A Systematic Review of *Kerivoula* Gray, 1842 (Chiroptera: Vespertilionidae: Kerivoulinae) from Thailand

Bounsavane Douangboubpha

A Thesis Submitted in Fulfillment of the Requirement for the Degree of

Doctor of Philosophy in Biology

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Major Program	Doctor of Philosophy in Biology

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I hereby certify that this work has not already been accepted in substance for any degree, and is not being concurrently submitted in candidature for any degree.

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ABSTRACT

A systematic study of the genus *Kerivoula* Gray, 1842 from Thailand was undertaken based on morphology, acoustics and genetics. Seven species, *K. papillosa, K. kachinensis, K. hardwickii, K. titania, K. pellucida, K. krauensis* and *K. minuta*, were included in the study. One, *K. krauensis,* is recorded for the first time from the country. Two other species, *K. picta* and *K. whiteheadi*, which had been recorded previously from the country were not available to examine for the present study. The results of morphological and genetic analyses show that the bats in this genus consist of several species complexes, including the *K. papillosa* complex, the *K. hardwickii* complex and the *K. titania* complex. Acoustic analysis indicates that echolocation call characters are significantly different between species, although, there is considerably overlap in each parameter among species.

A detailed study of the *K. papillosa* species complex, based on data from throughout South-east Asia, indicated that it includes three distinct species, of which one is referable to an undescribed species, *Kerivoula* spA. The other two are *K. papillosa* and *K. malayana* respectively The results also show that specimens previously referred to *K. lenis* from the Sundaic Subregion are discrete from those from India and are here considered as an undescribed species, *Kerivoula* spB.

In case of the *K. hardwickii* species complex, both morphological and genetic analysis show that the bats previously referred to *K. hardwickii* consist of several cryptic species, which are divided into two type, ‘domed-skull’ type and ‘flat-skull type. The specimens with a ‘domed-skull’ type are here considered referable to *K. hardwickii,* which is itself an apparant species complex. Those with the ‘flat-skull’ type are referred to the *K. depressa* complex, which also appears to include several cryptic species. More data are required to analyse these latter two complexes in detail.

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CHAPTER 1
GENERAL INTRODUCTION

1.1. Order Chiroptera

Bats are in Order Chiroptera. They are one of the most species order of mammals with 202 genera and > 1,116 species worldwide (Simmons, 2005). Its number is only less than rodents. Bats are almost distributed throughout the world although the majority are in tropical or subtropical regions (Corbet and Hill, 1992).

1.1.1. Systematics

Based on morphology, bats, were previously included in the Superorder Archontra (Novacek, 1992), including Orders Primates (primates), Scandentia (three shrews), and Dermoptera (flying lemurs). However, recent genetic studies suggest that the Order Chiroptera is included in the Superorder Laurasiatheria (Waddell et al., 1999; Madsen et al., 2001), including Orders Eulipotyphla (eulipotyphlan insectivores), Pholidota (pangolins), Carnivora (carnivores), Perissodactyla (perissodactyls), and Cetartiodactyla (cetartiodactyls).

The history of bat systematics is complex and confusing. The classification used today is based on the system developed by Miller (1907). However, Miller's system was only for Microchiroptera. In the past, morphological study placed all non-echolocating bats in the suborder Megachiroptera (fruit bats or megabats) and echolocating bats in the suborder Microchiroptera (Insectivorous bats or Microbats) (sensu Simmons and Geisler, 1998). However, recent DNA studies disagree with the morphology. They place the echolocating bats in superfamily Rhinolophoidea with those of megabats (sensu Springer et al., 2001). However, the DNA studies show some different clusters, such as Murphy et al. (2001) which included the family Nycteridae in the superfamily Rhinolophoidea and placed this superfamily in the Microchiroptera. However, Lui et al. (2001) included the Emballonuroidea as a sister-taxon of the megabats rather than the Rhinolophoidea. The most recent DNA studies suggest that the Rhinolophoidea is a sister-taxon of the megabats rather than others (Springer et al., 2001; Teeling et al., 2005). The classification, both based on

Table 1.1. Summary tradition classification based on morphology (sensu Simmons and Geisler, 1998) and modern classification based on DNA (sensu Spring et al., 2001; Teeling et al., 2005).

Traditional classification	Modern classification
Order Chiroptera	Order Chiroptera
Suborder Megachiroptera	Suborder Yinpterochiroptera
Family Pteropodidae	Superfamily Pteropodoidea
Suborder Microchiroptera	Family Pteropodidae
Superfamily Emballonuroidea	Superfamily Rhinolopoidea
Family Emballonuridae	Family Rhinolophidae
Infraorder Yinochiroptera	Family Hipposideridae
Superfamily Rhinopomatoidea	Family Rhinopomatidae
Family Craseonycteridae	Family Megadermatidae
Family Rhinopomatidae	Family Craseonycteridae
Superfamily Rhinolophoidea	Suborder Yangochiroptera
Family Nycteridae	Superfamily Emballonuroidea
Family Megadermatidae	Family Nycteridae
Family Rhinolophidae	Family Emballonuridae
Infraorder Yangochiroptera	Superfamily Noctilionoidea
Family Mystacinidae	Family Noctilionidae
Superfamily Noctilionoidea	Family Furipteridae
Family Noctilionoidae	Family Thyropteridae
Family Mormoopidae	Family Phyllostomidae
Family Phyllostomidae	Family Mormoopidae
Superfamily Molossoidea	Family Mystacinidae
Family Antrozoidae	Family Mezopodidae
Family Molossidae	Superfamily Vespertilionoidea
Superfamily Vespertilionoidea	Family Natalidae
Family Vespertilionidae	Family Vespertilionidae
Superfamily Nataloidea	Family Miniopteridae
Family Myzopodidae	Family Molossidae
Family Thyropteridae	
Family Furipteridae	
Family Natalidae	

morphology (traditional classification) and genetics (modern classification – Figure 1.1.), is summarised in Table 1.1.

1.2. Family Vespertilionidae

The Vespertilionidae is the largest family of Order Chiroptera, with 48 genera and > 407 species known to science (Simmons, 2005). The bats of the family Vespertilionidae occur throughout the world, including some isolated oceanic islands

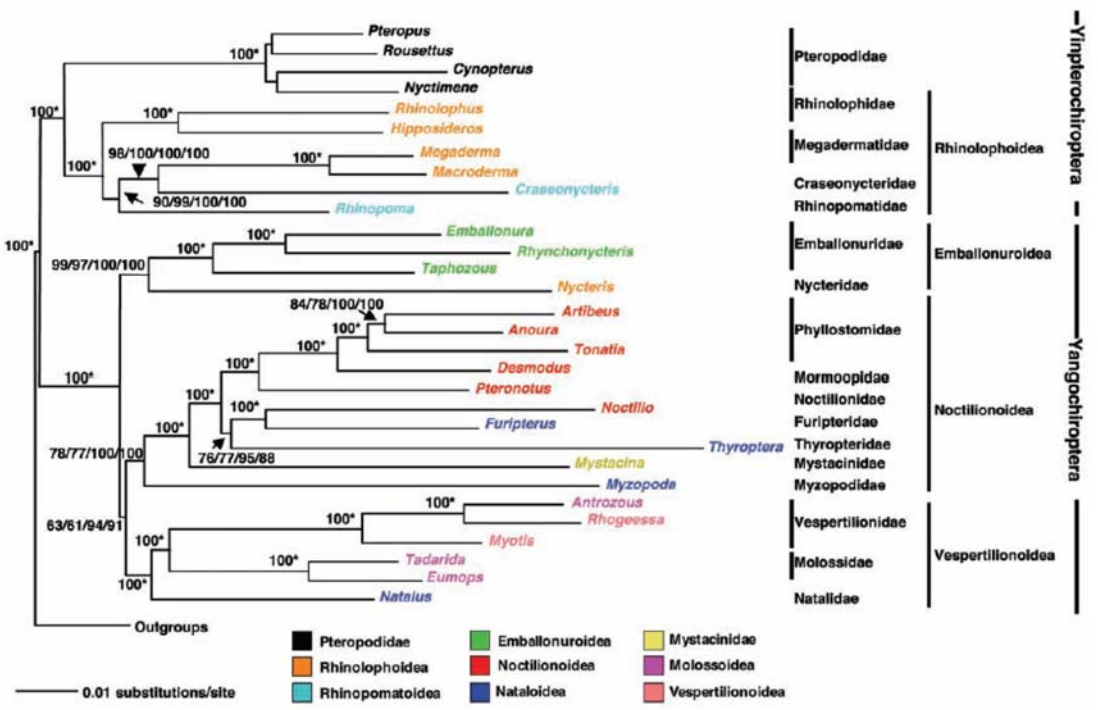

Figure 1.1. Modern classification based on genetic analysis of the Order Chiroptera (from Teeling et al., 2005).

and island groups. The exceptions are the polar and near polar regions (Figure 1.2.). The member of the family are found in a wide variety of environments ranging from tropical forests to arid semi-desert and desert regions as well as throughout the cool temperate regions of the world (Hill and Smith, 1984).

Generally, the muzzle is simple, sometime with tubular nostrils (subfamily Murininae). The eyes are usually quite small and often hidden by the thick fur on the face. The ears of the member of the family Vespertilionidae are generally small and simple in structure, but some species have very long ears. The tragus is usually a simple tongue-shaped structure, but it too may be long and vary in form. The skull and dentition vary among genera and species. The skull of most small vespertilionids is delicate (i.e. *Kerivoula* and *Pipistrellus*), whereas those of large species are heavy and relatively massive (i.e. *Scotophillus* and *Lasiurus*). The skulls of some species are extremely flat (i.e. *Tylonycteris* and *Mimetillus moloneyi*).

The classification of the family Vespertilionidae is confusing. Previously, it included the genus *Miniopterus* in the subfamily Miniopterinae (sensu Hill and Smith,

Table 1.2. Classification of family Vespertilionidae following Simmons (2005).

Family Vespertilionidae	Tribe Vespertilionini
Subfamily Vespertilioninae	Genus *Chalinolobus*
Tribe Eptesicini	Genus *Eudiscopus*
Genus *Arielulus*	Genus *Falsistrellus*
Genus *Eptesicus*	Genus *Glauconycteris*
Genus *Hesperoptenus*	Genus *Histiotus*
Tribe Lasiurini	Genus *Hypsugo*
Genus *Lasiurus*	Genus *Ia*
Tribe Nycticeiini	Genus *Laephotis*
Genus *Nycticeinops*	Genus *Mimetillus*
Genus *Nycticeius*	Genus *Neoromicia*
Genus *Scoteanax*	Genus *Philetor*
Genus *Scotoecus*	Genus *Tylonycteris*
Genus *Scotomanes*	Genus *Vespadelus*
Genus *Scotophilus*	Genus *Vespertilio*
Genus *Scotorepens*	Tribe Antrozoini
Tribe Nyctophilini	Genus *Antrozous*
Genus *Nyctophilus*	Genus *Bauerus*
Genus *Pharotis*	Genus *Baeodon*
Tribe Pipistrellini	Genus *Rhogeessa*
Genus *Glischropus*	Subfamily Myotinae
Genus *Nyctalus*	Genus *Cistugo*
Genus *Pipistrellus*	Genus *Lasionycteris*
Genus *Scotozous*	Genus *Myotis*
Tribe Plecotini	Subfamily Murininae
Genus *Barbastella*	Genus *Harpiocephalus*
Genus *Corynorhinus*	Genus *Murina*
Genus *Euderma*	Subfamily Kerivoulinae
Genus *Idionycteris*	Genus *Kerivoula*
Genus *Otonycteris*	Genus *Phoniscus*
Genus *Plecotus*	

1984). However, recent genetic studies suggest that the genus *Miniopterus* should be included in its own family, the Miniopteridae (sensu Hoofer and van den Bussche, 2003). The most recent classification of the family Vespertilionidae is summarised in Table 1.2.

1.3. Genus *Kerivoula*

Genus *Kerivoula* Gray, 1842 is a large genus in the family Vespertilionidae, which currently comprises 22 species (Table 1.3.) (Simmons, 2005; Bates et al., 2004;

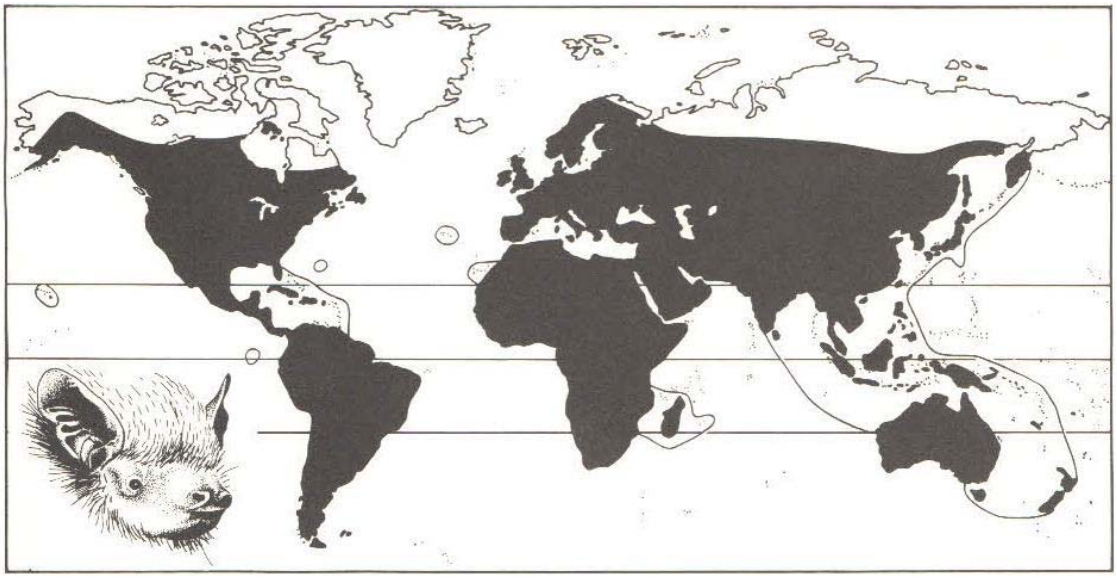

Figure 1.2. Distribution of bats in the family Vespertilionidae (from Hill and Smith, 1984).

2007; Francis et al., 2007). Its geographical range includes sub-Saharan Africa, India to South China, throughout South-east Asia to Philippines and New Guinea (Corbet and Hill, 1992). The genus is characterized by its funnel-like ears with the tragus is long, narrow and has a pointed tip. The fur is long and woolly and often covers much of the face. The nostrils are small and slightly protuberant. The skull usually has a high domed braincase (although, some species, *K. kachinensis* and *K. titania*), have a flattened braincase) and long rostrum.

Currently, the genus *Kerivoula* is included in the subfamily Kerivoulinae, together with genus *Phoniscus* Miller, 1905. Its classification (following Springer et al., 2001; Teeling et al., 2002; Hoofer and van den Bussche, 2003) is summarised in Table 1.4.

1.3.1. Research on genus *Kerivoula* in Thailand

The first *Kerivoula* known from Thailand was *K. minuta* Miller, 1898 which was described from Trong, Lower Siam (= Lay Song Hong, Trang, South Thailand). Subsequently, *K. bicolor* Thomas, 1904 was described from Biserat, Jalor, Malay Peninsula (= Yala, peninsular Thailand), although later Hill (1965) considered to be a subspecies of *K. whiteheadi* Thomas, 1894. Another new species of *Kerivoula*,

Table 1.3. List of species of the genus *Kerivoula*, including conservation status and geographical range. Conservation status follows IUCN (2013). DD = Data Deficient, EN = Endangered, LC = Least Concern, NT = Near Threatened and VU = Vulnerable.

No	Species	Conser. status	Geographical range
1	*K. africana*	EN	Tanzania
2	*K. agnella*	DD	Papua New Guinea
3	*K. argentata*	LC	Uganda, Kenya to South Africa
4	*K. cuprosa*	DD	Congo, Cameroon
5	*K. eriophora*	DD	Ethiopia
6	*K. flora*	VU	Borneo, Lesser Sunda
7	*K. hardwickii*	LC	Sri Lanka, India to Philippines
8	*K. intermedia*	NT	Malaysia, Borneo
9	*K. kachinensis*	LC	South-east Asia
10	*K. krauensis*	DD	Malaysia
11	*K. lanosa*	LC	Guinea, Liberia to South Africa
12	*K. lenis*	LC	India, Malaysia, Borneo
13	*K. minuta*	NT	Thailand, Malaysia, Borneo
14	*K. muscina*	LC	New Guinea
15	*M. myrella*	DD	Lesser Sundas, Papua New Guinea
16	*K. papillosa*	LC	South-east Asia to Sulawesi
17	*K. pellucida*	NT	Thailand to Philippines
18	*K. phalaena*	LC	Liberia to Congo
19	*K. picta*	LC	Sri Lanka, India to Moluccas
20	*K. smithii*	LC	Nigeria to Kenya
21	*K. titania*	LC	South-east Asia
22	*K. whiteheadi*	LC	Thailand to Philippines

namely *K. picta* Pallas, 1767 (= *Cerivoula picta*) was recorded form the country by Flower (1900). Seventeen years later, Gyldenstolpe (1917) reported another new species record, *K. hardwickii* Horsfield, 1824, from the country. Gyldenstolpe (1919) listed in the following *Kerivoula* species from Thailand: *K. hardwickii, K. picta, K. minuta,* and *K. whiteheadi* (= *K. bicolor*). Osgood (1934) published a record of *K. picta* from northern Thailand, which he referred to the subspecies *bellissima* Thomas, 1906, which was originally described from Pak-hi, Guangdong in southern China. Shamel (1942) also reported *K. picta* from Chiang Mai Province, northern Thailand.

Thirty years later, Hill (1975) reported two species, *K. hardwickii* and *K. picta*. Contrary to Osgood (1934), he included all specimens of *K. picta* from north-eastern and central Thailand in the nominate race, *picta*. Subsequently, he restricted the taxon *bellissima* to southern China and Hainan (Corbet and Hill, 1992). In respect

Table 1.4. The classification of the genus *Kerivoula,* after Simmons (2005).

Kingdom Animalia
Phylum Chordata
Class Mammalia
Order Chiroptera
Suborder Yangochiroptera
Superfamily Vespertilionoidea
Family Vespertilionidae
Subfamily Kerivoulinae
Genus *Kerivoula*

of *K. hardwickii*, Hill (1975) suggested that in addition to the nominate form, *hardwickii*, a distinct subspecies *depressa* Miller, 1906 might also be present. This latter taxon was described from Biapo, Carin Hills, southern Myanmar (Burma) as a distinct species from *K. hardwickii* based on its smaller ears, short tibia, smaller foot, lower and more flattened braincase, narrower palatal and narial emarginations. It was included in *K. hardwickii* by Ellerman and Morrison-Scott (1951) based on suggestions by Tate (1941). This taxonomic arrangement was also followed by Hill (1965).

Lekagul and McNeely (1977) reported four species, including *K. hardwickii* (with the subspecies *depressa* restricted to Tenasserim Range and the nominate form found elsewhere), *K. picta, K. minuta* and *K. whiteheadi*. Yenbutra and Felten (1986) also reported the same four species. They referred material from Chiang Mai Province, northern Thailand and Phetchabun Province, north-eastern Thailand to *K. minuta*, although subsequent authors considered that this species is restricted to the southern part of the country (Corbet and Hill, 1992; Simmons, 2005; Francis, 2008). It is probably the specimens of *K. minuta* from Chiang Mai and Phetchabun are referable to undescribed species. Later, Hendrichsen et al. (2001) referred a specimen from Chiang Mai Province in the collection of British Museum (Natural History) (BMNH.78.2385) to *K. flora* Thomas, 1914, a view followed by Vanitharani et al. (2003). Later, Bates et al. (2007) referred this specimen to their new taxon, *K. titania*.

McBee et al. (1986) reported an additional species, *K. papillosa* Temminck, 1840, from Surat Thani Province in peninsular Thailand. Subsequently, Vanitharani et al. (2003) noted that this material might be referable to *K. lenis* Thomas, 1916.

Anwarali et al. (2010) compared measurements of McBee et al. (1986) specimen (CM 88164, FA = 43.3 mm) with *K. lenis* and *K. papillosa* and noted that it is more closely related to *K. lenis* in term of size and skull morphology. *K. lenis* is only known from India, peninsular Malaysia and Borneo (Vanitharani et al., 2003; Simmons, 2005; Francis, 2008). Its distributional range suggests that it may prove to be widespread in mainland South-east Asia, especially Myanmar and Thailand.

Corbet and Hill (1992) summarized the mammals of the Indomalayan region and reported the same five species from Thailand, namely *K. picta, K. minuta, K. whiteheadi, K. hardwickii* and *K. papillosa*. Robinson et al. (1995) published the results of some small mammal surveys in the western part of Thailand and included two species, *K. hardwickii* and *K. papillosa*. Later, Robinson et al. (1996) published the result of bat surveys from the same area but reported only *K. hardwickii*.

Simmons (2005) reported five species from Thailand and based on Hendrichsen et al (2001), commented that *K. flora* also probably occurred there. Bumrungsri et al. (2006) listed six species from the country including one *K. pellucida* Waterhouse, 1845, which was a new record for Thailand. After that, Soisook et al. (2007) recorded one other new species, *K. kachinensis* Bates et al., 2004. Then Bates et al. (2007) described a new species, *K. titania*, from mainland South-east Asia, including Thailand.

The recent genetic study suggested that our current understanding of the genus *Kerivoula* significantly underestimates its diversity, such that, for example, *K. hardwickii* and *K. papillosa/K. lenis* are in reality a complex for cryptic species (Francis, 2008; Anwarali et al., 2010; Francis et al., 2010). The current study seeks to review the taxonomic status of all species in the genus from Thailand using a range of morphology, acoustic characters and genetics.

1.4. Objectives

The present study aims to:

- Undertake a taxonomic review of the genus *Kerivoula* in Thailand, with reference to all species but with particular emphasize on cryptic species.
- Undertake a detailed analysis of the *Kerivoula* species complex based on data from throughout South-east Asia.

CHAPTER 2

Morphology, acoustics and genetics of the genus *Kerivoula* (Chiroptera: Vespertilionidae: Kerivoulinae) in Thailand

ABSTRACT

Following extensive field work in Thailand (2010-2013) and the examination of numerous museum specimens, this chapter reviews and examines the taxonomy of the genus *Kerivoula* in Thailand, based on morphology, acoustic characters, and genetics. Seven species, *Kerivoula papillosa, K. kachinensis, K. hardwickii, K. titania, K. pellucida, K. krauensis* and *K. minuta*, were analysed in detail. Thai specimens of two species, *K. picta* and *K. whiteheadi*, were not available for study. The results of the morphological and genetic analyses, show that bats in this genus consist of several species complexes, comprising a range of cryptic species. This is especially the case for *K. papillosa*, *K. hardwickii* and *K. titania*. In their totality, acoustic characters are significantly different between species, although the individual parameters overlap considerably. The taxonomic status of each taxon is discussed.

2.1. INTRODUCTION

A series of recent morphological and genetic studies show that bats in the genus *Kerivoula* Gray, 1842 include a number of cryptic species complexes, especially in the *K. papillosa* Temminck, 1840/*K. lenis* Thomas, 1916 complex and the *K. hardwickii* Horsfield, 1824 complex (Anwarali et al., 2010; Francis et al., 2010; Hasan and Abdullah, 2011).

Recent genetic analysis reveal that bats referred to *K. papillosa* and *K. lenis* include at least four monophyletic types (Francis et al., 2010). Payne and Francis (1985) noted that the bats referred to *K. papillosa* from Borneo include more than one species. Similarly, Kingston et al. (1999) found that the Malaysian *K. papillosa* comprises two size classes: *K. papillosa* S[mall] (FA: 37.8-40.0 mm) and *K. papillosa* L[arge] (FA: 40.5-45.0 mm). The authors also indicate that acoustic characters can be

used for specific identification within the genus. Later, Vanitharani et al. (2003) referred *K. papillosa* S to the taxon *K. lenis*.

Anwarali et al. (2010) studied the morphology and genetics of Malaysian *Kerivoula*. The results show that bats referred to *K. papillosa* include more than one morphotype and monophyletic type, including *K. papillosa* S[mall] (FA: 39.5-43.0 mm and GTL: 16.9-17.3 mm) and *K. papillosa* L[arge] (FA: 45.0-46.5 mm and GTL: 17.7-18.0 mm). The authors also referred material of a third *Kerivoula* taxa with a forearm length of 38.7-38.9 mm and a skull length of 15.7-16.2 mm to *K. lenis*. Hasan and Abdullah (2011) studied the morphology of Malaysian *Kerivoula* and found a similar result to that of Anwarali et al. (2010) in which the bats referred to *K. papillosa* include more than one morphotype, namely *K. papillosa* S (FA: 41.2-43.7 mm and GTL: 17.8-18.3 mm) and *K. papillosa* L (FA: 44.7-47.3 mm and GTL: 18.4-18.8 mm).The authors referred material of *K. papillosa* S to *K. p. malayana.* This is in contrast to Anwarali et al. (2010) who referred material of *K. papillosa* S to *K. p. papillosa*. The authors also referred material with forearm lengths of 39.9-40.9 mm and a skull length of 16.8 mm to *K. lenis*.

In the case of *K. hardwickii*, Hill (1975) referred material from Chiang Mai Province, Thailand with domed braincases to the nominate race *K. h. hardwickii* and material from Phetchabun Province with flattened skulls to the subspecies *K. h. depressa*. Later, Lekagul and McNeely (1988) suggested that the taxon *depressa* is found in the western Thailand, whereas *hardwickii* is found in the remainder of the country. Corbet and Hill (1992) noted that specimens from the western part of the range of *K. hardwickii* (from India to Vietnam) have relatively flattened skulls. Bates et al. (2007) suggested that the taxon with the smaller, flat-head (BH<5.1 mm) may prove to be *K. depressa* Miller, 1906a whereas that with the slightly larger, domed-skull (BH>5.1 mm) may be referable to the true *K. hardwickii*. Recent genetic studies also suggest that bats currently referred to *K. hardwickii* include several different species (Francis, 2008; Francis et al., 2010): available names include *fusca* Dobson, 1871, locality unknown; *depressa* from South-eastern Myanmar; *engana* Miller, 1906b from Western Sumatra; *crypta* Wroughton and Ryley, 1913 from Southern India, and *malpasi* Phillips, 1932 from Sri Lanka (sensu Corbet and Hill, 1992). However, most authors (Corbet and Hill, 1992; Simmons, 2005) currently treat these

names as synonyms of *K. hardwickii* and recent genetic and morphological studies of Malaysian *K. hardwickii* show that there is only one morphotype and monophyletic type (Anwarali et al., 2010; Hasan and Abdullah, 2011).

In Thailand, Yenbutra and Felten (1986) referred material from Chiang Mai and Phetchabun Provinces to *K. minuta*. However, the known range of this taxon is currently considered to be limited to the southern part of Thailand (Corbet and Hill, 1992; Simmons, 2005; Francis, 2008). It is suggested that this material from northern Thailand is referable to an undescribed species. A recent genetic study showed two monophyletic clades of *K. minuta* (Francis et al., 2010). However, a comparable morphological study showed only one form (Anwarali et al., 2010; Hasan and Abdullah, 2011). Additionally, *K. minuta* is essentially similar to *K. intermedia* Hill and Francis, 1984 from Borneo, which is only differentiated from *K. minuta* by its larger skull (Hill and Francis, 1984; Francis, 2008; Anwarali et al., 2010). However, these two species are different genetically (Anwarali et al., 2010; Francis et al., 2010).

In the recent years, several new species were described from the region, including *K. kachinensis* Bates et al., 2004; *K. titania* Bates et al., 2007 and *K. krauensis* Francis et al., 2007. In addition, there have been some changes to the rank of individual taxa, for example with the elevation of *K. lenis* to specific status (Vanitharani et al., 2003). However, it appears that the species diversity of the genus *Kerivoula* is still underestimated and further taxonomic revision is needed.

The present study aims to examine the taxonomic status of bats in the genus *Kerivoula* in Thailand based on morphology, acoustics and genetics. It is based on extensive field work (2010-2013), a thorough examination of museum specimens and a thorough review of the literature.

2.2. MATERIAL AND METHODS

2.2.1. Field work

In the present study, bats were captured at sixteen localities in six provinces of Thailand (Figure 2.1. and Table 2.1.) using four-bank harp traps (Francis, 1989) and mist-nets. The harp traps were set on natural trails, over small streams and across paths in forest understorey. Harp traps were erected before sunset and left over night.

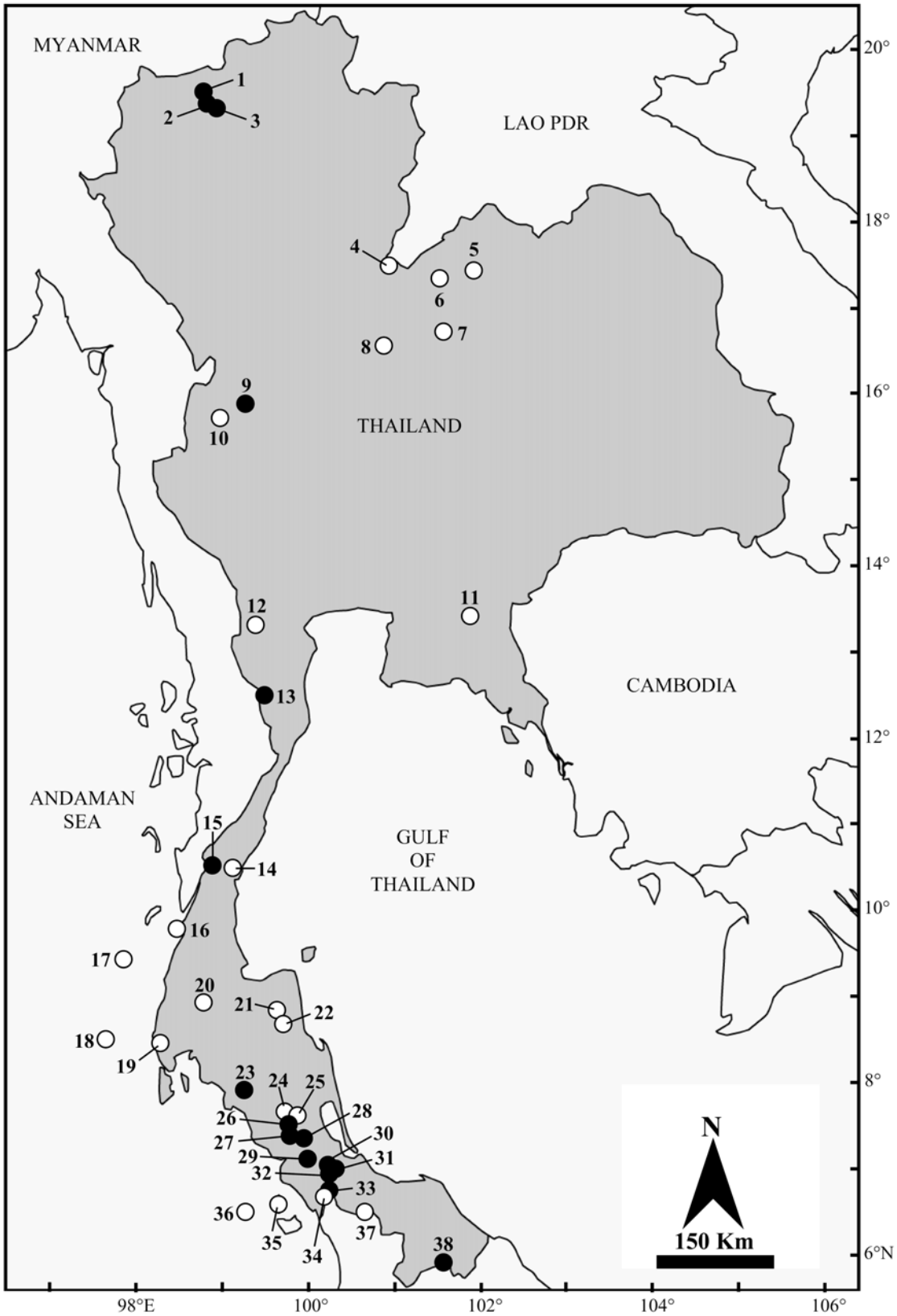

Figure 2.1. Localities in Thailand from which *Kerivoula* specimens were examined in this study; black symbols represent localities visited; open symbols are for museum specimens. For list of localities see Appendix 3.

Table 2.1. List of localities of the specimens examined in the present study.

No	Locality	Province	Co-ordinate
1	Khun Mae Ngai GS.	Chiang Mai	19°30’33”N, 98°49’57”E
2	Hui Mae Kok RS.	Chiang Mai	19°22’25”N, 98°50’05”E
3	Chiang Dao WRS.	Chiang Mai	19°21’51”N, 98°55’23”E
4	Phou Suan Sai NP.	Loei	17°30’39”N, 100°57’07”E
5	Phu Suan Sai NP.	Loei	17°28’00”N, 101°58’00”E
6	Phu Loung WS.	Loei	17°20’34”N, 101°33’49”E
7	Namnao NP.	Phetchabun	16°45’06”N, 101°33’44”E
8	Thung Salang Luang NP.	Phisanoulok	16°34’16”N, 100°52’34”E
9	Mae Wong NP.	Tak	c.o. 15°54’N, 99°12’E
10	East Thung Yai Naresuan WS.	Tak	15°44’00”N, 98°59’06”E
11	Angruenai WS.	Chachuengsao	13°24’44”N, 101°52’44”E
12	Pha Chi WS.	Ratchaburi	13°18’30”N, 99°24’51”E
13	Pa La-U RS.	Prachuap Khiri Khan	12°32’17”N, 99°27’48”E
14	Khao Kaew	Chumphon	10°30’18”N, 99°07’09”E
15	South Klom Luang Chumporn WS.	Ranong	10°31’02”N, 98°54’09”E
16	Mo Koh Payam NP.	Ranong	9°48’41”N, 98°26’08”E
17	Surin Islands NP.	Phang Nga	9°26’45”N, 97°52’18”E
18	Mu Koh SimilanNP.	Phang Nga	8°39’46”N, 97°39’10”E
19	Lumpee Waterfall	Phang Nga	8°27’55”N, 98°17’34”E
20	Khao Sok NP.	Surat Thani	c.o. 8°57’N, 98°48’E
21	Khao Nan NP.	Nakhon Si Thammarat	8°51’56”N, 99°37’25”E
22	Krungching, Khao Luang NP.	Nakhon Si Thammarat	c.o. 8°42’N, 99°41’E
23	Khao Pra-Bang Kram WS.	Krabi	7°55’31”N, 99°15’47”E
24	Ban Nai Khao	Trang	7°42’28”N, 99°41’10”E
25	Khao Pu-Khao Ya NP.	Patthalung	c.o. 7°40’N, 99°52’E
26	Khao Chong WEC.	Trang	7°33’02”N, 99°46’54”E
27	Sai Rung Waterfall	Trang	7°25’27”N, 99°46’10”E
28	Priwan Waterfall	Phatthalung	7°23’48”N, 99°58’40”E
29	Phu Pha Phet RS.	Satun	7°07’56”N, 100°00’27”E
30	Had Sai Khao Waterfall,	Songkhla	7°02’40”N, 100°12’31”E
31	Kuan Khao Wang FP.	Songkhla	7°00’28”N, 100°18’45”E
32	Ton Nga Chang WS.	Songkhla	6°56’44”N, 100°14’28”E
33	Pha Dam RS.	Songkhla	6°47’13”N, 100°13’34”E
34	Taleban NP.	Satun	6°39’25”N, 100°09’03”E
35	Tarutao Island	Satun	6°39’30”N, 99°40’00”E
36	Adang-Rawi Islands	Satun	6°32’57”N, 99°16’52”E
37	Khao Nam Khang NP.	Songkhla	6°06’30”N, 101°04’28”E
38	Hala-Bala WS.	Narathiwat	5°48’01”N, 101°50’00”E

Mist-nets were used to capture bats in similar locations to the harp traps, but were more often used in open spaces. The mist-nets were set at the same time as the harp traps and taken down at 22.00 hours.

The species, sex, age (adult or juvenile) and the reproductive condition (pregnant or lactating) were determined in the field. Initial species identification was made in the field following Francis (2008), Corbet and Hill (1992) and Payne and Francis (1985). Adults or juveniles were identified by the presence of unfused epiphyses of phalanges and metacarpal joints (Brunet-Rossinni and Wilkinson, 2009). The reproductive status of female bats was determined by examining the nipples (Racey, 2009).

A number of specimens were taken for the study of morphometrics, especially cranial and dental characters, and as vouchers to support genetic studies. The body mass and some external characters were measured, including head and body, forearm, ear, tail, tibia and foot. In addition, co-ordinates were recorded using a GPS and habitats were described.

2.2.2. Sound records and analysis

Echolocation calls were recorded when the bats were free flying in room or alternatively when they were free flying in an artificial enclosure comprising mosquito nets for a roof and walls. The calls were detected with a Pettersson Ultrasound Detector D 1000, which were set at 10x expansion rate.

The sounds were analyzed using the software BatSound Pro v3.1 (Pettersson Elektronik AB) following Kingston et al. (1999) and Preatoni et al. (2005). For each call, four parameters were measured. They included: MinF: minimum frequency – measured on the spectrogram via a large measurement cursor placed at the top end of the spectrogram (Figure 2.2.); MaxF: maximum frequency – measured on the spectrogram via a large measurement cursor placed at the bottom end of spectrogram (Figure 2.2.); MaxEF: maximum energy frequency – measured by evaluating the power spectrum maximum, FFT (Fast Fourier Transforms) size 1024 and a Hanning window (applying the BatSound Power Spectrum function to the selection enclosed between start time and end time cursors) (Figure 2.3.); MidF: middle frequency – measured by evaluating a power spectrum maximum over a marking cursor

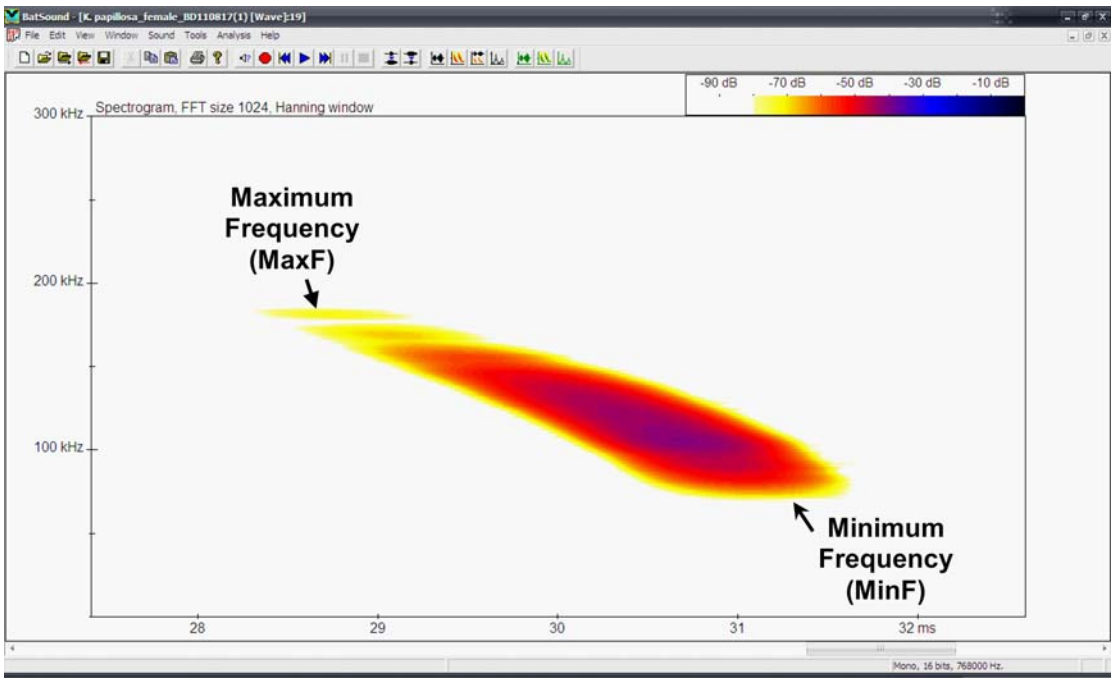

Figure 2.2. Maximum frequency and minimum frequency measurements of *K. papillosa*.

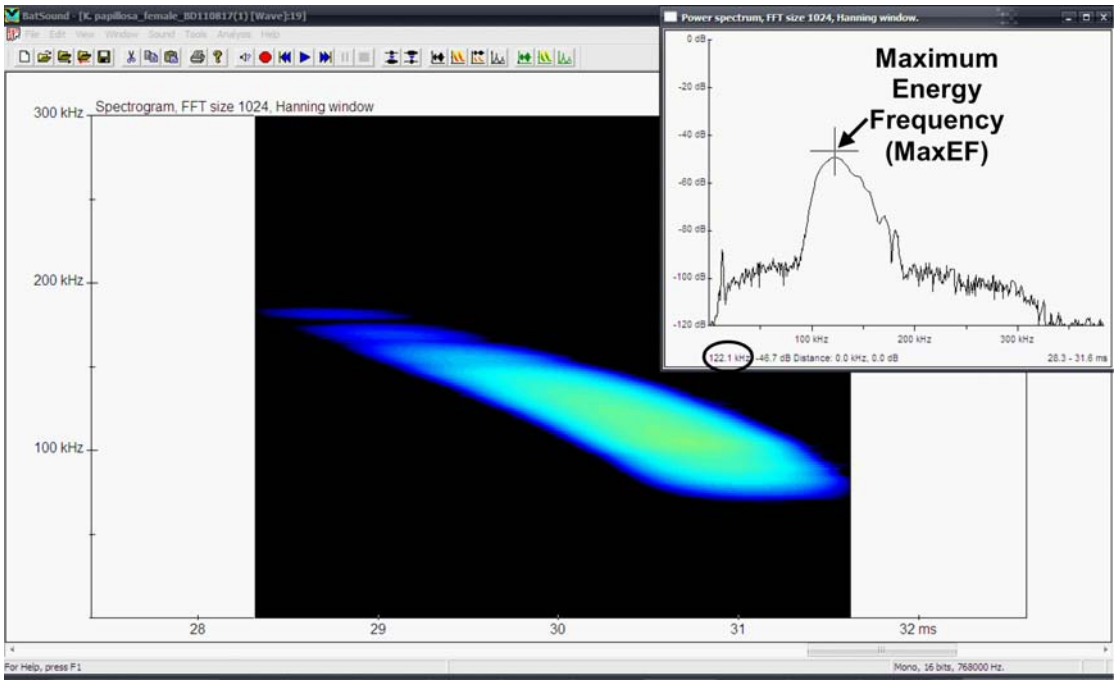

Figure 2.3. Maximum energy frequency measurement of *K. papillosa*.

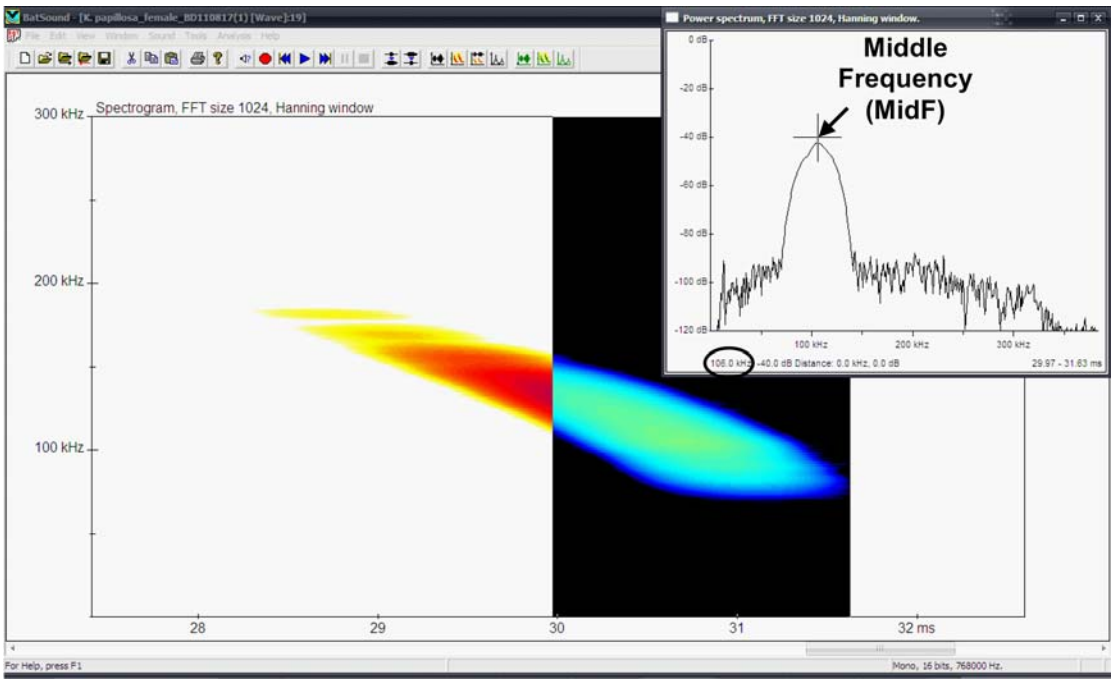

Figure 2.4. Middle frequency measurement of *K. papillosa*.

previously placed at half time (Figure 2.4.). To determine whether there were significant differences in each parameter between taxa, a series of One-Way ANOVA were run at a confidence limit of 95%.

2.2.3. Measurements

In this study, 155 voucher specimens were measured. They are held in the collections of the Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University, Thailand (PSUZC) and the Hala-Bala Wildlife Research Station, Thailand (HBWRS).

External and skull measurements were taken with a digital caliper to the nearest 0.01 mm, following Bates and Harrison (1997) and Bates et al. (2004) (Figures 2.5. and 2.6.). Body mass was measured with a Pesola Spring balance. Measurements included: HB: head and body – from the tip of the snout to the anus, ventrally; FA: forearm length – from the extremity of the elbow to the extremity of the carpus with the wings folded; EL: ear length – from the lower border of the external auditory meatus to the tip of the pinna; TL: tail length – from the tip of the

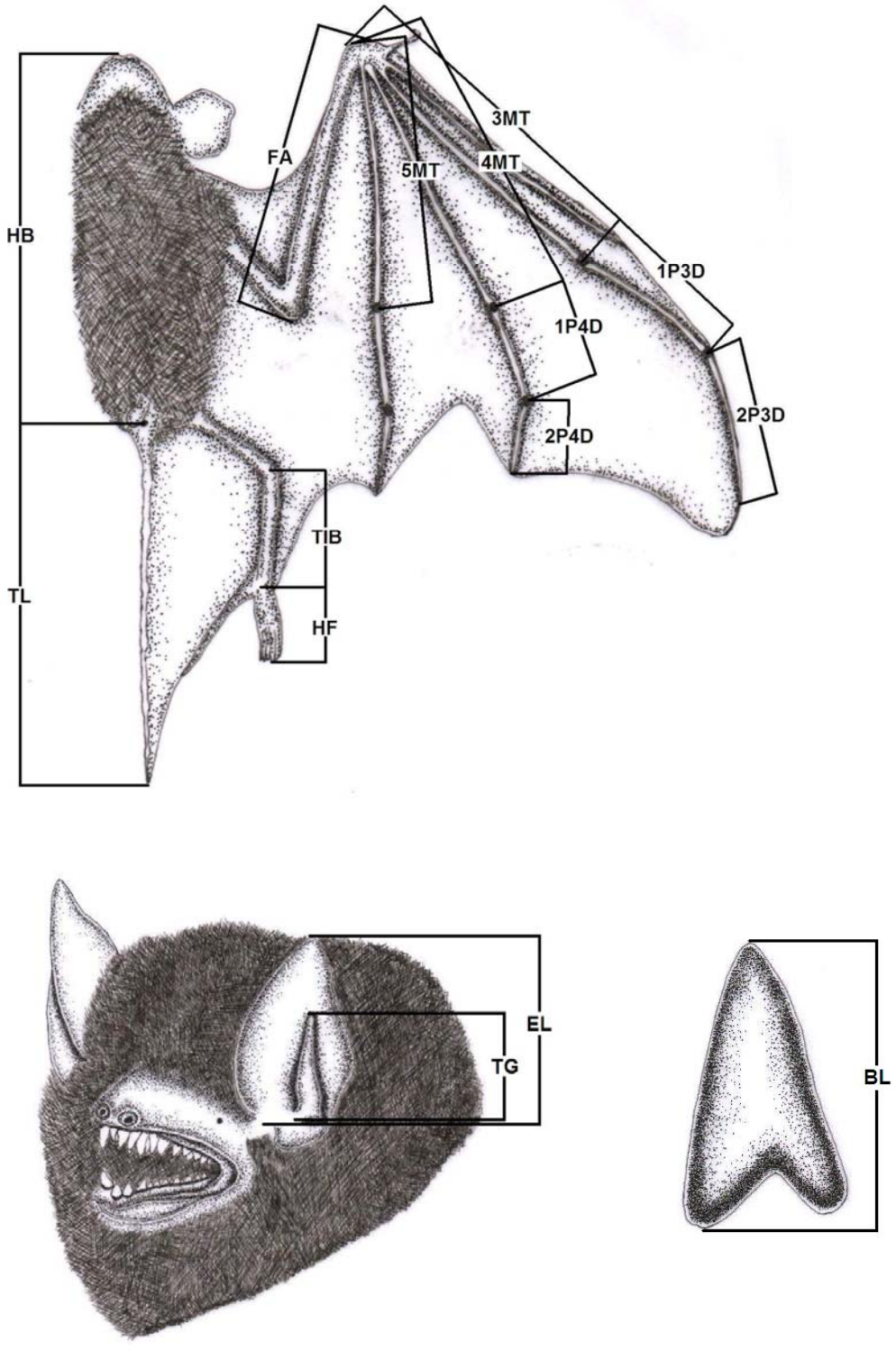

Figure 2.5. External and bacular measurements of *Kerivoula*.

