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A review of the *Murina cyclotis* complex (Chiroptera: Vespertilionidae) with descriptions of a new species and subspecies

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Until recently, the taxon *Murina cyclotis* was considered to be a widespread species, albeit one that exhibited considerable individual, sexual and geographical variation. Subsequently however, it was recognised that this taxon was in fact a complex of species. As such, in 2012, two larger forms were recognised as separate and distinct species, namely: *M. peninsularis* in the Sunda region and *M. fionae* in Laos and Vietnam. In the current paper, a new cryptic species of the *cyclotis*-complex is described from peninsular Thailand based on a combination of external, craniodental and genetic differences. In addition, the population previously referred to *M. cyclotis* from the Nicobar Islands is described as a new subspecies of this new species. Despite this work and the research of others, the taxonomy of *M. cyclotis* still requires further study. The description of *M. peninsularis* is emended and the extensive variation in its morphological characters is addressed. The diagnostic characters of each taxon, as well as the additional data on ecology, zoogeography, distribution, echolocation and genetics, where available, are summarised and discussed.

Key words: cryptic species, DNA barcode, Southeast Asia, taxonomy, tube-nosed bat, Thailand, zoogeography

Introduction

Francis *et al*. (2010) suggested that Southeast Asian *Murina* have high cryptic diversity. Intensive field surveys using harp traps in forested areas, coupled with more rigorous taxonomic analysis, including genetic studies, support this suggestion. The total number of the *Murina* species recorded from the region is increasing rapidly such that to date, 20 of the 34 species of *Murina* currently known to science are from Southeast Asia (Simmons, 2005; Francis, 2008; Csorba *et al.*, 2011; Eger and Lim, 2011; Francis and Eger, 2012; Soisook *et al.*, 2013).

Murina cyclotis Dobson, 1872, until recently, was considered to be one of the most widely distributed species of the genus. As formerly understood (sensu Corbet and Hill, 1992), it was thought to comprise three subspecies: *M. c. cyclotis* from India to mainland Southeast Asia; *M. c. peninsularis* Hill, 1964 from peninsular Thailand to Malaysia and Indonesia; and *M. c. eileenae* Phillips, 1932 restricted to Sri Lanka. However, now it is regarded as

a species complex (Francis *et al.*, 2010; Francis and Eger, 2012) with the Sundaic taxon '*M. c. peninsularis*' treated as a separate species *M. peninsularis* by Francis and Eger (2012) and the large Indochinese form, referred previously to the taxon '*peninsularis'* by Matveev and Csorba (2007) and to '*Murina* sp. B' by Francis *et al.* (2010), described as a new species, *M. fionae* Francis and Eger, 2012.

During 2011–2013, specimens of *Murina* belonging to the *'cyclotis*-complex' were examined. This material of *M. cyclotis*, *M.* cf. *cyclotis*, *M. fionae*, and *M. peninsularis* from mainland Southeast Asia with some additional specimens from India, Malaysia and Indonesia, was made available for study from various museums in Asia, Europe and North America (Appendix). Based on external, craniodental and bacular morphology, as well as genetic differences, specimens of *M.* cf. *cyclotis* from peninsular Thailand, including one (ROM 110439) collected from Krabi Province, peninsular Thailand are here described as a new species. Specimens currently referred to *M. cyclotis* from Nicobar Islands, are described as a distinct subspecies of the new species herein.

Materials and Methods

Specimens of *Murina* deposited in various collections were examined by at least one of the authors, the list and acronyms of the museums/collections are as follows: Natural History Museum, London, UK (BMNH); Harrison Institute, Sevenoaks, UK (HZM); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Museum of Texas Tech University, Texas Tech University, Lubbock, Texas, USA (TTU/TK); Zoological Museum, Universiti Malaysia Sarawak, Sarawak, Malaysia (UNIMAS), Royal Ontario Museum, Toronto, Ontario, Canada (ROM); Institute of Ecology and Biological Resources, Vietnamese Academy of Science and Technology, Hanoi, Vietnam (IEBR); Kim Hy Nature Reserve Collection, Vietnam (NF); Museum Zoologicum Bogoriense, Indonesian Institute of Sciences [LIPI], Bogor, Indonesia (MZB); Princess Maha Chakri Sirindhorn Natural History Museum [here after PSUNHM], Prince of Songkla University [PSU], Hat Yai, Thailand (PSUZC); and the Thailand Natural History Museum, Pathum Thani, Thailand (THNHM). Bat specimens held in local wildlife research stations of the Department of National Park, Wildlife and Plant Conservation (DNP) in Thailand were also examined; these included reference collections in Chiangdao Wildlife Research Station, Chiang Mai (CDWRS) and Halabala Wildlife Research Station, Narathiwat (HBRWS).

Additional specimens were collected during field surveys in Thailand undertaken jointly between 2010 and 2013 by PSU and the wildlife teams of the DNP. The new material was collected from the following localities:

Surat Thani Province — a series of field surveys was conducted between 2010 and 2011 by PS for the study of small mammal and bird diversity in Rajjaprabha Dam, under the 'Plant Genetic Conservation Project under the Royal Initiation of Her Royal Highness Princess Maha Chakri Sirindhorn (RSPG)' (8°57'N, 98°47'E, 80 metres above sea level [hereafter m a.s.l.]; Loc. 1, Fig. 1). Specimens were collected in a harp trap and mist nets in secondary evergreen forest. Two species of *Murina* were collected including *M. suilla* (Temminck, 1840) and *Murina* sp. (described below) together with 25 other species of bats (P. Soisook, S. Bumrungsri, P. Sookbangnop, and U. Pimsai, unpublished data).

Trang Province — a field survey was conducted around Ton Tae Waterfall, Pa Lien District (7°19'N, 99°50'E, 60 m a.s.l.; Loc. 2, Fig. 1), on 11 January 2012. A specimen of *M. suilla* and a *Murina* sp. were collected in a harp trap set across forest trail in lowland evergreen forest. The other insectivorous bats found in the same site included *Rhinolophus lepidus* Blyth, 1844, *R. affinis* Horsfield, 1823, *R. malayanus* Bonhote, 1903 and *Kerivoula hardwickii* (Horsfield, 1824).

Phattalung Province — a field survey was conducted around Ton Phrae Thong Waterfall, Kong Ra District (7°29'N, 99°54'E, 70 m a.s.l.; Loc. 3, Fig. 1), on 13 March 2012. A specimen of *Murina* sp. was collected in a harp trap set by a stream, between a tree and a small bamboo grove. The other insectivorous bats found in the same area included *R. affinis*, *R. coelophyllus* Peters, 1866, *R. lepidus*, *Hipposideros atrox* K. Andersen, 1918, *H. bicolor* (Temminck, 1834), *H. larvatus* (Horsfield, 1823) and *H. pendleburyi* Chasen, 1936.

Songkhla Province — a field survey was conducted around Pha Dam Waterfall, Hat Yai District (6°49'N, 100°13'E, 150 m a.s.l.; Loc. 4, Fig. 1), between 4–7 February 2012. The area is covered by evergreen forest. Specimens of *M. peninsularis* and *M. suilla* were collected in a harp trap set across a forest trail. The other insectivorous bats found in this site included *Nycteris tragata* (K. Andersen, 1912), *R. affinis*, *R. trifoliatus* (Temminck, 1834), *H. atrox*, *H. doriae* (Peters, 1871), *Hesperoptenus blanfordi* (Dobson, 1877), *Tylonycteris pachypus* (Temminck, 1840), *K. hardwickii*, *K. pellucida* (Waterhouse, 1845), *K. minuta* Miller, 1898 and *Phoniscus atrox* Miller, 1905.

Satun Province — a field survey was undertaken at Wang Tai Nan Waterfall, Manang District (7°10'N, 100°00'E, 240 m a.s.l.; Loc. 5, Fig. 1). The area is characterised by lowland primary evergreen forest. Bats were captured in harp traps set across forest trails. Bat species found at this site included *N. tragata*, *R. affinis*, *R. malayanus*, *R. stheno* (K. Andersen, 1905), *R. robinsoni* (K. Andersen, 1918), *R. coelophyllus*, *H. atrox*, *H. larvatus*, *H. diadema* (E. Geoffroy Saint-Hillaire, 1813), *K. hardwickii*, *K. pellucida* and *K. minuta.*

Narathiwat Province — a series of field survey was conducted between September and October 2012 in Bala Forest, Halabala WS (ca. 5°48'N, 101°50'E, 200 m a.s.l.; Loc. 6, Fig. 1 — see Bumrungsri *et al.*, 2006 for more details of the area). Bats were captured in a harp trap set across forest trails or over small streams. Specimens of *M. suilla*, *M. peninsularis*, *M. aenea* Hill, 1964 and *M. rozendaali* Hill and Francis, 1984 were collected. Other insectivorous bats captured during the survey included *R. lepidus*, *R. trifoliatus*, *R. affinis*, *R. acuminatus* Peters, 1871, *H. atrox*, *H. bicolor*, *Pipistrellus stenopterus* (Dobson, 1975), *Harpiocephalus harpia* (Temminck, 1840), *K. papillosa* (Temminck, 1840), *K. pellucida*, *K. minuta*, *Ph. atrox* and *Ph. jagorii* (Peters, 1866).

External measurements were taken with a dial caliper to the nearest 0.1 mm in the field. Specimens are preserved in 70% ethanol. Some specimens were prepared as dry study skins. Skulls and some bacula were extracted. Craniodental measurements were taken with a digital caliper (to the nearest 0.01 mm) under a microscope. Definitions of measurements followed

Bates and Harrison (1997), Csorba *et al.* (2011) and Francis and Eger (2012) unless otherwise stated. All measurements are in mm except for MASS which is in grams: MASS: body mass of the bat (newly sacrificed) — taken with 10 g Pesola scale to the nearest 0.1 g; FA: forearm length, from the extremity of the elbow to the extremity of the carpus with the wings folded; HB: head and body length, from the tip of the snout to the base of the tail, dorsally; TAIL: tail length, from the tip of the tail to its base adjacent to the anus; HF: hind foot length, from the extremity of the heel behind the os calcis to the extremity of the longest digit, not including the hair or claws; TIB: length of tibia, from the knee joint to the ankle; 5MET, 4MET, 3MET: length of the metacarpal of the fifth, fourth and third digits respectively, taken from the extremity of the carpus to the distal extremity of each metacarpal; 3D1PH, 3D2PH: first/second phalanx respectively of the third digit — taken from the proximal to the distal extremity of the phalanx; E: ear length, from the lower border of the external auditory meatus to the tip of the pinna; TRG: tragus length, as ear length but to the tip of the tragus; GTL: greatest length of skull, the greatest antero-posterior length of the skull, taken from the most projecting point at each extremity; CBL: condylobasal length, from the exoccipital condyle to the anterior part of the upper incisor; CCL: condylo-canine length, from an exoccipital condyle to the anterior alveolus of a canine; ZB: zygomatic breadth, the greatest width of the skull across the zygomatic arches; BB: breadth of braincase, greatest width of the braincase at the posterior roots of the zygomatic arches; BCH: braincase height — from the basisphenoid at the level of the hamular processes to the highest part of the skull, including the sagittal crest (if present), MW: mastoid width, greatest width across the mastoid; IC: interorbital constriction, the least width of the interorbital constriction; LW: lacrimal width, greatest width across the lacrimal tubercles at the rostral margins of the orbits; C–M^3 : maxillary toothrow length, from the front of the upper canine to the back of the crown of the third upper molar; C–P^4: upper canine–premolar length, from the front of the upper canine to the back of the crown of the second premolar; M^3–M^3: palatal width, taken across the outer borders of the third upper molar, taken at the widest part; C^1–C^1: greatest anterior palatal width measured across the outer borders of the canines, taken at the widest part; C–M_3: mandibular toothrow length, from the front of the lower canine to the back of the crown of the third lower molar; M: mandible length, from the most posterior part of the condyle to the most anterior part of the mandible; CPH: least height of the coronoid process — from the tip of the coronoid process to the apex of the indentation on

