

A new species of *Kerivoula* (Chiroptera: Vespertilionidae) from Southeast Asia

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A new species of *Kerivoula* is described from Seima Biodiversity Conservation Area, Cambodia. It is widely distributed in mainland Southeast Asia, with referred material from 12 additional localities in Myanmar, Thailand, Lao PDR and Vietnam. Superficially similar to *Kerivoula flora*, it is distinguished by its flattened skull, a character shared with the larger, recently described, *Kerivoula kachinensis*. It is known from a variety of habitat types, both pristine and disturbed, including deciduous dipterocarp forest, moist evergreen and semi-evergreen forest, forest on limestone karst and upper montane forest.

Key words: *Kerivoula* sp. nov., Cambodia, Myanmar, Thailand, Lao PDR, Vietnam, taxonomy, skull morphology

INTRODUCTION

Between 1997 and 2000, a series of bat surveys were conducted in six protected areas of Vietnam. Fifty-nine species were recorded including two *Kerivoula*, which were represented by seven specimens collected from Pu Mat National Park, Nghe An Province and Kon Ka Kinh Nature Reserve, Gia Lai Province. Five of these specimens were referred to *K. hardwickii* and two to *K. flora* (Hendrichsen *et al.*, 2001);

however these authors further commented that, although these latter two specimens agreed in many characters (with *K. flora*), there were some differences, and that the record should be considered provisional until more material was available. Subsequently, together with an additional specimen from Thailand, they were included as *K. flora* in Vanitharani *et al.* (2003) in which the dentition of specimen HZM.1.32607 from Kon Ka Kinh Nature Reserve was illustrated. In 2007, further single specimens of *Kerivoula*,

comparable to the provisional *K. flora* of Hendrichsen *et al.* (2001), were collected in Vietnam from Kim Hy Nature Reserve and Ba Be National Park in Bac Kan Province, and at Da Krong Nature Reserve in Quang Tri Province. In addition, a specimen from Ben En National Park, Than Hoa Province was found in the collections of the Hungarian Natural History Museum, Budapest.

In 1997 and 1998, several specimens were collected from Louang Namtha, Vientiane, Khammouane and Attapu Provinces in Lao PDR. They were listed as *Kerivoula* sp. in Francis *et al.* (1999) with a remark that they were intermediate in size between *K. hardwickii* and *K. papillosa*. Subsequently, DNA 'barcodes' were obtained from several of these specimens and from a subsequent specimen collected in April, 2003 from Namdee Hill, Myanmar. They were found to be similar to each other, but very distinct from any other species currently recognized from mainland Southeast Asia, with a genetic divergence > 12% from all other species examined (included as *K. cf. flora* in Fig. 3 of Francis *et al.*, 2007). The specimen from Myanmar, which was listed as *Kerivoula* sp. in Struebig *et al.* (2005), was one of three *Kerivoula* collected at the same locality. Of the other two, one was described as a species new to science, *Kerivoula kachinensis* Bates *et al.*, 2004 and the other is referred to *K. cf. hardwickii* (Struebig *et al.*, 2005). More recently, in July, 2005 and January, 2006, three specimens were collected from Seima Biodiversity Conservation Area in eastern Cambodia. Since the above material differs from all currently described taxa, it is proposed to describe a new species of *Kerivoula*.

MATERIALS AND METHODS

Field Surveys

Kerivoula sp. nov. was collected from 13 localities in mainland Southeast Asia. Each locality is

briefly described below. Geographical co-ordinates are included in the 'Distribution' section below.

In Myanmar, Namdee Hill was one of 25 localities surveyed in March–April, 2003 by a team from the University of Mandalay and the UK. Twenty-three bat species were collected, including one specimen of *Kerivoula* sp. nov. (Struebig *et al.*, 2005). In Thailand, Doi Pui is one of three prominent mountain peaks in Doi Suthep National Park which is situated to the west of Chiang Mai. It was registered in 1981 and has a total area of 26,100 ha. It comprises high mountains composed of many ridge systems and serves as the source of headwaters for the Ping river tributaries. The vegetation includes hill evergreen, dry dipterocarp, mixed deciduous, and pine forest.

In Lao PDR, surveys in the vicinity of the Nam Ha NBCA in Louang Namtha Province took place from 20 April–2 May 1998, using mainly harp traps and some limited mist netting. A variety of habitats were sampled including evergreen and semi-evergreen lowland and hill forest with various degrees of disturbance, as well as some dry dipterocarp forest. Thirty-one species were captured. At Phou Khao Khouay NBCA, Vientiane Province, surveys were carried out from 2–6 June 1997 and from 3–6 February 1998 primarily using harp traps. Although the sampling effort was rather limited (7 nights), 25 species were caught in an area of partially logged semi-deciduous forest mixed with evergreen riverine forest. Surveys at Hin Nam No NBCA in Khammouane Province were carried out from 10–18 February 1998. The area consists of extensive limestone karst with some large caves, interspersed with heavily disturbed forest consisting of a mixture of dry dipterocarp forest, and semi-evergreen or evergreen forests along the river edges. Harp traps were mainly set within the forest and 25 species of bats were captured. Dong Amphan National Biodiversity Conservation Area (NBCA) in Attapu Province was surveyed for bats between 26 April and 30 May 1997 using up to eight 4-bank harp traps set each night across trails, narrow roads, small streams, or gaps in the forest, as well as a few mist nets, set occasionally across larger streams, rivers or ponds. The area includes a mixture of moist riverine forest, and dry dipterocarp forest with various levels of disturbance, as well as a major river, the Xe Kaman. Forty-one species of bats were identified.

In Cambodia, Seima Biodiversity Conservation Area, Mondul Kiri Province was surveyed for bats in July, 2005 and January, 2006. A former logging concession, it comprises 303,400 ha of grasslands, secondary deciduous dipterocarp forest mixed with bamboo, and some evergreen hill forest. Annual precipitation averages between 1,700 and 1,800 mm. The wet

season is from May to October, with the wettest months being June and September. The underlying geology of the area is basalt with some sandstones, shales, and alluvium but no limestone karst (SCW, 2006).