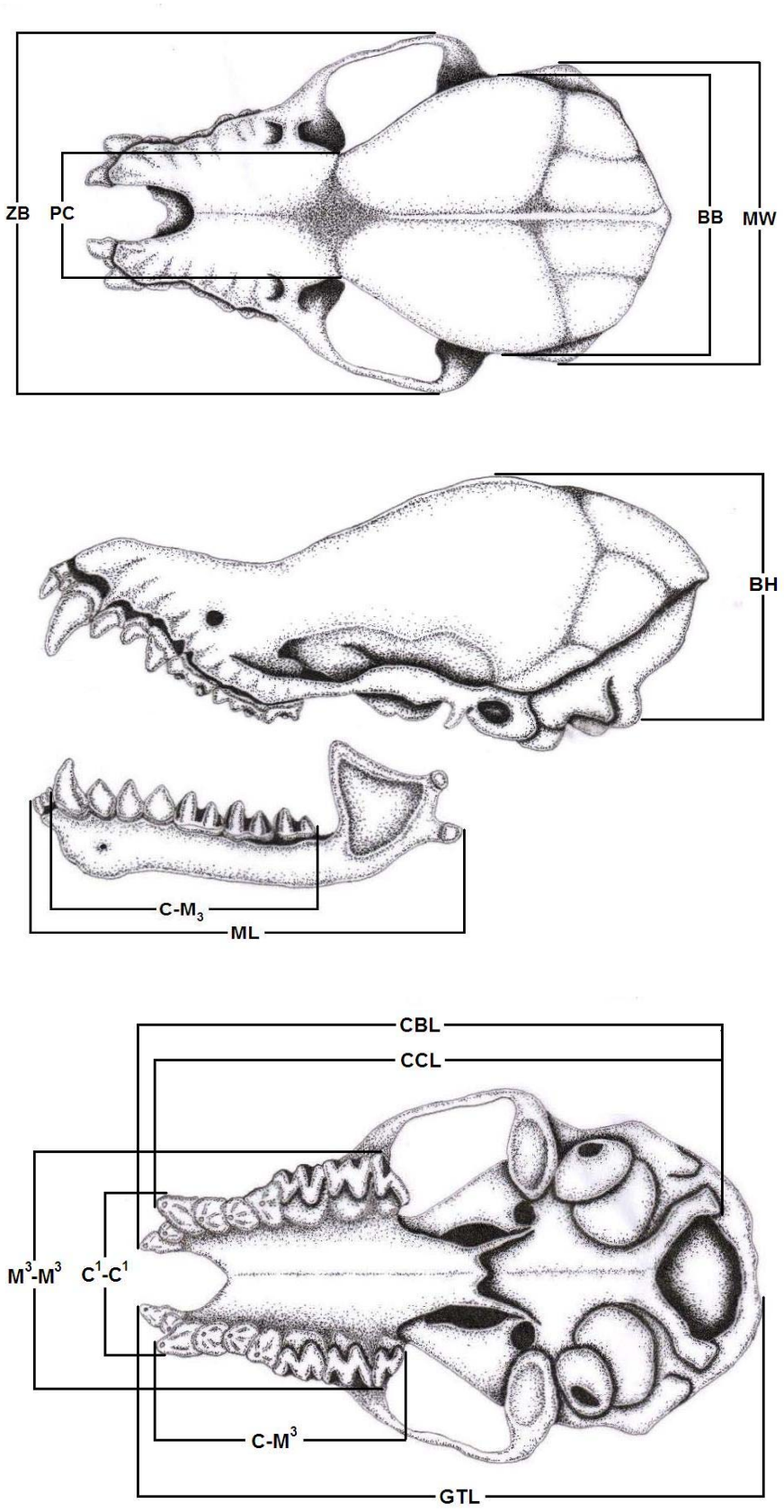

Figure 2.6. Cranio-dental measurements of *Kerivoula*.

tail to its base adjacent to the anus; TIB: tibia – from the knee joint to the extremity of the heel behind the os calcis; HF: foot – from the extremity of the heel behind the os calcis to the extremity of the longest digit, not including the hairs or claws; 3MT, 4MT, 5MT: third, fourth, fifth metacarpal lengths, respectively – from the extremity of the carpus to the distal extremity of the third, fourth and fifth metacarpals respectively; 3D1P, 3D2P, 4D1P, 4D2P: first and second phalanges of the third and fourth digits, respectively – from the proximal to the distal extremity of the phalanges; W: body mass (g); GTL: greatest length of skull – the greatest antero-posterior diameter of the skull, from the most projecting point at each extremity regardless of what structure forms these points; CCL: condylo-canine length – from the exoccipital condyle to the alveolus of the canine; CBL: condylo-basal length – from the exoccipital condyle to the alveolus of the anterior incisor; MW: mastoid width – the greatest distance across the mastoid region; ZB: zygomatic breadth – the greatest width of the skull across the zygomata; BB: breadth of braincase – greatest breadth of the braincase at the posterior roots of the zygomatic arches; BH: braincase height – taken from the basisphenoid to the highest part of the skull; PC: postorbital constriction – the narrowest width across the constriction posterior to the orbits; ML: mandible length – from the most posterior part of the condyle to the most anterior part of the mandible, including the lower incisors; C^1-C^1: anterior palatal width – taken across the outer borders of the upper canine; M^3-M^3: posterior palatal width – taken across the outer borders of the upper third molar; C-M^3: upper toothrow length – from the front of the upper canine to the back of the crown of the third molar; C-M_3: lower toothrow length – from the front of the lower canine to the back of the crown of the third lower molar.

2.2.4. Morphological analysis

To determine whether there were significant differences in metric characters between taxa, a series of *t*-tests were run at a confidence limit of 95%. Principal Component Analysis (PCA), performed on the correlative matrix, was used for multivariate comparisons.

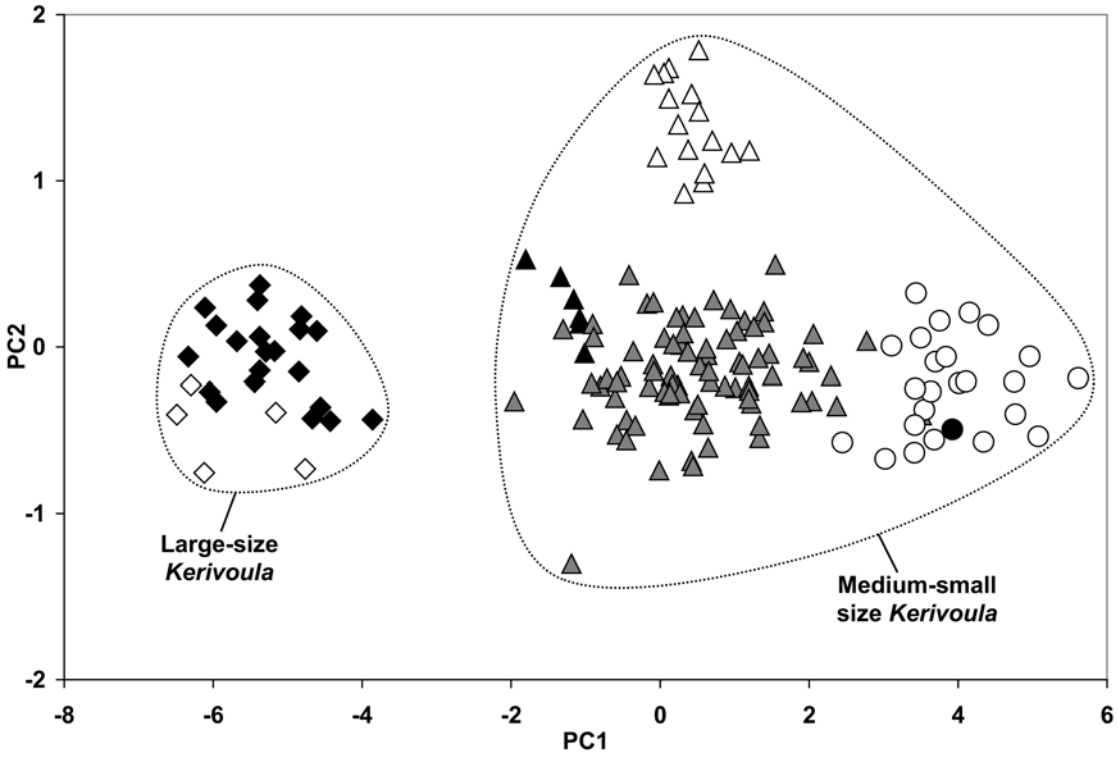

Figure 2.7. PCA of the external measurements between first and second principal components based on nine metric characters. Black diamonds represent *K. papillosa*, open diamonds are *K. kachinensis*, black triangles are *K. titania*, grey triangles are *K. hardwickii*, open triangles are *K. pellucida*, black circle is *K. krauensis* and open circles are *K. minuta*.

2.2.4. Genetic analysis

The deoxyribonucleic acid (DNA) was extracted from wing punches and cytochrome *c* oxidase (COI) was amplified and sequenced following the standard protocols published in Anwarali et al. (2010) and Francis et al. (2010). Additional, published sequences were included in the analysis, namely for *K. lenis* (TK 152052 and TK 152178), *K.* cf. *lenis* (ROM MAM 110520), *K. kachinensis* (EBD 25122), *K. picta* (ROM MAM 106371), *K. krauensis* (SMF 83824), *K. intermedia* (TK 153621), *K. hardwickii* (INECOL M0071 and INECOL M0108) and *K. minuta* (INECOL M0111 and INECOL M0112). These were available in the Barcode of Life Database (www.boldsystems.org) and are published in Anwarali et al. (2010) and/or Francis et al. (2010).

Phylogenetic reconstruction was undertaken using Neighbor-joining (NJ) with a Kimura 2-parameter (K2) model in the software MEGA version 5.1 (Kimura, 1980;

Table 2.2. Eigenvectors and eigenvalues of principal component analysis of nine external measurements of 154 specimens of seven species of *Kerivoula*.

Character	Eigenvector		
	1	2	3
FA	-0.34	-0.27	-0.25
TIB	-0.33	0.17	0.04
3MT	-0.34	-0.16	-0.31
4MT	-0.34	-0.09	-0.31
5MT	-0.34	-0.06	-0.28
3D1P	-0.34	-0.08	0.00
3D2P	-0.33	0.42	0.31
4D1P	-0.32	0.62	0.16
4D2P	-0.31	-0.54	0.74
Eigenvalue	8.23	3.27	2.34
% of total variation explained	91.40	94.66	97.01

Tamura et al., 2011) at bootstrap method for 1,000 replications. The divergent distance between and within taxa was generated using the Kimura 2-parameter model in the software MEGA version 5.1 (Kimura, 1980; Tamura et al., 2011).

2.3. RESULTS

2.3.1. Morphometrics

External measurements were available for 154 specimens from the study area. Principal Component Analysis (PCA) based on nine external characters shows that the bats in the genus *Kerivoula* from the study area are divided into two main groups (Figure 2.7. and Table 2.2.), comprising a 'large-size' group and a 'medium-small' size group (Table 2.3.).

Specimens within the 'large-size' group are here referable to *K. papillosa* and *K. kachinensis*. External measurements are similar in size between these two species, except tail (TL), tibia (TIB), third metacarpal (3MT) and fourth metacarpal (4MT), which average significantly larger in *K. kachinensis*; in contrast, the first phalanx on the fourth digit (4D1P) is significantly shorter (Tables 2.3. and 2.4.). In addition, the fur on the dorsal surface is slightly darker at the base in *K. kachinensis* whereas it is paler in *K. papillosa* (Figure 2.8.). The fur on the ventral surface does not differ between these two species but does exhibit individual variation.

Table 2.3. External measurements (mm) and body mass (g) of seven species of *Kerivoula*. HB – head and body; FA – forearm; EL – ear; TL – tail; TIB – tibia; HF – foot; 3MT, 4MT, 5MT – third, fourth, fifth metacarpals; 3D1P, 3D2P, 4D1P, 4D2P – first and second phalanges of third and fourth digits; W – body mass. Mean, range and standard deviation. Sample sizes differing from those reported under *n* are given in parentheses.

n	Sex	HB	FA	EL	TL	TIB	HF	3MT	4MT	5MT
					Kerivoula papillosa					
21	♂♂♀♀	40.3-52.2	39.1-42.3	13.1-17.4	47.7-56.4	18.8-23.2	7.9-9.9	42.3-46.2	40.9-45.5	39.4-43.5
		45.6, 2.8	40.6, 0.9	14.4, 0.9	51.1, 2.5	20.8, 1.2	9.2, 0.5	43.8, 0.9	42.6, 1.0	41.1, 1.0
					Kerivoula kachinensis					
5	♂♂♀	44.7-49.9	41.0-42.1	12.9-14.8	52.7-59.4	21.7-23.6	8.7-9.7	44.5-45.5	43.2-44.5	41.3-42.8
		48.0, 2.5	41.5, 0.5	14.2, 0.8	56.0, 2.7	22.9, 0.7	9.1, 0.4	45.0, 0.5	43.7, 0.5	41.9, 0.6
					Kerivoula hardwickii					
81	♂♂♀♀	32.0-42.5	28.9-35.7	10.6-15.0	33.8-47.9	15.2-19.4	6.5-8.4	31.6-38.1	30.1-37.6	28.3-35.9
		36.9, 2.0	32.8, 1.4	12.8, 0.9	41.3, 3.0	17.4, 0.8	7.6, 0.4	35.0, 1.4	34.0, 1.4	32.7, 1.4
					Kerivoula titania					
6	♂♂♀♀	38.4-41.0	34.1-35.9	12.5-13.8	48.1-53.5	18.8-19.8	7.3-7.8	35.2-36.4	34.7-35.9	33.4-34.4
		39.5, 1.0	34.8, 0.7	13.1, 0.5	50.1, 2.0	19.4, 0.3	7.6, 0.2	35.7, 0.5	35.2, 0.4	34.0, 0.4
					Kerivoula pellucida					
16	♂♂♀♀	35.4-41.4	29.2-32.1	13.2-16.3	44.0-51.2	16.3-19.5	6.7-7.8	33.6-35.6	32.8-34.6	31.5-33.6
		37.4, 1.7	30.9, 0.8	14.8, 0.9	47.2, 2.1	17.9, 0.8	7.3, 0.3	34.3, 0.5	33.6, 0.5	32.5, 0.5
					Kerivoula krauensis					
1	♂	31.6	30.8	12.1	33.1	14.6	7.5	31.5	29.9	28.3
					Kerivoula minuta					
24	♂♂♀♀	28.2-39.0	25.3-29.4	7.9-11.6	30.6-42.3	12.0-14.8	6.1-7.1	27.9-32.1	26.4-30.8	25.3-30.3
		31.4, 2.4	28.0, 1.1	9.8, 0.4	37.0, 3.0	13.9, 0.6	6.5, 0.2	30.2, 1.2	28.9, 1.1	27.9, 1.2

Table 2.3. Continued.

n	Sex	3D1P	3D2P	4D1P	4D2P	W
			Kerivoula papillosa			
21	♂♂♀♀	18.9-22.8	18.6-22.6	12.5-13.9	9.1-10.4	6.5-9.0
		21.0, 1.0	21.1, 0.9	13.2, 0.5	9.7, 0.4	7.9, 0.7 (11)
			Kerivoula kachinensis			
5	♂♂♀	19.7-22.2	19.1-21.4	11.8-13.3	9.0-10.5	6.3-8.0
		21.4, 1.0	20.5, 1.0	12.7, 0.7	9.9, 0.7	7.1, 0.7
			Kerivoula hardwickii			
81	♂♂♀♀	14.7-18.8	13.3-18.0	8.7-11.9	6.4-10.5	3.0-5.5
		16.6, 0.8	16.1, 1.0	10.5, 0.6	7.9, 0.6	4.1, 0.6 (44)
			Kerivoula titania			
6	♂♂♀♀	18.1-19.4	17.4-19.0	11.0-12.3	8.3-8.8	4.0-5.0
		18.7, 0.5	18.0, 0.6	11.7, 0.5	8.6, 0.2	4.5, 0.5
			Kerivoula pellucida			
16	♂♂♀♀	15.0-16.7	17.0-19.3	11.1-12.4	6.7-8.6	3.7-5.5
		15.8, 0.5	18.0, 0.8	11.8, 0.4	7.3, 0.4	4.6, 0.6 (11)
			Kerivoula krauensis			
1	♂	13.6	13.0	8.3	6.3	-
			Kerivoula minuta			
24	♂♂♀♀	12.5-14.9	12.8-15.8	7.9-9.4	6.3-8.4	2.5-3.5
		13.9, 0.7	14.2, 0.7	8.9, 0.4	7.1, 0.5	2.6, 0.3 (16)

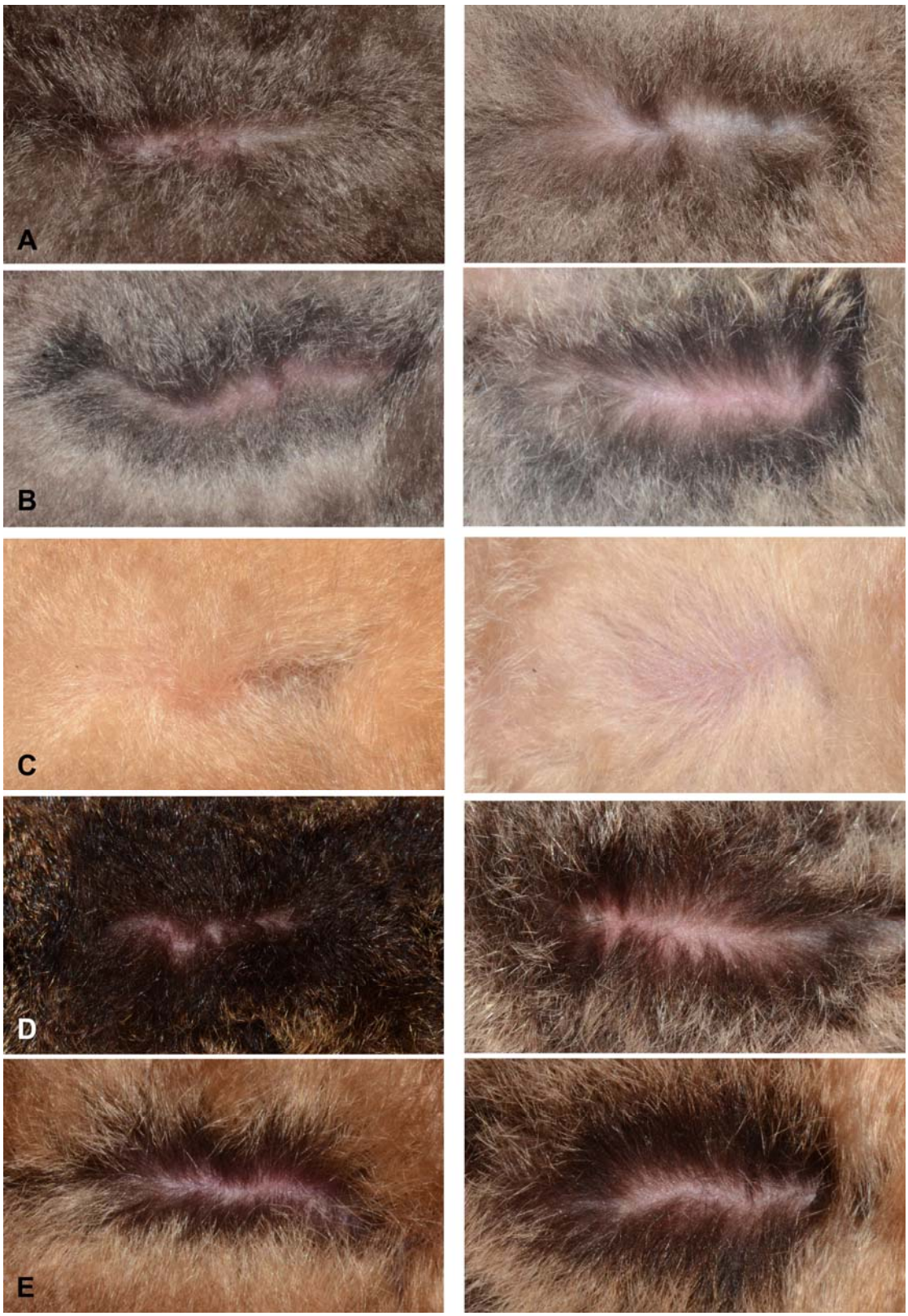
A
B
C
D
E

Figure 2.8. The dorsal (left) and ventral (right) pelage of five species of *Kerivoula*. A – *K. papillosa*, PSUZC-MM2013.28, ♂, Hala-Bala Wildlife Research Station, Narathiwat Province; B – *K. hardwickii*, PSUZC-MM2013.22, ♂, Phu Pha Phet Ranger Station, Khao Bantad Wildlife Sanctuary, Satun Province; C – *K. pellucida*, PSUZC-MM2013.24, ♂, Phu Pha Phet Ranger Station, Khao Bantad Wildlife Sanctuary, Satun Province; D – *K. krauensis*, PSUZC-MM2013.25, ♂, Hala-Bala Wildlife Research Station, Narathiwat Province; E – *K. minuta*, BD130825.3, ♂, Phu Pha Phet Ranger Station, Khao Bantad Wildlife Sanctuary, Satun Province. No scale.

Material within the 'medium-small' size group is here referable to *K. hardwickii*, *K. titania, K. pellucida, K. krauensis* and *K. minuta*. Specimens referred to *K. hardwickii* average significantly smaller than those of specimens referred to *K. titania*, except ear (EL), foot (HF) and third metacarpal (3MT) lengths which are not significantly different (Tables 2.3. and 2.5.). *Kerivoula hardwickii* is significantly smaller in some features and larger in others as compared to *K. pellucida*, with the exception the lengths of head and body (HB), third (3MT), fourth (4MT) and fifth (5MT) metacarpals, and second phalanx of third digit (3D2P), which are not significantly different. The measurements of *K. titania* are significantly larger than those of *K. pellucida*, except the second phalanx of third digit (3D2P) and the first phalanx of fourth digit (4D1P). External measurements were available for only one specimen of *K. krauensis* which is smaller than *K. hardwickii*, *K. titania* and *K. pellucida* (Table 2.3.). *K. minuta* is significantly smaller than those of other species in the 'medium-small' group.

Pelage colour does not differ between *K. hardwickii* and *K. titania* but does exhibit individual variation within species (Figure 2.8.). However, pelage colour can be used to discriminate between *K. pellucida*, *K. krauensis* and *K. minuta* and between these species and *K. hardwickii* and *K. titania*. The fur of specimens referred to *K. hardwickii* and *K. titania* is dark grey or grey brown with a uniform dark grey at the base. This contrasts to the orange-brown with pale hair base in all of *K. pellucida*. *K. krauensis* differs in having golden hair tips whereas those of *K. minuta* are a uniform dark brown.

A hundred and fifty-five skulls were measured. The multivariate analysis based on twelve cranial and dental characters shows that the bats in this genus are divided into three groups, including 'large-size', 'medium-size' and 'small-size'

Table 2.4. Comparison between *K. papillosa* and *K. kachinensis*. Levels of significance (*P*-value) based on series of *t*-test. External and cranio-dental measurements (mm) presented as mean ± SD; ns = not significant.

Characters	*K. papillosa*	*K. kachinensis*	*P*-value
External characters			
HB	45.6 ± 2.8	48.0 ± 2.5	ns
FA	40.6 ± 0.9	41.5 ± 0.5	ns
EL	14.4 ± 0.9	14.2 ± 0.8	ns
TL	51.1 ± 2.5	56.0 ± 2.7	<0.01
TIB	20.8 ± 1.2	22.9 ± 0.7	<0.01
HF	9.2 ± 0.5	9.1 ± 0.4	ns
3MT	43.8 ± 0.9	45.0 ± 0.5	<0.01
4MT	42.6 ± 1.0	43.7 ± 0.5	<0.03
5MT	41.1 ± 1.0	41.9 ± 0.6	ns
3D1P	21.0 ± 1.0	21.4 ± 1.0	ns
3D2P	21.1 ± 0.9	20.5 ± 1.0	ns
4D1P	13.2 ± 0.5	12.7 ± 0.7	<0.05
4D2P	9.7 ± 0.4	9.9 ± 0.7	ns
Cranio-dental characters			
GTL	17.3 ± 0.3	17.5 ± 0.2	ns
CCL	15.4 ± 0.3	15.6 ± 0.2	ns
CBL	15.9 ± 0.3	16.1 ± 0.2	ns
MW	8.4 ± 0.2	8.7 ± 0.1	0.03
ZB	10.5 ± 0.3	10.4 ± 0.1	ns
BB	7.9 ± 0.2	8.3 ± 0.1	<0.01
BH	6.9 ± 0.3	5.6 ± 0.1	<0.01
PC	3.4 ± 0.2	3.6 ± 0.1	<0.04
ML	12.6 ± 0.2	12.3 ± 0.2	<0.01
C^1-C^1	4.3 ± 0.1	4.2 ± 0.1	ns
M^3-M^3	6.5 ± 0.2	6.5 ± 0.1	ns
C-M^3	7.0 ± 0.1	6.8 ± 0.1	<0.02
C-M_3	7.5 ± 0.2	7.2 ± 0.1	<0.01

groups (Figure 2.9.; Tables 2.6. and 2.7.).

The bats with 'large-skull' size include two species, *K. papillosa* and *K. kachinensis*. Specimens of *K. papillosa* are similar in skull length to those of *K. kachinensis* except mandible (ML), upper (C-M^3) and lower (C-M_3) toothrows which are significantly longer in *K. papillosa* (Tables 2.4. and 2.7.). They are narrower in some features, such as mastoid width (MW), breadth of braincase (BB) and postorbital constriction (PC). Most characteristically, they have a higher braincase (BH) such as that the skull of *K. papillosa* is high and domed braincase (BH > 6.3

Table 2.5. Comparison between *K. hardwickii*, *K. titania* and *K. pellucida*. Levels of significance (*P*-value) based on series of *t*-test. External and cranio-dental measurements (mm) presented as mean ± SD; ns = not significant.

Characters	*K. hardwickii*	*K. titania*	*P*-value	*K. hardwickii*	*K. pellucida*	*P*-value	*K. titania*	*K. pellucida*	*P*-value
Extrnal characters									
HB	36.9 ± 2.0	39.5 ± 1.0	<0.01	36.9 ± 2.0	37.4 ± 1.7	ns	39.5 ± 1.0	37.4 ± 1.7	<0.02
FA	32.8 ± 1.4	34.8 ± 0.7	<0.01	32.8 ± 1.4	30.9 ± 0.8	<0.01	34.8 ± 0.7	30.9 ± 0.8	<0.01
EL	12.8 ± 0.9	13.1 ± 0.5	ns	12.8 ± 0.9	14.8 ± 0.9	<0.01	13.1 ± 0.5	14.8 ± 0.9	<0.01
TL	41.3 ± 3.0	50.1 ± 2.0	<0.01	41.3 ± 3.0	47.2 ± 2.1	<0.01	50.1 ± 2.0	47.2 ± 2.1	<0.01
TIB	17.4 ± 0.8	19.4 ± 0.3	<0.01	17.4 ± 0.8	17.9 ± 0.8	0.02	19.4 ± 0.3	17.9 ± 0.8	<0.01
HF	7.6 ± 0.4	7.6 ± 0.2	ns	7.6 ± 0.4	7.3 ± 0.3	<0.03	7.6 ± 0.2	7.3 ± 0.3	0.04
3MT	35.0 ± 1.4	35.7 ± 0.5	ns	35.0 ± 1.4	34.3 ± 0.5	ns	35.7 ± 0.5	34.3 ± 0.5	<0.01
4MT	34.0 ± 1.4	35.2 ± 0.4	<0.05	34.0 ± 1.4	33.6 ± 0.5	ns	35.2 ± 0.4	33.6 ± 0.5	<0.01
5MT	32.7 ± 1.4	34.0 ± 0.4	<0.04	32.7 ± 1.4	32.5 ± 0.5	ns	34.0 ± 0.4	32.5 ± 0.5	<0.01
3D1P	16.6 ± 0.8	18.7 ± 0.5	<0.01	16.6 ± 0.8	15.8 ± 0.5	<0.01	18.7 ± 0.5	15.8 ± 0.5	<0.01
3D2P	16.1 ± 1.0	18.0 ± 0.6	<0.01	16.1 ± 1.0	18.0 ± 0.8	ns	18.0 ± 0.6	18.0 ± 0.8	ns
4D1P	10.5 ± 0.6	11.7 ± 0.5	<0.01	10.5 ± 0.6	11.8 ± 0.4	<0.01	11.7 ± 0.5	11.8 ± 0.4	ns
4D2P	7.9 ± 0.6	8.6 ± 0.2	<0.02	7.9 ± 0.6	7.3 ± 0.4	<0.01	8.6 ± 0.2	7.3 ± 0.4	<0.01
Cranio-dental characters									
GTL	14.6 ± 0.5	15.5 ± 0.1	<0.01	14.6 ± 0.5	14.4 ± 0.3	ns	15.5 ± 0.1	14.4 ± 0.3	<0.01
CCL	12.9 ± 0.4	13.7 ± 0.1	<0.01	12.9 ± 0.4	12.7 ± 0.2	ns	13.7 ± 0.1	12.7 ± 0.2	<0.01
CBL	13.4 ± 0.5	14.2 ± 0.1	<0.01	13.4 ± 0.5	13.2 ± 0.3	ns	14.2 ± 0.1	13.2 ± 0.3	<0.01
MW	7.4 ± 0.2	7.8 ± 0.2	<0.01	7.4 ± 0.2	7.1 ± 0.1	<0.01	7.8 ± 0.2	7.1 ± 0.1	<0.01
ZB	8.6 ± 0.3	9.1 ± 0.1	<0.01	8.6 ± 0.3	8.1 ± 0.1	<0.01	9.1 ± 0.1	8.1 ± 0.1	<0.01
BB	7.3 ± 0.2	7.7 ± 0.2	<0.01	7.3 ± 0.2	6.9 ± 0.1	<0.01	7.7 ± 0.2	6.9 ± 0.1	<0.01
BH	5.5 ± 0.4	5.4 ± 0.1	ns	5.5 ± 0.4	5.9 ± 0.1	<0.01	5.4 ± 0.1	5.9 ± 0.1	<0.01
PC	3.3 ± 0.1	3.3 ± 0.1	ns	3.3 ± 0.1	3.0 ± 0.1	<0.01	3.3 ± 0.1	3.0 ± 0.1	<0.01
ML	10.1 ± 0.4	10.7 ± 0.1	<0.01	10.1 ± 0.4	9.9 ± 0.2	ns	10.7 ± 0.1	9.9 ± 0.2	<0.01

Table 2.5. Continued.

Characters	*K. hardwickii*	*K. titania*	*P*-value	*K. hardwickii*	*K. pellucida*	*P*-value	*K. titania*	*K. pellucida*	*P*-value
C^1-C^1	3.5 ± 0.2	3.6 ± 0.1	ns	3.5 ± 0.2	3.1 ± 0.1	<0.01	3.6 ± 0.1	3.1 ± 0.1	<0.01
M^3-M^3	5.4 ± 0.2	5.6 ± 0.1	<0.03	5.4 ± 0.2	5.1 ± 0.1	<0.01	5.6 ± 0.1	5.1 ± 0.1	<0.01
C-M^3	5.5 ± 0.2	6.0 ± 0.1	<0.01	5.5 ± 0.2	5.5 ± 0.1	ns	6.0 ± 0.1	5.5 ± 0.1	<0.01
C-M_3	5.8 ± 0.2	6.3 ± 0.1	<0.01	5.8 ± 0.2	5.8 ± 0.2	ns	6.3 ± 0.1	5.8 ± 0.2	<0.01

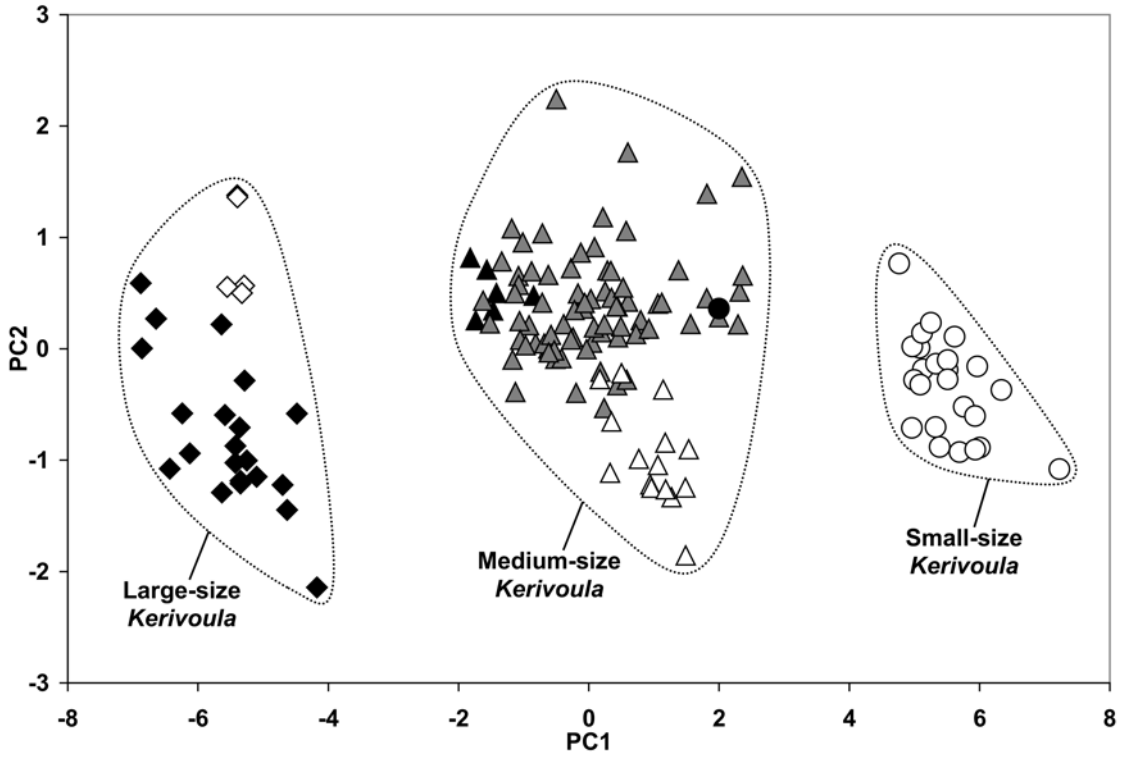

Figure 2.9. PCA of the cranial and dental measurements between first and second principal components based on twelve metric characters. Black diamonds represent *K. papillosa*, open diamonds are *K. kachinensis*, black triangles are *K. titania*, grey triangles are *K. hardwickii*, open triangles are *K. pellucida*, black circle is *K. krauensis* and open circles are *K. minuta*.

mm), whereas it is flattened (BH < 5.7 mm) in *K. kachinensis* (Figure 2.10.). However, interestingly, the skulls of specimens referred to *K. papillosa* vary from markedly domed in some specimens to more flattened in others. Here they are considered to conform to five morphotypes (Figure 2.6.), which also show some difference in greatest skull length.

Bats in the 'medium-skull' size group include *K. hardwickii*, *K. titania, K. pellucida* and *K. krauensis*. The skull measurements of *K. hardwickii* average significantly smaller than those of *K. titania* except braincase height (BH), postorbital constriction (PC) and anterior palatal width (C^1-C^1) which are not significantly different (Tables 2.5. and 2.7.). The skulls of *K. hardwickii* are similar in length to those of *K. pellucida*, but are broader but not as high compared to the latter species. The specimens of *K. titania* are larger than those of *K. pellucida*. Cranio-dental measurements of *K. krauensis* were available for only one specimen which tends to be

Table 2.6. Eigenvectors and eigenvalues of principal component analysis of twelve cranio-dental measurements of 151 specimens of seven species of *Kerivoula*.

Characters	Eigenvector		
	1	2	3
GTL	-0.30	-0.06	-0.04
CCL	-0.30	-0.05	0.01
CBL	-0.30	-0.06	0.02
MW	-0.30	0.13	-0.01
BB	-0.28	0.30	-0.43
BH	-0.26	-0.42	-0.69
PC	-0.24	0.79	-0.09
ML	-0.30	-0.13	0.17
C^1-C^1	-0.29	0.01	0.31
M^3-M^3	-0.29	-0.08	0.42
C-M^3	-0.30	-0.17	0.15
C-M_3	-0.30	-0.13	0.08
Eigenvalue	10.90	4.50	1.94
% of total variation explained	90.86	95.36	97.30

smaller than other species in this group (Table 2.9.).

The skulls of specimens referred to *K. hardwickii* include several forms, but can be divided into 'flat' and 'domed' morphotypes (Figures 2.10., 2.12. and 2.13.), with variable skull lengths. The 'domed-skull' morphotype clearly differs from that flat skull of *K. titania.* However, the 'flat-skull' morphotype of *K. hardwickii* is much more similar to *K. titania*. In the case of *K. pellucida*, the skull is more bulbous and the braincase rises abruptly from rostrum. The skull of *K. krauensis* is similar to those of *K. hardwickii* but is more flattened than those 'domed-skull' and higher than those 'flat-skull' of the latter species.

Bats within the 'small-skull' size group are all referable to *K. minuta*, which is differentiated from all other local *Kerivoula* species by its smaller size (Table 2.7.). The braincase is intermediate between flattened and domed; it is elevated but not abruptly so, only rising slightly above the rostrum (Figure 2.10.).

2.3.2. Acoustics

Acoustic data are available for twenty individuals of six species including *K. papillosa* (6), *K. hardwickii* (6), *K. titania* (2), *K. pellucida* (1), *K. krauensis* (1) and *K. minuta* (5). One-way ANOVA showed that all measurement parameters of the

Table 2.7. Cranio-dental measurements of seven species of *Kerivoula*. GTL – greatest skull length; CCL – condylo-canine length; CBL – condylo-basal length; MW – mastoid width; ZB – zygomatic breadth; BB – breadth of braincase; BH – braincase height; PC – postorbital constriction; ML – mandible length; C^1-C^1 – anterior palatal width; M^3-M^3 – posterior palatal width; C-M^3 – upper toothrow length; C-M_3 – lower toothrow length. Mean, range and standard deviation. Sample sizes differing from those reported under *n* are given in parentheses.

n	Sex	GTL	CCL	CBL	MW	ZB	BB	BH	PC
				Kerivoula papillosa					
21	♂♂♀♀	16.6-17.8	14.9-16.0	15.4-16.5	8.1-9.0	10.0-11.1	7.4-8.2	6.3-7.4	3.0-3.8
		17.3, 0.3	15.4, 0.3	15.9, 0.3	8.4, 0.2	10.5, 0.3	7.9, 0.2	6.9, 0.3	3.4, 0.2
				Kerivoula kachinensis					
5	♂♂♀	17.2-17.7	15.3-15.9	15.9-16.4	8.5-8.7	10.3-10.4	8.2-8.4	5.5-5.7	3.5-3.7
		17.5, 0.2	15.6, 0.2	16.1, 0.2	8.7, 0.1	10.4, 0.1	8.3, 0.1	5.6, 0.1	3.6, 0.1
				Kerivoula hardwickii					
82	♂♂♀♀	13.4-15.6	11.8-13.7	12.1-14.3	6.9-7.9	8.0-9.2	6.7-7.8	4.3-6.2	3.1-3.7
		14.6, 0.5 (81)	12.9, 0.4 (80)	13.4, 0.5 (80)	7.4, 0.2 (81)	8.6, 0.3 (74)	7.3, 0.2	5.5, 0.4 (81)	3.3, 0.1
				Kerivoula titania					
6	♂♂♀♀	15.4-15.6	13.5-13.9	14.1-14.4	7.5-7.9	9.0-9.2	7.5-7.9	5.2-5.6	3.3-3.4
		15.5, 0.1	13.7, 0.1	14.2, 0.1	7.8, 0.2	9.1, 0.1	7.7, 0.2	5.4, 0.1	3.3, 0.1
				Kerivoula pellucida					
16	♂♂♀♀	14.0-14.9	12.3-13.1	12.8-13.7	6.9-7.4	7.9-8.4	6.6-7.0	5.7-6.1	2.8-3.2
		14.4, 0.3 (15)	12.7, 0.2	13.2, 0.3 (15)	7.1, 0.1	8.1, 0.1 (15)	6.9, 0.1	5.9, 0.1	3.0, 0.1
				Kerivoula krauensis					
1	♂	13.3	12.0	12.5	7.0	8.1	7.0	5.5	3.2
				Kerivoula minuta					
24	♂♂♀♀	11.1-12.3	9.9-10.8	10.3-11.4	5.8-6.5	6.7-7.5	5.3-6.1	4.0-4.5	2.6-3.2
		11.8, 0.3	10.5, 0.2	11.0, 0.3	6.3, 0.1	7.2, 0.2 (21)	5.6, 0.2	4.3, 0.1	2.9, 0.1

Table 2.8. Continued.

n	Sex	ML	C^1-C^1	M^3-M^3	C-M^3	C-M_3
			Kerivoula papillosa			
21	♂♂♀♀	12.1-13.0	4.1-4.6	6.2-6.9	6.8-7.2	7.1-7.8
		12.6, 0.2	4.3, 0.1	6.5, 0.2	7.0, 0.1	7.5, 0.2
			Kerivoula kachinensis			
5	♂♂♀	12.1-12.6	4.1-4.3	6.4-6.6	6.7-7.0	7.1-7.3
		12.3, 0.2	4.2, 0.1	6.5, 0.1	6.8, 0.1	7.2, 0.1
			Kerivoula hardwickii			
82	♂♂♀♀	9.1-10.8	3.1-3.9	4.9-5.9	4.9-6.0	5.1-6.3
		10.1, 0.4	3.5, 0.2 (80)	5.4, 0.2	5.5, 0.2	5.8, 0.2
			Kerivoula titania			
6	♂♂♀♀	10.6-10.8	3.5-3.6	5.4-5.7	5.9-6.1	6.1-6.5
		10.7, 0.1	3.6, 0.1	5.6, 0.1	6.0, 0.1	6.3, 0.1
			Kerivoula pellucida			
16	♂♂♀♀	9.6-10.2	2.8-3.3	4.9-5.3	5.2-5.7	5.4-6.1
		9.9, 0.2	3.1, 0.1 (15)	5.1, 0.1	5.5, 0.1	5.8, 0.2
			Kerivoula krauensis			
1	♂	9.4	3.0	5.1	5.0	5.2
			Kerivoula minuta			
24	♂♂♀♀	7.8-8.6	2.6-2.9	4.3-5.0	4.1-4.7	4.2-4.8
		8.2, 0.2	2.8, 0.1	4.7, 0.1	4.5, 0.1	4.6, 0.1

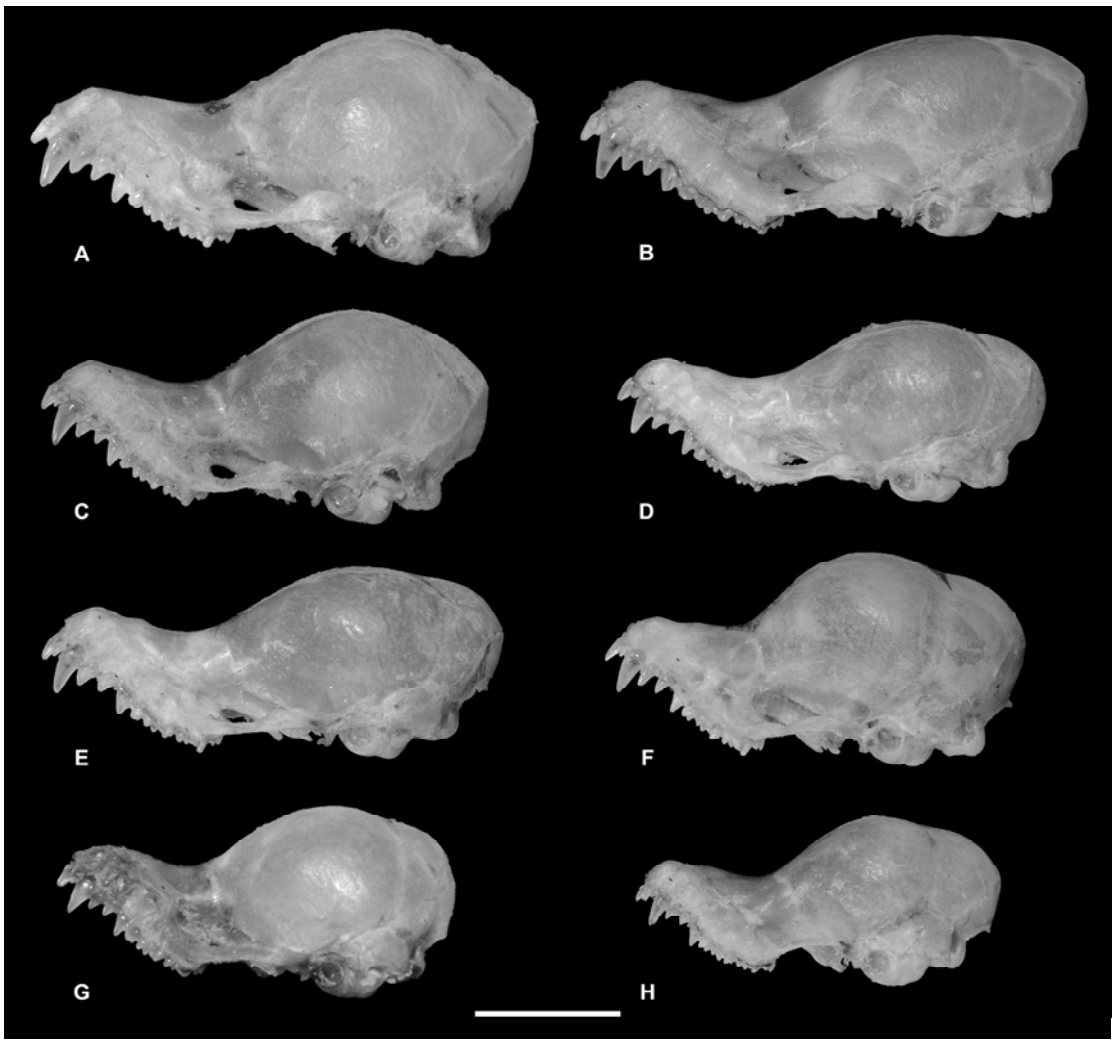

Figure 2.10. The skull of seven species of *Kerivoula*. A – *K. papillosa*, PSUZC-MM2011.2, ♂, Khao Chong Wildlife Education Centre, Khao Bantad Wildlife Sanctuary, Trang Province; B – *K. kachinensis*, PSUZC-MM2007.243, ♂, Phou Suan Sai National Park, Loei Province; C – *K. hardwickii* ('domed-skull' type), PSUZC-MM2012.160, ♂, Phu Pha Phet Ranger Station, Khao Bantad Wildlife Sanctuary, Satun Province; D – *K. hardwickii* ('flat-skulled' type), PSUZC-MM2011.19, ♀, Chiang Dao Wildlife Research Station, Chiang Mai Province; E – *K. titania*, PSUZC-MM2011.18, ♂, Khun Mae Ngai Suard Station, Chiang Dao Wildlife Sanctuary, Chiang Mai Province; F – *K. pellucida*, PSUZC-MM2011.12, ♀, Hala-Bala Wildlife Research Station, Narathiwat Province; G – *K. krauensis*, PSUZC-MM2013.25, ♂, Hala-Bala Wildlife Research Station, Narathiwat Province; and H – *K. minuta*, PSUZC-MM2011.5, ♀, Hala-Bala Wildlife Research Station, Narathiwat Province. Scale: 5 mm.

