博士論文

Morphological variation and systematic study of tube-nosed and woolly bats in Vietnam

（ベトナム産テングコウモリ類およびウーリーコウモリ類の
形態学的変異と系統分類に関する研究）

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ABSTRACT

Doctoral Dissertation

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Three genera *Murina*, *Harpiocephalus* and *Harpoila* of tube-nosed bats (Murininae) and two genera *Kerivoula* and *Phoniscus* of woolly bats (Kerivoulinae) are currently recognized. The members of these groups are small to medium-sized or slightly large bats of the vesper bats (Vespertilionidae) with a distribution throughout Asia, from northeastern Pakistan, eastwards to Siberia, Korea and Japan, southwards to northeastern Australia, except for Kerivoulinae, which have a wider range to Africa.

Recent studies indicated that the species number of *Murina* rapidly increased with thirty-five recorded species from Southeast Asia. The subfamily Kerivoulinae is currently contains twenty-six species. However, the taxonomic status of both subfamilies remains problematic by appear the complex species, particularly the intraspecific variation of possible crytic species, *Kerivoula hardwikii* as well as the generic status of *Kerivoula* and *Phoniscus*.

Recent studies on the species diversity and taxonomy of afore-mentioned groups were based on diagnostic characters (e.g., fur color, forearm length, and skull characters) to identify the species. Nevertheless, comprehensive skull morphometric analyses based on sufficient number of specimens and species have never been carried out for these subfamilies.

In this study, field surveys were conducted from 2001 to 2014 in forty-three sites of twenty-eight provinces of Vietnam and a collection of 424 specimens of tube-nosed and woolly bats was examined for morphological characteristics. Based on morphometric variation among and within species, I intended to identify and evaluate the interspecific and intraspecific variation in skull size and shape. In additional I discussed the taxonomic, relationships of distribution, habitat use and the morphological diversification of tube-nosed and woolly bats in Vietnam. Principal component analysis (PCA) and Canonical variate analysis (CVA) were used for multivariate analysis of craniodental measurements, skull size and shape of all species. Moreover, karyological data of seven species were also provided. Principal findings of the study

are arranged as follows:

1) The genus *Murina*: Morphological diversification were found among sympatric species pairs and between sexes of *Murina* in Vietnam. The diversification of sexual dimorphism in genus *Murina*, which *M. harrisoni* showed that the differences in skull size and shape might be due to the functional limitations and compensation of the skull. Further investigation suggests that morphological variability also exists in the nasal capsule or braincase and this is possibly in relation to echolocation function, that echolocation may have strongly affected for the complicated morphological and species diversity.

2) The subfamily Kerivoulinae: *Phoniscus* clearly separated from *Kerivoula* based on measurements of the braincase height, interorbital width, and the shape of anterior part of the palatal bones. Statistic analysis also revealed the morphological variation in the skull shape of *Kerivoula hardwickii* in Vietnam. This suggests a possible separation of three morphotypes, representing cryptic species supported by statistic differences variation in skull size/shape and teeth.

3) In this study, detail morphology, distribution, and taxonomic note of the subfamily Murininae were provided. Vietnam harbors the highest species diversity of Murininae with fifteen recorded species. Five of them are common species, found in more than ten localities and six species have limited distribution ranges of which four are rare species. Kon Tum Province in the Central Highlands of Vietnam has the highest number of bat species with ten recorded species. The results also indicated that the forearm length and the skull length are significantly different among sympatric species pairs and intraspecific differences between sexes. It is assumed that the skull size and shape are affected by food habits and echolocation function, while the forearm and external morphology is more related to fly behavior and aerial niche use of the Murininae species.

4) The study first provided the largest karyotype results of seven species in Vietnam, of which, five are newly recorded for the bat fauna from Vietnam. Species of *Murina* and *Harpiola* shared similar karyotypes, while *Harpiocephalus* differs from both afore-mentioned genera by having one more pair of chromosome and it is suggested that to have evolved by the inversion of the acrocentric pair in the *Murina* karyotype during the evolution of the genus *Harpiocephalus*. Except for *Harpiocephalus*, conservative trends in chromosome re-arrangement in the subfamily Murininae were confirmed in this study.

CHAPTER I

General Introduction

1. 1. Overview of bat study in Vietnam

Biodiversity of Vietnam has drawn special attentions of scientists for several reasons. Sterling *et al*. (2006) indicated that, firstly the country harbors a globally significant diversity of species; secondly, scientists have described an unexpectedly large number of new species since 1992; and thirdly, a high proportion of known species are endemic to the country. Tordoff *et al*. (2012) showed Key Biodiversity Areas provide geographic targets for the expansion of protected area coverage, and identify sites for urgent conservation action, which the Indo-Burma is the Hotspot areas in the world includes Cambodia, Lao PDR, Myanmar (Burma), Thailand, Vietnam, and plus parts of southern China.

Regarding the Vietnamese bat fauna, Hong (1980) firstly listed 76 species, and then Huynh *et al*. (1994) provided a checklist of Vietnamese mammals, including 65 bat species. Since 1997, bats of Vietnam have received an initial attention from foreign specialists, and the numbers of bat species recorded from the country have been remarkably increased. Bates and Harrison (1997) and Bate *et al*. (1997) provided new records of three species of *Pipistrellus* and five species of *Myotis* from Vietnam. Khoi (2000) listed 88 species. Hendrichsen *et al*. (2001) listed 59 bat species with six new species to the country; Borissenko and Kruskop (2003) listed 95 species and provided an overview of the bat fauna of Vietnam with noteworthy records of new *Myotis* species from the country. Lunde *et al*. (2003a) recorded some of globally rare species of the family. Recent surveys of Vietnamese and foreign scientists reported a high level of species diversity of bats from Vietnam as Bates *et al*. (1997), Trai *et al*. (1999), Dang *et al*. (2000), Khoi (2000), Son *et al*. (2000), Tordoff *et al*. (2000), Trai *et al*. (2000), Son (2001), Hendrichsen *et al.* (2001), Thong *et al*. (2001), Lunde *et al*. (2003b), Son *et al*. (2003), Thong *et al*. (2003), Son *et al*. (2004), Son and Thong (2004), Thong and Viet (2004), Thong *et al*. (2004), Tien *et al*. (2004), Son (2005), Son and Thong (2005), Thong *et al*. (2005), Furey and Tu (2006), Abramov *et al*. (2006), Thong *et al*. (2006), Abramov *et al*. (2007), Bates *et al*. (2007), Csorba *et al*. (2007), Lunde *et al*. (2007), Khoi *et al*. (2007), Son and Csorba (2007); Son and Nghia (2007), Thong *et al*. (2007), Borissenko *et al*., (2008), Kruskop *et al*. (2008), Thong and Furey (2008), Thong *et al*. (2008), Abramov *et al*. (2009), Furey *et al*. (2009); Son *et*

al. (2009a, b, c), Thong *et al*. (2009), Furey *et al*. (2010), Son *et al*. (2010), Thong *et al*. (2010), Csorba *et al*. (2011), Minh *et al*. (2011); Phuong and Son (2011), Son and Thong (2011), Son *et al*. (2011), Thong (2011), Thong *et al*. (2011), Abramov *et al.* (2012), Dang *et al*. (2012), Thong *et al*. (2012a, b), Son *et al*. (2013), Csorba *et al*. (2014); Görföl *et al*. (2014), Thanh *et al*. (2014), Thong *et al*. (2014a, b, c), Son *et al*. (2015a, b), Tu *et al*. (2015a, b), Thanh *et al*. (2015) Son *et al*. (2016). As a result of these surveys numerous new species have been discovered from Vietnam, and the list of bats has regularly updated from Vietnam by Thong *et al*. (2004) (117 species), Kuznetsov (2006) (102 species), Can *et al*. (2008) (112 species), Dang and Canh (2009) (112 species). Kruskop (2013) provided and updated list of bats from Vietnam consisting of 117 species, however, the results remained incompletely studied and taxonomic assignment many taxa is still unclear, and lack specimen for analyses, for example: *Pteropus vampyrus*, *P. hypomelanus*, *Macroglossus minimus*, *Hipposideros ater*, *H. lylei*, *H. pratti*, *Rhinolophus lepidus*, *Rhinolophus subbadius*, *Rh. siamensis*, *Rh. yunnanensis*, *Murina leucogaster*, *Myotis chinensis*, *M. nipalensis*, *Pipistrellus ceylonicus*, *Nyctatus noctula*, *Eptesicus serotinus*, ect. It can be concluded that the taxonomy status of bats in Vietnam still remains problems, and be messily confused by recent publications.

1. 2. Overview of tube-nosed (Murininae) and woolly bats (Kerivoulinae) from Vietnam:

Osgood (1932) listed two species *M. cyclotis* and *M. tubinaris* from Vietnam, which *M. tubinaris* was synonymized with *M. huttoni* by Ellerman and Morrison-Scott (1951), but considered as a distinct species by Hill (1964). Bourret (1942) listed *Harpiocephalus harpia* from central part of Vietnam. Ever since, Van Peenen *et al*. (1969) listed seven species of tube-nosed and woolly bats from Vietnam: *Harpiocephalus harpia*, three species of *Murina species* (*M. cyclotis*, *M. huttoni*, and *M. tubinaris*), and three species of *Kerivoula* (*K. hardwickii*, *K. papillosa*, and *K. picta*). Huynh *et al*. (1994) also reported same species based on the list of Van Peenen *et al*. (1969). Hendrichsen *et al*. (2001) recorded *M. leucogaster* for the first time from the central Vietnam, and listed two species of *Harpiocephalus* (*H. harpia* and *H. mordax*), and two species of *Kerivoula* (*K. hardwickii* and *K. flora*) from the country. Thong *et al*. (2006) reported new country recorded of *K. kachinensis* and genus *Phoniscus* as well as *P. jagorri* from Vietnam. Kruskop *et al*. (2006) new recorded the genus *Harpiola* for Vietnam with species *H. isodon*. Bates *et al*. (2007) described a new species *K. titania* from Cambodia and first recorded for Vietnam. Csorba *et al*. (2007) described another new species, *Murina tiensa* from Vietnam.

Two other new species, *M. harpioloides* was described by Kruskop and Eger (2008) from Central Highlands, and *M. eleryi* was described by Furey *et al*. (2009) from the northern of Vietnam. Csorba *et al*. (2011) described three new species (*M. cineracea*, *M. beelzebub* and *M. walstoni*) from Vietnam and Cambodia. These authors also indicated that *M. tubinaris* does not occur in Vietnam and previous records of *M. tubinaris* from country should be treated as *M. cineracea* (Csorba *et al*. 2011). However, Francis and Eger (2012) subsequently considered that *M. cineracea* was a junior synonym of *M. feae* and *M. tiensa* as a junior of *M. harrisoni*. These authors also described two new species, *M. annamitica* and *M. fionae* from Lao and first recorded for Vietnam. Most, recently, Kruskop (2013) recorded an additional species of *Murina* from Northwest of Vietnam, viz. *M. chrysochaetes*.

1. 3. Natural features of Vietnam

Topography (Figs. 1. 1)

The total area of Vietnam is approximately 331.212 km^2 with the mountains and hill covering fourth-fifth of the country territory. It extends from the upper Red River drainage near the Tropic of Cancer at $23^0$23'N southwards $8^0$30'N at Ca Mau Point with a linear distance of about 1,600 km. The inland border of Vietnam with China, Laos, and Cambodia extends for 4,639 km, while the coastline along the Gulf of Tonkin, East Sea, and Gulf of Thailand is about 3,440 km in length with Paracel and Sparatly islands (Rundel, 1999; Sterling *et al*. 2006).

The North of Vietnam has a relatively large area of uplands extending above 2,000 m, and a number of peaks reaching 2,500−3,000 m elevation, includes the Northeast, Northwest Region and the Red River Delta. The Northeast Region stretches from the Red River Valley to the Gulf of Tonkin with mountainous area scattered between 300−1600 m elevation, and Tay Con Linh, the highest mountain of elevations of 2,531 m at the peak. The Northwest Region is comprised of mountains that run from the north of the Sino-Vietnamese border to the west of Thanh Hoa Province, Fansipan Mountain, which measures elevations of 3,143 m at the peak and Ta Giang Phin is only slightly lower at 3,096m elevation. Southwest of this massif lies an area of complex folded parent material termed the Song Da and Dien Bien Phu synclinoria and the Song Ma anticlinorium. To the south of the Song Da (Black) River, the Ta P'ing, Son La and Moc Hau plateaus which reach to as much as 1,800 m elevation are separated by deep valleys. The highest peaks to the south of the Song Da River are Sam Sao (1,896 m) and Pha Luong (1,884 m). The southern part of the country is well known for the lowland of Mekong Delta,

approximately 40,000 km^2 with an average elevation of under elevations of 10 m (Rundel, 1999; Averyanov *et al*., 2003; Tordoff *et al*., 2004; Sterling *et al*., 2006).

The Truong Son Range (or Annamite Range) in Central Vietnam is the main uplands in Indochina, and spreading over Laos, Vietnam, and Cambodia, from northwest to Southeast and the highest peak in the central Annamites of Vietnam is Phu Lai Lang which reaches elevation of 2,711 m near the Lao border (Rundel, 1999; Bain and Hurley, 2011). The Truong Son Mountains is continued by Kon Tum Massif, with elevations over 500 m elevation, with the highest peak at Ngoc Linh Mount (2,598 m), and joins the lower uplift of Pleiku Plateau, at about elevation of 800−1400 m, in Gia Lai Province (Rundel, 1999; Averyanov *et al*., 2003; Tordoff *et al*., 2004; Sterling *et al*., 2006).

River Basins (Fig. 1. 1)

Two broad river basins and deltas form distinct geomorphic regions of Vietnam. The Red River rises in the mountains of Yunnan Province in China, and flows southeast for more than 1,127 km, finally emptying into the Gulf of Tonkin through a broad delta area. The chief tributaries of the Red River are the Song Da (Black) and Song Chay (Clear) rivers. The southwestern region of Vietnam below Ho Chi Minh City is formed by the extensive triangle of the Mekong delta. This low-lying terrain is largely composed of Quaternary sediments deposited by the river, which here branches into a series of channels to form its broad delta. Although major tributaries join the Mekong within Vietnam, extensive areas of the eastern slopes of the southern Annamite region of Vietnam drain westward into Cambodia where they eventually join the Mekong. This separation of drainage basins has had a significant historical association with the levels of human impact in the southern Annamite Region (Rundel, 1999; Sterling *et al*., 2006; Bain and Hurley, 2011).

Climates

Rundel (1999) and Averyanov *et al*. (2003) stated that the climate of Vietnam can be divided into seven types: (1) Monsoon tropical climate with cold winter and summer rains; (2) Monsoon tropical climate with cold winter and summer-autumn rains; (3) Monsoon tropical climate with warm winter-autumn-winter rains; (4) Monsoon tropical climate with warm winter and autumn-winter rains; (5) Monsoon tropical climate with warm winter and summer rains; (6) Monsoon subequatorial climate with summer rains; and (7) Monsoon tropical climate associated with mountains.

Vegetation types

Averyanov *et al*. (2003) indicated the vegetation of Vietnam is belonging to the Indochinese Floristic Region, comprising six zones: Sikang-Yunnan, South Chinese, North Indochinese, Central Annamese, South Annamese, and South Indochinese.

Zoogeographic background (Figs. 1. 1 and 1. 2)

Tordoff *et al*. (2004), Sterling *et al*. (2006), Can *et al*. (2008), Sang *et al*. (2009) showed eight geographic divisions in Vietnam: the Northwest Region, the Northeast Region, the Red River Delta, the North Central Region, the South Central Region, the Central Highlands, the Southeast Region, and the Mekong Delta (Fig. 1. 2).

Based on geographic distribution of primates in Vietnam, Fooden (1996) allocated 22 species or well-defined subspecies to nine zoogeographic groups and proposed two major patterns of the distribution as follow: (1) four of the six non-macaque groups are essentially restricted to the eastern part of the Indochinese Peninsula, east of the Mekong River; and (2) species and subspecies in seven of the nine groups reach their northern or southern limits of distribution in central Vietnam, at 14–17^{0}N. The first pattern suggests that the Mekong River has been an important barrier to westward dispersal of non macaque primates in continental Southeast Asia. The second pattern suggests that a zoogeographic barrier formerly extended east and west across Vietnam at ca. 14–17^{0}N (Fig. 1. 1 and 1. 2).

1. 4. Outlines of the dissertation

Specific objectives:

This study focuses on the skull variations in tube-nosed bats of the genus *Murina* and in the woolly bats of the subfamily Kerivoulinae from Vietnam. Taxonomy of the subfamily Murininae in Vietnam is also reviewed. Many species in genus *Murina* and *Kerivoula* have restricted geographical distribution and some are currently known only from a single or very few specimens deposited in the museum collections (Hendrichsen *et al*., 2001; Kruskop and Eger, 2008; Eger and Lim, 2011; Csorba *et al*., 2011; Kruskop, 2013). Based on the newly collected material from Vietnam, I have investigated intraspecific and interspecific variations in the skull size and shape of *Murina* and Kerivoulinae species using multivariate analysis. Specific objectives of this study are: 1) to identify the differences in skull size and shape of tube-nosed bats of the genus *Murina* (Chapter II) and a comprehensive review of the subfamily Murininae

in Vietnam and karyological results was conducted in this study (Chapter IV). 2) to identify the differences in skull size and shape of woolly bats of the genus *Phoniscus* and *Kerivoula* and confirm the variation in skull size and shape of *Kerivoula hardwickii* populations (Chapter III).

Bat specimens were collected from 43 sites of national park (NP) and nature reserve (NR) of 28 provinces of Vietnam (Fig. 1. 3). The field surveys were conducted from 2001 to 2014 with special focus on the poorly explored areas (Appendix 1. 1): Lao Cao province (Hoang Lien mountain) [1], Ha Giang province (Tay Con Linh mountain) [2], Cao Bang province (Phia Oac-Phia Den NR) [5], Lang Son (Huu Lien NR) [8], the border with Laos: Son La province (Ta Sua NR, Co Ma area, Xuan Nha NR) [13, 14, 15], Phu Tho (Xuan Son NP with Ten mountain) [12], Thanh Hoa province (Pu Hu NR, Pu Luong NR, Ben En NP, Xuan Lien NR) [16, 17, 20, 19], Nghe An province (Pu Huong NR, Pu Mat NP) [21, 22], Ha Tinh province (Vu Quang NP) [23], Quang Binh province [Phong Nha-Ke Bang NP) [24], Quang Tri province (Bac Huong Hoa NR) [25], Thua Thien-Hue province (Bach Ma NP) [26], Quang Nam province (Ngoc Linh NR) [27, 28], Kon Tum province (Ngoc Linh NR and Chu Mom Ray NP) [29, 31], the border between Vietnam and Cambodia: Kon Tum province (Ngoc Linh NR and Chu Mom Ray NP) [29, 31], Gia Lai province (Kon Ka Kinh NP) [32], Dak Lak province (Yok Don NP and Chu Yang Sin NP) [34, 35], and Binh Phuoc province [Bu Gia Map NP) [41]. I also conducted field survey in two offshore islands of Vietnam: Bai Tu Long in Quang Ninh province [9] and Phu Quoc island in Kien Giang province [43]. Collections of 252 specimens of tube-nosed bats and 172 specimens of woolly bats have been examined for this study, most of which I examined morphologically.

Outlines of the results:

First, in Chapter II, I reveal the result of multivariate analysis of the skull size and shape in tube-nosed bats of the genus *Murina* in Vietnam. Next, in Chapter III, I present the first results of morphological analysis of the skull size and shape of woolly bats of the subfamily Kerivoulinae from Vietnam. In Chapter IV, I address first karyological analyses was conducted and a review of the subfamily Murininae in Vietnam. Finally, I general discussion and conclusion the findings on tube-nosed, woolly bats from Vietnam and discuss on remaining problems clarified and further studies (Chapter V).

Fig. 1. 1. The border, topography, and river basins of Vietnam (*in* Sterling *et al*., 2006).

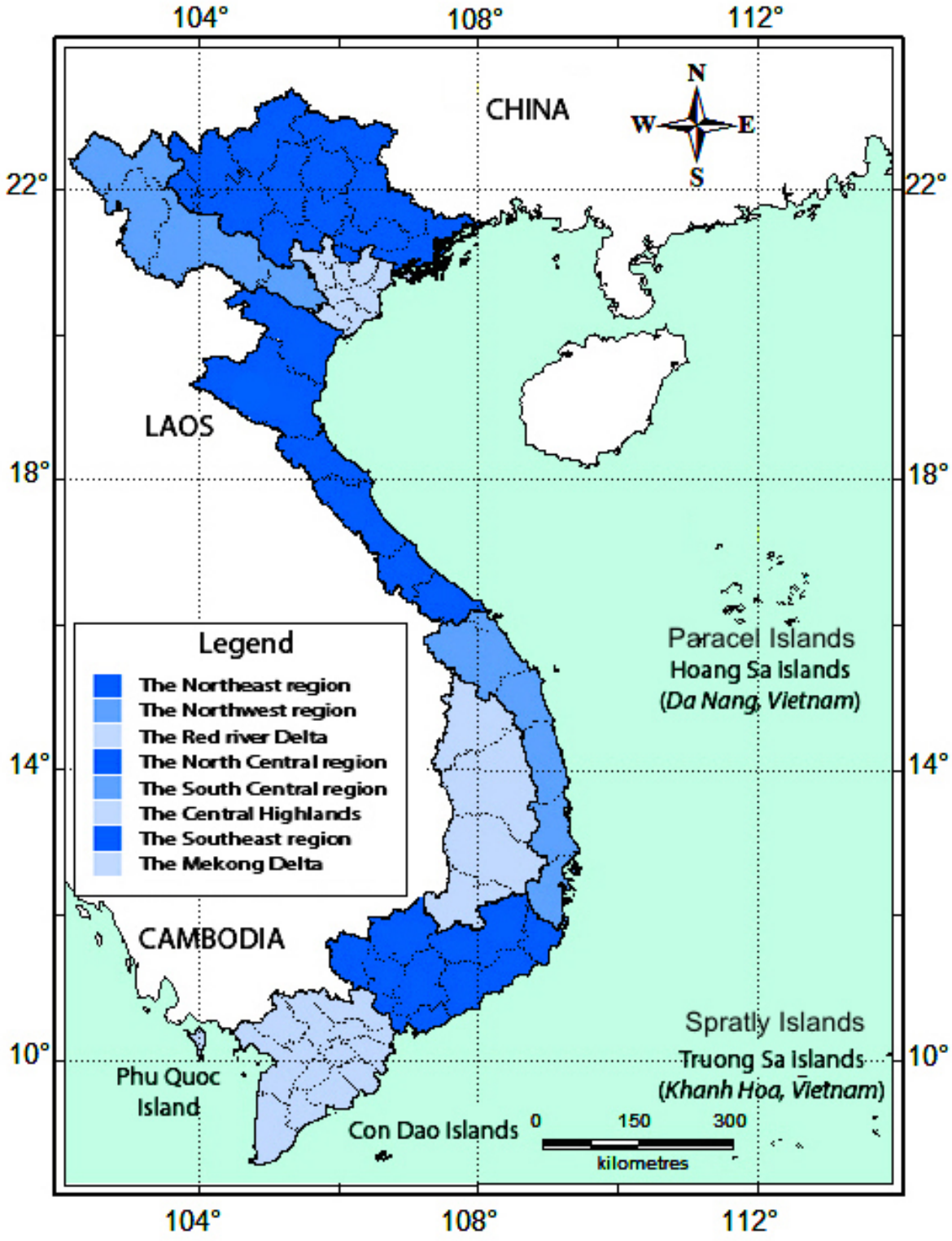

Fig. 1. 2. The geographic divisions in Vietnam (follow Tordoff *et al*., 2004; Sterling *et al*., 2006, Can *et al*., 2008, and Sang *et al*., 2009).

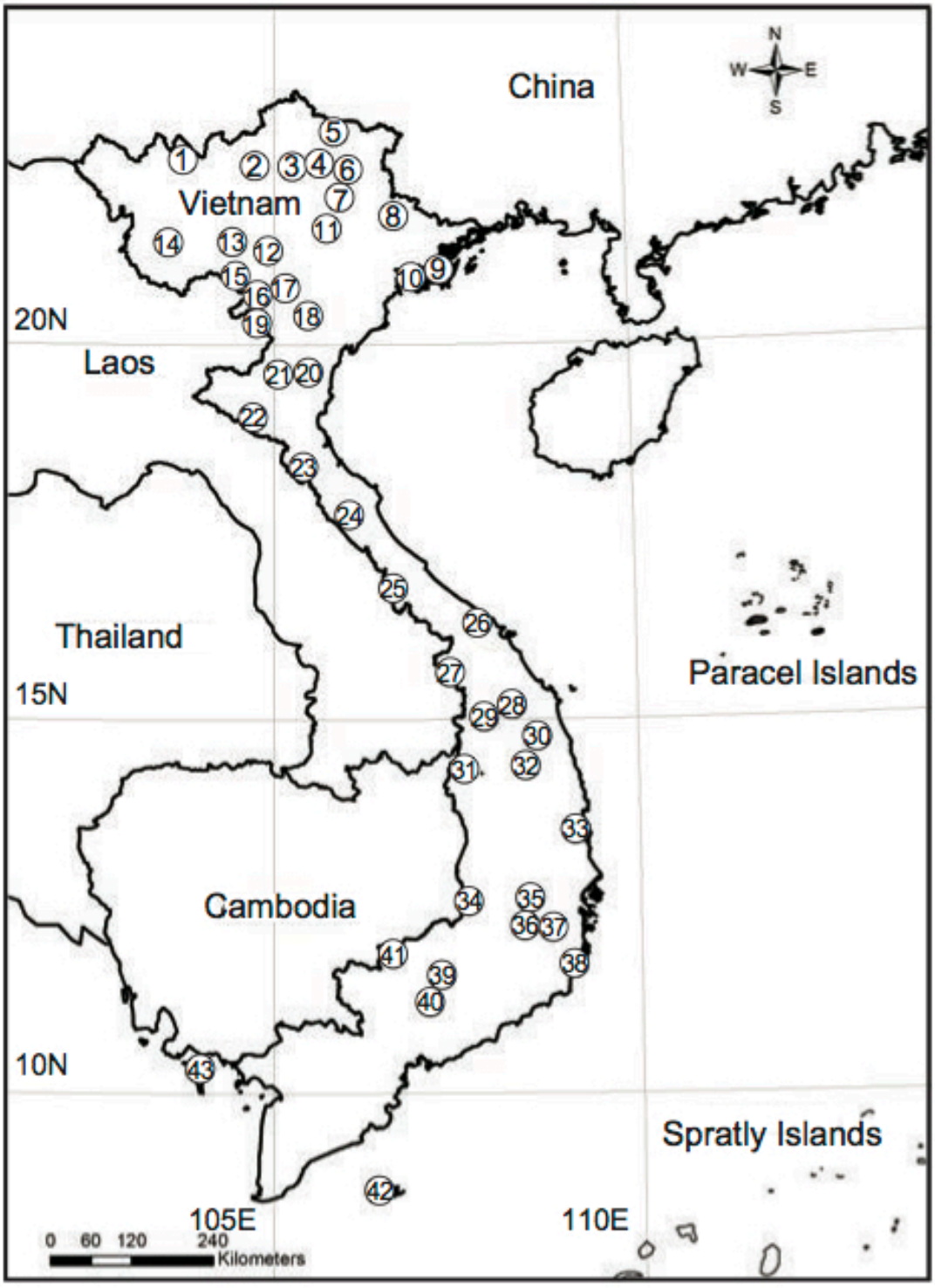

Figure 1. 3. The study sites in Vietnam.