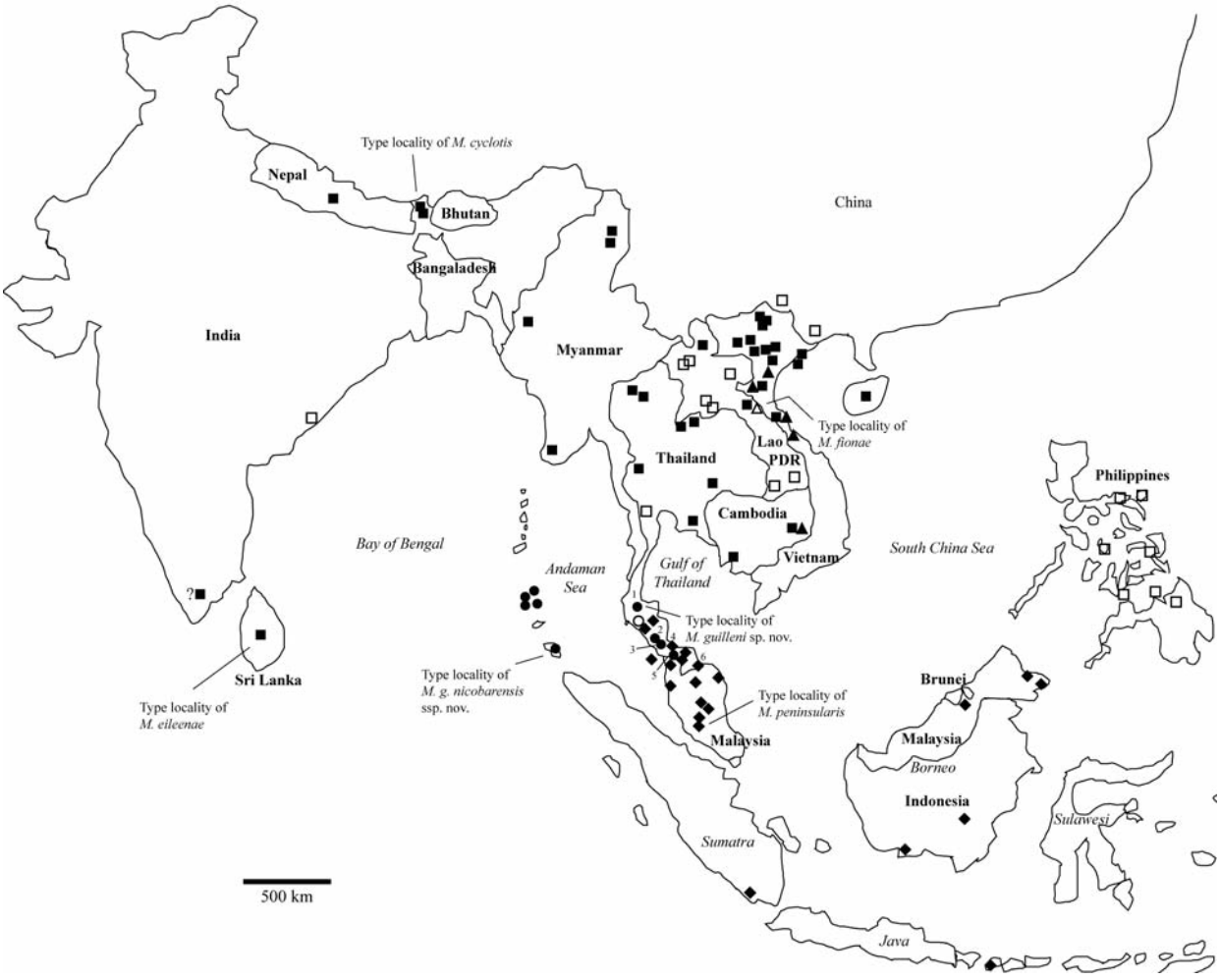

FIG. 1. Distribution of *M. guilleni* sp. nov. (circles), *M. cyclotis* (squares), *M. fionae* (triangles) and *M. peninsularis* (diamonds). The black symbols refer to specimens examined by the authors, whereas the blank symbols refer to records from literature or released individuals. The list of specimens and samples are included in the Appendix

the inferior surface of the ramus adjacent to the angular process; TRM_1: length of the trigonid of the first lower molar — measured on the lingual side of the tooth when viewed from above, from the most anterior part to the most posterior part of the trigonid cusp; TAM_1: length of the talonid of the first lower molar — measured on the lingual side of the tooth when viewed from above, from the most posterior part of the trigonid cusp to the most posterior part of the talonid; BL: greatest length of the baculum — measured from the most posterior to the most anterior part. Drawings were made under microscope with a camera lucida by PS. Statistical analysis was performed in R 2.14 (R Development Core Team, Vienna, www.R-project.org).

Calls were recorded from individual bats flying freely in a 4 × 4 m room or in a 3 × 3 m enclosure made from mosquito nets. During the study, two recorders were used: either a Pettersson D-1000X ultrasound detector set in 10× time-expansion mode and a sampling rate of 768 kHz or a Pettersson D-240X set in 10× time expansion mode connected to an iRiver iHP-120 Multi-Codec Jukebox Recorder. Calls were transferred to a computer for analysis in BatSound — Sound Analysis Version 4.1.4 (Pettersson Electronics and Acoustic AB). Four call parameters were measured including: start frequency [*sf*] and terminal frequency [*tf*] (in kHz) measured by using the measurement cursor in the spectrogram, the frequency of maximum energy [*fmaxe*] measured in the power spectrum, and call duration [*d*] (in ms) measured by using the marking cursor in the amplitude window. A sampling frequency of 44.10 kHz was used and produced a spectrogram using Automatic Fast Fourier Transforms (FFT) with a Hanning window. At least ten calls with good signal-to-noise ratio from each individual were chosen for analysis.

Genetic material were taken from the wing membrane, tongue or liver and stored in 1.5 ml microtubes with absolute alcohol. Tissue materials were analysed following standard protocols of DNA extraction, gene amplification, and nucleotide sequencing as outlined in Francis *et al.* (2010) and Ivanova *et al.* (2012) for mammalian DNA Barcode analyses. The cytochrome oxidase-I (COI) gene of 657 bp sequences from our samples were analysed using the Neighbour-joining tree algorithms (NJ) implemented within the Barcode of Life Data Systems (BOLD) using *Harpiocephalus harpia* as an outgroup (e.g., Khan *et al.*, 2010). In addition, public data were included for specimens of the *cyclotis*-complex from other geographical areas; these were published in Francis *et al.* (2010) and deposited in BOLD. Genetic divergence values between samples were calculated using the Kimura 2-parameter model.

Systematic Description

Murina cyclotis Dobson, 1872
Round-eared tube-nosed bat

Murina cyclotis Dobson, 1872: 210; Darjeeling, NE India.
Murina eileenae Phillips, 1932: 329; Mousakande, Gammaduwa, East Matale Hills, Sri Lanka.

Description and taxonomic notes

This is a small-medium sized tube-nosed bat with a FA of 29.4–36.8 mm (Table 1). Females have an average larger body size than males, with a mean FA of 33.9 mm versus 30.7 mm, respectively. Ear length (E) is 12.0–17.6 mm. However, the shape of the pinna is variable between individuals, from broadly round with a convex anterior border to narrower, somewhat more elliptical and less convex. Dorsal pelage is dark grey basally and orange-brown at the hair tips; the pelage extends onto the tail membrane and the hind feet. The hairs of the ventral pelage are grey basally with light grey to whitish-brown tips (Fig. 2b) or with a light orange-brown tinge in some individuals. Each wing membrane is attached near the base of the claw of the outer toe. In the skull, the GTL is 15.86–18.18 mm and the CCL is 13.60–16.17 mm (Table 2). The rostral profile is relatively long with a well-defined concavity in the interorbital region (Fig. 3b). The braincase is relatively low, with a BCH of 6.08–7.22 mm (Table 2), and the sagittal crest is well-defined (Fig. 3b). The upper canine exceeds the P^4 in height. The height of the P^2 is about two-thirds that of the P^4. In occlusal view, the shape of P^2 and P^4 are rounded and similar in size (Fig. 4b). The M^1 and M^2 are without mesostyles, and their labial surfaces have a U-shaped indentation. In the lower dentition, P_2 and P_4 are equal in height and about two-thirds that of the C_1. The crown area of the P_2 is slightly more than half that of the P_4 (Fig. 4b). The talonid of the M_1 is between half and two-thirds the crown area of its respective trigonid, averaging 59.60% in males and 60.52% in females, the range for both sexes is 46.51–71.79% (n = 23). The entoconids of the M_1 and M_2 are equal or exceeded in height by their hypoconids. The baculum is very small (BL 0.8 mm). The dorsal surface is arched upwards and the ventral surface is deeply concave. The anterior border has a distinct concavity and it is M-shaped on the posterior border (Fig. 5b).

Although regarded as a subspecies of *M. cyclotis* by some authors (Ellerman and Morrison-Scott, 1951; Eisenberg and McKay, 1970; Corbet and Hill, 1992), the four specimens of *eileenae* we examined from Sri Lanka (including the holotype) are very similar morphologically to *cyclotis* from elsewhere in its range. The differences, including those in the original description of Phillips (1932), such as having less bright pelage colour and darker wing membranes are actually very slight as noted by Hill (1964). Following Koopman (1993), Bates and Harrison (1997), Molur *et al.* (2002) and Simmons (2005), we regard *eileenae* as a synonym of *M. cyclotis.*

However, much of the taxonomy of *M. cyclotis* remains unresolved, especially since morphological and genetic data from India are difficult to access, particularly from the type locality. In Indochina, extreme morphological variation has been observed,

TABLE 1. External measurements (in mm) and body mass (MASS) (in gram) of *M. g. guilleni*, *M. g. nicobarensis*, *M. cyclotis, M. fionae* and *M. peninsularis*. Sample sizes of male and female specimens examined, $\bar{x}$ ± SD, minimum and maximum values are given. A sample size that differs from the total number of specimens is given in italics. Definitions of measurements are provided in the Materials and Methods section

n/sex	FA	E	TRG	HB	TAIL	TIB	HF	5MET	4MET	3MET	3D1PH	3D2PH	MASS
						M. guilleni guilleni sp. nov.							
6♂♂	33.2 ± 0.7	13.7 ± 1.4	8.6 ± 0.5	48.0 ± 3.2	35.9 ± 4.0	18.4 ± 0.8	8.5 ± 0.6	31.0 ± 0.4	29.5 ± 0.9	31.5 ± 0.6	15.0 ± 0.4	14.4 ± 0.2	6.5 ± 0.3
	31.9–34.0	11.4–15.2	8.3–9.2, *3*	43.2–51.6	28.1–39.2	17.7–19.7	7.7–9.4	30.6–31.8	29.2–31.3	30.9–32.6	14.3–15.3	14.0–14.5	6.0–6.8, *5*
3♀♀	35.4 ± 0.5	14.4 ± 0.8	–	48.2 ± 0.2	39.1 ± 3.1	18.9 ± 0.8	8.2 ± 0.2	31.1, *1*	29.2, *1*	31.4, *1*	15.3, *1*	14.4, *1*	5.7 ± 2.5
	35.0–35.9	13.5–15.1	–	48.0–48.3	35.9–42.0	18.1–19.7	8.0–8.4	–	–	–	–	–	3.0–8.0
						M. guilleni nicobarensis ssp. nov.							
3♂♂	34.0 ± 1.4	13.7 ± 0.9	7.7 ± 0.2	43.7 ± 2.1	38.3 ± 1.2	17.8, *1*	8.1 ± 0.3	–	–	–	–	–	–
	32.6–35.3	12.7–14.5	7.6–8.0	42.0–46.0	37.0–39.0	–	7.8–8.3	–	–	–	–	–	–
2♀♀	34.0, 34.4	14.2, *1*	–	44.0, *1*	34.0, *1*	–	8.2, *1*	–	–	–	–	–	–
						M. cyclotis							
36♂♂	30.7 ± 0.9	14.0 ± 1.3	8.1 ± 0.6	42.3 ± 2.3	34.9 ± 3.9	17.6 ± 1.1	7.9 ± 0.6	29.0 ± 1.6	28.3 ± 1.7	29.2 ± 1.5	13.6 ± 0.4	13.0 ± 0.7	5.0, 5.8, *2*
	29.4–33.0, *35*	12.0–17.6, *17*	6.8–9.3, *13*	38.7–46.4, *16*	26.2–39.0, *17*	14.5–19.3, *18*	6.5–8.8, *17*	25.1–31.8, *16*	24.7–31.9, *16*	26.5–32.4, *16*	12.8–14.5, *16*	11.1–14.1, *16*	–
40♀♀	33.9 ± 1.0	14.5 ± 1.0	7.9 ± 0.9	45.1 ± 2.8	37.4 ± 2.5	18.8 ± 0.9	8.3 ± 0.8	32.3 ± 1.2	31.4 ± 1.3	32.0 ± 1.2	14.8 ± 0.7	14.4 ± 0.9	6.1, *1*
	31.6–36.8	12.7–16.0, *17*	5.8–9.2, *14*	41.1–50, *17*	32.0–41.1, *17*	17.3–20.3	7.0–9.7, *17*	30.8–35.1, *11*	29.7–34.4, *11*	30.4–34.9, *11*	13.7–16.2, *11*	12.7–15.4, *11*	–
						M. fionae							
7♂♂	35.1 ± 0.7	14.2 ± 1.3	7.6 ± 0.6	45.4 ± 3.4	37.3 ± 2.5	19.6 ± 0.6	8.8 ± 0.5	33.5 ± 0.7	32.6 ± 1.1	33.6 ± 0.8	15.6 ± 0.7	14.9 ± 0.3	–
	34.5–36.3	12.1–15.6, *6*	6.8–8.4, *6*	41.0–51.0, *6*	33.7–40.6, *6*	19.1–20.5, *6*	7.8–9.3, *6*	32.5–34.1, *4*	31.1–33.4, *4*	32.5–34.2, *4*	14.7–16.4, *4*	14.5–15.2, *4*	–
6♀♀	37.3 ± 1.6	15.2 ± 0.3	7.1 ± 1.0	46.3 ± 8.4	37.2 ± 2.1	20.6 ± 0.4	8.6 ± 0.8	33.8, 36.0, *2*	33.3, 34.7, *2*	34.9, 35.4, *2*	16.7, 16.9, *2*	15.5, 15.6, *2*	6.6, *1*
	35.5–40.1	14.9–15.5, *3*	6.2–8.2, *3*	37.3–54.0, *3*	35.0–39.1, *3*	20.2–21.1, *3*	7.8–9.3, *3*	–	–	–	–	–	–
						M. peninsularis							
23♂♂	35.7 ± 1.3	14.2 ± 1.7	8.4 ± 0.9	46.6 ± 3.0	38.7 ± 3.3	19.5 ± 1.0	7.8 ± 0.9	33.3 ± 1.5	32.7 ± 1.3	34.0 ± 1.5	15.9 ± 0.9	15.1 ± 1.0	7.0 ± 0.9
	33.8–38.1, *22*	11.9–18.8, *13*	7.4–10.3, *8*	39.9–50.1, *14*	32.4–42.8, *12*	18.2–21.6, *14*	5.6–9.1, *14*	31.3–36.8, *12*	29.9–35.4, *11*	32.0–37.6, *11*	14.5–17.6, *11*	13.8–16.8, *11*	5.5–8.3, *9*
19♀♀	37.7 ± 1.2	15.1 ± 1.2	8.3 ± 0.5	49.9 ± 3.7	42.3 ± 1.9	19.3 ± 2.5	9.0 ± 0.8	35.6 ± 0.5	35.1 ± 0.6	36.5 ± 0.6	17.1 ± 0.8	15.8 ± 0.3	9.7 ± 1.1
	34.5–39.4	13.0–17.0, *12*	7.6–9.0, *9*	42.0–55.1, *12*	38.5–46.0, *12*	11.1–21.0, *14*	7.1–10.0, *14*	35.0–36.5, *9*	34.0–36.4, *9*	35.7–37.7, *9*	15.4–18.2, *9*	15.5–16.4, *9*	8.5–11.9, *12*