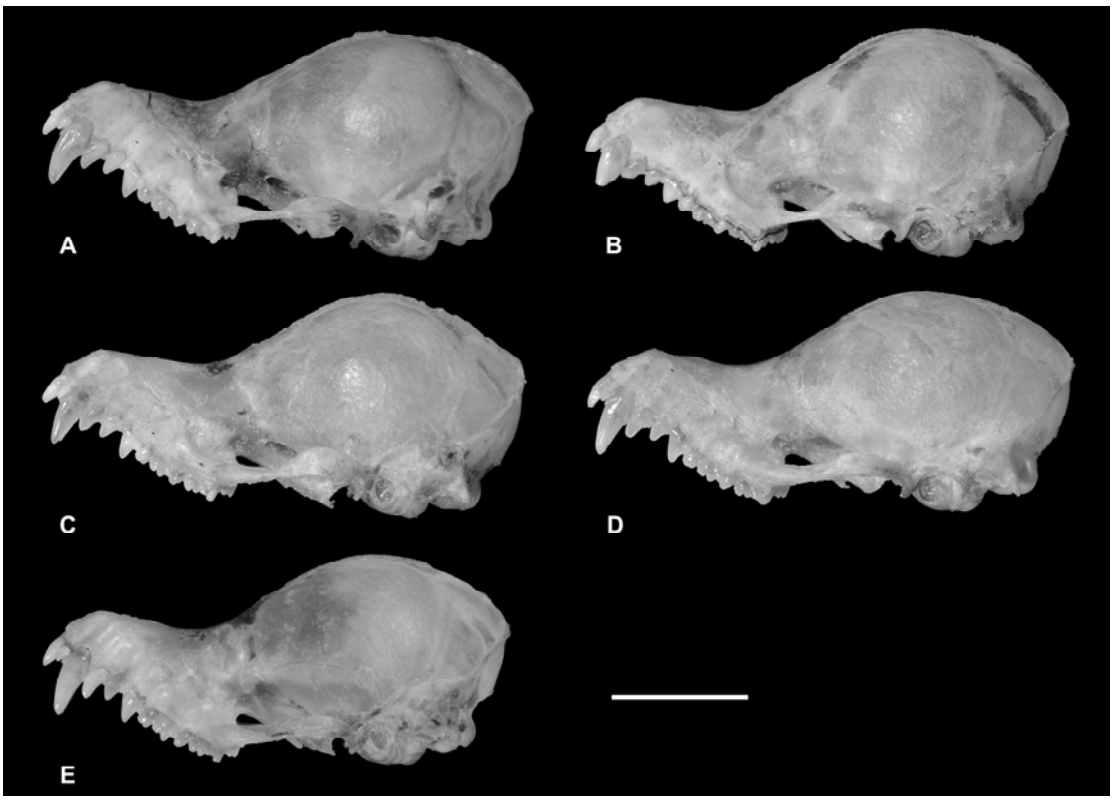

Figure 2.11. Variation in skull morphology in *K. papillosa*. A – HBWRS2010.3, ♂, Khao Nam Khang National Park, Songkhla Province; B – PSUZC-MM2011.10, ♀, Hala-Bala Wildlife Research Station, Narathiwat Province; C – PSUZC-MM2011.2, ♂, Khao Chong Wildlife Education Centre, Khao Bantad Wildlife Sanctuary, Trang Province; D – PSUZC-MM2008.57, ♂, Pha Chi Wildlife Sanctuary, Ratchaburi Province; and E – PSUZC-MM2011.53, ♀, South Klom Luang Chumporn Wildlife Sanctuary, Ranong Province. Scale: 5 mm.

sound, on average, significantly differ from each other (Table 2.8.). The minimum frequency (MinF) of all available species shows a large overlap in range between each other, except for *K. krauensis* and *K. pellucida,* which are slightly lower than others (Figures 2.14. and 2.15.). The maximum frequency (MaxF) is slightly lower in *K. papillosa* (169.0-207.7 kHz) and *K. minuta* (160.1-193.5 kHz) while it is relatively higher in *K. hardwickii* (194.0-245 kHz), *K. titania* (217.0-243.0 kHz), *K. pellucida* (210.0-235.0 kHz) and *K. krauensis* (205.0-241.0 kHz). The maximum energy frequency (MaxEF) and middle frequency (MidF) show a large overlap between species.

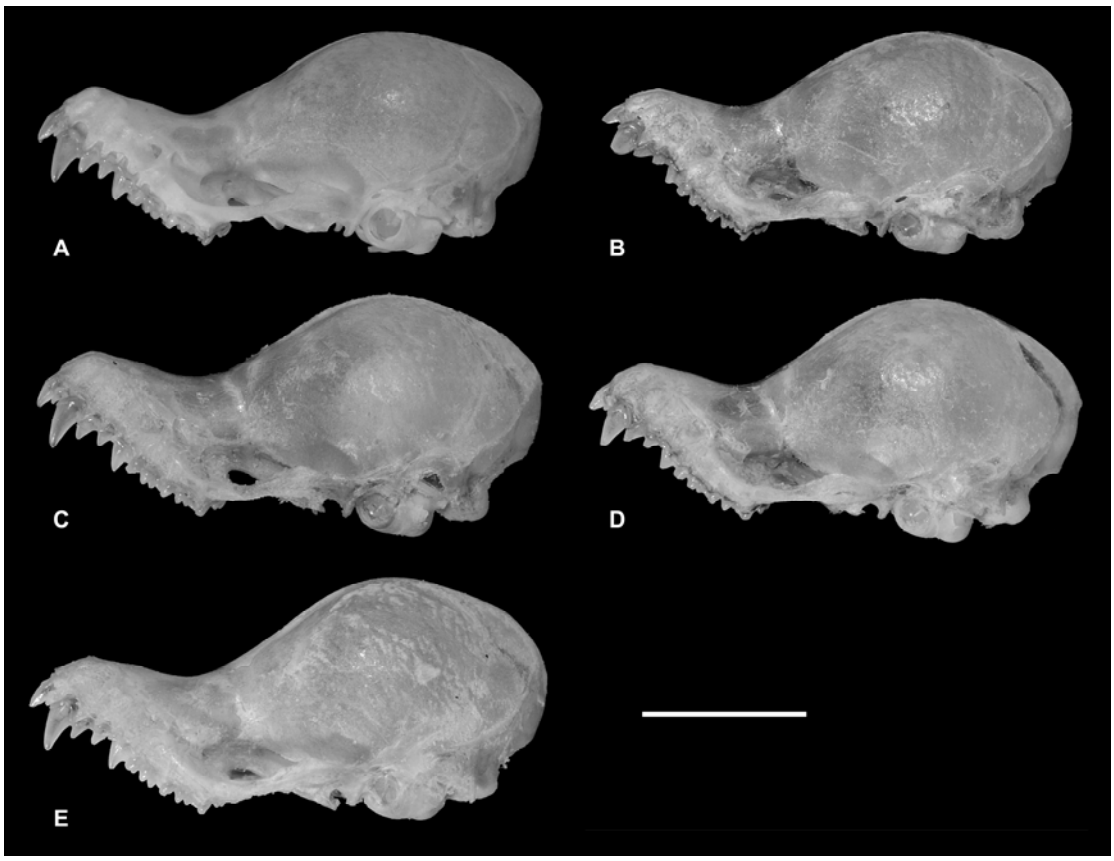

Figure 2.12. Variation in morphology of the 'domed-skull' type of *K. hardwickii*. A – PSUZC-MM2005. 204, ♀, Ton Nga Chang Wildlife Sanctuary, Songkhla Province; B – PSUZC-MM2012.161, ♂, Khao Pra-Bang Kram Wildlife Sanctuary, Krabi Province; C – PSUZC-MM2012.160, ♂, Phu Pha Phet Ranger Station, Khao Bantad Wildlife Sanctuary, Satun Province; D – PSUZC-MM2012.162, ♂, Khao Pra-Bang Kram Wildlife Sanctuary, Krabi Province; and E – PSUZC-MM2008.131, ♀, Tarutao Island, Tarutao National Park, Satun Province. Scale: 5 mm.

2.3.3. Genetics

Twenty-nine sequences are available for Thai specimens, ten for *K. papillosa*,twelve for *K. hardwickii*, two for *K. titania*, one for *K. pellucida* and three for *K. minuta*. Eleven sequences for eight taxa, in the Barcode of Life Database, were included in the analysis, namely: *K. lenis* (2), *K.* cf. *lenis* (1), *K. kachinensis* (1), *K. hardwickii* (2), *K. krauensis* (1), *K. picta* (1), *K. minuta* (2) and *K. intermedia* (1). The phylogenetics shows that the sequences from the study area together with others from region can be divided into fifteen monophyletic clades. The nine clades of Thai material have an average 14.7 % divergence from each other (Figure 2.16.).The sequences referable to *K. papillosa* from the study area are divided into three

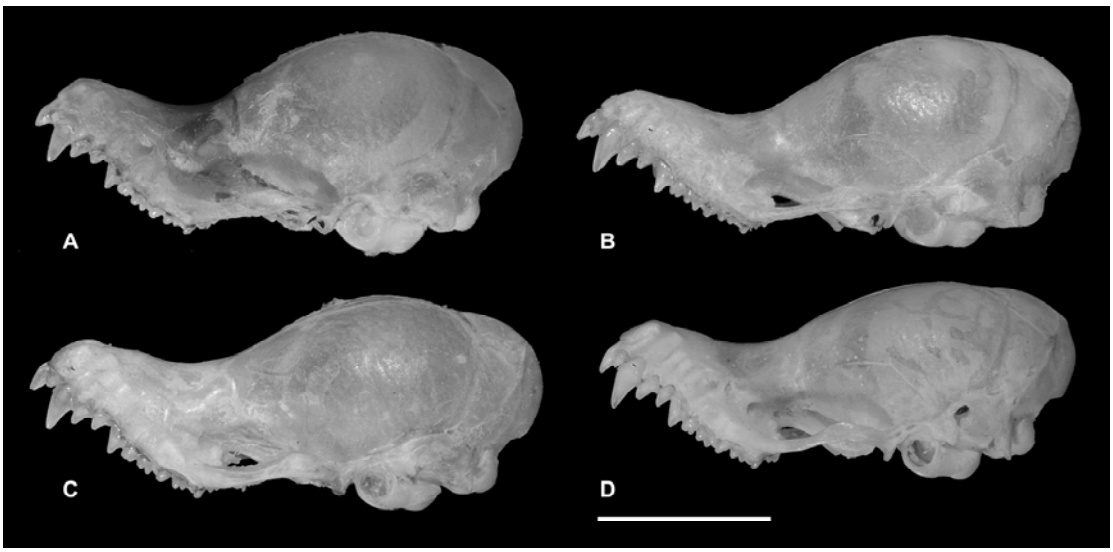

Figure 2.13. Variation in the morphology of the 'flat-skull' type of *K. hardwickii*. A – PSUZC-MM2012.166, ♂, Khao Luang National Park, Nakhon Si Thammarat Province; B – PSUZC-MM2011.17, ♂, Khun Mae Ngai Suard Station, Chiang Dao Wildlife Sanctuary, Chiang Mai Province; C – PSUZC-MM2011.52, ♂, Pa La-U Ranger Station, Kaeng Krachan National Park, Prachuap Khiri Khan Province; D – PSUZC-MM2005.201, ♂, Hauy Nam Chan, Phu Laung Wildlife Sanctuary, Loei Province. Scale: 5 mm.

monophyletic clades, with 8.14 % divergence from each other (Table 2.9.). The clade of *K. papillosa* A has a 5.15 % divergence from the clade of *K. papillosa* B; the clade *K. papillosa* C has a 14.18 % and 12.96 % divergence from clades *K. papillosa* A and *K. papillosa* B, respectively (Table 2.10.).

Similarly, the bats referable to *K. hardwickii* are also divided into three monophyletic clades, with an average of 9.11% divergence between each other (Table 2.9.). *K. hardwickii* A is 13.28 % divergent from *K. hardwickii* B and 16.21 % divergent from *K. hardwickii* C; *K. hardwickii* B is 17.94 % divergent from *K. hardwickii* C (Table 2.11.). Moreover, the clade of *K. hardwickii* A is 8.87% divergent within the clade. However, clades, *K. hardwickii* B and *K. hardwickii* C are < 0.01% and 1.88% divergent within their clades, respectively.

The sequences of *K. titania* are 5.25 % divergent within the clade and the sequences referable to *K. minuta* averaged 1.11% divergent within the species (Table 2.9.). Only one sequence from Thailand is available for *K. pellucida* and no sequence is available for *K. kachinensis* and *K. krauensis*.

Table 3.8. Four parameters of echolocation calls (kHz) of six species of *Kerivoula*. MinF – minimum frequency, MaxF – maximum frequency, MaxEF – maximum energy frequency and MidF – middle frequency. Mean, range and standard deviation. Numbers in parentheses under species names represent the numbers of bats and pulses of echolocation calls, respectively.

Parameter	***K. papillosa*** **(6, 138)**	***K. hardwickii*** **(6, 89)**	***K. titania*** **(2, 15)**	***K. pellucida*** **(1, 14)**	***K. krauensis*** **(1, 67)**	***K. minuta*** **(5, 80)**	***P*-value**
MinF	60.0-89.8	62.0-87.0	74.8-90.0	35.0-49.0	44.0-62.0	54.0-97.2	
	73.5 ± 5.8	75.3 ± 5.3	82.6 ± 4.2	40.6 ± 5.3	51.3, 4.4	81.4 ± 10.3	<0.01
MaxF	169.0-207.7	194.0-245.0	217.0-243.0	210.0-235.0	205.0-241.0	160.1-193.5	
	189.9 ± 8.1	220.4 ± 11.6	227.0 ± 7.4	220.4 ± 8.5	224.8, 9.3	178.4 ± 8.9	<0.01
MaxEF	109.9-161.4	129.5-186.4	137.7-168.7	130.1-161.1	136.8-166.8	108.2-137.6	
	138.8 ± 10.6	151.1 ± 13.3	157.0 ± 7.6	142.4 ± 8.0	146.7, 8.7	126.0 ± 6.3	<0.01
MidF	97.8-147.8	102.0-150.6	113.1-148.4	102.0-138.0	114.3-140.2	89.4-125.1	
	116.0 ± 11.5	129.1 ± 9.9	133.1 ± 10.8	126.0 ± 9.2	134.6, 4.5	113.2 ± 7.5	<0.01

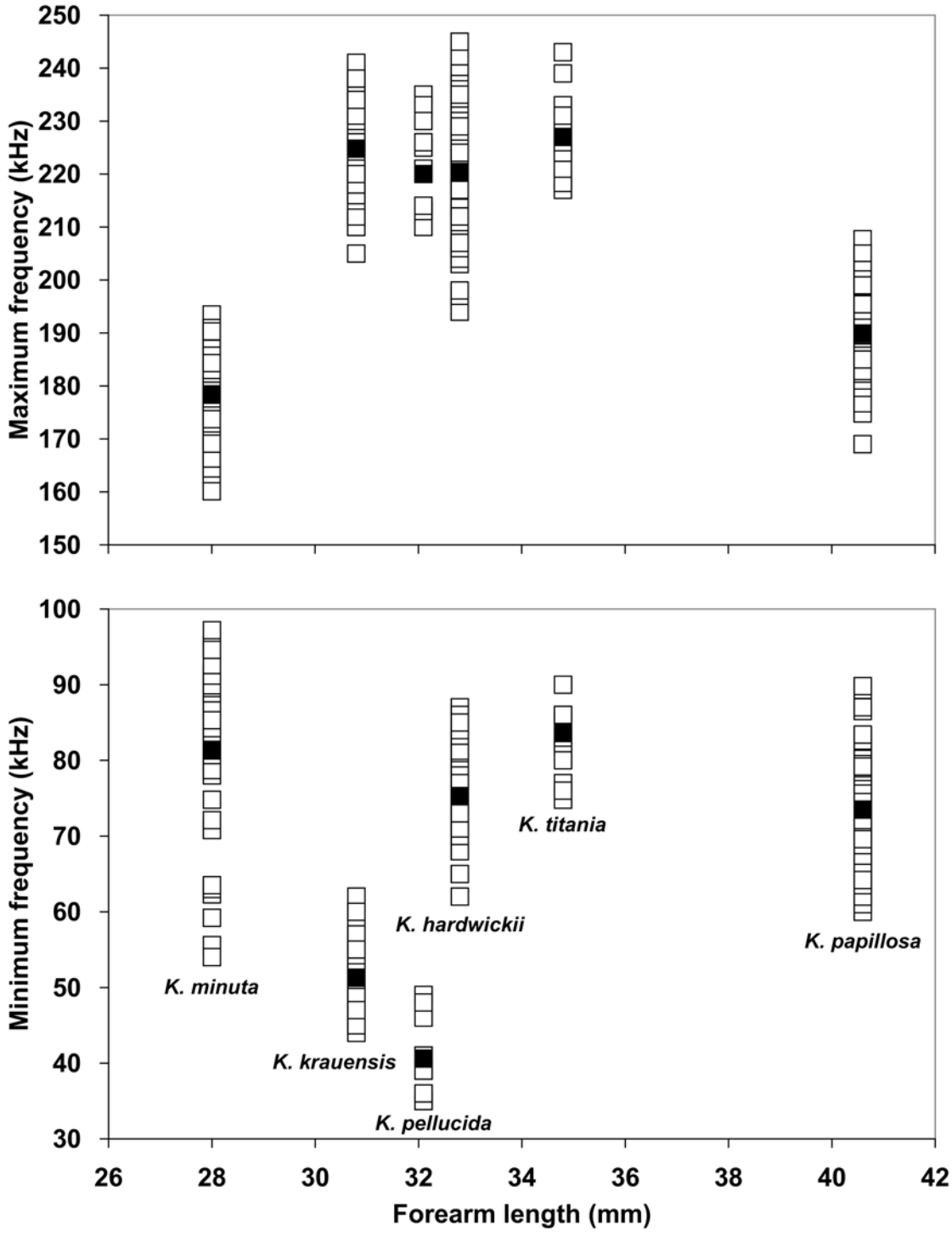

Figure 2.14. Relationship between mean forearm length and maximum frequency and minimum frequency of sixe species of *Kerivoula*. Open symbols represents the frequency of each call parameter and black symbols are the mean values of the call parameters.

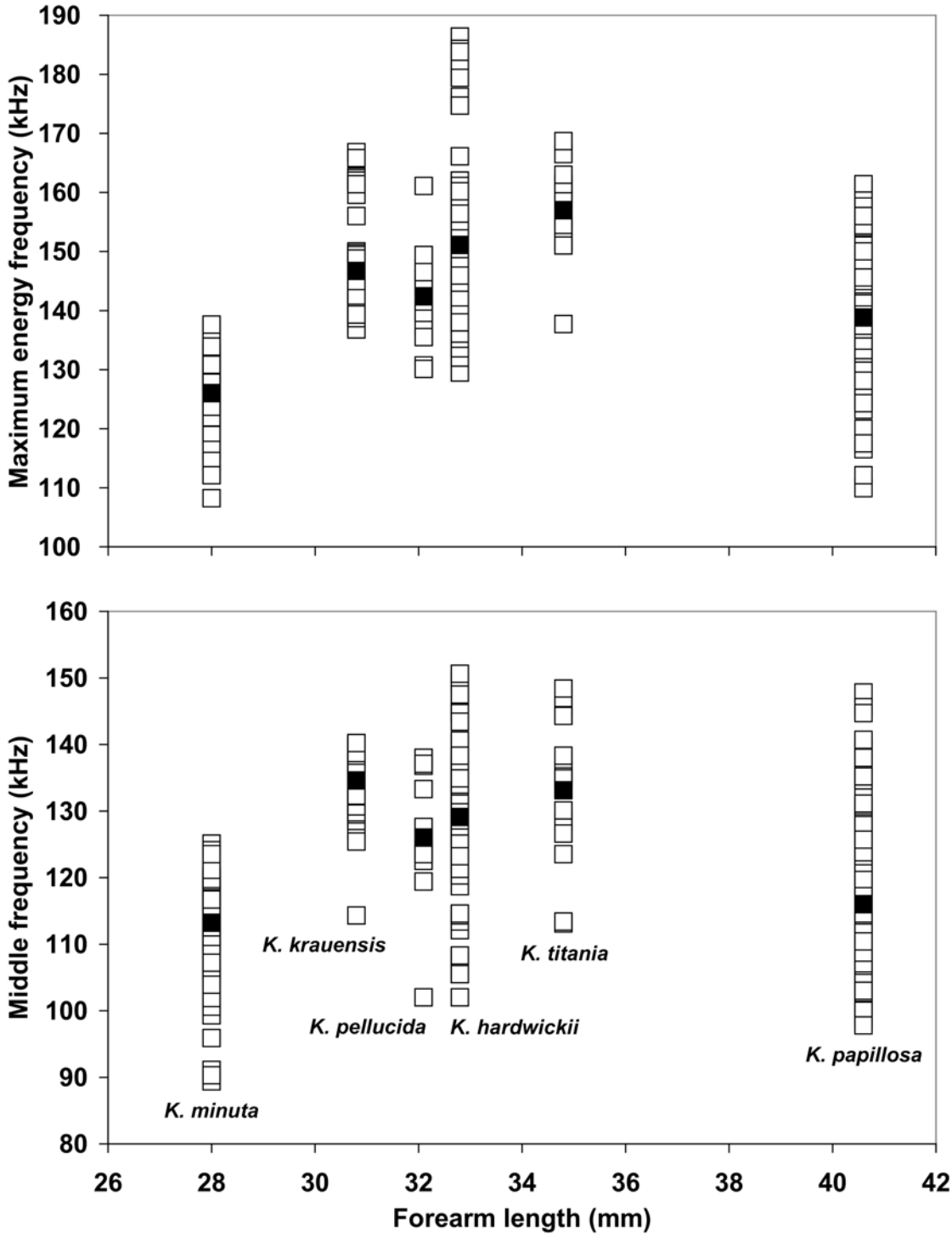

Figure 2.15. Relationship between mean forearm length and maximum energy frequency and middle frequency of six species of *Kerivoula*. Open symbols represents the frequency of each call parameter and black symbols are the mean values of the call parameters.

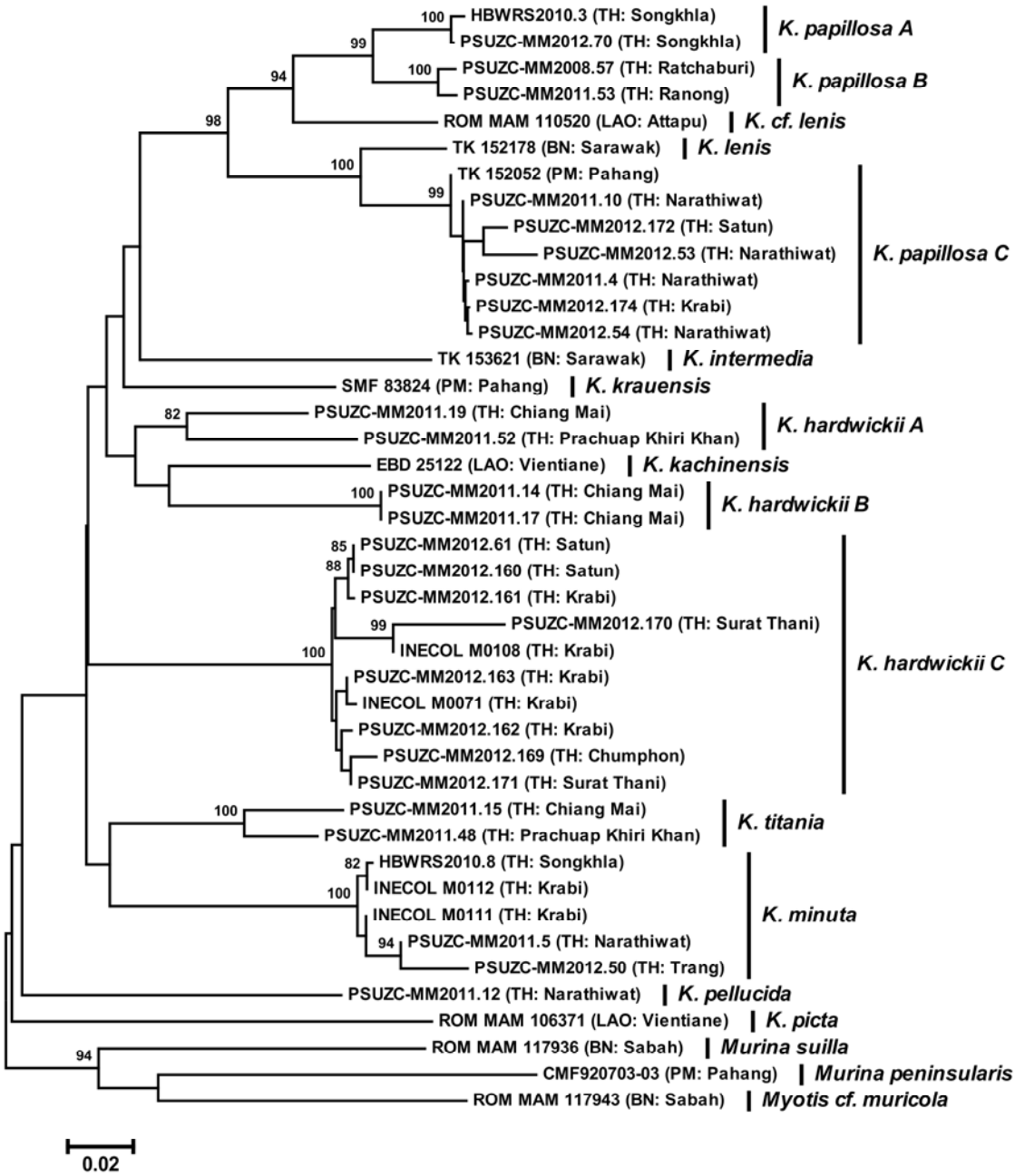

Figure 2.16. Phylogeny based on cytochrome *c* oxidase (COI) of 28 sequences of five species of *Kerivoula* from Thailand together with 11 sequences of seven species from the South-east Asian region in GenBank.

2.4. DISCUSSION

Morphologically, specimens referred to *K. papillosa* suggest that there are five morphotypes (Figure 2.11.) whereas the genetics results indicate only three monophyletic clades (Figure 2.16.). However, the genetic analysis in this study is only

Table 2.9. Average percentage of Kimura 2-parameter distance values within and between taxa of *Kerivoula* based on cytochrome *c* oxidase (COI). The left scores in bold represent the percentage difference between taxa and right scores in bold are the standard deviation percentages. PM = peninsular Malaysia, BN = Borneo, LAO = Lao PDR, NA = not available.

No	Taxon	*n*	1	2	3	4	5	6	7	8	9	10	11
1	*K. papillosa*	10	**8.14/0.86**	0.72	1.38	2.22	1.76	1.96	2.22	2.37	2.53	2.03	2.01
2	*K. lenis* PM & BN	2	6.95	**5.77/1.01**	1.63	2.26	1.76	2.10	2.18	2.29	2.57	2.12	2.12
3	*K. lenis* LAO	1	12.85	14.55	**NA**	2.37	1.76	2.14	2.44	2.45	2.49	2.13	2.09
4	*K. kachinensis*	1	22.47	21.46	21.44	**NA**	1.60	1.86	2.23	2.61	2.73	2.29	2.30
5	*K. hardwickii*	14	20.25	19.39	18.75	15.35	**9.11/0.86**	1.63	1.91	1.98	2.21	1.66	1.91
6	*K. titania*	2	19.11	18.70	18.32	15.27	15.98	**5.25/1.14**	2.48	2.33	2.52	1.80	2.16
7	*K. pellucida*	1	21.58	20.57	22.49	19.67	20.07	20.42	**NA**	2.78	2.45	2.29	2.47
8	*K. krauensis*	1	18.78	16.57	17.48	17.33	14.88	15.51	20.49	**NA**	3.23	2.34	2.24
9	*K. picta*	1	26.60	25.51	23.34	25.15	23.68	22.24	23.15	24.39	**NA**	2.81	2.67
10	*K. minuta*	5	21.84	20.56	20.02	21.17	17.38	15.04	20.32	15.85	25.92	**1.11/0.21**	2.24
11	*K. intermedia*	1	18.98	19.12	17.50	19.54	18.77	16.81	22.56	15.12	23.87	19.26	**NA**

Table 2.10. Average percentage of Kimura 2-parameter distance values within and between taxa of *K. papillosa* and *K. lenis* based on cytochrome *c* oxidase (COI). The left scores in bold represent percentage difference between taxa and right scores in bold are the standard deviation percentage. PM = peninsular Malaysia, BN = Borneo, LAO = Lao PDR, NA = not available.

No	Taxon	*n*	1	2	3	4	5	6
1	*K. papillosa* A	2	**0.46/0.26**	0.93	1.69	1.70	1.71	1.42
2	*K. papillosa* B	2	5.15	**1.08/0.38**	1.60	1.58	1.51	1.33
3	*K. papillosa* C	6	14.18	12.96	**1.24/0.27**	0.25	0.98	1.83
4	*K. lenis* PM	1	13.43	12.01	0.83	**NA**	0.99	1.83
5	*K. lenis* BN	1	13.34	11.07	5.73	5.77	**NA**	1.76
6	*K. lenis* LAO	1	9.87	8.94	15.14	14.60	14.50	**NA**

based on cytochrome *c* oxidase (COI). Further study, including cytochrome *b* (*Cytb*) and/or nuclear genes may help considerably in resolving the taxonomy of this species complex (Anwarali et al., 2010; Nesi et al., 2011; Francis and Eger, 2012; Thong et al., 2012; Lin et al., 2013). Since, currently, there are no additional supporting data, the specimens referred to *K. papillosa* are here separated into three distinct taxa or monophyletic clades.

The clade of *K. papillosa* A is 5.15 % divergent from the *K. papillosa* B monophyletic clade. It also has a larger skull and a higher braincase than *K. papillosa* B. Specimens of *K. papillosa* A are here assigned to the taxon *malayana* Chasen, 1940 on the basis of size. The correct name for this taxon would be *K. malayana*. In comparison to specimens of *malayana* listed in the type description by Chasen (1940), the four specimens from peninsular Thailand have a similar forearm length (40.7-43.4 mm), but slightly smaller skull length (18.2-18.4 mm), mastoid width (8.7 mm), breadth of braincase (8.4 mm) and upper toothrow length (7.6 mm). In terms of genetics, the Thai specimens of this taxon cluster together with those referred to *K. papillosa* S in Anwarali et al. (2010); these latter specimens were collected from Krau Wildlife Research, Pahang in peninsular Malaysia, which is close to the type locality of *malayana* (Ginting Bedai, Selangor-Pahang boundary, Malaysia).

The clade of *K. papillosa* B includes two size-different morphotypes (Figures 2.11D. and 2.11E.), which are 'large-size' (FA: 42.1-42.3 mm and GTL: 17.0-17.1 mm) and 'small-size' (FA: 39.4-40.2 mm and GTL: 16.6-17.0 mm). Genetically, there is only 1.08 % divergence within the clade. On the basis of genetics, they are here

Table 2.11. Average percentage of Kimura 2-pparameter distance values within and between taxa of *K. hardwickii* based on cytochrome *c* oxidase (COI). The left scores in bold represent percentage difference between taxa and right scores in bold are the standard deviation percentage.

No	Taxon	1	2	3
1	*K. hardwickii* A	**8.87/1.26**	1.51	1.76
2	*K. hardwickii* B	13.28	**0.00/0.00**	2.11
3	*K. hardwickii* C	16.21	17.94	**1.88/0.28**

included together as a taxon, until there is more evidence to support a separation. The specimens of *K. papillosa* B from throughout the study area are difficult to assign to any particular named taxon. Only two pre-existing names appear to be available, *K. p. papillosa* Temminck, 1840 from Bantam, north-western Java and *K. lenis* Thomas, 1916 from Calcutta, Bengal, India. Others, such as *K. flora* Thomas, 1914 from Flores, Lesser Sunda Islands have similar forearm length (39.5 mm) but a smaller skull (GTL: 16.0 mm; C-M^3: 6.2 mm).

K. papillosa B has a smaller forearm length than the 43.2 mm and 44.5 mm of the holotype and co-type ('a') of *papillosa* listed by Dobson (1876) and Tate (1941), but has a similar skull length to those from Java (<17.0 mm) examined by Chasen (1940). The Thai specimens of this clade have a similar forearm length (37.2-40.2 mm) and skull length (16.4-17.1 mm) to those of *K. lenis* examined by Vanitharani et al. (2003). However, genetically, it is separated from those *K. lenis* and *K. papillosa* reported by Anwarali et al. (2010) and Francis et al. (2010) in the Barcode of Life Database (Figure 2.16.). Clearly, further research is required, particularly in South-east Asia and India, to help assign *K. papillosa* B with certainty to its correct taxon. It is also possible that it may represent a new and as yet undescribed species. However, without additional studies, especially in the type localities of *papillosa* and *lenis*, it will be difficult to prove that it is not referable to one or other of these two taxa.

Specimens within the clade of *K. papillosa* C show morphological variation (Figures 2.11B. and 2.11C.), but are similar in size. Genetically, material of this clade is clustered together, with a 1.24 % divergence within the clade. Thai specimens have smaller forearm length than those of the holotype and co-type of *K. papillosa* listed by Dobson (1876) and Tate (1941), but a longer skull than that examined by Chasen

(1940). The specimens average larger in external and cranio-dental measurements than those of *K. lenis* (Vanitharani et al., 2003). Genetic comparison shows that a sequence of *K. lenis* from peninsular Malaysia (TK 152052) is clustered together in this clade, while another (TK 152178) from Borneo is separated by a 5.73 % divergence (Anwarali et al., 2010). However, the specimens from peninsular Malaysia and Borneo are smaller than Thai specimens (Anwarali et al., 2010). In addition, the taxonomic status of *K. lenis* from throughout its range is unclear. Genetically, *K.* cf. *lenis* from Lao PDR does not cluster with the *K. lenis* from peninsular Malaysia and Borneo, as there is > 14 % divergence (Anwarali et al., 2010; Francis et al., 2010). Since there is currently a lack of comparative material and genetic information from India, it is difficult to assign the correct name to this taxon.

The specimens referred to *K. kachinensis* Bates et al., 2004 on the basis of their large size and flat skull are clearly different from other species in the genus and are comparable to the description and measurements of *K. kachinensis* in Bates et al. (2004), Thong et al. (2006) and Soisook et al. (2007).

Material referred to *K. hardwickii* includes several forms which can be divided into two main morphotypes, 'domed' and 'flat' skulls (Figure 2.10.). The specimens with 'domed-skull' vary in both size and morphology (Figure 2.12.), but the result of genetic analysis shows that all available sequences of specimens with domed-skulls cluster together in a monophyletic clade (*K. hardwickii* C), with a 1.88 % divergence from each other. However, this study is only based on COI. A further study with *Cytb* and a nuclear gene could be of considerable interest to clarify whether there arecryptic species 'hidden' within this taxon (Anwarali et al., 2010; Nesi et al., 2011; Francis and Eger, 2012; Thong et al., 2012; Lin et al., 2013). Since there is no additional supporting information, specimens with domed-skulls are here assigned to *hardwickii*. Other taxa, such as *fusca* and *engana*, are considered to be synonyms of *hardwickii* on the basis of similar skull morphology with only minor differences in colour of the pelage (Dobson, 1876; Chasen, 1940; Hill, 1965).

The specimens with 'flat-skulls' are similar both in size and morphology (Figure 2.13.), but the genetics differ and cluster into two monophyletic clades (*K. hardwickii* A and *K. hardwickii* B), which may represent two distinct species. Only one pre-existing name appears to be available, *depressa*. Other, such as *crypta* and

malpasi are considered to be synonyms of *depressa*. The taxon *crypta* has a relatively flattened braincase and the taxon *malpasi* differs only in pelage colour, and is geographically isolated (Bates and Harrison, 1997). Bates et al. (2007) suggest that the correct name for the bats with smaller, flat-headed skulls (BH < 5.1 mm) may be *K. depressa*. However, since the genetic analysis shows there are potentially two cryptic species within the taxon, without additional study, especially in the type locality of *depressa* (SE Myanmar), it will very difficult to prove which one is referable to the taxon *depressa* and which is referable to an undescribed species.

The specimens referred to *K. titania* on the basis of their slightly larger, flat-skulls are comparable to the description of *K. titania* by Bates et al. (2007). Genetically, this taxon may comprise two cryptic species, which are similar both in size and morphology. Specimens from Prachaup Khiri Khan Province, Thailand cluster in a different clade from others that originated from northern Thailand and elsewhere in South-east Asia. Further study will be of considerable interest to resolve the relationships within this taxon.

Specimens referred to *K. pellucida* are distinguished from other species in the genus by their orange-brown pelage and high and bulbous skull, the braincase of which rises abruptly from the rostrum; this corresponds to descriptions given in Hill (1965), Corbet and Hill (1992) and Francis (2008). In case of *K. krauensis*, it distinguished from all other species by its dorsal pelage (shiny golden hair tips with dark brown bases) and slightly flattened skull (Francis et al., 2007). Specimens here referred to *K. minuta* are distinguished from *K. intermedia* by their smaller more bulbous skulls; this agrees with the findings of Miller (1898), Hill and Francis (1984) Corbet and Hill (1992) and Francis (2008) and with the genetic results in which the Thai material clusters with those referred to *K. minuta* from peninsular Malaysia and Borneo and is separated from those of *K. intermedia* from peninsular Malaysia and Borneo (Figure 2.16.).

Kingston et al. (1999) suggested that the echolocation calls of six species of *Kerivoula* (*K. papillosa, K. lenis, K. pellucida, K. krauensis, K. intermedia* and *K. minuta*) from Malaysia can be used to assist with their identification. Analysis showed that there is a significant difference in average call characters between species (Table 2.8.). However, there is also a large overlap in the ranges of all measured parameters

(Figures 2.14. and 2.15.). The present study supports the findings of Kingston et al. (1999).

CHAPTER 3

A Review of the *Kerivoula papillosa* Species Complex and *K. lenis* (Chiroptera: Vespertilionidae: Kerivoulinae) from South-east Asia

ABSTRACT

Following extensive field work in Thailand (2010-2013) and the examination of numerous museum specimens, this chapter reviews and examines the taxonomy of the *Kerivoula papillosa* species complex and *K. lenis* from South-east Asia based on morphology and genetics. The results indicate that material of *K. papillosa* and *K. lenis* from throughout South-east Asia are distinguished into four species. Specimens previously referred to *K. papillosa* L[arge] and *K. papillosa* S[mall] are here assigned to *K. papillosa* and *K. malayana* respectively, whereas *K. lenis* from Sundaic Subregion are here referable the new taxon, *Kerivoula* spB. In addition, specimens from Thailand are also referable to other undescribed species, *Kerivoula* spA. Further detail of each taxon are discussed.

3.1. INTRODUCTION

The recent morphology and genetic analysis showed that the taxonomic status of *Kerivoula papillosa* Temminck, 1840 and *K. lenis* Thomas, 1916 is complex and unclear (Vanitharani et al., 2003; Francis et al., 2007; 2010; Anwarali et al., 2010; Hasan and Abdullah, 2011). *K. papillosa* was described from Bantam, west of Java together with specimen from Padang, west of Sumatra (Temminck, 1840). Later, Dobson (1876) and Dobson (1878) listed some external measurements of the type specimen in Leiden Museum and restricted the type locality to Java. Tate (1940) designated the co-type based on specimen ‘a’ from Bantam of Java and specimen ‘b’ from Sumatra in the Leiden Museum and noted that this species should be restricted to specimens from Java. Chasen (1940) described the taxon *malayana* as a subspecies of *K. papillosa* from Selangor-Pahang boundary, peninsular Malaysia on the basis of a larger skull size than the nominate race *papillosa*. However, Tate (1941) suggested

that the taxon *malayana* is essentially similar to the taxon *papillosa*.

Kerivoula lenis was described on the basis of a single specimen from Calcutta, north-east India. It was considered to be closely allied to *K. papillosa* but with a smaller size (Thomas, 1916). Tomes (1858) referred this material to *K. papillosa* and also reported other material from Sri Lanka. However, Blanford (1888-1891) mentioned that the status of material from Sri Lanka was less certain, nor was it absolutely proved that the first specimen was from India, though this was probable.

Tate (1941) suggested the following taxa, *malayana, lenis* and perhaps *jagorii* Peters, 1866, were all near relatives of *K. papillosa*. However, the taxon *jagorii* is currently included in the genus *Phoniscus* Miller, 1905 (sensu Hill, 1965; Corbet and Hill, 1992; Simmons, 2005). Later, Ellerman and Marrison-Scott (1951) included the taxa *malayana* and *lenis* as a subspecies of *K. papillosa*. This was followed by Hill (1965), Corbet and Hill (1992) and Bates and Harrison (1997). They also noted that the taxon *lenis* is smaller in size than *papillosa* and *malayana*.

Payne and Francis (1985) suggested that the bats referred to *K. papillosa* in Borneo might include more than one species. This view was supported by Kingston et al. (1999) who divided material of *K. papillosa* from Malaysia into two arbitrary size classes: *K. papillosa* L[arge] (FA: 40.5-45.0 mm) and *K. papillosa* S[mall] (FA: 37.8-40.0 mm). Later, Vanitharani et al. (2003) reported the second locality for the taxon *lenis* in peninsular India and considered this taxon to be species rank, *K. lenis*. They also referred the *K. papillosa* S in Kingston et al. (1999) to this species.

Later, a genetic analysis of the genus *Kerivoula* showed that the bats referred to *K. lenis* and *K. papillosa* included more than one species (Francis et al., 2007; 2010). Anwarali et al. (2010) referred material of the large Malaysian *Kerivoula* to three taxa, including *K. lenis* (FA: 38.7-38.9 mm and GTL: 15.7-16.2 mm), *K. papillosa* S[mall] (FA: 39.5-43.0 mm and GTL: 16.9-17.3 mm) and *K. papillosa* L[arge] (FA: 45.0-46.5 mm and GTL: 17.7-18.0 mm). They suggested that *K. papillosa* S should be referable to the nominate race *K. p. papillosa* and *K. papillosa* L is provisionally referable to *K. p. malayana* on the basis of skull size. However, they mentioned the taxonomic status of *K. papillosa* is unclear and it may be referable to an undescribed species. The authors also noted that the genetics of *K. lenis* from Peninsular Malaysia and Borneo is different from what is called *K. lenis* from Laos. Moreover, the

karyotypes of *K. papillosa* and *K. lenis* are more complex. Similarly, Hasan and Abdullah (2011) classified the large Malaysian *Kerivoula* into three taxa, including *K. papillosa* L[arge] (FA: 44.7-47.3 mm and GTL: 18.4-18.8 mm), *K. papillosa* S[mall] (FA: 42.2-43.7 mm and GTL: 17.8-18.3 mm) and *K. lenis* (FA: 39.9-40.9 mm and GTL: 16.8 mm). In contrast to Anwarali et al. (2010), the authors referred material of *K. papillosa* L to an undescribed species and those of *K. papillosa* S to the taxa *K. p. malayana* on the basis of size.

In Thailand, McBee et al. (1986) first reported *K. papillosa* from Surat Thani Province, peninsular Thailand and then Robinson et al. (1995) reported an additional location from Thung Yai Naresuan Wildlife Sanctuary, Western Thailand. Subsequently, Vanitharani et al. (2003) suggested that it was unclear if the material from peninsular Thailand was true *K. papillosa* or possible *K. lenis*. On the basis of skull size and morphology, the specimen included in McBee et al. (1986) is more closely related to *K. lenis*, but the forearm length (43.4 mm) is longer than those of *K. lenis* (Anwarali et al., 2010). However, the status of material from western Thailand is unclear, it would appear to either *K. papillosa* or *K. lenis*.

In the current study, the taxonomic status of *K. papillosa* is examined in detail, using a combination of morphometric characters and genetic data. The study is based on recently extensive field work in Thailand (2010-2013), specimens in thee museum and a thorough review of the literature.

3.2. MATERIAL AND METHODS

3.2.1. Measurements

In this study, thirty-one voucher specimens were measured. They are held in the Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University, Thailand (PSUZC); Halabala Wildlife Research Station, Thailand (HBWRS); Harrison Institute, UK (HZM); Museum Zoologicum Bogoriense, Indonesia (MZB); Museum of Texas Tech University, USA (TTU); and the Natural History Museum, London (formerly the British Museum (Natural History)), UK (BMNH).

Measurements (in mm) were taken with a digital caliper, except body mass (in gram) which taken with Pesola Spring balance, and where relevant followed Bates and Harrison (1997), Bates et al. (2004) and Zubaid and Davison (1987). They included: HB: head and body length – from the tip of the snout to the anus, ventrally; FA: forearm length – from the extremity of the elbow to the extremity of the carpus with the wings folded; EL: ear length – from the lower border of the external auditory meatus to the tip of the pinna; TL: tail length – from the tip of the tail to its base adjacent to the anus; TIB: tibia length – from the knee joint to the extremity of the heel behind the os calcis; HF: foot length – from the extremity of the heel behind the os calcis to the extremity of the longest digit, not including the hairs or claws; 3MT, 4MT, 5MT: third, fourth, fifth metacarpal lengths respectively – from the extremity of the carpus to the distal extremity of the third, fourth and fifth metacarpals respectively; 3D1P, 3D2P, 4D1P, 4D2P: first and second phalanges of the third and fourth digit respectively – from the proximal to the distal extremity of the phalanges; 3D1Px100/3MT – % length of the first phalanx of the third digit relative to its metacarpal; BL: baculum length – from the extremity of the base to extremity of the tip; GTL: greatest length of the skull – the greatest antero-posterior diameter of the skull, from the most projecting point at each extremity regardless of what structure forms these points; CCL: condylo-canine length – from the exoccipital condyle to the alveolus of the canine; CBL: condylo-basal length – from the exoccipital condyle to the alveolus of the anterior incisor; MW: mastoid width – the greatest distance across the mastoid region; ZB: zygomatic breadth – the greatest width of the skull across the zygomata; BB: breadth of braincase – greatest width of the braincase at the posterior roots of the zygomatic arches; BH: braincase height – taken from the basisphenoid to the highest part of the skull; BHx100/BB – % high of the braincase relative to its breadth; PC: postorbital constriction – the narrowest width across the constriction posterior to the orbits; ML: mandible length – from the most posterior part of the condyle to the most anterior part of the mandible, including the lower incisors; C^1-C^1: anterior palatal width – taken across the outer borders of the upper canine; M^3-M^3: posterior palatal width – taken across the outer borders of the third molar; C-M^3: upper toothrow length – from the front of the upper canine to the back of the crown of

the third upper molar; C-M_3: lower toothrow length – from the front of the lower canine to the back of the crown of the third lower molar.