In Vietnam, Ba Be National Park, Bac Kan Province, covers an area of 10,048 ha and was originally established as a protected area in 1977. The park is centred on the 500 ha Ba Be lake, the largest natural freshwater mountain lake in Vietnam, which is surrounded by evergreen forest on limestone in primary and secondary condition. Annual precipitation in Bac Kan province averages between 1,300 and 1,600 mm and the wet season runs from May to September, with the wettest months being July and August. An ongoing field survey began at Ba Be and Kim Hy in 2006. Kim Hy Nature Reserve, Bac Kan Province, covers an area of 15,461 ha in and was established as a reserve in 1998. Elevations at the site range from ca. 250–1,000 metres and its natural vegetation is limestone forest and sub-montane dry evergreen forest (MacKinnon, 1997). The south, centre and west of the nature reserve comprise a large area of limestone karst which is almost entirely forested, while the north and east of the reserve are, in contrast, characterised by a mosaic of swidden fields, secondary vegetation and remnant patches of forest. Ben En National Park is in Thanh Hoa Province and has a total area of a 16,634 ha, of which 14% is covered with artificial lakes. The vegetation comprises forest, rice paddy, and bamboo. Bat specimens were collected in November, 1998. Pu Mat National Park was surveyed for bats between July and October, 1998 by Ben Hayes and Thomas Howard. Created as a reserve in 1993, Pu Mat is situated in the Annamite Mountains (centred on 18°58'N, 104°46'E) in Nghe An Province. The Reserve has an area of 93,400 ha. Its western perimeter lies on the border of Lao PDR. The elevation ranges from 50 to 1,841 metres and the dominant vegetation is tropical semi-evergreen and evergreen forest. There are many limestone caves in the buffer zone. Thirty-nine species of bat were recorded (Hendrichsen *et al.*, 2001). Da Krong Nature Reserve was established in 2001. The area comprises 40,526 ha and covers one of the few remaining extensive patches of lowland forest in the Greater Annamites ecoregion. Kon Ka Kinh Nature Reserve was surveyed for bats by Ben Hayes in March–April, 1999. With an area of 28,000 ha and centred on 14°20'N, 108°22'E, it was created as a reserve in 1986 and is situated in Gia Lai province in central-south Vietnam. The vegetation mainly comprises upper montane forest, evergreen forest and agricultural land. Fourteen species of bat were recorded (Hendrichsen *et al.*, 2001).

Measurements

All external measurements were taken using digital calipers. Cranial and dental measurements of the holotype were taken using calipers and a graticule in a Leica MZ8 stereo microscope. The definitions of the measurements are as follows: FA*: forearm length, from the extremity of the elbow to the extremity of the carpus with the wings folded; TAIL*: tail length, from the tip of the tail to its base adjacent to the anus; HF*: foot, from the tip of the longest digit, excluding the claw, to the extremity of the heel, behind the os calcis; TIBIA*: 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; 3d1p*: length of the first phalanx of the third digit; 3d2p*: length of the second phalanx of the third digit; EAR*: ear length, from the lower border of the external auditory meatus to the tip of the pinna; GTL*: greatest length of skull, the greatest antero-posterior length of the skull, taken from the most projecting point at each extremity; CBL*: condylo-basal length, from an exoccipital condyle to the alveolus of the anterior incisor; CCL*: condylo-canine length, from an exoccipital condyle to the alveolus of the anterior canine; ZB*: zygomatic breadth, the greatest width of the skull across the zygomatic arches; BB*: breadth of braincase, taken at the posterior roots of the zygomatic arches; GBB: greatest width of the braincase; BH: braincase height, taken from the basisphenoid to the highest part of the skull; PC: post-orbital constriction, the narrowest width across the orbits; C–M³*: maxillary tooththrow length, from the front of the upper canine to the back of the crown of the third upper molar; M²–M^{2ext}: external palatal width, taken across the outer borders of the second upper molar, taken at the widest part; M²–M^{2int}: internal palatal width, taken across the inner borders of the second upper molar, taken at the narrowest part; BOW: basioccipital width, taken at narrowest point between the cochleae; C–M₃*: mandibular tooththrow length, from the front of the lower canine to the back of the crown of the third lower molar; C¹–C^{1int}: anterior palatal width measured across the inner borders of the canines, taken at the narrowest part; MDL*: mandible length, from the most posterior part of the condyle to the most anterior part of the mandible. MDLH: posterior mandibular height, taken from the apex of the concavity adjacent to the angular process on the inferior border of the ramus to the tip of the coronoid process. Measurements marked with a star (*) are illustrated in Figs. i–v in Bates and Harrison (1997). Body mass (MASS) was taken using a 60 g Pesola scale.

Specimens included in this study are held in the collection of Vu Dinh Thong, Institute of Ecology and Biological Resources, Hanoi (CMR and VN), Estacion Biologica Doñana, Spain (EBD), Kim Hy Nature Reserve Collection, Vietnam (NF), Natural History Museum, London (BMNH), the Harrison Institute, UK (HZM), the Hungarian Natural History Museum (HNHM), the Royal Ontario Museum (ROM), and Naturhistorisches Museum, Wien (NMW).

SYSTEMATIC DESCRIPTION

Kerivoula titania sp. nov.

Holotype

HNHM 2005.81.58., adult ♀, body in alcohol, skull extracted, collected by G. Csorba, H. S. Hong and C. Chen, 15 July, 2005.

Measurements (in mm): forearm (FA): 33.6; fifth (5MET), fourth (4MET) and third (3MET) metacarpal lengths respectively: 32.4, 33.9, 34.5; tibia (TIBIA): 18.8; ear (EAR): 12.8; greatest skull length (GTL): 15.2; condylobasal length (CBL): 14.1; condylo-canine length (CCL): 13.5; zygomatic breadth (ZB): 8.5; breadth of braincase (BB): 7.0; greatest breadth of braincase (GBB): 7.5; braincase height (BH): 5.2; postorbital constriction (PC): 3.2; upper toothrow length (C–M³): 6.0; external palatal width (M²–M^{2ext}): 5.3; internal palatal width (M²–M^{2int}): 2.7; anterior internal palatal width (C¹–C^{1int}): 2.0; lower toothrow length (C–M₃): 6.3; mandible length (MDL): 10.3; mandibular height (MDHL): 2.9. Mass: 4.0 g.

Type Locality

Seima Biodiversity Conservation Area, Mondul Kiri Province, Cambodia, 12°10.49'N, 106°58.55'E, 290 m a.s.l.

Paratypes

Cambodia — HZM.3.38179 (formerly HNHM 2005.81.54.), Seima Biodiversity Conservation Area, Mondul Kiri Province, Cambodia, 12°15.44'N, 107°03.49'E, 360

m a.s.l., adult ♀, body in alcohol, skull extracted, collected by G. Csorba, H. S. Hong and C. Chen, 15 July, 2005; HNHM 2006.34.27, Seima Biodiversity Conservation Area, Mondul Kiri Province, Cambodia, 12°15.44'N, 107°03.49'E, 360 m a.s.l., adult ♂, body in alcohol, skull extracted, collected by G. Csorba, G. Ronkay, Y. Saksang and L. Duval, 27 January, 2006.

Referred Material

Myanmar — HZM.2.35962 (Field No. MA.030411.1), Namdee Hill, Bhamo Township, Kachin State, Myanmar, 24°34.203'N, 97°07.501'E, adult ♀, body in alcohol, skull extracted, collected by Matthew Struebig, Sai Sein Lin Oo, Sein Sein Win, Moe Moe Aung and Aye Aye Nwe, 11 April, 2003. *Thailand* — BMNH. 78.2385, Doi Pui, Muang, Chiang Mai, Thailand, centred on 18°50'N, 98°53'E, adult ♂, dry skin with skull extracted, collected by Kitti Thonglongya, 6 October, 1967. *Lao PDR* — ROM.118395, Outskirts of Ban Phoulán, Nam Ha NBCA, Louang Namtha, 20°44'N, 101°10'E, pregnant ♀, specimen in alcohol, collected by A. Guillén, 29 April, 1998; EBD.25120, Phou Khao Khouay NBCA, Vientiane, 18°26'N, 102°57'E, adult ♀, specimen in alcohol, collected by A. Guillén, 4 June, 1997; ROM.118093, Ban Xam Kang, Hin Nam No NBCA, Khammouane, 17°34'N, 105°50'E, adult ♀, specimen in alcohol, collected by C. M. Francis, 11 February, 1998; ROM.110573, ROM.110584, ROM.110591 (adult ♂♂), ROM.110575, ROM.110586 (adult ♀♀), Xe Kaman, Dong Amphan NBCA, Nam Kama, Attapu, 15°05'N, 107°17'E, specimens in alcohol, collected by C. M. Francis, 16–17 May, 1997. *Vietnam* — HNHM 2007.27.8., Ba Be National Park, Bac Kan Province, 22°24.673'N, 105°37.591'E, adult ♀, body in alcohol, skull extracted, collected by Neil