CHAPTER II

Multivariate analysis of the skull size and shape in tube-nosed bats of the genus *Murina* (Chiroptera: Vespertilionidae) from Vietnam

2. 1. Introduction

Bats of the genus *Murina* Gray, 1842 (Vespertilionidae: Murininae) have a wide distribution range from Pakistan eastward to Japan, northward into Russia and southward through Peninsular Malaysia and Indonesia to northern Australia (Kuo *et al.*, 2009; Furey *et al.*, 2009; Francis and Eger, 2012). Species number of this genus has remarkably increased from 17 species in 2005 (Simmons, 2005) to 35 species in 2013, including 18 newly described species from South and Southeast Asia, making this genus one of the most interesting diversified bat groups for the study of species diversity and taxonomy (Csorba and Bates, 2005; Csorba *et al*., 2007; Kruskop and Eger, 2008; Furey *et al*., 2009; Kuo *et al*., 2009; Eger and Lim, 2011; Csorba *et al*., 2011; Ruedi *et al*., 2012; Francis and Eger, 2012; Kruskop, 2013; Soisook *et al*., 2013a, b). These findings have been based on the extensive effort for collecting specimens and finding diagnostic characters to define species limits using morphological quantitative difference among species such as fur color, forearm length and skull characters. Nevertheless, comprehensive skull morphometric analyses based on sufficient number of specimens and species has never been carried out for the genus *Murina*. Study of morphometric variation among and within species is, therefore, expected to identify and evaluate both the interspecific and intraspecific variation in combination with size and shape factors; and to discuss the mechanisms of the morphological diversification.

In Vietnam, 12 species of *Murina* are currently known to occur (Table 2. 1), accounting for 34.3% of the total number of the genus in the world (Hendrichsen *et al*., 2001; Csorba *et al*., 2007; Kruskop and Eger, 2008; Furey *et al*., 2009; Csorba *et al*. 2011; Francis and Eger, 2012; Kruskop, 2013). Herewith, I follow Csorba and Bates (2005), Csorba *et al*. (2007) and Thong *et al*. (2011a) to recognize *M. tiensa* as a species distinct from *M. harrisoni* (Csorba and Bates, 2005; Csorba *et al*., 2007; Thong *et al*., 2011), in contrast to the view of Francis and Eger (2012) who categorized *M. tiensa* as a junior synonym of *M. harrisoni*. To minimize the effect of extensive geographic variation or the possibility of examining cryptic species, intensive morphometric study should be initially carried out in each of the given target area. Having the highest diversity of the genus in the Indomalayan region, as compared to the eight species

recorded from Laos (Francis and Eger, 2012), four species from Cambodia (Csorba *et al*., 2011; Ith *et al*., 2011), and seven species from Thailand (Bumrungsri *et al*., 2006, Soisook *et al*., 2013b), the study of Vietnamese *Murina* will have potential for further extension and contribution to the understanding of morphological variation and taxonomic reassessment in the Indomalayan region and also in Asia, and in the world as well. In this study, I focus on the skull morphometric variation in combination with size and shape factors by using principal component analysis (PCA), and then discuss interspecific and intraspecific variation patterns in relation to species discrimination, species taxonomy and diversification, and sexual dimorphism.

2. 2. Materials and methods

Morphometric characters

A total of 150 skulls, consisting of 69 females and 81 males of 11 species were measured to the nearest 0.01 mm using a digital caliper (NTD12-15PMX, Mitutoyo Co., Kawasaki, Japan) under an Olympus SZ61 stereomicroscope (Tokyo, Japan) (Table 2. 2). Only fully-grown adult specimens were included in this study. The age was assessed following Racey (1990) and Kruskop (2013). One species *M. leucogaster* could not be analyzed, because no specimen was available for detailed study. Voucher specimens were deposited in the collections of the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam; Hungarian Natural History Museum (HNHM), Budapest, Hungary; and the Zoological Museum of Moscow University (ZMMU), Moscow, Russia (Appendix 2. 2). In this study, I used 33 measurements for statistical analysis (Table 2. 2, Fig. 2. 1) including the 15–20 most frequently used ones for taxonomic comparison between *Murina* species (e.g., Csorba and Bates, 2005; Csorba *et al*., 2007; Furey *et al*., 2009; Csorba *et al*., 2011; Eger and Lim, 2011; Francis and Eger, 2012) and additional measurements developed by us.

Statistical analyses

The sexes were analyzed separately in this study, because females are reported larger than males in *Murina bicolor*, *M. gracilis*, and *M. recondita* (Kuo *et al*., 2009). I calculated mean values and standard deviations of the 33 measurements. PCA was conducted with the software PAST (Hammer *et al*., 2001) to evaluate morphological variations among the 11 species, as well as between males and females of *M. annamitica*, *M. feae*, and *M. cyclotis*, that have sufficient sample size for testing sexual dimorphism.

For the PCA, I conducted two analyses using (1) raw data to assess size factor using PC1 score that represents overall size (Barlow *et al*., 1995; Lindenfors *et al*., 2007), and (2) standardized data (raw score/geometric mean) to assess shape factor (Jungers *et al*., 1995) using each of PC scores that have eliminated size factors. Both the raw data and standardized data were log-transformed (Blackith and Reyment, 1971; Reyment, 1971). Differences in the mean values of the principal components among samples (species or sex) were examined by analysis of variance (one-way ANOVA), and pairwise comparisons were made with Tukey's test ($P < 0.05$) for more than three samples and with F and t-tests ($P < 0.05$) among taxa for comparison between sexes. The higher factor loadings (positive and negative) of PCA (PCs1, 2, and 3) were selected follows Elizabeth (2006) and James (2009).

2. 3. Results

Craniodental measurements of the maximum, minimum, mean values, and standard deviations are presented in Table 2. 3. Skull size was represented as the total length of the skull (STOTL). STOTL was the greatest in *M. tiensa* and *M. fionae*, which did not overlap with those of the most other species except *M. cyclotis* and *M. huttoni* with little overlapping (Fig. 2. 2). The ranges of STOTL overlapped among the six medium-sized species: *M. huttoni*, *M. cyclotis*, *M. beelzebub*, *M. annamitica*, *M. walstoni*, and *M. feae* (Fig. 2. 2). Three species (*M. eleryi*, *M. chrysochaetes*, and *M. harpioloides*) showed the smallest skull size, with ranges overlapping within the cluster. Similar trends were observed for the other craniodental measurement (Table 2. 3 and Fig. 2. 2). The ML, which represented mandible size, was also greatest in *M. tiensa* and *M. fionae* and was the smallest in *M. eleryi*, *M. chrysochaetes*, and *M. harpioloides* (Table 2. 3 and Fig. 2. 2).

The factor loadings for PCA of log-transformed raw data are shown in Table 2. 4. The PC1 was interpreted to represent a size component, because all character factor loadings were positive, which explains the 67.22% total variance in the males and 72.29% total variance in the females. The PC1 factor loading CW, CL, cp4L, CP4L, C1C1W, BasW, CM3L, cm3L, and CPH were relatively higher in both sexes. Only PC1 of log-transformed raw data was considered in this study, while the shape factor could be evaluated with PCA using log-transformed standardized data, as mentioned in Materials and methods.

In the males, the range of values showed difference for size of each group (Fig. 2. 2, one-way ANOVA). The PC1 scores of *M. tiensa* overlapped with those of *M. fionae* (Tukey test, $P >$

0.05), and the values for both the species were larger than those for the other species ($P < 0.05$). The PC1 scores for the species were in the following order: *M. huttoni*, *M. cyclotis*, *M. beelzebub*, *M. annamitica*, *M. walstoni*, and *M. feae*. The lowest PC1 score was for *M. eleryi.* The score for *M. huttoni* was significantly larger than that for *M. cyclotis* ($P < 0.05$). The scores for *M. cyclotis*, *M. annamitica*, *M. beelzebub*, and *M. walstoni* overlapped ($P > 0.05$) and were larger than that for *M. feae* ($P < 0.05$).

In the females (Fig. 2. 2), the PC1 values of *M. tiensa* overlapped only with those of *M. fionae* ($P > 0.05$), which was greater than the values for the other species ($P < 0.05$), followed by the medium-sized *M. huttoni*, *M. cyclotis*, *M. annamitica*, *M. beelzebub*, *M. walstoni*, and *M. feae*. The lowest PC1 scores were observed in *M. harpioloides*, followed by *M. chrysochaetes* and *M. eleryi*. PC1 scores for *M. huttoni* and *M. cyclotis* overlapped ($P > 0.05$), although the values were greater than those for *M. annamitica*, *M. beelzebub*, *M. walstoni*, and *M. feae* ($P < 0.05$). The PC1 scores of *M. feae* were smaller than those of the other medium-sized bats ($P < 0.05$), except for the score of *M. walstoni*.

By using log-transformed standardized data in the PCA, PCs 1, 2, and 3 were interpreted as shape components (Table 2. 4 and Fig. 2. 3). In males, 42.51% of the variances could be explained using PC1, with high factor loadings for cp4L, CPH, CP4L, CW, CL (positive) and M1L, M2L (negative) (Table 2. 4). PC2 explained 12.80% of the variances, with high factor loadings for BasW, M2L, CL (positive) and BCH, P4L, BCW, IOW (negative). PC3 explained 7.92% of the variances, with the high loading factors for BCH, BasW (positive) and CW, CL (negative). In the plots for PC 1 and 2 scores, *M. tiensa*, *M. fionae*, *M. huttoni, M. cyclotis*, *M. annamitica*, and *M. eleryi* formed a separate 2-dimensional space from the plots of other species, with almost no overlaps, whereas *M. feae*, *M walstoni,* and *M. beelzebub* overlapped with one another (Fig. 2. 3). In plots for PC2 and PC3 scores, PC3 values were well overlapped among species (Fig. 2. 3).

For females, PCs 1, 2, and 3 explained 49.12%, 14.93%, and 6.49% of the variances (Table 2. 4), with high factor loadings in PC1 for M2L, M1L, IOW (positive), and CPH, CL, CW, cp4L, CP4L (negative); in PC2 for M1taW, M2taW, P4L, P4W (positive) and BasW, BCH (negative); and in PC3 for RL, CL, BasW (positive) and P4L (negative) (Table 2. 4). In the plots for PCs 1 and 2 (Fig. 2. 3), the *M. chrysochaetes* and *M. harpioloides* plots were distinct from plots of the other species. *Murina tiensa* and *M. cyclotis* overlapped in plots, although such pair

was distinct from the other species. *Murina feae* overlapped with *M. walstoni*, *M. beelzebub*, and *M. eleryi*. In the plots for PCs 2 and 3 (Fig. 2. 3), *M. tiensa* was distinct from the others ($P < 0.05$) in having greater PC3.

Sexual dimorphism was assessed by the principal component analyses (Table 2. 5) based on both log-transformed raw data and log-transformed standardized data in each of the three species: *M. annamitica*, *M. feae*, and *M. cyclotis*. For the PCA from the log-transformed raw data, PC1 was considered as a size component because all the characters had positive factor loadings, which explains 27.16% of total variances in *M. annamitica*, 39.53% in *M. feae*, and 58.95% in *M. cyclotis* (Table 2. 5). PC1 scores were greater in the females than in the males, without overlaps in *M. cyclotis* (males: mean = –0.785 [range = –2.102~–0.214], females: 1.004 [0.336~1.989]; *F* and *t*-tests, $t = 14.924$ [$P < 0.05$]). PC1 scores were greater in females than in males, with overlaps in *M. annamitica* (males: –0.033 [–0.081~0.034]; females: 0.036 [–0.039~0.0912]; *F* and *t*-tests, $t = 3.9276$ [$P < 0.05$]), and were not different between the sexes in *M. feae* (males: –0.373 [–1.937~1.162]; females: 0.397 [–1.547~1.483]; *F* and *t*-tests, $t = 1.642$ [$P > 0.05$]) (Table 2. 5).

In *M. cyclotis*, *F* and *t*-tests were carried out to assess differences in characters between sexes. Differences were found in CCL, CW, CL, C1C1W, PWC1C1, PWM3M3, ZYW, MAW, RW, RL, PBL CM3L, P4M3L, M1M3L, M1taW, M2taW, cp4L, cm3L, p4m3L, m1m3L, and CPH, where females were larger than males. In *M. annamitica*, *F* and *t*-tests showed that only STOTL, CM3L, and ML were found to be different, in which females were larger than males. Difference in any character was not found in *M. feae* (Table 2. 5).

The *F* and *t*-tests indicated significant differences in PC 1, 2, and 3 scores of the log-transformed standardized data between sexes only in *M. cyclotis* for PC1 (21.16% of the total variances; $t = –7.75$, $P < 0.05$) and PC2 (14.52%; $t = 3.64$, $P < 0.05$). The high factor loadings in PC1 were CL, CW, BCH, IOW, and BCW; those in PC2 was BasW, followed by P4L and P4W. For PC3, the highest factor loadings were BasW, M2L, P4W, and P4L (Table 2. 5). In the plots for PCs 1 and 2, males and females were separated, with minimal overlaps; males showed higher PC1 scores and smaller PC2 scores, whereas females were associated with lower PC1 scores and higher PC2 scores (Fig. 2. 4).

2. 4. Discussion

The results of the present study showed that *Murina* species recorded in Vietnam can be divided into three different size classes as follows: large species (*M. tiensa* and *M. fionae*), medium-sized species (*M. huttoni*, *M. cyclotis*, *M. beelzebub*, *M. annamitica*, *M. walstoni*, and *M. feae*) and small species (*M. eleryi*, *M. harpioloides*, and *M. chrysochaetes*). These three size clusters almost do not overlap in overall skull size, as shown by the STOTL, ML and log-transformed raw data PC1 scores. From the PC1 factor loadings, there may be positive allometry of CW, CL, CP4L, cp4L, CM3L, cm3L, and CPH that are related to canine and premolar teeth, as shown by the slightly larger PC1 factor loadings compared to the other measurements. The larger species may have more robust canines and premolars than the smaller species. On the other hand, within the same size clusters, several species-pairs partly or largely overlap in overall size such as the medium-sized *M. beelzebub*, *M. annamitica*, *M. walstoni*, and *M. feae*. In this study, *M. leucogaster* was not analyzed, but according to the GLT value (18.9 mm, equivalent to STOTL) reported by Hendrichsen *et al*. (2001), the species probably belongs to the large-sized cluster, which includes *M. tiensa* and *M. fionae*. Each size group was further differentiated by shape. Different ecological adaptations especially for food habits are suggested to have produced the species and morphological diversity. Postawa *et al*. (2012) discussed that differentiation in skull morphology of the insectivorous bats is known to correlate with size of prey, hardness of consumed insects, or a combination of these factors; and some congeneric species pairs can utilize similar food habits in allopatry, but they in sympatry, had partitioned the food items and changed skull morphology as character displacements, e.g. between *Myotis evotis* and *M. auriculus* (Husar, 1976; Gannon and Rácz, 2006) and between *Plecotus auritus* and *P. austriacus* (Postawa *et al*., 2012). In Vietnam, 11 species of *Murina* are divided into three different size classes and further differentiated in shape. This morphological divergence suggests that each species developed different food habits and facilitated the adaptation in skull morphology through the complex character displacements and food partitions among several sympatric species pairs.

In the PCs 1, 2, and 3 of the log-transformed standardized data, shape differences were detected among species. Among size overlapping species such as the medium-sized species previously mentioned, the plots of PCs 1 and 2 showed that *M. cyclotis* did not overlap with the other species except the overlapping with *M. tiensa* in females, as in Fig. 2. 3. In the males,

shape differences among species are suggested from the higher factor loadings to be distinct in the canines, first upper and lower premolars, and molars, as well as in the coronoid process. The braincase may be also important, but interspecific variation patterns in the braincase might be different between the sexes, and only that of the males might be distinct. These characteristics (dentition, coronoid process, and braincase) have often been mentioned in the taxonomy of *Murina* species (Csorba and Bates, 2005; Csorba *et al*., 2007; Kruskop and Eger, 2008; Furey *et al*., 2009; Kuo *et al*., 2009; Csorba *et al*., 2011; Eger and Lim, 2011; Francis and Eger, 2012; Ruedi *et al*., 2012), and in this study relevant measurements were proved to be useful to distinguish species.

Corbet and Hill (1992), Koopman (1994), Csorba *et al*. (2007), Furey *et al*. (2009), and Kuo *et al.* (2009) discussed that species in the genus *Murina* can be divided into two groups: "*suilla*-group" and "*cyclotis*-group," based on the relative size of the crown area of canines, the first and second upper premolars and the position of the incisors. Further, Corbet and Hill (1992), Csorba and Bates (2005), Csorba *et al*. (2007), Matveev and Csorba (2007), and Furey *et al*. (2009), Csorba *et al*. (2011) included *M. leucogaster*, *M. beelzebub*, *M. feae*, *M. walstoni*, *M. eleryi*, *M. chrysochaetes*, and *M. harpioloides* in the "*suilla*-group" and *M. tiensa*, *M fionae*, *M. huttoni*, *M. cyclotis,* and *M. annamitica* in the "*cyclotis*-group." In this study, the overall size of members of the "*cyclotis*-group" was larger than that of the "*suilla*-group," with overlaps in the log-transformed raw data PC1 values between *M. annamitica* and *M. beelzebub*. However, the STOTL value of *M. leucogaster* (not examined in this study), which was previously classified as a member of the *suilla*-group, indicates that this species is similar in size to *M. tiensa* and *M. fionae*, which are the two largest species of the *cyclotis*-group in Vietnam. Therefore, overall size is not a suitable indicator for differentiating the *suilla*-group from the *cyclotis*-group. On the other hand, the log-transformed standardized data for PCs 1 and 2 almost completely separated the two groups based solely on PC1 values. As previously mentioned, PC1 was strongly correlated with CW, CL, M1L, M2L, CP4L, cp4L, and CPH, and the *cyclotis*-group has larger values for CL, CW, CP4L, cp4L, and CPH, and smaller values for M1L and M2L compared to that of the *suilla*-group. Previous studies have focused on the relative basal dimensions of the upper canine and premolars and the position of the first and second incisors to separate the two groups. The findings of this study provide additional morphological differences expressed as the trends of morphometric values as shown above in relation to the upper canines, the second upper premolars, the molars, as well as the coronoid process, between the two groups. Particularly, in

the 2-dimensional plots between length and width ratios of the canine to the second upper premolars (CL/P4L versus CW/P4W; Fig. 2. 5), *suilla*-group and *cyclotis*-group showed different positions with range overlapping. Further studies would be required to evaluate more effective discrimination of the *cyclotis*-group and *suilla*-group using several morphometric characters by analyzing specimens of *M. leucogaster* and other *Murina* species not recorded in Vietnam.

Several bat species showing sexual size dimorphisms generally have larger females compared to males (e.g., Myers, 1978; Matveev, 2005; Fukui *et al*., 2005; Lindenfors *et al*., 2007; Thong *et al*., 2011; Lisón *et al*., 2014). Recent results also suggest that females are larger than males in the genus *Murina* in Southeast Asia (Kuo *et al*., 2009; Thong *et al*., 2011; Francis and Eger, 2012). In this study, I analyzed the detailed patterns of sexual size dimorphism in selected *Murina* species and found that the extent of sex-biased size dimorphism differs among species. On one hand, *M. cyclotis* has characteristically larger females. On the other hand, in *M. annamitica*, the differences are less extensive and the sexes overlap in size, only character STOTL, CM3L and ML was found to be significant ($P < 0.05$), whereas *M. feae* shows no sexual dimorphism. Francis and Eger (2012) discussed that the morphological variation in *M. cyclotis* is complicated by a strong sexual dimorphism in size. My results confirm the different extent and patterns of sex-biased variation in combination with size and shape factors among species in the genus *Murina*. In the most extensive sexual dimorphism in this study is the case of *M. cyclotis*, and significant differences both in size and in the skull shape with respect to the canines, first upper premolar, braincase, and upper molars were clarified; the factor loadings indicated that the first and second upper molars and lower molars in females were longer and larger than those in males, and the braincase of males showed a more pronounced dome shape than that of females.

Recently, Lisón *et al*. (2014) reported sex-biased variations in the wing size in *Myotis myotis*, showing that the females are larger than males and that the differences may be because of reproductive advantages, trophic niche segregation, and greater ability to move. The sexual dimorphism that I observed in some species of *Murina* may also be influenced by similar factors. Comparative ecological studies, including the annual cycle of reproductive events for sexually dimorphic species, are necessary to understand the biological mechanisms and evolutionary forces that influence the characteristics.

In conclusion, this study revealed morphometric divergences in skulls of 11 species of *Murina* in Vietnam separating three size clusters, and cases of sexual dimorphism patterns that were considerably different among species. Ecological adaptations for food habit might have produced morphological diversification among species and sexes of *Murina* in Vietnam, probably through interactions of sympatric species pairs. The results also indicated that a combination of the skull size and shape could separate *Murina* species in Vietnam and may contribute to elucidating new taxa and to developing a morphological identification key for the species from Vietnam and surrounding regions.

Table 2. 1. *Murina* species recorded in Vietnam and the number of specimens used in this study.