3.2.2. Morphometric analysis

To determine whether there were significant differences between taxa, a series of *t*-test were run at a confidence limit of 95%. Principal Components Analysis (PCA) performed on the correlation matrix was used for multivariate comparisons.

3.2.3. Genetic analysis

In this study, the deoxyribonucleic acid (DNA) was extracted from wing membrane. An 657 base pairs (bp) fragment of the mitochondrial nuclear, cytochrome *c* oxidase (COI), was amplified and sequenced. The DNA extraction, amplification and sequencing followed the standard protocol published in Anwarali et al. (2010) and Francis et al. (2010).

Ten sequences of material referred to *K. papillosa* from the study area were available for the study. Twenty-nine sequences of material referred to *K. papillosa*, *K. lenis*, *K.* cf. *papillosa* and *K.* cf. *lenis* from throughout the region (Lao PDR, Vietnam, Malaysia and Borneo) and three sequences referred to *K. kachinensis* from Lao PDR and Vietnam, all of which are deposited in the Barcode of Life Databank (www.boldsystems.org), were used to compare with material from Thailand. The sequences of specimens from Thailand were also obtained with sequences of all other species of *Kerivoula*, as well as *Phoniscus*, from throughout South-east Asia in the Barcode of Life Databank (www.boldsystem.org), as well as GenBamk.

A phylogenetic reconstruction was undertaken using the software MEGA version 5.1 (Kimura, 1980; Tamura et al., 2011). The Kimura 2-parameter (K2) substitution model was used as it was the best fit model (Nei and Kumar, 2000; Tamura et al., 2011). A phylogenetic reconstruction was run using the bootstrap method at 1,000 replications. The COI genetic distance matrix was generated using the Kimura 2-parameter model with gamma-distributed rates in the MEGA version 5.1 and run with bootstrap method at 1,000 replications.

3.3. RESULTS

Following the results above, morphology shows that there are five morphotypes included in the specimens of *K. papillosa* (Figure 2.11.). However, the genetic analysis shows that there are only three distinct species included in the specimens of *K. papillosa* from Thailand (Figure 2.16.). Based on both morphology and genetics, the specimens of *K. papillosa* from Thailand are considered to three distinct species and are initially classified as *K. papillosa* A, *K. papillosa* B and *K. papillosa* C.

3.3.1. Morphometrics

External measurements were available for thirty-one specimens from the study area. A multivariate analysis based on nine external characters shows that most of specimens of *K. papillosa* from Thailand are overlapped grouping between each other and some overlap with *K. lenis* from peninsular Malaysia, Sumatra and Borneo, but discrete from *K. papillosa* L[arge] and *K. lenis* from from India (Figure 3.1.; Table 3.1.). In addition, the specimens of *K. papillosa* B are divided into two groups, including 'large-size' group and 'small-size' group.

The specimens of *K. papillosa* A from Thailand and peninsular Malaysia average smaller than specimens of *K. papillosa* L[arge] from Sumatra and Borneo, except head and body (BH), ear (EL), tail (TL), fifth metacarpal (5MT), first phalanx of third and fourth digits (3D1P and 4D1P) which are not significant differences (Tables 3.2. and Table 3.3.). However, most of external characters of specimens of *K. papillosa* A are not significant differences from those of 'small-size' *K. papillosa* B and *K. papillosa* C, except head and body (HB), tibia (TIB) and first phalanx of third digit (3D1P) which are larger than those of latter two species, whereas the specimens of *K. papillosa* A average larger than those of *K. lenis* from peninsular Malaysia, Sumatra and Borneo, except ear (EL), tail (TL), foot (HF), metacarpals (MTs) and second phalanx of four digit (4D1P) lengths which are not significant difference. Specimens of *K. papillosa* A appear to be similar external size to 'large-size' *K. papillosa* B ($n = 2$), but are larger than *K. lenis* from India ($n = 1$) but the sample size is too small to make any meaningful conclusion.

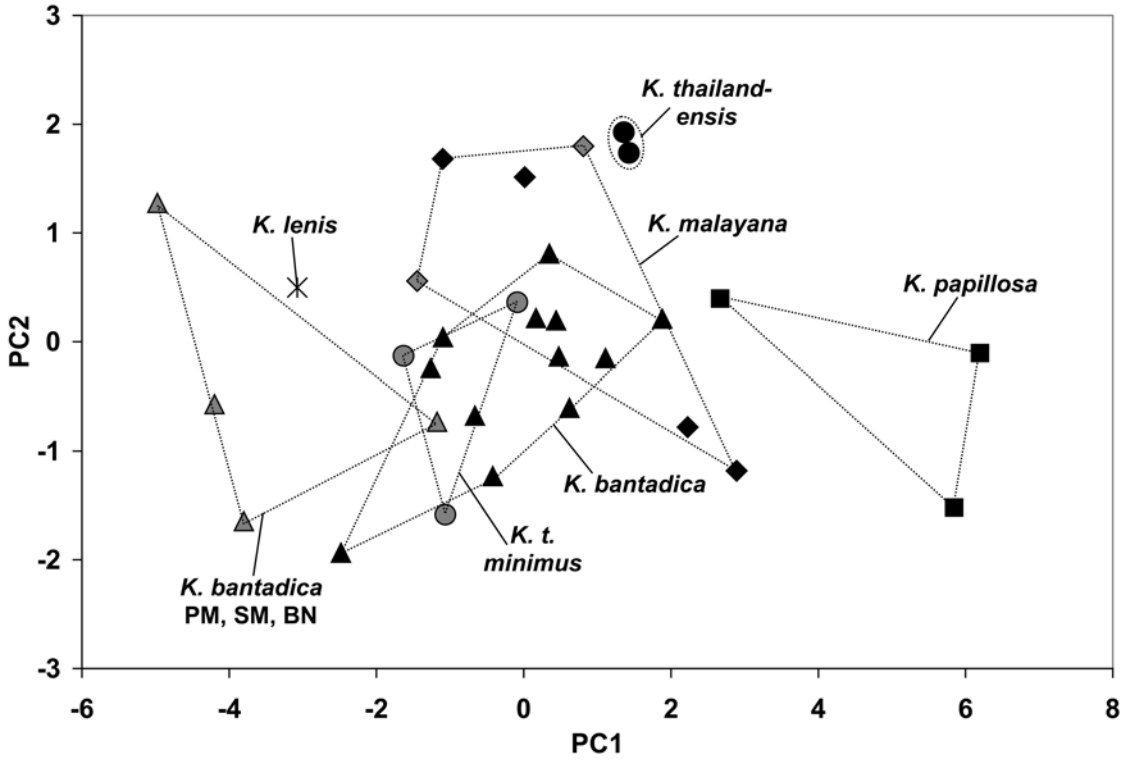

Figure 3.1. PAC between first and second principal components based on nine external metric characters for specimens of *Kerivoula*. Black squares represent *K. papillosa*, black diamonds are *K. malayana* from Thailand; grey diamonds are *K. malayana* from peninsular Malaysia; black circles are *Kerivoula* spA; grey circles are *Kerivoula* subspA; black triangles are *Kerivoula* spB from Thailand; grey triangles are *Kerivoula* spB from peninsular Malaysia, Sumatra and Borneo; and black star is *K. lenis*.

Specimens of *K. papillosa* B 'large-size' are larger than those of *K. papillosa* B 'small-size' and *K. lenis* from India, peninsular Malaysia, Sumatra and Borneo, whereas it is similar to those of *K. papillosa* C (Table 3.2.), but the sample size is too small to make any meaningful conclusion. Specimens of *K. papillosa* B 'small-size' are smaller than those of *K. papillosa* L[arge], except head and body (HB), ear (EL), tail (TL), third metacarpal (3MT) and second phalanx of four digit (4D2P) which are not significant difference, whereas it is similar to those of *K. papillosa* C and *K. lenis* from peninsular Malaysia, Sumatra and Borneo, except first phalanx of four digit (4D1P) which is smaller than that of *K. papillosa* C (Table 3.4.). Specimens of *K. papillosa* B 'small-size' are larger than *K. lenis* from India in some characters.

Table 3.1. Eigenvectors and eigenvalues of PCA of nine external measurements of 31 specimens of five species and a subspecies of *Kerivoula*. See also Figure 3.4.

Character	Eigenvector		
	1	**2**	**3**
FA	0.38	0.02	-0.11
TIB	0.30	0.42	-0.31
3MT	0.37	-0.23	0.06
4MT	0.36	-0.39	0.14
5MT	0.37	-0.32	0.12
3D1P	0.37	0.09	-0.27
3D2P	0.28	0.45	-0.32
4D1P	0.35	-0.11	0.23
4D2P	0.16	0.55	0.79
Eigenvalue	6.05	1.13	0.81
% total of variation Explained	67.26	79.78	88.78

Specimens of *K. papillosa* C average smaller than those of *K. papillosa* L[arge], except ear (EL), tail (TL) and second phalanx of four digit (4D2P) which are not significant difference (Table 3.5.). However, specimens of *K. papillosa* C are larger than those of *K. lenis* from peninsular Malaysia, Sumatra and Borneo, except ear (EL), foot (HF), first and second phalanges of third digit (3D1P and 3D2P) which are not significant difference. In addition, specimens of *K. papillosa* C are larger than specimen of *K. lenis* from India, but the sample size of latter species are small.

Pelage colour is not difference between species, but does exhibit individual variation. Most specimens have dark grey on the dorsal surface and paler on ventral surface, but some individuals have pale brown on the dorsal surface with slightly paler on ventral surface (Figure 3.2.).

Baculum is similar in size between specimens from Thailand (Table 3.2.), but they are difference in morphology. The baculum of *K. papillosa* A is triangular shape, with slightly long and large bifid base (Figure 3.3.), whereas baculum of *K. papillosa* B 'large-size' slightly large parallel tip, with slightly large and short bifid base. Baculum of *K. papillosa* C includes two morphotypes, one has triangular shape with short and narrow bifid base, whereas it is large and short bifid base with narrow parallel tip. There is no any baculum of *K. papillosa* B 'small-size' available in the present study.

Table 3.2. External measurements (in mm) and body mass (in g) of five species and a subspecies of *Kerivoula*. HB – head and body; FA – forearm; EL – ear; TL – tail; TIB – tibia; HF – foot; 3MT, 4MT, 5MT – third, fourth, fifth metacarpal, respectively; 3D1P, 3D2P, 4D1P, 4D2P – first and second phalanges of third and fourth digit, respectively; 3D1Px100/3MT – % length of first phalanx of third digit relative to the third metacarpal; BL – baculum; BM – body mass. mean, range and standard deviation, sample sizes differing from those reported under *n* are given in parentheses. [a]data from Dobson (1876), [b]from Tate (1941), [c]from Chasen (1940), and [d]data from Thomas (1916).

n	sex	HB	FA	EL	TL	TIB	HF	3MT	4MT	5MT
					Kerivoula papillosa Holotype					
1	?	55.9[a]	43.2[a]	16.5[a]	55.9[a]	22.9[a]	–	–	–	–
					Kerivoula papillosa Co-type ('a')					
1	♀	–	44.5[b]	–	–	–	–	–	–	–
					Kerivoula papillosa (*K. papillosa* L[arge])					
3	♂♂♀	45.8-51.7	42.6-44.4	12.3-14.6	49.1-51.6	23.1-24.0	10.1-10.7	44.4-48.3	43.9-46.6	42.2-45.1
		48.9, 3.0	43.5, 0.9	13.6, 1.2	50.6, 1.3	23.4, 0.5	10.5, 0.3	46.8, 2.1	45.7, 1.5	43.9, 1.5
					Kerivoula malayana Holotype					
1	♀	52.0[c]	43.4[c]	–	52.0[c]	–	–	–	–	–
					Kerivoula malayana (*K. papillosa* A)					
6	♂♂♀♀	46.1-52.2	39.5-42.0	13.3-15.3	49.2-53.6	21.1-22.0	9.3-9.9	42.3-46.4	40.9-45.5	39.4-43.5
		49.5, 2.6 (4)	40.9, 1.0	14.3, 1.0 (4)	50.6, 2.1 (4)	21.6, 0.4	9.5, 0.3 (4)	43.9, 1.4	42.4, 1.9	41.2, 1.7
					Kerivoula spA (*K. papillosa* B 'large-size)					
2	♂♂	44.4, 43.6	42.3, 42.1	14.1, 13.1	47.7, 52.6	23.2, 22.8	9.5, 9.4	44.2, 44.1	41.7, 41.7	39.8, 40.9
					Kerivoula spA subspA (*K. papillosa* B 'small-size)					
3	♀♀	40.3-45.3	39.4-40.2	14.0-14.6	47.9-55.1	18.8-21.4	9.0-9.9	42.9-44.2	42.2-43.0	40.4-40.9
		43.5, 2.8	39.8, 0.4	14.3, 0.3	50.9, 3.8	19.9, 1.3	9.3, 0.5	43.7, 0.7	42.5, 0.4	40.7, 0.3
					Kerivoula spB (*K. papillosa* C)					
12	♂♂♀♀	40.5-47.3	39.1-42.0	13.5-17.4	48.0-56.4	19.4-22.4	7.9-9.6	42.8-44.8	41.8-43.6	40.4-42.4
		45.0, 2.0	40.4, 0.7	14.6, 1.0	51.5, 2.5	20.4, 0.7	9.0, 0.5	43.7, 0.8	42.6, 0.5	41.2, 0.7

Table 3.2. Continued.

n	**sex**	**HB**	**FA**	**EL**	**TL**	**TIB**	**HF**	**3MT**	**4MT**	**5MT**
					Kerivoula spB (*K. lenis* Malaysia, Sumatra, Borneo)					
4	♂♂♀♀	40.1, 42.9	38.0-39.7	14.7, 15.1	46.0, 48.2	18.2-20.1	9.3, 9.6	40.0-44.1	37.8-42.5	36.8-40.8
		(2)	39.0, 0.7	(2)	(2)	19.1, 0.8	(2)	42.2, 1.7	40.3, 1.9	38.9, 1.6
					Kerivoula lenis Holotype					
1	?	–	41.0[d]	–	–	–	–	42.5[d]	–	–
					Kerivoula lenis India					
1	♂	39.1	38.8	13.9	49.5	21.0	8.8	42.2	40.6	39.4

Table 3.2. Continued.

n	sex	3D1P	3D2P	4D1P	4D2P	3D1Px100/3MT	BL	W
				Kerivoula papillosa Holotype				
1	?	–	–	–	–	–	–	–
				Kerivoula papillosa Co-type ('a')				
1	♀	–	–	–	–	–	–	–
				Kerivoula papillosa (*K. Papillosa* L[arge])				
3	♂♂♀	22.7-24.0	22.1-22.8	13.5-14.7	9.2-10.2	48.6-51.0	–	–
		23.4, 0.7	22.4, 0.4	14.1, 0.6	9.7, 0.5	50.0, 1.2		
				Kerivoula malayana Holotype				
1	♀	–	–	–	–	–	–	–
				Kerivoula malayana (*K. papillosa* A)				
6	♂♂♀♀	20.0-22.8	21.2-22.7	12.0-13.8	9.1-10.3	47.4-51.5	0.7	8.0-8.2
		21.4, 1.0	22.0, 0.6	12.9, 0.7	9.7, 0.4	48.8, 1.6	(1)	8.1, 0.1 (2)
				Kerivoula spA (*K. papillosa* B 'large-size')				
2	♂♂	22.4, 21.7	22.2, 21.7	13.2, 13.1	9.8, 10.4	50.6, 49.1	0.7	7.0, 8.0
				Kerivoula spA subspA (*K. papillosa* B 'small-size'				
3	♀♀	18.9-21.1	19.7-21.5	12.8-13.0	9.5-10.0	44.0-47.9	–	6.5
		20.3, 1.2	20.5, 0.9	12.9, 0.1	9.7, 0.3	46.3, 0.3		(1)
				Kerivoula spB (*K. papillosa* C)				
12	♂♂♀♀	19.2-21.6	18.6-22.1	12.5-13.9	9.1-10.2	45.0-49.2	0.7, 0.8	7.0-9.0
		20.8, 0.7	21.0, 0.8	13.3, 0.5	9.7, 0.4	47.5, 1.3	(2)	8.0, 0.6 (8)
				Kerivoula spB (*K. lenis* Malaysia, Sumatra, Borneo)				
4	♂♂♀♀	18.4-21.1	18.8-21.3	11.6-11.9	8.6-9.5	43.7-49.9	–	–
		19.8, 1.1	20.0, 1.1	11.8, 0.1	9.2, 0.4	46.9, 2.6		
				Kerivoula lenis Holotype				
1	?	20.0[d]	–	–	–	–	–	–
				Kerivoula lenis India				
1	♂	19.0	18.9	12.0	10.0	45.0	–	–

Table 3.3. External and cranio-dental measurements (in mm) of *K. malayana*, *K. papillosa*, *Kerivoula* spA subspA and *Kerivoula* spB presented as mean ± SD. *P* = significance value, based on *t*-test; ns = not significant.

Characters	*K. malaya-na* (*K. pa-piloca* A)	*K. papillo-sa* (*K. pa-pillosa* L)	*P*-value	*K. malaya-na* (*K. pa-piloca* A)	*Kerivoula* spA sub-spA (*K. papillosa* B 'small-size'	*P*-value
External characters						
HB	49.5 ± 2.6	48.9 ± 3.0	ns	49.5 ± 2.6	43.5 ± 2.8	0.031
FA	40.9 ± 1.0	43.5 ± 0.9	0.006	40.9 ± 1.0	39.8 ± 0.4	ns
EL	14.3 ± 1.0	13.6 ± 1.2	ns	14.3 ± 1.0	14.3 ± 0.3	ns
TL	50.6 ± 2.1	50.6 ± 1.3	ns	50.6 ± 2.1	50.9 ± 3.8	ns
TIB	21.6 ± 0.4	23.4 ± 0.5	<0.001	21.6 ± 0.4	19.9 ± 1.3	0.019
HF	9.5 ± 0.3	10.5 ± 0.3	0.008	9.5 ± 0.3	9.3 ± 0.5	ns
3MT	43.9 ± 1.4	46.8 ± 2.1	0.041	43.9 ± 1.4	43.7 ± 0.7	ns
4MT	42.4 ± 1.9	45.7 ± 1.5	0.037	42.4 ± 1.9	42.5 ± 0.4	ns
5MT	41.2 ± 1.7	43.9 ± 1.5	ns	41.2 ± 1.7	40.7 ± 0.3	ns
3D1P	21.4 ± 1.0	23.4 ± 0.7	0.017	21.4 ± 1.0	20.3 ± 1.2	ns
3D2P	22.0 ± 0.6	22.4 ± 0.4	ns	22.0 ± 0.6	20.5 ± 0.9	0.021
4D1P	12.9 ± 0.7	14.1 ± 0.6	0.043	12.9 ± 0.7	12.9 ± 0.1	ns
4D2P	9.7 ± 0.4	9.7 ± 0.5	ns	9.7 ± 0.4	9.7 ± 0.3	ns
Cranio-dental characters						
GTL	17.7 ± 0.2	18.5 ± 0.2	<0.001	17.7 ± 0.2	16.9 ± 0.2	<0.001
CCL	15.9 ± 0.1	16.8 ± 0.3	<0.001	15.9 ± 0.1	15.1 ± 0.2	<0.001
CBL	16.4 ± 0.1	17.3 ± 0.3	<0.001	16.4 ± 0.1	15.6 ± 0.2	<0.001
MW	8.4 ± 0.1	9.2 ± 0.3	0.005	8.4 ± 0.1	8.1 ± 0.0	<0.001
ZB	10.9 ± 0.2	11.4 ± 0.1	<0.001	10.9 ± 0.2	10.1 ± 0.2	<0.001
BB	8.3 ± 0.2	8.6 ± 0.2	0.033	8.3 ± 0.2	7.6 ± 0.2	0.001
BH	7.1 ± 0.2	7.5 ± 0.3	0.015	7.1 ± 0.2	6.5 ± 0.2	0.005
PC	3.7 ± 0.1	3.7 ± 0.2	ns	3.7 ± 0.1	3.2 ± 0.2	0.003
ML	12.9 ± 0.3	13.7 ± 0.3	<0.001	12.9 ± 0.3	12.4 ± 0.2	0.036
C^1-C^1	4.5 ± 0.1	4.8 ± 0.1	0.001	4.5 ± 0.1	4.2 ± 0.1	<0.001
M^3-M^3	6.7 ± 0.1	6.9 ± 0.2	0.022	6.7 ± 0.1	6.2 ± 0.0	<0.001
C-M^3	7.2 ± 0.1	7.6 ± 0.2	0.002	7.2 ± 0.1	6.9 ± 0.1	0.005
C-M_3	7.7 ± 0.2	8.1 ± 0.2	0.001	7.7 ± 0.2	7.4 ± 0.2	ns

Thirty-six skulls were examined for the present study. A multivariate analysis shows that specimens of *K. papillosa* A are discrete from other taxa, where as *K. papillosa* B are grouped together with *K. papillosa* B 'large-size', but discrete from *K. papillosa* B 'small-size' and *K. lenis* from India, and some overlap with *K. lenis* from peninsular Malaysia, Sumatra and Borneo (Figure 3.4.; Table 3.6.). Those of

Table 3.3. Continued.

Characters	*K. malaya-na* (*K. pa-piloca* A)	*Kerivoula* spB (*K. papillosa* C)	*P*-value	*K. malaya-na* (*K. pa-piloca* A)	*Kerivoula* spB (*K. lenis* PM, SM, BN)	*P*-value
External characters						
HB	49.5 ± 2.6	45.0 ± 2.0	0.003	49.5 ± 2.6	41.5 ± 1.2	0.020
FA	40.9 ± 1.0	40.4 ± 0.7	ns	40.9 ± 1.0	39.0 ± 0.7	0.011
EL	14.3 ± 1.0	14.6 ± 1.0	ns	14.3 ± 1.0	14.9 ± 0.3	ns
TL	50.6 ± 2.1	51.5 ± 2.5	ns	50.6 ± 2.1	47.1 ± 1.6	ns
TIB	21.6 ± 0.4	20.4 ± 0.7	0.002	21.6 ± 0.4	19.1 ± 0.8	<0.001
HF	9.5 ± 0.3	9.0 ± 0.5	ns	9.5 ± 0.3	9.5 ± 0.2	ns
3MT	43.9 ± 1.4	43.7 ± 0.8	ns	43.9 ± 1.4	42.2 ± 1.7	ns
4MT	42.4 ± 1.9	42.6 ± 0.5	ns	42.4 ± 1.9	40.3 ± 1.9	ns
5MT	41.2 ± 1.7	41.2 ± 0.7	ns	41.2 ± 1.7	38.9 ± 1.6	ns
3D1P	21.4 ± 1.0	20.8 ± 0.7	ns	21.4 ± 1.0	19.8 ± 1.1	0.039
3D2P	22.0 ± 0.6	21.0 ± 0.8	0.018	22.0 ± 0.6	20.0 ± 1.1	0.006
4D1P	12.9 ± 0.7	13.3 ± 0.5	ns	12.9 ± 0.7	11.8 ± 0.1	0.020
4D2P	9.7 ± 0.4	9.7 ± 0.4	ns	9.7 ± 0.4	9.2 ± 0.4	ns
Cranio-dental characters						
TL	17.7 ± 0.2	17.3 ± 0.2	<0.001	17.7 ± 0.2	16.7 ± 0.1	<0.001
CCL	15.9 ± 0.1	15.3 ± 0.1	<0.001	15.9 ± 0.1	14.8 ± 0.1	<0.001
CBL	16.4 ± 0.1	15.9 ± 0.2	<0.001	16.4 ± 0.1	15.3 ± 0.1	<0.001
MW	8.4 ± 0.1	8.4 ± 0.2	<0.001	8.4 ± 0.1	8.4 ± 0.2	0.002
ZB	10.9 ± 0.2	10.5 ± 0.2	<0.001	10.9 ± 0.2	10.5 ± 0.3	0.014
BB	8.3 ± 0.2	7.9 ± 0.2	<0.001	8.3 ± 0.2	7.9 ± 0.1	0.005
BH	7.1 ± 0.2	6.9 ± 0.2	ns	7.1 ± 0.2	6.8 ± 0.1	ns
PC	3.7 ± 0.1	3.3 ± 0.1	<0.001	3.7 ± 0.1	3.4 ± 0.2	0.015
ML	12.9 ± 0.3	12.6 ± 0.2	0.039	12.9 ± 0.3	12.4 ± 0.6	ns
C^1-C^1	4.5 ± 0.1	4.3 ± 0.2	0.006	4.5 ± 0.1	4.2 ± 0.1	<0.001
M^3-M^3	6.7 ± 0.1	6.5 ± 0.2	0.008	6.7 ± 0.1	6.2 ± 0.2	<0.001
C-M^3	7.2 ± 0.1	7.0 ± 0.1	0.002	7.2 ± 0.1	6.7 ± 0.2	<0.001
C-M_3	7.7 ± 0.2	7.4 ± 0.2	0.011	7.7 ± 0.2	7.2 ± 0.4	0.021

K. papillosa B, *K. papillosa* C and *K. lenis* clearly discrete from *K. papillosa* L[arge]. The skull measurements of *K. papillosa* A are smaller than those of *K. papillosa* L[arge], except postorbital constriction (PC) which is not significant difference (Tables 3.3. and 3.7.), whereas they are larger than those of *K. papillosa* B, *K. papillosa* C and those referred to *K. lenis*, except lower toothrow length (C-M_3) which is not difference between *K. papillosa* A and *K. papillosa* B 'small-size', braincase height (BH) which is not difference between *K. papillosa* A and *K. papillosa* C, braincase height (BH) and mandible length (ML) which are not different between

Table 3.4. External and cranio-dental measurements (in mm) of *K. papillosa*, *Kerivoula* spA subspA and *Kerivoula* spB, presented as mean ± SD. PM = Peninsular Malaysia, SM = Sumatra, BN = Borneo. *P* = significance value, based on *t*-test; ns = not significant.

Characters	***Kerivoula* spA sub-spA (*K. papillosa* B 'small-size')**	***K. papillo-sa* (*K. pa-pillosa* L)**	***P*-value**	***Kerivoula* spA sub-spA (*K. papillosa* B 'small-size')**	***Kerivoula* spB (*K. papillosa* C)**	***P*-value**	***Kerivoula* spA sub-spA (*K. papillosa* B 'small-size')**	***Kerivoula* spB (*K. lenis* PM, SM, BN)**	***P*-value**
External characters									
HB	43.5 ± 2.8	48.9 ± 3.0	ns	43.5 ± 2.8	45.0 ± 2.0	ns	43.5 ± 2.8	41.5 ± 1.2	ns
FA	39.8 ± 0.4	43.5 ± 0.9	0.003	39.8 ± 0.4	40.4 ± 0.7	ns	39.8 ± 0.4	39.0 ± 0.7	ns
EL	14.3 ± 0.3	13.6 ± 1.2	ns	14.3 ± 0.3	14.6 ± 1.0	ns	14.3 ± 0.3	14.9 ± 0.3	ns
TL	50.9 ± 3.8	50.6 ± 1.3	ns	50.9 ± 3.8	51.5 ± 2.5	ns	50.9 ± 3.8	47.1 ± 1.6	ns
TIB	19.9 ± 1.3	23.4 ± 0.5	0.013	19.9 ± 1.3	20.4 ± 0.7	ns	19.9 ± 1.3	19.1 ± 0.8	ns
HF	9.3 ± 0.5	10.5 ± 0.3	0.029	9.3 ± 0.5	9.0 ± 0.5	ns	9.3 ± 0.5	9.5 ± 0.2	ns
3MT	43.7 ± 0.7	46.8 ± 2.1	ns	43.7 ± 0.7	43.7 ± 0.8	ns	43.7 ± 0.7	42.2 ± 1.7	ns
4MT	42.5 ± 0.4	45.7 ± 1.5	0.026	42.5 ± 0.4	42.6 ± 0.5	ns	42.5 ± 0.4	40.3 ± 1.9	ns
5MT	40.7 ± 0.3	43.9 ± 1.5	0.022	40.7 ± 0.3	41.2 ± 0.7	ns	40.7 ± 0.3	38.9 ± 1.6	ns
3D1P	20.3 ± 1.2	23.4 ± 0.7	0.016	20.3 ± 1.2	20.8 ± 0.7	ns	20.3 ± 1.2	19.8 ± 1.1	ns
3D2P	20.5 ± 0.9	22.4 ± 0.4	0.029	20.5 ± 0.9	21.0 ± 0.8	ns	20.5 ± 0.9	20.0 ± 1.1	ns
4D1P	12.9 ± 0.1	14.1 ± 0.6	0.025	12.9 ± 0.1	13.3 ± 0.5	<0.001	12.9 ± 0.1	11.8 ± 0.1	ns
4D2P	9.7 ± 0.3	9.7 ± 0.5	ns	9.7 ± 0.3	9.7 ± 0.4	ns	9.7 ± 0.3	9.2 ± 0.4	ns
Cranio-dental characters									
GTL	16.9 ± 0.2	18.5 ± 0.2	<0.001	16.9 ± 0.2	17.3 ± 0.2	ns	16.9 ± 0.2	16.7 ± 0.1	0.003
CCL	15.1 ± 0.2	16.8 ± 0.3	<0.001	15.1 ± 0.2	15.3 ± 0.1	0.014	15.1 ± 0.2	14.8 ± 0.1	0.017
CBL	15.6 ± 0.2	17.3 ± 0.3	<0.001	15.6 ± 0.2	15.9 ± 0.2	0.042	15.6 ± 0.2	15.3 ± 0.1	0.030
MW	8.1 ± 0.0	9.2 ± 0.3	<0.001	8.1 ± 0.0	8.4 ± 0.2	ns	8.1 ± 0.0	8.4 ± 0.2	0.016
ZB	10.1 ± 0.2	11.4 ± 0.1	<0.001	10.1 ± 0.2	10.5 ± 0.2	ns	10.1 ± 0.2	10.5 ± 0.3	0.011

Table 3.4. Continued.

Characters	***Kerivoula* spA sub-spA (*K. papillosa* B 'small-size')**	***K. papillosa* (*K. papillosa* L)**	***P*-value**	***Kerivoula* spA sub-spA (*K. papillosa* B 'small-size')**	***Kerivoula* spB (*K. papillosa* C)**	***P*-value**	***Kerivoula* spA sub-spA (*K. papillosa* B 'small-size')**	***Kerivoula* spB (*K. lenis* PM, SM, BN)**	***P*-value**
BB	7.6 ± 0.2	8.6 ± 0.2	<0.001	7.6 ± 0.2	7.9 ± 0.2	0.030	7.6 ± 0.2	7.9 ± 0.1	0.008
BH	6.5 ± 0.2	7.5 ± 0.3	0.002	6.5 ± 0.2	6.9 ± 0.2	0.039	6.5 ± 0.2	6.8 ± 0.1	0.010
PC	3.2 ± 0.2	3.7 ± 0.2	0.005	3.2 ± 0.2	3.3 ± 0.1	ns	3.2 ± 0.2	3.4 ± 0.2	ns
ML	12.4 ± 0.2	13.7 ± 0.3	<0.001	12.4 ± 0.2	12.6 ± 0.2	ns	12.4 ± 0.2	12.4 ± 0.6	ns
C^1-C^1	4.2 ± 0.1	4.8 ± 0.1	<0.001	4.2 ± 0.1	4.3 ± 0.2	ns	4.2 ± 0.1	4.2 ± 0.1	ns
M^3-M^3	6.2 ± 0.0	6.9 ± 0.2	0.001	6.2 ± 0.0	6.5 ± 0.2	ns	6.2 ± 0.0	6.2 ± 0.2	0.032
C-M^3	6.9 ± 0.1	7.6 ± 0.2	0.001	6.9 ± 0.1	7.0 ± 0.1	ns	6.9 ± 0.1	6.7 ± 0.2	ns
C-M_3	7.4 ± 0.2	8.1 ± 0.2	0.001	7.4 ± 0.2	7.4 ± 0.2	ns	7.4 ± 0.2	7.2 ± 0.4	ns

Table 3.5. External and cranio-dental measurements (in mm) of *K. papillosa*, and *K. bantadica* sp. nov., presented as mean ± SD. PM = Peninsular Malaysia, SM = Sumatra, BN = Borneo. *P* = significance value, based on *t*-test; ns = not significant.

Characters	***Kerivoula* spB (*K. papillosa* C)**	***Kerivoula* spB (*K. lenis* PM, SM, BN)**	***P*-value**	***Kerivoula* spB (*K. papillosa* C)**	***K. papillosa* (*K. papillosa* L)**	***P*-value**	***Kerivoula* spB (*K. lenis* PM, SM, BN)**	***K. papillosa* (*K. papillosa* L)**	***P*-value**
External characters									
HB	45.0 ± 2.0	41.5 ± 1.2	0.037	45.0 ± 2.0	48.9 ± 3.0	0.015	41.5 ± 1.2	48.9 ± 3.0	ns
FA	40.4 ± 0.7	39.0 ± 0.7	0.003	40.4 ± 0.7	43.5 ± 0.9	<0.001	39.0 ± 0.7	43.5 ± 0.9	0.001
EL	14.6 ± 1.0	14.9 ± 0.3	ns	14.6 ± 1.0	13.6 ± 1.2	ns	14.9 ± 0.3	13.6 ± 1.2	ns
TL	51.5 ± 2.5	47.1 ± 1.6	0.035	51.5 ± 2.5	50.6 ± 1.3	ns	47.1 ± 1.6	50.6 ± 1.3	ns
TIB	20.4 ± 0.7	19.1 ± 0.8	0.012	20.4 ± 0.7	23.4 ± 0.5	<0.001	19.1 ± 0.8	23.4 ± 0.5	<0.001
HF	9.0 ± 0.5	9.5 ± 0.2	ns	9.0 ± 0.5	10.5 ± 0.3	<0.001	9.5 ± 0.2	10.5 ± 0.3	0.031
3MT	43.7 ± 0.8	42.2 ± 1.7	0.021	43.7 ± 0.8	46.8 ± 2.1	0.001	42.2 ± 1.7	46.8 ± 2.1	0.023
4MT	42.6 ± 0.5	40.3 ± 1.9	0.001	42.6 ± 0.5	45.7 ± 1.5	<0.001	40.3 ± 1.9	45.7 ± 1.5	0.011
5MT	41.2 ± 0.7	38.9 ± 1.6	0.001	41.2 ± 0.7	43.9 ± 1.5	<0.001	38.9 ± 1.6	43.9 ± 1.5	0.009
3D1P	20.8 ± 0.7	19.8 ± 1.1	ns	20.8 ± 0.7	23.4 ± 0.7	<0.001	19.8 ± 1.1	23.4 ± 0.7	0.004
3D2P	21.0 ± 0.8	20.0 ± 1.1	ns	21.0 ± 0.8	22.4 ± 0.4	0.014	20.0 ± 1.1	22.4 ± 0.4	0.016
4D1P	13.3 ± 0.5	11.8 ± 0.1	0.001	13.3 ± 0.5	14.1 ± 0.6	0.025	11.8 ± 0.1	14.1 ± 0.6	0.001
4D2P	9.7 ± 0.4	9.2 ± 0.4	0.045	9.7 ± 0.4	9.7 ± 0.5	ns	9.2 ± 0.4	9.7 ± 0.5	ns
Cranio-dental characters									
GTL	17.3 ± 0.2	16.7 ± 0.1	<0.001	17.3 ± 0.2	18.5 ± 0.2	<0.001	16.7 ± 0.1	18.5 ± 0.2	<0.001
CCL	15.3 ± 0.1	14.8 ± 0.1	<0.001	15.3 ± 0.1	16.8 ± 0.3	<0.001	14.8 ± 0.1	16.8 ± 0.3	<0.001
CBL	15.9 ± 0.2	15.3 ± 0.1	<0.001	15.9 ± 0.2	17.3 ± 0.3	<0.001	15.3 ± 0.1	17.3 ± 0.3	<0.001
MW	8.4 ± 0.2	8.4 ± 0.2	ns	8.4 ± 0.2	9.2 ± 0.3	<0.001	8.4 ± 0.2	9.2 ± 0.3	0.001
ZB	10.5 ± 0.2	10.5 ± 0.3	ns	10.5 ± 0.2	11.4 ± 0.1	<0.001	10.5 ± 0.3	11.4 ± 0.1	<0.001
BB	7.9 ± 0.2	7.9 ± 0.1	ns	7.9 ± 0.2	8.6 ± 0.2	<0.001	7.9 ± 0.1	8.6 ± 0.2	<0.001
BH	6.9 ± 0.2	6.8 ± 0.1	ns	6.9 ± 0.2	7.5 ± 0.3	<0.001	6.8 ± 0.1	7.5 ± 0.3	0.004

Table 3.5. Continued.

Characters	***Kerivoula* spB (*K. papillosa* C)**	***Kerivoula* spB (*K. lenis* PM, SM, BN)**	***P*-value**	***Kerivoula* spB (*K. papillosa* C)**	***K. papillosa* (*K. papillosa* L)**	***P*-value**	***Kerivoula* spB (*K. lenis* PM, SM, BN)**	***K. papillosa* (*K. papillosa* L)**	***P*-value**
PC	3.3 ± 0.1	3.4 ± 0.2	ns	3.3 ± 0.1	3.7 ± 0.2	<0.001	3.4 ± 0.2	3.7 ± 0.2	0.015
ML	12.6 ± 0.2	12.4 ± 0.6	ns	12.6 ± 0.2	13.7 ± 0.3	<0.001	12.4 ± 0.6	13.7 ± 0.3	0.002
C^1-C^1	4.3 ± 0.2	4.2 ± 0.1	ns	4.3 ± 0.2	4.8 ± 0.1	<0.001	4.2 ± 0.1	4.8 ± 0.1	<0.001
M^3-M^3	6.5 ± 0.2	6.2 ± 0.2	0.027	6.5 ± 0.2	6.9 ± 0.2	<0.001	6.2 ± 0.2	6.9 ± 0.2	<0.001
C-M^3	7.0 ± 0.1	6.7 ± 0.2	0.006	7.0 ± 0.1	7.6 ± 0.2	<0.001	6.7 ± 0.2	7.6 ± 0.2	<0.001
C-M_3	7.4 ± 0.2	7.2 ± 0.4	ns	7.4 ± 0.2	8.1 ± 0.2	<0.001	7.2 ± 0.4	8.1 ± 0.2	0.001

Figure 3.2. Three species and a subspecies of *Kerivoula*. A – *K. malayana*, PSUZC-MM2013.28, ♀, Hala-Bala Wildlife Sanctuary, Narathiwat Province; B – *Kerivoula* spA, PSUZC-MM2008.57, ♂, Pha Chi Wildlife Sanctuary, Ratchaburi Province; C – *Kerivoula* subspA, PSUZC-MM2011.53, ♀, South Klom Luang Chumporn Wildlife Sanctuary, Ranong Province; D – *Kerivoula* spB, Field No. BD131122.1, ♂, Hala-Bala Wildlife Sanctuary, Narathiwat Province. No scale.

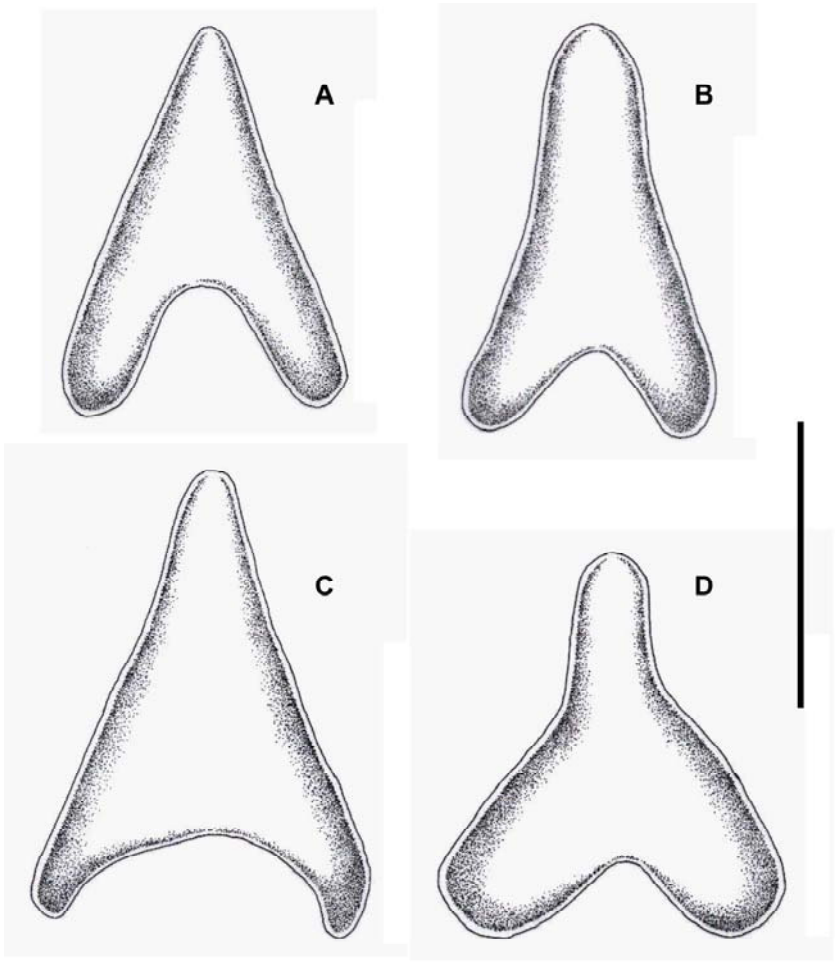

Figure 3.3. Dorsal view of baculum of three species of *Kerivoula*. A – *K. mamalaya*, HBWRS2010.3, Watershed Management Station, Khao Nam Khang National Park, Songkhla Province; B – *Kerivoula* spA, PSUZC-MM2008.56, Pha Chi Wildlife Sanctuary, Ratchaburi Province; C – *Kerivoula* spB, PSUZC-MM2011.2, Khao Chong Wildlife Education Centre, Khao Bantad Wildlife Sanctuary, Trang Province; D – *Kerivoula* spB, PSUZC-MM2005.123, Hala-Bala Wildlife Sanctuary, Narathiwat Province. Scale: 0.5 mm.

K. papillosa A and *K. lenis* from peninsular Malaysia, Sumatra and Borneo. Specimens of *K. papillosa* B 'large-size' (n = 2) and *K. lenis* from India (n = 1) are smaller than those of *K. papillosa* A but the sample size is too small to make any meaningful conclusion.

Specimens of *K. papillosa* B 'large-size' are similar skull size to those of *K. papillosa* C, but larger than those of *K. papillosa* B 'small-size' and those referred to *K. lenis* (Tables 3.7.). However, the skull measurements of *K. papillosa* B 'small-size' are similar to those of *K. papillosa* C, except condylo-canine length (CCL), condylo-

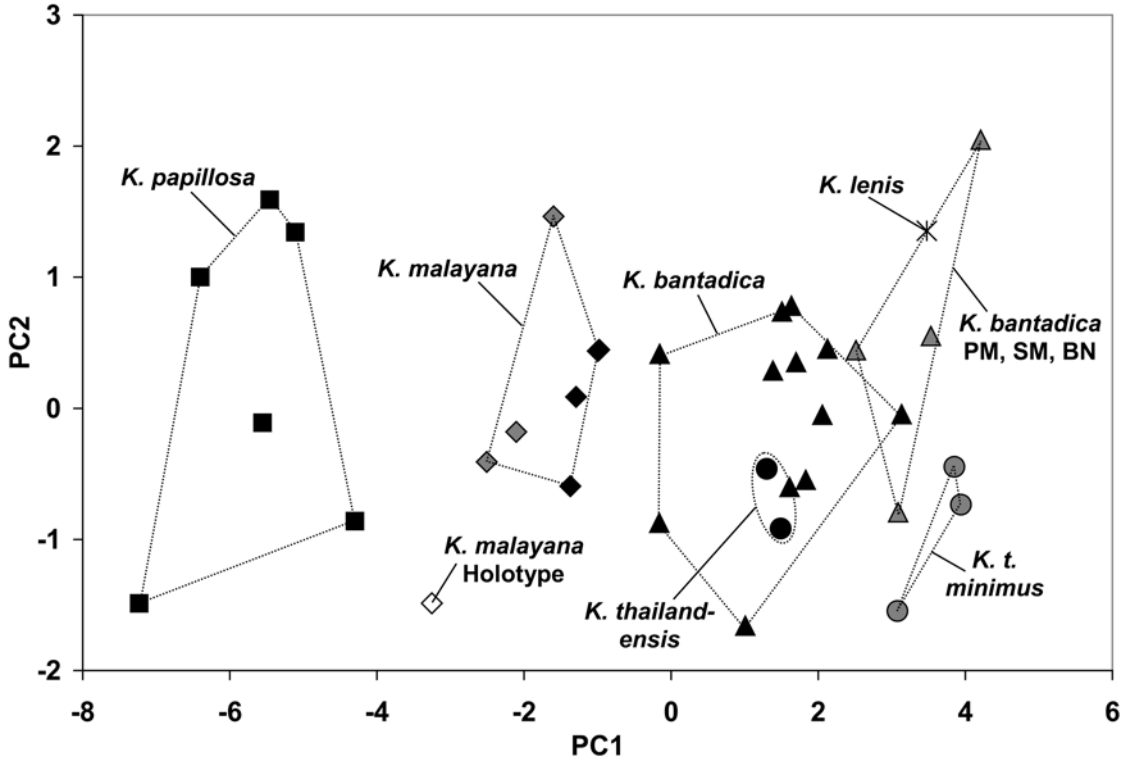

Figure 3.4. PAC between first and second principal components based on thirteen cranial and dental metric characters for specimens of *Kerivoula*. Black squares represent *K. papillosa*, black diamonds are *K. malayana* from Thailand; grey diamonds are *K. malayana* from peninsular Malaysia; open diamond is holotype of *K. malayana*; black circles are *Kerivoula* spA; grey circles are *Kerivoula* subspA; black triangles are *Kerivoula* spB from Thailand; grey triangles are *Kerivoula* spB from peninsular Malaysia, Sumatra and Borneo; and black star is *K. lenis*.

basal length (CBL), breadth of braincase (BB) and braincase height (BH) which average smaller, whereas they are larger in some characters or smaller in some characters than those of *K. lenis* from peninsular Malaysia, Sumatra and Borneo, except postorbital constriction (PC), mandible length (ML), anterior palatal width (C^1-C^1), and upper and lower toothrow lengths (C-M^3 and C-M_3) which are no significant difference (Tables 3.4. and 3.7.).

Specimens of *K. papillosa* C are similar to those of *K. lenis* from peninsular Malaysia, Sumatra and Borneo, except greatest skull length (GTL), condylo-canine length (CCL), condylo-basal length (CBL), posterior palatal length (M3-M3) and upper toothrow length (C-M3) which are significant larger than those of latter species (Tables 3.5. and 3.7.). In addition, specimens of *K. papillosa* C are larger skull than

Table 3.6. Eigenvectors and eigenvalues of PCA of thirteen cranio-dental measurements of 36 specimens of five species and a subspecies of *Kerivoula*. See also Figure 3.5.