Furey, Gabor Csorba and Vu Dinh Thong, 1 May 2007; NF.050207.2, Vu Muon commune, Bac Thong district, Kim Hy Nature Reserve, Bac Kan Province, 22°14.835'N, 105°58.693'E, adult ♀, body in alcohol, skull extracted, collected by Neil Furey, 5 February 2007; HNHM 2000.84.8, Ben En National Park, Than Hoa Province, centred on 19°35'N, 105°27'E, adult ♂, body in alcohol, skull extracted, collected by Frontier, 7 November, 1998; HZM. 5.31779 (Field No. PM.42), Pu Mat National Park, Nghe An Province, centred on 18°58'N, 104°46'E, adult ♀, body in alcohol, skull extracted, collected by Ben Hayes and Thomas Howard, October, 1998; HNHM 2007.27.43., Da Krong Nature Reserve, Quang Tri Province, centred on 16°37'N, 106°47'E, subadult ♂, body in alcohol, skull extracted, collected by Nguyen Truong Son, Pham Duc Tien, Nguyen Thien Tao and Gabor Csorba, 18 May 2007; HZM.1.32607 (Field No. KKK-4), Kon Ka Kinh Nature Reserve, Gia Lai Province, 14°19.150'N, 108°24.529'E, adult ♂, body in alcohol, skull extracted, collected by Ben Hayes, 24 March, 1999.

Diagnosis

This is a medium-sized *Kerivoula*, with a forearm length of 32.4–35.9 mm and a condylo-canine length of 13.4–13.9 mm (Tables 1 and 2). The skull is characterised by its flattened braincase (Fig. 1); its height (BH = 5.2–5.7 mm) is 67.2–72.0% of its greatest width (GBB).

Description

This is a medium-sized *Kerivoula*, with a forearm length of 32.4–35.9 mm (Table 1). The nostrils are slightly protuberant and downward facing. The muzzle, including the lips but excluding the nostrils, is hairy (Fig. 2). The ears are large and virtually naked, with just a few short hairs on their posterior surfaces; the anterior border of each is convex; the tip is rounded off and there is a distinct concavity just below the tip on the posterior border. The tragus is narrow and tall (8.5–9.1 mm); the anterior margin is virtually straight until near the tip, where it is very slightly convex; the posterior margin is concave and has a small hook-shaped basal lobe (projection) at the widest part, above and below which are shallow concavities. The hairs on the

TABLE 1. External measurements (in mm) and mass (in grams) of *K. titania*, *K. flora*, *K. lenis*, *K. kachinensis* and *K. hardwickii* (sensu Corbet and Hill, 1992); FA: forearm length; TAIL: tail length; HF: foot length; TIBIA: tibia length; EAR: ear length; MASS: body mass. Sample size (*n*), mean, standard deviation and range are shown. Sample sizes differing from those reported under *n* are given in brackets

| Species | <i>n</i> | FA | TAIL | HF | TIBIA | EAR | MASS |
|-----------------------|----------|---------------|--------------|------------|--------------|---------------|-------------|
| <i>K. titania</i> | 7♂♂ | 33.8, 0.6 | 49.1, 2.5 | 7.7, 0.2 | 18.8, 0.3 | 14.0, 0.7 | 5.0, 1.6 |
| | | 32.9–34.4 | 46.3–53.0 | 7.5–8.1[6] | 18.4–19.1 | 12.9–15.0 | 4.0–7.9[5] |
| | 11♀♀ | 34.3, 0.9 | 49.3, 1.9 | 7.9, 0.4 | 19.1, 0.5 | 14.1, 0.6 | 5.1, 0.9 |
| | | 32.4–35.9 | 45.8–52.2[9] | 7.1–8.3[9] | 18.5–19.7[5] | 12.8–14.8[8] | 4.0–6.9[5] |
| <i>K. flora</i> | 2♂♀ | 38.7 | 48.7[1] | 8.3[1] | 19.5 | 15.3 | 6.4[1] |
| | | 38.4, 39.0 | | | 19.3, 19.6 | 14.6, 15.9 | |
| <i>K. lenis</i> | 5♂♀ | 39.4, 1.9 | 48 | 8.7 | 19.7, 1.3 | 13.8[1] | * |
| | | 37.2–41.0 | | | 18.2–20.7[3] | | |
| <i>K. kachinensis</i> | 4♂♀ | 42.7, 0.8 | 53.4, 2.3 | 8.9, 0.7 | 22.7, 0.7 | 11.9, 1.6 | 7.5, 0.5 |
| | | 41.6–43.4 | 50.5, 56.1 | 8.5, 10.0 | 21.8, 23.5 | 10.0–13.5 | 7.0–8.3 |
| <i>K. hardwickii</i> | 23♂♂ | 31.4, 1.1 | 42.3, 3.8 | 6.8, 0.6 | 16.0, 0.9 | 12.3, 1.5 | 4.4, 1.6 |
| | | 29.6–33.2[19] | 38.0–45.0[3] | 6.0–7.5[9] | 15.3–17.0[3] | 9.7–14.6[8] | 3.5–8.1[10] |
| | 22♀♀ | 33.1, 1.2 | 41.0, 4.0 | 6.9, 1.1 | 16.0[1] | 12.6, 1.9 | 4.7, 1.4 |
| | | 31.2–34.6[19] | 35.0–47.0 | 4.2–8.0 | | 10.2–15.0[12] | 3.5–7.4[6] |

TABLE 2. Cranial and dental measurements (in mm) of *K. titania*, *K. flora*, *K. lenis*, *K. kachinensis* and *K. hardwickii* (sensu Corbet and Hill, 1992); GTL: greatest length of skull; CBL: condylobasal length; CCL: condylo-canine length; ZB: zygomatic breadth; BB: breadth of braincase; GBB: greatest breadth of braincase; BH: braincase height; PC: postorbital constriction; C-M³: upper toothrow length; M²-M^{2ext}: external palatal width; C-M₃: lower toothrow length; M: mandible length. Sample size (*n*), mean, standard deviation and range are shown. Sample sizes differing from those reported under *n* are given in brackets