Species	Number		Traditionally accepted species
	Male	Female	
M. chrysochaetes	-	1	Eger and Lim (2011)
M. harpioloides	-	1	Kruskop and Eger (2008)
M. eleryi	3	3	Furey *et al*. (2009)
M. feae	17	17	Francis and Eger (2012)
M. walstoni	3	3	Csorba *et al*. (2011)
M. annamitica	11	10	Francis *et al*. (2012)
M. beelzebub	4	3	Csorba *et al*. (2011)
M. cyclotis	25	32	Corbet and Hill (1992), Simmons (2005), Francis and Eger (2012), Soisook *et al*. (2013)
M. huttoni	3	4	Corbet and Hill (1992), Simmons (2005), Francis and Eger (2012)
M. fionae	5	1	Francis and Eger (2012)
M. tiensa	2	3	Csorba *et al*. (2007)
M. leucogaster	-	-	Corbet and Hill (1992), Hendrichsen *et al*. (2001), Simmons (2005)
Total	81	69	

Table 2. 2. List of craniodental measurements used to this study

Character	Explanation
	Cranium
STOTL	Total length of the skull (from the anterior rim of the alveolus of the first upper incisor to the most projecting point of the occipital region)
CCL	Condylo-canine length (distance from the exoccipital condyle to the most anterior part of the canine)
PWC1C1	Anterior palatal width (least distance between the inner borders of the upper canines)
PWM3M3	Posterior palatal width (least distance between the inner borders of the last upper molars)
C1C1W	Width across the upper canines (greatest width across the outer borders of the upper canines)
M3M3W	Width across the upper molars (greatest width across the outer crowns of the last upper molars)
ZYW	Zygomatic width (greatest width of the skull across the zygomatic arches)
MAW	Mastoid width (greatest distance across the mastoid region)
IOW	Interorbital width (least width of the interorbital constriction)
BCW	Braincase width (greatest width of the braincase)
BCH	Braincase height (from the basisphenoid at the level of the hamular processes to the highest part of the skull, including the sagittal crest, if present)
RW	Rostral width at the level of the infraorbital foramina
RL	Rostral length (from posterior margin of the infraorbital foramen the anterior tim of the alveolus of the first upper)
PBL	Width of the palatal bone immediately posterior to the last upper molars
BasW	Width between the cochleae
CM3L	Maxillary toothrow length (distance from the front of upper canine to the back of the crown of the third molar)
P4M3L	Molariform toothrow length, from the posterior upper premolar to the last upper molar
M1M3L	Upper molar crown length
CW	Upper canines width
CL	Upper canines length
P4W	Posterior upper second premolar width
P4L	Posterior upper second premolar length
M1L	First upper molar length
M2L	Second upper molar length
M1taW	First upper molar talon width
M2taW	Second upper molar talon width

CP4L	Upper canine-premolar length (from the front of the upper canine to the back of the crown of the posterior premolar)
	Mandible
ML	Mandible length (distance from the anterior rim of the alveolus of the first lower incisor to the most posterior part of the condyle)
cm3L	Mandibular tooth row length (distance from the front of the lower canine to the back of the crown of the third lower molar)
p4m3L	Posterior lower premolar to the last lower molar length
m1m3L	Lower molars crown length
cp4L	Lower canine-premolar length (distance from the front of the lower canine to the back of the crown of the posterior premolar)
CPH	Least height of the coronoid process (distance from the tip of the coronoid process to the apex of the indentation on the inferior surface of the ramus adjacent to the angular process)

Table 2. 3. Craniodental measurements (mm) of eleven *Murina* species from Vietnam

Character	*M. chrysochaetes*	*M. harpioloides*	*M. eleryi*		*M. feae*		*M. walstoni*		*M. annamitica*	
	♀ (1)	♀ (1)	♀ (3)	♂ (3)	♀ (16)	♂ (17)	♀ (3)	♂ (3)	♀ (10)	♂ (11)
STOTL	14.72	14.53	14.21 – 15.16	14.64 – 14.77	15.13 – 16.10	14.91– 16.30	15.15 – 15.45	15.39 – 15.73	16.30 – 17.16	15.63 – 16.47
			14.72 ± 0.48	14.71 ± 0.07	15.70 ± 0.36	15.39 ± 0.39	15.34 ± 0.16	15.59 ± 0.18	16.77 ± 0.27	16.16 ± 0.26
CCL	12.82	12.34	12.24 – 13.16	12.54 – 12.60	13.01 – 14.16	12.77 – 14.30	13.29 – 13.53	13.54 – 13.66	13.60 – 15.05	13.93 – 14.65
			12.71 ± 0.46	12.56 ± 0.03	13.73 ± 0.34	13.9 ± 0.42	13.43 ± 0.13	13.60 ± 0.06	14.50 ± 0.50	14.24 ± 0.23
PWC1C1	1.99	1.77	1.72 – 1.96	1.65 – 1.70	1.66 – 2.03	1.65 – 2.03	1.96 – 1.99	1.84 – 2.00	1.75 – 2.19	1.73 – 2.03
			1.85 ± 0.12	1.68± 0.03	1.88 ± 0.09	1.84 ± 0.10	1.97 ± 0.02	1.91 ± 0.08	1.97 ± 0.15	1.87 ± 0.11
PWM3M3	3.01	2.89	2.77 – 2.95	2.57 – 2.95	2.85 – 3.43	2.83 – 3.36	3.07 – 3.20	3.18 – 3.19	3.05 – 3.36	2.95 – 3.40
			2.88 ± 0.09	2.77 ± 0.19	3.15 ± 0.16	3.10 ± 0.15	3.14 ± 0.07	3.19 ± 0.01	3.20 ± 0.12	3.13 ± 0.12
C1C1W	3.63	3.42	3.23 – 3.60	3.22 – 3.54	3.42 – 3.96	3.26 – 4.00	3.96 – 4.02	3.82 – 4.10	3.87 – 4.27	3.66 – 4.16
			3.45 ± 0.20	3.42 ± 0.17	3.68 ± 0.15	3.59 ± 0.20	4.00 ± 0.03	3.96 ± 0.14	4.07 ± 0.13	3.96 ± 0.15
M3M3W	4.93	4.86	5.00 – 5.15	4.63 – 5.21	5.03 – 5.71	4.99 – 5.45	5.37 – 5.83	5.81 – 5.92	5.39 – 5.84	5.20 – 5.70
			5.05 ± 0.08	4.99 ± 0.32	5.37 ± 0.22	5.21 ± 0.16	5.58 ± 0.23	5.86 ± 0.06	5.56 ± 0.15	5.43 ± 0.20
ZYW	8.41	8.13	8.00 – 8.31	7.82 – 8.20	8.15 – 9.32	8.15 – 8.94	8.83 – 9.31	9.00 – 9.34	8.94 – 9.53	8.65 – 9.63
			8.13 ± 0.16	8.03 ± 0.19	8.88 ± 0.32	8.63 ± 0.27	9.08 ± 0.24	9.19 ± 0.17	9.23 ± 0.20	9.06 ± 0.33
MAW	7.62	7.37	7.10 – 7.40	7.06 – 7.49	7.17 – 7.73	7.00 – 7.68	7.44 – 7.60	7.70 – 7.84	7.66 – 8.24	7.54 – 8.20
			7.30 ± 0.17	7.25 ± 0.22	7.44 ± 0.17	7.31 ± 0.17	7.50 ± 0.09	7.79 ± 0.08	7.99 ± 0.19	7.73 ± 0.22
IOW	4.17	4.11	4.18 – 4.28	4.17 – 4.25	4.20 – 4.68	4.13 – 4.40	4.11 – 4.33	3.96 – 4.24	4.17 – 4.65	3.99 – 4.38
			4.25 ± 0.05	4.21 ± 0.04	4.39 ± 0.13	4.27 ± 0.09	4.19 ± 0.12	4.11 ± 0.14	4.33 ± 0.15	4.20 ± 0.10
BCW	7.28	7.21	7.09 – 7.23	7.14 – 7.35	7.11 – 7.85	6.96 – 7.79	6.92 – 7.25	7.24 – 7.45	7.28 – 7.89	7.09 – 7.84
			7.14 ± 0.08	7.22 ± 0.11	7.49 ± 0.23	7.33 ± 0.27	7.12± 0.18	7.38 ± 0.12	7.62 ± 0.18	7.48 ± 0.23
BCH	6.33	6.36	5.70 – 6.01	5.78 – 5.90	5.74 – 6.51	5.71 – 6.45	5.99 – 6.30	5.91 – 6.58	6.23 – 6.88	6.21 – 6.94
			5.81 ± 0.18	5.84 ± 0.06	6.16 ± 0.20	6.12 ± 0.25	6.18 ± 0.16	6.28 ± 0.34	6.52 ± 0.25	6.54 ± 0.25

RW	4.02	4.12	3.57 – 4.05	3.45 – 3.55	3.89 – 4.68	3.83 – 4.45	4.06 – 4.45	4.18 – 4.53	4.28 – 4.67	4.06 – 4.56
			3.86 ± 0.25	3.49 ± 0.06	4.27 ± 0.22	4.20 ± 0.23	4.20 ± 0.21	4.40 ± 0.19	4.43 ± 0.15	4.36 ± 0.15
RL	3.3	3.13	3.05 – 3.09	2.77 – 3.10	3.10 – 3.72	3.08 – 3.64	3.16 – 3.30	3.22 – 3.43	3.31 – 3.75	3.30 – 4.03
			3.08 ± 0.02	2.92 ± 0.17	3.44 ± 0.19	3.38 ± 0.16	3.22 ± 0.07	3.32 ± 0.11	3.55 ± 0.15	3.61 ± 0.23
PBL	6.56	6.73	6.34 – 6.54	6.25 – 6.40	6.03 – 7.13	6.00 – 7.00	6.59 – 7.10	6.74 – 7.03	6.52 – 7.70	6.36 – 7.05
			6.44 ± 0.10	6.33 ± 0.08	6.67 ± 0.31	6.42 ± 0.28	6.84 ± 0.22	6.92 ± 0.16	7.14 ± 0.40	6.78 ± 0.24
BasW	1.39	1.52	1.34 – 1.42	1.17 – 1.33	1.15 – 1.59	1.15 – 1.53	1.35 – 1.44	1.40 – 1.70	1.28 – 1.70	1.30 – 1.77
			1.37 ± 0.05	1.23 ± 0.09	1.42 ± 0.12	1.35 ± 0.12	1.40 ± 0.05	1.56 ± 0.15	1.47 ± 0.13	1.52 ± 0.13
CM3L	4.66	4.68	4.48 – 4.89	4.53 – 4.84	4.89 – 5.38	4.82 – 5.26	5.27 – 5.48	5.34 – 5.39	5.23 – 5.69	5.19 – 5.60
			4.72 ± 0.22	4.72 ± 0.16	5.17 ± 0.15	4.99 ± 0.23	5.39 ± 0.11	5.37 ± 0.03	5.51 ± 0.16	5.37 ± 0.13
P4M3L	3.65	3.62	3.62 – 3.71	3.42 – 3.65	3.70 – 4.10	3.64 – 4.04	3.93 – 4.13	3.95- 4.02	3.89 – 4.06	3.72 – 3.92
			3.65 ± 0.05	3.54 ± 0.12	3.89 ± 0.11	3.78 ± 0.12	4.04 ± 0.10	3.98 ± 0.04	3.95 ± 0.05	3.81 ± 0.06
M1M3L	2.88	2.82	2.87 – 2.94	2.68 – 2.89	2.78 – 3.25	2.79 – 3.22	3.09 – 3.26	3.12 – 3.28	3.05 – 3.22	2.88 – 3.15
			2.91 ± 0.04	2.81 ± 0.12	3.01 ± 0.11	2.92 ± 0.12	3.17 ± 0.09	3.18 ± 0.09	3.11 ± 0.05	3.00 ± 0.09
CW	0.8	0.7	0.85 – 0.88	0.77 – 0.82	0.85 – 1.03	0.85 – 0.99	1.02 – 1.05	0.97 – 1.06	1.01 – 1.15	0.99 – 1.13
			0.86 ± 0.02	0.80 ± 0.03	0.93 ± 0.05	0.90 ± 0.06	1.03 ± 0.02	1.01 ± 0.05	1.08 ± 0.04	1.05 ± 0.05
CL	0.07	0.81	0.73 – 0.87	0.74 – 0.80	0.80 – 1.03	0.85 – 1.01	0.90 – 1.01	0.90 – 0.93	0.95 – 1.13	0.95 – 1.05
			0.81 ± 0.07	0.76 ± 0.03	0.92 ± 0.06	0.91 ± 0.05	0.95 ± 0.06	0.92 ± 0.02	1.05 ± 0.06	1.01 ± 0.03
P4W	0.98	0.99	1.03 – 1.13	0.99 – 1.05	1.14 – 1.35	1.03 – 1.28	1.21 – 1.36	1.22 – 1.32	1.09 – 1.35	1.08 – 1.26
			1.10 ± 0.06	1.02 ± 0.03	1.20 ± 0.07	1.16 ± 0.08	1.31 ± 0.08	1.26 ± 0.05	1.19 ± 0.07	1.16 ± 0.06
P4L	0.86	0.87	0.95 – 1.07	0.90 – 1.05	0.98 – 1.31	0.95 – 1.26	1.11 – 1.20	1.11 – 1.13	1.12 – 1.22	1.10 – 1.23
			1.00 ± 0.06	0.97 ± 0.08	1.14 ± 0.08	1.10 ± 0.10	1.15 ± 0.05	1.12 ± 0.01	1.17 ± 0.03	1.15 ± 0.05
M1L	1.17	1.23	1.24 – 1.30	1.18 – 1.22	1.25 – 1.47	1.23 – 1.44	1.38 – 1.45	1.38 – 1.42	1.18 – 1.39	1.18 – 1.34
			1.26 ± 0.03	1.20 ± 0.02	1.34 ± 0.07	1.31 ± 0.06	1.41 ± 0.04	1.40 ± 0.02	1.32 ± 0.06	1.25 ± 0.05
M2L	1.02	1.09	1.21 – 1.27	1.08 – 1.18	1.20 – 1.46	1.12 – 1.29	1.32 – 1.39	1.28 – 1.41	1.24 – 1.40	1.17 – 1.34
			1.23 ± 0.03	1.13 ± 0.05	1.27 ± 0.07	1.22 ± 0.05	1.36 ± 0.04	1.33 ± 0.07	1.31 ± 0.05	1.24 ± 0.05

M1taW	1.3	1.28	1.19 – 1.49	1.24 – 1.38	1.39 – 1.63	1.30 – 1.60	1.39 – 1.67	1.24 – 1.39	1.25 – 1.44	1.24 – 1.52
			1.38 ± 0.17	1.31 ± 0.07	1.48 ± 0.07	1.43 ± 0.07	1.49 ± 0.16	1.32 ± 0.08	1.34 ± 0.06	1.34 ± 0.08
M2taW	1.32	1.28	1.30 – 1.52	1.28 – 1.45	1.23 – 1.68	1.27 – 1.63	1.59 – 1.73	1.34 – 1.50	1.41 – 1.59	1.34 – 1.57
			1.43 ± 0.12	1.34 ± 0.09	1.44 ± 0.12	1.39 ± 0.11	1.66 ± 0.07	1.41 ± 0.08	1.48 ± 0.06	1.47 ± 0.08
CP4L	2.02	1.96	1.98 – 2.21	1.97 – 2.11	2.20 – 2.32	2.10 – 2.40	2.36 – 2.57	2.35 – 2.38	2.47 – 2.71	2.35 – 2.63
			2.12 ± 0.12	2.03 ± 0.07	2.33 ± 0.09	2.29 ± 0.11	2.47 ± 0.11	2.37 ± 0.02	2.57 ± 0.08	2.51 ± 0.08
ML	9.94	9.31	9.28 – 9.71	9.49 – 9.55	9.80 – 10.86	9.63 – 10.64	10.40 – 11.81	10.62 – 10.74	10.96 – 11.47	10.13 – 10.98
			9.44 ± 0.24	9.51 ± 0.03	10.31 ± 0.33	10.08 ± 0.31	10.67 ± 0.24	10.67 ± 0.06	11.17 ± 0.14	10.63 ± 0.24
cm3L	5.08	5.13	5.12 – 5.47	4.92 – 5.24	5.17 – 5.79	4.75 – 5.74	5.71 – 5.90	5.85 – 5.94	5.76 – 6.20	5.73 – 6.14
			5.27 ± 0.18	5.04 ± 0.17	5.55 ± 0.18	5.43 ± 0.25	5.78 ± 0.10	5.88 ± 0.05	6.03 ± 0.17	5.90 ± 0.14
p4m3L	3.96	3.91	3.93 – 4.05	3.81 – 4.10	4.02 – 4.52	3.96 – 4.53	4.29 – 4.51	4.39 – 4.68	4.47 – 4.60	4.20 – 4.43
			4.01 ± 0.07	3.93 ± 0.15	4.28 ± 0.15	4.20 ± 0.14	4.42 ± 0.12	4.54 ± 0.15	4.54 ± 0.04	4.34 ± 0.07
m1m3L	3.33	3.3	3.34 – 3.40	3.16 – 3.55	3.33 – 3.75	3.24 ± 3.72	3.60 – 3.77	3.61 ± 3.90	3.64 – 3.75	3.45 – 3.64
			3.37 ± 0.03	3.26 ± 0.10	3.56 ± 0.13	3.50 ± 0.13	3.71 ± 0.10	3.76 ± 0.15	3.69 ± 0.03	3.53 ± 0.05
cp4L	1.83	1.86	1.88 – 2.02	1.88 – 2.02	1.98 – 2.30	1.94 – 2.25	2.14 – 2.50	2.28 – 2.32	2.30 – 2.73	2.30 – 2.64
			1.97 ± 0.13	1.93 ± 0.08	2.15 ± 0.11	2.12 ± 0.13	2.35 ± 0.19	2.31 ± 0.02	2.51 ± 0.14	2.47 ± 0.09
CPH	3.51	3.25	2.85 – 3.23	2.85 – 3.17	3.11 – 3.69	3.01 – 3.63	3.67 – 3.69	3.32 – 3.65	3.80 – 4.35	3.49 – 4.12
			3.14 ± 0.34	3.06 ± 0.18	3.54 ± 0.19	3.37 ± 0.17	3.68 ± 0.01	3.49 ± 0.17	3.99 ± 0.17	3.81 ± 0.21

Value given as minimum-maximum (above) and mean ± standard deviation (below) (if n≥3).

Table 2. 3. Continue

Character	*M. beelzebub*		*M. cyclotis*		*M. huttoni*		*M. fionae*		*M. huttoni*		*M. tiensa*	
	♀ (4)	♂ (3)	♀ (25)	♂ (32)	♀ (3)	♂ (4)	♀ (1)	♂ (5)	♀ (3)	♂ (4)	♀ (2)	♂ (3)
STOTL	16.75 – 16.97	16.40 – 16.61	16.70 – 18.28	16.08 – 17.66	17.85 – 18.10	16.71 – 17.85	19.08	17.86– 18.23	17.85 – 18.10	16.71 – 17.85	18.18 – 19.30	18.20 – 18.39
	16.84 ± 0.11	16.51 ± 0.11	17.45 ± 0.41	16.60 ± 0.40	18.01 ± 0.14	17.45 ± 0.51		18. 04 ± 0.16	18.01 ± 0.14	17.45 ± 0.51		18.30 ± 0.10
CCL	14.68 – 15.01	14.50 – 14.57	14.86 – 16.14	13.98 – 14.98	15.70 – 16.50	15.04 – 16.30	16.56	15.86 – 16.21	15.70 – 16.50	15.04 – 16.30	16.06 – 16.99	15.90 – 16.25
	14.85 ± 0.14	14.54 ± 0.04	15.35 ± 0.33	14.52 ± 0.28	16.07 ± 0.40	15.52 ± 0.55		16.00 ± 0.13	16.07 ± 0.40	15.52 ± 0.55		16.10 ± 0.18
PWC1C1	1.96 – 2.07	1.95 – 2.04	1.92 – 2.41	1.74 – 1.93	1.87 – 2.30	2.02 – 2.20	2.15	1.92 – 2.20	1.87 – 2.30	2.02 – 2.20	2.25 – 2.42	2.05 – 2.25
	2.02 ± 0.05	1.98 ± 0.05	2.03 ± 0.08	1.86 ± 0.05	2.15 ± 0.24	2.09 ± 0.08		2.08 ± 0.11	2.15 ± 0.24	2.09 ± 0.08		2.13 ± 0.11
PWM3M3	3.33 – 3.37	2.27 – 3.24	3.15 – 3.45	2.81 – 3.13	3.32 – 3.35	3.20 – 3.34	3.42	3.33 – 3.66	3.32 – 3.35	3.20 – 3.34	3.47 – 3.47	3.23 – 3.48
	3.35 ± 0.02	2.84 ± 0.51	3.26 ± 0.07	3.03 ± 0.09	3.34 ± 0.02	3.24 ± 0.07		3.45 ± 0.13	3.34 ± 0.02	3.24 ± 0.07		3.31 ± 0.15
C1C1W	3.92 – 3.97	3.82 – 3.87	4.10 – 4.53	3.71 – 4.10	4.17 – 6.10	4.19 – 4.65	4.82	4.49 – 4.67	4.17 – 6.10	4.19 – 4.65	4.87 – 5.33	4.70 – 4.94
	3.95 ± 0.02	3.85 ± 0.03	4.27 ± 0.12	3.97 ± 0.09	4.89 ± 1.06	4.39 ± 0.19		4.56 ± 0.07	4.89 ± 1.06	4.39 ± 0.19		4.83 ± 0.12
M3M3W	5.57 – 5.76	5.25 –5.81	5.36 – 6.07	5.15 – 5.91	5.80 – 5.95	5.60 – 5.94	6.22	6.22 – 6.45	5.80 – 5.95	5.60 – 5.94	5.99 – 6.50	5.63 – 5.98
	5.68 ± 0.08	5.52 ± 0.28	5.71 ± 0.17	5.51 ± 0.17	5.88 ± 0.08	5.76 ± 0.14		6.32 ± 0.09	5.88 ± 0.08	5.76 ± 0.14		5.81 ± 0.18
ZYW	9.25 – 9.60	8.95 – 9.73	9.61 – 10.31	8.90 – 9.62	9.45 – 10.18	9.13 – 9.76	11.29	10.33 – 10.61	9.45 – 10.18	9.13 – 9.76	10.75 – 11.47	10.47 – 10.55
	9.41 ± 0.14	9.29 ± 0.40	9.94 ± 0.20	9.35 ± 0.17	9.80 ± 0.37	9.46 ± 0.34		10.47 ± 0.11	9.80 ± 0.37	9.46 ± 0.34		10.51 ± 0.04
MAW	7.91 – 8.17	7.76 – 8.08	8.00 – 8.72	7.58 – 8.08	8.33 – 8.60	8.12 – 8.60	9.21	8.64 – 8.80	8.33 – 8.60	8.12 – 8.60	9.08 – 9.53	8.82 – 9.16
	8.02 ± 0.11	7.91 ± 0.16	8.27 ± 0.21	7.91 ± 0.13	8.50 ± 0.15	8.40 ± 0.23		8.71 ± 0.06	8.50 ± 0.15	8.40 ± 0.23		8.99 ± 0.17
IOW	4.69 – 4.82	4.41 – 4.73	4.04 – 4.51	3.87 – 4.38	8.45 – 4.80	4.32 – 4.44	5.03	4.46 – 4.75	8.45 – 4.80	4.32 – 4.44	4.30 – 4.53	4.32 – 4.34
	4.77 ± 0.06	4.60 ± 0.17	4.26 ± 0.11	4.17 ± 0.13	4.64 ± 0.18	4.40 ± 0.05		4.63 ± 0.11	4.64 ± 0.18	4.40 ± 0.05		4.37 ± 0.6
BCW	7.84 – 8.04	7.80 – 8.13	7.46 – 8.16	7.28 – 7.90	7.70 – 8.40	7.49 – 8.05	8.83	7.96 – 8.43	7.70 – 8.40	7.49 – 8.05	7.93 – 8.01	7.61 – 7.98
	7.94 ± 0.08	8.01 ± 0.18	7.75 ± 0.19	7.62 ± 0.16	8.10 ± 0.36	7.81 ± 0.24		8.21 ± 0.19	8.10 ± 0.36	7.81 ± 0.24		7.74 ± 0.21
BCH	6.52 – 6.73	6.44 – 6.75	6.27 – 7.49	5.97 – 7.15	6.57 – 6.87	6.10 – 7.12	8.08	7.02 – 7.81	6.57 – 6.87	6.10 – 7.12	6.59 – 7.23	6.40 – 6.78
	6.58 ± 0.10	6.59 ± 0.16	6.67 ± 0.27	6.62 ± 0.27	6.77 ± 0.17	6.50 ± 0.44		7.35 ± 0.36	6.77 ± 0.17	6.50 ± 0.44		6.60 ± 0.19
RW	4.54 – 4.68	4.11 – 4.59	4.17 – 4.72	3.72 – 4.13	4.33 – 4.40	4.28 – 4.39	5.6	5.02 – 5.39	4.33 – 4.40	4.28 – 4.39	5.04 – 5.09	4.48 – 4.69

	4.63 ± 0.06	4.30 ± 0.26	4.35 ± 0.13	3.98 ± 0.10	4.36 ± 0.04	4.32 ± 0.05		5.29 ± 0.16	4.36 ± 0.04	4.32 ± 0.05		4.59 ± 0.11
RL	3.63 – 3.86	3.39 – 3.97	3.47 – 3.88	3.06 – 3.40	3.63 – 3.99	3.28 – 3.52	4.78	3.82 – 4.40	3.63 – 3.99	3.28 – 3.52	3.97 – 4.14	3.77 – 4.02
	3.72 ± 0.11	3.60 ± 0.32	3.60 ± 0.10	3.27 ± 0.11	3.77 ± 0.19	3.42 ± 0.10		4.08 ± 0.23	3.77 ± 0.19	3.42 ± 0.10		3.92 ± 0.13
PBL	6.98 – 7.23	7.05 – 7.07	7.16 – 8.10	6.44 – 7.10	7.62 – 7.88	7.05 – 7.62	8.48	7.70 – 8.06	7.62 – 7.88	7.05 – 7.62	7.51 – 8.20	7.45 – 8.02
	7.09 ± 0.13	7.06 ± 0.01	7.53 ± 0.25	6.82 ± 0.19	7.77 ± 0.13	7.34 ± 0.25		7.87 ± 0.14	7.77 ± 0.13	7.34 ± 0.25		7.68 ± 0.30
BasW	1.60 – 1.71	1.64 – 1.80	1.39 – 1.70	1.24 – 1.66	1.79 – 2.00	1.60 – 1.90	2.16	1.73 – 2.04	1.79 – 2.00	1.60 – 1.90	1.89 – 1.92	1.84 – 1.93
	1.65 ± 0.05	1.72 ± 0.08	1.57 ± 0.09	1.48 ± 0.12	1.93 ± 0.12	1.78 ± 1.13		1.89 ± 0.11	1.93 ± 0.12	1.78 ± 1.13		1.89 ± 0.05
CM3L	5.47– 5.70	5.44 – 5.54	5.55 – 5.89	5.16 – 5.55	6.04 – 6.06	5.76 – 6.05	6.39	6.10 – 6.38	6.04 – 6.06	5.76 – 6.05	6.30 – 6.65	6.25 – 6.31
	5.59 ± 0.10	5.47 ± 0.06	5.73 ± 0.11	5.41 ± 0.10	6.05 ± 0.01	5.92 ± 0.12		6.21 ± 0.10	6.05 ± 0.01	5.92 ± 0.12		6.28 ± 0.03
P4M3L	4.05 – 4.20	4.04 – 4.11	3.86 – 4.14	3.63 – 3.81	4.30 – 4.39	4.15 – 4.35	4.32	4.16 – 4.43	4.30 – 4.39	4.15 – 4.35	4.37 – 4.57	4.27 – 4.29
	4.15 ± 0.07	4.09 ± 0.04	3.96 ± 0.09	3.75 ± 0.05	4.33 ± 0.05	4.25 ± 0.08		4.26 ± 0.12	4.33 ± 0.05	4.25 ± 0.08		4.28 ± 0.01
M1M3L	3.07 – 3.30	3.12 – 3.22	2.90 – 3.30	2.65 – 2.90	3.30 – 3.39	3.29 – 3.38	3.31	3.17 – 3.36	3.30 – 3.39	3.29 – 3.38	3.46 – 3.58	3.29 – 3.37
	3.20 ± 0.10	3.15 ± 0.06	3.01 ± 0.10	2.82 ± 0.05	3.34 ± 0.05	3.33 ± 0.04		3.27 ± 0.27	3.34 ± 0.05	3.33 ± 0.04		3.32 ± 0.04
CW	0.95 – 1.03	0.92 – 0.99	1.07 – 1.32	0.95 – 1.13	1.15 – 1.17	1.15 – 1.30	1.35	1.29 – 1.52	1.15 – 1.17	1.15 – 1.30	1.42 – 1.63	1.32 – 1.32
	0.98 ± 0.04	0.95 ± 0.04	1.19 ± 0.06	1.06 ± 0.06	1.16 ± 0.01	1.17 ± 0.09		1.44 ± 0.09	1.16 ± 0.01	1.17 ± 0.09		1.32 ± 0.00
CL	0.93 – 1.01	0.89 – 0.96	1.02 – 1.31	0.92 – 1.10	1.16 – 1.22	1.17 – 1.20	1.35	1.30 – 1.40	1.16 – 1.22	1.17 – 1.20	1.41 – 1.59	1.30 – 1.38
	0.98 ± 0.03	0.94 ± 0.04	1.17 ± 0.07	1.04 ± 0.04	1.18 ± 0.03	1.14 ± 0.05		1.35 ± 0.04	1.18 ± 0.03	1.14 ± 0.05		1.33 ± 0.04
P4W	1.11 – 1.29	1.20 – 1.31	1.19 – 1.49	1.11 – 1.36	1.27 – 1.43	1.25 – 1.36	1.32	1.32 – 1.45	1.27 – 1.43	1.25 – 1.36	1.46 – 1.47	1.32 – 1.40
	1.22 ± 0.08	1.26 ± 0.06	1.31 ± 0.07	1.24 ± 0.06	1.37 ± 0.09	1.30 ± 0.05		1.39 ± 0.05	1.37 ± 0.09	1.30 ± 0.05		1.35 ± 0.04
P4L	1.11 – 1.29	1.08 – 1.27	1.13 – 1.45	1.10 – 1.32	1.24 – 1.30	1.17 – 1.29	1.21	1.26 – 1.43	1.24 – 1.30	1.17 – 1.29	1.12 – 1.52	1.10 – 1.21
	1.19 ± 0.07	1.19 ± 0.10	1.28 ± 0.07	1.22 ± 0.06	1.28 ± 0.03	1.22 ± 0.05		1.37 ± 0.07	1.28 ± 0.03	1.22 ± 0.05		1.17 ± 0.06
M1L	1.35 – 1.43	1.39 – 1.48	1.13 – 1.45	1.10 – 1.31	1.37 – 1.54	1.43 – 1.52	1.34	1.33 – 1.53	1.37 – 1.54	1.43 – 1.52	1.50 – 1.51	1.33 – 1.50
	1.39 ± 0.03	1.43 ± 0.05	1.28 ± 0.05	1.20 ± 0.05	1.43 ± 0.09	1.48 ± 0.04		1.40 ± 0.08	1.43 ± 0.09	1.48 ± 0.04		1.43 ± 0.09
M2L	1.33 – 1.40	1.31 – 1.40	1.10 – 1.32	1.02 – 1.30	1.35 – 1.45	1.35 – 1.50	1.26	1.23 – 1.46	1.35 – 1.45	1.35 – 1.50	1.40 – 1.43	1.36 – 1.41
	1.36 ± 0.03	1.36 ± 0.05	1.20 ± 0.07	1.15 ± 0.07	1.39 ± 0.07	1.43 ± 0.07		1.35 ± 0.10	1.39 ± 0.07	1.43 ± 0.07		1.38 ± 0.03
M1taW	1.31 – 1.47	1.32 – 1.53	1.34 – 1.65	1.18 – 1.37	1.35 – 1.60	1.48 – 1.52	1.34	1.46 – 1.68	1.35 – 1.60	1.48 – 1.52	1.69 – 1.76	1.60 – 1.75