Character	Eigenvector		
	1	2	3
GTL	-0.30	0.06	0.16
CCL	-0.29	0.06	0.19
CBL	-0.30	0.06	0.22
MW	-0.28	0.34	-0.01
ZB	-0.28	0.13	-0.13
BB	-0.27	0.39	-0.21
BH	-0.23	0.49	0.20
PC	-0.24	-0.04	-0.77
ML	-0.28	-0.19	0.40
C^1-C^1	-0.29	-0.14	-0.15
M^3-M^3	-0.28	-0.29	-0.07
C-M^3	-0.29	-0.36	0.00
C-M_3	-0.27	-0.43	0.06
Eigenvalue	10.14	0.86	0.59
% total of variation Explained	77.99	84.59	89.10

K. lenis from India, but the sample size is too small for the latter taxon.

The skull morphology of specimens from Thailand is clearly different between each taxon and different from those of *K. papillosa* L[arge] and *K. lenis* from India (Figure 3.5.). The skull of *K. papillosa* A is similar to those of *K. papillosa* L[arge], whereas it is higher braincase than those of other taxa. In addition, the skull of *K. papillosa* B included two morphotypes which are different in the braincase shape, the skull of *K. papillosa* B 'large-size' is without depression on its parietal region whereas it occurs in *K. papillosa* B 'small-size'. The skull morphology of *K. papillosa* C included two morphotypes which are mainly different braincase, one has domed braincase and other has flattened braincase (Figure 3.6.).

In addition, the skull morphology of *K. papillosa* A corresponds to the skull of specimens referred to *K. papillosa* S[mall] from peninsular Malaysia. The domed skull type of *K. papillosa* C corresponds to those of *K. lenis* from peninsular Malaysia and Borneo and the flattened type corresponds to that of *K. lenis* from Borneo. However, those of *K. lenis* from Sundic subregion are clear different from the skull of *K. lenis* from India.

Table 3.7. Cranial and dental measurements (in mm) of five species and a subspecies of *Kerivoula*. GTL – greatest skull length; CCL – condylo-canine length; CBL – condylo-basal length; MW – mastoid width; ZB – zygomatic breadth; BB – breadth of braincase; BH – braincase height; BHx100/CBL – % height of braincase height relative to condylo-basal length; BHx100/BB – % height of braincase height relative to breadth of braincase; PC – postorbital constriction; ML – mandible length; C^1-C^1 – anterior palatal width; M^3-M^3 – posterior palatal width; C-M^3 – upper toothrow length; CM_3 – lower toothrow length. [a]data from Tate (1941), [b]from Chasen (1940), [c]from Thomas (1916) and [d]Vanitharani et al. (2003).

n	**sex**	**GTL**	**CCL**	**CBL**	**MW**	**ZB**	**BB**	**BH**	**BHx100/CBL**
				Kerivoula papillosa Co-type ('a')					
1	♀	–	–	–	–	–	–	–	–
				Kerivoula papillosa (*K. papillosa* L[arge])					
6	♂♂♀	18.4-18.8	16.4-17.1	16.9-17.6	8.8-9.6	11.3-11.5	8.2-8.8	7.1-7.8	40.6-45.7
		18.5, 0.2	16.8, 0.3	17.3, 0.3	9.2, 0.3	11.4, 0.1	8.6, 0.2	7.5, 0.3	43.1, 2.1
				Kerivoula malayana Holotype					
1	♀	18.0 (18.2[b])	15.5	16.2	10.8 (8.7[b])	11.4[b]	8.0 (8.4[b])	7.2	46.5
				Kerivoula malayana (*K. papillosa* A)					
7	♂♂♀♀	17.4-17.9	15.7-16.1	16.2-16.5	8.6-9.0	10.6-11.1	8.0-8.6	6.8-7.4	41.2-45.4
		17.7, 0.2	15.9, 0.1	16.4, 0.1	8.4, 0.1	10.9, 0.2	8.3, 0.2	7.1, 0.2	43.0, 1.4
				Kerivoula spA (*K. papillosa* B 'large-size')					
2	♂♂	17.1, 17.0	15.4, 15.3	15.9, 15.7	8.4, 8.4	10.4, 10.4	8.1, 8.0	6.7, 6.5	42.2, 41.1
				Kerivoula spA subspA (*K. papillosa* B 'small-size')					
3	♀♀	16.6-17.0	14.9-15.2	15.4-15.8	8.1-8.1	10.0-10.3	7.4-7.7	6.3-6.7	40.1-43.2
		16.9, 0.2	15.1, 0.2	15.6, 0.2	8.1, 0.0	10.1, 0.2	7.6, 0.2	6.5, 0.2	42.0, 1.7
				Kerivoula spB (*K. papillosa* C)					
12	♂♂♀♀	17.0-17.6	15.0-15.6	15.5-16.2	8.1-8.6	10.2-10.9	7.6-8.1	6.6-7.3	41.2-45.5
		17.3, 0.2	15.3, 0.1	15.9, 0.2	8.4, 0.2	10.5, 0.2	7.9, 0.2	6.9, 0.2	43.6, 1.3
				Kerivoula spB (*K. lenis* Malaysia, Sumatra, Borneo)					
4	♂♂♀♀	16.6-16.9	14.7-14.8	15.3-15.4	8.1-8.5	10.1-10.8	7.7-7.9	6.8-6.9	44.5-45.1
		16.7, 0.1	14.8, 0.1	15.3, 0.1	8.4, 0.2	10.5, 0.3	7.9, 0.1	6.8, 0.1	44.7, 0.3

Table 3.7. Continued.

n	sex	GTL	CCL	CBL	MW	ZB	BB	BH	BHx100/CBL
					Kerivoula lenis Holotype				
1	?	–	–	–	–	8.7[c]	–	–	–
					Kerivoula lenis India				
1	♂	17.1	15.1	15.7	8.2	10.0	8.1	6.9	44.0

Table 3.7. Continued.

n	**sex**	**PC**	**ML**	**C^1-C^1**	**M^3-M^3**	**C-M^3**	**C-M_3**
			Kerivoula papillosa Co-type ('a')				
1	♀	3.5[a]	–	–	–	7.5[a]	–
			Kerivoula papillosa (*K. papillosa* L[arge])				
6	♂♂♀	3.6-4.1	13.4-14.2	4.6-4.9	6.6-7.2	7.4-7.9	7.9-8.4
		3.7, 0.2	13.7, 0.3	4.8, 0.1	6.9, 0.2	7.6, 0.2	8.1, 0.2
			Kerivoula malayana Holotype				
1	♀	3.9	13.2	4.9	6.9	7.6 (7.6[b])	8.1
			Kerivoula malayana (*K. papillosa* A)				
7	♂♂♀♀	3.4-3.8	12.3-13.1	4.4-4.6	6.6-6.9	7.0-7.4	7.4-7.9
		3.7, 0.1	12.9, 0.3	4.5, 0.1	6.7, 0.1	7.2, 0.1	7.7, 0.2
			Kerivoula spA (*K. papillosa* B 'large-size')				
2	♂♂	3.4, 3.6	12.6, 12.4	4.3, 4.4	6.5, 6.6	7.1, 7.0	7.5, 7.5
			Kerivoula spA subspA (*K. papillosa* B 'small-size')				
3	♀♀	3.0-3.4	12.2-12.5	4.2-4.3	6.2-6.2	6.8-7.0	7.2-7.6
		3.2, 0.2	12.4, 0.2	4.2, 0.1	6.2, 0.0	6.9, 0.1	7.4, 0.2
			Kerivoula spB (*K. papillosa* C)				
12	♂♂♀♀	3.2-3.5	12.1-12.8	4.1-4.6	6.2-6.9	6.8-7.2	7.1-7.8
		3.3, 0.1	12.6, 0.2	4.3, 0.2	6.5, 0.2	7.0, 0.1	7.4, 0.2
			Kerivoula spB (*K. lenis* Malaysia, Sumatra, Borneo)				
4	♂♂♀♀	3.2-3.6	11.6-12.9	4.1-4.2	6.0-6.4	6.5-6.8	6.7-7.6
		3.4, 0.2	12.4, 0.6	4.2, 0.1	6.2, 0.2	6.7, 0.2	7.2, 0.4
			Kerivoula lenis Holotype				
1	?	3.2[c] (3.4[d])	11.9[e]	3.3[c] (4.2[e])	6.0[d]	6.7[c] (6.5[d])	7.2[c]
			Kerivoula lenis India				
1	♂	3.5	12.0	4.0	6.2	6.7	6.9

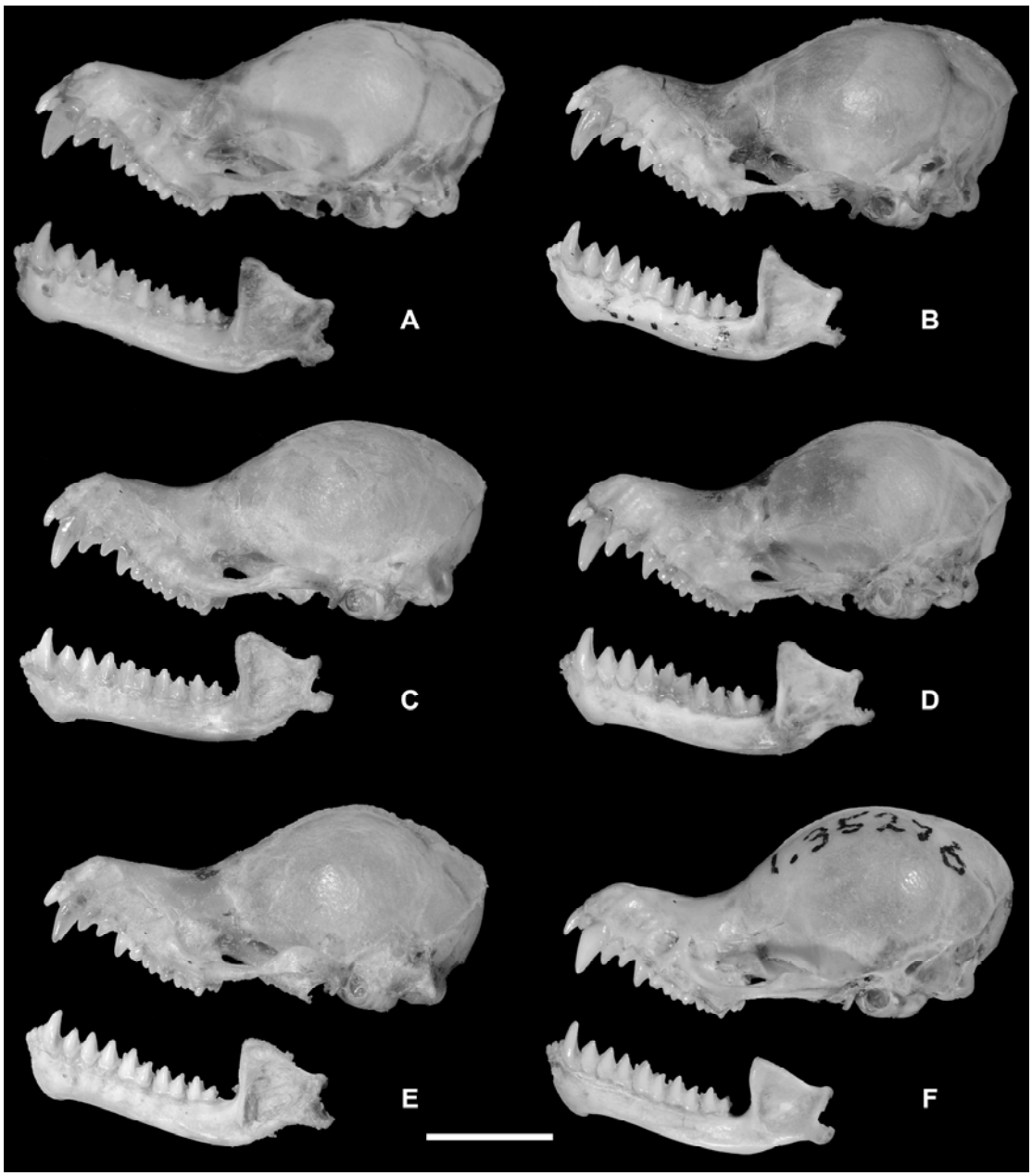

Figure 3.5. Lateral view of skull of five species and a subspecies of *Kerivoula*. A – *K. papillosa*, MZB35887, ♂, Way Canguk, Lampung, Sumatra; B – *K. malayana*, HBWRS2010.3, ♂, Watershed Management Station, Khao Nam Khang National Park, Songkhla Province, Thailand; C – *Kerivoula* spA, PSUZC-MM2008.56, ♂, Pha Chi Wildlife Sanctuary, Ratchaburi Province, Thailand; D – *Kerivoula* subspA, PSUZC-MM2011.53, ♀, South Klom Luang Chumporn Wildlife Sanctuary, Ranong Province, Thailand; E – *Kerivoula* spB, PSUZC-MM2011.2, ♂, Khao Chong Wildlife Education Centre, Khao Bantad Wildlife Sanctuary, Trang Province, Thailand; F – *K. lenis*, HZM.1.35276, ♂, Therkumalai Estate, Tamil Nadu, India. Scale: 5 mm.

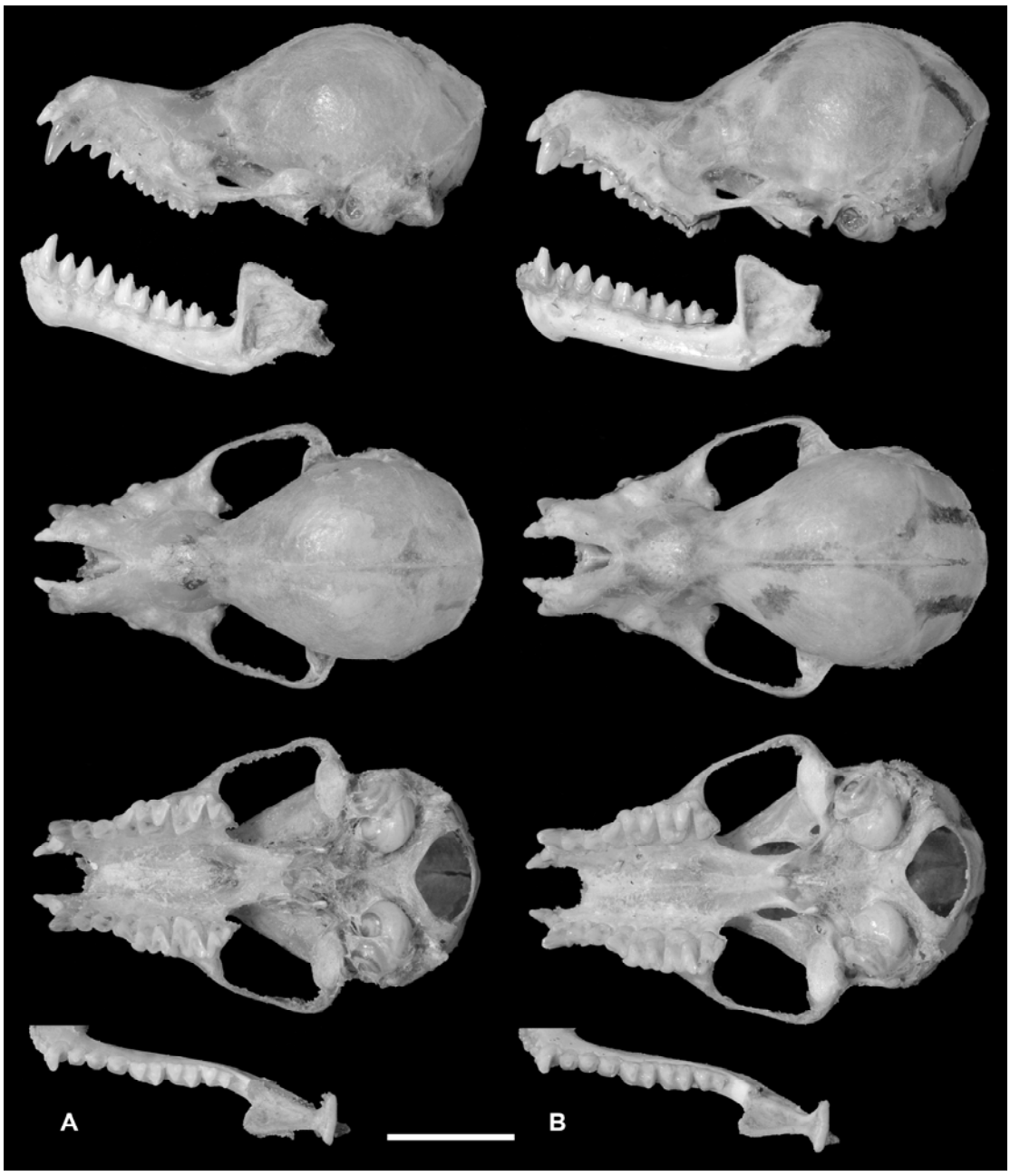

Figure 3.6. Skull variation of *Kerivoula* spB. A – PSUZC-MM2011.2, ♂, Khao Chong Wildlife Education Centre, Khao Bantad Wildlife Sanctuary, Trang Province, Thailand; B – PSUZC-MM2011.10, ♀, Hala-Bala Wildlife Sanctuary, Narathiwat Province, Thailand. Scale: 5 mm.

3.3.2. Genetics

Thirty-nine sequences of specimens referred to *K. papillosa* and *K.* cf. *lenis* are available in the present study. The phylogenetics shows that the sequences from

the study area together with others from the region can be divided into five monophyletic clades (Figure 3.7.). The sequences of *K. papillosa* A from Thailand are clustered together with those of specimens of *K. papillosa* S[mall] from peninsular Malaysia and Borneo, with genetic divergent of 1.34% (Table 3.8.). Sequences of *K. papillosa* A are separated from those of *K. papollosa* B, with genetic divergent 5.63%.

Sequences of *K. papillosa* C from Thailand is clustered together with the sequences of *K. lenis* from peninsular Malaysia, with genetic distance of 1.07%, but is separated from those of *K. lenis* from Borneo, with genetic divergent of 6.95% (Figure 3.7.; Table 3.8.). In addition, sequences of *K. papillosa* C are also separated from those referred to *K.* cf. *lenis* and *K. papillosa* from Lao PDR and Vietnam, with the genetic divergent of 15.00%. The clade of *K. papillosa* C is different from those of *K. papillosa* A and *K. papillosa* B by > 13%. Sequences of *K. papillosa* L[arge] from Borneo are separated from those of *K. papillosa* A, *K. papillosa* B and *K. papillosa* C, with genetic divergent > 16%.

3.4. SYSTEMATIC DESCRIPTIONS

As results, both in term of morphological and genetic differences, indicate that there are five distinct species of large *Kerivoula* with domed-skull within the study area. Specimens previously referred *K. papillosa* L[arge] from Sumatra and Borneo (sensu Anwarali et al., 2010) are here assigned to *K. papillosa* on the basis of size. As noted above, the specimens of *K. papillosa* L[arge] would appear comparable to the forearm length (43.2 mm – Figure 3.8.) and tibia length (22.9 mm) of holotype of *K. papillosa* as listed by Dobson (1876) (Tables 3.2.). In addition, they also would appear comparable to the forearm length (44.5 mm – Figure 3.8.), postorbital constriction (3.5 mm) and upper toothrow length (7.5 mm) of co-type of *K. papillosa* as listed by Tate (1941) (Tables 3.2. and 3.7.).

In case of *K. papillosa* A, the specimens from Thailand and peninsular Malaysia would appear comparable to the forearm length (40.7-43.2 mm, 43.4 mm for holotype) in the type description of the taxon *malayana* (Figure 3.8.; Table 3.2.). In addition, the skull measurement of *K. papillosa* A also would appear comparable to

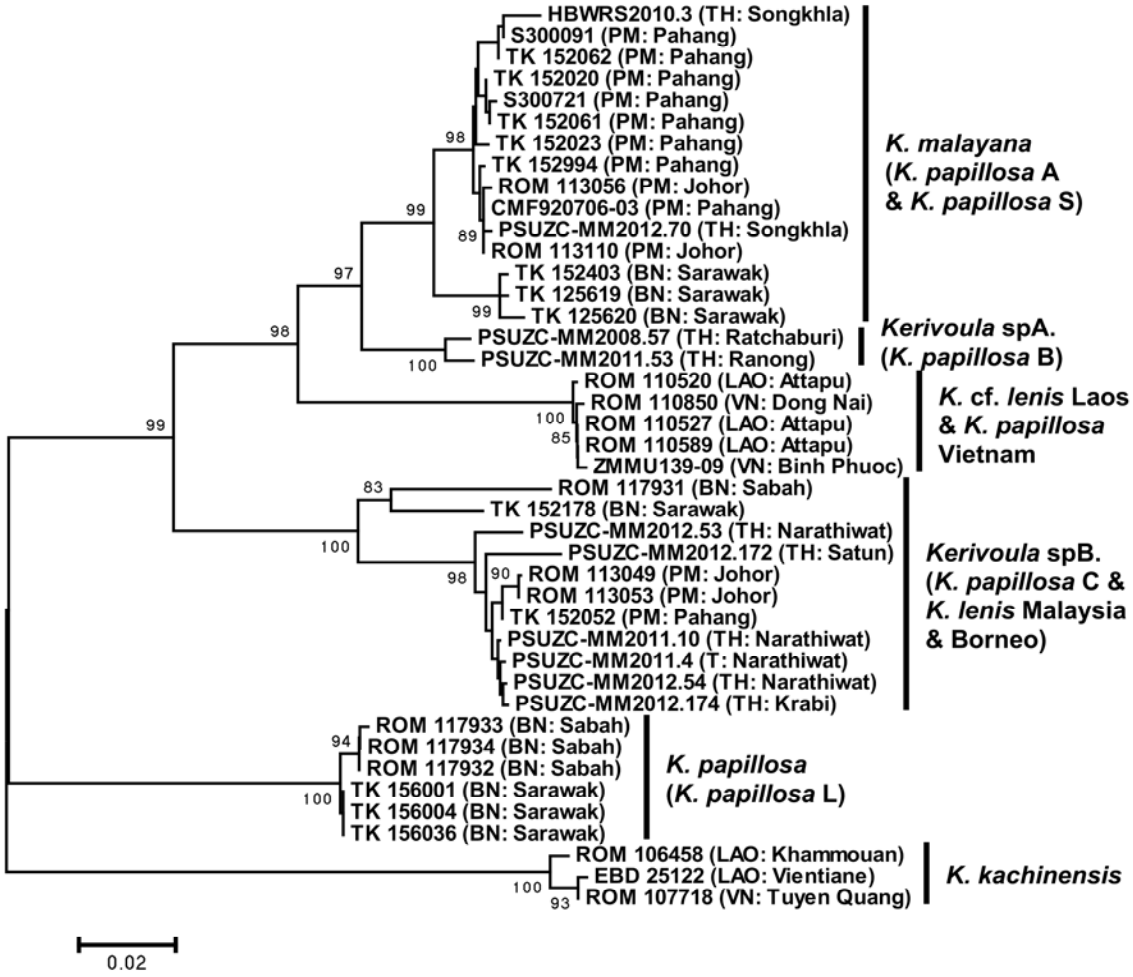

Figure 2.7. Neighbour-joining phylogeny based on cytochrome *c* oxidase (COI) sequences of *Kerivoula*, including *K. papillosa*, *K. malayana, K. thailandensis* sp. nov., *K. bantadica* sp. nov., *K.* cf. *lenis* and *K. kachinensis*, which included sequences from throughout region in the DNA Barcode of Life Database to comparison. Distance scale: 0.02.

Table 3.8. Average percentage of Kimura 2-parameter distance values of cytochrome *c* oxidase (COI) sequences within and between species of large *Kerivoula*. Below data present an average percentage between taxa and above data is standard deviation.

No	Species	*n*	1	2	3	4	5	6	7
1	*K. malayana* (*K. papillosa* A & *K. papillosa* S)	15	**1.34/0.27**	0.88	1.38	1.67	1.65	1.86	2.33
2	*Kerivoula* spA. (*K. papillosa* B)	2	5.63	**1.08/0.38**	1.38	1.65	1.55	2.05	2.45
3	*K.* cf. *lenis* LAO (*K. papillosa* VN)	5	9.93	9.95	**0.18/0.11**	1.86	1.77	2.25	2.31
4	*Kerivoula* spB. (*K. papillosa* C & *K. lenis* PM)	9	13.75	13.42	15.00	**1.07/0.32**	0.99	2.01	2.28
5	*Kerivoula* spB. (*K. lenis* BN)	2	13.88	13.43	15.50	6.95	**5.19/0.97**	1.91	2.25
6	*K. papillosa* (*K. papillosa* L)	6	16.48	18.41	20.78	17.87	17.57	**0.31/0.16**	2.07
7	*K. kachinensis*	3	22.59	222.57	21.69	22.25	22.45	18.98	**0.41/0.20**

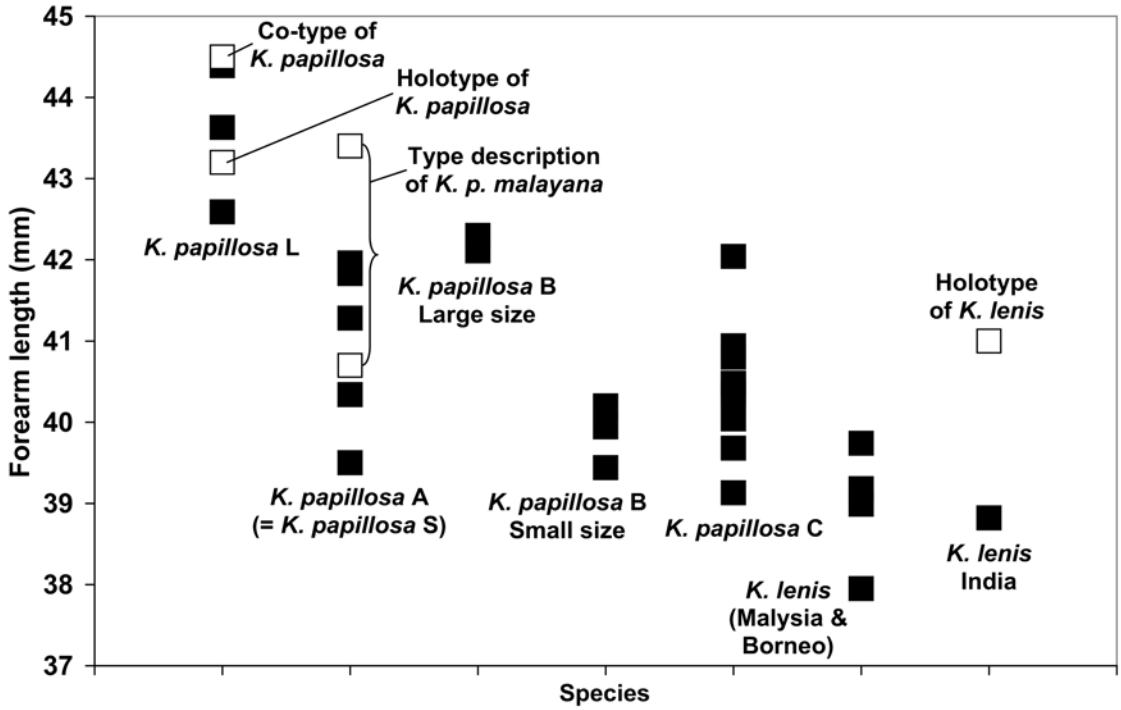

Figure 3.8. Comparison of the forearm length of seven taxa of large *Kerivoula.*

the skull measurements of the holotype of the taxon *malayana* (Figure 3.4.; Table 3.7.). Moreover, the skull morphology of Thai and Malaysian specimens also corresponds to holotype of the taxon *malayana*. Based on correspond in both size and morphology, the specimens of *K. papillosa* A are here assigned to the taxon *malayana* and based on different morphometrics and genetics from *K. papillosa* (Figures 3.1. and 3.4., Tables 3.2., 3.3. and 3.7.), it is considered as a distinct from *K. papillosa* and revaluated from subspecies to species level, *K. malayana*.

Specimens of *K. papillosa* B is difference in both morphology and genetic from those of *K. papillosa* and *K. malayana*. The PCA of external characters and skull measurements divided specimens of *K. papillosa* B into two groups, including 'large size' and 'small size' (Figures 3.1. and 3.4.; Tables 3.2. and 3.7.). The skulls of these two groups are also difference in morphology (Figure 3.5.). However, the genetic analysis shows that the specimens of these two groups are clustered together (Figure 3.7.), with the genetic divergent only 1.08% (Table 3.8.). Their distributions are isolated, the specimens of 'large-size' group are only known in Indochinese subregion and the specimens of 'small-size' group are only known in Sundaic subregion (Figure

3.9.). Based on different size and skull morphology, and geographical isolation, specimens of large *K. papillosa* B are here considered as a undescribed species, *Kerivoula* spA and specimens of small *K. papillosa* B are here considered as a distinct sunspecies of *Kerivoula* spA, *Kerivoula* spA subspA.

The morphology suggested that specimens of *K. papillosa* C are included two morphotypes (Figures 3.3. and 3.6.), but the genetic analysis shows that the sequences of *K. papillosa* C is clustered together (Figure 3.7.), with genetic divergent 1.07% (Table 3.8.). In addition, the sequences of *K. papillosa* C is clustered together with sequences of specimens from peninsular Malaysia, but separated from those of *K. lenis* from Borneo, with genetic divergent 6.95%. However, cytochrome *b* analysis shows that the sequence of *K. lenis* from peninsular Malaysia is clustered together, with genetic divergent only 3.9% (Anwaeali et al., 2010). Specimens of *K. papillosa* C are different morphology and genetic from those of other known species in the region. In addition, the skull morphology of *K. papillosa* C also difference from the skull of *K. lenis* from India. There is no any sequence of *K. lenis* from India are available for the present study. However, they are separated geography, the specimens of *K. papillosa* C are only known from the Sundaic subregion and the specimens of *K. lenis* are only known from India. Based on different skull morphology and geographical isolation, the specimens of *K. papillosa* C or *K. lenis* from peninsular Malaysia and Borneo are considered as a distinct species from *K. lenis* from India and are here assigned to undescribed species, *Kerivoula* spB.

The descriptions of three species and a subspecies found in Thailand are given below, together with comparison to other known taxa, distribution, ecology and behaviour.

***Kerivoula malayana* Chasen, 1940**

Malayan Woolly Bat

Kerivoula papillosa malayana Chasen, 1940; Ginting Bedai, Selangor-Pahang boundary, Malaysia, 2300ft.

Description

Kerivoula malayana has a forearm length of 39.5-42.0 mm (based on the

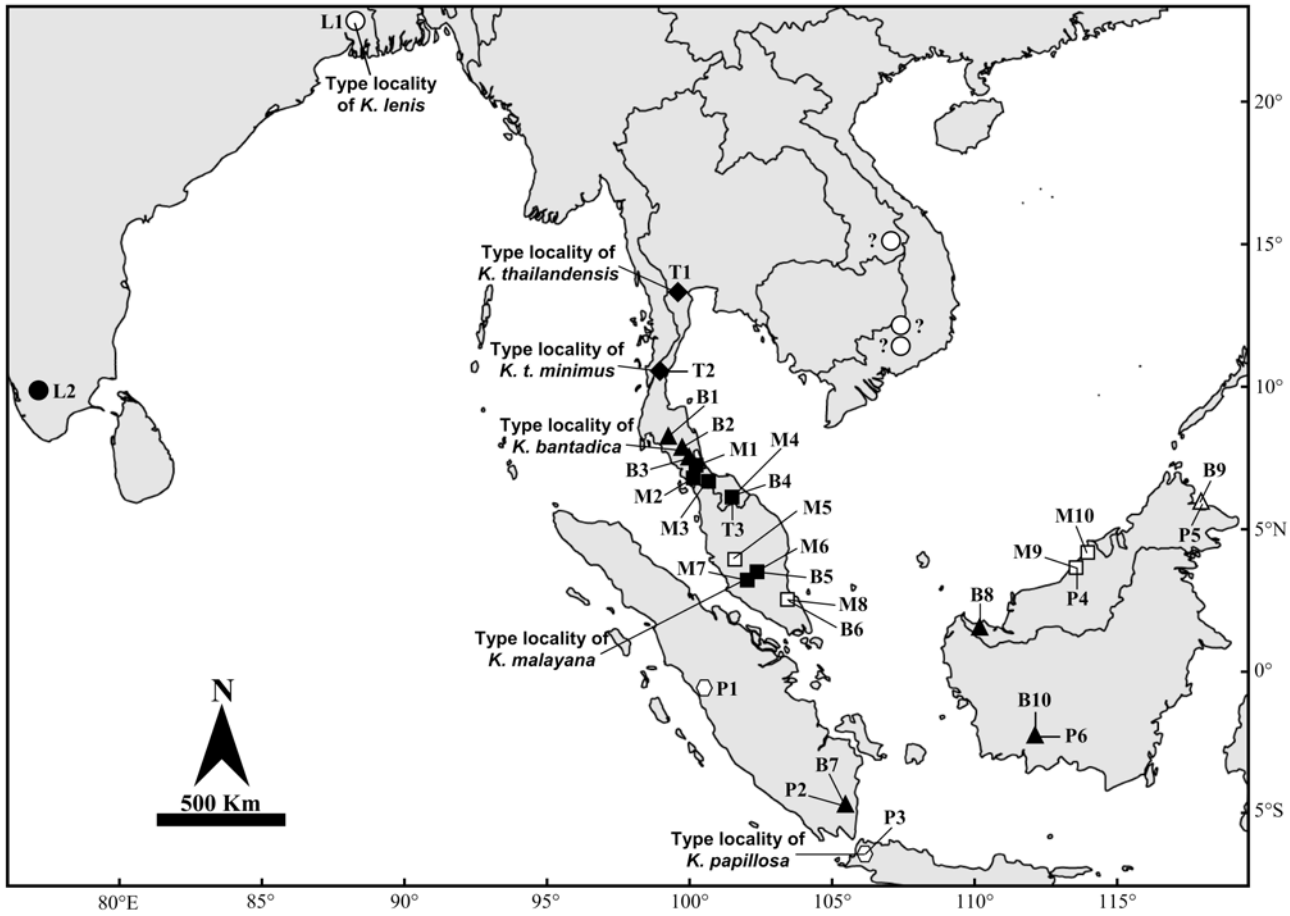

Figure 3.9. Distribution map of five species of *Kerivoula* from throughout region, including *K. papillosa* (hexagons), *K. malayana* (squares), *K. thailandensis* (diamonds), *K. bantadica* (triangles) and *K. lenis* (circles). Black symbols represent localities where specimens were examined in the present study, open symbols are literature records and genetic representation, question mark (?) are localities where specimens uncertain.

specimens listed above), 43.4 mm for holotype listed by Chasen (1940) (Table 3.2.). The fur on dorsal surface is clearly divided into three bands, dark grey-brown at the base, light grey in the mid-part and grey brown at the tip (Figure 3.2A.). The ventral surface is divided into two bands, dark grey at the base and pale at the tip. The fur is sometimes dark orange adjacent to the muzzle. Each wing and the interfemoral are dark grey-brown. The nostrils are slightly protuberant and downward facing. The muzzle is hairly, except the upper and lower lips and around nostrils. The ears are large and virtually naked, the anterior border is convex and the tip is rounded off. The tragus is tall (9.0-9.4 mm) and slender, with a very small lobe (projection) on its posterior border; its tip is ill-pointed. In the wing, the fourth metacarpal (4MT: 40.9-45.5 mm) exceeds the fifth (5MT: 39.4-43.5 mm) in length, but is shorter than the third (3MT: 42.3-46.2 mm). The first phalanx of the third digit (3D1P: 20.2-22.8 mm) is relatively long (47.4-47.5%) of the length of the third metacarpal). The feet are relatively large and each wing membrane is attached to the base of the outer toe. The baculum is small, with a length of 0.7 mm. Its shape is triangular with long bifid proximal processes (Figure 3.3A.).

The skull is large with condylo-basal length of 16.2-16.5 mm (Table 3.7.). The mastoid width (MW: 8.6-9.0 mm) exceeds the breadth of the braincase (BB: 8.0-8.6 mm). When viewed in lateral profile, the skull has high braincase, without a depression on its parietal region (Figure 3.5B.); the anterior part of the braincase is not abruptly elevated above the rostrum. The braincase height (BH: 6.8-7.4 mm) is about 41.2-45.4% of the condylo-basal length. The sagittal crest is low. The rostrum is relatively long and narrow, without a sulcus. The narial pit of the rostrum is is U-shaped and well-developed. Each zygoma is narrow on its anterior part and with a well-defined dorsal process on it posterior part. In each half mandible, the coronoid process is well-developed (CPH: 4.6-4.9 mm) and exceeds the height of the lower canine.

The upper toothrow length (C-M^3) is 7.1-7.4 mm (7.6 mm for holotype) (Table 3.7.). The first upper incisor (I^2) is small, without a secondary cusp. The second upper incisor (I^3) is very small, about one third to one half the height of I^2 and equal in crown area; it is compressed between I^2 and the upper canine (C^1). The upper canine (C^1) is large and robust, with a well-defined cingulum on its internal border

and shallow longitudinal groove on its internal border. The first upper premolar (P^2) exceeds the second (P^3) in height, but is shorter than the third (P^4); P^2 exceeds P3 in crown area, but smaller than P^4; they are compressed in the toothrow. The first and second upper molars (M^1 and M^2) have a typical W-shaped cusp pattern, with well developed para-, meso- and metastyles. In the third upper molar (M^3), the metastyle is absent. The lower incisors are tricuspid, each with a well-developed central cusp; in the third (I_3) the outer cusps are less developed. The lower canine (C_1) is slender, with a well-defined cingulum on its antero-internal border and a shallow longitudinal groove on its posterior border. The first lower premolar (P_2) is slightly shorter than the second (P_3) in height, but exceeds the third (P_4); they are similar in crown area and compressed in the toothrow. In the lower molars, the protoconid and hypoconid are well-developed, especially in the first (M_1) and the second (M_2).

Taxonomic notes and comparison

Seven specimens were compared to the measurements of the taxon *malayana* Chasen, 1940, which are similar to the forearm length of 40.7-43.4 mm, mastoid width of 8.7 mm and braincase breadth of 8.4 mm, but slightly smaller skull length of 8.2-8.4 mm and upper toothrow length of 7.6 mm. In examination of a slightly damaged skull of the holotype of *malayana* (BM(NH).47.1438), it is similar size in some essentials (Table 3.7.) and closely resemble morphology to Thai and Malaysian specimens.

Chasen (1940) described the taxon *malayana* as a subspecies of *K. papillosa* Temminck, 1840 on the basis of its larger skull. However, Tate (1941) examined co-type ('a') of *K. papillosa* from Java and suggested that the race is not especially larger. Multivariate analyses based on nine external characters (Figure 3.1., Table 3.1.) and thirteen cranio-dental characters (Figure 3.4., Table 3.6.) show that specimens of *K. malayana* form a group that is discrete from *K. papillosa*.

In terms of skull morphology, *K. malayana* has a higher braincase than *K. papillosa* without a depression on its parietal region; the braincase is less abrupty elevated above the rostrum less abrupt. In terms of genetics, *K. malayana* is differentiated by 16.50% from *K. papillosa* (Figures 3.7. and 3.10., Table 3.8.).

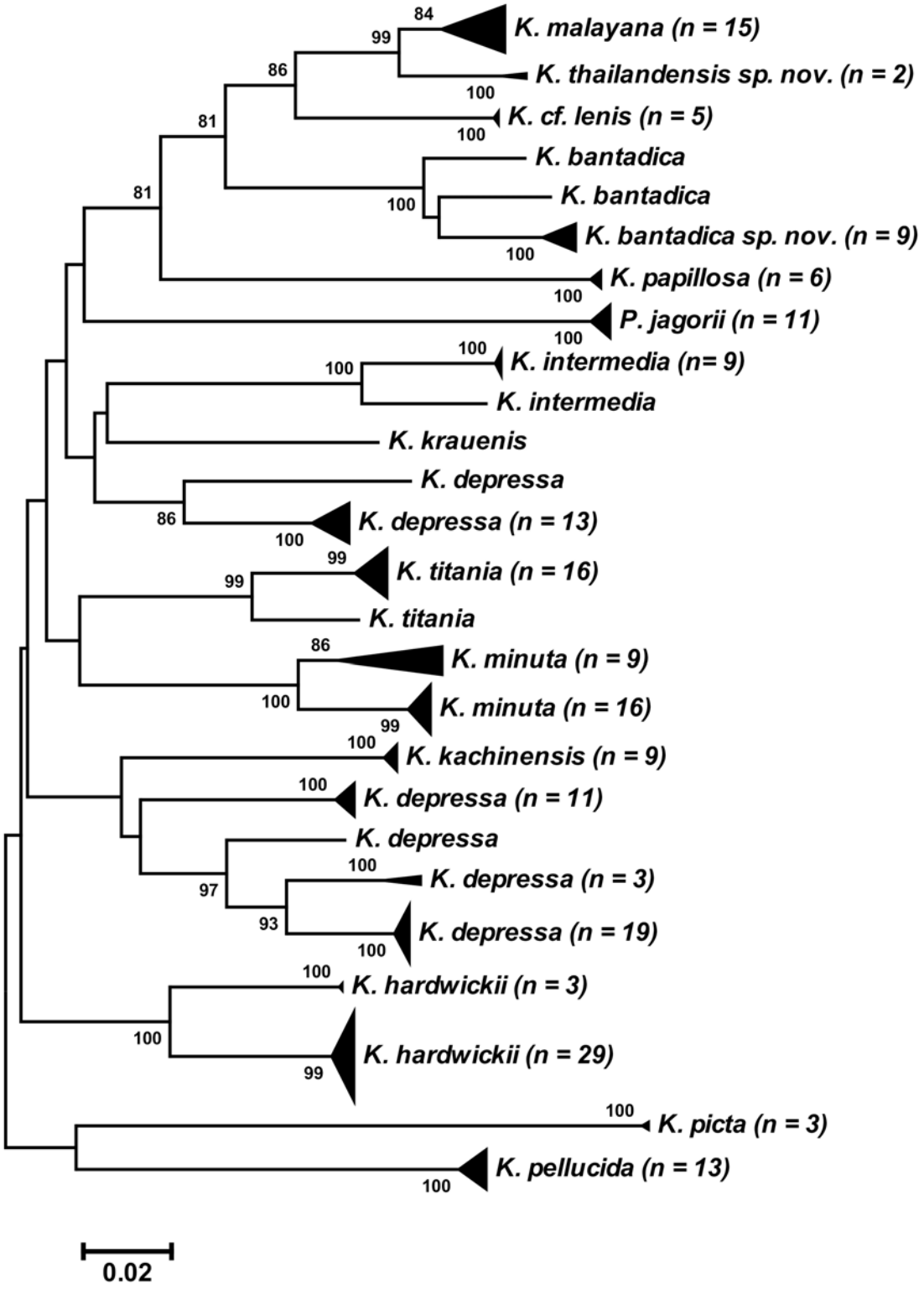

Figure 3.10. Neighbour-joining phylogeny based on cytochrome *c* oxidase (COI) sequences of *Kerivoula*, as well as *Phoniscus*, which included sequences from throughout region in the DNA Barcode of Life Database to comparison. Distance scale: 0.02.

The taxon *malayana* is similar in external characters to *K. lenis* Thomas, 1916, but the skull of *malayana* is larger in most but not all measurements (Figures 3.1., 3.4. and 3.8.; Tables 3.2. and 3.7.). The braincase of *K. lenis* is bulbous and it rises abruptly above the rostrum, whereas it is high but less abrupt in *malayana* (Figure 3.5.).

There is no genetic data, which can be unequivocally attributed to *K. lenis*. However, there are five sequences of specimens provisionally referred to *K. lenis* from Lao PDR (3 specimens) and Vietnam (2 specimens, initially referred to *K. papillosa*). They differ from *K. malayana* by 10.02% (Figures 3.7. and 3.10., Table 3.8.). However, the identification of these specimens from Lao PDR and Vietnam remains in doubt and they were not seen during the present study.

Distribution

As understood here, *Kerivoula malayana* is known from peninsular Thailand, Malaysia and Borneo (Figure 3.9.). In Thailand, it was collected from Songkhla Province: Kuan Khao Wang Forest Park (7°00'N, 100°18'E, 50 m a.s.l.) [loc. M1] (PSUZC Collection); Watershed Management Ranger, Khao Nam Khang National Park (6°06'N, 101°04'E, 73 m a.s.l.) [loc. M2] (HBWRS Collection); Satun Province: Taleban National Park (6°39'N, 100°09'E) [loc. M3] (PSUZC Collection); Narathiwat Province: Hala-Bala Wildlife Sanctuary (5°48'N, 101°50'E, 100 m a.s.l.) [loc. M4] (PSUZC Collection). In peninsular Malaysia, it was collected from Pahang State: Taman Negara (c.o. 4°30'N, 101°28'E) [loc. M5] (TTU Collection – GenBank); Krau Game Reserve (3°35'N, 102°10'E, 92 m a.s.l.) [loc. M6] (TTU Collection); Selangor-Pahang boundary: Ginting Bedai (c.o. 3°24'N, 101°50') [loc. M7 – type locality] (BM(NH) Collection); Johor State: Endau Rompin National Park (2°53'N, 103°26'E) [loc. M8] (ROM Collection – GenBank). In Borneo, it was collected from Sarawak: Niah National Park (c.o. 3°50'N, 113°20'E) [loc. M9] (TTU Collection – GenBank); Similajau National Park (c.o. 4°04'N, 113°52'E) [loc. M10] (UNIMAS Collection – GenBank).

Ecology and behaviour

In Thailand, *Kerivoula malayana* has been found in a variety of habitats at the

altitude of 50-100 m a.s.l., in tropical rainforest and lowland evergreen forest, as well as secondary forest. In Malaysia, it has been found in the area of lowland evergreen dipterocarp forest (Kingston et al., 1999). Late lactating female has been found in February.

***Kerivoula* spA.**

Description

This is a large *Kerivoula* with a forearm length of 42.1-42.3 mm (Table 3.2.). The fur on the dorsal surface is clearly divided into three bands, with dark grey-brown base, light grey at the mid-part and grey-brown tip (Figure 3.2B.). The ventral surface is divided into two bands, with dark grey base and paler or light brown tip, sometime paler with dark grey patch of the fur presents under chin. The wing and interfemoral membranes are dark grey-brown. The nostrils are slightly protuberant and downward facing. The muzzle is hairy, except the upper lip around the nostrils and lower lip. The ears are large and virtually naked, except a few short hairs presents on their posterior surface; the anterior border of each is convex; the tip is rounded off. The tragus is tall (10.0-10.4 mm); its anterior margin is slightly curve to the tip; its posterior margin is explained and convex around the base, with very small lobe (projection) at the base; the tip is round. In the wing, the fourth metacarpal (4MT: 41.7 mm) exceeds the fifth (5MT: 39.8-40.9 mm) in length, but shorter than the third (3MT: 44.1-44.2 mm). The first phalange of third digit (3D1P: 21.7-22.4 mm) is relatively long, about 49.1-50.6% of the length of the relative long third metacarpal. The feet are relatively large, with wing membrane attached to the base of the outer toe. The baculum is small, with a length of 0.7 mm. Its shape is narrow, triangular and characteristically bifid base; the base is slightly expanded with relatively short proximal processes; the tip is relatively narrow with rounded tip (Figure 3.3B.). In the dorsal profile, the baculum is curve from the middle downward to its sides.

The skull has a condylo-basal length of 15.7-15.9 mm (Table 3.7.). The mastoid width (MW: 8.4 mm) exceeds the breadth of the braincase (BB: 8.0-8.1 mm). When viewed in lateral profile; the braincase is flattened without depression on its

parietal region, less abrupt from the rostrum (Figure 3.5C.). The braincase height (BH: 6.5-6.7 mm), between 41.1-42.2% of the condylo-basal length. The sagittal crest is absent. The rostrum is relatively long and narrow, without sulcus. The narial pit of the rostrum is well-developed, it is U-shaped. Each zygoma is narrow with a small dorsal process on its posterior part. The basioccipital space is relatively broad (BOW: 1.7-1.8 mm). In each half of the mandible, the coronoid process is well-developed (CPH: 4.5-4.7 mm), exceeds the height of the lower canine (C_1).