| Species | <i>n</i> | GTL | CBL | CCL | ZB | BB | GBB | BH |
|-----------------------|----------|---------------|---------------|---------------|-------------|-------------|-------------|-------------|
| <i>K. titania</i> | 4♂♂ | 15.5, 0.2 | 14.1, 0.2 | 13.5, 0.1 | 8.9, 0.2 | 7.2, 0.3 | 7.7, 0.1 | 5.5, 0.1 |
| | | 15.2–15.7 | 13.9–14.3[3] | 13.4–13.7[3] | 8.7–9.1[3] | 6.9–7.6 | 7.6–7.8 | 5.3–5.6 |
| | 6♀♀ | 15.6, 0.2 | 14.1, 0.3 | 13.7, 0.2 | 9.0, 0.2 | 7.1, 0.3 | 7.7, 0.2 | 5.4, 0.2 |
| <i>K. flora</i> | 3♂♀ | 15.2–15.8 | 13.7–14.5 | 13.5–13.9 | 8.5–9.2 | 6.8–7.6 | 7.4–8.0 | 5.2–5.7 |
| | | 15.7, 0.5 | 14.5, 0.4 | 13.9, 0.4 | 9.5, 0.4 | 7.2, 0.1 | 7.5, 0.2 | 6.3, 0.1 |
| | | 15.3–16.2 | 14.1–14.9 | 13.5–14.4 | 9.1–9.8 | 7.2–7.3 | 7.4–7.8 | 5.9–6.4 |
| <i>K. lenis</i> | 5♂♀ | 16.8, 0.4 | 15.4, 0.2 | 14.8, 0.3 | 10.2, 0.5 | 7.4, 0.3 | 7.9, 0.2 | 6.8, 0.2 |
| | | 16.4–17.1[4] | 15.2–15.5[3] | 14.5–15.1[4] | 9.6–10.6[4] | 7.1–7.7[4] | 7.7–8.2[4] | 6.7–7.0[4] |
| <i>K. kachinensis</i> | 4♂♀ | 17.6, 0.4 | 16.4, 0.3 | 15.9, 0.4 | 10.4, 0.3 | 7.9, 0.2 | 8.2, 0.1 | 5.3, 0.2 |
| | | 17.1 17.9 | 16.1 16.7 | 15.5–16.3 | 10.2 10.7 | 7.6 8.2 | 8.1–8.4 | 5.1–5.5 |
| <i>K. hardwickii</i> | 23♂♂ | 13.9, 0.4 | 12.7, 0.5 | 12.2, 0.4 | 8.2, 0.3 | 6.6, 0.2 | 7.1, 0.2 | 5.1, 0.4 |
| | | 13.1–14.7 | 11.8–13.5[22] | 11.4–12.9[22] | 7.6–8.7[16] | 6.2–7.0 | 6.8–7.3 | 4.6–5.9 |
| | 23♀♀ | 14.2, 0.4 | 13.0, 0.5 | 12.5, 0.4 | 8.4, 0.3 | 6.7, 0.2 | 7.1, 0.2 | 5.1, 0.4 |
| | | 13.7–14.8[19] | 12.2–13.6[19] | 11.9–13.2[20] | 7.9–8.8[12] | 6.3–7.3[21] | 6.8–7.5[21] | 4.7–5.8[20] |

dorsal surface are greyish. They are clearly divided into three bands, being black basally, light grey in the mid-parts and dark grey on the distal half. On the ventral surface, the roots are black and the tips whitish, tinged with grey-brown. The wing and tail membranes are a translucent grey. There is a scattering of hairs on the posterior margin of the interfemoral membrane but there is no definite fringe. In the wings, the fifth metacarpal (5MET = 33.2, 30.3–34.5, *n* = 9) is shorter than the fourth (4MET = 34.1, 31.7–35.3, *n* = 9) and third (3MET = 34.8, 31.6–36.6, *n* = 9) and is about equal to forearm length. The first phalanx of the third digit (3d1p = 17.8–18.9 mm, *n* = 3) is shorter than the second (3d2p = 20.1–22.1 mm, *n* = 3). A slightly enlarged fleshy callosity, oval in shape, which measures 1.5–1.7 mm in width × 2.4–2.5 mm (*n* = 3) in length, is present on the ball of the first digit (thumb) of each wing. The wings are attached to the base of the first phalanx of the outer toes. The soles of the feet are normal, without a fleshy pad or callosity.

The skull has a condylo-canine length of 13.4–13.9 mm (Table 2). The narial pit of the rostrum is large. The rostral sulcus is well developed. The postorbital constriction is narrower than the posterior part of the rostrum. The braincase is broad and distinctly flattened (Figs. 1 and 3). In the bony palate, the widest part is adjacent to the margin between m^1 and m^2 , (m^2 - m^{2int} = 2.7–2.9 mm, *n* = 3). It narrows towards the canines (c^1 - c^{1int} = 2.0–2.1 mm, *n* = 3) but is not especially convergent. The basioccipital space is relatively broad (BOW = 1.6–1.8 mm, *n* = 3) and the basioccipital pits are shallow. In the mandible, the coronoid process is well developed (MDLH = 2.9–3.3 mm, *n* = 3), considerably exceeding the condyle in height.

Upper toothrow length (C-M³) is 5.8–6.2 mm. In the upper dentition, the first incisor (I²) is unicuspid and with a cingulum on its internal posterior border. The second incisor (I³) is compressed between I² and the canine (C¹) and is equal to I² in crown area; it has a well defined cingular cusp on its internal aspect. The canine (C¹) has

TABLE 2. Extended

| Species | <i>n</i> | BH/CCL × 100 | BH/GBB × 100 | PC | C-M ³ | M ² -M ^{2ext} | C-M ₃ | M |
|-----------------------|----------|---------------|---------------|-------------|------------------|-----------------------------------|------------------|--------------|
| <i>K. titania</i> | 4♂♂ | 40.9, 1.9 | 70.8, 1.3 | 3.3, 0.0 | 6.0, 0.2 | 5.4, 0.2 | 6.3, 0.2 | 10.4, 0.2 |
| | | 38.8–42.5[3] | 69.4–72.0[3] | 3.2–3.3 | 5.8–6.2 | 5.1–5.6 | 6.0–6.4 | 10.3–10.6 |
| | 6♀♀ | 39.6, 1.8 | 69.0, 1.7 | 3.4 | 6.1, 0.1 | 5.6, 0.2 | 6.4, 0.1 | 10.6, 0.2 |
| | | 38.1–41.8[4] | 67.2–71.3[4] | 3.2–3.6[4] | 6.0–6.2 | 5.3–5.7 | 6.3–6.5 | 10.3–10.8 |
| <i>K. flora</i> | 3♂♀ | 44.9, 1.2 | 83.2, 3.9 | 3.3, 0.1 | 6.2, 0.2 | 5.7, 0.1 | 6.7, 0.4 | 11.3, 0.8 |
| | | 43.9–46.2 | 79.8–87.4 | 3.2–3.5 | 6.0–6.5 | 5.6–5.8 | 6.3–7.1 | 10.6–12.1 |
| <i>K. lenis</i> | 5♂♀ | 46.0, 1.3 | 86.3, 3.5 | 3.4, 0.2 | 6.7, 0.1 | 6.3, 0.3 | 7.3, 0.2 | 12.1, 0.3 |
| | | 44.5–47.2[4] | 82.4–89.3[4] | 3.1–3.6[4] | 6.6–6.8 | 6.0–6.6 | 7.2–7.6 | 11.8–12.4[4] |
| <i>K. kachinensis</i> | 4♂♀ | 33.5, 0.5 | 64.6, 1.5 | 3.6, 0.1 | 6.8, 0.1 | 6.4, 0.0 | 7.3, 0.2 | 12.5, 0.2 |
| | | 32.8 34.0 | 62.9–66.4 | 3.5–3.7 | 6.6–6.9 | 6.4–6.4 | 7.1–7.5 | 12.2–12.7 |
| <i>K. hardwickii</i> | 23♂♂ | 41.9, 2.5 | 71.9, 4.7 | 3.1, 0.1 | 5.3, 0.2 | 5.0, 0.2 | 5.6, 0.2 | 9.4, 0.3 |
| | | 37.4–47.0[22] | 64.4–80.4 | 2.9–3.4 | 5.0–5.7 | 4.7–5.5 | 5.2–6.1[22] | 8.8–10.0[22] |
| | 23♀♀ | 40.8, 2.4 | 71.4, 5.0 | 3.2, 0.1 | 5.5, 0.2 | 5.2, 0.2 | 5.8, 0.2 | 9.9, 0.4 |
| | | 35.9–44.9[19] | 65.5–79.8[20] | 3.0–3.4[20] | 5.2–5.8 | 4.9–5.6[22] | 5.4–6.2[22] | 9.2–10.6[22] |