notably in hair colour and ear shape (as above). However, curiously there is remarkably little variation in craniodental characters. Further intensive taxonomic study of this species, with a combination of morphological and genetic data, especially for Indian specimens, would be of particular interest.

Specimens of *M. cyclotis* from the Philippines, which previously have not been assigned to any subspecies (e.g., Corbet and Hill 1992; Ingle and Heaney, 1992; Simmons, 2005) were not available for examination in this study. Based on the description, together with the measurements of four specimens

FIG. 2. Four *Murina* species: (a) *M. guilleni* sp. nov., ♂, PSUZC-MM 2013.15 (paratype), from peninsular Thailand, (b) *M. cyclotis*, ♂, PSUZC-MM 2006.179, from NE Thailand, (c) *M. fionae*, ♂, T.160811.3, from Vietnam, (d) *M. peninsularis*, ♂, PSUZC-MM 2012.12, from peninsular Thailand. Not to scale

(FA 36–39 mm, CCL 15.8–16.8 mm, C–M^3 5.9–6.3 mm) and drawings provided in Ingle and Heaney (1992), it appears that they agree closely with either *M. peninsularis* from the Sundaic subregion or *M. fionae* from Indochina (see below). However, currently, it is too speculative to assign this population to either taxa. Further study with genetic data from a series of specimens from the Philippines is required.

Echolocation

Based on two individuals from Loei Province, northeast Thailand, it is apparent that *M. cyclotis* uses typical broadband frequency-modulated (FM) signals with an *fmaxe* of 96.3, 109.0 kHz and *d* of 1.5, 2.3 ms. The *sf* and *tf* are 141.0, 163.0 kHz and 56.0, 72.0 kHz, respectively.

Ecology and habitat

Murina cyclotis is recorded from a range of forest habitats, including lowland, wet and hill evergreen forest, mixed deciduous forest and dry dipterocarp forest; elevations range from about sea level (PSUZC) to 1,650 m a.s.l. (BMNH). In April 2008, a pregnant female was captured in a harp trap, which was set over a streamlet in evergreen forest in Ratchaburi Province, western Thailand. This individual was subsequently released (PS, unpublished data).

Distribution

Murina cyclotis ranges from India (see also Bates and Harrison, 1997), Sri Lanka, and Nepal to Myanmar, Laos (see also Francis and Eger, 2012; Thomas *et al.*, 2013), Vietnam, China (Guangxi and Hainan Island), Thailand (north of the Isthmus of Kra), Cambodia and the Philippines (see Heaney *et al.*, 1998) (Fig. 1, Appendix).

Murina guilleni sp. nov.
(Figs. 1–9, Tables 1–3)

Holotype

PSUZC-MM 2010.22 (field number PS100 419.2), adult male, body in alcohol, skull and baculum extracted, collected by P. Soisook on 19 April 2010.

Type locality

Rajjaprabha Dam, Ban Takhun District, Surat Thani Province, peninsular Thailand, 8°57'N, 98°47'E, 80 m a.s.l. (Loc. 1, Fig. 1).

Paratypes

PSUZC-MM 2010.23 (field number PS100419.3), lactating female; PSUZC-MM 2011.42 (field number PS110831.6), adult female, from the same site as the holotype; PSUZC-MM 2012.7 (field number PS120111.2), adult male, from Ton Tae Waterfall, Pa Lien District, Trang Province, Thailand; PSUZCMM 2013.15 (field number PS130625.1), adult male, from Wang Tai Nan Waterfall, Manang District, Satun Province, Thailand; PSUZC-MM 2012.8 (field number PS120313.6), adult male, Ban Ton St., Khao Bantad WS, Phattalung, S. Thailand; PSUZC-MM 2008.3 (field number SB080103.4), adult male, Yaroi Waterfall, Taleban NP., Satun, S. Thailand; PSUZC-MM 2007.350 (field number SB071222.1), adult male, Ban Vang Pha, Songkhla, S. Thailand; PSUZC-MM 2007.154 (field number SB070224.1), Makling Waterfall, Rattaphum, Songkhla, S. Thailand.

Referred specimens

ROM 110439 (field number AGS 970412-01), adult female, from Khao Nor Chuchi Reserve (= Khao Pra Bang Kram WS), Klong Tom District, Krabi Province, Thailand. Referred specimens from the Nicobar Islands are listed below in *M. guilleni* ssp. nov.

Diagnosis

This is a small-medium sized *Murina* with an average FA of 34.0 mm (range 31.9–35.9 mm). Males have a slightly smaller body size than females, with an average FA of 33.5 and 34.9 mm respectively. The dorsal pelage is grey basally with orange-brown tips. The ventral pelage is less bright, being uniformly dark grey except around the neck and over the chest where the hairs have a dark grey base and are tinged with orange-brown at the tip (Fig. 2a). Each plagiopatagium is dark brown and attached to the side of the foot near the base of the claw of the outer toe. The GTL is 16.40–18.10 mm, and the CCL is 14.47–15.76 mm. The upper and lower canines exceed the respective premolars in height (Fig. 3a). The upper premolar (P^2) is sub-equal to about two-thirds the height of the P^4. The first and second upper molars (M^1 and M^2) are without a mesostyle and the labial surfaces have a V-shaped indentation (Fig. 4a). The crown area of the talonid of the first lower molar (M_1) is about half to two thirds that of its respective trigonid.

Measurements of the holotype (in mm) are as follows: FA: 34.0, E: 12.6, HB: 48.0, TAIL: 35.2, HF:

TABLE 2. Craniodental measurements (in mm) of *M. g. guilleni*, *M. g. nicobarensis*, *M. cyclotis, M. fionae* and *M. peninsularis*. Sample sizes of male and female specimens examined, $\bar{x} \pm$ SD; minimum and maximum values are given. A sample size that differs from the total number of specimens is given in italics. Definitions of measurement are included in the Materials and Methods section

n/sex	GTL	CBL	CCL	ZB	BB	BCH	MW	IC	LW
					M. guilleni guilleni sp. nov.				
6♂♂	17.10 ± 0.43	15.46 ± 0.33	14.85 ± 0.26	9.60 ± 0.22	7.76 ± 0.06	6.68 ± 0.12	8.12 ± 0.11	4.34 ± 0.07	5.16 ± 0.05
	16.40–17.54	14.93–15.83	14.47–15.19	9.29–9.93	7.65–7.82	6.57–6.91	8.00–8.28	4.24–4.44	5.09–5.23
3♀♀	17.65 ± 0.50	16.10 ± 0.32	15.43 ± 0.34	9.92 ± 0.15	7.64 ± 0.11	6.94 ± 0.16	8.34 ± 0.14	4.32 ± 0.12	5.34 ± 0.05
	17.12–18.10	15.79–16.43	15.09–15.76	9.75–10.02	7.53–7.74	6.78–7.10	8.18–8.43	4.20–4.44	5.31–5.40
					M. guilleni nicobarensis ssp. nov.				
3♂♂	17.22 ± 0.38	15.55 ± 0.38	14.96 ± 0.38	9.43 ± 0.32	7.88 ± 0.22	6.66 ± 0.09	8.03 ± 0.31	4.41 ± 0.05	5.21 ± 0.05
	16.87–17.62	15.26–15.98	14.65–15.38	9.12–9.75	7.73–8.13	6.57–6.74	7.68–8.29	4.37–4.46	5.18–5.27
2♀♀	17.45, *1*	15.65, *1*	15.00, 15.01	9.23, 9.52	7.55, 8.01	6.72, 6.79	7.93, 8.35	4.44, 4.46	5.20, *1*
					M. cyclotis				
36♂♂	16.47 ± 0.34	14.97 ± 0.40	14.45 ± 0.34	9.36 ± 0.31	7.64 ± 0.22	6.49 ± 0.30	7.90 ± 0.26	4.17 ± 0.12	4.95 ± 0.24
	15.86–17.08, *27*	14.00–15.67, *27*	13.60–15.12	8.78–10.05, *35*	7.16–8.10	6.08–7.22, *34*	7.11–8.48	3.92–4.48	4.26–5.42, *27*
38♀♀	17.21 ± 0.47	15.85 ± 0.48	15.22 ± 0.41	9.84 ± 0.29	7.71 ± 0.19	6.5 ± 0.24	8.20 ± 0.21	4.25 ± 0.13	8.71 ± 0.27
	16.60–18.18, *25*	14.95–16.86, *24*	14.34–16.17	9.33–10.43, *37*	7.40–8.17	6.10–7.21, *37*	7.64–8.58	3.99–4.52	4.67–5.85, *23*
					M. fionae				
7♂♂	18.54 ± 0.56	16.80 ± 0.45	16.21 ± 0.46	10.48 ± 0.36	8.1 ± 0.24	7.25 ± 0.33	8.65 ± 0.27	4.66 ± 0.19	5.72 ± 0.30
	17.53–19.26	15.99–17.49	15.32–16.87	9.78–10.89	7.75–8.39	6.53–7.50	8.10–8.91	4.26–4.85	5.11–6.07
6♀♀	18.80 ± 0.43	17.06 ± 0.35	16.43 ± 0.35	10.56 ± 0.28	8.20 ± 0.27	7.18 ± 0.19	8.69 ± 0.31	4.51 ± 0.21	5.44 ± 0.18
	18.12–19.19	16.48–17.45	15.82–16.73	10.19–10.85	7.84–8.49	6.98–7.48	8.22–8.92	4.23–4.75	5.15–5.61
					M. peninsularis				
23♂♂	17.79 ± 0.31	16.06 ± 0.33	15.52 ± 0.41	10.36 ± 0.38	8.12 ± 0.19	7.32 ± 0.32	8.74 ± 0.27	4.57 ± 0.19	5.47 ± 0.25
	17.39–18.52, *17*	15.68–16.91, *17*	14.90–16.41	9.76–11.31	7.72–8.48	6.79–8.22	8.32–9.39	4.31–4.97, *22*	4.97–5.86, *16*
17♀♀	18.70 ± 0.52	17.11 ± 0.41	16.40 ± 0.36	10.80 ± 0.27	8.22 ± 0.22	7.48 ± 0.34	9.02 ± 0.34	4.68 ± 0.12	5.88 ± 0.20
	17.59–19.33, *13*	16.11–17.69, *13*	15.53–16.89, *16*	10.12–11.22	7.70–8.58	7.10–8.37	8.08–9.62	4.46–4.88, *16*	5.47–6.21, *13*