	1.42 ± 0.07	1.42 ± 0.11	1.45 ± 0.10	1.30 ± 0.05	1.44 ± 0.14	1.50 ± 0.02		1.56 ± 0.10	1.44 ± 0.14	1.50 ± 0.02		1.68 ± 0.08
M2taW	1.42 – 1.61	1.54 – 1.66	1.46 – 1.76	1.26 – 1.49	1.45 – 1.73	1.55 – 1.77	1.56	1.59 – 1.88	1.45 – 1.73	1.55 – 1.77	1.79 – 1.86	1.68 – 1.78
	1.54 ± 0.09	1.59 ± 0.06	1.57 ± 0.09	1.38 – 0.06	1.55 ± 0.15	1.68 ± 0.10		1.71 ± 0.12	1.55 ± 0.15	1.68 ± 0.10		1.74 ± 0.05
CP4L	2.42 – 2.62	2.42 – 2.50	2.64 – 3.11	2.45 – 2.80	2.92 – 2.96	2.70 – 2.99	3.16	3.14 – 3.36	2.92 – 2.96	2.70 – 2.99	3.16 – 3.24	3.03 – 3.16
	2.49 ± 0.09	2.47 ± 0.04	2.85 ± 0.12	2.72 ± 0.15	2.91 ± 0.05	2.82 ± 0.12		3.13 ± 0.14	2.91 ± 0.05	2.82 ± 0.12		3.11 ± 0.07
ML	11.00 – 11.48	10.73 – 11.11	10.90 - 12.34	10.44 – 12.14	12.15 – 12.25	11.85 – 11.95	12.85	12.18 – 12.44	12.15 – 12.25	11.85 – 11.95	12.61 – 13.27	12.50 – 12.89
	11.25 ± 0.21	10.90 ± 0.19	11.73 ± 0.33	11.22 ± 0.41	12.19 ± 0.05	11.84 ± 0.14		12.29 ± 0.12	12.19 ± 0.05	11.84 ± 0.14		12.76 ± 0.22
cm3L	5.95 – 6.04	5.82 – 5.87	5.97 – 6.46	5.41 – 6.06	6.58 – 6.70	6.34 – 6.80	6.81	6.64 – 7.72	6.58 – 6.70	6.34 – 6.80	6.81 – 7.43	6.82 – 6.95
	5.99 ± 0.04	5.84 ± 0.03	6.20 ± 0.16	5.90 – 0.15	6.63 ± 0.06	6.55 ± 0.20		6.97 ± 0.43	6.63 ± 0.06	6.55 ± 0.20		6.87 ± 0.07
p4m3L	4.49 – 4.75	4.53 – 4.59	4.35 – 4.69	3.96 – 4.40	4.79 – 4.89	4.77 – 4.90	4.88	4.79 – 5.08	4.79 – 4.89	4.77 – 4.90	4.92 – 5.49	4.95 – 5.06
	4.61 ± 0.12	4.55 ± 0.03	4.51± 0.10	4.26 ± 0.10	4.83 ± 0.06	4.83 ± 0.06		4.92 ± 0.11	4.83 ± 0.06	4.83 ± 0.06		4.99 ± 0.06
m1m3L	3.76 – 3.92	3.72 – 3.83	3.47 – 3.82	3.28 – 3.46	3.85 – 3.93	3.80 – 4.07	3.99	3.84 – 4.03	3.85 – 3.93	3.80 – 4.07	3.91 – 4.42	3.86 – 4.00
	3.84 ± 0.08	3.78 ± 0.06	3.58 ± 0.10	3.40 ± 0.06	3.88 ± 0.04	3.95 ± 0.12		3.91 ± 0.09	3.88 ± 0.04	3.95 ± 0.12		3.92 ± 0.07
cp4L	2.31 – 2.32	2.25 – 2.30	2.56 – 3.03	2.42 – 2.80	2.70 – 2.78	2.80 – 2.90	3.13	3.01 – 3.21	2.70 – 2.78	2.80 – 2.90	3.07 – 3.36	3.11 – 3.22
	2.30 ± 0.02	2.25 ± 0.07	2.79 ± 0.12	2.64 ± 0.10	2.75 ± 0.04	2.78 ± 0.09		3.12 ± 0.08	2.75 ± 0.04	2.78 ± 0.09		3.17 ± 0.05
CPH	3.69 – 4.08	3.68 – 3.73	4.32 – 5.06	3.85 – 4.21	4.17 – 4.50	4.25 – 4.28	5.1	4.39 – 4.70	4.17 – 4.50	4.25 – 4.28	4.99 – 5.22	4.94 – 5.04
	3.88 ± 0.16	3.70 ± 0.03	4.66 ± 0.19	4.14 ± 0.12	4.38 ± 0.19	4.18 ± 0.10		4.41 ± 0.12	4.38 ± 0.19	4.18 ± 0.10		4.98 ± 0.06

Value given as minimum-maximum (above) and mean ± standard deviation (below) (if n≥3).

Table 2. 4. Character factor loadings for principal components analysis of the log-transformed raw data (PC1) and log-transformed standardized data (PCs 1, 2, and 3) of *Murina* species from Vietnam.

Character	Raw data		Standardized data					
	Male	Female	Male			Female		
	PC1	PC1	PC1	PC2	PC3	PC1	PC2	PC3
STOTL	0.133	0.147	0.030	-0.181	0.096	-0.013	-0.086	-0.133
CCL	0.150	0.160	0.041	-0.115	0.098	-0.030	-0.096	-0.122
PWC1C1	0.126	0.108	-0.089	-0.010	0.127	0.073	-0.201	-0.211
PWM3M3	0.092	0.081	-0.125	-0.080	-0.058	0.124	-0.057	-0.150
C1C1W	0.211	0.215	0.109	0.068	0.002	-0.117	-0.144	0.048
M3M3W	0.125	0.112	-0.032	-0.163	-0.010	0.069	0.032	-0.122
ZYW	0.154	0.165	0.043	-0.130	0.075	-0.040	-0.042	-0.069
MAW	0.140	0.133	0.018	-0.122	0.069	0.015	-0.152	-0.042
IOW	0.046	0.018	-0.192	**-0.224**	0.075	**0.259**	-0.086	-0.090
BCW	0.070	0.067	-0.101	**-0.271**	0.186	0.146	-0.132	-0.131
BCH	0.106	0.106	-0.010	**-0.277**	**0.234**	0.060	**-0.210**	-0.161
RW	0.142	0.088	-0.164	0.165	-0.185	0.141	-0.095	0.142
RL	0.127	0.164	-0.137	0.132	-0.094	0.026	-0.076	**0.485**
PBL	0.141	0.146	-0.017	-0.042	0.058	-0.021	-0.122	-0.157
BasW	**0.270**	**0.177**	0.074	**0.557**	**0.720**	0.011	**-0.441**	**0.355**
CM3L	**0.180**	**0.169**	0.052	0.019	0.025	-0.032	0.019	0.015
P4M3L	0.107	0.078	-0.140	0.006	0.003	0.151	0.038	0.026
M1M3L	0.097	0.061	**-0.213**	0.088	-0.056	0.196	0.042	0.117
CW	**0.304**	**0.330**	**0.297**	0.186	**-0.252**	**-0.346**	0.188	0.206
CL	**0.301**	**0.350**	**0.287**	**0.230**	**-0.223**	**-0.376**	0.150	**0.374**
P4W	0.159	0.161	0.033	-0.122	-0.116	-0.034	**0.251**	-0.182
P4L	0.155	0.192	0.094	**-0.273**	0.001	-0.099	**0.253**	**-0.255**
M1L	0.087	0.029	**-0.292**	0.200	-0.132	**0.263**	0.147	0.129
M2L	0.109	0.032	**-0.258**	**0.239**	-0.111	**0.285**	0.204	0.171
M1taW	0.114	0.127	-0.120	-0.017	-0.161	0.041	**0.370**	-0.053
M2taW	0.124	0.136	-0.125	0.032	-0.155	0.040	**0.408**	-0.050
CP4L	**0.271**	**0.268**	**0.298**	-0.028	-0.121	**-0.236**	0.031	0.003
ML	0.170	0.179	0.095	-0.116	0.064	-0.062	-0.045	-0.086
cm3L	**0.220**	**0.168**	0.083	0.110	-0.108	-0.034	-0.016	0.037
p4m3L	0.138	0.115	-0.095	0.082	-0.035	0.084	0.032	0.073

m1m3L	0.102	0.073	-0.190	0.063	-0.016	0.174	0.045	0.106
cp4L	**0.318**	**0.317**	**0.410**	0.058	-0.157	**-0.342**	-0.010	-0.063
CPH	**0.265**	**0.327**	**0.335**	-0.062	0.158	**-0.377**	**-0.196**	-0.211
Eigenvalue	0.028	0.034	0.040	0.012	0.007	0.055	0.017	0.007
% variance	67.22	72.29	42.51	12.80	7.92	49.12	14.93	6.49

Boldface numerals: High (positive and negative) factor loading. 8 higher values of character factor loadings were selected in PC1 of raw data. 8, 7, and 4 character factor loadings were also selected in PCs 1, 2, and 3 of standardized data.

Table 2. 5. Character factor loadings of the principal components analysis of three *Murina* species by using the log-transformed raw data (PC1) and log-transformed standardized data (PCs 1, 2 and 3).

Character	Raw Data			Standardized Data		
	M. annamitica	*M. feae*	*M. cyclotis*	*M. cyclotis*		
	PC1	PC1	PC1	PC1	PC2	PC3
STOTL	0.179	0.072	0.115	0.152	-0.041	-0.111
CCL	0.145	0.096	**0.133**	0.103	0.005	-0.159
PWC1C1	0.373	0.149	**0.187**	0.040	0.189	-0.194
PWM3M3	0.188	0.174	**0.173**	-0.002	0.159	-0.085
C1C1W	0.204	0.211	**0.188**	-0.035	0.025	-0.061
M3M3W	0.180	0.136	0.098	0.161	-0.172	-0.100
ZYW	0.190	0.157	**0.143**	0.040	0.052	-0.082
MAW	0.220	0.073	**0.111**	0.118	-0.045	-0.033
IOW	0.199	0.053	0.060	**0.231**	-0.126	0.051
BCW	0.176	-0.006	0.047	**0.234**	-0.053	0.058
BCH	0.068	0.032	0.027	**0.376**	-0.081	0.128
RW	0.191	0.175	**0.207**	-0.139	0.114	-0.066
RL	0.056	0.135	**0.213**	-0.136	0.124	-0.215
PBL	0.244	0.159	**0.229**	-0.082	0.175	-0.273
BasW	0.106	0.180	0.145	0.218	**0.687**	**0.524**
CM3L	0.177	0.169	**0.152**	0.025	-0.008	-0.013
P4M3L	0.122	0.136	**0.137**	0.026	-0.021	0.004
M1M3L	0.084	0.112	**0.174**	-0.073	-0.032	-0.054
CW	0.168	0.344	**0.298**	**-0.456**	-0.049	-0.001
CL	0.180	0.181	**0.321**	**-0.474**	0.055	0.197
P4W	0.124	0.219	0.181	-0.139	**-0.271**	**0.296**
P4L	0.110	0.345	0.149	-0.098	**-0.370**	**0.270**
M1L	0.038	0.098	0.185	-0.107	-0.023	0.102
M2L	0.175	0.157	0.153	0.021	-0.049	**0.367**
M1taW	0.120	0.206	**0.195**	-0.141	0.005	0.054
M2taW	0.115	0.209	**0.195**	-0.104	-0.027	0.026
CP4L	0.168	0.243	0.170	0.104	-0.141	-0.095
ML	0.146	0.138	0.131	0.158	-0.055	-0.190
cm3L	0.150	0.177	**0.141**	0.026	-0.104	-0.026
p4m3L	0.106	0.147	**0.150**	-0.015	-0.063	0.031

m1m3L	0.115	0.137	**0.138**	0.017	-0.064	0.024
cp4L	0.221	0.175	**0.152**	0.102	-0.074	-0.126
CPH	0.288	0.229	**0.273**	-0.150	**0.280**	-0.246
Eigenvalue	0.003	0.006	0.009	0.008	0.006	0.005
% variance	27.16	39.53	58.95	21.16	14.52	11.56

Boldface numerals: High (positive and negative) factor loading in *M. cyclotis*. 21 higher values of character factor loadings were selected in PC1 of raw data. 5, 4, and 3 character factor loadings were also selected in PCs1, 2, and 3 of standardized data.

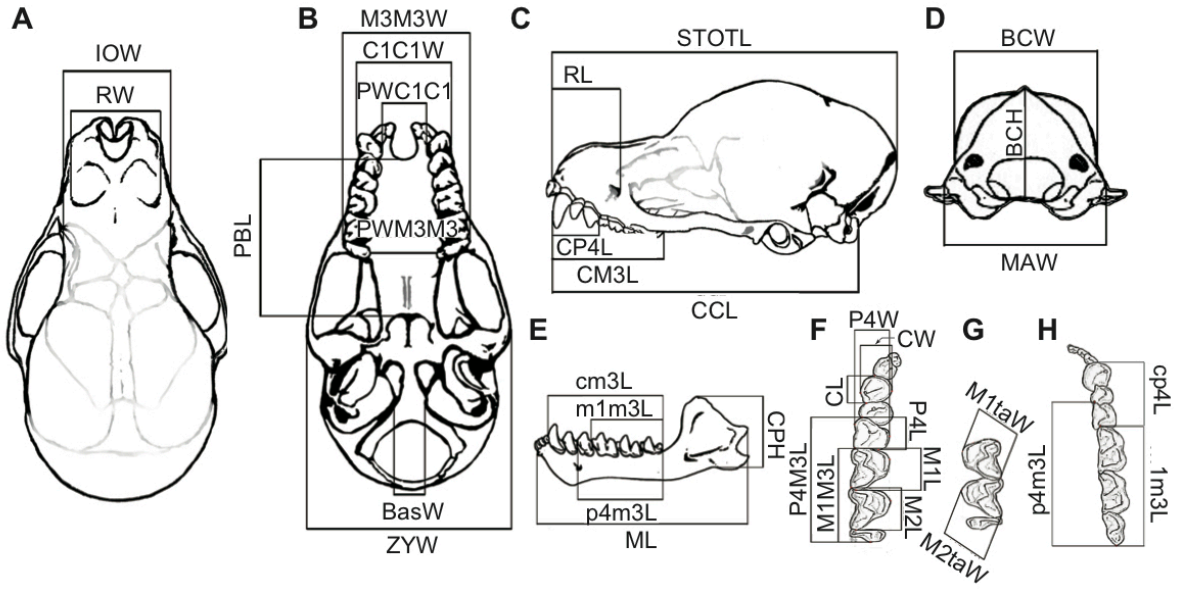

Figure 2. 1. Dorsal (A), ventral (B), lateral (C) and posterior (D) views of the cranium and mandible (E), and upper (F, G) and lower (H) dentition showing measurements. See Table 1 for abbreviations of the measurements.

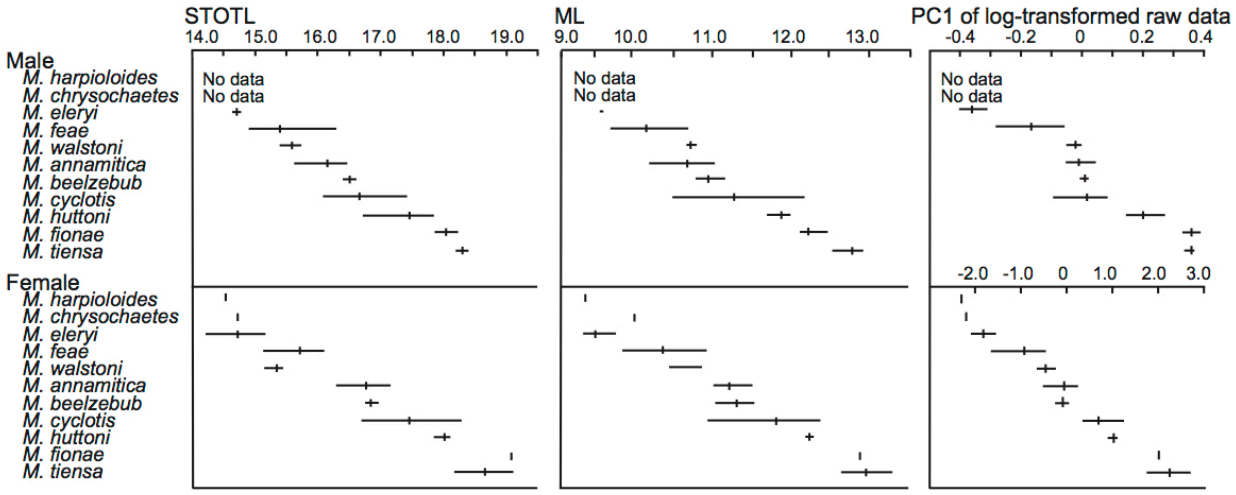

Figure 2. 2. Range (minimum value to maximum value in horizontal line) and mean value (in vertical bar) of total length of the skull (STOTL), mandible length (ML), and PC1 scores of log-transformed raw data of *Murina* species from Vietnam.

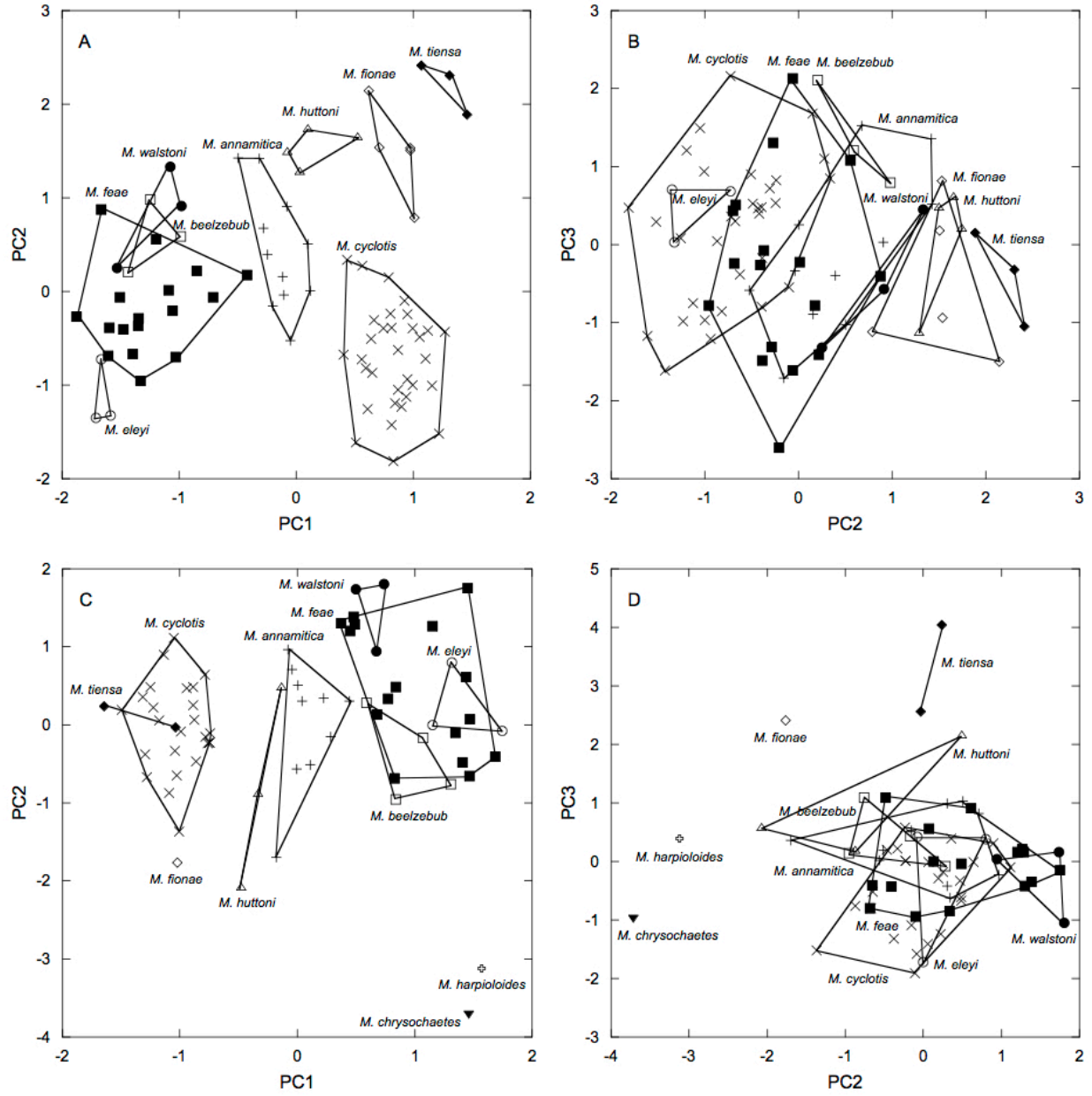

Figure 2. 3. Scatterplots of scores of the first and second and the second and third principal component axes based on log-transformed standardized data for males (A, B) and females (C, D) of 11 *Murina* species from Vietnam.

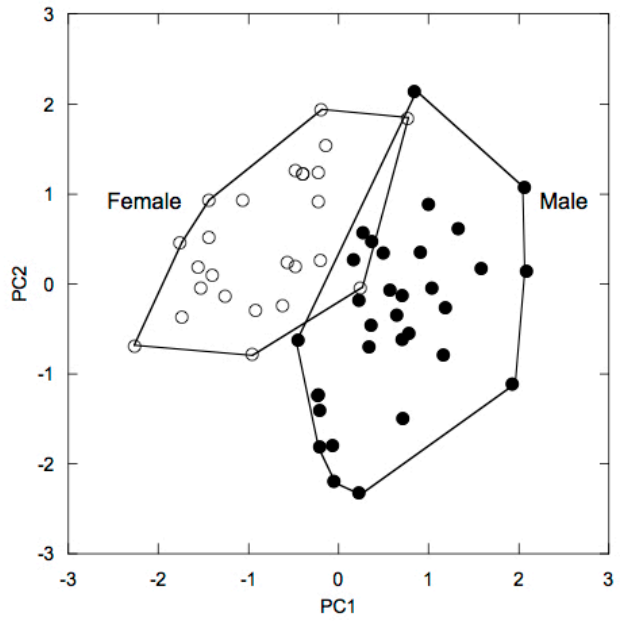

Figure 2. 4. Scatterplots of score of the first two principal component axes between males and females based on log-transformed standardized data for *Murina cyclotis* from Vietnam.