a well defined cingulum on its internal border; the shaft is smooth on its outer side, without a deep longitudinal groove; its posterior part is without a conspicuous cutting edge. The three upper premolars are compressed in the toothrow; their transverse diameters (width) slightly exceed their respective longitudinal diameters (length) (Fig. 3). The second upper premolar (P³) is 80% of the crown area of the first (P²), whilst the third (P⁴) is about 60% of the crown area of the first molar (M¹). The first (M¹) and second (M²) upper molars have well developed para-, meso-, and metastyles. The third molar (M³) has the metastyle absent. In the lower dentition, the first and second incisors (I₁, I₂) are tricuspid. The third incisor (I₃) is smaller, with a well defined central cusp but no lateral cusps. The canine has a cingular cusp on its antero-internal border. The three lower premolars are compressed in the toothrow; their lengths exceed their widths. The crown area of the second premolar (P₃) is about 90% that of the first (P₂). The crown area of the talonid of the first lower molar (M₁) slightly exceeds that of the second (M₂). In the third molar (M₃), the talonid is reduced to about 70% that of the trigonid.

Etymology

Named after Titania, the Queen of the Fairies from William Shakespeare's "A Midsummer Night's Dream". The name is chosen to reflect the nymph-like nature of this forest bat. The proposed English name is 'Titania's woolly bat'.

Comparative Material

Kerivoula cf. *hardwickii* — Cambodia: Seima Biodiversity Conservation Area, HNHM 2005.81.27., HNHM 2005.81.39., HNHM 2005.81.55., HNHM 2005.81.59., HNHM 2005.82.16., HNHM 2005.82.24., HNHM 2005.82.37., HNHM 2006.34.25.–26., HNHM 2006.34.30.–33., HNHM 2006.34.47., HNHM 2006.34.52.; M' Lou Prey Village, HZM.10.33789, HZM.11.33790; BMNH.60.8.28.28; India: Kardibetta Forest, BMNH.12.8.25.2 (holotype of *crypta*); Darjeeling, BMNH.16.3.25.31; Jaintia Hills, BMNH.21.1.6.32; Indonesia: Java, BMNH.9.1.5.418/419/420/422/424, BMNH.10.4.6.22, BMNH.79.11.15.61, NMW 30545, 30550; Kalimantan, HZM.11.36540; Malaysia: BMNH.60.1582; Myanmar: Namdee Hill, HZM.10.35963; Nam Tamai, BMNH.50.432/433/434/435/438; Sri Lanka: Pallama, HZM.3.31606; Kumbalgamuwa, BMNH.31.4.7.1 (holo-

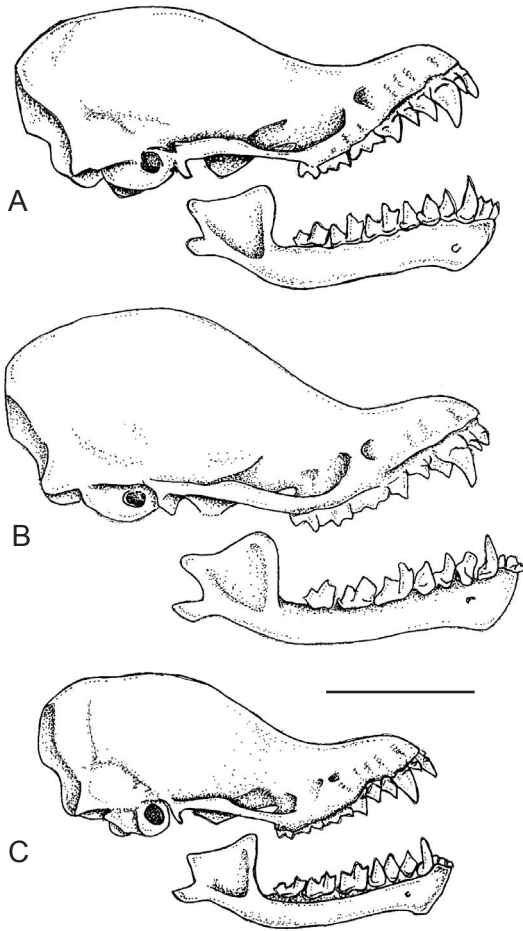


FIG. 1. Lateral views of the cranium and right mandible of (A) *K. titania*, HNHM 2005.81.58 (holotype), Seima Biodiversity Conservation Area, Cambodia, (B) *K. flora*, BMNH.97.4.18.22 (holotype), South Flores, Indonesia and (C) *K. hardwickii*, HZM.4.31763, Pu Mat National Park, Vietnam. Scale = 5 mm

type of *malpasi*); *Thailand*: no exact locality, BMNH.78.2386; *Vietnam*: Kon Ka Kinh Nature Reserve, HZM.7.32604/8.32605/9.32606; Pu Mat National Park, HZM.4.31763, HZM.6.31778.

Kerivoula flora — *Indonesia*: South Flores, BMNH. 97.4. 18.22 (holotype of *flora*); *Malaysia*: Gomontong, Sabah, BMNH.84.2081; Mount Kinabalu, Sabah, BMNH.84.2062.

Kerivoula kachinensis — *Myanmar*: Namdee Hill, Bhamo Township, HZM.1.

35288 (holotype of *kachinensis*); *Vietnam*: Chu Mom Ray National Park, CMR-28, CMR-25; Kim Hy Nature Reserve, VN014-S411.

Kerivoula lenis — *India*: Calcutta, BMNH.79.11.21.126 (holotype of *lenis*); Therkumalai, HZM.1.35276; *Malaysia*: Pasoh Forest Reserve, Negeri Sembilan, BMNH.1988.46; Sepilok, Sabah, BMNH.84.2071/2075.