TABLE 2. Extended

n/sex	C–P^4	C–M^3	M^3–M^3	C^1–C^1	C–M$_3$	M	CPH	TRM$_1$	TAM$_1$
				M. guilleni guilleni sp. nov.					
5♂♂	2.81 ± 0.07	5.58 ± 0.12	5.54 ± 0.16	4.19 ± 0.07	6.00 ± 0.09	11.38 ± 0.21	4.63 ± 0.21	0.81 ± 0.01	0.43 ± 0.04
	2.69–2.85	5.44–5.72	5.36–5.80	4.12–4.31, *5*	5.83–6.12	11.13–11.74	4.33–4.93	0.80–0.82	0.40–0.48
3♀♀	2.81 ± 0.13	5.67 ± 0.21	5.79 ± 0.10	4.34 ± 0.09	6.18 ± 0.22	12.11 ± 0.21	5.10 ± 0.05	0.82 ± 0.02	0.47 ± 0.03
	2.69–2.94	5.50–5.91	5.68–5.87	4.28–4.44	6.01–6.43	11.95–12.34	5.05–5.15	0.80–0.84	0.44–0.50
				M. guilleni nicobarensis ssp. nov.					
3♂♂	2.50, 2.60, *2*	5.52 ± 0.20	5.55 ± 0.30	3.98 ± 0.10	6.08 ± 0.20	11.5 ± 0.40	4.17 ± 0.20	0.83 ± 0.00	0.47 ± 0.10
	–	5.39–5.71	5.24–5.71	3.90–4.13	5.91–6.21	11.27–11.96	4.01–4.44	0.80–0.86	0.42–0.56
2♀♀	2.78, 3.05	5.70, 5.73	5.27, 5.31	3.86, 4.16	6.19, 6.26	11.47, 11.74	4.15, 4.20	–	–
				M. cyclotis					
36♂♂	2.66 ± 0.16	5.41 ± 0.15	5.39 ± 0.18	4.00 ± 0.14	5.84 ± 0.14	11.17 ± 0.30	4.14 ± 0.21	0.79 ± 0.03	0.47 ± 0.05
	2.21–2.96	5.12–5.68	5.07–5.79, *35*	3.73–4.27	5.57–6.18	10.52–11.68, *35*	3.77–4.60, *35*	0.74–0.84, *13*	0.40–0.56, *13*
38♀♀	2.76 ± 0.19	5.61 ± 0.19	5.57 ± 0.19	4.25 ± 0.14	6.11 ± 0.16	11.86 ± 0.35	4.71 ± 0.27	0.82 ± 0.04	0.49 ± 0.04
	2.21–3.11	5.06–6.00	5.18–6.05	4.00–4.68, *37*	5.75–6.49, *37*	11.32–12.78, *37*	4.16–5.30	0.76–0.90, *10*	0.40–0.54, *10*
				M. fionae					
7♂♂	3.03 ± 0.22	6.14 ± 0.24	6.03 ± 0.16	4.64 ± 0.23	6.65 ± 0.21	12.48 ± 0.39	4.64 ± 0.25	0.90 ± 0.06	0.49 ± 0.05
	2.68–3.24	5.72–6.40	5.74–6.25	4.18–4.88	6.30–6.95	11.99–13.19	4.24–4.88	0.82–1.00, *6*	0.44–0.54, *6*
6♀♀	2.79 ± 0.08	6.11 ± 0.21	6.06 ± 0.24	4.57 ± 0.17	6.63 ± 0.25	12.82 ± 0.18	5.08 ± 0.22	0.88 ± 0.07	0.51 ± 0.03
	2.70–2.89, *5*	5.78–6.32	5.71–6.24	4.34–4.72	6.33–6.89	12.56–13.01	4.70–5.36	0.80–0.92, *3*	0.48–0.54, *3*
				M. peninsularis					
22♂♂	2.99 ± 0.15	5.76 ± 0.18	5.72 ± 0.18	4.66 ± 0.25	6.31 ± 0.42	11.92 ± 0.39	4.86 ± 0.29	0.87 ± 0.05	0.43 ± 0.03
	2.73–3.3, *17*	5.52–6.09	5.45–6.22	4.28–5.28	5.94–8.02	11.25–12.92, *21*	4.30–5.33	0.79–1.00, *15*	0.38–0.50, *15*
17♀♀	2.90 ± 0.74	6.07 ± 0.18	5.94 ± 0.15	4.97 ± 0.17	6.55 ± 0.21	12.75 ± 0.41	5.51 ± 0.39	0.91 ± 0.04	0.46 ± 0.04
	0.14–3.36	5.68–6.39	5.69–6.20, *16*	4.46–5.26, *16*	6.28–6.94, *16*	12.09–13.59	4.72–6.08, *16*	0.84–1.00, *12*	0.40–0.52, *12*

8.1, TIB: 19.6, 3MET: 31.4, 4MET: 29.2, 5MET: 31.1, 3D1PH: 15.3, 3D2PH: 14.4, GTL: 17.03, CBL: 15.62, CCL: 14.88, ZB: 9.72, BB: 7.74, BCH: 6.57, MW: 8.15, IC: 4.31, LW: 5.17; C–M^3: 5.44, C–P^4: 2.85, C^1–C^1: 4.16, M^3–M^3: 5.80, C–M_3: 6.00, M: 11.43, CPH: 4.78, TRM_1: 0.8; TAM_1: 0.4, BL: 1.0, MASS: 6.5 g.

Etymology

The species is named in honour of Antonio Guillén-Servent, who collected the first specimen of this species (ROM 110439) from Krabi, peninsular Thailand in 1997. The proposed English name is 'Guillén's Tube-nosed bat'.

Description

This is a small-medium sized *Murina* with a FA of 31.9–35.9 mm, HB 42.0–51.6 mm and a body mass of 3.0–8.0 g (Table 1). Males are slightly smaller than females, with an average FA of 33.5 mm vs. 34.9 mm, and a CCL of 14.88 vs. 15.26 mm (Tables 1 and 2). The ear is 11.4–15.2 mm in height, and is rounded with no distinct emargination on the posterior border of the pinna. The tragus is white and short, 7.6–9.2 mm, which is more than half the height of the ear (Fig. 2a). The dorsal pelage is grey basally with orange-brown tips. The ventral pelage is almost uniformly dark grey, although around the neck and chest there is an orange-brown tinge.

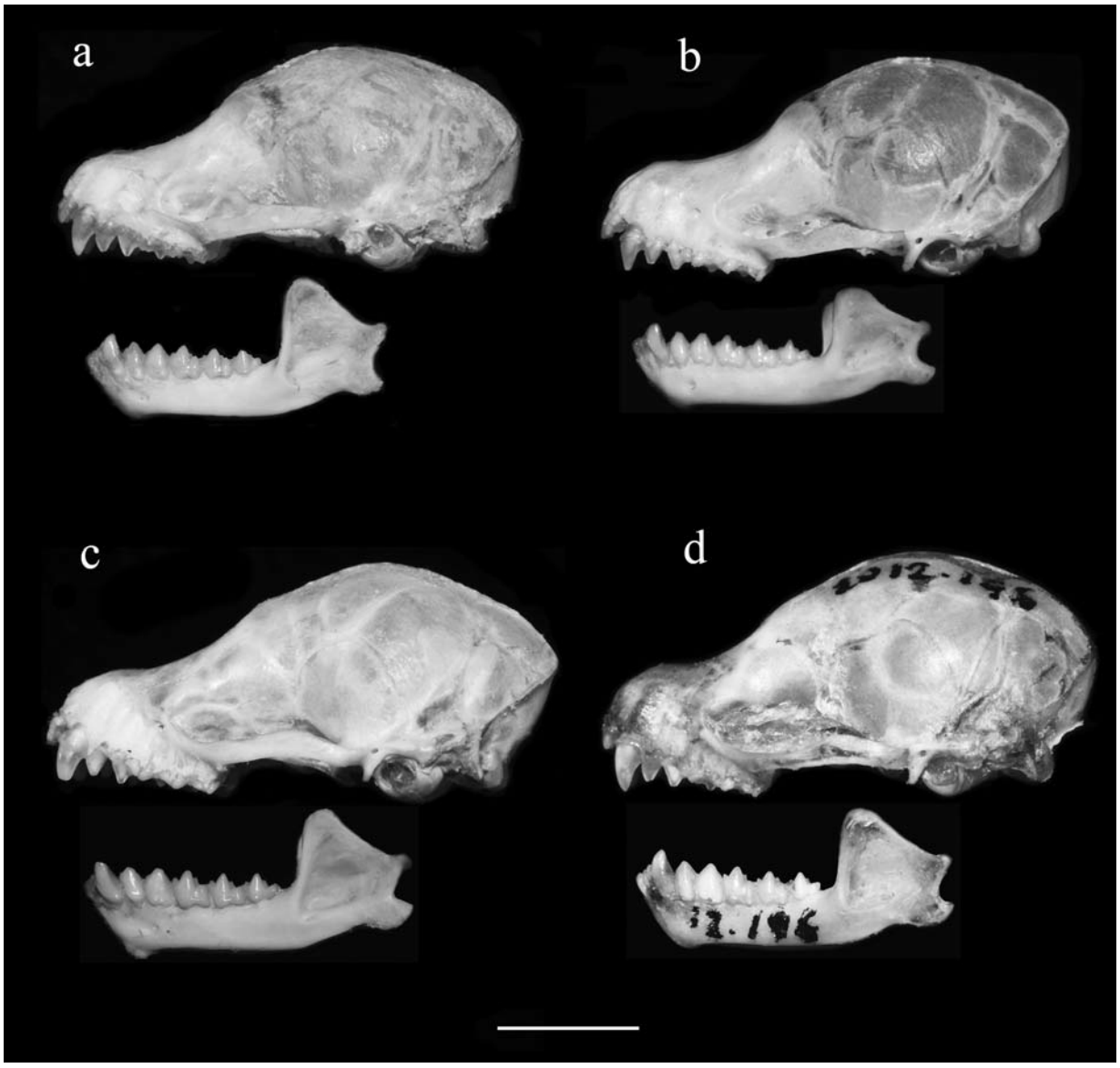

FIG. 3. Lateral view of the skulls of four *Murina* species: (a) *M. guilleni* sp. nov., ♂, PSUZC-MM 2010.22 (holotype), from peninsular Thailand, (b) *M. cyclotis*, ♂, PSUZC-MM 2006.179, from NE Thailand, (c) *M. fionae*, ♂, field no. 025, from Vietnam, (d) *M. peninsularis*, ♂, PSUZC-MM 2012.196, from peninsular Thailand. Scale = 5 mm

In the wings, each plagiopatagium is naked and dark brown in colour, and is attached to the distal phalanx, near the base of the claw of the outer toe. The third metacarpal (3MET), 30.9–32.6 mm, is the longest but only slightly longer than the fifth metacarpal (5MET), which is 30.6–31.8 mm. The fourth metacarpal (4MET) is the shortest, 29.2–31.3 mm (Table 1). The first (3D1PH) and second phalanges (3D2PH) of the third digit are 14.3–15.3 mm and 14.0–14.5 mm, respectively. The feet are covered with orange-brown hairs dorsally and are relatively small, 7.7–9.4 mm, 43.5–47.7% of tibia length (17.7–19.7 mm). Orange-brown hairs are also found on the back of the uropatagium. The tail is 28.1–42.0 mm in length.

In the skull, the greatest length (GTL) is 16.40–18.10 mm, CBL 14.93–16.43 mm, and CCL 14.47–15.76 mm (Table 2). Each zygoma is thin and without a distinct dorsal process; the breadth (ZB) is 9.12–10.02 mm. The breadth of braincase (BB) and mastoid (MW) are 7.53–8.13 mm and 7.68–8.43 mm, respectively. In lateral view, the rostrum is relatively short and exhibits only a slight concavity. The basioccipital pit is shallow. The braincase is relatively high, with the BCH of 6.57–7.10 mm, and the sagittal crest is poorly developed, with a slight