The upper toothrow length (C-M^3) is 7.0-7.1 mm (Table 3.7.). The first upper incisor (I^2) is small, without second cusp. The second upper incisor (I^3) is very small, about one half the height of I^2 and equals in crown area; it is compressed between the upper canine (C^1) and I^2. The upper canine (C^1) is slender and robust, with a well-defined cingulum on its internal border and shallow longitudinal groove on its external border. The first upper premolar (P^2) exceeds the second (P^3) in the height, but shorter than the third (P^4); P^2 is similar to P^3 but smaller than P^4 in crown area; they are compressed in the toothrow, except P^3 which is slightly intruded from the toothrow. The first and second upper molars (M^1 and M^2) have a typical W-shaped cusp, with well-developed para-, meso- and metastyles. In the third upper molar (M^3), the metastyle is absent. The first and second lower incisors (I_1 and I_2) are tricuspid. In the third lower incisor (I_3); the central cusp is well-defined, with or without lateral cusps, if it is present it is very small. The lower canine (C_1) is small, with a well-defined cingulum on its antero-internal border and shallow longitudinal groove on its posterior border. The first lower premolar (P_2) is shorter than the second (P_3) in height, but similar to the third (P_4); P_2 is similar to P_3 but smaller than P_4 in crown area; they are compressed in the toothrow. In the lower molar, the protoconid and hypoconid are well-developed, especially in the second (M_2) and the third (M_3).

Proposed name

The proposed species name is *Kerivoula thailandensis* is derived from Thailand where the type series was collected and *ensis* (Latin for ‘belonging to’). Its proposed English name is ‘Thailand woolly bat’.

Comparison with other taxa

Kerivoula spA is smaller than those of *K. papillosa* in both external and skull (Figures 3.1., 3.4. and 3.8.; Tables 3.1., 3.2., 3.6. and 3.7.). The skull of *K. papillosa* has a high braincase whereas those of *Kerivoula* spA have more flattened (Figure 3.5.). Genetically, the sequences of *Kerivoula* spA is separated clustering from those of *K. papillosa* (Figures 3.7. and 3.10.), with genetic divergent > 17% (Table 3.8.).

Kerivoula spA is similar external measurements to those of *K. malayana* Chasen, 1940 (Table 3.2.). The colour of the pelage is similar between these two species, but sometimes with pale fur on the ventral surface in *K. malayana* (Figure 3.2.). The tragus of the latter taxon has a well-defined basal lobe on its posterior margin, whereas it lacks or very small in *Kerivoula* spA. The baculum is differentiated by triangular shape with more ill-pointed tip and wide base in the *K. malayana* (wider and more rounded tip and narrower base in *Kerivoula* spA) (Figure 3.3.). The skull of *Kerivoula* spA is clearly smaller than those of *K. malayana* (Table 3.7.). The skull is higher in *K. malayana*, whereas it is more flattened in *Kerivoula* spA (Figure 3.5.). In addition, the genetics is difference clustering between *Kerivoula* spA and *K. malayana* (Figures 3.7. and 3.10.), with 5.23% divergence from each other (Table 3.8.).

Kerivoula spA is larger external measurements than those of *K. lenis* Thomas, 1916 (Table 3.2.). The skull of the new species, *Kerivoula* spA, is similar in some metric characters to those of *K. lenis* but larger in some measurements (Table 3.7.). The skull of *Kerivoula* spA is more flattened with the braincase is less abrupt from the rostrum, whereas that of *K. lenis* is more bulbous with the braincase is abrupt from the rostrum (Figure 3.5.). No any genetics of *K. lenis* from India is available for the comparison. However, the genetics of material which would be referable to *K. lenis* from Lao PDR (originally referred to *K.* cf. *lenis*) and Vietnam (originally referred to *K. papillosa*) is different cluttering from that of *Kerivoula* spA (Figures 3.7. and 3.10.), with 9.29% divergence from each other (Table 3.8.).

Kerivoula spA is similar size to those of *K. kachinensis* Bates et al., 2004 (FA: 40.1-43.4 mm, CBL: 15.2-16.7 mm, C-M3: 6.2-7.2 mm) listed by Bates et al. (2004), Thong et al. (2006) and Soisook et al. (2007). Externally, *K. kachinensis* differs from those of *Kerivoula* spA by darker base of the fur. The tragus of *K. kachinensis* has a well-defined basal lobe on its posterior margin. The skull of *K. kachinensis* is flat

(BH: 5.2-5.9 mm – Bates et al., 2004; Soisook et al., 2007). The genetics of *K. kachinensis* is different clustering with those of *Kerivoula* spA, with > 22% divergence from each other (Figures 3.7. and 3.10., Table 3.8.).

Kerivoula spA is larger than those of *K. flora* Thomas, 1914a (FA: 37.0-39.0 mm, CBL: 14.3-14.9 mm and C-M^3: 6.1-6.2 mm); *K. myrella* Thomas, 1914b (FA: 37.5-38.5 mm, GTL: 13.8-14.6 mm and C-M^3: 5.8-6.1 mm); *K. hardwickii* Horsfield, 1824 (FA: 30.0-38.5 mm, CBL: 12.2-13.8 mm and C-M^3: 4.8-6.0 mm), which includes *fusca* Dobson, 1871, *depressa* Miller, 1906a, *engana* Miller, 1906b, *crypta* Wroughton and Ryley, 1913 and *malpasi* Phillips, 1932; *K. titania* Bates et al., 2007 (FA: 32.4-35.9 mm, CBL: 13.7-14.5 mm and C-M^3: 5.8-6.2 mm); *K. pellucida* Waterhouse, 1845 (FA: 28.5-33.5 mm, CBL: 12.5-13.0 mm and C-M^3: 5.3-5.6 mm), which includes *bombifrons* Lyon, 1911; *K. krauensis* Francis et al., 2007 (FA: 28.7-31.2 mm, CBL: 11.5-11.7 mm and C-M^3: 4.9-5.0 mm); *K. picta* Pallas, 1767 (FA: 32.5-39.0 mm, CBL: 12.7-13.8 mm and C-M^3: 5.1-6.0 mm), which includes *bellissima* Thomas, 1906; *K. whiteheadi* Thomas, 1894 (FA: 27.5-31.0 mm, CBL: 11.8-11.9 mm and C-M^3: 5.0 mm), which includes *pusilla* Thomas, 1894 and *bicolor* Thomas, 1904; *K. intermedia* Hill and Francis, 1984 (FA: 26.7-30.7 mm, CBL: 11.1-11.8 mm and C-M^3: 4.6-5.0 mm) and *K. minuta* Miller, 1898 (FA: 24.8-29.3 mm, CBL: 10.0-11.1 mm and C-M^3: 4.1-4.5 mm) listed by Thomas (1914b), Hill (1965), Hill and Rozendaal (1989), Corbet and Hill (1992), Bates et al. (2007), Francis et al. (2007) and Francis (2008) (Table 3.9.). Genetically, *Kerivoula* spA is separated clustering from most above species (Figure 3.10.), except *K. flora, K. myrella* and *K. whiteheadi* which the genetics available for comparison, with genetic divergent > 17%.

Distribution

To date, *Kerivoula* spA is only known from Mae Nam Pha Chi Wildlife Sanctuary, Ratchaburi Province, Thailand (13°18'N, 99°24'E) [loc. T1, Figure 3.9.] (PSUZC Collection).

Ecological notes

Kerivoula spA was collected in the harp traps which were set across a seasonal

Table 3.9. Character matrix of eighteen species of *Kerivoula* currently recognized from Asia. Data is based on the present study, Thomas (1914b), Hill (1965), Hill and Rozendaal (1989), Corbet and Hill (1992), Bates et al. (2004), Thong et al. (2006), Bates et al. (2007), Soisook et al. (2007), Francis et al. (2007) and Francis (2008).

No	Species	FA	CBL	C-M^3	Distribution
1	*K. papillosa*	42.6-44.5	16.9-17.6	7.4-7.9	Sumatra, Java and Borneo
2	*K. malayana*	39.5-43.4	16.2-16.5	7.0-7.6	Thailand, Malaysia and Borneo
3	*Kerivoula* spA	39.4-42.3	15.4-15.9	6.8-7.1	Thailand
4	*Kerivoula* spB	38.0-42.0	15.3-16.2	6.5-7.2	Thailand, Malaysia, Sumatra and Borneo
5	*K. lenis*	38.8-41.0	15.7	6.7	India
6	*K. kachinensis*	40.1-43.4	15.2-16.7	6.2-7.2	South-east Asia
7	*K. flora*	37.0-39.0	14.3-14.9	6.1-6.2	Borneo, Lesser Sunda
8	*K. myrella*	37.5-38.5	13.8-14.6	5.8-6.1	Lesser Sundas, Papua New Guinea
9	*K. agnella*	34.5-37.5	13.8	5.7-6.0	Papua New Guinea
10	*K. hardwickii*	30.0-38.5	12.2-13.8	4.8-6.0	Sri Lanka, India to Philippines
11	*K. titania*	32.4-35.9	13.7-14.5	5.8-6.2	South-east Asia
12	*K. pellucida*	28.5-33.5	12.5-13.0	5.3-5.6	Thailand to Philippines
13	*K. krauensis*	28.7-31.2	11.5-11.7	4.9-5.0	Thailand and Malaysia
14	*K. picta*	32.5-39.0	12.7-13.8	5.1-6.0	Sri Lanka, India to Moluccas
15	*K. muscina*	32.4	12.8	5.7	New Guinea
16	*K. whiteheadi*	27.5-31.0	11.8-11.9	5.0	Thailand to Philippines
17	*K. intermedia*	26.7-30.7	11.1-11.8	4.6-5.0	Malaysia, Borneo
18	*K. minuta*	24.8-29.3	10.0-11.1	4.1-4.5	Thailand, Malaysia, Borneo

stream at an altitude of 431 metres in primary evergreen forest. The Wildlife Sanctuary is characterised by steeply rugged mountains which are parts of the Tenasserim Mountain Range, with the Pha Chi River runs through the western part of the sanctuary. The forest types in the wildlife sanctuary also compresses of dry evergreen, mixed deciduous and dipterocarp forest (Soisook et al., 2010).

***Kerivoula* spA subspA.**

Description

Kerivoula spA subspA has a forearm length of 39.4-40.2 mm (Table 3.2.). The fur on the dorsal surface is divided into the bands: dark grey base, pale at the mid-part and slightly dark grey-brown tip. Ventral surface is two colour bands: dark grey base and paler grey-brown tip (Figure 3.2C.). The colour on the ventral is sometime light brown under chin. The wing and interfemoral membrane are dark grey. The nostrils are slightly protuberant and downward facing. The muzzle is hairy, except the upper lip around the nostril and lower lip. The ears are large and virtually naked, except a few short hairs presents on their posterior surface; the anterior border of each is convex and the tip is rounded off. The tragus is tall (TL: 8.4-9.8 mm); its anterior margin is slightly curve to the tip and its posterior margin is explained and convex around the base, with a small lobe (projection) at the base; the tip is round. In the wing, the fourth metacarpal (4MT: 42.3-43.0 mm) exceeds the fifth (5MT: 40.4-40.9 mm) in length, but shorter than the third (3MT: 42.9-44.2 mm). The first phalanx of third digit (3D1P: 18.9-21.1 mm) is relatively short, between 44.0-47.9% of the length of the relative long third metacarpal. The feet are relatively large, with wing membrane attached to the base of the outer toe.

The skull has a condylo-basal length of 15.4-15.8 mm (Table 3.7.). The mastoid width (MW: 8.1 mm) exceeds the breadth of braincase (BB: 7.4-7.7 mm). When view in lateral profile, the skull has flattened braincase and slightly slopes backward to the lambda (Figure 3.5D.). The braincase height (BH: 6.3-6.7 mm) is about 40.1-43.2% of the condylo-basal length. The sagittal crest is very low. The rostrum is relatively long and narrow, without sulcus. The narial pit of the rostrum is

well-developed, it is U-shaped. Each zygoma is narrow with a small dorsal process on its posterior part. The basioccipital space is relatively broad (BOW: 1.7-1.8 mm). In each half of the mandible, the coronoid process is well-developed (CPH: 4.3-4.5 mm), exceeds the height of the lower canine (C_1).

The upper toothrow length (C-M^3) is 6.8-7.0 mm (Table 3.7.). The first upper incisor (I^2) is small, without second cusp. The second upper premolar (I^3) is very small, about one half the height of I^2 and slightly exceeds I^2 in crown area; it is compressed between I^2 and the upper canine (C^1). The upper canine (C^1) is relative large, with a small cingulum on its antero-internal border and a shallow longitudinal groove on its internal border. The first upper premolar (P^2) exceeds the second (P^3) in height, but shorter than the third (P^4); P^2 exceeds or equals to P^3 in crown area, but smaller than P^4; they are compressed in the toothrow. the first and second upper molar (M^1 and M^2) have a typical W-shaped cusp, with well-developed para-, meso- and metastyles. In the third upper molar (M^3), the metastyle is absent. The lower incisors are tricuspid, with well-developed the central cusp, especially in the third lower incisor (I_3); in I_3, the outer cusps are less developed. The lower canine (C_1) is slender, with a well-defined cingulum on its antero-internal border and a shallow longitudinal groove on it posterior border. The second lower premolar (P_3) is slightly shorter than the first (P_2) in height, but slightly exceeds the third (P_4); they equal in crown area and are compressed in the toothrow. In the lower morlas, the protocolnid and hypoconid are well-developed, especially in the first (M_1) and the second (M_2).

Proposed name

The proposed subspecies name is *Kerivoula thailandensis minimus* which is derived from its diagnostically smaller size than the nominate race (Latin for *minimus*).

Comparison with other taxa

Kerivoula spA subspA is smaller size than the nominate race *Kerivoula* spA (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.4., 3.6. and 3.7.). The fur colour is the same as the nominate race (Figure 3.2.). The skull of *Kerivoula* subspA is more flattened than in the nominate race (Figure 3.5.). Genetically, *Kerivoula* subspA is clustered

with that of the nominate race with the genetic different 1.08% (Figure 3.7.; Table 3.8.).

Similar to the nominate race *Kerivoula* spA, the new subspecies *Kerivoula* spA subspA is smaller than those of *K. papillosa* in both external and skull (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.4., 3.6. and 3.7.). The skull of *K. papillosa* has a high braincase whereas those of *Kerivoula* spA subspA have more flattened braincase (Figure 3.5.). The genetics of *Kerivoula* spA subspA is clustered together with that of *Kerivoula* spA which is separated from those of *K. papillosa* (Figure 3.7.; Table 3.8.).

The new subspecies, *Kerivoula* sp A subspA, is overlap external size to those of *K. malayana*, but smaller skull size than those of the latter taxon (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.4., 3.6. and 3.7.). The skull of the latter species is higher than those of the new subspecies (Figure 3.5.). The genetic of the new subspecies is separated from those of *K. malayana* with the genetic different > 5% (Figure 3.7.; Table 3.8.).

The new subspecies, *Kerivoula* spA subspA is similar in both external and skull size to those of *K. lenis* (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.4. and 3.6.). The skull of *K. lenis* is more bulbous and higher than the new subspecies (Figure 3.5.). For further detail of comparison to other *Kerivoula* see in the nominate race *Kerivoula* spA.

Distribution

To date, *Kerivoula* spA subspA is only known from peninsular Thailand, where it was collected from South Klom Luang Chumporn Wildlife Sanctuary, Ranong Province, Thailand (10°31'N, 98°54'E; 67 m a.s.l.) [Loc. T2, Figure 3.9.] (PSUZC Collection) and Hala-Bala Wildlife Sanctuary, Narathiwat Province, Thailand (5°48'N, 101°50'E, 100 m a.s.l.) [loc. T3, Figure 3.9.] (PSUZC Collection).

Ecological notes

The holotype was caught by harp trap set across a small stream in the secondary forest, at altitude of 67 m, which is surrounded by fruit orchards and rubber plantations. Other material was also caught by harp traps set on natural trail under

forest storey in the lowland tropical rainforest nearby peat swamp forest, at an altitude of 100 m.

Kerivoula spB.

Description

Kerivoula spB has a forearm length of 39.1-40.2 mm (Table 3.2.). The fur on the dorsal surface varies from grey to brown-grey, it is divided into three bands: dark grey base, pale at the mid-part and grey or brown-grey tip (Figure 3.2D.). On the ventral surface is paler than those on the dorsal surface, it is divided into bands: dark grey base and paler grey or brown-grey tip. The wing and interfemoral membranes are dark grey. The nostrils are slightly protuberant and downward facing. The muzzle is hairy, except the upper lip around the nostrils and lower lip. The ears are relatively large and virtually naked, except a few short hairs presents on their posterior surface; the anterior border of each is convex; the tip is rounded off. The tragus is slender and relatively long (8.2-10.4 mm); its anterior margin is slightly curve to the tip; its posterior margin is explained and convex around the base, with very small lobe (projection) on it base. In the wing, the fourth metacarpal (4MT: 41.8-43.6 mm) exceeds the fifth (5MT: 40.4-42.4 mm) in length, but shorter than the third (3MT: 42.8-44.8 mm). The first phalanx of third digit (3D1P: 19.2-21.6 mm) is relatively short, between 44.0-50.6 % of the length of the relative long third metacarpal. The feet are relatively large, with wing membrane attached at the base of outer toe. The baculum is small, with a length of 0.7-0.8 mm. It is triangular shape, narrow tip and broadly explained base; it is bifid base with short, broad or narrow proximal processes (Figure 3.3C&D.). In dorsal profile, the baculum is curve from the middle downward to its sides.

The skull has a condylo-basal length of 15.5-16.2 mm (Table 3.7.). The mastoid width (MW: 8.1-8.6 mm) exceeds the breadth of braincase (BB: 7.5-8.1 mm). When viewed in lateral profile, the braincase is high and domed-shaped, sometimes is slightly flattened, with slopes backward on its parietal region (Figures 3.5E. and 3.6.). The braincase height (BH: 6.6-7.3 mm) is 41.2-45.5% of the condylo-basal length.

The sagittal crest is very low or absent. The rostrum is relatively short and narrow, without sulcus. The narial pit of the rostrum is well-developed, it is U-shaped. Each zygoma is narrow with a well-defined dorsal process on its posterior par. The basioccipital space is relatively broad (BOW: 1.6-2.0 mm). In each half mandible, the coronoid process is well-developed (CPH: 4.5-4.9 mm), exceeds the height of the lower canine (C_1).

The upper toothrow length (C-M^3) is 6.8-7.2 mm (Table 3.7.). The first upper incisor (I^2) is small, without second cusp. The second upper incisor (I^3) is very small, about one third to one half the height of I^2 and equal in crown area; it is compressed between I^2 and the upper canine (C^1). The upper canine (C^1) is relative small, with a small cingulum on its antero- and postero-internal border and shallow longitudinal groove on its internal border. The first upper premolar (P^2) exceeds the second (P^3) in height, slightly exceeds or shorter than the third (P^4); P^2 is slightly exceeds P^3 in crown area, but much smaller than P^4; they are compressed in the toothrow. The first and second upper molars (M^1 and M^2) have a typical W-shaped cusp, with well-developed para-, meso- and metastyles. In the third upper molar (M^3), the metastyle is absent. The lower incisors are tricuspid, with well-defined central cusp, especially in the third (I_3); in I_3, the outer cusps are less developed. The lower canine (C_1) is slender, with a small cingulum on its antero-internal border and a shallow longitudinal groove on its posterior border. The first lower premolar (P_2) slightly exceeds or equals to the second (P_3) in height; the third (P_4) is slightly shorter or equals to P_2 and P_3; they equal in crown area and are compressed in the toothrow. In the lower molars, the protocolnid and hypoconid are well-developed, especially in the first (M_1) and the second (M_2).

Proposed name

The proposed species name is *Kerivoula* spB which is derived from Khao Bantad Mountain, Thailand where the most specimens were collected and *ica* (Latin for ‘belonging to’). Its proposed English name is ‘Khao Bantad woolly bat’.

Comparison with other taxa

Thai specimens of *Kerivoula* spB include two morphotypes which are similar

size, but mainly different baculum and skull morphology (Figures 3.3. and 3.6.). However, the genetic analysis shows that the sequences of Thai specimens are clustered in one monophyletic clade (Figure 3.7.), with genetic divergent of 1.07 % (Table 3.8.). Specimens from peninsular Malaysia and Sumatra correspond skull morphology to one of Thai specimens. In addition, the sequences of specimens from peninsular Malaysia are clustered with those from Thailand (Figure 3.7.). Two specimens from Borneo also correspond to other type of Thai specimens. However, the genetics of specimens from Borneo are separated clustering from those of Thai specimens (Figure 3.7.), with the genetic divergent of 6.95 % (Table 3.8.). In addition, specimens of *Kerivoula* spB from Thailand are larger size than those from peninsular Malaysia, Sumatra and Borneo in both external and skull (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.5., 3.6. and 3.7.).

Kerivoula spB is smaller than those of *K. papillosa* in both external and skull (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.5., 3.6. and 3.7.). The skull of *Kerivoula* spB is more bulbous and more domed braincase with the parietal region slopes backward whereas the skull is high and without depression on its parietal region in those of *K. papillosa* (Figure 3.5.). In addition, the genetics of *Kerivoula* spB is separated clustering from those of *K. papillosa* (Figures 3.7. and 3.10.) with genetic divergent > 17 % (Table 3.8.).

Thai specimens of *Kerivoula* spB is similar external characters to those of *K. malayana*, but those from peninsular Malaysia, Sumatra and Borneo are smaller than those of *K. malayana* (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.3., 3.6. and 3.7.). The baculum is similar in size but different morphology, the baculum of *Kerivoula* spB is triangular with small and short proximal processes and sometimes with parallel around the tip, it is triangular with long proximal processes in *K. malayana* (Figure 3.3.). The skull of *Kerivoula* spB is bulbous and domed braincase with slope backward on its parietal region, whereas it is high and without depression on it parietal region in *K. malayana* (Figure 3.5.). In addition, the genetics of *Kerivoula* spB is separated clustering from those of *K. malayana* (Figures 3.7. and 3.10.) with genetic difference > 13 % (Table 3.8.).

Thai specimens of *Kerivoula* spB is similar in both external and skull to those of *Kerivoula* spA, but those from peninsular Malaysia, Sumatra and Borneo are

averaged smaller than *Kerivoula* spA (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.6. and 3.7.). *Kerivoula* spB is similar external size to those of *Kerivoula* spA subspA but average larger skull (those from peninsular Malaysia, Sumatra and Borneo average smaller than *Kerivoula* spA subspA). The baculum of *Kerivoula* spB is more explained base than that of *Kerivoula* spA but narrower tip (Figure 3.3.). The skull of *Kerivoula* spA is more bulbous and domed braincase than those of *Kerivoula* spB (Figure 3.5.). Genetically, the sequences of *Kerivoula* spB are separated clustering from those of *Kerivoula* spA (Figures 3.7. and 3.10.) with genetic different > 12 % (Table 3.8.).

Specimens of *Kerivoula* spB are similar size to those of *K. lenis* (Figures 3.1. and 3.4.; Tables 3.1., 3.2., 3.6. and 3.7.). The skull of *Kerivoula* spB is domed braincase with slopping backward on its parietal region, whereas it is bulbous and without depression on its parietal region (Figure 3.5.). There is no genetics available for specimens of *K. lenis* from India in the present study. However, the sequences of specimens from Lao PDR and Vietnam which would be referable to *K. lenis* are separated clustering from those of *Kerivoula* spB (Figures 3.7. and 3.10.) with genetic different > 15 % (Table 3.8.).

Kerivoula spB average smaller than those of *K. kachinensis* listed by Bates et al. (2004), Thong et al. (2006) and Soisook et al. (2007). The fur of *K. kachinensis* is darker base and the tragus has a well-defined basal lobe on its base. The skull of *Kerivoula* spB is high whereas that of *K. kachinensis* is flat. Genetically, those of *Kerivoula* spB are separated clustering from those of *K. kachinensis* (Figures 3.7. and 3.10.) with genetic divergent > 21 % (Table 3.8.).

Some specimens of *Kerivoula* spB have a similar forearm (39.5 mm), third metacarpal (40.0 mm), first phalanx of third digit (19.0 mm), mastoid width (10.0 mm) and breadth of braincase (8.0 mm) to holotype of *K. flora* Thomas, 1914, but larger skull length (16. mm), anterior palatal width (3.8 mm) and upper toothrow length (6.3 mm).

Similar to *K. flora*, specimens of *K. myrella* Thomas, 1914 listed in type description has a similar forearm (37.5-38.5 mm), third metacarpal (40.0 mm) and breadth of braincase (7.7 mm) to some specimens of *Kerivoula* spB, but shorter first

phalanx of third digit (17.2 mm), skull length (14.6), anterior palatal width (3.9 mm) and upper toothrow length (6.1 mm).

Kerivoula spB is also larger than *K. hardwickii*, *K. titania, K. pellucida, K. krauensis, K. picta, K. whiteheadi, K. intermedia* and *K. minuta* (Corbet and Hill, 1992; Bates et al., 2007; Francis et al., 2007; Francis, 2008) (Table 3.9.) and the genetics is also separated from those of above taxa (Figure 3.10.).

Distribution

To date, *Kerivoula* spB is known from Thailand, Malaysia, Sumatra and Java (Figure 3.9.). In Thailand, it was collected from Krabi Province: Khao Pra-Bang Kram Wildlife Sanctuary (7°55'N, 99°15'E) [loc. B1] (PSUZC Collection); Trang Province: Khao Chong Wildlife Education Centre, Khao Bantad Wildlife Sanctuary (7°33'N, 99°46'E) [loc. B2] (PSUZC Collection); Satun Province: Phu Pha Phet Ranger Station, Khao Bantad Wildlife Sanctuary (7°07'N, 100°00'E) [loc. B3] (PSUZC Collection); Narathiwat Province: Hala-Bala Wildlife Sanctuary (5°48'N, 101°50'E, 100 m a.s.l.) [loc. B4] (PSUZC Collection). In Malaysia, it is collected from Pahang State: Krau Game Reserve (3°35'N, 102°10'E, 92 m a.s.l.) [loc. B5] (TTU Collection); Johor State: Endau Rompin National Park (2°53'N, 103°40'E) [loc. B6) (ROM Collection – GenBank). In Sumatra: Lampung: Way Canguk (c.o. 5°16'N, 104°10'E) [loc. B7, Figure 3.8.] (MZB Collect-ion). Borneo: Sarawak: Kubah National Park (1°36'N, 110°11'E, 139 m a.s.l.) [loc. B8] (TTU Collection); Sabah: Sepilok Forest Reserve (5°85'N, 117°96E) [loc. B9] (ROM Collection – GenBank); Central Kalimantan: Tanjung Puting National Park (approx. 2°16'S, 112°00'E) [loc. B10] (HZM Collection).

Ecology and behaviour

In Thailand, *Kerivoula* spB was collected at a variety of forest types, including secondary forest to primary tropical rainforest. It tends to be tolerant of disturbed habitats. In Malaysia, it was collected in the area of lowland evergreen dipterocarp forest (Kingston et al., 1999). Late lactating females have been found in March, April and May.

3.5. DISCUSSION

The study supports that the bats formerly referred to *K. papillosa* and *K. lenis* are species complex. It also supports the view of Francis (2008), Anwarali et al. (2010), Francis et al. (2007; 2010) and Hasan and Abdullah (2011). The specimens here referred to *K. papillosa* are not clear whether they referable to true *K. papillosa* or yet undescribed species. According to Dobson (1876) and Tate (1941), the specimens formerly referred to *K. papillosa* type L[arge] in Anwarali et al. (2010) and Hasan and Abdullah (2011) would be referable to true *K. papillosa* based on more similar size to the type specimens than those referable here (Tables 3.2. and 3.7.). However, without additional studies, especially in the type locality of *K. papillosa*, it is very difficult to conclude which taxon is referable to *K. papillosa*. Further studies, including morphological and molecular analysis of type specimen and material from type locality would be help resolve the taxonomic problem of these taxa.

In addition, the morphology indicates that specimens here are referred to *Kerivoula* spB included two taxa (Figures 3.3. and 3.6.), which were found sympatrically at three localities (Khao Pra-Bang Kram Wildlife Sanctuary in Krabi Province [loc. B1, Figure 3.9.], Khao Chong Wildlife Research Centre in Trang Province [loc. B2, Figure 3.9.], and Hala-Bala Wildlife Sanctuary in Narathiwat Province [loc. B4 Figure 3.9.]). However, the genetic analysis based on COI is clustered together in one clade (Figure 3.7.). Although, the present genetic study is based on a single gene which it is not a sufficient for species recognition (Baker and Bradley, 2006). A combination of multiple data set of gene would be of considerable interest to help resolve of incomplete lineage sorting or introgression through a past hybridization of genetic variation within species (Anwarali et al., 2010; Francis et al., 2010).

The genetic analysis also shows that specimens from peninsular Thailand and Malaysia are distinct clusters from those of Borneo with > 6% divergence from each other (Figures 3.7. and 3.10.; Table 3.8.). An examination of specimens from peninsular Malaysia and Borneo shows that these specimens closely resemble in size, but differ in skull morphology. These two morphotypes are the same as two types of Thai specimens. It suggests that these two morphotypes could represent different taxa.

However, the cytochrom *b* analysis of specimens from peninsular Malaysia and Borneo is only 3.9% different from each other (see Table 1 in Anwarali et al., 2010).

In terms of *K. lenis*, it was known from India, Malaysia and Borneo (Vanitharani et al., 2003; Francis, 2008; Anwarali et al., 2010; Hasan and Abdullah, 2011). The present study shows that *K. lenis* is only restricted to India and the specimens from Malaysia and Borneo represent to other taxon, which is here primarily classified to *K. papillosa*. The taxonomic status of material from Lao PDR and Vietnam is not clear whether it is referable to true *K. lenis* or yet undescribed species. The genetic analysis shows that the material from Lao PDR and Vietnam is different from those of formerly referred to *K. lenis* from Malaysia and Borneo. However, those specimens are not available to examine in the present study. It is clear that further studies, including molecular analysis of material from India and morphological analysis of specimens from Lao PDR and Vietnam would be help to assign the name for these specimens.

CHAPTER 4

A Morphological and Phylogenetic Analysis of *Kerivoula hardwickii* species Complex (Chiroptera: Vespertilionidae) from Southeast Asia

ABSTRACT

Currently, *Kerivoula hardwickii* is considered to be a widespread species, which includes multiple subspecies. However, recent genetic analysis suggests that it is a species complex, comprising several distinct taxa, which exhibit many similar morphological features. The assigning of the correct name to each of these taxa is complicated by the paucity of detail in most of the type descriptions and the poor condition of the holotypes themselves, a number of which are damaged. In the current paper, material is assigned two distinct species complexes, *K. hardwickii* and *K. depressa*. Their amended descriptions, distribution and ecology are included. In addition, the taxonomic status of each is discussed.

4.1. INTRODUCTION

Kerivoula hardwickii Horsfield, 1824 was described from Java. According to Corbet and Hill (1992), its range extends from Sri Lanka and India to South China, throughout Southeast Asia to the Philippines and Lesser Sunda Islands. Hill (1965) recognised several distinct forms but his view was not followed by Corbet and Hill (1992) or Simmons (2005). However, recent studies show that bats referred to this species do include multiple forms, which although closely similar in morphology, differ genetically (Francis, 2008; Francis et al., 2010).

Dobson (1876) included the taxon *K. fusca* Dobson, 1871, unknown locality, as a synonym of *K. hardwickii*. Subsequently, Chasen (1940) considered the taxon *K. engana* Miller, 1906b from Enggano Island, western Sumatra to be a subspecies. Tate (1941) suggested that seven taxa appeared to be "closely allied to *hardwickii* (as opposed to *pusilla* and its relatives)". In addition to *fusca* and *engana,* these included *flora* Thomas, 1914 from Flores, Lesser Sunda Islands, Indonesia; *whiteheadi*

Thomas, 1894 from Luzon, Philippines; *depressa* Miller, 1906a from south-eastern Myanmar; *crypta* Wroughton and Ryley, 1913 from southern India and *malpasi* Phillips, 1932 from central Sri Lanka. Later, Ellerman and Morrison-Scott (1951) included the taxon *fusca* as a synonym of *K. h. hardwickii* and the forms *depressa, crypta* and *malpasi* as subspecies of *K. hardwickii*. The taxa *engana, flora,* and *whiteheadi* were omitted as they were extralimital to the study area of their research.

Hill (1965) also considered the taxon *fusca* to be a synonym of the nominate race *hardwickii.* He included the taxa *depressa, engana, flora, crypta* and *malpasi* as subspecies. Subsequently, Hill and Rozendaal (1989) considered the taxon *flora* as a distinct species based on its larger size, relatively longer and narrower rostrum, and relatively narrower palate. Corbet and Hill (1992) noted that the specimens of *K. hardwickii* from the western part of the range (from India to Vietnam) have skulls with a relatively flattened braincase. Later, Bates and Harrison (1997) referred material of *K. hardwickii* from the Indian Subcontinent to the taxon *depressa* and included the taxa *crypta* and *malpasi* as synonyms of this subspecies. Recently, Bates et al. (2007) suggested that the taxon with a smaller, flat skull (braincase height (BH) < 5.1 mm) may prove to be a valid species and that the correct name would be *K. depressa* and that with a slightly larger, domed skull (BH > 5.1 mm) would be *K. hardwickii*.

In the present study, new and previous material of *K. hardwickii* from mainland Southeast Asia (Myanmar, Thailand, Lao PDR, Vietnam and Cambodia) is examined in detail, using a combination of morphological and genetic information. This study is primarily based on specimens in natural history museum collections and a thorough review of the existing literature.

4.2. MATERIAL AND METHODS

4.2.1. Measurements

Ninety-six specimens were measured. They are held in the collections of Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University, Thailand (PSUZC); Harrison Institute, UK (HZM); Centre for

Biodiversity Conservation, Royal University of Phnom Penh, Cambodia (CBC) and Faculty of Environmental Sciences, National University of Laos, Lao PDR (FES).

Measurements were taken with a digital caliper, except body mass which is taken with a Pesola spring balance, and followed Bates and Harrison (1997), Bates et al. (2004) and Zubaid and Davison (1987). Measurements included: HB: head and body – from the tip of the snout to the anus, ventrally; FA: forearm length – from the extremity of the elbow to the extremity of the carpus with the wing folded; EL: ear length – from the lower border of the external auditory meatus to the tip of the pinna; TG: tragus length – from the base of the tragus to the extremity of the tip; TL: tail length – from the tip of the tail to its base adjacent to the anus; TIB: from the knee joint to the extremity of the heel behind the os calcis; HF: foot – from the extremity of the heel behind the os calcis to the extremity of the longest digit, not including the hairs or claws; 3MT, 4MT, 5MT: third, fourth, fifth metacarpal length, respectively – from the extremity of the carpus to the distal extremity of the third, fourth and fifth metacarpal respectively; 3D1P, 3D2P, 4D1P, 4D2P: first and second phalanges of the third and fourth digits, respectively – from the proximal to the distal extremity of the phalanges; W: body mass (in gram); BL: baculum length – from the extremity of the longest proximal process to the tip of the baculum; GTL: greatest length of the skull – from the greatest antero-posterior diameter of the skull, from the most projecting point at each extremity regardless of what structure forms this points; CCL: condylo-canine length – from the exoccipital condyle to the anterior alveolus of the canine; CBL: condylo-basal length – from the exoccipital condyle to the alveolus of the anterior incisor; MW: mastoid width – the greatest distance across the mastoid region; ZB: zygomatic breadth – the greatest width of the skull across the zygomata; BB: breadth of the braincase – width of the braincase at the posterior roots of the zygomatic arches; BH: braincase height – from the basisphenoid to the highest part of the skull; PC: postorbital constriction – the narrowest width across the constriction posterior to the orbits; ML: mandible length – from the most posterior part of the condyle to the most anterior part of the mandible, including the lower incisors; C^1-C^1: anterior palatal width – taken across the outer borders of the upper canine; M^3-M^3: posterior palatal width – taken across the outer borders of the third upper molar; C-M^3: upper toothrow length – from the front of the upper canine to the back of the

crown of the third upper molar; C-M_3: lower toothrow length – from the front of the lower canine to the back of the crown of the third lower molar.

4.2.2. Morphological analysis

To determine whether there was sexual dimorphism within each taxon and significant differences in metric characters between the taxa, a series of *t*-tests were run at a confidence limit of 95%. Principal Component Analysis (PCA) performed on the correlation matrix was used for multivariate comparison.

4.2.3. Genetic analysis

DNA data were collected following the standard protocols of DNA extraction, gene amplification and nucleotide sequencing as presented in Anwarali et al. (2010) and Francis et al. (2010). The sequences referable to *K. hardwickii* from South China and Southeast Asia in the DNA Barcode of Life Database (www.boldsystems.org) were reversed and used for comparison. These sequences are published in Anwarali et al. (2010), Francis et al. (2010) and Kruskop (2011), together with additional sequences of *K. titania* and *K. pellucida.* Phylogenetic analyses were performed using Neighbour-joining (NJ) with Kimura 2-parameters (K2) model in the software MEGA version 5.1 (Kimura, 1980; Tamura et al., 2011). 1,000 replications were used for bootstrap support value. The genetic distance between and within taxa was generated using the Kimura 2-parameter (K2) model in the software MEGA version 5 (Kimura, 1980; Tamara et al., 2011).

4.3. RESULTS

4.3.1. Morphometrics

External measurements were available for 93 specimens from throughout Southeast Asia. Following Bates et al. (2007), they were initially classified as 'domed-skull' (*hardwickii, engana,* and *fusca*) and 'flat-skull' (*depressa, crypta,* and *malpasi*) types. Significant variation in external measurements between the sexes was found in eight characters for material with 'domed-skull' type and five characters for material with 'flat-skull' type (Table 4.1.). The material with 'domed-skull' type is

Table 4.1. External measurements (in mm) and body mass (in g) of *K. hardwickii* and *K. depressa*, including the type series. HB – head and body; FA – forearm; EL – ear; TL – tail; TIB – tibia; HF – foot; 3MT, 4MT, 5MT – third, fourth, fifth metacarpals, respectively; 3D1P, 3D2P, 4D1P, 4D2P – first and second phalanges of third and fourth digits, respectively; W: body mass. Minimum, maximum, mean and standard deviation; sample sizes differing from those reported under *n* are given in parentheses. *T*-test comparison for sexual dimorphism (sex. dim.; ns = not significant difference). Measurements of type series based on literature records; Dobson (1871) for *K. fusca*, Dobson (1876) for *K. hardwickii*, Miller (1906a) for *K. depressa*, Miller (1906b) for *K. engana*, Wroughton and Ryley (1913) for *K. crypta* and Phillips (1932) for *K. malpasi*.

n	Sex	HB	FA	EL	TL	TIB	HF	3MT	4MT	5MT
taxa with 'domed-skull' (sensu Bates et al., 2007)										
Kerivoula hardwickii Holotype										
1	?	–	30.5	12.7	–	15.2	–	–	–	–
Kerivoula fusca Holotype										
1	?	40.6	33.0	11.4	40.6	15.2	–	–	–	–
Kerivoula engana Holotype										
1	♂	43.0	33.0	13.0	42.0	17.6	8.0	–	–	–
Kerivoula hardwickii										
40	♂♂	32.0-41.5	28.9-34.5	11.4-15.0	35.6-45.8	15.6-18.9	6.5-8.4	32.1-37.2	30.9-35.6	30.0-34.7
		37.1, 2.0	32.5, 1.2	13.0, 0.8	40.9, 2.6	17.4, 0.7	7.5, 0.4	34.5, 1.1	33.6, 1.1	32.3, 1.1
22	♀♀	34.6-41.3	32.0-35.7	10.7-14.7	37.6-47.9	15.4-19.4	6.8-8.4	34.0-38.1	33.2-37.6	32.3-35.9
		38.0, 1.8	33.9, 1.0	13.0, 0.9	43.3, 2.9	17.8, 0.8	7.7, 0.4	36.0, 1.2	35.2, 1.1	34.0, 0.9
Sex. dim.		ns	<0.01	ns	<0.01	ns	ns	<0.01	<0.01	<0.01

Table 4.1. Continued.

n	Sex	HB	FA	EL	TL	TIB	HF	3MT	4MT	5MT
taxa with 'flat-skull' (sensu Bates et al., 2007)										
Kerivoula depressa Holotype										
1	♀	32.6	32.8	11.6	42.8	15.4	6.0	–	–	–
Kerivoula crypta Holotype										
1	♂	44.0	31.5	12.5	42.0	16.0	7.0	31.0	–	–
Kerivoula malpasi Holotype										
1	♀	43.0	32.0	15.0	–	–	5.0	–	–	–
Kerivoula depressa										
11	♂♂	32.5-37.8	28.9-33.2	10.6-13.8	33.8-42.7	15.2-17.3	6.9-7.6	31.6-35.6	30.1-34.3	28.3-33.6
		35.8, 1.9	31.3, 1.2	12.2, 0.8	39.3, 2.4	16.4, 0.7	7.3, 0.2	34.0, 1.3	32.7, 1.2	31.6, 1.5
20	♀♀	34.3-41.0	31.0-34.6	10.6-14.8	36.9-44.5	15.2-18.2	6.7-8.3	32.8-37.1	32.5-36.2	30.6-34.8
		36.8, 1.8	32.7, 1.0	12.1, 0.9	40.6, 2.1	16.8, 0.8	7.5, 0.4	35.2, 1.3	34.0, 1.1	32.8, 1.2
Sex. dim.		ns	<0.01	ns	ns	ns	ns	<0.03	<0.01	<0.03

Table 4.1. Continued.

n	Sex	3D1P	3D2P	4D1P	4D2P	W
taxa with 'domed-skull' (sensu Bates et al., 2007)						
Kerivoula hardwickii Holotype						
1	?	–	–	–	–	–
Kerivoula fusca Holotype						
1	?	–	–	–	–	–
Kerivoula engana Holotype						
1	♂	–	–	–	–	–
Kerivoula hardwickii						
40	♂♂	14.8-18.4	13.9-17.6	9.6-11.6	7.0-9.1	3.0-5.0
		16.4, 0.7	16.0, 0.8	10.5, 0.5	8.0, 0.4	4.0, 0.5 (22)
22	♀♀	15.3-18.4	15.0-18.0	9.9-11.7	7.2-10.5	3.7-5.5
		17.0, 0.7	16.6, 0.9	10.7, 0.5	8.2, 0.7	4.3, 0.6 (11)
Sex. dim.		<0.01	<0.01	<0.05	ns	ns
taxa with 'flat-skull' (sensu Bates et al., 2007)						
Kerivoula depressa Holotype						
1	♀	–	–	–	–	–
Kerivoula crypta Holotype						
1	♂	15.0	–	–	–	–
Kerivoula malpasi Holotype						
1	♀	–	–	–	–	–
Kerivoula depressa						
11	♂♂	14.7-16.4	13.3-16.6	8.7-11.8	6.4-8.4	3.0-8.1
		15.6, 0.6	15.0, 1.0	10.1, 0.9	7.3, 0.7	4.7, 2.2 (6)
20	♀♀	15.0-18.8	14.0-17.6	9.5-11.9	7.0-8.6	4.0-7.4
		16.4, 1.0	15.6, 0.9	10.5, 0.6	7.6, 0.4	4.9, 1.1 (8)
Sex. dim.		<0.04	ns	ns	ns	ns

Table 4.2. External and cranio-dental measurements (in mm) of males and females of *K. hardwickii* and *K. depressa*, presented as x ± SD. *P* = significance value, based on *t*-test; ns = not significant difference.

Characters	♂♂		*P*-value
	Domed-skull form (*K. hardwickii*)	**Flat-skull form (*K. depressa*)**	
	External characters		
HB	37.1 ± 2.0	35.8 ± 1.9	ns
FA	32.5 ± 1.2	31.3 ± 1.2	<0.01
EL	13.0 ± 0.8	12.2 ± 0.8	<0.01
TL	40.9 ± 2.6	39.3 ± 2.4	ns
TIB	17.4 ± 0.7	16.4 ± 0.7	<0.01
HF	7.5 ± 0.4	7.3 ± 0.2	ns
3MT	34.5 ± 1.1	34.0 ± 1.3	ns
4MT	33.6 ± 1.1	32.7 ± 1.2	<0.03
5MT	32.3 ± 1.1	31.6 ± 1.5	ns
3D1P	16.4 ± 0.7	15.6 ± 0.6	<0.01
3D2P	16.0 ± 0.8	15.0 ± 1.0	<0.01
4D1P	10.5 ± 0.5	10.1 ± 0.9	<0.05
4D2P	8.0 ± 0.4	7.3 ± 0.7	<0.01
	Cranial and dental characters		
GTL	14.6 ± 0.3	13.9 ± 0.4	<0.01
CCL	12.9 ± 0.3	12.2 ± 0.4	<0.01
CBL	13.5 ± 0.3	12.7 ± 0.4	<0.01
MW	7.4 ± 0.2	7.0 ± 0.2	<0.01
ZB	8.7 ± 0.2	8.1 ± 0.1	<0.01
BB	7.3 ± 0.2	7.0 ± 0.2	<0.01
BH	5.7 ± 0.2	4.8 ± 0.3	<0.01
PC	3.3 ± 0.1	3.1 ± 0.1	<0.01
ML	10.1 ± 0.2	9.6 ± 0.3	<0.01
C^1-C^1	3.5 ± 0.1	3.2 ± 0.1	<0.01
M^3-M^3	5.4 ± 0.1	5.0 ± 0.1	<0.01
C-M^3	5.6 ± 0.1	5.1 ± 0.2	<0.01
C-M_3	5.9 ± 0.1	5.5 ± 0.2	<0.01

significantly larger than the material with 'flat-skull' type in all external measurements except foot (HF), which is not significantly different (Table 4.2.). A multivariate analysis based on nine external characters shows a large overlap between the material of the two skull forms, here referred to as *hardwickii* and *depressa* (Figure 4.1. and Table 4.3.).

The colour of pelage does not differ consistently between the taxa but does

Table 4.2. Continued.

Characters	♀♀		*P*-value
	Domed-skull form (*K. hardwickii*)	**Flat-skull form (*K. depressa*)**	
	External characters		
HB	38.0 ± 1.8	36.8 ± 1.8	<0.04
FA	33.9 ± 1.0	32.7 ± 1.0	<0.01
EL	13.0 ± 0.9	12.1 ± 0.9	<0.01
TL	43.3 ± 2.9	40.6 ± 2.1	<0.01
TIB	17.8 ± 0.8	16.8 ± 0.8	<0.01
HF	7.7 ± 0.4	7.5 ± 0.4	ns
3MT	36.0 ± 1.2	35.2 ± 1.3	<0.04
4MT	35.2 ± 1.1	34.0 ± 1.1	<0.01
5MT	34.0 ± 0.9	32.8 ± 1.2	<0.01
3D1P	17.0 ± 0.7	16.4 ± 1.0	<0.04
3D2P	16.6 ± 0.9	15.6 ± 0.9	<0.01
4D1P	10.7 ± 0.5	10.5 ± 0.6	ns
4D2P	8.2 ± 0.7	7.6 ± 0.4	<0.01
	Cranial and dental characters		
GTL	14.9 ± 0.4	14.1 ± 0.3	<0.01
CCL	13.2 ± 0.3	12.6 ± 0.3	<0.01
CBL	13.7 ± 0.3	13.1 ± 0.3	<0.01
MW	7.6 ± 0.2	7.3 ± 0.2	<0.01
ZB	8.8 ± 0.3	8.3 ± 0.2	<0.01
BB	7.3 ± 0.2	7.1 ± 0.2	<0.01
BH	5.6 ± 0.2	4.9 ± 0.2	<0.01
PC	3.3 ± 0.1	3.3 ± 0.1	ns
ML	10.3 ± 0.3	9.8 ± 0.4	<0.01
C^1-C^1	3.6 ± 0.1	3.4 ± 0.1	<0.01
M^3-M^3	5.5 ± 0.2	5.2 ± 0.2	<0.01
C-M^3	5.7 ± 0.2	5.3 ± 0.2	<0.01
C-M_3	6.0 ± 0.2	5.6 ± 0.2	<0.01

exhibit individual variation. In all taxa, the fur on the dorsal surface is clearly divided into three bands. It is dark grey to dark grey-brown at the base, paler in the midpart and grey or brown at the tip. On the ventral surface, the hair bases are dark and the tips greyish (Figure 4.2.).