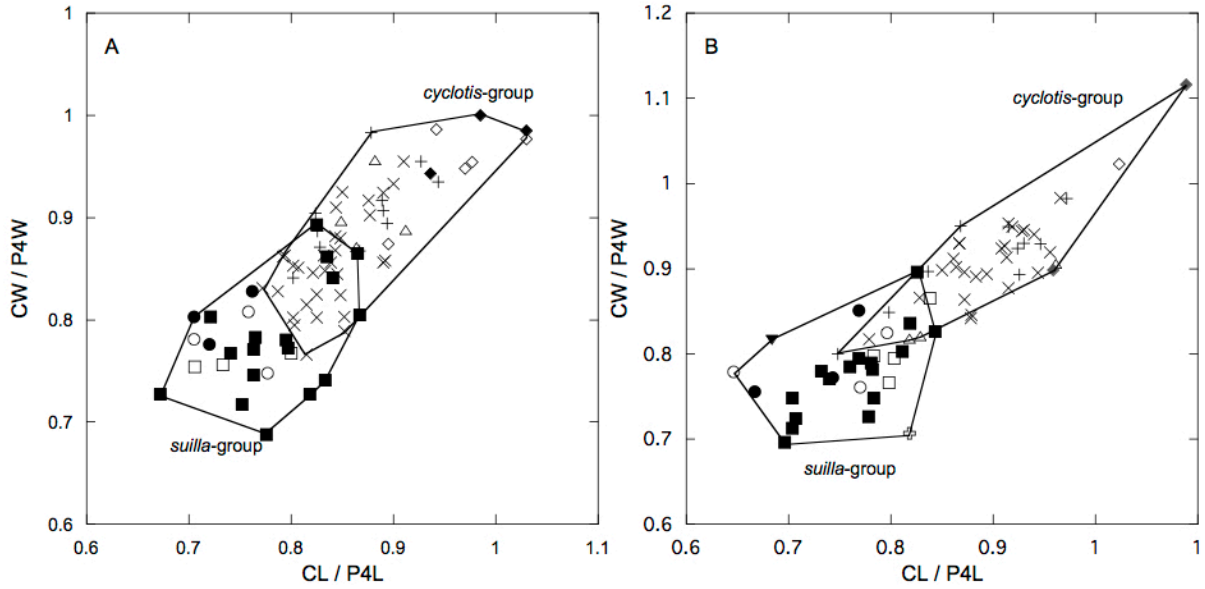

Figure 2. 5. Scatter plots between length ratio (CL/P4L) and width ratio (CW/P4W) of upper canine and second upper premolar of *Murina cyclotis* group and *M. suilla* group for males (A) and females (B). Symbol for each species is the same as Fig. 2. 3.

CHAPTER III

A morphological analysis of the skull size and shape of Kerivoulinae (Chiroptera: Vespertilionidae) from Vietnam

3. 1. Introduction

The East and Southeast Asia region is substantially high in species diversity of tube-nosed bat (*Murina*), which 18 newly described, making this genus one of the most in diversified bat groups in this region. In Vietnam, 13 species recorded for country, however, for comprehensive skull morphometric analysis based on sufficient number of specimens and species have never been carried out for the genus *Murina*. In Chapter II, I first examined the mutivariate analysis of the skull size and shape of the 11 *Murina* species and my analysis indicated significant differences of the size and shape skull and sexual dimorphism of this gorup. The result is based to provide the diagnostic characters for ther further stidies on the taxonomic of *Murina* and also provided the method for the other group on mutivatiate anylisis. In this Chapter, I continued to examine a comprehensive morphological analysis of the skull size and shape of woolly bats, Kerivoulinae (Vestertilionidae: Chiroptera) from Vietnam, while have never been carried out for these subfamily from this country.

Recent studies on Asian bats have indicated that Asia harbors a number of species complexes that present challenges for establishing the taxonomy (Bates *et al*., 2004; Bates *et al*., 2007; Francis *et al*., 2010; Soisook *et al*., 2013b). This is mainly due to cryptic forms and the limited number of voucher specimens available for morphological comparisons (Faisal *et al*., 2010). Since 2000, numerous new species of the family Vespertilionidae have been described in Southeast Asia including some species of Kerivoulinae (Francis *et al*., 1999; Bates et al., 2004; Bates *et al*., 2007), and undescribed species may yet be common in the natural forest in Southeast Asia (Fooden, 1996; Kingston *et al*., 1999). Within the family, one of the taxa with a high number of cryptic forms and an unresolved taxonomy is the subfamily Kerivoulinae (Fooden, 1996; Francis *et al*. 2010).

Gray (1842) established the genus *Kerivoula* and has selected *Vespertilio pictus* (Pallas, 1767) as the type species. Subsequently, Miller (1905) has described a new genus and species, *Phoniscus atrox*, and established the subfamily Kerivoulinae and in addition, this author provided the diagnostic characteristics of *Kerivoula* Gray, 1842 and *Phoniscus* Miller, 1905. The generic rank of *Phoniscus* was recognized by several authors (Thomas, 1914; Troughton,

1929), however, it was considered by other scholars to merely be a subgenus of *Kerivoula* (Tate, 1941; Laurie and Hill, 1954; Ryan, 1965; Koopman, 1993, 1994). *Phoniscus* can be distinguished from *Kerivoula* based on the following diagnostic characteristics: the upper canine with a well-defined longitudinal groove on the buccal face (versus smoothly rounded in *Kerivoula*), the second upper incisor is much reduced (versus developed in *Kerivoula*), and the anterior part of the rostrum is broader than in *Kerivoula* and anterior palatal emargination is distinctively broader than deep (versus deeper in *Kerivoula*) (Tate, 1941; Hill, 1965; Corbet and Hill, 1992).

In Southeast Asia, the subfamily Kerivoulinae currently contains nine species of *Kerivoula* (including *K. lenis*) and two species of *Phoniscus* (Corbet and Hill, 1992; Vanitharani *et al*., 2003; Simmon, 2005). Three new species of *Kerivoula* have recently been described in the region: *K. kachinensis* in Myanmar (Bates *et al*., 2004), *K. titania* in Cambodia and Vietnam (Bates *et al*., 2007) and *K. krauensis* in Peninsular Malaysia (Francis *et al*., 2007). In addition, *K. titania* was recently recorded from China (Wu *et al*., 2012). Morphological and genetic comparisons suggested that *K. hardwickii* is a species complex, that contains at least three forms (Bates *et al*., 2007; Francis *et al*., 2007; Francis *et al*., 2010). The comparison of braincase height showed that at least two different forms exist: a smaller, flat-headed species, that may be *K. depressa* (Miller, 1906) and a slightly larger dome-skulled taxon, *K. hardwickii* (Horsfield, 1824) (Bates *et al*., 2007). Karyotype, phylogenetic and morphological studies of *Kerivoula* species conducted in Malaysia indicated that this genus includes three different morphotypes (Faisal *et al*., 2010). The morphological analysis of Malaysian *Kerivoula* was done, and as the results, six grouping of *Kerivoula* were identified and *K. papillosa* provided evidence that the species includes two distinctive groups based on size (Hasan and Abdullah, 2011). These studies showed that *Kerivoula* encompasses a group of cryptic species and that the diversity of the woolly bats is still underestimated.

In Vietnam, one *Phoniscus* and five *Kerivoula* species have been recorded (Hendrichsen *et al*., 2001; Thong *et al*., 2006, Bates *et al*. 2007; Can *et al*., 2008; Kruskop, 2013). Among them, six species have been recorded in Laos (Francis *et al*., 2007; Thomas *et al*., 2013), five species are known in Thailand (Bates *et al*., 2007; Soisook *et al*., 2007, 2011), and four species have been identified in Cambodia (Bates *et al*., 2007; Kingsada *et al*., 2011; Phauk *et al*., 2013). As the specific content of *K. hardwickii* has been considered as a group of cryptic species (Bates *et*

al., 2007; Francis *et al*., 2007, 2010) and in genusl the taxonomy of the Kerivoulinae in Southeast Asia is highly problematic (Thong *et al*., 2006), I examined a large number of skulls of Kerivoulinae in Vietnam and used multivariate analysis to investigate the morphological differences of the species within the subfamily.

3. 2. Materials and Methods

Morphometric characteristics and measurements

Skulls of 113 females and 59 males were measured to the nearest 0.01 mm using a digital caliper (Mitutoyo model NTD12-15PMX, Mitutoyo Corp., Kawasaki, Japan) under an SZ40 stereomicroscope (Olympus, Tokyo, Japan). I osteometrically examined 23 cranial and dental measurements (Table 3. 1 and Fig. 3. 1) including the 15 measurements that have been frequently used for taxonomic comparisons between Kerivoulinae species and the other species of bats Hill, 1965; Corbet and Hill, 1992; Bates and Harrison, 1997; Hendrichsen *et al*., 2001; Vanitharani *et al*., 2003; Bates *et al*., 2004; Thong *et al*., 2006; Bates *et al*., 2007; Francis *et al*., 2007; Soisook *et al*., 2007; Faisal *et al*., 2010; Hasan and Abdullah, 2011; Kruskop, 2013). The notation used in describing the first upper and lower incisor is I1/i1, second upper and lower incisor is I2/i2, as for the premolars, first upper/lower premolar is P2/p2, and the second upper/lower premolar is P3/p3, whereas the third upper/lower premolars is P4/p4 (Tate, 1941; Hill, 1965; Vanitharani *et al*., 2003; Thong *et al*., 2006). Only fully grown adult specimens were included in this study (Racey, 1990; Kruskop, 2013).

Voucher specimens used in this study are deposited in the collection of the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam and the Hungarian Natural History Museum (HNHM), Budapest, Hungary. Registration numbers of each specimen are provided in Appendix 3. 3. I compared 23 original cranial and dental measurements of my collections (Table 3. 1) with previous descriptions and using relevant references (Miller, 1905, 1907; Tate, 1941; Hill, 1965; Vanitharani *et al*., 2003; Bates *et al*., 2004; Thong *et al*., 2006; Bates *et al*., 2007; Kruskop, 2013). Six species of Kerivoulinae, namely: *K. kachinensis*, *K. hardwickii*, *K. papillosa*, *K. picta*, *K. titania* and *Phoniscus jagorii* were tentatively identified (Fig. 3. 9).

The species of Kerivoulinae examined in this study are shown in Table 3. 2. The braincase height can be used as one of the characteristics to separate *Kerivoula* species (Corbet and Hill, 1992; Bates *et al*., 2004; Thong *et al*., 2006; Bates *et al*., 2007). The specimens of *K. hardwickii* used in this study originate from various geographical populations. I referred to this

characteristic and used the locality data of the specimens to confirm the geographic morphological variations of *K. hardwickii*. Finally, I postulate the three geographic populations in this species (Fooden, 1996; Averyanov *et al*., 2003; Tordoff *et al*., 2004; Sterling *et al*., 2006; Bain and Hurley, 2011). Each population name in the *K. hardwickii* was assigned the locality symbol: the northern (N), the central (C), and the southern (S) populations as arranged in Table 3. 2. The N and S populations originated only from one locality, whereas the C population originated from multiple geographical sites in the center of Vietnam (Table 3. 2 and Figs. 3. 2, 3. 9).

Statistical analyses

I calculated the mean values and standard deviations from the 23 craniodental measurements, with the two sexes analyzed separately (Table 3. 3). Measurement data were applied to assess significant differences of the size and shape within Kerivoulinae. Principal component analysis (PCA) was conducted with the software PAST Statistics (Hammer *et al*., 2001) to evaluate morphological variations among the six Kerivoulinae populations. The higher factor loadings (positive and negative) of PCA were selected by percent of variance.

Canonical variate analysis (CVA) was used in Genstat version 10 (Payner, 1987) to confirm the distinctiveness between groups after PCA. For the PCA and CVA, I conducted the two analyses using (1) log-transformed raw data to assess the size (Barlow *et al*. 1997; Reyment, 1971; Blackith and Reyment, 1971) and (2) log-transformed standardized data (raw score/geometric mean) to examine the shape (Jungers *et al*., 1995).

Differences in the craniodental measurements and the mean values of the principal components among populations were examined by one-way analysis of variance (ANOVA), and pairwise comparisons were made with Tukey's test ($P < 0.05$) for more than three samples with F and t-tests ($P < 0.05$) among taxa for comparison between sexes. The higher factor loadings (positive and negative) of PCA (PCs1, 2, and 3) and coefficients of discriminate function (positive and negative) of CVA (CVAs 1, 2) were selected follow Elizabeth (2006) and James (2009).

3. 3. Results

Descriptive statistics of craniodental measurements are presented in Table 3. 3. On the results of the multiple comparisons, one-way ANOVA indicated the greatest length of skull

(GTL) was the largest in *K. kachinensis* and *K. papillosa*, which were distinctly separated from the other species of Kerivoulinae. The *P. jagori* and *K. titania* showed intermediate skull size and distinguished them from other species. The N, C, S populations, and *K. picta* showed smallest skull size (Fig. 3. 9). In females, the GTL values of N, C, S populations, and *K. picta* do not overlap, however, in males, N, C populations, and *K. picta* do not have overlapping ranges of GTL (Table 3. 3 and Fig. 3. 3) and showed smallest size of skull. In addition, mandibular length (ML) was the greatest in the female of *K. papillasa* and *K. kachinensis*, and smallest in the three *K. hardwickii* populations. In the males, ML is the greatest in the *K. papillosa* only. Moreover, *K. kachinensis* and *P. jagori* are overlapped (Fig. 3. 3). However, the S population has greater mean values of GTL and ML than the N and C populations (Fig. 3. 3). Similar trends were also observed in the other measurement, such as CCL, UCCW, UP3P3W, UP4P4W, M3M3W, CP4L, CM3L, BasW, ZYW, BB, MAW, and cm3L, in which the largest was found in *K. papillosa* and *K. kachinensis*, medium in *K. titania, P. jagori*, and smallest in N, C, and S populations (Table 3. 3).

Using one-way ANOVA, the differences in the size clearly separated three groups of Kerivoulinae in both sexes. The factor loadings for PCA of the log-transformed raw data are provided in Table 3. 4. All characteristic factor loadings were positive in raw data. PC1 was a size component, which explains the 83.10% total variance in the males and 86.05% total variance in females. The high factor loadings of the both sexes are demonstrated by the following measurements: CCL, UCCW, UP2P2W, UP3P3W, CP4L, CM3L, P4M3L, PBL, BasW, ZYW, ML, cm3L, cp4L, and CPH (Table 3. 4). The PC1 scores indicated that Kerivoulinae is divided into three groups (Tukey's test, $P < 0.05$) (Fig. 3. 4). In the females (Fig. 3. 5), higher factor loadings in the PC1 indicated the larger size in *K. papillosa* (mean: 1.649, range: 1.474~1.791), which overlapped with *K. kachinensis* (1.308, 0.892~1.918), but were significantly larger than the other populations of Kerivoulinae ($P < 0.05$). The medium-sized species, such *P. jagori* (0.583~0.784) were larger than *K. titania* (PC1 mean: –0.026; range: –0.389~0.319) and significantly larger than the small-sized group that included *K. picta* (–0.746) and *K. hardwickii* populations (–1.046; –1.470~–0.641) ($P < 0.05$).

In males (Fig. 3. 5), the species of the largest size is *K. papillosa* (range: 2.151~2.283), which is larger than *K. kachinensis* (mean: 1.577, range: 1.260~1.987) ($P < 0.05$). The species of medium size was *P. jagori* (1.498~1.628), which is larger than *K. titania* (0.316,

0.093~0,499) (P<0.05), and both *P. jagori* and *K. titania* were significantly larger than the other small-sized *K. hardwickii* populations (–0.751, –1.592~0.096) (P < 0.05), and *K. picta* (–0.102).

In addition, the statistic results in both sexes indicated that the PC1 mean score of the S population (female: –0.916 and male: –0.400) was larger than that of the N (female: –1.051 and male: –0.892) and C (female: –1.119 and male: 0.950) populations.

Using log-transformed standardized data in the PCA, PCs 1, 2, and 3 were interpreted as shape components (Table 3. 4 and Fig. 3. 6). In females, PC1 explained 30.13% of the variance. The data show the highest factor loading for IOW, followed by BCH, GBCW, and PALW in negative axes; BasW, cp4L, CPH, and UCCW in positive axes in Table 3. 4. PC2 explained 18.75% of the variance, with the highest factor loading for BCH, CP4L, cp4L followed cm3L by in negative axes; PALW and BasW in positive axes. PC3 showed CPH, PALW, and UCCW in positive axes; BasW in the negative axes, which was the highest factor loading of 13.89% of the variance. In the plots for PC1 and 2 scores of the both sexes, *K. kachinensis*, *K. papillosa* and *K. picta* formed a separated two-dimensional space from the plots of the other species, with almost no overlap (P<0.05) (Fig. 3. 6). In males, 25.48% of the variance could be explained using PC1, with the highest factor loading for BCH followed by CP4L and IOW in positive axes; BasW, PALW, UP2P2W, UCCW, GBCW in negative axes in Table 3. 4. PC2 explained 23.62% of the variance with high negative factor loadings for IOW, PALW, and GBCW; cm3L, cp4L, and CPH in positive axes. PC3 accounted for 12.25% of the variance, with the highest factor loadings for BasW in positive axes; UCCW, UP2P2W, and UP4P4W in negative axes in Table 3. 4. Above results revealed that the overlap in N, C, and S populations of *K. hardwickii*, in which the skull shape of C population overlapped a part of the N and S populations from females, but the S population was separated from the N and C populations in the males (P < 0.05) (Fig. 3. 6).

Results of CVA are shown in Table 3.5. In log-transformed raw data, the CVA for females and males clearly separated the Kerivoulinae populations into the different groups (Fig. 3. 7). In the CVA of characteristics of females, the first canonical variable indicated the largest (positive and negative) coefficients of the discriminate function to be GBCW, UP4P4W, IOW, MAW, ZYW, UP2P2W, UCCW, and cm3L with percentage variation of 38.83%. The CCL, GBCW, GTL, MAW, BCH, CM3L, cm3L, and ML were higher (positive and negative) coefficients of the discriminate function in the second canonical variate of 38.07% (Table 3. 5). Furthermore,

the CVA for the characteristics of males separated the Kerivoulinae populations into the different groups. The first canonical variate had the highest (positive and negative) coefficients of the discriminate function with GBCW, UP3P3W, UP4P4W, CCL, cm3L, CP4L, CM3L, BCH, GTL, IOW, and UCCW at 56.07% of the percentage variation. The CM3L, ML, CCL, CP4L, IOW, BB, and cp4L were the highest (positive and negative) coefficients of the discriminate functions in the second canonical variate of 22.24% (Table 3. 5 and Fig. 3. 7).

The results from both PCA with higher positive and negative factor loadings and CVA with higher coefficients of the discriminate function of CCL, UCCW, UP2P2W, UP3P3W, CP4L, CM3L, IOW, GBCW, BCH, and cm3L (Tables 3. 4 and 3. 5) indicated clear differences between *Phoniscus* and *Kerivoula* and among *Kerivoula* populations (Figs. 3. 6, 3. 7).

I focused on the high factor loadings and higher and smaller coefficients of the discriminate function of UCCW, UP3P3W, IOW, GBCW, and BCH used ratio comparisons of BCH and GBCW, IOW and GBCW and UCCW, and UP3P3W to assess differences in the shape of neurocranium, interorbital region and rostrum between *Kerivoula* and *Phoniscus* (Figs. 3. 8, 3. 9). The results clearly showed that BCH and IOW are the effective diagnostic characteristics to reveal significant differences between populations. The skull of *Phoniscus* was considerably more dome-shaped and slightly inflated anteriorly with a braincase height over 89.04% of the greatest width of the braincase (BCH/GBCWx100) compared with the genus *Kerivoula* (Figs. 3. 8A, 3. 9) and the interorbital width over 54.90% of the greatest width of the braincase (IOW/GBCWx100) (versus narrower and slender in *Kerivoula*) (Fig. 3. 8B). The ratio of the upper canine distance (UCCW) and second upper premolar distance (UP3P3W) is 98.94%–99.73% in *Phoniscus*; however, it is < 98.80% in medium-sized and small-sized *Kerivoula* species and over 100% in large-sized species of *Kerivoula* and *K. picta* (Fig. 3. 8C). This result indicated that the anterior part of the palatal bones is parallel in *Phoniscus*, whereas they are anteriorly narrowed in *K. tinania*, N, C and S populations and anteriorly extended in *K. picta*, *K.papillosa* and *K. kachinensis* (Fig. 3. 8C). The characters for CCL, CM3L, CP4L, and cm3L also indicated the significant difference of the teeth, in which the second upper incisors are much reduced (versus developed in *Kerivoula*), the canines, second upper and lower premolars are narrow in *Phoniscus* (versus broader in *Kerivoula*). The genus *Phoniscus* is clearly separated from *Kerivoula* by significant differences in the dome-shaped skull, the shape of the nasal sinus and second upper and lower premolars.

The high factor loadings of PCA and the coefficients of the discriminate functions of CVA for CM3L, and CP4L (Tables 3. 4 and 3. 5) showed significant variation of N, C, and S populations. The character for BCH showed the variation in size and shape of skull within *K. hardwickii* populations. The ratio of braincase height and greatest width of the braincase of S (67.92% < BCH/GBCW x100 <80.91%) and N (60.78% < BCH/GBCW x 100 < 77.89%) populations showed a higher variation than C population (69.83% < BCH/GBCW x 100 < 76.13%) (Fig. 3. 8A). Therefore based on braincase shape of the *K. hardwickii* populations in Vietnam could be divided into three forms: the flattened braincase form containing the specimens from multiple sites in northern provinces, the slightly domed braincase form comprising the specimens from C and some specimens from multiple sites in northern provinces as well as one site (Dong Nai province) from southern provinces, and the distinctly domed braincase form consisting of the specimens from only in southern provinces (Figs. 3. 2 and 3. 8D).

I used two characters BCH and CM3L from the both sexes to compare the differences of *K. hardwickii* populations. The result indicated the significant difference of character BCH (P<0.05), which slightly domed braincase comprising of N, C, and S populations (4.79 mm < BCH < 5.60 mm, 67.92% < BCH/GBCW x 100 < 76.16%) larger than flattened braincase of N population (4.37 mm < BCH < 4.70 mm, 60.78% < BCH/GBCW x 100 < 65.72%), but smaller than distinctly domed braincase of S population (5.70 mm<BCH, 79.50% < BCH/GBCW x100) (Figs. 3. 8D, E, 3. 9). The character CM3L also indicated distinctly domed braincase of S population (5.36mm<CM3L) significant larger than flattened braincase of N population (CM3L<5.35 mm) (P<0.05) (Fig. 3. 8E). The result also pointed out the significant differences in the size related to the difference in the shape of second upper and lower premolars of *K. hardwickii* populations (Table 3. 6).

3. 4. Discussion

Multivariate analysis of skull size and shape is one of the most important methods to establish taxonomy of bats, particularly for species complexes, subspecies, and cryptic species, or to assess the geographical variations in the Southeast Asian region, where few taxonomical investigations have been carried out (Endo *et al*., 2003a, b, 2004, 2007; Hasan and Abdullah, 2011; Son *et al*., 2015b). In Vietnam, five *Kerivoula* species and *P. jagorii* were recorded recently (Hendrichsen *et al*., 2001; Thong *et al*., 2006; Bates *et al*., 2007; Can *et al*., 2008;

Kruskop, 2013). In this study, I used *P. jagorii* as an active representative of the genus *Phoniscus* for comparison with the genus *Kerivoula*. My analysis first time indicated that *P. jagorii* is a medium-sized species of Kerivoulinae, but larger than the medium-sized species (*K. tinania* and *K. picta*) by measurement CCL is announced in the first time ($P < 0.05$); however, *P. jagorii* overlapped with large-sized species of *K. kachinensis*. PC1 of log-transformed data showed high factor loadings as CCL, UCCW, UP1P1W, UP2P2W, UP4P4W, M3M3W, CP4L, CM3L, P4M3L, PBL, BasW, cm3L, and cp4L indicated the significant differences between *Phoniscus* and *Kerivoula*, which are mainly related to the rostrum, palatal bones, size of second upper incisors, first and second upper and lower premolars. The factor loading of PCA for PBL also showed significant differences in anterior palatal emargination that has been indicated by some previous studies. My results pointed out that the anterior palatal emargination in *Kerivoula* is distinctively deeper than in *Phoniscus*. Although DNA analysis unclearly supported the phylogenetic separation between *Kerivoula* and *Phoniscus* (Francis *et al*. 2010), the present morphological data, however, demonstrated that the *Kerivoula* and *Phoniscus* are clearly distinguished from each other and represent two separated genus.

PCs 1 and 2 from log-transformed standardized data and the CVA result showed high factor loadings and larger (positive and negative) coefficients of the discriminate function from both analysis to be CCL, UCCW, UP2P2W, CP4L, CM3L, IOW, GBCW, BCH, cm3L, cp4L, and CPH (Tables 3. 4 and 3. 5). I confirmed the high factor loadings of CP4L and cp4L and larger and smaller coefficients of the discriminate function of CM3L, CP4L, and cm3L demonstrated that the length of the first and second upper premolars was pointed, trenchant and the shape is elongated in *Phoniscus*, whereas ovate and circular in the *Kerivoula* species. CVA results showed larger (positive in female and negative in male) coefficients of the second discriminate function for GTL and CCL, can be related with significant difference of the shape of second upper incisor, which Hill (1965) has shown that the second upper incisor is much more reduced in *Phoniscus*, whereas more massive in *Kerivoula*. The larger coefficients of the discriminate functions for GBCW also indicated the braincase width is domed in *Kerivoula* (versus flattened in *Phoniscus*). I suggest that the development of the second upper incisors, shape of canines, second upper and lower premolars, interorbital region and shape of skull are considered to be the generic characteristics between *Phoniscus* and *Kerivoula*.

The *K. hardwickii* (Horsfield, 1824) was originally described from Java. Recent studies

suggested that *K. hardwickii* is a complex of cryptic species (Bates *et al*., 2007; Francis *et al*., 2007, 2010) and is widely distributed from Southern India to Nepal and from Southern China to Southeast Asia (Horfield, 1821-24; Hill, 1965; Hill, 1983; Hill and Francis, 1984; Hill and Rozendaal, 1989; Koopman, 1989, Corbet and Hill, 1992; Koopman, 1993, 1994; Bates and Harrison, 1997; Wang, 2003; Matthew *et al*., 2005; Simmon, 2005; Francis *et al*., 2007; Vishakha *et al*., 2007; Kruskop, 2013; Thomas *et al*., 2013; Phauk *et al*., 2013). Members of this complex are common and widely distributed species throughout Vietnam (Can *et al*., 2008; Kruskop, 2013).