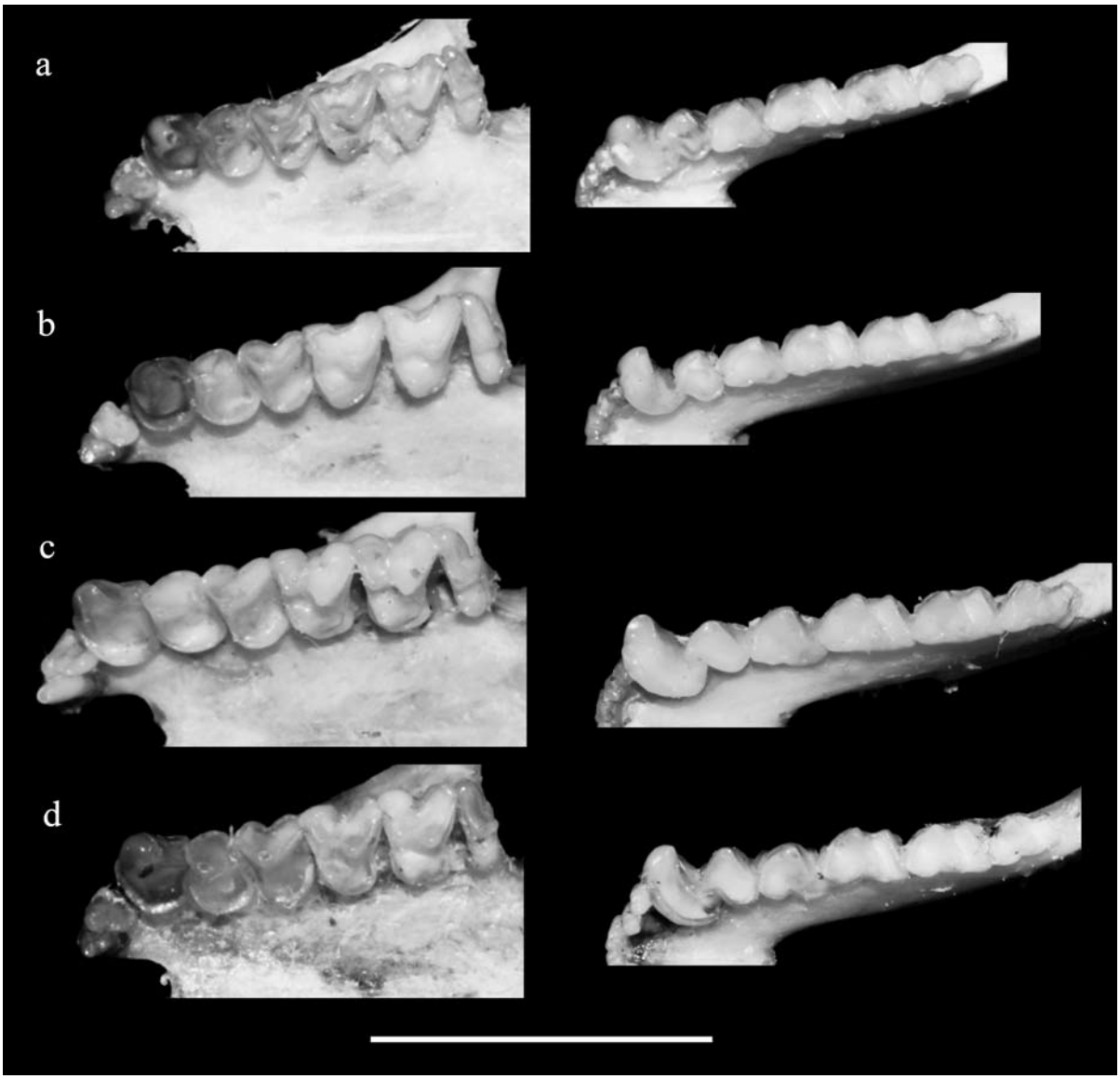

FIG. 4. Occlusal view of left upper (left of each pair) and right lower dentition (right of each pair) of four species of *Murina*: (a) *M. guilleni* sp. nov, ♂, PSUZC-MM 2010.22 (holotype), from peninsular Thailand, (b) *M. cyclotis*, ♂, PSUZC-MM 2006.179, from NE Thailand, (c) *M. fionae*, ♂, field no. 025, from Vietnam, (d) *M. peninsularis*, ♂, PSUZC-MM 2012.196, from peninsular Thailand. Scale = 5 mm

indication over the anterior part of the braincase (Fig. 3a). The upper toothrows converge anteriorly; the width at C^1–C^1 (3.86–4.44 mm) is 68.30–78.08% of that at M^3–M^3 (5.24–5.87 mm). The upper canine–second upper premolar length (C–P^4; 2.50–3.05 mm) is 45.53–52.39% of the maxillary toothrow length (C–M^3; 5.39–5.91 mm). The inner upper incisor (I^2) and the outer upper incisor (I^3) are about equal in height. I^2 is placed almost in line with I^3, so that in lateral view, I^2 is almost obscured by I^3 (Fig. 3a). The upper canine (C^1) is relatively large in comparison to the first (P^2) and second upper premolars (P^4). The crown area and the height of the P^2 are about two-thirds to subequal that of P^4, and are about subequal to that of the upper canine (Fig. 4a). P^2 and P^4 are both wider than long and somewhat elliptical in shape. The first (M^1) and second molars (M^2) are without a mesostyle, and the labial surface of both teeth is concave with a well-defined V-shape.

In the lower jaw, the mandible length (M) is 11.13–12.34 mm. The lower incisors (I_1 to I_3) are all tricuspidate. The mandibular toothrow length (C–M_3) is 5.83–6.43 mm. The height of the lower canine (C_1) exceeds that of the first (P_2) and second lower premolars (P_4), which are equal in height. P_2 is about half the crown area of the C_1 and about two-thirds that of the P_4. The anterior and posterior basal cusps of P_2 are partially placed above the posterior border of C_1 and the anterior border of P_4 (Fig. 4a). P_4 is relatively large and rectangular in shape, with a crown area about two-thirds that of the lower canine. The talonid of the first (M_1) and second lower molars (M_2) is about half to two thirds that of its respective trigonid in size; 50.00–70.00% and 50.00–73.68% in M_1 and M_2, respectively. The height of the hypoconid exceeds that of its entoconid in both M_1 and M_2. The coronoid process is well developed, 4.01–5.15 mm in height.

The baculum is heart shaped, with a M-shape on the anterior margin and a pointed projection on the posterior margin. The greatest length of the baculum (BL) is 1.0 mm and the width is 0.8 mm. The dorsal surface is arched upwards and the ventral surface is deeply concave (Fig. 5a).

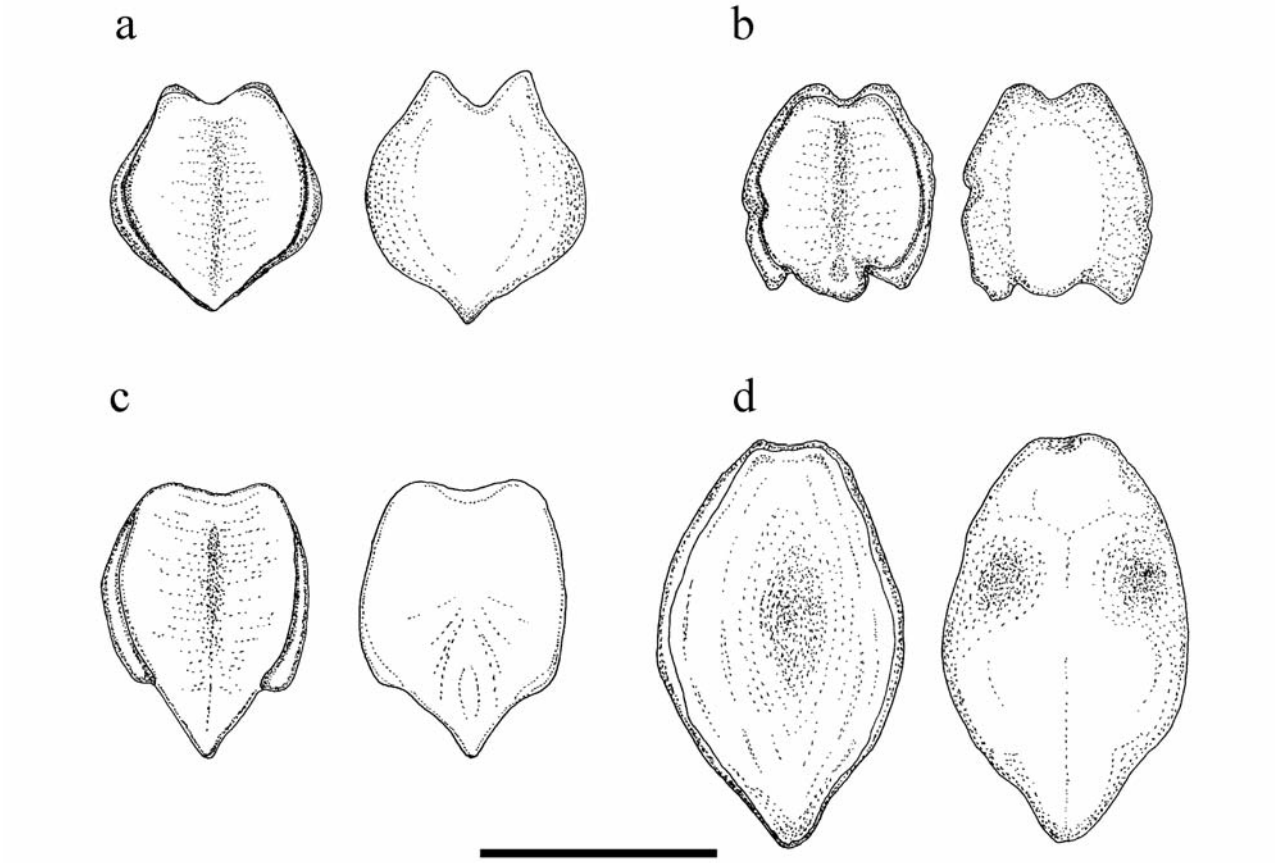

FIG. 5. Ventral (left of each pair) and dorsal (right) views of the bacula of four species of *Murina*: (a) *M. guilleni* sp. nov., PSUZC-MM 2010.22 (holotype), from peninsular Thailand, (b) *M. cyclotis,* PSUZC-MM 2005.203, from SE Thailand, (c) *M. fionae*, field no. 18, from Vietnam, (d) *M. peninsularis*, PSUZC-MM 2006.160, from peninsular Thailand. Scale = 1 mm

Echolocation

Murina guilleni emits typical broadband frequency-modulated (FM) signals with the energy distributed throughout the call. The *fmaxe* of two male specimens was 120.1–155.7 kHz, with a *d* of 1.8–3.8 ms. The *sf* and *tf* were 175.0–184.0 kHz and 53.0–63.0 kHz, respectively. The call parameters of a female specimen were similar to those of the two male specimens, except for the *sf* which was lower, 159.0–167.0 kHz; other measurements overlap, *tf* of 50.0–57.0 kHz, *fmaxe* of 120.7–157.7 kHz, and *d* of 2.4–3.0 ms.

Ecology and habitat

This species is found in disturbed secondary forest and undisturbed primary evergreen forest in peninsular Thailand. It was captured along forest trails, by a stream, and in the understorey. It shares these habitats with several other insectivorous bat species (see Method section). In April 2010, a pair of male and female specimens was captured together in harp trap at the type locality; the female appeared to be lactating. The female specimen ROM 110439 collected from Khao Pra Bang Kram WS on 12 April 1997 was also lactating (A. Guillén-Servent, personal communication). In the Nicobar Islands, India, specimens were collected in gallery forests (see below; BA, unpublished data).

Distribution

Currently, this species has been found in seven localities in six provinces of peninsular Thailand and five localities in the Nicobar Islands (Fig. 1, Appendix). It was found sympatrically with the larger species, *M. peninsularis*, but there is no overlap in geographical range with *M. fionae* or *M. cyclotis* (Fig. 1).

Discussion

Comparison with Other Species

Murina guilleni is very similar to *M. cyclotis.* However, it can be distinguished by its relatively larger size and various craniodental characters. Although the size of *M. guilleni* falls within at least part of the range of *M. cyclotis*, the mean scores of all the measurements in both sexes show that it is generally larger (Tables 1 and 2). In *M. guilleni*, males and females have an average FA of 33.5 mm and 34.9 mm, and a CCL of 14.88 and 15.26 mm, respectively. These exceeds those of *M. cyclotis*, which has an average FA of 30.7 mm and 33.9 mm and CCL of 14.45 mm and 15.22 mm, in males and females, respectively (Fig. 6, Tables 1 and 2). The dorsal pelage of *M. guilleni* resembles that of *M. cyclotis* but differs somewhat in the ventral pelage, in which *M. guilleni* is duller being dark grey rather than the whitish-brown of *M. cyclotis* (Fig. 2). In the skull, the rostral concavity is less pronounced in *M. guilleni* than in *M. cyclotis.* The braincase of *M. guilleni* is more domed and higher, with an average BCH of 6.68 mm and 6.86 mm in males and females, respectively, whereas the comparable figures for *M. cyclotis* are 6.49 mm and 6.57 mm (Fig. 3, Table 2). The first upper premolar (P^2) of *M. guilleni* is about two-thirds to subequal that of the second (P^4) in height crown area, whereas in *M. cyclotis*, the height of P^2 is two-thirds and the crown area about equal to that of the P^4. The relative size of the talonid in comparison to its respective trigonid of the first (M_1) and second lower (M_2) molars of *M. guilleni* is smaller, about half to two-thirds, whereas in *M. cyclotis* this proportion is variable from more or less about half to about two-third (Fig. 4).

In the baculum, the posterior margin of *M. guilleni* is pointed whereas it is M-shaped in *M. cyclotis* (Fig. 5). However, it is noteworthy that the baculum of *Murina* could be variable, and using bacular morphology in the identification of *Murina* species has not been widely accepted. Based on our examination, the baculum of *Murina* is generally very small, fragile and easy to crack, which may lead to misleading conclusions in species identification.

Murina guilleni is distinctly smaller in external and cranial characters compared to both *M. fionae* and *M. peninsularis* (Fig. 6, Tables 1 and 2). Although there is some overlap in measurements between larger female specimens of *M. guilleni* and smaller male specimens of *M. peninsularis*, comparison between the same sexes of both species can readily distinguish them apart. Besides size, the skulls of *M. fionae* and *M. peninsularis* are more robust, each with a massive upper canine and heavy rostrum (Fig. 3). *Murina guilleni* also differs from *M. fionae* and *M. peninsularis* in the general appearance of the pelage and the height of the P^2 (Figs. 2 and 3).