DISCUSSION

Comparison with Other Taxa

Kerivoula titania has a forearm length of 32.4–35.9 mm, which is comparable to that of *K. hardwickii* (Horsfield, 1824) (29.6–34.6 mm — sensu Corbet and Hill, 1992), which includes *fusca* Dobson, 1871, *engana* Miller, 1906a, *depressa* Miller 1906b, *crypta* Wroughton and Riley, 1913 and *malpasi* Phillips, 1932. However, in all absolute external, cranial and dental measurements *K. titania* averages larger than *K. hardwickii* (Tables 1 and 2), although the situation is complicated by the fact that *K. hardwickii* (sensu Corbet and Hill, 1992) appears to be a composite taxon, which genetic data suggest may comprise at least three species (Francis *et al.*, 2007). Morphologically, there appears to be a smaller flat-headed species (BH < 5.1 mm) (the correct taxon name for this may prove to be *K. depressa* Miller 1906b) and a slightly larger domed-skulled taxon (*K. hardwickii*) (BH > 5.1 mm; Fig. 4). That said, in skull length (GTL and CCL) and upper tooththrow length (C–M³), *K. titania* is absolutely larger than *K. hardwickii* and all forms currently referred to it with no overlap in the ranges and there is virtually no overlap in greatest breadth of braincase (GBB), mandible length (M) and lower tooththrow length (C–M₃). There are also differences in the pelage colour. On the dorsal



FIG. 2. *Kerivoula titania*, NF.050207.2. Kim Hy, Vietnam. Photograph by Neil Furey

surface, *K. titania* has hairs with black bases, pale grey mid-parts and dark grey tips. In *K. hardwickii*, the comparable hairs have dark brown bases, light brown mid-parts and medium brown tips. Genetically, specimens of *K. titania* from Myanmar and Lao PDR (referred to *K. cf. flora* in Fig. 3 of Francis *et al.*, 2007) are distinct from all those provisionally referred to *K. cf. hardwickii* with differences exceeding 12% in all comparisons.

In comparison to *K. papillosa* Temminck, 1840 (FA: 39.4–48.9; CCL: 15.4–17.1 mm — Bates *et al.*, 2004) and *K. lenis* Thomas, 1916 (FA: 37.2–41.0; CCL: 14.5–15.1 — Table 2), *K. titania* is considerably smaller in external and cranial characters. It is larger than *K. pellucida* Waterhouse, 1845 (and its synonym *bombifrons* Lyon, 1911) (CBL: 12.5–13.0 mm) and *K. muscina* Thomas, 1908 (CBL: 12.8 mm — Hill, 1965), all of which have the braincase abruptly elevated above the rostrum (Corbet and Hill, 1992); *pellucida* is also characterised by its large ears, fur colouration and

wing translucency. It is also larger than *K. whiteheadi* Thomas, 1894 and its synonyms *K. pusilla* Thomas, 1894 and *K. bicolor* Thomas, 1904 (CBL: 11.8–11.9 mm — Corbet and Hill, 1992) and is considerably larger than *K. minuta* Miller, 1898 (CBL: 10.0–11.1) and *K. intermedia* Hill and Francis, 1984 (CBL: 11.1–11.8 mm — Corbet and Hill, 1992). Based on measurements included in Vanitharani *et al.* (2003), *K. titania* slightly exceeds in size *K. myrelli* and *K. agnella*. However, unlike *K. titania*, the skulls of these latter taxa do not have ‘flattened’ crania. In addition, *K. agnella* from Papua New Guinea has a knife-like posterior cutting edge on each upper canine (C^1), whilst the C^1 of *K. myrelli* from the Lesser Sunda Islands is robust, exceeding the third upper premolar (P^4) in crown area. The canine (C^1) of *K. titania* is without a sharp posterior cutting edge and is about equal to P^4 in crown area (Fig. 3).

The general size of the skull and dentition of *K. titania* is most similar to those of *K. flora* Thomas, 1914 (for further details

see Hill and Rozendal, 1989). However, in contrast to *K. flora*, the braincase is flattened relative to its breadth. In *K. titania*, braincase height is 67.2–72.0% of greatest braincase width (BH/GBB × 100) whereas in *K. flora*, the comparable figure is

79.8–87.4%; in *K. lenis*, it is 82.4– 89.3% (Table 2) and in *K. papillosa* 80.6– 91.6% (Bates *et al.*, 2004). In comparison to *K. kachinensis*, which in Myanmar was collected at the same time and from the same locality as *K. titania*, the skull is less flattened. In

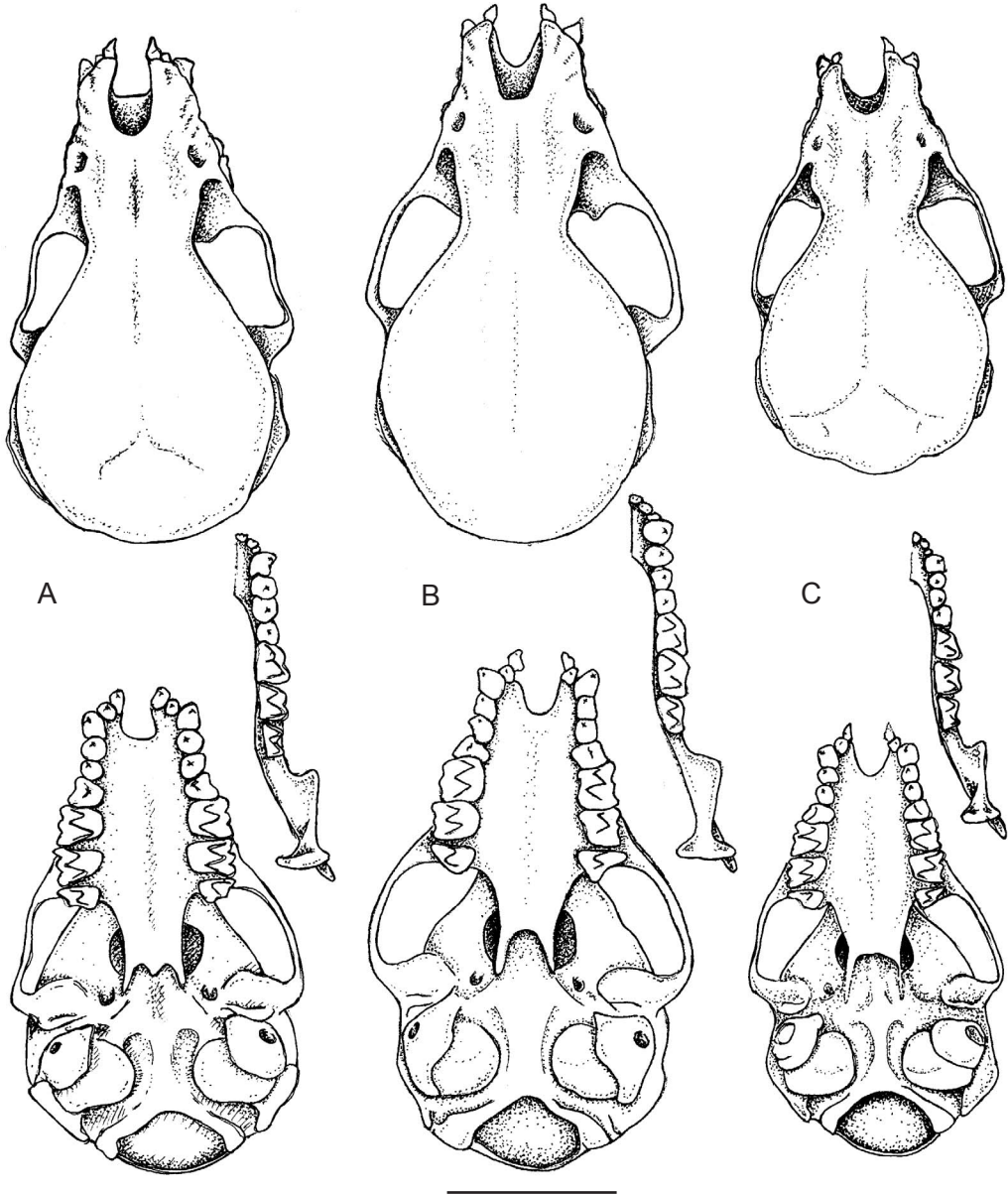


FIG. 3. Dorsal and ventral views of the cranium and dorsal view of the right mandible of (A) *K. titania*, HNHM 2005.81.58 (holotype), Seima Biodiversity Conservation Area, Cambodia, (B) *K. flora*, BMNH.97.4.18.22 (holotype), South Flores, Indonesia and (C) *K. cf. hardwickii*, HZM.4.31763, Pu Mat National Park, Vietnam. Scale = 5 mm