PCA results showed the *K. hardwickii* N, C and S populations overlapped in the size measurements and had large variation in the skull shape. However, the CVA result indicated the clear separation among the N, C, and S (Fig. 3. 7). My results first indicated important measurements, such CP4L, CM3L, and BCH (Tables 3. 4 and 3. 5), showed a statistically significant variation in teeth, skull size and shape among the three populations of *K. hardwickii* (Figs. 3. 5, 3. 6, 3. 8E, 3. 9) and the variation in the species composition is broadly correlated with the topography, habitat complexity and climate condition in Vietnam. Averyanov *et al*. (2003) have provided a phylogeographic review of eastern Indochina, and Fooden (1996) suggested that a zoogeographic barrier formerly extended from east to west across Vietnam at ca. 14–17^0 N [18] (Fig. 3. 2). My results support the hypothesis that the Annamite mountain chains act as a geographical barrier at ca. 14–17^0 N and the difference of the habitat and climate influence the morphological characteristics separating *K. hardwickii* populations.

The N and S populations may represent two distinct taxa. The C population shows variation in skull shape and is widely distributed from northern to southern of Vietnam, because this is an area with much fauna overlap of the Lower Mekong Watershed area and the Central Highlands area (Tordoff *et al*., 2004; Sterling *et al*., 2006; Bain and Hurley, 2011). Furthermore, I suggest that the Thanh Hoa and Dong Nai province (Fig. 3. 2) are the transition zones for the N population, with the Annamite mountains and S population, with the Central Highlands to the Mekong Delta (Fooden, 1996; Tordoff *et al*., 2004; Sterling *et al.,* 2006; Bain and Hurley, 2011) comprising an area of morphological differentiation, observed on the basis of the differences in skull shape among the N, C, and S populations. In conclusion, both areas contain specimens with a wide variation in skull shape.

Furthermore, I also suggest that the measurements such CM3L and CP4L, may be related

to the difference in the shape of the first and second upper premolars and BCH related to the significant difference in the size and shape of skull among the *K. hardwickii* populations and these differences may be due to the variation of habitats. Finally, my results, based on mutivariate analysis, demonstrate for the first time that significant differences in morphological characteristics indicate the presence of cryptic taxa of *Kerivoula* in Vietnam, which the results clearly showed the separation of three forms. This result will be the basis for a reassessment and reclassification of this group in Vietnam and Asia in the near future.

Table 3. 1. List of craniodental measurements used in this study and their abbreviations.

Character	
Cranium	
GTL	Greatest length of skull, the greatest antero-posterior length of the skull, taken from the most projecting point at each extremity
CCL	condylo-canine length, from an exoccipital condyle to the anterior edge of the anterior canine
UCCW	Anterior palatal width (least distance between the outer borders of the upper canines)
UP2P2W	Posterior palatal width: greatest width across the outer border first upper premolars from their buccal borders
UP3P3W	Posterior palatal width: Greatest width across the outer border second upper premolars from their buccal borders
UP4P4W	Greatest width across the outer border third upper premolars from their buccal borders
M3M3W	External palatal width, taken across the outer border of the third upper molar, taken at the widest part.
CP4L	Upper canine-premolar length (from the front of the upper canine to the back of the crown of the posterior premolar)
CM3L	Maxillary toothrow length (distance from the front of upper canine to the back of the crown of the third molar)
P4M3L	Molariform toothrow length, from the posterior upper premolar to the last upper molar
PALW	Palatal width
PBL	Palatal length
BasW	Width between the cochleae
IOW	Interorbital width (least width of the interorbital constriction)
ZYW	Zygomatic width (greatest width of the skull across the zygomatic arches
BB	Breadth of braincase at the posterior roots of zygomatic arches
GBCW	Greatest width of the braincase
MAW	Mastoid width (greatest distance across the mastoid region
BCH	Braincase height (from the basisphenoid at the level of the hamular processes to the highest part of the skull
Mandible	
ML	Mandible length (distance from the anterior rim of the alveolus of the first lower incisor to the most posterior part of the condyle
cm3L	Mandibular tooth row length (distance from the front of the lower canine to the back of the crown of the third lower molar)
cp4L	Lower canine-premolar length (distance from the front of the lower canine to the back of the crown of the posterior premolar)
CPH	Least height of the coronoid process (distance from the tip of the coronoid process to the apex of the indentation on the inferior surface of the ramus adjacent to the angular process)

Table 3. 2. Species, sex composition and locality of the specimens used in this study

Species*	Symbol of species	Sample		Traditionally-accepted subspecies	Geographic distribution followed Averyanov et al. (2003); Tordoff *et al*. (2004); Sterling *et al*. (2006); Bain and Hurley (2011)
		Female	Male		
Kerivoula kachinenis	K	30	8	Bates *et al*. (2004)	Northern, Center and Center highland Plateau.
*K. hardwickii** Northern population	N	21	18	Tate (1941), Hill (1965), Corbet and Hill (1992), Kruskop (2013)	The Northern of Vietnam from North Eastern, North Western and Red River Delta.
*K. hardwickii** Central population	C	13	4	Tate (1941), Hill (1965), Corbet and Hill (1992), Kruskop (2013)	From multiple geographical sites in the center of Vietnam.
*K. hardwickii** Southern population	S	8	10	Tate (1941), Hill (1965), Corbet and Hill (1992), Kruskop (2013)	South Eastern and Mekong Delta included Phu Quoc and Condao island.
K. papillosa	P	3	2	Tate (1941), Hill (1965), Corbet and Hill (1992), Kruskop (2013)	Only recorded in the South Eastern and Mekong Delta included Phu Quoc and Condao island.
K. picta	pi	1	1	Miller (1905), Tate (1941), Hill (1965), Corbet and Hill (1992), Kruskop (2013)	Widespread species
K. titania	T	35	14	Bates *et al*. (2007)	Northern to North Center Coast, South central Coast, Central Highland Plateau
Phoniscus jagorii	J	2	2	Tate (1941), Hill (1965), Corbet and Hill (1992), Kruskop (2013)	Northern and Southern

(*): *K. hardwickii* is separated to three geographic populations

Table 3. 3. Minimum, maximum, mean values (mm) and standard deviations for craniometric measurement in various populations of Kerivoulinae in Vietnam.

Character	*K. kachinensis*		*K. papillosa*		*K. picta*		*K. titania*		*Phoniscus jagorii*	
	♀ (30)	♂ (8)	♀ (3)	♂ (2)	♀ (1)	♂ (1)	♀ (35)	♂ (14)	♀ (2)	♂ (2)
GTL	17.17– 18.42	16.76 – 17.69	17.15 – 17.85	17.26 – 17.51	15.23	14.98	15.22 – 16.35	15.26 – 15.98	16.71 – 17.02	16.56 – 16.84
	17.81 ± 0.32	18.28 ± 0.37	17.44 ± 0.37				15.79 ± 0.26	15.57 ± 0.20		
CCL	15.23 – 16.44	15.08 – 15.79	15.52 – 15.91	15.34 – 15.53	13.07	13.04	13.33 – 14.18	13.10 – 13.92	14.76 – 15.26	14.64 – 14.81
	15.87 ± 0.31	15.41 ± 0.24	15.67 ± 0.21				13.82 ± 0.24	13.54 ± 0.21		
UCCW	4.13 – 4.66	3.88 – 4.52	4.50 – 4.70	4.57 – 4.72	3.32	3.33	3.30 – 3.77	3.37 – 3.67	3.60 – 3.63	3.50 – 3.73
	4.35 ± 0.13	4.23 ± 0.21	4.62 ± 0.11				3.55 ± 0.11	3.53 ± 0.08		
UP2P2W	4.19 – 4.82	3.94 – 4.55	4.42 – 4.67	4.33 – 4.44	3.12	3.28	3.55 – 3.92	3.54 – 3.78	3.59 – 3.75	3.67 – 3.61
	4.41 ± 0.13	4.23 ± 0.21	4.56 ± 0.13				3.72 ± 0.10	3.66 ± 0.07		
UP3P3W	4.14 – 4.82	3.81 – 4.43	4.39 – 4.61	4.36 – 4.41	3.25	3.38	3.65 – 3.99	3.65 – 3.88	3.63 – 3.84	3.74 – 3.69
	4.38 ± 0.14	4.19 ± 0.20	4.53 ± 0.12				3.81 ± 0.08	3.75 ± 0.07		
UP4P4W	4.39 – 5.75	4.85 – 5.49	5.42 – 5.57	5.31 – 5.34	4.34	4.34	4.45 – 4.84	4.48 – 4.78	4.37 – 4.77	4.52 – 4.58
	5.36 ± 0.22	5.14 ± 0.19	5.52 ± 0.09				4.66 ± 0.10	4.60 ± 0.09		
M3M3W	6.18 – 6.94	5.87 – 6.61	6.45 – 6.77	6.37 – 6.37	5.48	5.72	5.39 – 5.88	5.38 – 5.69	5.50 – 5.68	5.65 – 5.70
	6.46 ± 0.18	6.21 ± 0.24	6.58 ± 0.17				5.67 ± 0.12	5.54 ± 0.09		
CP4L	3.19 – 3.65	3.07 – 3.42	3.53 – 3.57	3.49 – 3.60	2.96	2.88	2.88 – 3.19	2.86 – 3.06	3.63 – 3.74	3.74 – 3.75
	3.40 ± 0.12	3.22 ± 0.12	3.55 ± 0.02				3.05 ± 0.07	2.98 ± 0.05		
CM3L	6.54 – 7.28	6.53 – 6.89	7.02 – 7.34	7.07 – 7.18	5.78	5.81	5.78 – 6.26	5.81 – 6.12	6.44 – 6.65	6.57 – 6.60
	6.86 ± 0.17	6.71 ± 0.12	7.21 ± 0.17				6.07 ± 0.10	5.97 ± 0.08		
P4M3L	4.18 – 4.80	4.61 – 4.50	4.53 – 4.68	4.58 – 4.62	3.76	3.77	3.06 – 4.18	3.82 – 3.98	3.67 – 400	3.89 – 3.93
	4.49 ± 0.13	4.32 ± 0.29	4.62 ± 0.08				3.97±0.24	3.90 ± 0.06		
PALW	1.92 – 2.32	1.91 – 2.13	1.76 – 1.95	1.78 – 1.81	1.96	1.98	1.52 – 2.00	1.67 – 1.89	1.94 – 2.11	1.77 – 2.00

	2.12 ± 0.12	2.02 ± 0.09	1.85 ± 0.10				1.79 ± 0.11	1.77 ± 0.07		
PBL	6.67 – 7.85	6.68 – 7.43	7.40 – 7.83	7.26 – 7.54	6.46	6.99	5.88 – 6.90	5.96 – 6.67	6.55 – 6.68	7.15 – 7.44
	7.31 ± 0.24	7.14 ± 0.30	7.62 ± 0.22				6.42 ± 0.27	6.38 ± 0.20		
BasW	1.65 – 2.31	1.70 – 1.90	1.82 – 2.09	1.86 – 1.89	1.29	1.4	1.49 – 1.91	1.53 – 1.83	1.52 – 1.59	1.68 – 1.71
	1.93 ± 0.15	1.81 ± 0.07	1.93 ± 0.14				1.74 ± 0.11	1.68 ± 0.10		
IOW	3.34 – 3.94	3.44 – 3.75	3.37 – 3.59	3.38 – 3.39	3.43	3.38	3.26 – 3.65	3.28 – 3.64	4.37 – 4.48	4.29 – 4.49
	3.63 ± 0.15	3.61 ± 0.09	3.45 ± 0.12				3.45 ± 0.09	3.41 ± 0.11		
ZYW	10.03 – 11.29	9.52 – 10.58	10.78 – 11.19	10.70 – 10.70	8.77	9.03	9.00 – 9.77	8.72 – 9.38	9.60 – 9.66	10.17 – 10.21
	10.54 ± 0.26	10.19 ± 0.39	10.95 ± 0.21				9.30 ± 0.18	9.08 ± 0.20		
BCH	5.21 – 5.88	5.28 – 5.78	6.63 – 6.88	6.69 – 6.76	5.22	5.7	5.04 – 5.83	5.15 – 5.70	7.14 – 7.15	7.54 – 7.65
	5.55 ± 0.17	5.56 ± 0.19	6.87 ± 0.24				5.48	5.47 ± 0.16		
GBCW	7.77 – 8.75	7.94 – 8.27	8.00 – 8.22	8.10 – 8.11	6.74	6.95	7.37 – 8.03	7.54 – 7.98	7.87 – 8.03	7.87 – 8.00
	8.23 ± 0.22	8.21 ± 0.16	8.08 ± 0.12				7.75 ± 0.16	7.74 ± 0.14		
BB	7.53 – 8.42	7.24 – 7.97	7.61 – 8.11	7.86 – 7.95	6.58	6.87	6.86 – 7.59	6.86 – 7.46	7.73 – 7.75	7.84 – 7.95
	7.88±0.23	7.70 ± 0.25	7.78 ± 0.29				7.15 ± 0.17	7.15 ± 0.20		
MAW	8.15 – 9.12	8.20 – 8.84	8.60 – 8.88	8.64 – 8.64	7.69	7.86	7.61 – 8.27	7.57 – 8.09	8.35 – 8.42	8.44 – 8.58
	8.72 ± 0.24	8.43 ± 0.21	8.77 ± 0.15				7.97 ± 0.17	7.85 ± 0.16		
ML	11.82 – 12.81	11.47 – 12.20	12.47 – 12.82	12.36 – 12.53	10.47	10.54	10.19 – 11.00	9.89 – 10.77	11.75 – 11.85	11.51 – 11.78
	12.28 ± 0.24	11.88 ± 0.24	12.62 ± 0.18				10.55 ± 0.24	10.31 ± 0.22		
cp4L	3.07 – 3.47	3.03 – 3.31	3.54 – 3.68	3.50 – 3.60	2.7	2.56	2.71 – 3.07	2.75 – 3.01	3.64 – 3.65	3.63 – 3.74
	3.33 ± 0.09	3.19 ± 0.10	3.61 ± 0.07				2.92 ± 0.07	2.85 ± 0.07		
cm3L	7.07 – 7.77	6.75 – 7.46	7.76 – 7.96	7.69 – 7.87	6	6.22	6.28 – 6.76	6.19 – 6.61	7.00 – 7.49	7.17
	7.38 ± 0.18	7.15 ± 0.21	7.88 ± 0.11				6.52 ± 0.11	6.39 ± 0.12		
CPH	3.37 – 4.12	3.43 – 4.00	4.17 – 4.60	4.16 – 4.55	2.89	2.8	2.86 – 3.43	2.86 – 3.22	3.65 – 3.68	3.82 – 3.88
	3.86 ± 0.18	3.63 ± 0.18	4.37 ± 0.22				3.10 ± 0.13	3.02 ± 0.13		

Value given as minimum-maximum (above) and mean ± standard deviation (below) (if n≥3)

Table 3. 3. Continue

Character	*K. hardwickii*-N		*K. hardwickii*-C		*K. hardwickii*-S	
	♀ (21)	♂ (18)	♀ (13)	♂ (4)	♀ (8)	♂ (10)
GTL	13.63 – 14.56	13.38 – 14.62	13.74 – 14.60	13.72 – 14.01	13.89 – 15.00	13.89 – 15.26
	13.63 ± 0.21	13.99 ± 0.32	14.19 ± 0.24	13.89 ± 0.12	14.55 ± 0.42	14.53 ± 0.37
CCL	11.94 – 12.98	11.88 – 12.81	12.19 – 12.88	11.98 – 12.26	12.16 – 13.15	12.17 – 13.22
	12.62 ± 0.22	12.34 ± 0.29	12.52 ± 0.18	12.11 ± 0.14	12.70 ± 0.37	12.69 ± 0.31
UCCW	3.17 – 3.58	3.00 – 3.56	3.24 – 3.50	3.11 – 3.35	3.37 – 3.62	3.32 – 3.68
	3.36 ± 0.11	3.28 ± 0.17	3.42 ± 0.12	3.22 ± 0.11	3.45 ± 0.11	3.47 ± 0.13
UP2P2W	3.20 – 3.61	3.08 – 3.62	3.28 – 3.55	3.17 – 3.37	3.37 – 3.62	3.39 – 3.68
	3.45 ± 0.10	3.35 ± 0.16	3.41 ± 0.09	3.26 ± 0.08	3.50 ± 0.10	3.52 ± 0.09
UP3P3W	3.28 – 3.68	3.16 – 3.58	3.33 – 3.64	3.19 – 3.44	3.48 – 3.69	3.49 – 3.65
	3.50 ± 0.11	3.38 ± 0.13	3.48 ± 0.11	3.31 ± 0.10	3.57 ± 0.09	3.57 ± 0.06
UP4P4W	4.05 – 4.56	3.94 – 4.57	4.10 – 4.48	4.01 – 4.27	4.25 – 4.47	4.27 – 4.60
	4.33 ± 0.13	4.21 ± 0.19	4.23 ± 0.14	4.13 ± 0.13	4.34 ± 0.10	4.44 ± 0.12
M3M3W	4.85 – 5.33	4.76 – 5.48	5.01 – 5.79	4.96 – 5.23	5.12 – 5.39	5.01 – 5.34
	5.15 ± 0.12	5.04 ± 0.19	5.19 ± 0.22	5.14 ± 0.12	5.22 ± 0.13	5.25 ± 0.12
CP4L	2.51 – 2.89	2.43 – 2.84	2.46 – 2.80	2.41 – 2.70	2.47 – 2.79	2.51 – 2.86
	2.64 ± 0.10	2.62 ± 0.12	2.61 ± 0.09	2.55 ± 0.13	2.67 ± 0.14	2.73 ± 0.10
CM3L	5.03 – 5.50	4.96 – 5.56	5.14 – 5.43	4.94 – 5.25	5.06 – 5.62	5.26 – 5.76
	5.27 ± 0.13	5.22 ± 0.18	5.30 ± 0.09	5.15 ± 0.14	5.45 ± 0.21	5.51 ± 0.13
P4M3L	2.64 – 3.65	3.27 – 3.69	3.34 – 3.62	3.21 – 3.55	3.24 – 3.86	3.52 – 3.81
	3.46 ± 0.21	3.46 ± 0.12	3.53 ± 0.09	3.43 ± 0.15	3.63 ± 0.20	3.68 ± 0.11
PALW	1.63 – 1.98	1.53 – 1.87	1.66 – 1.89	1.61 – 1.74	1.63 – 1.89	1.53 – 1.75
	1.78 ± 0.08	1.70 ± 0.10	1.78 ± 0.08	1.71 ± 0.02	1.75 ± 0.09	1.66 ± 0.07
PBL	5.35 – 6.08	5.13 – 5.87	5.32 – 6.71	5.40 – 6.12	5.79 – 6.08	5.63 – 6.11

	5.69 ± 0.21	5.65 ± 0.20	5.71 ± 0.16	5.69 ± 0.25	5.89 ± 0.17	5.90 ± 0.17
BasW	1.40 – 1.73	1.31 – 1.59	1.25 – 1.70	1.38 – 1.58	1.32 – 1.58	1.34 – 1.49
	1.57 ± 0.09	1.48 ± 0.07	1.44 ± 0.13	1.47 ± 0.10	1.43 ± 0.08	1.41 ± 0.05
IOW	3.11 – 3.57	2.94 – 3.53	3.20 – 3.60	3.03 – 3.31	3.20 – 3.28	3.23 – 3.48
	3.32 ± 0.12	3.24 ± 0.14	3.29 ± 0.11	3.21 ± 0.13	3.24 ± 0.03	3.38 ± 0.08
ZYW	7.93 – 8.78	7.29 – 8.89	7.74 – 8.58	8.11-8.50	8.36 – 8.94	8.33 – 9.04
	8.37 ± 0.23	8.16 ± 0.38	8.27 ± 0.25	8.35 ± 0.17	8.61 ± 0.28	8.64 ± 0.23
BCH	4.40 – 5.41	4.37 – 5.60	5.07 – 5.48	5.15 – 5.55	4.89 – 6.28	5.67 – 6.04
	4.78 ± 0.33	4.85 ± 0.32	5.24 ± 0.13	5.36 ± 0.17	5.62 ± 0.55	5.87 ± 0.14
GBCW	6.80 – 7.47	6.94 – 7.45	6.88 – 7.44	7.00 – 7.29	7.06 – 7.37	6.95 – 7.70
	7.21 ± 0.15	7.12 ± 0.14	7.21 ± 0.17	7.14 ± 0.12	7.16 ± 0.10	7.15 ± 0.22
BB	6.35 – 6.95	6.09 – 6.96	6.26 – 6.80	6.44 – 6.74	6.49 – 6.88	6.41 – 7.08
	6.68 ± 0.14	6.52 ± 0.26	6.54 ± 0.16	6.58 ± 0.12	6.62 ± 0.12	6.67 ± 0.20
MAW	7.18 – 7.61	6.82 – 7.47	6.97 – 7.57	7.05 – 7.50	7.19 – 7.58	7.18 – 7.86
	7.43 ± 0.12	7.24 ± 0.18	7.35 ± 0.18	7.27 ± 0.19	7.36 ± 0.17	7.37 ± 0.21
ML	9.13 – 9.91	8.80 – 9.67	9.02 – 9.55	8.75 – 9.34	9.14 – 10.00	9.09 – 10.13
	9.48 ± 0.24	9.19 ± 0.23	9.33 ± 0.15	9.08 ± 0.28	9.63 ± 0.30	9.62 ± 0.27
cp4L	2.33 – 2.81	2.15 – 2.62	2.35 – 2.64	2.25 – 2.41	2.35 – 2.63	2.49 – 2.71
	2.47 ± 0.12	2.41 ± 0.13	2.44 ± 0.09	2.34 ± 0.07	2.52 ± 0.08	2.56 ± 0.06
cm3L	5.42 – 5.89	5.25 – 5.98	5.50 – 5.83	5.13 – 5.59	5.30 – 6.04	5.64 – 6.08
	5.62 ± 0.14	5.56 ± 0.20	5.65 ± 0.10	5.45 ± 0.22	5.76 ± 0.26	5.85 ± 0.13
CPH	2.79 – 3.27	2.68 – 3.15	2.60 – 3.17	2.75 – 2.88	2.95 – 3.03	2.75 – 3.12
	2.98 ± 0.12	2.88 ± 0.15	2.89 ± 0.14	2.83 ± 0.06	2.98 ± 0.06	2.93 ± 0.13

Value given as minimum-maximum (above) and mean ± standard deviation (below) (if n≥3)

Table 3. 4. Character factor loadings for principal components analysis of the log-transformed raw data (PCs 1) and log-transformed standardized data (PCs 1, 2, and 3) of Kerivoulinae populations from Vietnam.

Measurement	Raw Data		Standardized Data					
	Female	male	Female			Male		
	PC 1	PC 1	PC1	PC2	PC3	PC1	PC2	PC3
GTL	0.198	0.196	-0.024	0.001	-0.015	-0.027	-0.029	0.074
CCL	**0.206**	**0.203**	0.008	0.023	0.031	-0.063	0.014	0.074
UCCW	**0.240**	**0.238**	**0.178**	0.097	**0.301**	**-0.114**	0.177	**-0.454**
UP2P2W	**0.229**	**0.212**	0.150	0.109	0.133	**-0.159**	0.054	**-0.352**
UP3P3W	**0.208**	**0.200**	0.069	0.076	0.054	-0.106	0.011	-0.246
UP4P4W	0.196	0.183	0.047	0.103	0.137	-0.099	-0.058	**-0.298**
M3M3W	0.203	0.187	0.039	0.064	0.056	-0.077	-0.085	-0.154
CP4L	**0.239**	**0.242**	0.079	**-0.242**	-0.076	**0.216**	0.175	0.250
CM3L	**0.238**	**0.248**	0.117	-0.154	-0.041	0.024	0.195	0.086
P4M3L	**0.226**	**0.207**	0.121	-0.131	-0.108	-0.042	0.079	-0.057
PALW	0.148	0.129	**-0.247**	**0.470**	**0.309**	**-0.312**	**-0.396**	-0.062
PBL	**0.223**	**0.226**	0.109	-0.032	0.017	0.030	0.073	0.231
BasW	**0.230**	**0.209**	**0.242**	**0.316**	**-0.752**	**-0.327**	0.027	**0.494**
IOW	0.090	0.114	**-0.521**	0.081	-0.023	**0.191**	**-0.470**	0.113
ZYW	**0.213**	**0.215**	0.040	-0.009	-0.006	0.009	0.037	-0.087
BB	0.158	0.170	-0.169	0.117	-0.092	0.007	-0.184	0.060
GBCW	0.122	0.131	**-0.286**	0.132	-0.177	**-0.105**	**-0.290**	0.106
MAW	0.152	0.151	-0.183	0.101	-0.110	-0.018	-0.218	0.097
BCH	0.117	0.171	**-0.472**	**-0.567**	-0.028	**0.785**	-0.168	-0.135
ML	**0.239**	**0.242**	0.118	-0.062	0.064	0.025	0.163	0.113
cm3L	**0.249**	**0.257**	0.149	**-0.206**	-0.049	0.050	**0.242**	0.161
cp4L	**0.283**	**0.296**	**0.217**	**-0.344**	0.023	0.029	**0.368**	0.065
CPH	**0.260**	**0.260**	**0.219**	0.058	**0.353**	0.082	**0.282**	-0.081
Eigenvalue	0.039	0.032	0.003	0.002	0.001	0.002	0.002	0.001
% variance	86.05	83.1	30.13	18.75	13.89	25.48	23.62	12.25

Boldface numerals: High (positive and negative) factor loading. 14 higher values of character factor loadings were selected in PC1 of raw data. 8, 6, and 4 higher values of character factor loadings were also selected in PCs 1, 2, and 3 of standardized data.

Table 3. 5. Coefficients of the discriminate function for canonical variate analysis of the log-transformed standardized data (CVs 1, 2) of Kerivoulinae populations from Vietnam.