A multivariate analysis based on one external (FA) and nine craniodental measurements (Table 3) of a total of 124 specimens clearly separates *M. cyclotis*, *M. fionae* and *M. peninsularis* from each other, whereas *M. guilleni* is situated midway between the three species (Fig. 7).

Genetic Analyses

Although quite similar morphologically, results from the genetic analyses showed approximately 15–17% divergence between *M. guilleni* from peninsular Thailand and *M. cyclotis* from Indochina. *Murina guilleni* also form a statistically supported (bootstrap > 80%) monophyletic sister clade with a genetic divergence value of 10% to a specimen identified as *M*. cf. *cyclotis* from India (Fig. 8). The morphological comparison of the external (i.e., FA of 34.2 mm), craniodental (i.e., CCL of 15.25 mm) and bacular characters of the male specimen (HZM 17.36447) from South India (Tamil Nadu) suggest that it is more similar to *M. guilleni* than specimens referred to *M. cyclotis* from elsewhere. However, with only a single specimen from the area, it is premature to determine whether this specimen represents a new species or belongs to a recognised species. Further study with more samples from the area and additional genetic analyses is recommended.

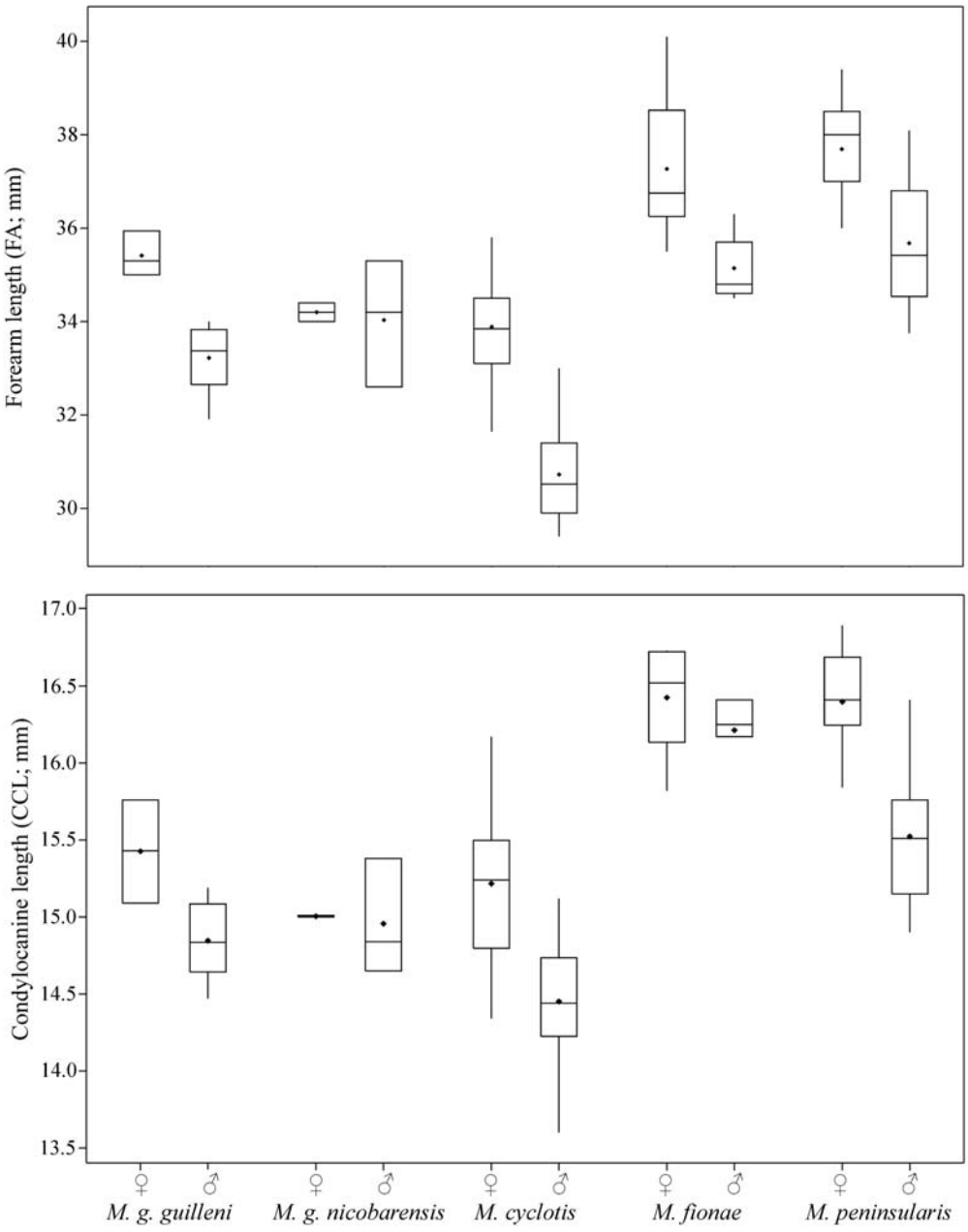

FIG. 6. Boxplots of the measurements of FA and CCL for females (left of each taxon) and males (right of each taxon) of *M. g. guilleni*, *M. g. nicobarensis*, *M. cyclotis*, *M. peninsularis* and *M. fionae*. The horizontal line within the boxes indicate median values and the black points indicate mean values

Murina guilleni nicobarensis subsp. nov.
(Figs. 1, 6–9, Tables 1–3)

Holotype

HZM 14.35312 (field number 15304336), adult male, body in alcohol, skull extracted, exact date not known.

Type locality

Great Nicobar Island, Nicobar Islands, India (7°8'N, 3°55'E).

Paratypes

HZM 12.35277 (field number TIL09 34), adult male, dry skin, skull extracted, from Tillanchong, Nicobar Islands, India; HZM 15.35319, adult female, body in alcohol, skull extracted, from Trinket, Nicobar Islands, India; HZM 13.35278 (field number 15322338), adult male, body in alcohol, skull extracted, from Camorta, Nicobar Islands, India; HNHM 2004.13.1 (field number BOMBAT27), adult female, body in alcohol, skull extracted, from Bompuka, Nicobar Islands, India.

Diagnosis

This taxon is described as a subspecies of *M. guilleni* based on its general similarity in external and craniodental characters. In contrast to the nominate race, males appear to be slightly larger than females in FA and skull size (Fig. 6, Tables 1 and 2). The dorsal and ventral pelage, as in the nominate subspecies, has a grey base with orange-brown tips on the back, and is uniformly dark grey on the underside.

Etymology

The subspecific name refers to the Nicobar Islands, where specimens of this taxon were collected.

Description and taxonomic notes

This is a small-medium sized *Murina* with a FA of 32.6–35.3 mm (Table 1) and a CCL of 14.65–15.38 mm (Table 2). The dorsal pelage is grey at the base and orange-brown at the tip. The ventral pelage is uniformly dark grey. Each wing is attached near the base of the claw of the outer toe. The braincase is relatively high, with a BCH of 6.57–6.79 mm and a poorly developed sagittal crest. The upper canine exceeds that of the P^4 in height. P^2 is about two-thirds the height and the crown area of P^4 (Fig. 9). The upper ($C–M^3$) and the lower ($C–M_3$) toothrow lengths are 5.39–5.73 mm and 5.91–6.26 mm, respectively. The height of the first and second (P_2 and P_4) lower premolars are about equal and about two-thirds that of the lower canine in height. The crown area of the talonid of M_1 and M_2 is about half to two-thirds that of the trigonid, and the entoconid is about equal in height to the hypoconid. The coronoid process (CPH) is 4.01–4.44 mm. The baculum is essentially similar to the nominate subspecies from peninsular Thailand.

TABLE. 3. Factor loading scores of the characters used in PCA (Fig. 7) and variance explained by the first and second components. Definitions of measurement are included in the Method section

Characters	PC1	PC2
FA	-0.313	0.115
CCL	-0.330	0.293
BB	-0.309	-0.373
BCH	-0.300	-0.454
MW	-0.327	-0.261
PCH	-0.308	-0.312
$C–M^3$	-0.320	0.381
$M^3–M^3$	-0.309	0.234
$C^1–C^1$	-0.327	-0.093
$C–M_3$	-0.319	0.426
Variance explained (%)	82.0	5.5

As in *M. g. guilleni*, the taxon *nicobarensis* is larger than *M. cyclotis* and smaller than *M. fionae* and *M. peninsularis*. It is, in general, very similar to the taxon *guilleni.* In the skull, the average skull size of *nicobarensis* is slightly larger in male specimens (i.e., CBL 15.55 mm, CCL 14.96 mm), and slightly smaller in female specimens (CBL 15.65 mm, CCL 15.00, 15.01 mm) than the mainland subspecies (CBL 15.46 mm, CCL 14.85 mm in male; and CBL 16.10 mm, CBL 15.43 in female) as described above (Table 2, Fig. 6). The height of the P^2 of *nicobarensis* is about two-thirds that of the P^4 (Fig. 9), whereas it is subequal in *guilleni.* The ventral pelage, although very similar to that of specimens from peninsular Thailand, is somewhat darker. A future study with a greater sample size and including genetics may prove that this geographically isolated population is specifically distinct.

Ecology and habitat

Specimens of *M. g. nicobarensis* were collected in mist nets set across streams in gallery forests. It was observed flying slowly in lower strata of the forest to the maximum height of 4.5 m above ground (BA, unpublished data).

Distribution

It is currently known from five specimens collected from the Nicobar Islands (Fig. 1, Appendix). Individuals of *Murina* similar to this species were also captured in Katchal, Nancowrie and Tressa where the bats were subsequently released (BA, unpublished data).

Murina fionae Francis and Eger, 2012
Fiona's tube-nosed bat

Murina peninsularis, Matveev and Csorba, 2007: 100.
Murina CMF sp. B Francis *et al*., 2010: 6.
Murina fionae Francis and Eger, 2012: 32; Pha Deng, ≈ 8 km E of Ban Navang, Khammouan Province, Laos.

Description and taxonomic notes

This is a medium-large sized *Murina* with a FA of 34.5–40.1 mm. The ear is rounded with a pinna height (E) of 12.1–15.6 mm (Table 1). The dorsal pelage is pale buff basally and orange-brown at the tips, with longer guard hairs scattered from the head, over the back and to the uropatagium. The ventral pelage is uniformly pale buff-orange, but more whitish near the chin (Fig. 2c). The third metacarpal (3MET) is about equal in length with the fifth (5MET), 32.5–35.4 mm and 32.5–36.0 mm, respectively. The fourth metacarpal (4MET) is the shortest, 31.1–34.7 mm (Table 1). Each plagiopatagium is attached to the distal phalanx near the base of the

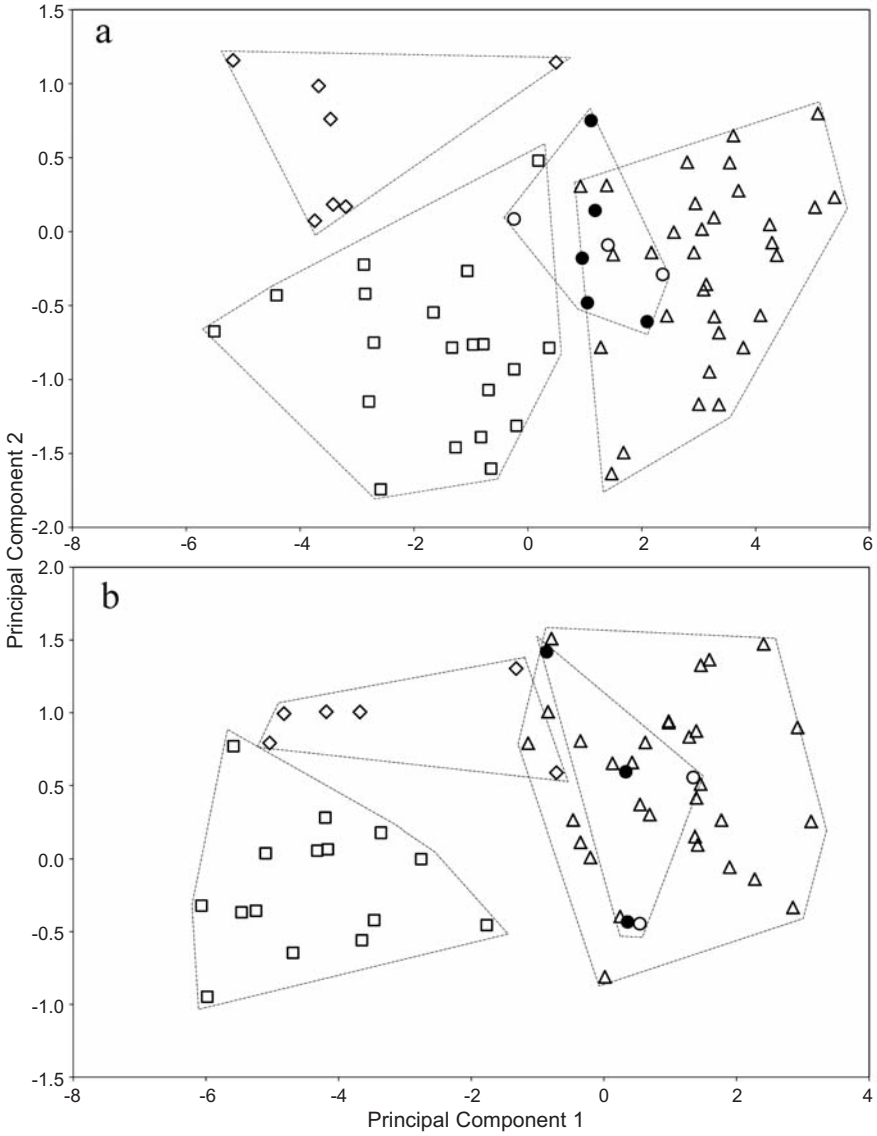

FIG. 7. Principal component analysis (first and second components) based on one external and nine craniodental characters of 67 male specimens (a), and 57 female specimens (b) of *M. g. guilleni* (black circles), *M. g. nicobarensis* (white circles), *M. cyclotis* (triangles), *M. fionae* (diamonds) and *M. peninsularis* (squares). Variance explained of the PC 1 and PC 2 are 82.0% and 5.5%, respectively. Loading scores are in Table 3