In contrast to hair colour, the baculum is different in both size and shape between taxa, except one taxon of the 'flat-skull' type (*depressa*) which is short. It is short with a straight shaft and slightly triangular tip in the 'domed-skull' type (*hardwickii*); it is short or long triangular shaft with or without long bifid base in the

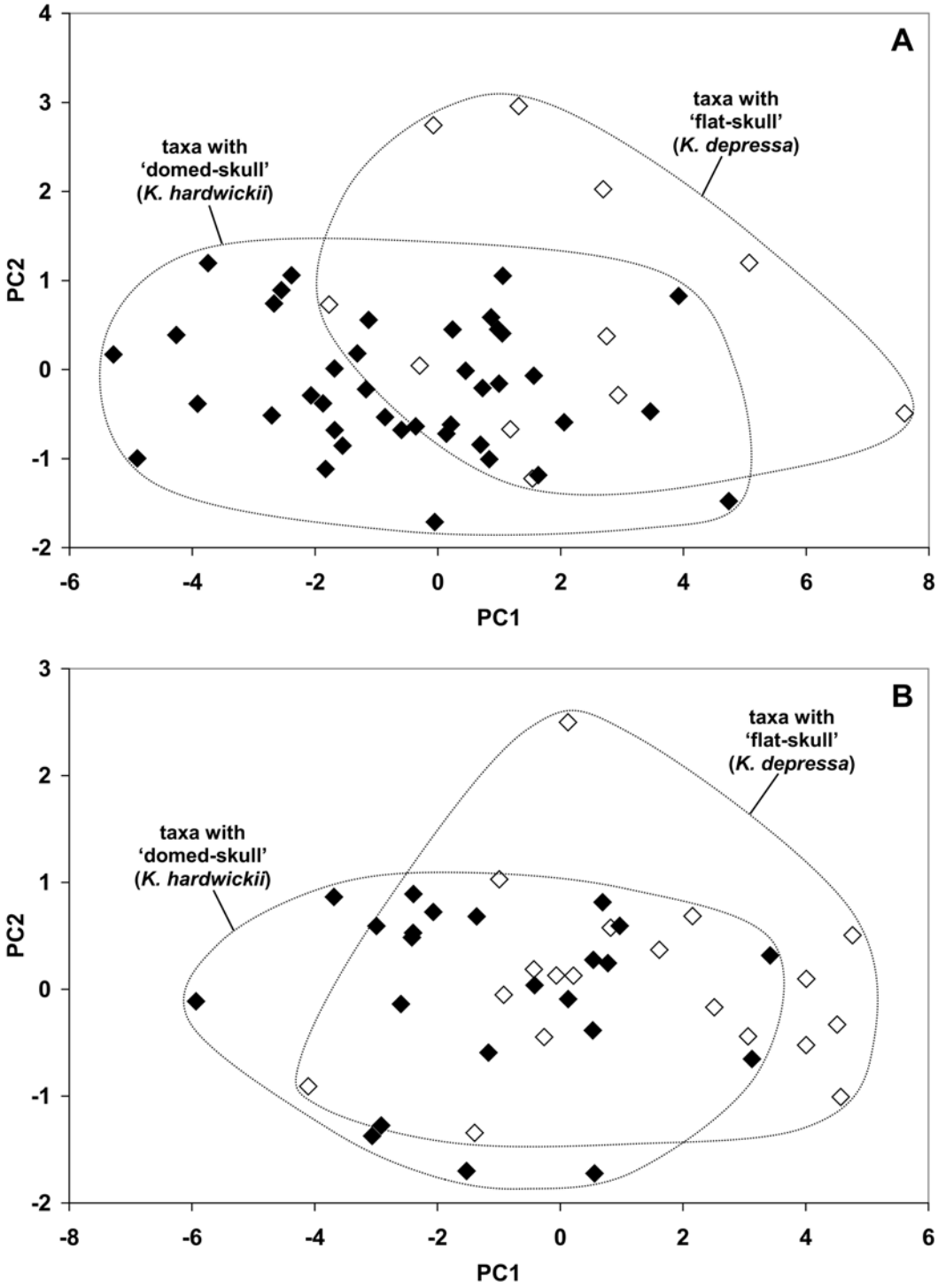

Figure 4.1. PCA between first and second principal components based on nine external metric characters for specimens of male (A) and female (B) separately. Black diamonds represent specimens with 'domed-skull' (*K. hardwickii*) and open diamonds are specimens with 'flat-skull' (*K. depressa*).

Figure 4.2. Two species of *Kerivoula*. A – *K. hardwickii*, ♀, PSUZC-MM2012.57, Pha Dam Ranger Station, Ton Nga Chang Wildlife Sanctuary, Songkhla Province, Thailand; B – *K. depressa*, ♀, PSUZC-MM2011.51, South Klom Luang Chumporn Wildlife Sanctuary, Ranong Province, Thailand.

'flat-skull' type (*depressa*) (Figure 4.3.).

Ninety-six skulls were measured. Ten cranial and dental characters were significantly different between males and females in the 'domed-skull' type (*hardwickii*); eight characters were different in the 'flat-skull' type (*depressa*) (Table 4.4.). As with the external characters, all skull measurements were significantly different between these two forms (Table 4.2.). A multivariate comparison based on twelve cranial and dental characters shows a minor overlap between the two taxa (Figure 4.4. and Table 4.5.). When condylo-basal length was plotted against braincase height in a bi-plot, these two taxa were separate from each other (Figure 4.5.).

Self-evidently, as illustrated in Figures 4.6. and 4.7., the height of the braincase is the major difference between the two forms. However, in addition, the material with a high braincase also has a depression of the parietal region of the braincase where it slopes backwards towards the lambda, and the rostrum is long. The material with a flat braincase is without a depression in its parietal region or slightly depression in some material and the rostrum is short in comparison to those of 'domed-skull' type. The dentition shows no significant different between the two taxa.

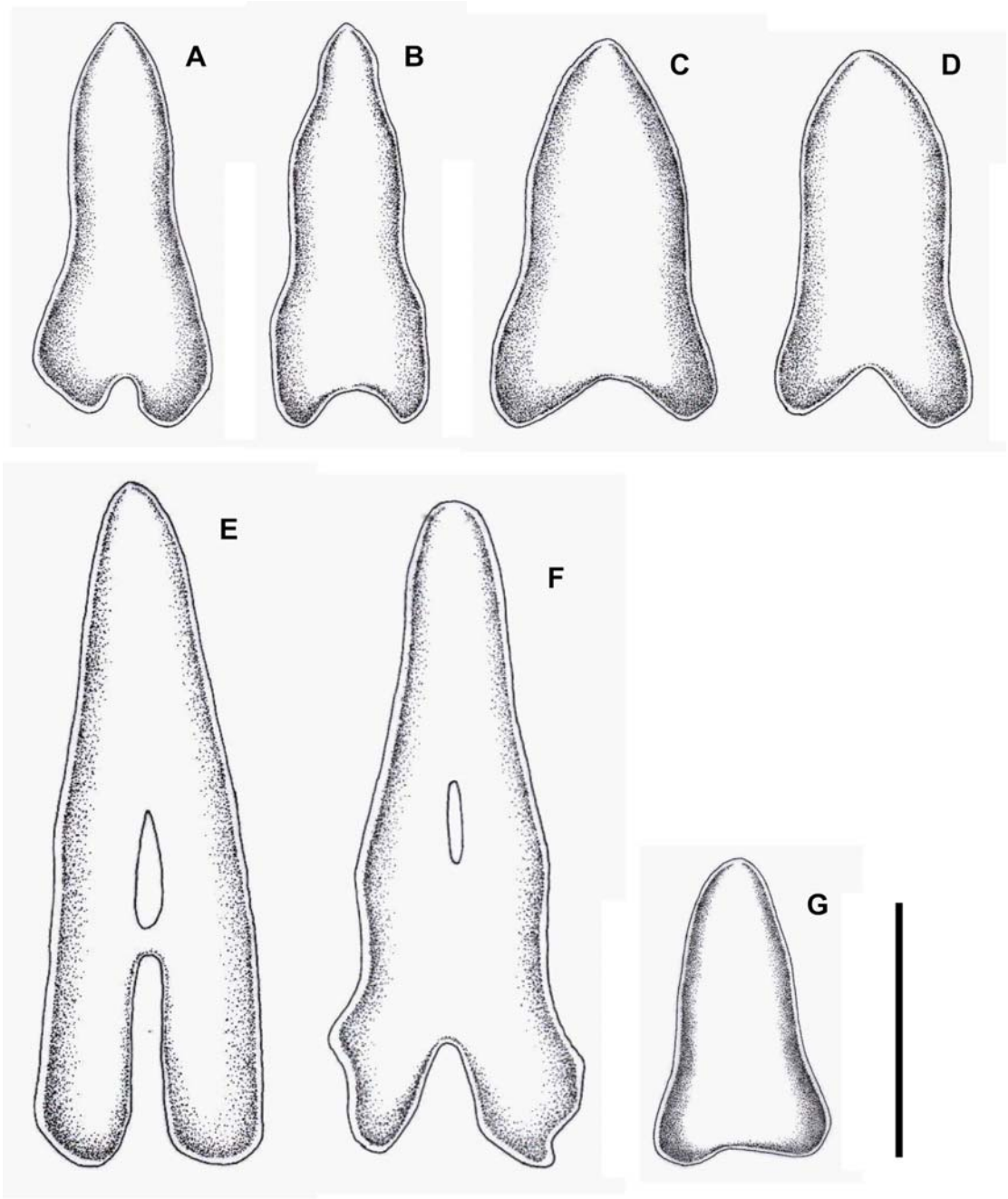

Figure 4.3. Dorsal view of baculum of the taxa with 'domed-skull' (*K. hardwickii*) (A-D) and the taxa with 'flat-skull' (*K. depressa*) (E-G). A – PSUZC-MM2007.271, Ton Nga Chang WS., Songkhla Province; B – PSUZC-MM2012.162, Khao Pra-Bang Kram WS., Krabi Province; C – PSUZC-MM2007.280, Ton Nga Chang WS., Songkhla Province; D – PSUZC-MM2012.171, Khao Sok NP., Surat Thani Province; E – PSUZC-MM2011.52, Kaeng Krachan NP., Prachuap Khiri Khan Province; F – PSUZC-MM2012.166, Khao Luang NP., Nakhon Si Thamarat Province; G – PSUZC-MM2011.17, Chiang Dao WS., Chiang Mai Province. Scale: 0.5 mm.

Table 4.3. Eigenvector and eigenvalue of PCA of nine external measurements of 93 specimens of males (51) and females (42) separately of taxa with 'domed-skull' (*K. hardwickii*) and taxa with 'flat-skull' (*K. depressa*).

Characters	Eigenvector					
	♂♂			♀♀		
	1	**2**	**3**	**1**	**2**	**3**
FA	-0.34	0.23	0.26	-0.35	0.21	0.03
TIB	-0.33	-0.17	0.27	-0.33	-0.21	0.10
3MT	-0.34	0.44	0.09	-0.34	0.44	0.15
4MT	-0.36	0.32	0.12	-0.36	0.36	-0.03
5MT	-0.36	0.30	-0.02	-0.35	0.37	-0.02
3D1P	-0.34	-0.29	-0.23	-0.34	-0.33	-0.17
3D2P	-0.34	-0.35	0.04	-0.35	-0.31	0.14
4D1P	-0.31	-0.04	-0.83	-0.28	-0.24	-0.79
4D2P	-0.29	-0.57	0.30	-0.29	-0.43	0.54
Eigenvalue	6.52	0.92	0.46	6.54	0.67	0.59
% total of variation explained	72.48	82.71	87.82	72.66	80.07	86.64

4.3.2. Phylogenetics

Sequences of fifteen voucher specimens were obtained for specimens from Thailand. Eight were for 'domed-skull' specimens (*K. hardwickii*), 4 for 'flat-skull' specimens (*depressa*), 2 for *K. titania* and one for *K. pellucida*. The result showed that the 'domed-skull' (*hardwickii*) form a monophyletic clade that is distinct, with an average 17.23% divergence, from the 'flat-skull' bats (*depressa*) (Figure 4.8., Table 4.6.). The 'domed-skull' type formed one monophyletic clade with 0.96% divergence within the group, whereas the 'flat-skull' type clade subdivided into three monophyletic clades with an average 13.21% divergence from each other. In addition, one clade of the 'flat-skull' type (specimen numbers PSUZC-MM2011.19 and PSUZC-MM2011.52) has an 8.30% divergence within the clade.

Seventy sequences referred to *K. hardwickii* or *K.* cf. *hardwickii* in the DNA Barcode of Life Database (www.boldsystems.org) were used for comparison with the sequences of Thai material. Twenty-six sequences grouped together with the 'domed-skull' type clade and forty-four grouped with the 'flat-skull' type clade (Figure 4.9.). To aid interpretation, sequences from the same localities with < 0.1% divergence from each other were removed from the phylogenetic trees. The phylogenetic analysis of

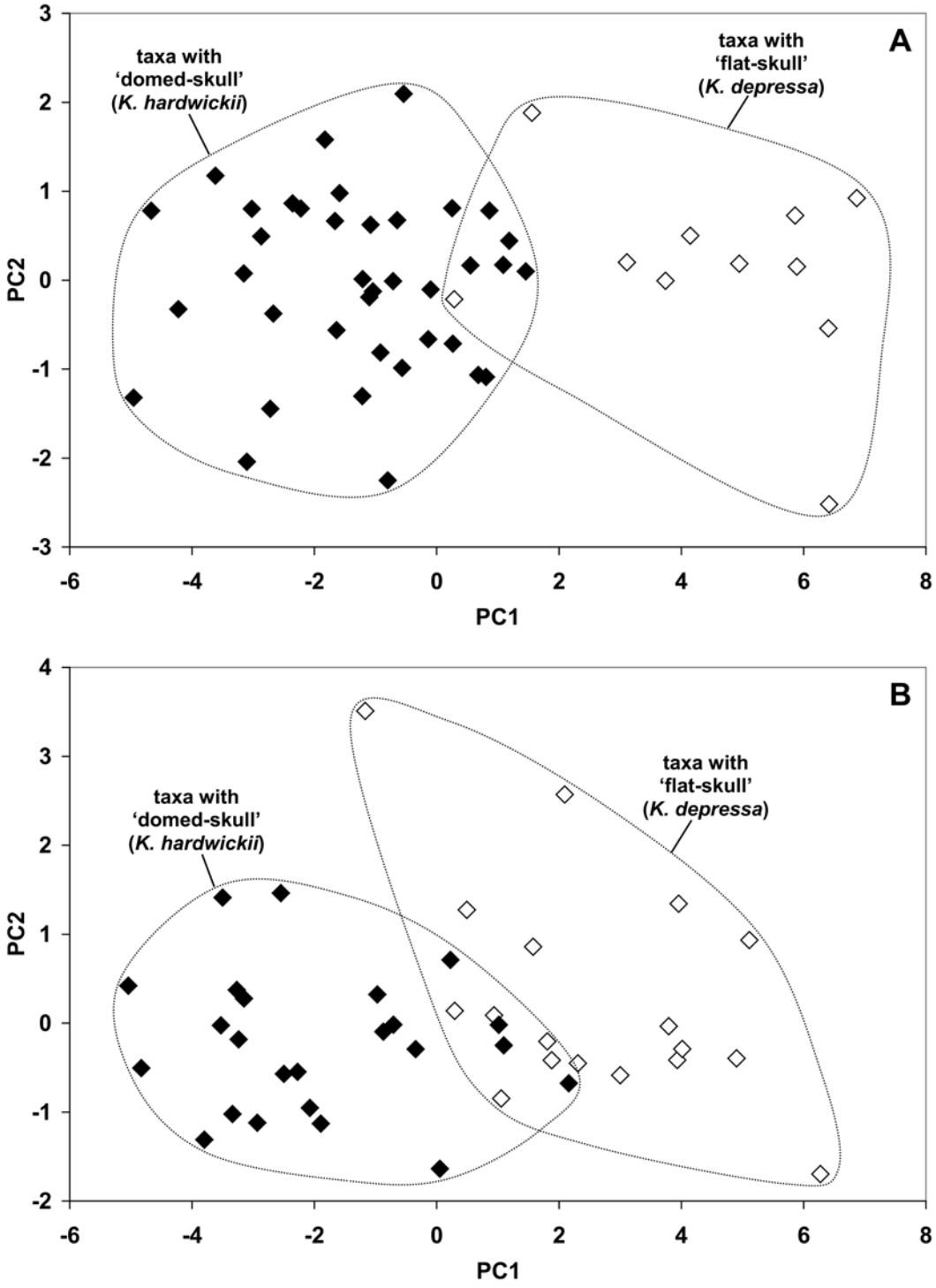

Figure 4.4. PCA between first and second principal components based on twelve cranio-dental metric characters for specimens of male (A) and female (B) separately. Black diamonds represent specimens with 'domed-skull' (*K. hardwickii*) and open diamonds are specimens with 'flat-skull' (*K. depressa*).

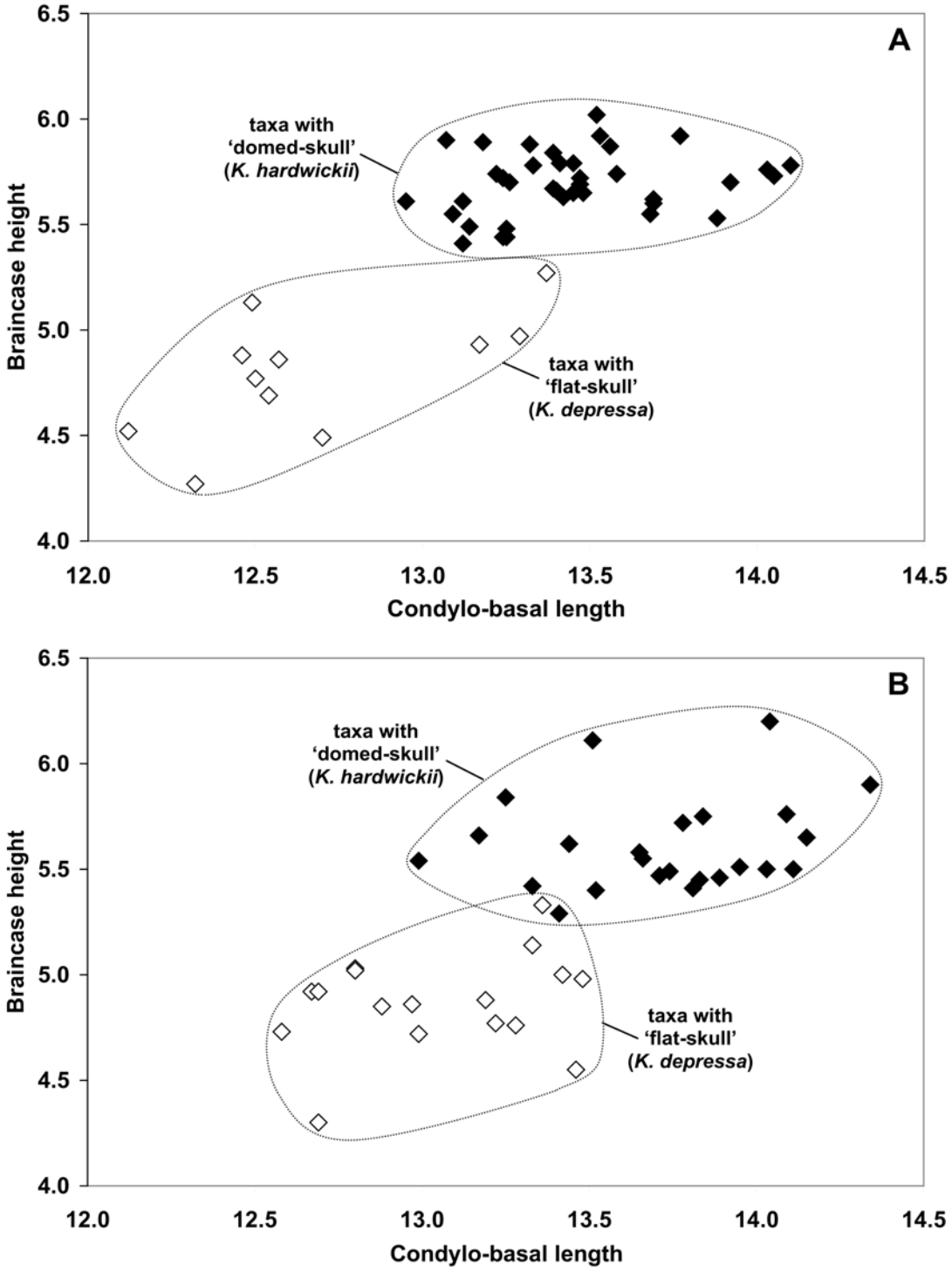

Figure 4.5. Bi-plot of condylo-basal length and braincase height (mm) specimens of male (A) and female (B) separately. Black diamonds represent specimens with 'domed-skull' (*K. hardwickii*) and open diamonds are specimens with 'flat-skull' (*K. depressa*).

the combined Thai and regional material shows an average 13.85% divergence between the two main clades (Table 4.7.). The sequences grouped with the 'domed-skull' type clade divided into a mainland group and a group originating from Borneo with an 8.32% divergence. The sequences grouped with the 'flat-skull' type clade divided into 6 groups with 5.79% divergence.

4.4. SYSTEMATIC DESCRIPTION

Both the morphological and genetic results indicate that specimens currently referred to *K. hardwickii* from throughout mainland South-east Asia include at least two distinct species. Specimens with a 'domed-skull' are here assigned to *K. hardwickii* and specimens with a 'flat-skull' are assigned to *K. depressa*.

Three pre-existing names appear to be available for the specimens with a 'domed-skull': *hardwickii* Horsfield, 1842 from Java; *fusca* Dobson, 1871, locality unknown (= Java in Chasen, 1940); and *engana* Miller, 1906b from Enggano, South-western Sumatra. The taxon *hardwickii* has forearm length of 30.5 mm and tibia length of 15.2 mm (Dobson, 1876) (Table 4.1.). This taxon has a characteristically globular skull (Horsfield, 1824). In case of the taxon *fusca*, it has a slightly longer forearm length (33.0 mm) than that of *hardwickii* but differs in the form of the ears and fur colour (Dobson, 1871). For the taxon *engana*, as the type description suggests it is similar in both skull and dentition to *hardwickii*, but larger in size (Miller, 1906b). On the basis of similar morphology, the two latter taxa are considered here as synonyms of *K. hardwickii*.

In the case of specimens with a 'flat-skull', three pre-existing names appear to be available: *depressa* Miller, 1906a from Myanmar, *crypta* Wroughton and Ryley, 1913 from South India and *malpasi* Phillips, 1932 from Sri Lanka. The taxon *depressa* was described as having a smaller and more flattened skull than the taxon *hardwickii* (Miller, 1906a). For the taxon *crypta*, it was described as being similar to *hardwickii* but smaller and darker in colour; there was apparently no difference in the skull between the two taxa (Wroughton and Ryley, 1913). However, Bates and Harrison (1997) mentioned that the taxon *crypta* is closely similar to *depressa* in having a flattened skull and considered it to be a synonym of the latter taxon. In case

Table 4.4. Cranial and dental measurements (in mm) of *K. hardwickii* and *K. depressa*. GTL – greatest length of the skull; CCL – condylo-canine length; CBL – condylo-basal length; MW – mastoid width; ZB – zygomatic breadth; BB – breadth of the braincase; BH – braincase height; PC – postorbital constriction; ML – mandible length; C^1-C^1 – anterior palatal width; M^3-M^3 – posterior palatal width; C-M^3 – upper toothrow length; C-M_3 – lower toothrow length. Minimum, maximum, mean and standard deviation; sample sizes differing from those reported under *n* are given in parentheses. *T*-test comparison for sexual dimorphism (sex. dim.; ns = not significant difference). Measurements of type series based on literature records; Miller (1906a) for *K. depressa*, Miller (1906b) for *K. engana* and Wroughton and Ryley (1913) for *K. crypta*. * – measurement method is difference from the present study.

n	Sex	GTL	CCL	CBL	MW	ZB	BB	BH
taxa with 'domed-skull' (sensu Bates et al., 2007)								
Kerivoula engana Holotype								
1	♂	14.6	–	13.6	–	9	7.4	6.6*
Kerivoula hardwickii								
40	♂♂	14.1-15.5	12.2-13.7	13.0-14.1	7.1-7.9	8.3-9.2	6.9-7.8	5.4-6.0
		14.6, 0.3	12.9, 0.3 (39)	13.5, 0.3 (39)	7.4, 0.2	8.7, 0.2 (36)	7.3, 0.2	5.7, 0.2
23	♀♀	14.1-15.6	12.8-13.7	13.0-14.3	7.3-7.8	8.1-9.1	6.8-7.6	5.4-6.2
		14.9, 0.4	13.2, 0.3	13.7, 0.3	7.6, 0.2	8.8, 0.3 (21)	7.3, 0.2	5.6, 0.2
Sex. dim.		<0.01	<0.01	<0.01	0.01	<0.03	ns	ns
taxa with 'flat-skull' (sensu Bates et al., 2007)								
***Kerivoula depressa* Holotype**								
1	♀	13.5	–	12.6	–	8.2	7.0	5.5*
***Kerivoula crypta* Holotype**								
1	♂	–	–	13.3	–	9.0	8.2	–
Kerivoula depressa								
12	♂♂	13.4-14.5	11.8-12.9	12.1-13.4	6.8-7.3	8.0-8.4	6.7-7.3	4.3-5.3
		13.9, 0.4	12.2, 0.4 (11)	12.7, 0.4 (11)	7.0, 0.2	8.1, 0.1 (10)	7.0, 0.2	4.8, 0.3
21	♀♀	13.5-14.6	12.0-13.0	12.6-13.5	7.0-7.6	8.0-8.8	6.8-7.4	4.3-5.3
		14.1, 0.3 (19)	12.6, 0.3 (19)	13.1, 0.3 (19)	7.3, 0.2 (19)	8.3, 0.2 (14)	7.1, 0.2	4.9, 0.2 (20)
Sex. dim.		ns	<0.01	0.01	<0.01	<0.01	ns	ns

Table 4.4. Continued.

n	Sex	PC	ML	C^1-C_1	M^3-M^3	C-M^3	C-M_3
			taxa with 'domed-skull' (sensu Bates et al., 2007)				
			Kerivoula engana Holotype				
1	♂	–	–	–	–	–	–
			Kerivoula hardwickii				
40	♂♂	3.1-3.5	9.7-10.5	3.2-3.7	5.1-5.7	5.3-5.8	5.6-6.1
		3.3, 0.1	10.1, 0.2	3.5, 0.1 (39)	5.4, 0.1	5.6, 0.1	5.9, 0.1
23	♀♀	3.2-3.5	9.8-10.8	3.4-3.9	5.1-5.9	5.3-6.0	5.4-6.3
		3.3, 0.1	10.3, 0.3	3.6, 0.1	5.5, 0.2	5.7, 0.2	6.0, 0.2
Sex. dim.		<0.01	<0.01	<0.01	ns	<0.01	<0.02
			taxa with 'flat-skull' (sensu Bates et al., 2007)				
			Kerivoula depressa Holotype				
1	♀	3.0	9.5	–	–	5.2	5.7
			Kerivoula crypta Holotype				
1	♂	–	–	–	5.5	5.5	–
			Kerivoula depressa				
12	♂♂	3.0-3.3	9.1-9.9	3.0-3.4	4.8-5.2	4.9-5.5	5.1-5.9
		3.1, 0.1	9.6, 0.3	3.2, 0.1	5.0, 0.1	5.1, 0.2	5.5, 0.2
21	♀♀	3.0-3.7	9.2-10.8	3.2-3.5	4.9-5.6	5.0-5.6	5.3-6.1
		3.3, 0.1	9.8, 0.4	3.4, 0.1 (20)	5.2, 0.2	5.3, 0.2	5.6, 0.2
Sex. dim.		ns	<0.04	<0.01	<0.01	<0.01	ns

of *malpasi*, it is similar to *hardwickii*, but with a relatively shorter tail and more rufescent colour (Phillips, 1932). Bates and Harrison (1997) considered *malpasi* to be a synonym of *depressa* differing only in minor details of pelage colour.but only commented on a colour difference. Here, the two taxa *crypta* and *malpasi* are assigned as synonyms of *K. depressa*.

***Kerivoula hardwickii* Horsfield, 1824**

Hardwicke's Woolly Bat

Kerivoula hardwickii Horsfield, 1824; Java.

Kerivoula fusca Dobson, 1871; locality unknown.

Kerivoula engana Miller, 1906b; Dua Island, about 1 mile from Enggano Island, Southwest of Sumatra.

External and bacular characters

Kerivoula hardwickii has a forearm length of 28.9-35.7 mm (Table 4.1.). The fur on the dorsal surface is grey or grey-brown and is divided into three bands - dark grey or dark grey-brown at the base, light grey or pale in the middle, and grey or grey-brown at the tip. On the ventral surface (Figure 4.2.), the fur has two colour bands, with grey or dark grey bases and paler tips. The ears are relatively short, with a rounded tip; the anterior part is smoothly concave. Each tragus is relatively short and narrow with a length of 6.8-8.8 mm; it is triangular in shape with a rounded tip and a well-defined basal lobe. The snout is short, covered by hairs except for the nostrils. In the wing, the fourth metacarpal exceeds the .fifth in length but is shorter than the third. The first phalanx of third digit is relatively long, between 44.3-51.0 % the length of the long third metacarpal. The tail is long, enclosed within the interfemoral membrane except for the extreme tip. The foot is relatively large, with a wing attached to the base of the toe. The baculum is small with a length of 0.7-0.8 mm. It varies in shape, sometime it is relatively narrow, in other specimens it is broader but the general configuration is always triangular but with slightly concave sides. The base is expanded and bifid. The tip is bluntly pointed or more rounded (Figure 4.3.).

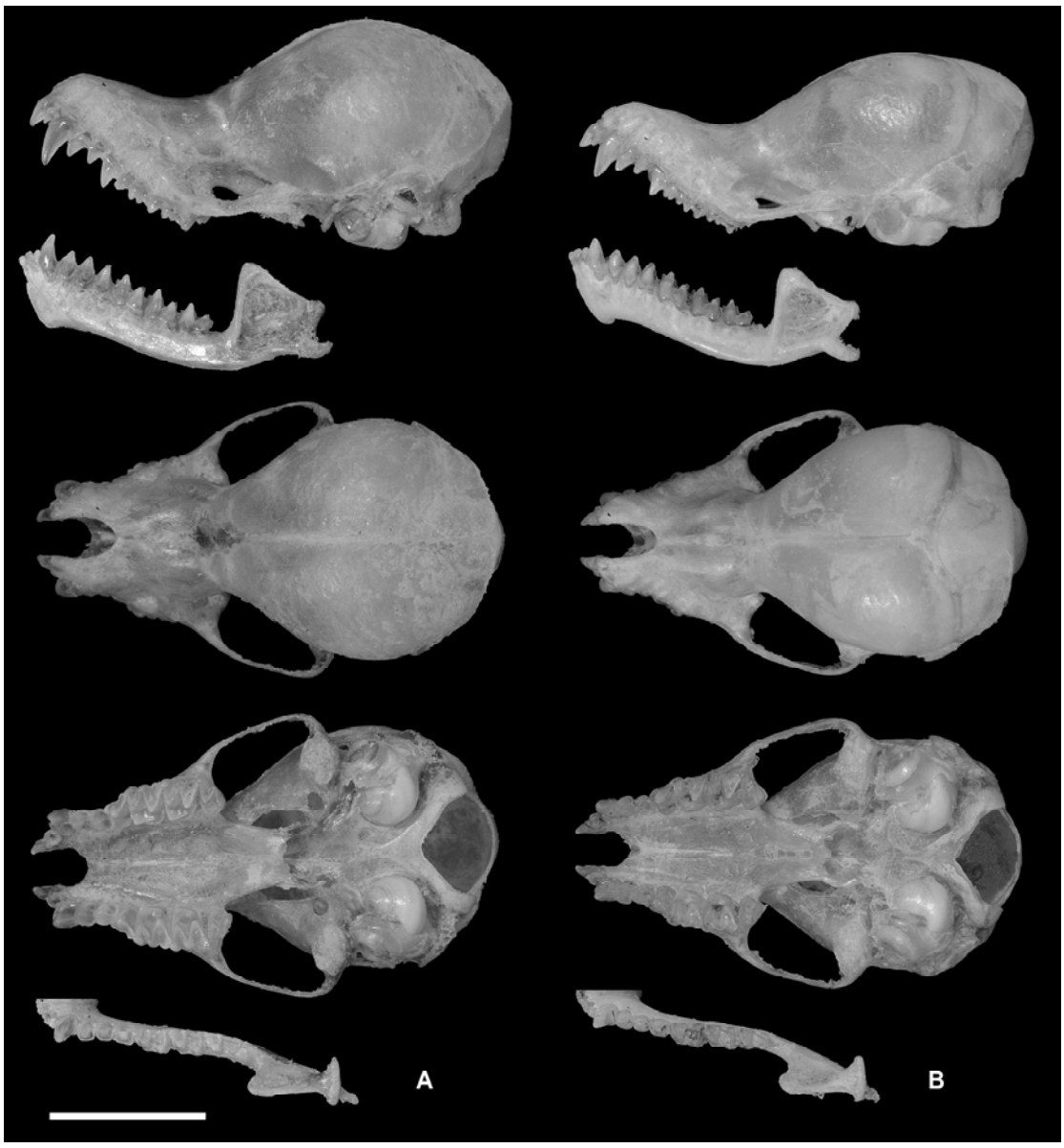

Figure 4.6. The skulls of two *Kerivoula*. A – taxon with 'domed-skull' (*K. hardwickii*), ♂, PSUZC-MM2012.160, Phu Pha Phet Ranger Station, Khao Bantad Wildlife Sanctuary, Satun Province, Thailand; B – taxon with 'flat-skull' (*K. depressa*), ♀, PSUZC-MM2007.281, Pha Dam Ranger Station, Ton Nga Chang Wildlife Sanctuary, Songkhla Province, Thailand. Scale: 5 mm.

Cranial and dental characters

The skull has a condylo-basal length of 13.0-14.3 mm. The mastoid width is 7.1-7.9 mm, which is narrower than the zygomatic breadth (Table 4.4.). When viewed in lateral profile, the skull is high, with a domed braincase (BH: 5.4-6.2 mm) and is with a slight depression in the parietal region (Figure 4.7.). Braincase height is 39.1-

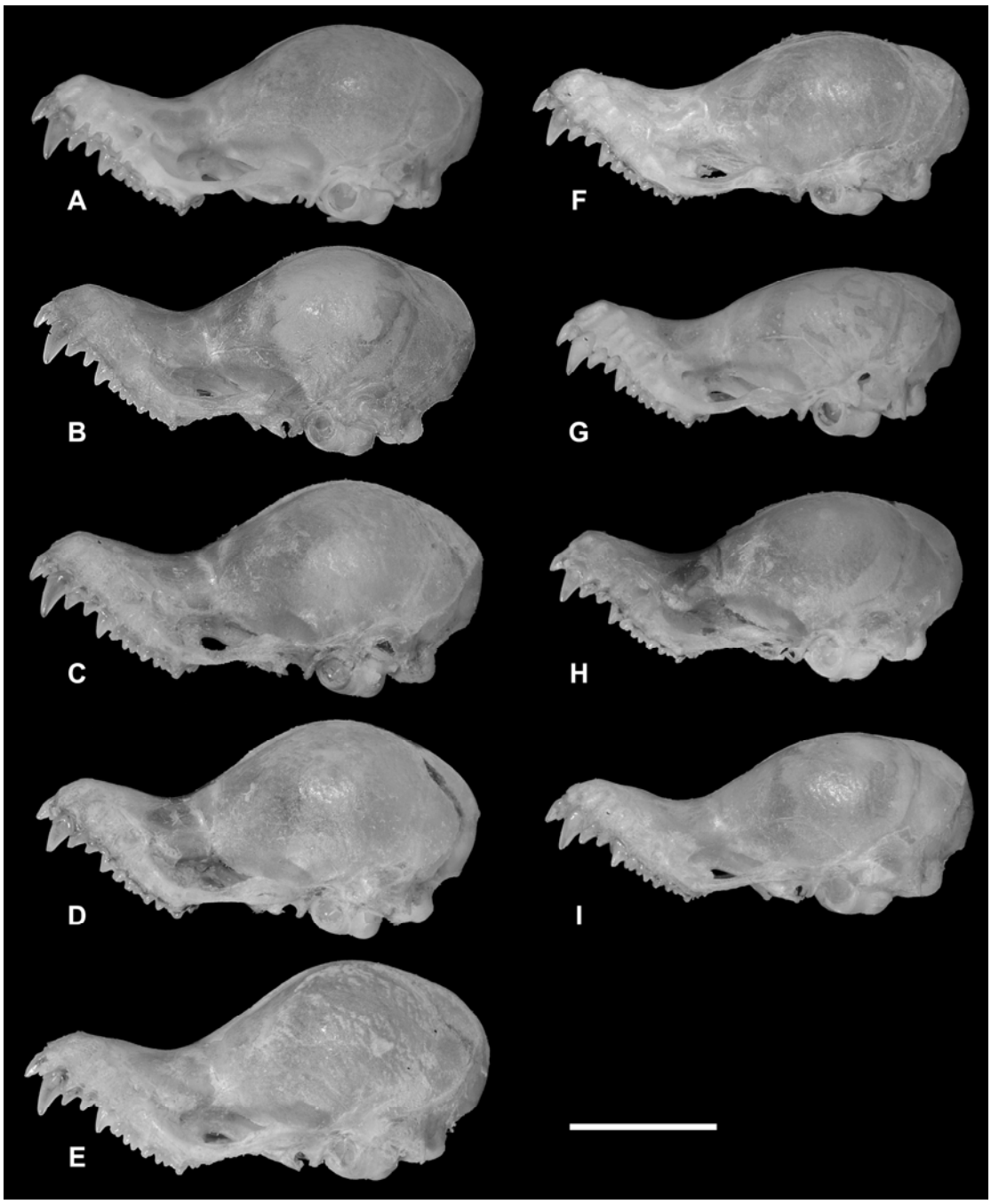

Figure 4.7. Lateral view of the skull of taxa with 'domed-skull' (*K. hardwickii*) (A-E) and the taxa with 'flat-skull' (*K. depressa*) (F-I). PSUZC-MM2005. 204, ♀, Ton Nga Chang WS., Songkhla Province; B – PSUZC-MM2012.161, ♂, Khao Pra-Bang Kram WS., Krabi Province; C – PSUZC-MM2012.160, ♂, Phu Pha Phet, Khao Bantad WS., Satun Province; D – PSUZC-MM2012.162, ♂, Khao Pra-Bang Kram WS., Krabi Province; and E – PSUZC-MM2008.131, ♀, Tarutao NP., Satun Province; F – PSUZC-MM2012.166, ♂, Khao Luang NP., Nakhon Si Thammarat Province; G – PSUZC-MM2011.17, ♂, Chiang Dao WS., Chiang Mai Province; H – PSUZC-MM2011.52, ♂, Kaeng Krachan NP., Prachuap Khiri Khan Province; I – PSUZC-MM2005.201, ♂, Phu Laung WS., Loei Province. Scale: 5 mm.

Figure 4.5. Eigenvector and eigenvalue of PCA of twelve cranio-dental measurements of 93 specimens of males (49) and females (42) separately of taxa with 'domed-skull' (*K. hardwickii*) and taxa with 'flat-skull' (*K. depressa*).

Characters	Eigenvector					
	♂♂			♀♀		
	1	**2**	**3**	**1**	**2**	**3**
GTL	-0.32	0.09	0.23	-0.33	-0.10	0.01
CCL	-0.32	0.13	0.14	-0.33	-0.08	0.05
CBL	-0.32	0.15	0.07	-0.32	-0.09	0.07
MW	-0.28	-0.21	0.37	-0.30	0.21	-0.31
BB	-0.23	-0.54	0.50	-0.22	0.28	-0.76
BH	-0.28	-0.09	-0.22	-0.27	-0.28	-0.24
PC	-0.19	-0.66	-0.47	-0.12	0.85	0.29
ML	-0.31	0.23	0.11	-0.31	0.07	0.28
C^1-C^1	-0.29	0.15	-0.38	-0.29	-0.05	-0.01
M^3-M^3	-0.29	-0.07	-0.32	-0.26	-0.11	0.13
C-M^3	-0.31	0.21	-0.08	-0.32	-0.16	0.19
C-M_3	-0.30	0.21	-0.04	-0.31	0.04	0.22
Eigenvalue	8.84	0.96	0.67	8.49	1.06	0.77
% total of variation explained	73.70	81.73	87.33	70.77	79.56	85.99

45.2% of the condylo-basal length. The sagittal crest is low or absent. The rostrum is relatively long and wide, with or without a sulcus. The narial pit is V-shaped or U-shaped. If present, the dorsal process on each zygoma is small or moderate in size and situated posteriorly. The coronoid process is well-developed and exceeds the height of the lower canine (C_1). The length of upper toothrow (C-M^3) is 5.3-6.0 mm. The first upper incisor (I^2) is relatively long and slender. The second upper incisor (I^3) is very small, about one third to one half the height of I^2; it is compressed between I^2 and C^1 and is in contact with C^1. The upper canine (C^1) is relatively large and robust. The first upper premolar (P^2) exceeds the second (P^3) in height, but is shorter than the third (P^4); P^3 is slightly intruded from the toothrow. The lower incisors are tricuspid with a well-developed central cusp, especially in the third (I_3). The lower canine (C_1) is small and slender. The second lower premolar (P_3) exceeds the third (P_4) in height, but is shorter than the first (P_2).

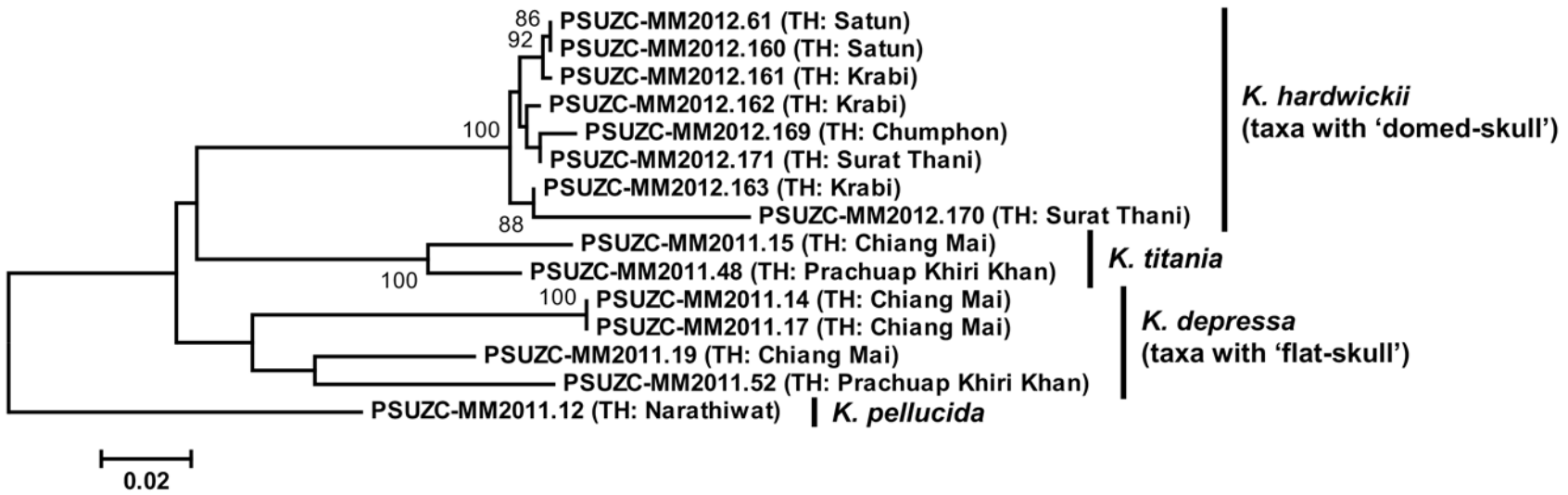

Figure 4.8. Neighbour-joining tree based on cytochrome *c* oxidase (COI) sequences of four Thai *Kerivoula*, including *K. hardwickii*, *K. depressa*, *K. titania* and *K. pellucida*.

Table 4.6. Averaged percentage of Kimura 2-parameter distance values of cytochrome *c* oxidase (COI) sequences within and between taxa of four Thai *Kerivoula*. NA = not available.

No	Taxon	*n*	1	2	3	4	5
1	*K. hardwickii*	8	**0.96/0.26**	2.41	1.95	2.03	2.36
2	*K. depressa* A	2	17.23	**0.00/0.00**	1.75	2.48	2.36
3	*K. depressa* B	2	15.08	13.21	**8.30/1.39**	1.66	2.10
4	*K. titania*	2	14.75	16.97	13.18	**4.46/1.08**	2.50
5	*K. pellucida*	1	16.69	17.19	16.76	17.76	**na**

Conservation status and distribution

Kerivoula hardwickii was included as 'Lower Risk: least concern' in the IUCN Red List (Rosell-Ambal et al., 2008).

Kerivoula hardwickii is known from southern Vietnam, southern Lao PDR, north and west Cambodia, east and peninsular Thailand, Malaysia, Sumatra, Java, Borneo, Philippines and Lesser Sunda Islands (sensu Corbet and Hill, 1992; Simmons, 2005; this study). Its distribution in Southeast Asia is mapped in Figure 4.10.

Ecology and behaviour

In Thailand, *Kerivoula hardwickii* has been found in a variety of habitats at the altitudes of 9-197 m a.s.l., including primary and secondary evergreen and mixed deciduous forests. It is tolerant of disturbed habitats, including rubber and orchard plantations, and also gardens. Pregnant females have been found from February to April and lactating females have been found during March to June (BD unpublished data).

***Kerivoula depressa* Miller, 1906**

Miller's Flat-headed Woolly Bat

Kerivoula depressa Miller, 1906a; Biapo, Carin Hills, Northeast Tounghoo, South Myanmar (Burma).

Kerivoula crypta Wroughton and Ryley, 1913; Karbidetta forest, Shimoga, South India.

Kerivoula malpasi Phillips, 1932; Kumbalgamuwa, Mulhalkelle district (c. 30 miles east of Kandy), Central Province, Sri Lanka, 3000 feet.

External and bacular characters

Kerivoula depressa has an average forearm length of 28.9-34.6 mm (Table 4.1.). The fur on dorsal surface is divided into bands, with dark grey bases, light grey or pale in the middle parts, and grey or grey-brown tips. On the ventral surface (Figure 4.2.), it has only two bands, with dark grey or grey-brown bases and paler tips. The ears and tragus are similar to those of *K. hardwickii*. The snout is short, covered by hairs except the nostrils. In the wing, the fourth metacarpal exceeds the fifth in length but is shorter than the third. The first phalanx of third digit is relatively short, between 42.6-50.9 % the length of the long third metacarpal. The tail is relatively long, enclosed within the interfemoral membrane except for the extreme tip. The feet are small, each wing is attached to the base of the outer toes. The baculum varies from small to long, with the length of 0.6-1.4 mm. Its shape is triangular with a long bifid base; although in one specimen the baculum is much shorter and the base scarcely bifid (Figure 4.3.).