Measurement	Female		Male	
	CV1	CV2	CV1	CV2
GTL	-28.86	**31.89**	**-63.97**	-28.74
CCL	-11.13	**75.16**	**44.39**	**-123.73**
UCCW	**-37.66**	24.71	**-37.19**	-9.15
UP2P2W	**-43.14**	15.7	6.83	36.7
UP3P3W	25.18	4.7	**81.54**	23.02
UP4P4W	**37.14**	-4.43	**72.36**	-27.49
M3M3W	-16.31	-3.07	17.32	15.29
CP4L	6.64	1.2	**-79.95**	**-70.96**
CM3L	4.66	**-61.35**	**-71.45**	**54.04**
P4M3L	-12.48	7.08	28.07	-2.9
PALW	3.98	2.56	20.7	-27.23
PBL	-6.86	17.15	-3.28	27.22
BasW	-1.02	5.27	17.9	-1.65
IOW	**31.15**	-8.32	**-63.66**	**-54.01**
ZYW	**-45.55**	-20.96	-9.02	16.78
BB	15.46	-6.28	-4.56	**-48.76**
GBCW	**40.45**	**59.09**	**99.94**	15.23
MAW	**29.03**	**27.16**	-2.33	-17.18
BCH	15.63	**-82.15**	**-67.17**	7.76
ML	-14.01	**-28.12**	34.27	**53.76**
cm3L	**-37.64**	**-37.51**	**34.91**	11.6
cp4L	-10.46	-19.71	13.55	39.16
CPH	-19.18	0.45	-11.53	31.77
Percentage variation	38.83	38.07	56.07	22.24

Boldface numerals: High (positive and negative) coefficients of the discriminate function. 8 higher values of coefficients of discriminate functions were selected in CVs1, 2 of female. 11 and 7 higher values of coefficients of discriminate functions were selected in CVs1, 2 of male.

Table 3. 6. Differences in size of braincase high and maxillary toothrow length and shape of first (P2) and second upper premolars (P3) of *K. hardwickii* populations.

Character	N flattened braincase	N, C and S slightly domed braincase	S distinctly domed braincase
Size of P2, P3	Small, P2>P3	Small, P2>P3	Large, P2=P3
Shape of P2, P3	Circular	Circular or ovate	Ovate
P2	Inner circular, outnet circular	Inner circular or oval, Outer slightly traight	Inner oval, outer oval
P3	Inner circular, outer circular	Inner circular, outer slightly circular	Inner oval, outer circular
Transverse diameters P2, P3	Equal their longitudinal diameters	Equal, exceeding their longitudinal diameters	Exceeding their longitudinal diameters
BCH (mm)	Less 4.7	4.89–5.60	Over 5.7
CM3L (mm)	Less 5.36	4.90–5.60	Over 5.36

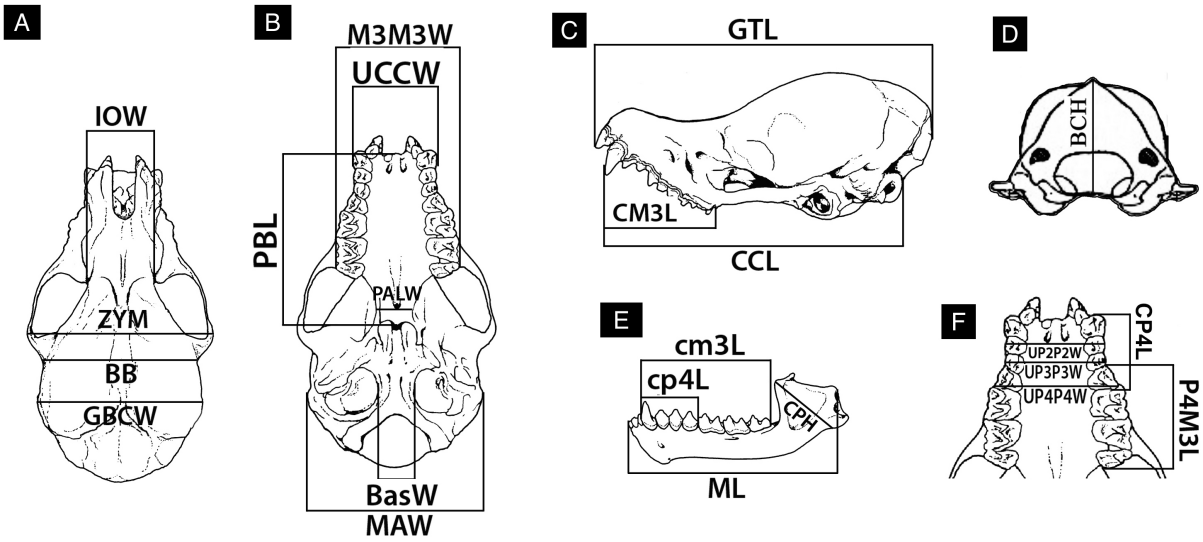

Fig. 3. 1. Dorsal (A), ventral (B), lateral (C) and posterior (D) views of the cranium and mandible (E), and upper (F) dentition showing measurements (see Table 3. 1).

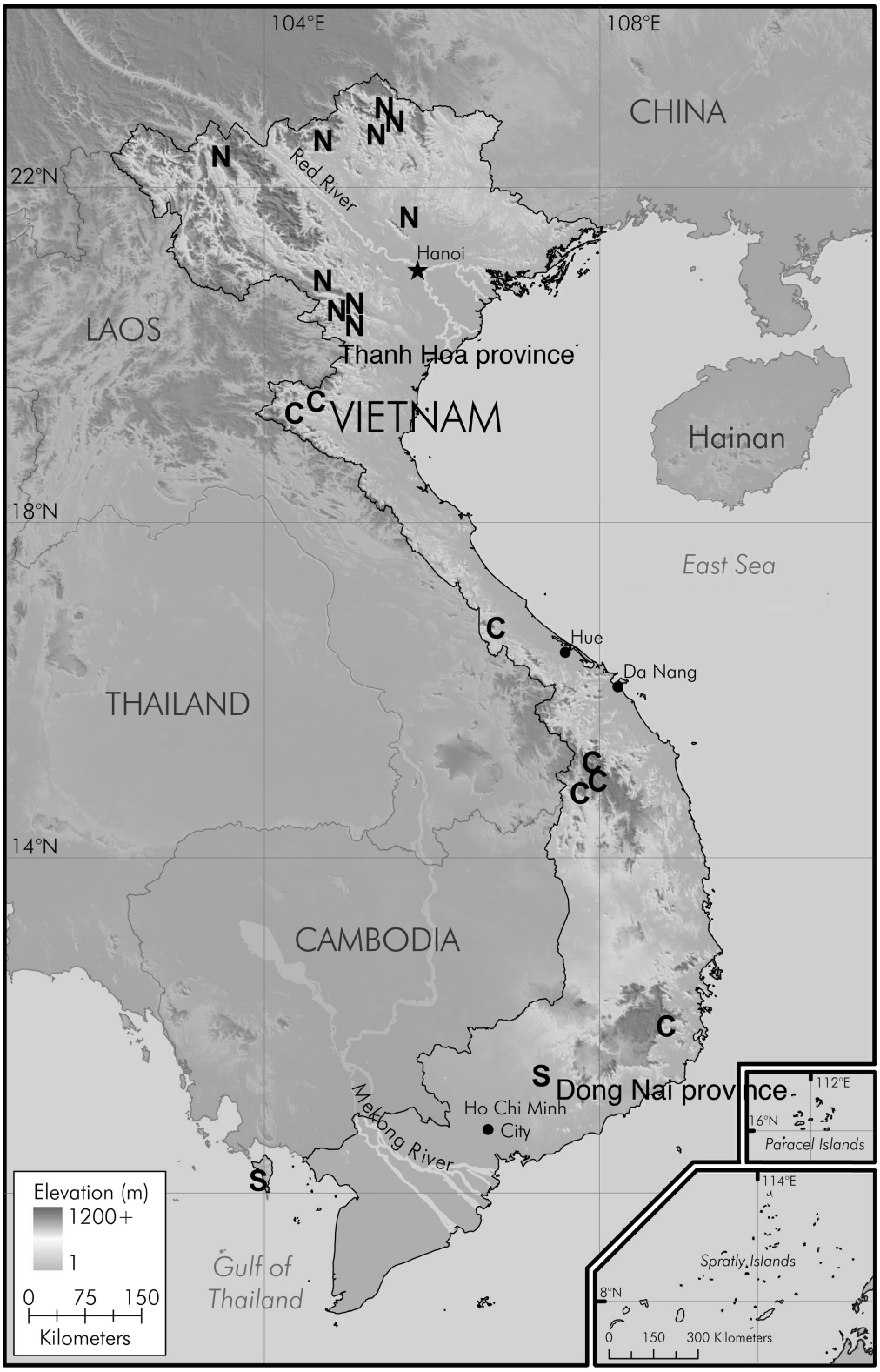

Fig. 3. 2. Map showing specimen localities of three *K. hardwickii* populations from Vietnam. N: northern population. S: southern population. C: widely distributed population, from multiple geographical sites in central of Vietnam. Symbols are explained in Table 3. 2.

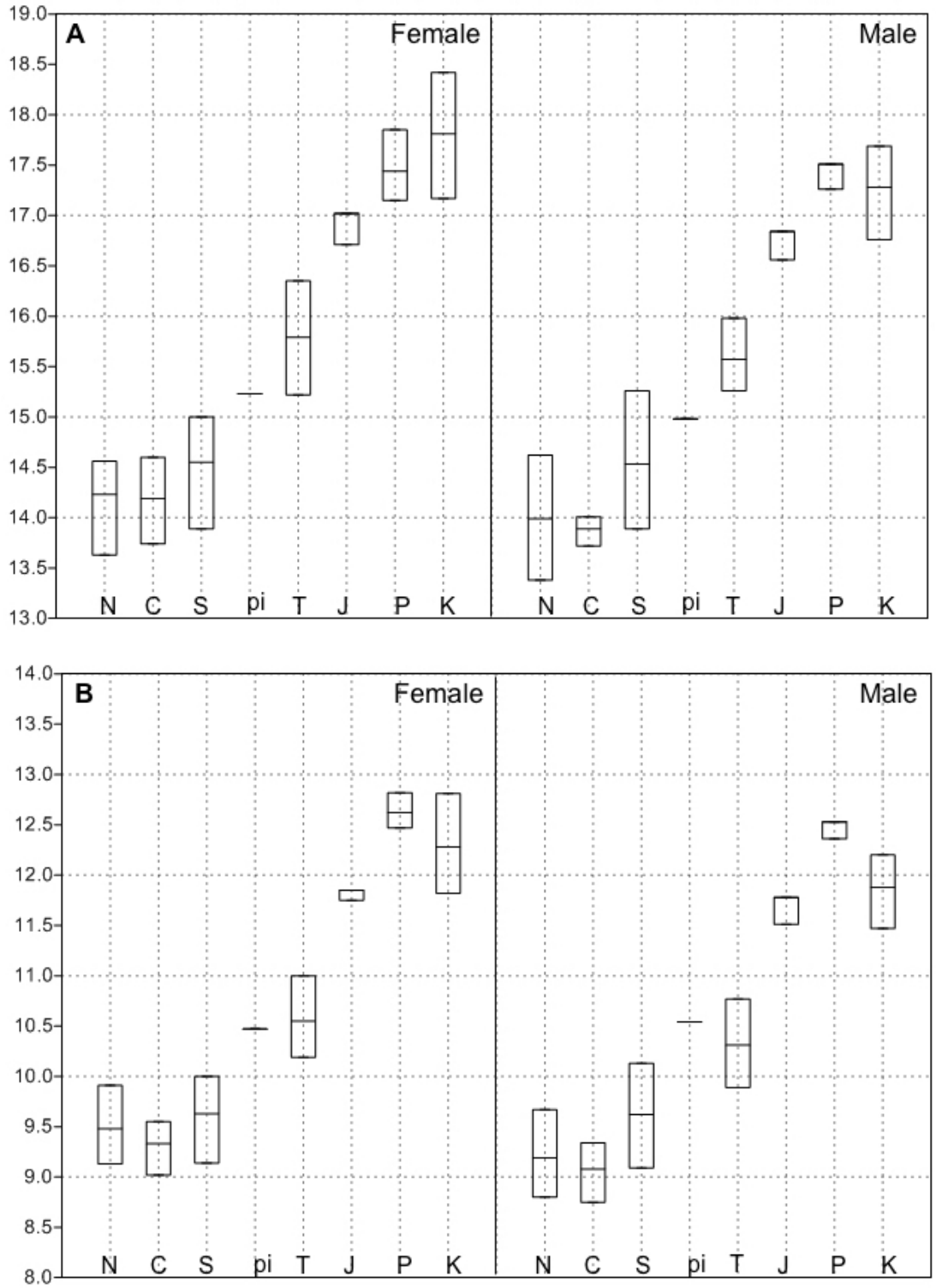

Fig. 3. 3. Range (minimum value to maximum value in boxplots) (mm) and mean value (in horizontal bar) (mm) of greatest length of the skull (A), mandible length (B) of Kerivoulinae populations from Vietnam. The line the top and bottom of boxplot: maximum and minimum value. The horizontal line within the boxes indicated mean value. Symbols are explained in Table 3. 2.

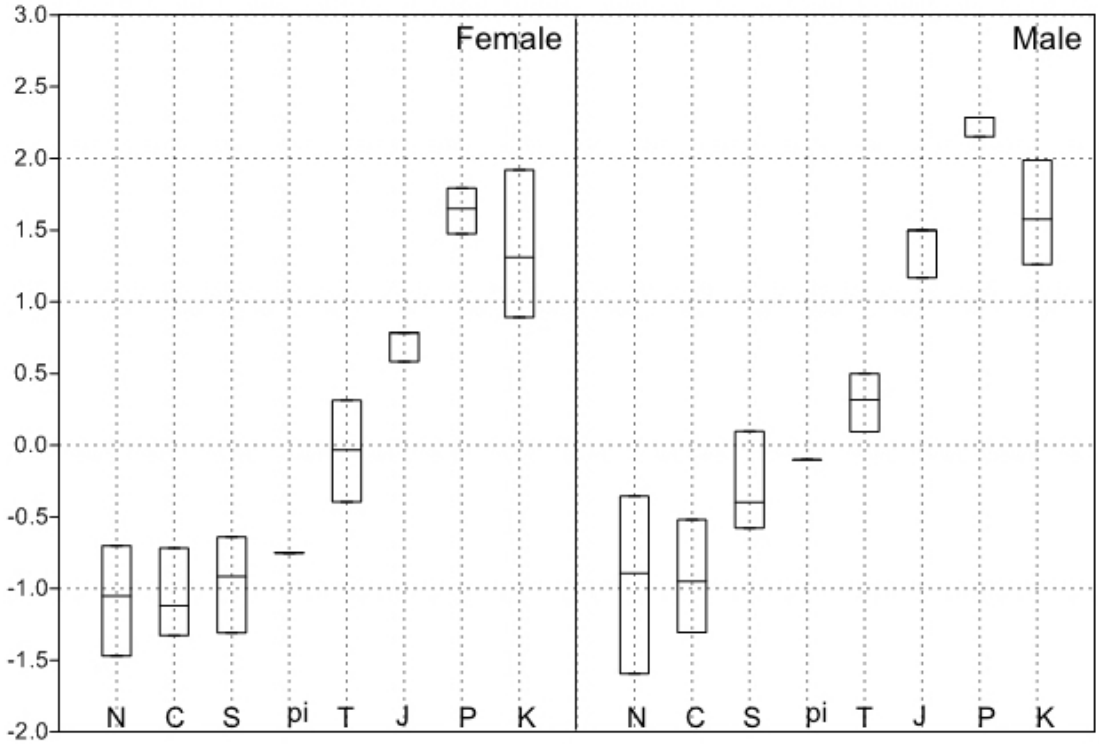

Fig. 3. 4. Range (minimum value to maximum value in boxplots) and mean value (in horizontal bar) of PC1 scores of log-transformed raw data of Kerivoulinae populations from Vietnam. The line the top and bottom of boxplot: maximum and minimum value. The horizontal line within the boxes indicated mean value. Symbols are explained in Table 3. 2.

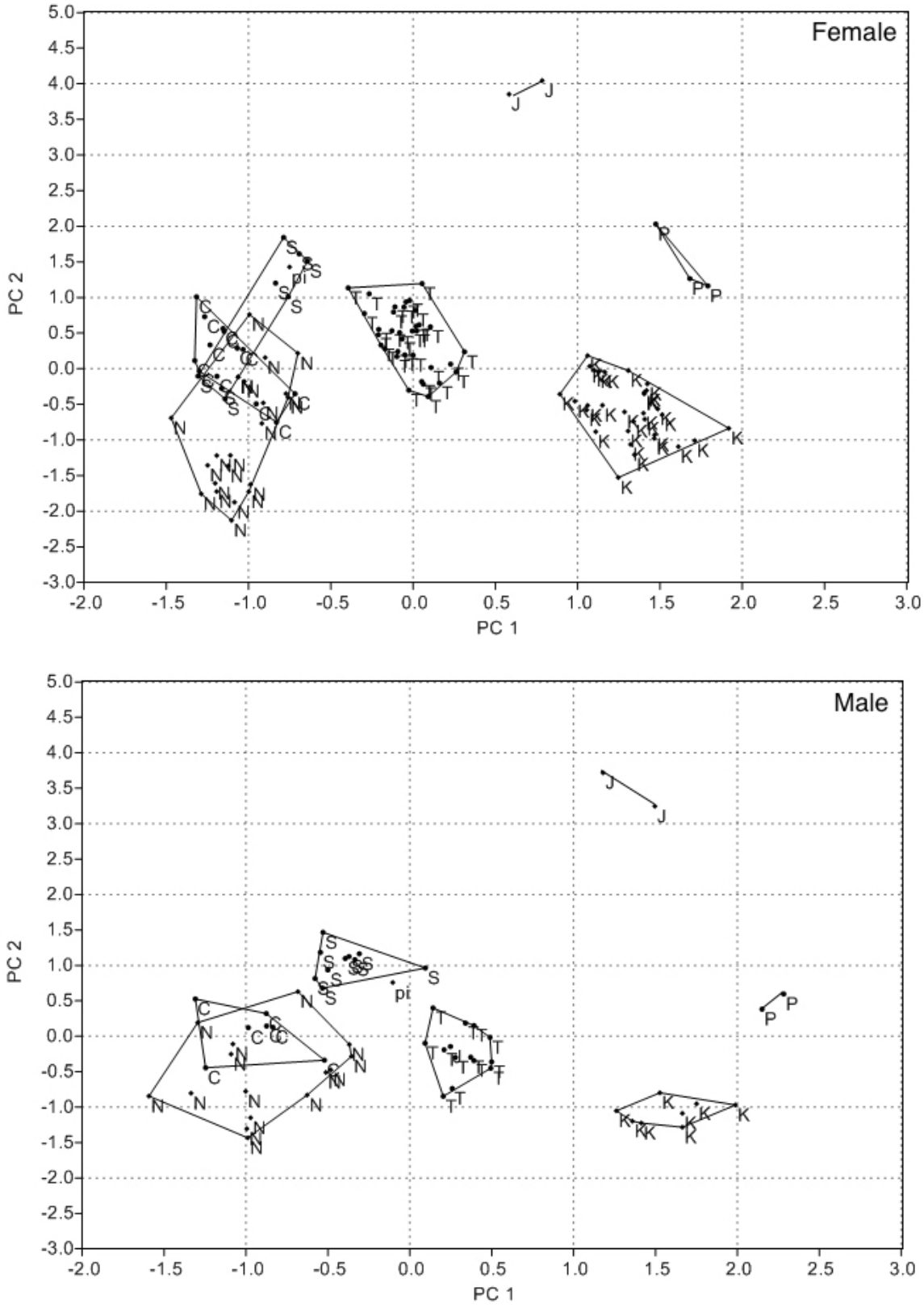

Fig. 3. 5. Scatterplots of scores of the PC1 and PC2 based on log-transformed raw data indicating the significant differences of the size of the females and the males of Kerivoulinae populations from Vietnam. Symbols are explained in Table 3. 2. Character factor loadings are shown in Table 3, 4.

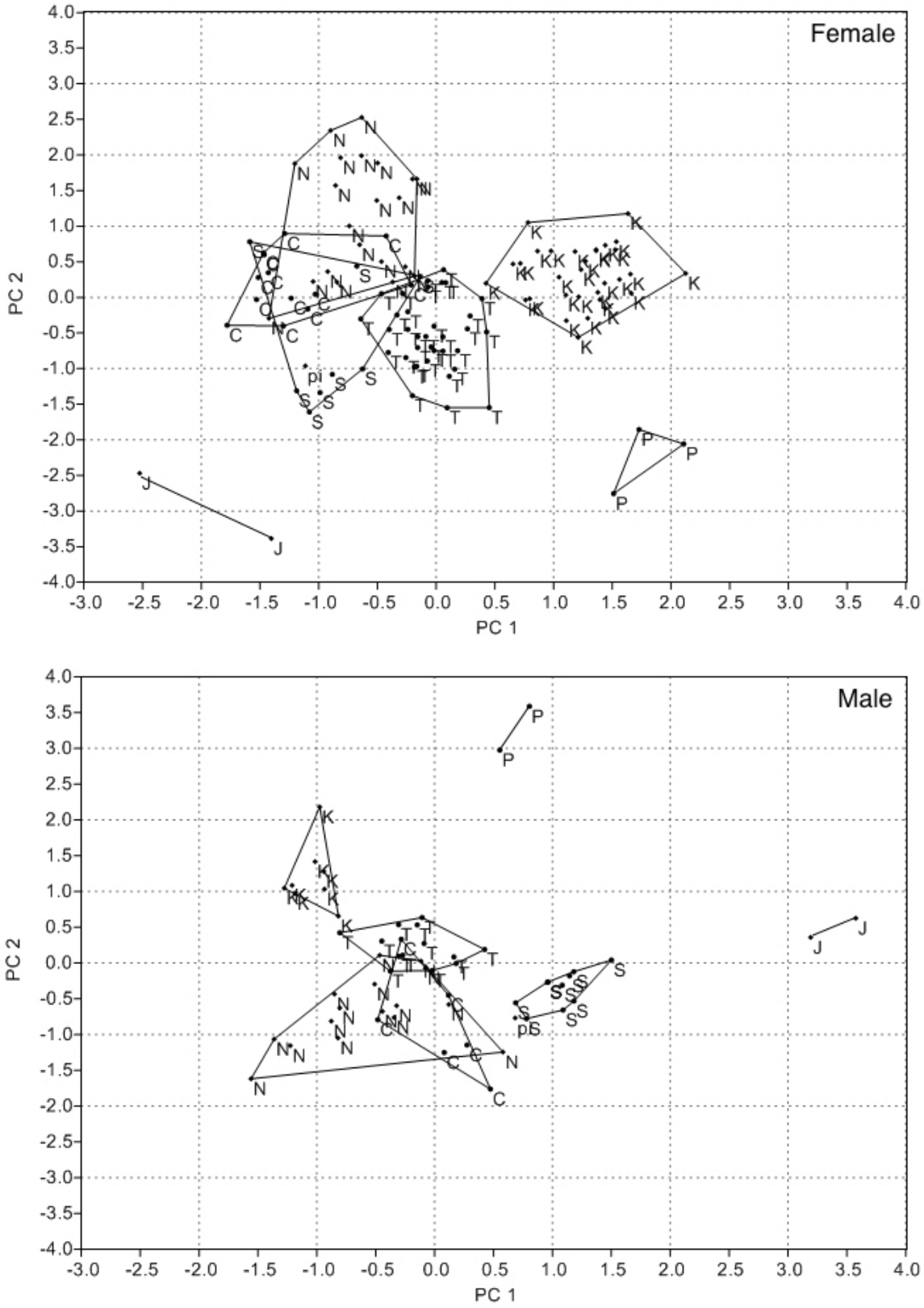

Fig. 3. 6. Scatterplots of scores of the first and second principal component axes based on log-transformed standardized data for females and males of Kerivoulinae populations from Vietnam. Symbols are explained in Table 3. 2. Character factor loadings are shown in Table 3, 4.

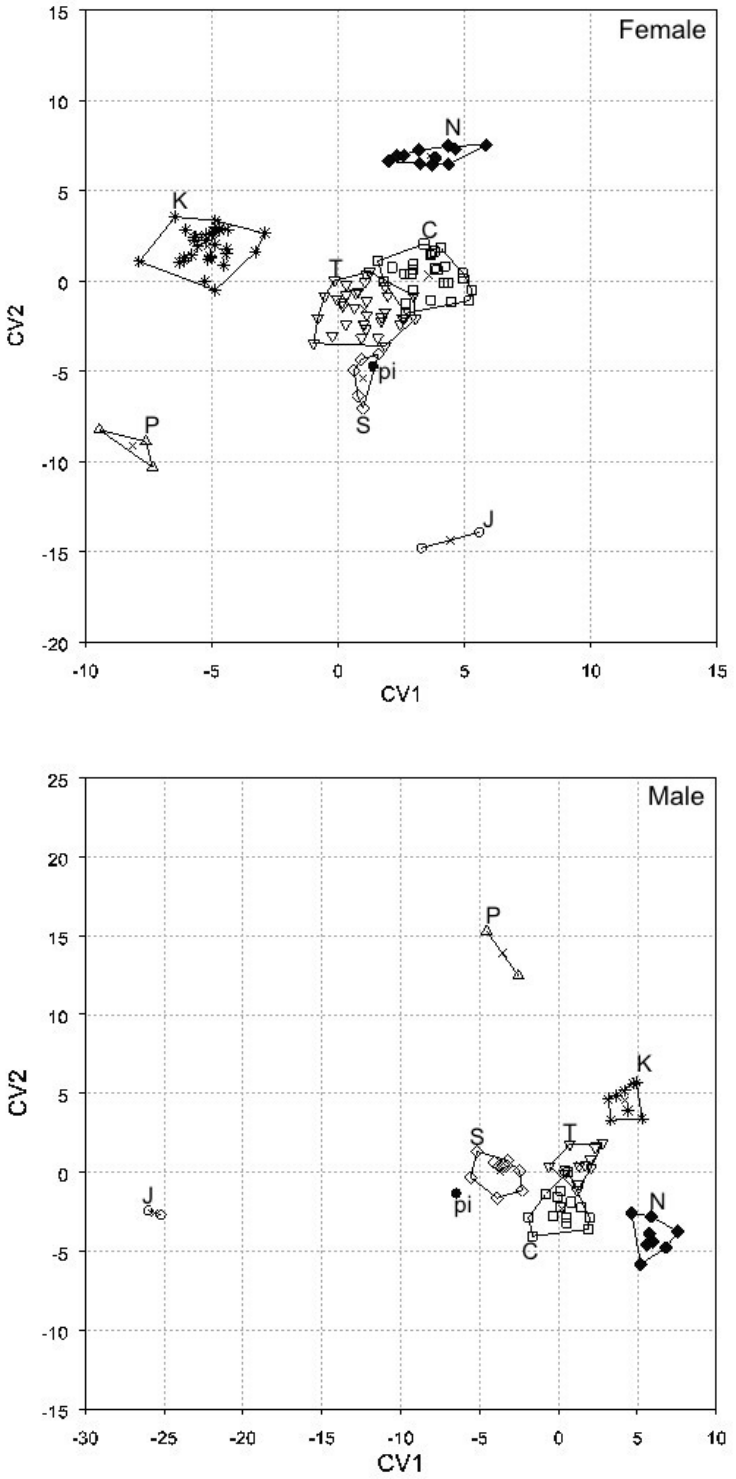

Fig. 3. 7. The visualized results of the canonical variate analysis among Kerivoulinae populations including three populations of *K. hardwickii*. Scattergrams showing the individual scores on the discriminant axes 1 (horizontal) and 2 (vertical). The locality symbols are explained in Table 3. 2. Female) the first function comprises 38.83% of the variance and the second function 38.07%. Male) the first function comprises 56.07% of the variance and the second function 22.24%. Coefficients of the discriminate functions are shown in Table 3.5.