claw. The skull is relatively large and heavily-built, with a GTL of 17.53–19.26 mm and the CCL of 15.32–16.87 mm (Table 2). The braincase is relatively high (BCH 6.53–7.50 mm) with a well-developed sagittal crest which is connected to the lambda (Fig. 3c). The maxillary toothrow length (C–M^3) is 5.72–6.40 mm, and is slightly convergent anteriorly, with the ratio between C^1–C^1 and M^3–M^3 of 72.76–80.34%. The upper canine (C^1) is rounded, very large, and greatly exceeds the second upper premolar (P^4) in size (Fig. 3c). The mesostyle of both the first (M^1) and second (M^2) upper molars is greatly reduced. The size of the talonid of the M_1 and M_2 is half that of the trigonid (Fig. 4c), and the entoconid is about equal in height to the hypoconid. The baculum is almost similar to that *M. guilleni* but somewhat less rounded and the pointed projection on the posterior margin is more elongated (Fig. 5c). The dorsal surface is arched upwards and the ventral surface is deeply concave with a total length (BL) of 1.1 mm.

Morphologically, *M. fionae* is very similar to *M. peninsularis* (see below). However, the skull size (for example, CCL) of *M. fionae* averages larger than that of *M. peninsularis* (Fig. 6, Table 2). The upper canine of *M. fionae* is more massive and its crown area greatly exceeds that of the second upper premolar whereas it only slightly exceeds it in *M. peninsularis.* In the DNA barcode, there is an approximately 16% difference between specimens from Laos and peninsular Thailand. Furthermore, geographically the two species are isolated from each other (Fig. 1). Clearly, the two taxa represent distinct species (Fig. 7).

Ecology and habitat

This species has been collected in wet, hill evergreen forest at an altitude of 830–1,140 m a.s.l. on the Annamite Mountains (Francis and Eger, 2012). The specimen from Cambodia (HNHM 2005.81.16) was collected in semi-deciduous forest at an altitude of 290 m.

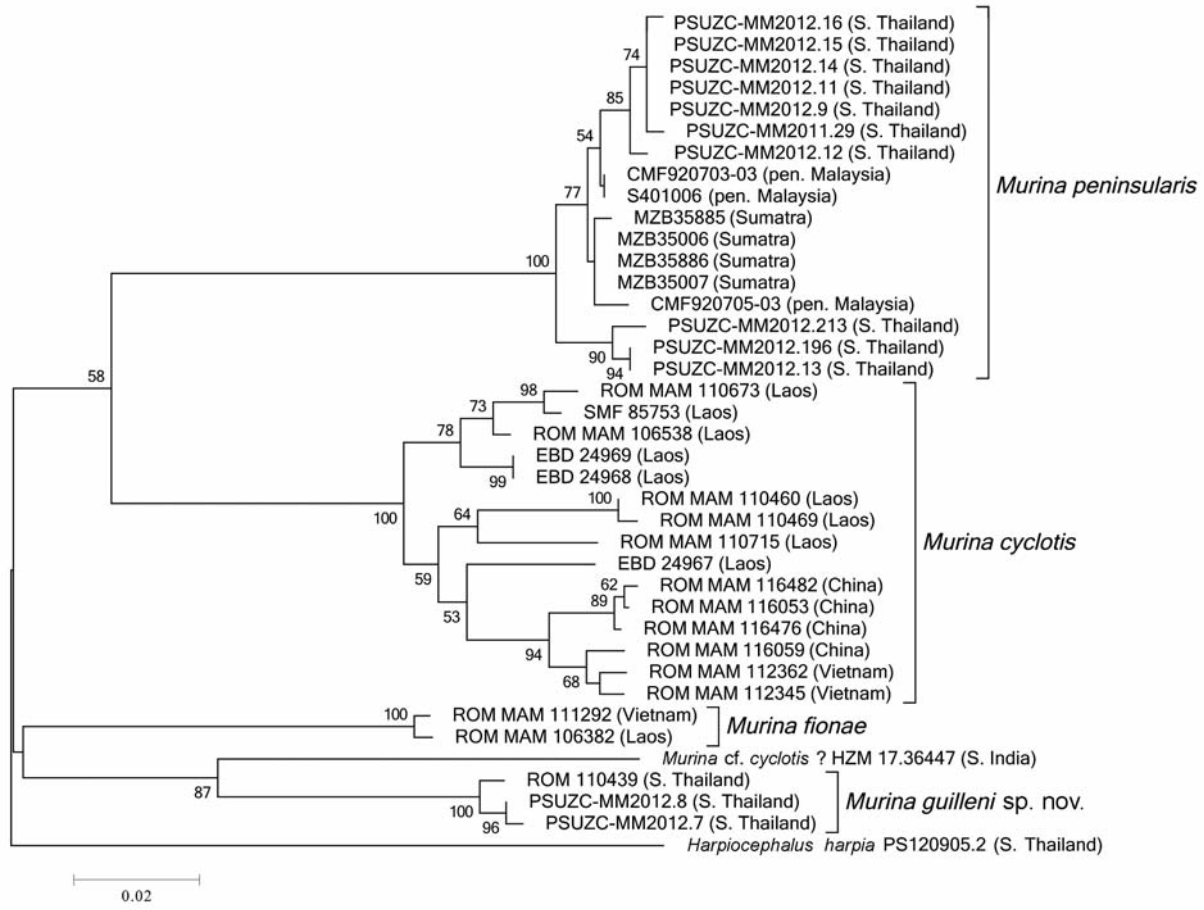

FIG. 8. Neighbour-joining tree based on DNA barcodes of *M. guilleni* sp. nov., *M. cyclotis*, *M. fionae* and *M. peninsularis*. Numbers close to tree branches/node indicate the NJ bootstrap support value

Distribution

Currently, *M. fionae* is known from Laos, Vietnam and Cambodia (Fig. 1, Appendix — see also Francis and Eger, 2012; Thomas *et al.*, 2013).

Murina peninsularis Hill, 1964
Peninsular tube-nosed bat

Murina cyclotis peninsularis Hill, 1964: 55; UIu Chemperoh, near Janda Baik, Bentong District, Pahang, Malaysia.

Redescription and taxonomic notes

This is a medium-large sized *Murina* with a FA of 33.8–39.4 mm. Males average smaller than females; mean FA of 35.7 mm (33.8–38.1 mm) vs. 37.7 mm (34.5–39.4 mm). The anterior border of the ear is curved and is without a distinct emargination on the posterior border; the tip is rounded and the height is 11.9–18.8 mm. The tragus is buff and relatively high; 7.4–10.3 mm, exceeding half the height of the pinna (Table 1). The dorsal pelage is buff basally and copper-brown to orange-brown at the tips with guard hairs of the same colour scattered over the dorsal side. The ventral pelage is relatively short, pale buff basally and greyish-brown at the tips but with more orange near the chin and on the side of the abdomen (Fig. 2d). In the wing, the third metacarpal (3MET) is slightly longer than the fifth (5MET); 32.0–37.7 mm and 31.3–36.8 mm, respectively; whereas the fourth (4MET) is the shortest, with 29.9–36.4 mm (Table 1). Each plagiopatagium is dark brown and attached to the distal phalanx near the base of the claw.

The skull is heavily-built and relatively large, with a GTL of 17.39–19.33 mm and CCL of 14.90–16.89 mm (Table 2). The braincase is domed with a well-developed sagittal crest (Fig. 3d). However, the braincase shape is variable, particularly in female specimens, from slightly domed to highly domed, with a BCH of 6.79–8.37 mm (Table 2). The rostrum is short and bulbous; it accommodates a massive upper canine, which exceeds the height and crown area of the second upper premolar (Figs. 3 and 4). The inner upper incisor (I^2) is placed lateral to the outer incisor (I^3) and is almost invisible in side view (Fig. 3d). The first upper premolar (P^2) is subequal to that of the second (P^4) in height, and about two-thirds in crown area (Figs. 3d and 4d). The first and second upper molars are without a mesostyle, and the labial surface has a deep V-shape indentation (Fig. 4d). The maxillary toothrows are almost parallel, with a ratio between C^1–C^1 and M^3–M^3 of 76.30–86.52%; the C–M^3 is 5.52–6.39 mm. All three lower incisors are tricuspidate. The first (P_2) and second (P_4) lower premolars are

FIG. 9. Skull of *M. g. nicobarensis* ssp. nov., ♂, HZM 14.35312 (holotype) from Great Nicobar Island, India. Scale = 5 mm

about equal in height and about two-thirds that of the lower canine. The talonid of the first and second lower molars (M_1 and M_2) is about half the size of its respective trigonid (Fig. 4d); the height of the entoconid is equal to, or slightly less than, that of its respective hypoconid.

The baculum is almost oval in shape; the anterior margin is rounded or very slightly concave, the posterior margin is pointed (Fig. 5d). The dorsal side is arched upwards and the ventral side is deeply concave. The total length of the baculum (BL) is 1.8 mm.

As mentioned above that the shape of the braincase is highly variable. External, dental and bacular morphology, however, show no significant differences between specimens examined. DNA barcodes also reveal a genetic distance of only about 1–2% among specimens from peninsular Thailand to Sumatra. However, further genetic studies, particularly between populations from the major islands of the Sunda, would be of particular interest. As above, although the measurements of specimens from the Philippines in Ingle and Heaney (1992) agree with *M. peninsularis*, it is not advisable to assign them to this species without examining relevant material.

Echolocation

Free-flying individuals of *M. peninsularis* collected in peninsular Thailand emitted typical broadband FM signals with the energy distributed almost evenly throughout the call. Based on call records of 10 individuals, the mean *fmaxe* is of 112.7 kHz (range 79.0–142.6 kHz); *sf* 163.3 kHz (range 139.0–182.0 kHz); *tf* 50.2 kHz (range 40.0–64.0 kHz). The *d* is of 2.6 ms (range 1.5–4.9 ms).

Ecology and habitat

In peninsular Thailand, it was mostly captured in harp traps set across forest trails or streams in both primary and secondary evergreen forests. During fieldwork in 2011–2012, female specimens were found to be pregnant between February and April, and lactating between April and July. In Sumatra, it was also captured in harp traps set in forest areas. In peninsular Malaysia, it was found from lowland to hill and montane terrain (e.g., Kingston *et al.*, 2006; Tingga *et al*., 2012). Its roosting behaviour is very little known, although an individual of *Murina* sp., with the size and colour comparable to this taxon, was found flying around banana trees in the afternoon during a search for a trapping site in peninsular Thailand. Kingston *et al.* (2006) reported an individual flying from a wild banana tree; it was subsequently caught in a mist net set nearby.

Distribution

Murina peninsularis is found in peninsular Thailand and Malaysia through to Sumatra, Borneo and Lombok (Fig. 1, Appendix).

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Appendix

List of specimens examined. Those that were included in the genetic analysis have the BOLD process ID in square brackets after the collection number

Murina guilleni sp. nov. — *Thailand*: ♂ PSUZC-MM 2010.22 (holotype), ♀ PSUZC-MM 2010.23 (paratype), Rajjaprabha Dam, Ban Takhun, Surat Thani, S. Thailand; ♂ PSUZC-MM 2012.7 (paratype) [BTSEA011-13], Ton Tae Waterfall, Pa Lien, Trang, S. Thailand; ♀ ROM 110439 [ABBM062-05], Khao Nor Chuchi Reserve (=Khao Pra Bang Kram WS.), Klong Tom, Krabi, S. Thailand; ♂ PSUZC-MM 2013.15 (paratype), Wang Tai Nan Waterfall, Manang, Satun, S. Thailand; ♂ PSUZC-MM 2012.8 [BTSEA013-13], Ban Ton St., Khao Bantad WS, Phattalung, S. Thailand; ♂ PSUZC-MM 2008.3, Yaroi Waterfall, Taleban NP., Satun, S. Thailand; ♂ PSUZC-MM 2007.350, Ban Vang Pha, Songkhla, S. Thailand; ♀ PSUZC-MM 2011.42, Rajjaprabha Dam, Ban Takhun, Surat Thani, S. Thailand; ♀ PSUZC-MM 2007.154, Makling Waterfall, Rattaphum, Songkhla, S. Thailand.