the specimens of *K. kachinensis* currently known from Myanmar and Vietnam (Thong *et al.*, 2006), braincase height averages 64.6% (62.9–66.4%) of greatest braincase width. The skull of *K. kachinensis* is also considerably larger (Table 2).

Habitat

In the Seima Biodiversity Conservation Area, Cambodia it was collected in four-bank harp-traps set in forest trails in mixed evergreen and deciduous forest. Specimens of *K. cf. hardwickii*, *K. kachinensis* and *K. papillosa* were also collected in the same area. There are no data on habitat available specifically for the specimen from Pu Mat National Park, Vietnam. However, as noted above, the area is situated in evergreen and montane forest and there are significant areas of limestone. In Kon Ka Kinh Nature Reserve, a specimen was collected flying over a small path, which runs along the ridge near the Kon Ka Kinh peak. The site is situated in pristine upper montane forest

at an altitude of 1,600 m. A specimen of *K. cf. hardwickii* was collected at the same site. The Kim Hy specimen was collected in a harp trap set at ca. 750 m a.s.l. on a limestone karst ridge-top on the western flank of the nature reserve. The area comprises a mosaic of valleys separated by karst ridges. Forests on the hillsides and ridge-tops are comparatively less disturbed than those in the valleys and retain both their structure and canopy cover. The Ba Be specimen was collected in a harp-trap at ca. 260 m a.s.l. in a forested gully located approximately midway between the eastern shore of Ba Be Lake and the national park headquarters. The gully is situated in an area of relatively steep terrain and dense, closed-canopy and regenerating forest on limestone karst. In Da Krong, the single individual was captured in a harp-trap, near a ridge-top in secondary forest on limestone.

In Myanmar, a single individual was collected at Namdee Hill, which is located near the settlement of Shet Shar on the eastern bank, north of the First Defile, of the

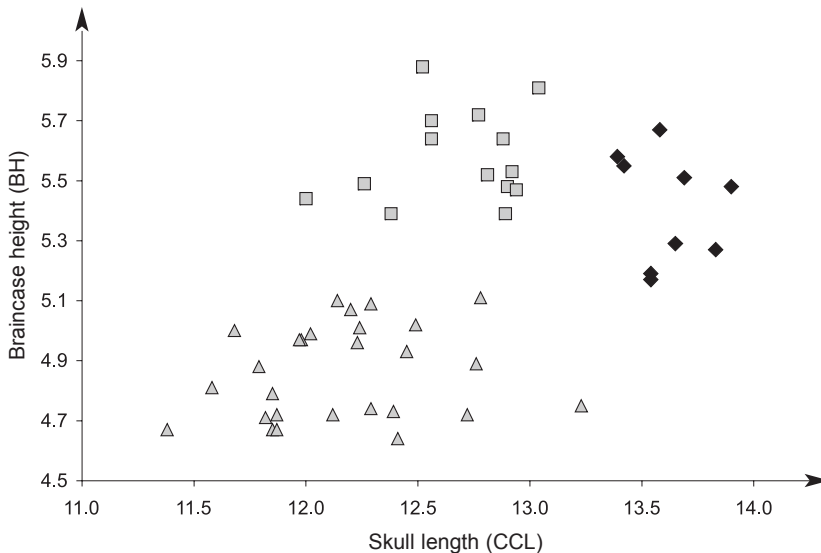


FIG. 4. Braincase height (in mm) compared to skull length (in mm) for three taxa of *Kerivoula*: *K. titania* (black diamonds), *K. hardwickii* (BH > 5.1 mm — grey squares), and *K. hardwickii* [? depressa] (BH < 5.1 mm — grey triangles). Specimens include holotype, paratypes and referred material of *K. titania*; the *K. hardwickii* specimens are listed in Comparative Material

Ayeyarwady River. Evergreen forest covers the hill and the immediate area but changes to mixed deciduous forest further away from the river. In April, 2003, approximately 2 ha of forest were being cleared for shifting cultivation at the edge of the river and it is likely that most of the forest in the area was heavily disturbed. There are a number of bamboo groves within the forest and two limestone caves near the top of the hill about 700 m from the forest edge (Struebig *et al.*, 2005). At Doi Pu in Thailand, there are significant areas of forest and limestone karst.

In Lao PDR, it was caught in harp traps in moist evergreen riverine forest along the upper reaches of the Xe Kaman River in Dong Amphan National Biodiversity Conservation Area (NBCA), Attapu Province. *K. cf. hardwickii* and *K. cf. lenis* (sensu Vanitharani *et al.*, 2003) were found at the same locality. At Phou Khao Khouay NBCA, it was collected, together with *K. cf. hardwickii* and *K. kachinensis*, in harp traps at three locations near the Tak Leuk waterfall, an area of partially logged semi-deciduous forest mixed with evergreen riverine forest. At Hin Nam No NBCA in Khammouane Province and at Nam Ha NBCA in Louang Nam Tha province, it was found with the more abundant *K. cf. hardwickii*, in disturbed dry dipterocarp forest, intermixed with semi-evergreen and evergreen forests. In Nam Ha NBCA, *K. kachinensis* was also present.

It is expected that this is a forest dependent bat. It is not known whether the species is more common around areas of limestone karst, or whether the number of records from areas with limestone merely reflects a bias in choice of collection sites by bat collectors.

Distribution

It is currently known from thirteen localities in five countries (Fig. 5): *Myanmar* —

Namdee Hill, Kachin State, 24°34.203'N, 97°07.501'E (Fig. 5, [loc. 1]); *Thailand* — Doi Pui, Muang, Chiang Mai, centred on 18°50'N 98°53'E [loc. 2]; *Lao PDR* — Outskirts of Ban Phoulán, Nam Ha NBCA, Louang Namtha, 20°44.17'N, 101°10'E [loc. 3]; Phou Khao Khouay NBCA, Vientiane, 18°26'N, 102°57'E [loc. 4]; Ban Xam Kang, Hin Nam No NBCA, Khammouane, 17°34'N, 105°50'E [loc. 5]; Nam Kama, Xe Kaman, Dong Amphan NBCA, Attapu, 15°05'N, 107°17'E [loc. 6]; *Cambodia* — Seima Biodiversity Conservation Area, Mondul Kiri Province, centred on 12°15.44'N, 107°03.49'E [loc. 7]; *Vietnam* — Ba Be National Park, Bac Kan Province, 22°24.673'N, 105°37.591'E [loc. 8]; Vu Muon commune, Bac Thong district, Kim Hy Nature Reserve, Bac Kan Province, 22°14.835'N, 105°58.693'E [loc. 9]; Ben En National Park, Than Hoa Province, centred on 19°35'N, 105°27'E [loc. 10] Pu Mat National Park, Nghe An Province, centred on 18°58'N, 104°46'E [loc. 11]; Da Krong Nature Reserve, Quang Tri Province, centred on 16°37'N, 106°47'E, [loc. 12]; Kon Ka Kinh Nature Reserve, Gia Lai Province, 14°19.150'N 108°24.529'E [loc. 13].