Cranial and dental characters

The skull averages smaller than those of *K. hardwickii*, with a condylo-basal length of 12.1-13.5 mm). The mastoid width is 6.8-7.6 mm, which is narrower than the zygomatic breadth (Table 4.4.). When viewed in lateral profile, the skull is relatively flat (BH: 4.3-5.1 mm) when compared to those of *K. hardwickii*, a slight depression in the parietal region is sometimes present (Figures 4.6. and 4.7.). Braincase height is 33.8-41.1% of the condylo-basal length. The sagittal crest is absent. The rostrum is short and narrow in comparison to those of *K. hardwickii*, with or without a shallow sulcus. The narial pit of the rostrum is V-shaped or U-shaped. When present the dorsal process on each zygoma is small and situated on the posterior part. The coronoid process of each half mandible is well-developed and exceeds the height of the lower canine (C_1). The length of upper toothrow (C-M^3) is 4.9-5.6 mm. The first upper premolar (I^2) is relatively long and slender. The second upper premolar (I^3) is very small, about one third to two thirds the height of I^2; it is

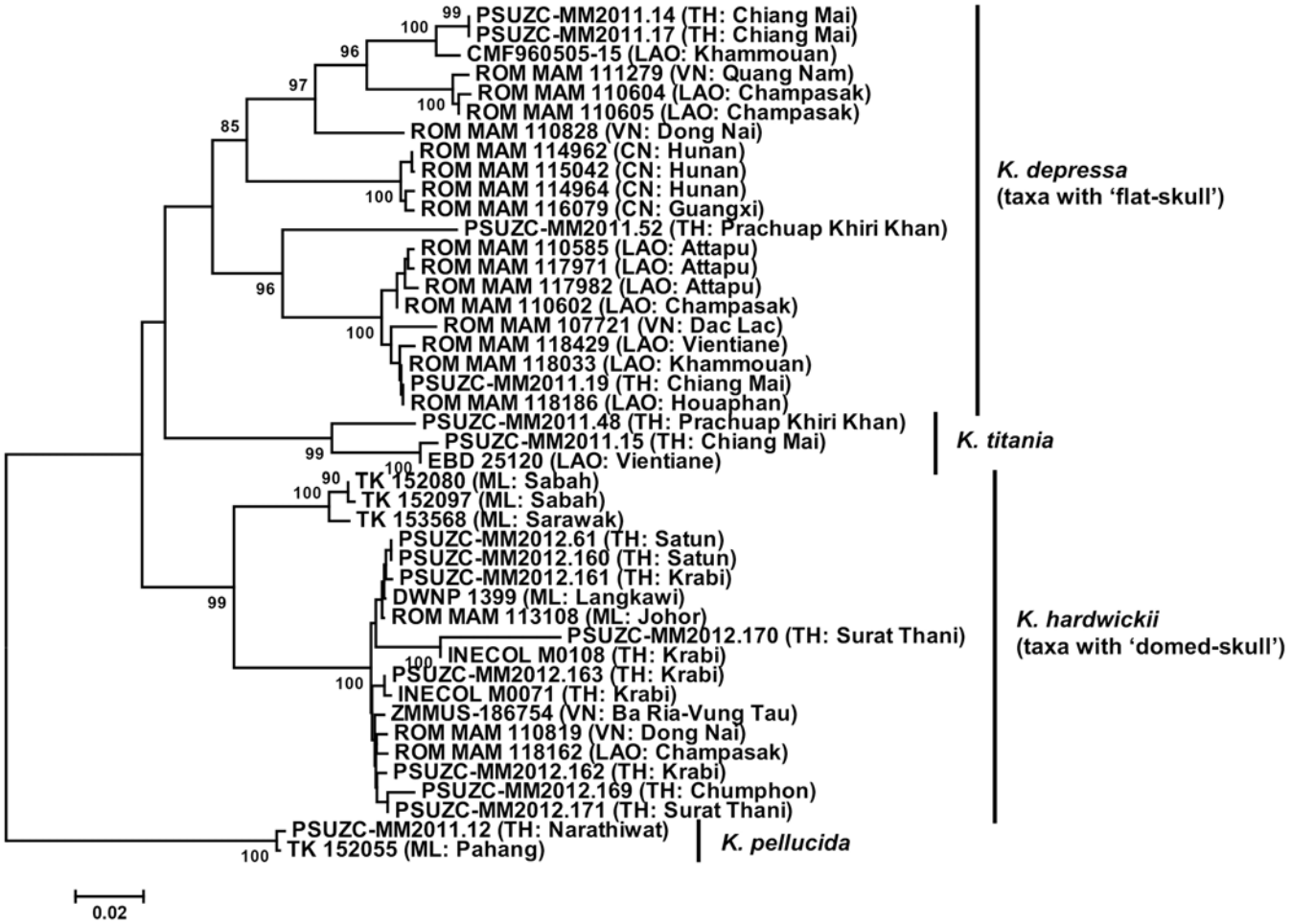

Figure 4.9. Neighbour-joining tree based on cytochrome *c* oxidase (COI) sequences of four Thai *Kerivoula*, including *K. hardwickii, K. depressa, K. titania* and *K. pellucida*, which included sequences from throughout region in the DNA Barcode of Life Database to comparison. Distance scale: 5% (0.05).

Table 4.7. Averaged percentage of Kimura 2-parameter distance values of cytochrome *c* oxidase (COI) sequences within and between taxa of four *Kerivoula*, including the sequences from the DNA Barcode of Life Database. NA = not available.

No	Taxon	*n*	1	2	3	4	5	6	7	8	9	10
1	*K. hardwickii* A	3	**0.88/0.30**	1.33	2.19	2.27	2.14	2.13	2.19	2.23	2.03	2.01
2	*K. hardwickii* B	15	8.32	**0.82/0.20**	2.27	1.93	2.21	2.09	2.37	2.30	2.06	2.29
3	*K. depressa* A	1	15.48	16.33	**na**	1.34	1.86	1.86	1.87	1.92	1.83	2.40
4	*K. depressa* B	9	15.89	13.85	8.35	**1.22/0.30**	1.66	1.70	1.93	1.94	1.77	2.30
5	*K. depressa* C	4	14.74	14.90	12.71	11.58	**0.54/0.23**	1.51	1.76	1.58	1.96	2.33
6	*K. depressa* D	1	14.62	14.33	13.32	11.81	9.84	**na**	1.16	1.20	2.49	2.10
7	*K. depressa* E	3	15.37	17.05	12.34	13.58	11.69	7.08	**1.10/0.36**	1.06	2.47	2.25
8	*K. depressa* F	3	15.48	16.45	13.63	14.15	10.52	6.78	5.79	**0.52/0.23**	2.28	2.54
9	*K. titania*	3	14.68	14.53	13.42	12.05	14.06	17.26	16.91	16.62	**2.94/0.72**	2.57
10	*K. pellucida*	2	13.36	16.43	17.75	16.71	16.88	15.25	16.93	18.29	17.81	**0.33/0.23**

compressed between I^2 and C^1 and is not in contact with C^1. The upper canine (C^1) is small and robust. The first upper premolar (P^2) exceeds the second (P^3) in the height, but is shorter than the third (P^4); P^3 is slightly intruded from the toothrow. The lower incisors are tricuspid with a well-developed central cusp, especially in the third (I_3). The lower canine (C_1) is small and slender. The second lower premolar (P_3) exceeds the third (P_4) in the height, but is shorter than the first (P_2) and is compressed in the toothrow.

Conservation status and distribution

As a synonym of *K. hardwickii*, *Kerivoula depressa* was included as 'Lower Risk: least concern' in the IUCN Red List (Rosell-Ambal et al., 2008).

Kerivoula depressa, as here understood, is known from Sri Lanka, India, South China, Myanmar, Thailand, Lao PDR, Vietnam and Cambodia (sensu Corbet and Hill, 1992; Simmons, 2005; this study). Its distribution in Southeast Asia is mapped in Figure 4.10.

Ecology and behaviour

In Thailand, *Kerivoula depressa* has been found in a variety of lowland and montane habitats, which include evergreen, mixed deciduous and dipterocarp forests at altitudes of 67-1,424 m a.s.l.,. It is tolerant of human-modified habitats, including rubber and orchard plantations. Pregnant females have been found in February to May and lactating females have been found in March to May (BD unpublished data).

4.5. DISCUSSION

Corbet and Hill (1992) suggested that specimens referred to *K. hardwickii* from India to Vietnam have relatively flattened braincases. The present study generally supports this view, based on both morphological and genetic data.

Our evidence indicates that the 'flat-skull' type of '*K. hardwickii'*, here referred to *K. depressa,* is primarily restricted to the Indochinese subregion (Figure 4.10.). In contrast, the 'domed-skull' type, *K. hardwickii*, is essentially restricted to the Sundaic subregion. However, there are exceptions to this distribution and in parts

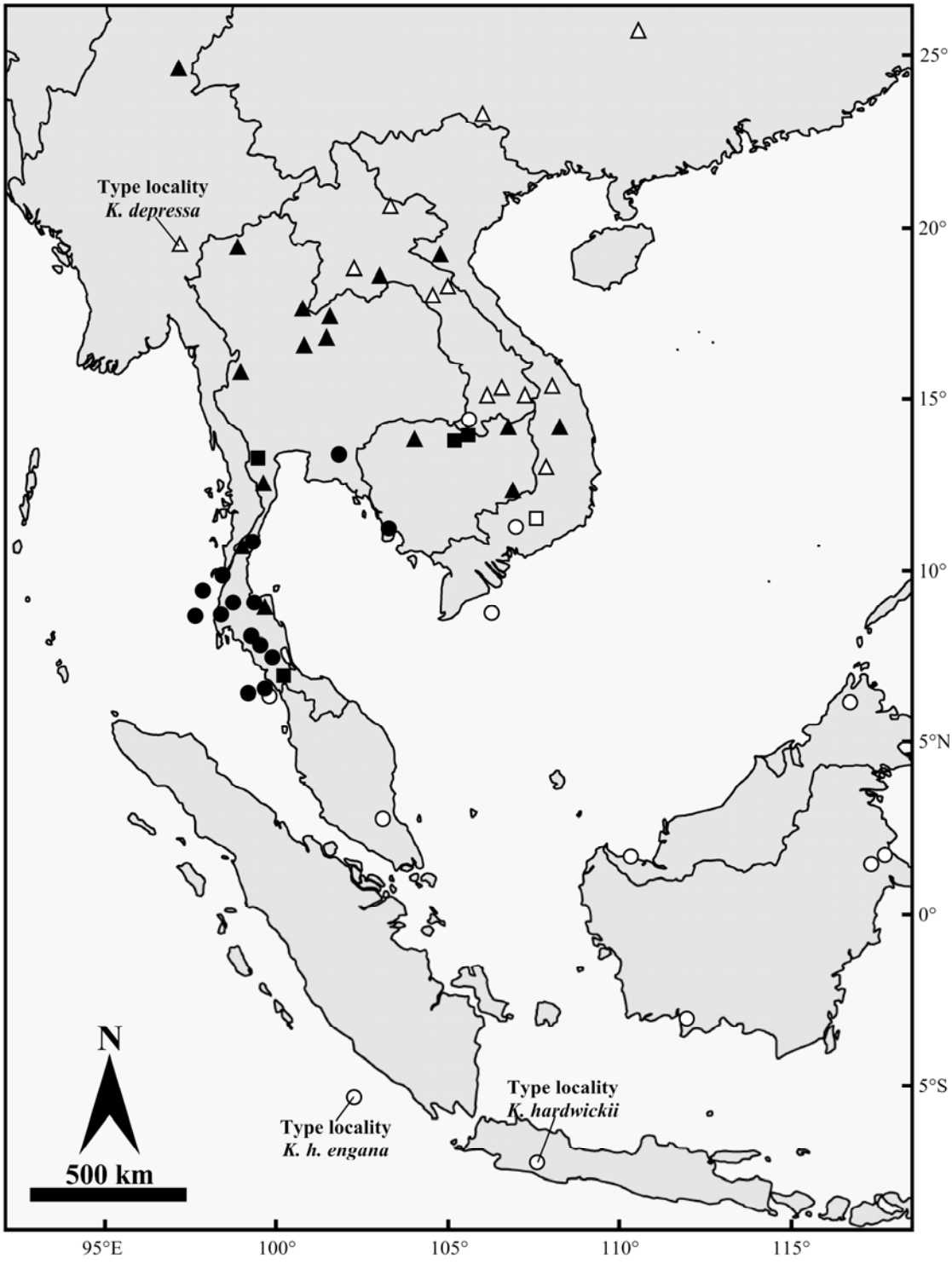

Figure 4.10. Distribution map of *K. hardwickii* (circles) and *K. depressa* (triangles). Square symbols represent sympatrical localities – black symbols represent the localities of voucher specimens used in this study and open symbols are genetics referred in GenBank and literature records, including Struebig et al. (2006a,b), Suyanto and Struebig (2007) and Anwarali et al. (2008).

of their ranges they are sympatric and have been found syntopically at some localities (Figure 4.10). These include Cat Tien National Park in Dong Nai Province of Vietnam (based on genetics – the DNA Barcode of Life Database), Baray Mounts and M'Lou Prey in Preah Vihear Province of Cambodia (based on morphology), and Pha Chi Wildlife Sanctuary in Ratchaburi Province and Ton Nga Chang Wildlife Sanctuary in Songkhla Province of Thailand (based on morphology).

Hill (1975) referred specimen from Chiang Mai, northern Thailand with a high braincase to *K. hardwickii.* However, this material may be referable to the recently described species, *K. titania* Bates et al., 2007, which is also known from Chiang Mai, northern Thailand. He also proposed that *K. depressa* may occur further to the south of Thailand. The current study supports the view that there is a wide overlap in the geographical ranges of the two taxa in eastern and peninsular Thailand.

Francis (2008) suggested that the bats previously referred to *K. hardwickii* include several taxa which have similar morphology but differ in genetics (see also Francis et al., 2010). However, the present study shows that bats previously referred to *K. hardwickii* (sensu Corbet and Hill, 1992) are clearly different in both morphology and genetics and can be divided into two distinct species, namely *K. hardwickii* and *K. depressa*. The result also suggests that the specimens with a 'domed-skull' (*K. hardwickii*) from Thailand and Cambodia include several forms with different morphology (Figures 4.3. and 4.7.). However, genetic analysis of the Thai specimens shows that there is only one monophyletic clade (Figure 4.8.) with a genetic divergence of 0.96 % (Table 4.6.). When Thai and Malaysian specimens are included, they also cluster in one monophyletic clade, with a genetic divergent < 0.88 % (Figure 4.9., Table 4.7.). However, the present study is based on mitochondrial DNA (mtDNA) region, COI. Baker and Bradley (2006) suggested that a study restricted to a single gene is not a sufficient for species recognition. Further study need to included more regional gene, especially nuclear gene to confirm there is morphological variation within the specimens of *K. hardwickii* or there is incomplete lineage sorting within genetic (Anwarali et al., 2010; Francis et al., 2010; Nesi et al., 2011; Lin et al., 2013). In contrast, the specimens with a 'flat-skull' (*K. depressa*) appear to represent several cryptic species with similar morphology (Figures 4.3. and 4.7.) and the genetic analysis includes several monophyletic clades (Figures 4.8. and

4.9.) with genetic divergent > 5 % (Tables 4.6. and 4.7.). However, without additional study, which ideally includes type specimens, it is very difficult to assign the correct name to each taxon.

The study supports the view that the taxonomy of the genus *Kerivoula* is still unresolved for many forms. This is reflected in the description, in recent years, of many new species, including: *K. kachinensis* Bates et al., 2004, *K. titania* Bates et al., 2007 and *K. krauensis* Francis et al., 2007 and the elevation of a former synonym of *K. papillosa* to species level *K. lenis,* by Vanitharani et al. (2003).

CHAPTER 5
GENERAL DISCUSSION

The present study increases the number of species of *Kerivoula* known from Thailand to 12 (Table 5.1.). It also supports the views of Francis (2008), Anwarali et al. (2010), Francis et al. (2010) and Hasan and Abdullah (2011) that *Kerivoula papillosa/K. lenis* and *K. hardwickii* (sensu Corbet and Hill, 1992; Vanitharani et al., 2003) are two species complexes.

Bats previously referred to *K. papillosa* are here considered to belong to three distinct species. Material previously referred to *K. papillosa* Large (sensu Anwarali et al., 2010; Hasan and Abdullah, 2011) is here referred to true *K. papillosa,* which is restricted to Sumatra, Java and Borneo (Figure 3.8.), whereas those referred to *K. papillosa* Small are here referable to the taxon *malayana,* which is considered to be a distinct species confined to peninsular Thailand and Malaysia and Borneo. The third taxon is only known from Thailand and is considered as an undescribed species, *Kerivoula* spA.

Bats previously referred to *K. lenis* from the Sundaic Subregion (sensu Anwarali et al., 2010; Francis et al., 2010; Hasan and Abdullah, 2011) are here considered as an undescribed species, *Kerivoula* sp. nov. B. True *K. lenis* is restricted to India. The taxonomy of specimens referred to *K. lenis* (sensu Francis et al., 2010) from the Indochinese Subregion (Lao PDR and Vietnam) is uncertain. Further studies may show that it is either *K. lenis* or more probably that it belongs to a new, undescribed species.

In the case of *K. hardwickii*, it was previously suggested that it was a species complex (Francis, 2008; Francis et al., 2010). The present study identified two distinct species, the 'domed-skull' type referred to *K. hardwickii* and the 'flat-skull' type referred to *K. depressa*. The morphology suggests that the specimens referred to *K. hardwickii* include several taxa (Figures 4.3. and 4.7.). However, this is not supported by the genetic analysis, which appears to indicate that there is only one taxon (Figures 4.8. and 4.9.), with genetic distances of < 1% (Tables 4.6. and 4.7.). However, the result from the present study is based on only one gene, COI.

Table 5.1. List of *Kerivoula* currently known from Thailand.

No	Species	Note
1	*K. malayana*	Previously considered as a subspecies of *K. papillosa*
2	*Kerivoula* sp A.	New species
3	*Kerivoula* sp B.	New species
4	*K. kachinensis*	
5	*K. titania*	
6	*K. hardwickii*	
7	*K. depressa*	Previously considered as a subspecies of *K. hardwickii*
8	*K. pellucida*	
9	*K. krauensis*	New record
10	*K. picta*	
11	*K. whiteheadi*	
12	*K. minuta*	

In contrast, specimens referred to *K. depressa* include several taxa which are supported by both morphology and genetics (Figures 4.3., 4.7., 4.8. and 4.9.; Tables 4.6. and 4.7.), including several undescribed species. Further study should be carried out to assign the correct name for each taxon.

The discovery of *K. krauensis* in Thailand, which is a northern range extension of 254 km, shows that it is more widespread than previously thought. This has implications for its conservation. Until now, its known range was restricted to a small area of approximately 530 km^2 in Krau Wildlife Reserve (Kingston et al., 1999, 2003, 2006). However, despite the range extension, it still appears that its population size is relatively small. In Krau Wildlife Reserve, its capture rate was < 0.4% of all bats (56/14,000 individuals), which is considerably less than the 15.3% for *K. intermedia,* 7.8% for *K. papillosa* and 5.9% for *K. pellucida* (Francis et al., 2007). This apparent low abundance of the population is also mirrored in Hala Bala, where despite intensive netting and harp trapping since 2003 (S. Bumrungsri, unpublished data), only one specimen has ever been collected.

Two species previously recorded for Thailand, *K. picta* and *K. whiteheadi*, were not found during the present study. *K. picta* has a widespread distribution and is known from India and Sri Lanka to the Moluccas. It suggests that this species is relatively rare to the region or possibly that it is difficult to collect in harp traps and/or nets. In the case of *K. whiteheadi*, it is only known from Yala Province, South

Thailand (= *K. bicolor*, currently considered as a subspecies of *K. whiteheadi*, *K. w. bicolor*).

In terms of biogeography, Thailand is divided into two zoogeographical subregions, with the Indochinese Subregion in the north and central part of the country and the Sundaic Subregion in the peninsula, with a transition zone in the Isthmus of Kra (Lekagul and McNeely, 1977; Corbet and Hill, 1992; Bruyn et al., 2005). Two species: *K. kachinensis* and *K. titania* are restricted to the Indochinese Subregion, while six species: *K. malayana, Kerivoula* spB., *K. pellucida, K. krauensis, K. whiteheadi* and *K. minuta*, are restricted to Sundaic Subregion, and other four are known to both subregions.

Within Sundaic Subregion, the genetic analysis shows that the populations from Borneo of *K. malayana, Kerivoula* spB., *K. hardwickii*, *K. intermedia* and *K. minuta* grouped separately from those of mainland (see also Anwarali et al., 2010). Francis et al. (2007) suggested that the South China Sea could be a geographical barrier which resulted in allopatric populations distinguishable by levels of genetic divergence between Peninsular Malaysia and Borneo. This result has also been observed in mammals (Ruedi and Fumagalli, 1996; Gorog et al., 2004), snakes and frogs (Inger and Voris, 2001), and termites (Gathorne-Hardy et al., 2002).

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Appendix 1. Gazetteer

Location	Province/State	Co-ordinate	Altitude
	India		
Therkumalai	Tamil Nadu	8°50'N, 77°21'E	800 m
	China		
Daweishan NP.	Hunan	28°25'N, 114°07'E	1,400 m
Shuhuangshan NR.	Hunan	26°25'N, 111°01'E	500 m
Jing Xin County Provincial NR.	Guangxi	23°07'N, 105°58'E	1,100 m
	Myanmar		
Nanti Hill Forest, Bhamo Township	Kachin	24°34'N, 97°07'E	
	Lao PDR		
Nam Ha NBCA	Louang Namtha	c.o. 20°23'N, 100°45'E	
Nam Et NBCA	Houaphan	c.o. 20°22'N, 103°32'E	
Vang Vieng	Vientiane	c.o. 18°58'N, 102°19'E	
Houi Nhang NR	Vientiane	18°04'N, 102°40'E	
Phou Khao Khouay NBCA	Vientiane	c.o. 18°23'N, 103°04'E	
Lak Sao	Khammouan	18°11'N, 104°58'E	
Nakai Plateau	Khammouan	17°58'N, 105°01'E	
Khammouan Limestone NBCA	Khammouan	c.o. 17°33'N, 105°04'E	
Hin Nam No NBCA	Khammouan	c.o. 17°30'N, 105°50'E	
Xe Kaman, Dong Amphan NBCA	Attapu	c.o. 14°55'N, 107°03'E	
Bolaven Plateau	Champasak	15°03'N, 106°33'E	
Dong Hua Sao NBCA	Champasak	c.o. 15°03'N, 106°05'E	
Dong Kanthung	Champasak	c.o. 14°15'N, 105°23'E	
	Vietnam		
Na Hang NR.	Tuyen Quang	22°19'N, 105°25'E	
Pu Mat Researve	Gnhe An	18°58'N, 104°46'E	
Nuoc Xa	Quang Nam	c.o. 15°12'N, 108°01'E	830 m
Kon Ka Kinh NR.	Gai Lai	14°19'N, 108°25'E	
Yok Don NP.	Dac Lac	12°52'N, 107°42'E	
Bu Gia Map NP.	Binh Phuoc	12°11'N, 107°12'E	540 m
Hon Ba Mts., Dien Khanh	Phu Khanh	12°05'N, 108°57'E	1,300 m
Cat Tien NP.	Dong Nai	11°25'N, 107°25'E	200 m
Vinh Cuu NR.	Dong Nai	11°22'N, 107°02'E	40 m
Con Son island, Con Dao NP.	Ba Ria-Vung Tau	8°41'N, 106°35'E	260 m
	Cambodia		
Baray Mounts, Preah Vihear PF.	Preah Vihear	14°01'N, 105°37'E	202 m
M'lou Prey	Preah Vihear	13°58'N, 105°16'E	
Botum Sakor NP.	Koh Kong	11°04'N, 103°20'E	

Appendix 1. Continued.

Location	Province/State	Co-ordinate	Altitude
O'Kasieb, Veun Sai District	Ratanakiri	14°03'N, 106°43'E	
Kbal Spean, Banteay Srey District	Siem Reap	13°41'N, 104°00'E	206 m
Seima BCA.	Mondulkiri	12°11'N, 107°01'E	311 m
Prek Kamaues	Kandal	11°26'N, 104°54'E	
	Thailand		
Khun Mae Ngai, Chiang Dao WS.	Chiang Mai	19°30'N, 98°49'E	
Hui Mae Kok, Chiang Dao WS.	Chiang Mai	19°22'N, 98°50'E	
Chiang Dao WRS.	Chiang Mai	19°21'N, 98°55'E	
Phou Suan Sai NP.	Loei	17°30'N, 100°57'E	
Na Haew, Phu Suan Sai NP.	Loei	17°28'N, 101°58'E	
Hauy Nam Chan, Phu Loung WS.	Loei	17°20'N, 101°33'E	
Namnao NP.	Phetchabun	16°45'N, 101°33'E	
Thung Salang Luang NP.	Phisanoulok	16°34'N, 100°52'E	
Mae Wong NP.	Tak	c.o. 15°54'N, 99°12'E	
East Thung Yai Naresuan WS.	Tak	15°44'N, 98°59'E	
Angruenai WS.	Chachuengsao	13°24'N, 101°52'E	
Pha Chi WS.	Ratchaburi	13°18'N, 99°24'E	
Pa La-U, Kaeng Krachan NP.	Prachuap Khiri Khan	12°32'N, 99°27'E	
Khao Kaew, Muang District	Chumphon	10°30'N, 99°07'E	
South Klom Luang Chumporn WS.	Ranong	10°31'N, 98°54'E	67 m
Koh Chang, Mo Koh Payam NP.	Ranong	9°48'N, 98°26'E	
North Surin Island, Surin Islands NP.	Phang Nga	9°26'N, 97°52'E	
Koh No. 8, Mu Koh SimilanNP.	Phang Nga	8°39'N, 97°39'E	
Lumpee Waterfall, Khao Lumpee-Had Thaymaung NP.	Phang Nga	8°27'N, 98°17'E	
Khao Sok NP.	Surat Thani	c.o. 8°57'N, 98°48'E	
Khao Nan NP.	Nakhon Si Thammarat	8°51'N, 99°37'E	
Krungching, Khao Luang NP.	Nakhon Si Thammarat	c.o. 8°42'N, 99°41'E	
Khao Pra-Bang Kram WS.	Krabi	7°55'N, 99°15'E	
Ban Nai Khao, Hui Yod District	Trang	7°42'N, 99°41'E	

Appendix 1. Continued.

Location	Province/State	Co-ordinate	Altitude
Khao Pu-Khao Ya NP.	Patthalung	c.o. 7°40'N, 99°52'E	
Khao Chong, Khao Bantad WS.	Trang	7°33'N, 99°46'E	
Sai Rung Waterfall, Khao Bantad WS.	Trang	7°25'N, 99°46'E	
Priwan Waterfall, Khao Bantad WS.	Phatthalung	7°23'N, 99°58'E	
Phu Pha Phet, Khao Bantad WS.	Satun	7°07'N, 100°00'E	
Had Sai Khao Waterfall, Rattaphum District	Songkhla	7°02'N, 100°12'E	
Kuan Khao Wang FP.	Songkhla	7°00'N, 100°18'E	50 m
Ton Nga Chang WS.	Songkhla	6°56'N, 100°14'E	
Pha Dam, Ton Nga Chang WS.	Songkhla	6°47'N, 100°13'E	
Taleban NP.	Satun	6°39'N, 100°09'E	
Tarutao Island, Tarutao NP.	Satun	6°39'N, 99°40'E	
Adang-Rawi Islands, Tarutao NP.	Satun	6°32'N, 99°16'E	
Khao Nam Khang NP.	Songkhla	6°06'N, 101°04'E	73 m
Hala-Bala WS.	Narathiwat	5°48'N, 101°50'E	100 m
	Peninsular Malaysia		
Kedah, Langkawi Island	Langkawi	c.o. 6°20'N, 99°47'E	
Taman Negara NP.	Pahang	c.o. 4°39'N, 102°28'E	
Krau Wildlife Reserve	Pahang	c.o. 3°43'N, 102°10'E	
Endau Rompin NP.	Johor	c.o. 2°31'N, 103°24'E	42 m
	Malaysian Borneo		
Niah NP.	Sarawak	c.o. 3°47'N, 113°46'E	
Similajau NP.	Sarawak	c.o. 3°30'N, 113°20'E	
Sibu, Bukit Aub	Sarawak	c.o. 2°14'N, 111°54'E	
Kubah NP.	Sarawak	c.o. 1°34'N, 110°10'E	
Lanjak Entimau WS.	Sarawak	c.o. 1°25'N, 112°06'E	
Mount Penrisen	Sarawak	c.o. 1°15'N, 110°08'E	
Sepilok Forest Reserve	Sabah	c.o. 5°51'N, 117°58'E	
Monggis Sub Station	Sabah	c.o. 5°48'N, 116°35'E	
Tabin Wildlife Reserve	Sabah	c.o. 5°04'N, 118°40'E	
Madai Caves	Sabah	4°43'N, 118°09'E	
	Indonesian Sumatra		
Way Canguk	Lampung	c.o. 5°16'N, 104°10'E	
	Indonesian Borneo		
Tanjung, Putin NP.	Central Kalimantan	2°16'S, 112°00'E	

Appendix 2. List of specimens examined in the present study.

Lacation	Country	Specimen number
	Kerivoula papillosa	
Niah NP.	B. Malaysia	TK156001, 156004, 156036
Way Canguk	S. Indonesia	MZB 35887, 35888
Tanjung, Putin NP.	B. Indonesia	HZM.1.36538
	Kerivoula malayana	
Kuan Khao Wang FP.	Thailand	PSUZC-MM2012.70
Khao Nam Khang NP.	Thailand	HBWRS2010.3
Taleban NP.	Thailand	PSUZC-MM2013.8
Hala-Bala WS.	Thailand	PSUZC-MM2013.28
Krau Game Reserve	P. Malaysia	TTU-M 108183, 108218, 108219
	***Kerivoula* spA.**	
Pha Chi WS.	Thailand	PSUZC-MM2008.56, 2008.57
South Klom Luang Chumporn WS.	Thailand	PSUZC-MM2011.53
Hala-Bala WS.	Thailand	PSUZC-MM2013.10, 2013.11
	***Kerivoula* spB.**	
Khao Pra-Bang Kram WS.	Thailand	PSUZC-MM2012.173, 2012.174
Khao Chong, Khao Bantad WS.	Thailand	PSUZC-MM2011.2, 2012.175, 2013.9
Phu Pha Phet, Khao Bantad WS.	Thailand	PSUZC-MM2012.172
Hala-Bala WS.	Thailand	PSUZC-MM2005.123, 2011.4, 2011.10, 2012.53, 2012.54, 2013.12
Krau Game Reserve	P. Malaysia	TTU-M 108210
Kubah NP.	B. Malaysia	TTU-M 108326
Way Canguk,	S. Indonesia	MZB 35008
Tanjung, Putin NP.	B. Indonesia	HZM.2.36539
	Kerivoula lenis	
Therkumalai	India	HZM.1.35276
	Kerivoula kachinensis	
Khun Mae Ngai., Chiang Dao WS.	Thailand	PSUZC-MM2011.16
Phou Suan Sai NP.	Thailand	PSUZC-MM2006.66, 2007.242, 2007.243
Namnao NP.	Thailand	PSUZC-MM2007.244
	Kerivoula titania	
Khun Mae Ngai., Chiang Dao WS.	Thailand	PSUZC-MM2011.18
Chiang Dao WRS.	Thailand	PSUZC-MM2011.15
Phou Suan Sai NP.	Thailand	PSUZC-MM2007.302, 2007.303
Namnao NP.	Thailand	PSUZC-MM2007.304
Pa La-U, Kaeng Krachan NP.	Thailand	PSUZC-MM2011.48

Appendix 2. Continued.

Lacation	Country	Specimen number
	Kerivoula kardwickii	
Angruenai WS.	Thailand	PSUZC-MM2005.200
Pha Chi WS.	Thailand	PSUZC-MM2007.343, 2007.344
Khao Kaew	Thailand	PSUZC-MM2012.169
Koh Chang, Mo Koh Payam NP.	Thailand	PSUZC-MM2011.20
North Surin Island, Surin Islands NP.	Thailand	PSUZC-MM2006.152, 2006.187, 2008.74
Lumpee Waterfall, Khao Lumpee-Had Thaymaung NP.	Thailand	PSUZC-MM2013.4
Koh No. 8, Mu Koh Similan NP.	Thailand	PSUZC-MM2008.77, 2008.78
Khao Pra-Bang Kram WS.	Thailand	PSUZC-MM2012.161, 2012.162, 2012.163, 2012.164, 2012.168
Khao Sok NP.	Thailand	PSUZC-MM2012.167, 2012.170, 2012.171, 2013.
Khao Nan NP.	Thailand	PSUZC-MM2007.286, 2007.287, 2007.311, 2007.312
Ban Nai Khao, Hui Yod District	Thailand	PSUZC-MM2007.285
Khao Chong, Khao Bantad WS.	Thailand	PSUZC-MM2007.282, 2007.284, 2012.113
Khao Pu-Khao Ya NP.	Thailand	HBWRS2010.7, 2010.11
Priwan Waterfall, Khao Bantad WS.	Thailand	PSUZC-MM2012.165
Phu Pha Phet, Khao Bantad WS.	Thailand	PSUZC-MM2012.160
Hin Sam Kon Waterfall, Rattaphum District	Thailand	PSUZC-MM2012.59
Kuan Khao Wang FP.	Thailand	PSUZC-MM2011.49, 2011.50
Ton Nga Chang WS.	Thailand	PSUZC-MM2007.270, 2007.271, 2007.276, 2007.277, 2007.280, 2007.283, 2007.289, 2012.62
Pha Dam, Ton Nga Chang WS.	Thailand	PSUZC-MM2007.152, 2007.279, 2012.57, 2012.58
Tarutao Island, Tarutao NP.	Thailand	PSUZC-MM2005.187, 2007.147, 2008.131, 2008.132, 2009.62, 2013.3
Adang-Rawi Islands, Tarutao NP.	Thailand	PSUZC-MM2008.79, 2009.40, 2009.41, 2012.60, 2012.61, 2013.5
Baray Mounts	Cambodia	CBC01273, 01274
M'lou Prey	Cambodia	HZM.11.33790
Botum Sakor NP.	Cambodia	CBC00480

Appendix 2. Continued.

Lacation	Country	Specimen number
	Kerivoula depressa	
Nanti Hill Forest	Myanmar	HZM.10.35963
Khun Mae Ngai, Chiang Dao WS.	Thailand	PSUZC-MM2011.17
Hui Mae Kok , Chiang Dao WS.	Thailand	PSUZC-MM2011.14
Chiang Dao WRS.	Thailand	PSUZC-MM2011.19
Phu Saun Sai NP.	Thailand	PSUZC-MM2006.166, 2007.272, 2007.273
Hauy Nam Chan, Phu Loung WS.	Thailand	PSUZC-MM2005.201, 2005.202
Namnao NP.	Thailand	PSUZC-MM2007.274, 2007.275
Thung Salang Luang NP.	Thailand	PSUZC-MM2006.165
Mae Wong NP.	Thailand	PSUZC-MM2013.26, 2013.27
East Thung Yai Naresuan WS.	Thailand	PSUZC-MM2008.75
Pu Nam Ron, Pha Chi WS.	Thailand	PSUZC-MM2007.345
Pa La-U, Kaeng Krachan NP.	Thailand	PSUZC-MM2011.52
South Klom Luang Chumporn WS.	Thailand	PSUZC-MM2011.51
Krungching, Khao Luang NP.	Thailand	PSUZC-MM2012.166
Pha Dam, Ton Nga Chang WS.	Thailand	PSUZC-MM2007.281
Tad Leuk Waterfall, Phou Khao Khouay NBCA.	Lao PDR	FES.MM.10.053
O'Kasieb	Cambodia	CBC00615, 00638, 00639, 01125, 01140
Baray Mts, Preah Vihear PF.	Cambodia	CBC01272
M'lou Prey	Cambodia	HZM.10.33789
Kbal Spean	Cambodia	CBC00946
Seima BCA.	Cambodia	CBC00479
Pu Mat Researve	Vietnam	HZM.4.31763, 6.31778
Kon Ka Kinh Nature Reserve	Vietnam	HZM.7.32604, 8.32605, 9.32606
	Kerivoula pellucida	
Khao Pra-Bang Kram WS.	Thailand	PSUZC-MM2012.176
Khao Pu Khao Ya NP.	Thailand	HBWRS2010.6, 2010.10
Phu Pha Phet, Khao Bantad WS.	Thailand	PSUZC-MM2013.24
Kuan Khao Wang FP.	Thailand	PSUZC-MM2011.46, 2011.47
Ton Nga Chang WS.	Thailand	PSUZC-MM2012.66, 2012.69, 2013.2
Khao Nam Khang NP.	Thailand	HBWRS2010.9
Hala-Bala WS.	Thailand	PSUZC-MM2011.12, 2011.13, 2012.55, 2012.56
	Kerivoula krauensis	
Hala-Bala WS.	Thailand	PSUZC-MM2013.25

Appendix 2. Continued.

Lacation	Country	Specimen number
	Kerivoula minuta	
Khao Chong, Khao Bantad WS.	Thailand	PSUZC-MM2011.1
Sai Rung Waterfall, Khao Bantad WS.	Thailand	PSUZC-MM2012.50
Phu Pha Phet, Khao Bantad WS.	Thailand	PSUZC-MM2013.19, 2013.20
Ton Nga Chang WS.	Thailand	PSUZC-MM2007.153, 2007.278, 2007.310, 2012.63, 2012.65, 2013.7
Khao Nam Khang NP.	Thailand	HBWRS2010.4, 2010.5, 2010.8
Hala-Bala WS.	Thailand	PSUZC-MM2011.3, 2011.5, 2011.6, 2011.7, 2011.8, 2011.9, 2012.51, 2012.52, 2012.108, 2012.110

Appenidix 3. List of genetic sequences of specimens from Thailand examined in the present study.

Location	Province	Specimen number
	Kerivoula malayana	
Kuan Khao Wang FP.	Songkhla	PSUZC-MM2012.70
Khao Nam Khang NP.	Songkhla	HBWRS2010.3
	***Kerivoula* spA.**	
Pha Chi WS.	Ratchaburi	PSUZC-MM2008.57
South Klom Luang Chumporn WS.	Ranong	PSUZC-MM2011.53
	***Kerivoula* spB.**	
Khao Pra-Bang Kram WS.	Krabi	PSUZC-MM2012.174
Phu Pha Phet, Khao Bantad WS.	Satun	PSUZC-MM2012.172
Hala-Bala WS.	Narathiwat	PSUZC-MM2011.4, 2011.10, 2012.53, 2012.54
	Kerivoula titania	
Chiang Dao WRS.	Chiang Mai	PSUZC-MM2011.15
Pa La-U, Kaeng Krachan NP.	Prachuap Khiri Khan	PSUZC-MM2011.48
	Kerivoula hardwickii	
Khao Kaew, Muang District	Chumphon	PSUZC-MM2012.169
Khao Sok NP.	Surat Thani	PSUZC-MM2012.170, 2012.171
Khao Pra-Bang Kram WS.	Krabi	PSUZC-MM2012.161, 2012.162, 2012.163
Phu Pha Phet, Khao Bantad WS.	Satun	PSUZC-MM2012.160
Adang-Rawi Islands, Tarutao NP.	Satun	PSUZC-MM2012.61
	Kerivoula depressa	
Khun Mae Ngai, Chiang Dao WS.	Chiang Mai	PSUZC-MM2011.17
Hui Mae Kok, Chiang Dao WS.	Chiang Mai	PSUZC-MM2011.14
Chiang Dao WRS.	Chiang Mai	PSUZC-MM2011.19
Pa La-U, Kaeng Krachan NP.	Prachuap Khiri Khan	PSUZC-MM2011.52
	Kerivoula minuta	
Sai Rung Waterfall, Khao Bantad WS.	Trang	PSUZC-MM2012.50
Khao Nam Khang NP.	Songkhla	HBWRS2010.8
Hala-Bala WS.	Narathiwat	PSUZC-MM2011.5
	Kerivoula pellucida	
Hala-Bala WS.	Narathiwat	PSUZC-MM2011.12

Appendix 4. List of genetic sequences from the DNA Barcode of Life Database (www.boldsystems.org), as well as GenBank, used to compare in the present study.

Location	Country	Specimens number
	Kerivoula papillosa	
Sepilok FR.	B. Malaysia	ROM 117932, 117933, 117934
Niah NP.	B. Malaysia	TK 156001, 156004, 156036
	Kerivoula malayana	
Taman Negara NP.	P. Malaysia	TK 152994
Krau Wildlife Reserve	P. Malaysia	S300091, 300721, CMF920706-03, TK 152020, 152023, 152061, 152062
Endau Rompin NP.	P. Malaysia	ROM 113056, 113110
Similajau NP.	B. Malaysia	TK 125619, 125620
Niah NP.	B. Malaysia	TK 152403
	***Kerivoula* spB.**	
Krau Wildlife Reserve	P. Malaysia	TK 152052
Endau Rompin NP.	P. Malaysia	ROM 113049, 113053
Sepilok Forest Reserve	B. Malaysia	ROM 117931
Kubah NP.	B. Malaysia	TK 152178
	Kerivoula cf. lenis	
Xe Kaman, Dong Amphan NBCA	Laos	ROM 110520, 110527, 110589
Bu Gia Map NP.	Vietnam	ZMMU 139-09
Cat Tien NP.	Vietnam	ROM 110850
	Kerivoula kachinensis	
Nam Ha NBCA	Laos	AGS980420-18
Nam Et NBCA	Laos	EBD 25747, ROM 118279
Phou Khao Khouay NBCA	Laos	EBD 25122, ROM 118063
Lak Sao	Laos	ROM 106458
Bolaven Plateau	Laos	ROM 110603
Na Hang NR.	Vietnam	ROM 107718
Bu Gia Map NP.	Vietnam	ZMMU 184667
	Kerivoula titania	
Bhamo Township	Myanmar	HZM 2.35962
Nam Ha NBCA	Laos	ROM 118395
Phou Khao Khouay NBCA	Laos	EBD 25120
Khammouan Limestone NBCA	Laos	ROM 118034
Hin Nam No NBCA	Laos	ROM 118093
Xe Kaman, Dong Amphan NBCA	Laos	ROM 110573, 110575, 110584, 110586
Na Hang NR.	Vietnam	ROM 107654, 107682, 107713
Nuoc Xa	Vietnam	ROM 111374, 111400
Hon Ba Mts., Dien Khanh	Vietnam	ZMMU 175149
	Kerivoula hardwickii	
Dong Kanthung	Laos	ROM 110721, 118153, 118162

Appendix 4. Continued.

Location	Country	Specimens number
Cat Tien NP.	Vietnam	ROM 110819, 110829, 110851, 110852
Vinh Cuu NR.	Vietnam	ZMMU 101-09
Con Son island, Con Dao NP.	Vietnam	ZMMU 186751, 186752, 186753, 186754, 186755, 186756, 186757
Khao Pra-Bang Kram WS.	Thailand	INECOL M0071, 0108
Endau Rompin NP.	P. Malaysia	ROM 113107, 113108, 113109
Kedah, Langkawi Island	P. Malaysia	DWNP 1399, 1409
Monggis Sub Station	B. Malaysia	TK 152080, 152097, 152115
Sibu, Bukit Aub	B. Malaysia	TK 153568
	Kerivoula depressa	
Daweishan NP.	China	ROM 114961, 114962, 114963, 114964, 115009, 115041, 115042, 115047
Shuhuangshan NR.	China	ROM 114918, 114944
Jing Xin County Provincial NR.	China	ROM 116079
Nuoc Xa	Vietnam	ROM 111337, 111362, 111363, 111272, 111273, 111274, 111275, 111276, 111277, 111278, 111279, 111280, 111281, 111282, 111283, 111298, 111299
Yok Don NP.	Vietnam	ROM 107721
Cat Tien NP.	Vietnam	ROM 110828
Nam Et NBCA	Laos	AGS980322-65, ROM 118186
Vang Vieng	Laos	ROM 118429
Nakai Plateau	Laos	CMF960505-15
Khammouan Limestone NBCA	Laos	ROM 118026, 118033
Hin Nam No NBCA	Laos	ROM 118092
Bolaven Plateau	Laos	ROM 110604, 110605
Dong Hua Sao NBCA	Laos	ROM 110602
Xe Kaman, Dong Amphan NBCA	Laos	ROM MAM 110556, 110585, 117971, 117982
	Kerivoula pellucida	
Taman Negara NP.	P. Malaysia	TK 153552, 153560, 153563
Krau Wildlife Reserve	P. Malaysia	CMF920705-02, DWNP 3912, TK 152055
Endau Rompin NP.	P. Malaysia	ROM 113021, 113022, 113023, 113057
Niah NP.	B. Malaysia	TK 152398
Similajau NP.	B. Malaysia	UNIMAS 00554
	Kerivoula picta	
Houi Nhang NR	Laos	ROM 106371, 117884

Appendix 4. Continued.

Location	Country	Specimens number
Prek Kamaues	Cambodia	HZM 1.35275
	Kerivoula krauensis	
Krau Wildlife Reserve	Malaysia	SMF 83824
	Kerivoula intermedia	
Krau Wildlife Reserve	P. Malaysia	CMF920703-04, 920704-04, TK 152019, 152021, 152060
Tabin Wildlife Reserve	B. Malaysia	SMF 83720
Lanjak Entimau WS.	B. Malaysia	TK 153609, 153619, 153621, 153638
	Kerivoula minuta	
Khao Pra-Bang Kram WS.	Thailand	INECOL M0111, 0112
Krau Wildlife Reserve	P. Malaysia	CMF920704-03
Taman Negara NP.	P. Malaysia	DWNP 2132, TK 152022, 152995, 152996, 152999, 153564
Endau Rompin NP.	P. Malaysia	ROM 113016, 113072
Sibu, Bukit Aub	B. Malaysia	TK 153567, 153588
Kubah NP.	B. Malaysia	TK 152194
Lanjak Entimau WS.	B. Malaysia	TK 153663, 153668
Mount Penrisen	B. Malaysia	TK 152206, 152249
Monggis Sub Station	B. Malaysia	TK 152075, 152079
Tabin Wildlife Reserve	B. Malaysia	SMF 83722
Madai Caves	B. Malaysia	CMF960523-39
	Phoniscus jagorii	
Jing Xin County Provincial NR.	China	ROM 116221
Nam Et NBCA	Laos	EBD 24977
Vang Vieng	Laos	INECOL M0127
Nakai Plateau	Laos	ROM 106483
Khammouan Limestone NBCA	Laos	CMF980124-10, ROM 110668, 118025, 118035
Dong Kanthung	Laos	CMF980228-114, ROM 110722, 110725
	Murina peninsularis	
Krau Wildlife Reserve	Malaysia	CMF920703-03
	Murina suilla	
Sepilok Forest Reserve	Malaysia	ROM 117936
	Myotis* cf. *muricola	
Tuaran, Sabah	Malaysia	ROM MAM 117943

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Educational Attainment

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List of Publication and Proceeding

Douangboubpha, B., S. Bumrungsri, C. Satasook, W. Wanna, P. Soisook, and P.J.J. Bates. Morphology, acoustics and genetics of the genus *Kerivoula* (Chiroptera: Vespertilionidae: Kerivoulinae) in Thailand. Mammalia (Submitted).

Douangboubpha, B., S. Bumrungsri, P. Soisook, S. Karapan, and P.J.J. Bates. The discovery of *Kerivoula krauensis* (Chiroptera: Vespertilionidae) in southern peninsular Thailand provides new information on the distribution and conservation status of this data deficient species. Songklanakarin Journal of Science and Technology (accepted).

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