Murina guilleni nicobarensis ssp. nov. — *India*: ♂ HZM 14.35312 (holotype), Great Nicobar Island, Nicobar Islands; ♂ HZM 12.35277 (paratype), Tillanchong, Nicobar Islands;

APPENDIX. Continued

♂ HZM 13.35278 (paratype), Camorta, Nicobar Islands; ♀ HNHM 2004.13.1 (paratype), Bompuka, Nicobar Islands; ♀ HZM 15.35319, Trinket, Nicobar Islands (paratype).

Murina cyclotis — *India*: ♂ BMNH 9.4.4.4 (holotype), Darjeeling, NE. India; ♂ BMNH 16.3.25.28, Gopaldara, Darjeeling, NE. India; ♂ BMNH 16.3.25.29, Pashok, Darjeeling, NE. India; ♂ BMNH 20.6.24.1, Teesta Valley, West Bengal, NE. India; ♂ HZM 17.36447 [ABBM421-05], Tamil Nadu, S. India; — *Sri Lanka*: ♂ BMNH 31.9.4.2 (holotype of *eileenae*); ♂ BMNH 59.5.31.63; ♂ BMNH 66.5543; ♂ BMNH 72.42.56, Mousakande, Gammaduwa; — *Nepal*: ♂ HNHM 98.7.3, Island Jungle Resort, Chitwan NP, Nepal; — *Myanmar*: ♀ HZM 17.35961, Madanyan Forest, Manse Township, Kachin, N. Myanmar; ♀ BMNH 50.484, Sumka Uma, Kachin, N. Myanmar; ♀ BMNH 16.3.26.3; ♀ BMNH 16.3.26.4, Chin Hills, W. Myanmar; ♀ BMNH 16.3.26.89, 50 miles from Kindat, Sagaing, W. Myanmar; — *China*: ♀ ROM MAM 116482 [ABBM461-05]; ♂ ROM MAM 116476 [ABBM460-05], Shiwandashan National Reserve, Guangxi, S. China; ♂ ROM MAM 116053 [ABBM447-05]; ♀ ROM MAM 116059 [ABBM448-05], Jing Xin County Provincial Nature Reserve, Guangxi, S. China; ♂ field number B050023, Hainan Island; — *Vietnam*: ♂ NF 160906.4; ♂ NF 170906.5; ♀ NF 030706.6; ♀ NF 170906.4; ♀ NF 230706.4, Kim, Hy Nature Reserve, Bac Kan, N. Vietnam; HZM 5.31760, Ke Bang, Quang Binh, C. Vietnam; ♂ HNHM 98.3.3, Pac Ban Village, Tuyen Quang, N. Vietnam; ♂ HNHM 2000.84.3, Ben En NP., Thanh Hoa; ♂ HNHM 2010.42.3; ♂ field number T.291107.3; ♀ field number T.241107.2; ♀ field number T.251107.1, Son La, N. Vietnam; ♂ field number T.050808.8, Bai Tu Long NP, Quang Ninh, N. Vietnam; ♂ field number T.120806.2; ♂ field number T.230408.1; ♀ field number T.220908.1, Cat Ba Island, Hai Phong, N. Vietnam; ♂ field number 11, Than Sa, Thai Nguyen, N. Vietnam; ♂ field number B46, Pu Hoat NR., Nghe An, C. Vietnam; ♀ HZM 1.30708; ♀ HNHM 208.23.1, Cuc Phong NP., Ninh Binh, N. Vietnam; ♀ HZM 3.31526; ♀ HZM 9.31777, Pu Mat NP., Nghe An, C. Vietnam; ♀ BMNH 1997.384, Na Hang NR., Tuyen Quang, N. Vietnam; ♀ field number T85; ♀ field number T03; ♀ field number T.270308.2, Me Linh, Vinh Phuc, N. Vietnam; ♀ HNHM 2007.27.7; ♀ NTS 1597, Ba Be NP., Bac Kan, N. Vietnam; ♀ field number T.010908.10; ♀ field number T.010908.6, Tam Dao, Vinh Phuc, N. Vietnam; ♀ field number T.210708.2; ♀ field number T.260607.2; ♀ field number T.270607.1; ♀ PSUZC-MM 2011.54, Phuong Vien, Phu Tho, N. Vietnam; ♀ field number T.290708.6, Xuan Son, Phu Tho, N. Vietnam; ♀ field number 06, Tamtri, Tam Ky, Quang Nam, C. Vietnam; ♀ ROM MAM 112362 [BM399-04]; ♀ ROM MAM 112345 [ABBM456-05], Lan Dat, 4 km W. of Huu Lien, Lang Son, N. Vietnam; — *Laos*: ♂ BMNH 1999.854, Ban Vieng, Khammouan, C. Laos; ♀ BMNH 1999.51, Tham Houay Si, 6.5 km SW. of Ban Vieng, Khammouan, C. Laos; ♀ field number BD100320.2; ♀ field number BD100320.5, Vang Vieng, Vientiane, C. Laos; ♀ ROM MAM 110673 [BM056-03], Phou Khao Kouay, Vientiane, C. Laos; ♂ SMF 85753 [ABBM389-05], Ban Keng Bit, Nam Kading, Khammouan, C. Laos; ♀ ROM MAM 106538 [BM110-03], Nam Pakkatan, Nakai Plateau, Khammouan, C. Laos; ♂ EBD 24968 [ABBM297-05]; ♂ EBD 24969 [ABBM298-05], Nam Khan, Nam Et NBCA, Louangprabang, N. Laos; ♀ ROM MAM 110469 [ABBM154-05], Xe Kaman, Attapu, S. Laos; ♀ ROM MAM 110715 [BM159-03], Dong Kanthung, Champasak, S. Laos; ♀ EBD 24967 [ABBM255-05], near Ban Chak, Nam Et NBCA, Houaphan, N. Laos; ♀ MHNG 1926.033, Sopkhang, Phongsaly, N. Laos; — *Thailand*: ♂ BMNH 82.164, Doi Inthanon NP., Chom Thong, Chiang Mai, N. Thailand; ♂ BMNH 78.2383, Tham Tab Tao, Fang, Chiang Mai, N. Thailand; ♂ BMNH 82.165, Doi Pha Hom Pok, Fang, Chiang Mai, N. Thailand; ♀ PSUZC-MM 2011.32, Chiangdao WS, Chiang Mai, N. Thailand; ♀ THNHM M-821, Klong Lan NP., Kampangphet, NW. Thailand; ♂ PSUZC-MM 2006.179; ♀ PSUZC-MM 2006.178, Phu Suan Sai NP., Na Haew, Loei, NE. Thailand; ♂ TISTR 54-7170, Phu Rua, Loei, NE. Thailand; ♂ THNHM M-735, Mo Sing To, Khao Yai NP., Nakhon Ratchasima, NE. Thailand; ♀ THNHM M-775, Dong Sua Parn, Khao Yai NP., Nakhon Ratchasima, NE. Thailand; ♂ PSUZC-MM 2005.203, Klong Klang Khao Ang Ru Nai WS., Chacherngsao, SE. Thailand; — *Cambodia*: ♂ HNHM 2007.49.10, Phnom Samkos, Pursat, W. Cambodia; ♂ HNHM 2006.34.38; ♂ HNHM 2005.81.33; ♀ HNHM 2005.81.48, Seima BCA, Mondol Kiri, E. Cambodia; ♀ HNHM 2006.34.2, Bokor NP., Kampot, SW. Cambodia.

Murina fionae — *Vietnam*: ♂ field number 025; ♂ field number 12; ♂ field number 18, Tam Tri, Tam Ky, Quang Nam, C. Vietnam; ♂ HZM 8.31764; ♂ HZM 6.31759, ♂ HZM 7.31762, Phong Nha, C. Vietnam; ♂ HNHM 2007.50.3; ♀ HNHM 2007.50.4, Huong Hoa Nature Reserve, Quang Tri, C. Vietnam; ♀ HZM 10.31776, Pu Mat NP., Nghe An, C. Vietnam; ♀ HZM 11.32353, Kon Cha Rang Nature Reserve, Gai Lai, C. Vietnam; ♀ HZM 4.31761, Ke Bang, Quang Binh, C. Vietnam; ♀ HNHM 2008.23.7, Pu Huong, Nghe An, C. Vietnam; ♀ ROM MAM 111292 [BM366-04], Ngoc Linh Nature Reserve, 10 Km SW Nuoc Xa, Quang Nam, C. Vietnam; — *Laos*: ♀ ROM MAM 106382 [BM318-04], Pha Deng, 8km E Ban Navang, Khammouan, C. Laos; — *Cambodia*: ♀ HNHM 2005.81.16, Seima BCA, Mondol Kiri, E. Cambodia.

Murina peninsularis — *Thailand*: ♂ PSUZC-MM 2012.9 [BTSEA016-13]; ♂ PSUZC-MM 2012.11 [BTSEA019-13]; ♂ PSUZC-MM 2012.12; ♀ PSUZC-MM 2012.14 [BTSEA020-13], Khao Pra Bang Kram WS, Klong Tom, Krabi, S. Thailand; ♀ PSUZC-MM 2007.349, Huay Lek, Khao Nan NP., Nop Pitam, Nakhon Sithammarat, S. Thailand; ♂ PSUZC-MM 2011.29 [BTSEA015-13], Khao Pu Khao Ya NP., Phattalung, S. Thailand; ♂ PSUZC-MM 2007.348, Kachong, Khao Bantad WS., Trang, S. Thailand; ♂ PSUZC-MM 2006.160, Taleban NP., Satun, S. Thailand; ♂ PSUZC-MM 2008.137, Talow Udang St., Tarutao Island, Satun, S. Thailand; ♂ PSUZC-MM 2012.10; ♂ PSUZC-MM 2012.12 [BTSEA036-13]; ♀ PSUZC-MM 2012.15 [BTSEA037-13]; ♀ PSUZC-MM 2012.16 [BTSEA035-13], Pha Dum Waterfall, Ton Nga Chang WS, Songkhla, S. Thailand; ♂ PSUZC-MM 2007.336; ♂ PSUZC-MM 2011.30; ♀ PSUZC-MM 2006.120; ♀ PSUZC-MM 2012.155; ♀ PSUZC-MM 2012.156, Ton Nga Chang WS, Songkhla, S. Thailand; ♂ PSUZC-MM 2012.13 [BTSEA024-13]; ♂ PSUZC-MM 2012.196 [BTSEA047-13]; ♀ PSUZC-MM 2012.212; ♀ PSUZC-MM 2012.213 [BTSEA030-13], Hala-Bala WS., Wang, Narathiwat, S. Thailand; — *Malaysia*: ♂ BMNH 64.771 (holotype); ♀ BMNH 64.772 (paratype), Ulu Chemperoh, Janda Baik, Pahang, peninsular Malaysia; ♂ BMNH 73.630; ♀ BMNH 67.1607, Gunong Benom Base Camp, Bentong, Pahang, peninsular Malaysia; ♀ TK 153526, Taman Negara, Pahang, peninsular Malaysia; ♂ CMF 920703-03 (Research Collection of Charles Francis) [BM486-04]; ♂ CMF 920705-03 (Research Collection of Charles Francis)

APPENDIX. Continued

[BM485-04], Kuala Lampat, Pahang, peninsular Malaysia; ♀ field number ? S401006 [ABBSI080-05], Krau Wildlife Reserve, Pahang, peninsular Malaysia; ♀ BMNH 1880.744, Pinang, peninsular Malaysia; ♀ BMNH 75.1294, Sungei Relembany Camp, Ulu Setiu, Besut, Trengganu, peninsular Malaysia; ♂ BMNH 73.631, Pahang, peninsular Malaysia; ♂ BMNH 68.845, Batu Pahat, Kangar, Perlis, peninsular Malaysia; ♂ BMNH 64.773, Fraser Hill, Selangor, peninsular Malaysia; ♂ TK 172744, Lojing Highlands, Kelantan, peninsular Malaysia; ♂ BMNH 78.1543, Melinau, Gunung Mulu NP., Sarawak, Borneo; ♂ BMNH 82.556; ♀ BMNH 84.2019; ♀ TK 168706, Sepilok, Sabah, Borneo; ♂ BMNH 84.2020, Lumerau, Sabah, Borneo; — *Indonesia*: ♂ MZB 35006; ♂ MZB 35007; ♀ MZB 35885; ♀ MZB 35886, Way Canguk, Bukit Barisan Selatan NP., Lampung, Sumatra; ♂ MZB 23925; ♂ MZB 31945, Marawi, Kalimantan, Borneo; ♀ HZM 18.36541, Tanjung Putting National Park, C. Kalimantan, Borneo; ♀ MZB 29315, Nusa Tenggara Barat, Lombok.