Taxonomic and Behavioural Notes

Kerivoula titania, after *K. kachinensis*, is the second species of *Kerivoula* from Asia that has recently been described with a flattened skull. As noted above, a provisional review of *Kerivoula hardwickii* (sensu Corbet and Hill, 1992) suggests that two or possibly three cryptic species may be present within this taxon and that at least one has a flattened skull. If this is the case, then it is apparent that there are pairings of 'flat' and 'domed-species' in at least three size classes: *K. kachinensis* and *K. lenis*; *K. titania* and *K. flora*; and *K.?* *depressa* and *K. hardwickii*. It is possible that a comprehensive taxonomic revision of the genus

(as currently understood), involving both morphological and molecular systematics, may suggest that two distinct subgenera are present. Existing genetic data based on the

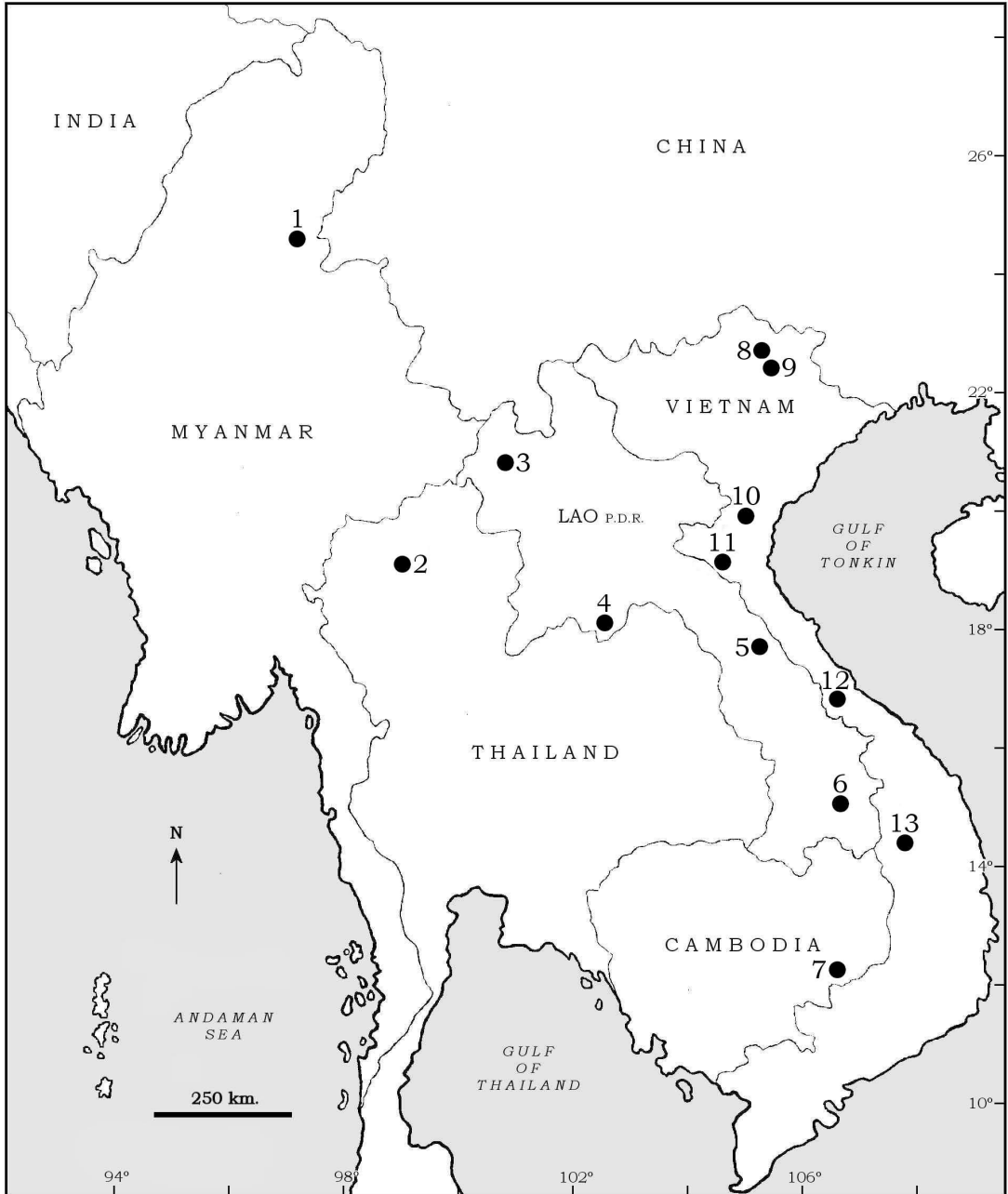


FIG. 5. Distribution of *Kerivoula titania*. [1] Namdee Hill, Kachin State; [2] Doi Pui, Muang, Chiang Mai; [3] Outskirts of Ban Phoulan, Louang Namtha; [4] Phou Khao Khouay, Vientiane; [5] Ban Xam Kang, Khammouane; [6] Xe Kaman, Attapu; [7] Seima Biodiversity Conservation Area, Mondul Kiri Province; [8] Ba Be National Park, Bac Kan Province; [9] Vu Muon commune, Kim Hy Nature Reserve, Bac Kan Province; [10] Ben En National Park, Than Hoa Province; [11] Pu Mat National Park, Nghe An Province; [12] Da Krong Nature Reserve, Quang Tri Province; [13] Kon Ka Kinh Nature Reserve, Gia Lai Province

mtDNA gene cytochrome oxidase I (Francis *et al.*, 2007) show such large divergences among all species that they cannot be used to infer branching orders reliably. Further genetic analyses will be required using slower evolving genes to determine phylogenetic relationships.

Nothing is known of the roosting behaviour of *K. titania*. However, its flattened cranium suggests it prefers sites with narrow restricted entrances, possibly including under the bark of trees or in narrow cracks or crevices.

The female specimen from Ba Be National Park, Vietnam collected on 1 May 2007 was in late pregnancy, as was a specimen collected on 29 April 1998 in Nam Ha NBCA, Lao PDR. Elsewhere in Lao, two females collected on 16 and 17 May 1997 in Dong Amphan NBCA, as well as two out of three collected in Phou Khao Khouay NBCA on 2–4 June 1997 were lactating. In contrast, an adult female specimen collected on 11 February 1998 in Hin Nam No NBCA was not noticeably reproductively active (C. M. Francis, unpublished data).

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