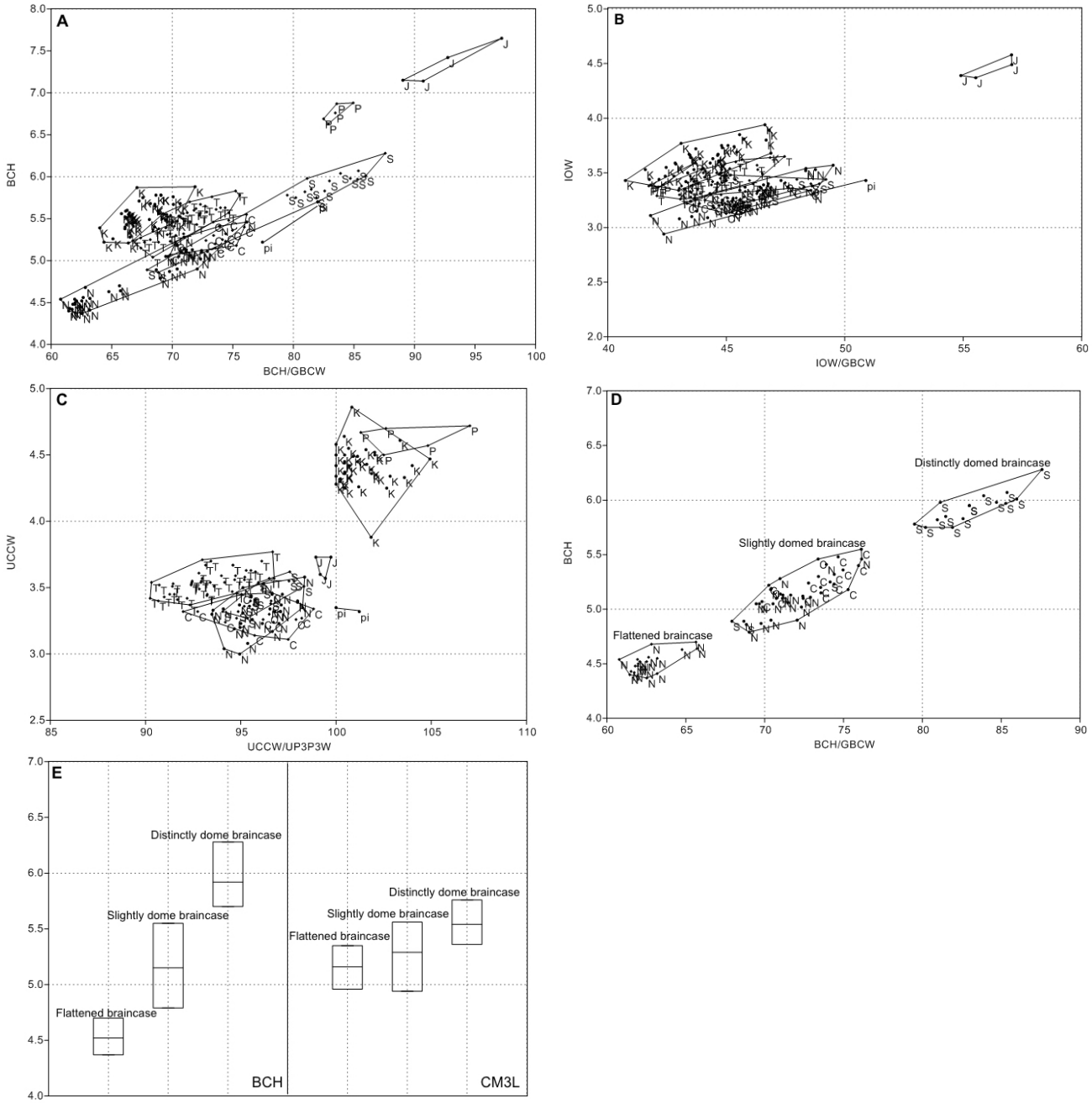

Fig. 3. 8. Scatter plots of Kerivoulinae (A) and *K. hardwickii* populations (D) between braincase height and greatest width of the braincase ratio (x axis: %; y axis: mm), Interorbital width and greatest width of the braincase ratio (B) (x axis: %; y axis: mm), anterior palatal width and posterior palatal width (C) (x axis: %; y axis: mm) of Kerivoulinae populations and the differences measurement of characters BCH and CM3L of *Kerivoula hardwickii* populations (E) (x axis: *K. hardwickii* populations; y axis: mm, range: minimum value to maximum value in boxplots and mean value in horizontal bar). Symbol for each species is the same as Table 3. 2.

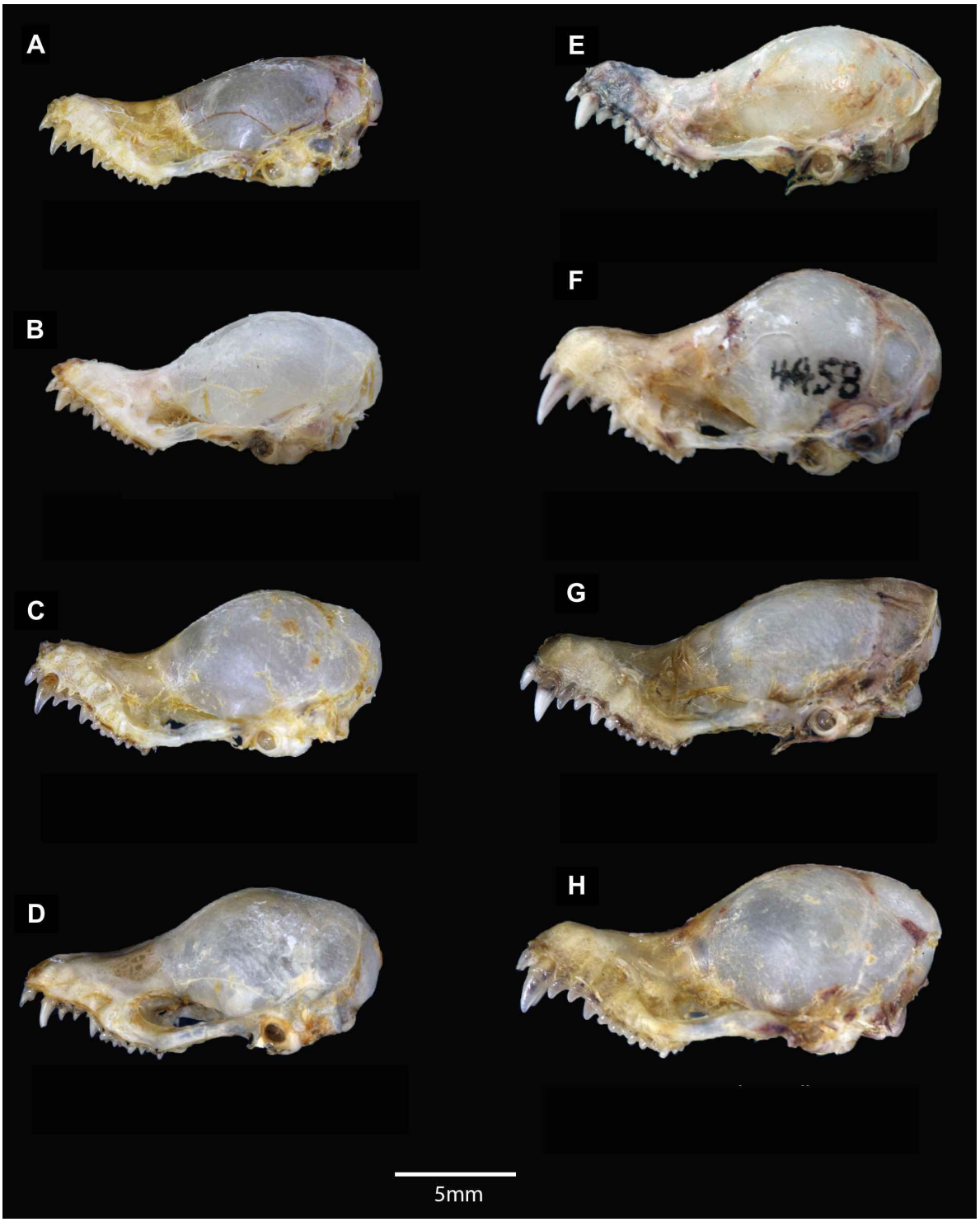

Fig. 3. 9. Skull of six species of Kerivoulinae. A) *K. hardwickii* N population (flattened braincase form): IEBR-M2938 (female); B) *K. hardwickii* C population (slightly domed braincase form): IEBR-M2217 (male); C) *K. hardwickii* S population (distinctly domed braincase form): IEBR-M2907 (female); D) *K. pcita*: IEBR-M12 (female); E) *K. titania*: IEBR-M5359 (male); F) *Phoniscus jagorii*: IEBR-M4458 (male); G) *K. kachinensis*: IEBR-M5626 (female); H) *K. papillosa*: IEBR-M4417 (male).

CHAPTER IV

Morphological biodiversity and taxonomic study of tube-nosed bats of subfamily Murininae in Vietnam

4. 1. Introduction

Throughtout Chapter II and III, I examined a morphological analysis of the skull size and shape of tube-nosed and woolly bats. The results showed that both groups have clearly significant differences in size and shape among the interspecific and intracspecific species. This morphological divergence suggests that each species developed different food habit and facilitated the adaptation in skull morphology through the complex character displacement and food partitions among several sympatric species pairs. The result also suggests that a zoogeographic barrier formerly extended from east to west across Vietnam at ca. 14–17^{0}N and two transition zones for bat species. In this Chapter, based on the largest speices and specimens, I examined the references including reviews of tube-nosed bat of subfamily Murininae in Vietnam.

Species of the subfamily Murininae are small in medium-sized bats of the Family Vespertilionidae. They are distributed throughout Asia from northeastern Pakistan, eastern Siberia, Korea to Japan to northeastern Australia. Diagnostic characters are the combination of: tubular nostrils; thick and woolly fur; furred forearms, hind limbs, proximal parts of wing membranes, and upper surface of interfemoral membrane; and two premolars in both the upper and lower toothrows, where the first premolars are unusually well-developed (Tate, 1941; Corbet and Hill, 1992; Koopman, 1994; Simmons, 2005; Kuo *et al.*, 2006, 2009; Francis and Eger, 2012).

Simmons (2005) listed 17 species of the genus *Murina* Gray, 1842 and subsequent studies have described further 21 species, mostly from southern Asia (Csorba and Bates, 2005; Bumrungsri *et al.*, 2006; Csorba *et al.*, 2007, Kruskop and Eger, 2008; Furey *et al.*, 2009; Kuo *et al.*, 2009; Eger and Lim, 2011; Csorba *et al.*, 2011; Ruedi *et al.*, 2012; Francis and Eger, 2012; Soisook *et al.*, 2013a, b). Inventory studies have been recently conducted in many Southeast Asian countries such as Thailand (10 species; Bumrungsri *et al.*, 2006; Soisook, 2011; Soisook *et al.*, 2013a, b), Laos (8 species; Francis and Eger, 2012), Cambodia (5 species; Csorba and Bates, 2005; Matveev and Csorba, 2007; Csorba *et al.*, 2011; Ith *et al.*, 2011), and Myanmar (4

species; Bates *et al.*, 2000; Matthew *et al*., 2005), indicating that the genus *Murina* includes interesting forest bats with high species diversity in Asia.

The subfamily Murininae also includes two genera, *Harpiocephalus* Gray, 1842 and *Harpiola* Thomas, 1915. The validity of the genus *Harpiocephalus* has been widely accepted, whereas the taxonomic rank of *Harpiola* has been controversial and considered either a separate genus (Tate, 1941; Bhattacharyya, 2002; Kuo *et al.*, 2006) or a subgenus of *Murina* (Ellerman and Morrison-Scott, 1951; Corbet and Hill, 1992; Koopman, 1994; Simmons, 2005). The phylogenetic reconstruction of Francis *et al.* (2010) based on sequences of the cytochrome c oxidase subunit I (COI) demonstrated that, contrary to the morphological distinctiveness, genetic analyses did not separate *Harpiola* and *Harpiocephalus* from the species of *Murina*.

Vietnam possesses the highest known species diversity of the Murininae in the world. Kuznetsov (2006) and Can *et al.* (2008) listed 6 species of Murininae in Vietnam, and Kruskop (2013) recognized twelve *Murina*, one *Harpiola*, and one *Harpiocephalus* species from Vietnam after incorporating information from recent studies (Csorba *et al.*, 2007; Kruskop and Eger, 2008; Furey *et al.*, 2009; Csorba *et al.*, 2011). Son *et al.* (2015b) analysed morphometric variation of the skull of Vietnamese *Murina* and documented considerable interspecific and sexual variations in size and shape of the skull, possibly reflecting food adaptations from interactions of sympatric species. In addition, the existence of sexual dimorphism and the extent of differences among species were documented by Son *et al.* (2015b), indicating that the complicated patterns of sexual differences can be the cause of taxonomic confusion among the species.

In this study, I review the taxonomic status of all Vietnamese species belonging to the subfamily Murininae. The species diversification of the subfamily and distribution patterns of tube-nosed bats within Vietnam are also discussed. Karyotypes also first studies in Murininae.

4. 2. Materials and Methods

Bats were collected through surveys conducted in 43 protected areas of 28 provinces in Vietnam from 2001 to 2014 (Table 4. 1, Fig. 4. 1, and Appendix 4. 4). Three-bank harp traps and mist nets were set at ground level, frequently across trails, streams, and rivers in different habitat types in secondary and primary forests. Mist nets and harp traps were checked every 20 min before dusk from 17:30 until 23:00. Harp traps were left open until around 06:00. Most captured bats were released at the capture site after recording standard measurements. Selected

specimens were prepared as voucher specimens. These were fixed in 95% ethanol, followed by preservation in 70% ethanol for about 12 h; tissue samples (usually liver or muscle) were preserved in 95% ethanol.

A total of 252 specimens were examined in this study (Appendix 4. 4). Voucher specimens were kept in the Institute of Ecology and Biological Resources, Hanoi, Vietnam (IEBR); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Harrison Institution, Sevenoaks, United Kingdom (HZM); Royal Ontario Museum, Toronto, Canada (ROM); Natural History Museum, London, United Kingdom (BMNH); Zoological Museum at Moscow University, Moscow, Russia (ZMMU); and Muséum National d'Histoire Naturelle, Paris, France (MNHN). Chinese specimens deposited in the College of Life Science, Guangzhou University, Guangzhou, China (IBHG) were also investigated.

Morphological examination

Terminology of external, skull, and dental morphology followed Bates and Harrison (1997), Csorba and Bates (2005), Csorba *et al.* (2007), Furey *et al.* (2009) and Csorba *et al.* (2011). Abbreviations used for the dental nomenclature were incisor (I/i_n), canine (C/c), premolar (P/p_n), and molar (M/m_n), with premaxillary and maxillary teeth denoted by uppercase and mandibular teeth by lowercase letters. Only adult specimens were used for statistical analyses. Age was determined following Anthony (1988).

The following external measurements were taken to the nearest 0.1 mm: HB, head and body from the tip of nose to the base fundament; FA, forearm length from the extremity of the elbow to the extremity of the carpus with the wings folded; T, tail length from the tip of tail to its base fundament; HF, hind foot from the tip of the longest digit, excluding claw, to the extremity of the heel, behind the os calcis; TIB, tibia length from the knee joint to ankle; E, ear length from the lower border of external auditory meatus where it joins with the body to the tip of pinna; and weight (in gram).

Craniodental and mandibular measurements were taken to the nearest 0.01mm following Son *et al.* (2015a, b) (Fig. 4. 2): STOTL, total length of skull from the anterior rim of the alveolus of the first upper incisor to the most projecting point of the occipital region; CCL (condyle – canine length), from the exoccipital condyle to the most anterior part of the canine; C1C1W, greatest width across the outer borders of the upper canines; M3M3W, greatest width across the outer crowns of the last upper molars; ZYW (zygomatic width), greatest width of the

skull across the zygomatic arches; MAW (mastoid width), greatest distance across the mastoid region; IOW (interorbital width), least width of the interorbital constriction; BCW (braincase width), greatest width of the braincase; BCH (braincase height), from the basisphenoid at the level of the hamular processes to the highest part of the skull, including the sagittal crest (if present); CM3L (maxillary toothrow length), from the front of upper canine to the back of the crown of the third molar; CP4L (upper canine-premolar length), from the front of the upper canine to the back of the crown of the posterior premolar; ML (mandible length), from the anterior rim of the alveolus of the first lower incisor to the most posterior part of the condyle; cm3L (mandibular toothrow length), from the front of the lower canine to the back of the crown of the third lower molar; cp4L (lower canine-premolar length), from the front of the lower canine to the back of the crown of the posterior premolar; CPH (least height of the coronoid process), from the tip of the coronoid process to the apex of the indentation on the inferior surface of the ramus adjacent to the angular process.

Multivariate analyses

To study individual variation in *M. harrisoni*, I used all 15 craniodental and mandibular measurements to conduct two PCA analyses with the software PAST (Hammer *et al.*, 2001) using (1) raw data to assess size factors using the PC1 score that represents overall size (Barlow *et al.*, 1995; Lindenfors *et al.*, 2007), and (2) standardized data (raw score/geometric mean) to assess the shape factor (Jungers *et al.*, 1995) using each of the PC scores that have eliminated size factors. Both the raw data and standardized data were log-transformed (Blackith and Reyment, 1971; Reyment 1971). The higher factor loadings (positive and negative) of PCA were selected follows Elizabeth (2006) and James (2009).

Karyotype analyses

Chromosomal preparations were made with culture cells of tail bone or ear tissue following the method of Harada and Yosida (1978). The tissue sample was cultured with Eagle's MEM medium supplemented with 12% calf serum, 3% calf serum and a few non-essential amino acids (l-glutamine, l-serine, sodium pyruvate). Diploid chromosome number (2n) and fundamental number (FN, as the total number of autosomal arms) was then calculated.

4. 3. Results of taxonomic accounts

4. 3. 1. Genus *Murina* Gray, 1842

Diagnostic characters

Small to medium-sized bats with tubular nostrils and dense woolly pelage. I2/3 C1/1 P2/2 M3/3=34. Height of upper incisors is distinctly less than that of the corresponding canines. I3 is not contact with C. M3 is developed.

Taxonomic notes

Two morphogroups, namely "*suilla*–group" and "*cyclotis*–group", differing in the relative size and position of the upper incisors, canines, premolars, and ratio of upper canine and second upper premolar have been widely accepted (Corbet and Hill, 1992; Koopman, 1994; Csorba and Bates, 2005; Csorba *et al.*, 2007; Furey *et al.*, 2009; Kuo *et al.*, 2009; Soisook *et al.*, 2013b; Son *et al.*, 2015b). As an important characteristic, crown area of the upper canine is less than that of P4 in the "*suilla*–group", and is equal to or exceeds that of P4 in the "*cyclotis*–group". Although I recognize the usefulness of these characteristics for identification of the species, these morphogroups do not represent the separated phylogenetic lineages. Therefore, morphological characteristics are referred hereafter as "*suilla*–type" dentition and "*cyclotis*–type" dentition without using the term "group".

Murina leucogaster Milne-Edwards, 1872

Murina leucogaster Milne-Edwards, 1872: 252; Type locality: Moupin, Sichuan, China.

Murina leucogaster: Hendrichsen *et al.*, 2001: 102.

Distribution

Northeast India, Nepal, western Thailand, Vietnam, and southern China (Milne-Edwards, 1872; Tate, 1941; Hill, 1964; Corbet and Hill, 1992; Bates and Harrison, 1997; Hendrichsen *et al.*, 2001; Simmons, 2005; Smith and Xie, 2008).

In Vietnam (Fig. 4. 1): Nghe An (Pu Mat NP) [22] (Hendrichsen *et al.*, 2001).

Diagnostic descriptions

Large species with "*suilla*–type" dentition (Table 4. 2, 4. 4). Wing membranes are greyish-brown, the muzzle is dark, and the ears are relatively narrow and short. There is a basal notch in the outer margin of ears. Pelage is thick and woolly, with hairs covering the interfemoral membrane and toes. The dorsum is ferruginous red with dark brown roots; ventrum is pale yellow with dark grey roots on the flanks. Wing is attached at the base of the toe claw and the

tail is hairy.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is domed. Sagittal and lambdoid crests are relatively weak. I2 is partly anterior to I3. C is slightly highter than or subequal to P4. C basal area is smaller than that of P4. P2 is small with a basal area one-third that of P4. M1 and M2 mesostyles are weakly developed. In the mandible, talonids on the lower molars are smaller than the corresponding trigonids.

I measured a female skull (HZM 1.31758) from Vietnam and a male skull (IBHG 10122) from Sichuan Province, China (Table 4. 4).

Taxonomic note

Milne-Edwards (1871) originally described *M. leucogaster* from Moupin, Szechwan, China. In Vietnam, Hendrichsen *et al.* (2001) only recorded one specimen from Pu Mat National Park, Nghe An Province and no further specimens were found.

Murina harrisoni Csorba and Bates, 2005

Murina huttoni: Hendrichsen *et al.*, 2001: 103 (part).

Murina harrisoni Csorba and Bates, 2005: 2; Type locality: O Tuk Chehn, Kirirom National Park, Kompong Speu Province, Cambodia; Wu *et al.*, 2010: 277; Francis and Eger, 2012: 29; Thomas *et al.*, 2013: 231.

Murina tiensa Csorba, Thong, Bates and Furey, 2007: 3; Type locality: An Tinh commune, Na Ri district of Kim Hy Nature Reserve, Bac Kan Province, Vietnam, about 750 m above sea level.

Distribution

Vietnam, Laos, Cambodia, Myanmar, Thailand, southern China including Hainan Island (Csorba and Bates, 2005; Csorba *et al.*, 2007; Wu *et al.*, 2010; Francis and Eger, 2012).

In Vietnam (Fig. 4. 1): Son La (Co Ma and Thuan Chau district) [13], Phu Tho (Xuan Son NP) [12], Bac Kan (Kim Hy NR) [6], Hai Phong (Cat Ba NP) [10], Vinh Phuc (Tam Dao NP) [11], Thanh Hoa (Xuan Lien) [19], Nghe An (Pu Mat NP) [22], Dak Lak (Yok Don NP) [34] (Csorba *et al.*, 2007; Thong *et al.*, 2011; Francis and Eger, 2012, This study).

Description

Large species with "*cyclotis*–type" dentition (Tables 4. 2, 4. 3, 4. 4; Fig. 4. 3). The ear is round and large. The hairs of the dorsal fur are pale-based, light, yellowish-red, gradually darkening towards the tip. The ventral pelage is uncoloured whitish or light grey. Plagiopatagium attached to the base of the toe claw.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum not inflated and the braincase is flat. Sagittal and lambdoid crests are well developed. I2 is lateral to I3. C is much higher than P4. C basal area equals or slightly larger than that of P4. P2 height is subequal to P4; its basal area is two-third or almost equals that of P4. M1 and M2 mesostyles are weakly developed. Lower canines are well developed. The height of p2 is about equal to that of the p4; m1 and m2 have well-developed talonids, and have a well-defined hypoconids and entoconids.

Taxonomic note

Csorba and Bates (2005) described *M. harrisoni* as a new species from Cambodia. Subsequently, Csorba *et al.* (2007) described another species, *M. tiensa* from Vietnam, and mentioned that *M. tiensa* differs from *M. harrisoni* by the insertion point of the wing membrane, and rostral characteristics where the anterior part of the rostrum is almost straight in *M. tiensa*, and more bulbous in *M. harrisoni*. Francis and Eger (2012) regarded *M. tiensa* as a junior synonym of *M. harrisoni* in examining specimens from Laos, Thailand, China and Vietnam, and concluded that the morphological characteristics separating the two species were actually intraspecies variation. DNA sequence variation among these specimens indicated two distinct clades, but the divergence of all specimens was less than 5–6%. Thereafter, Wu *et al.* (2010) reported the species as *M. harrisoni* from Hainan Island, China, and Son *et al.* (2015b) recognized *M. tiensa* instead of *M. harrisoni* for specimens from Vietnam.

To clarify the relationship between *M. harrisoni* and *M. tiensa*, I examined specimens from the collections of HZM, HNHM, IEBR, ROM, and IBHG. Plots between size PC1 (PCA of log-transformed raw data) and shape PC1 (PCA of log-transformed standardized data) are given in Fig. 4. 7. In size PC1, females were larger than males with little overlap. Size PC1 and shape PC1 (based on log-transformed standardized data) had a negative correlation. Size PC1 explained 76.2% of the variance, and all characters had positive loading factors between 0.090~0.459. The shape PC1 explained 33.6% of the variance, and CPH (–0.586, negative), BCW (0.472, positive), and IOW (0.442, positive) showed high factor loadings. Holotypes of *M. harrisoni* and *M. tiensa* (both females) plotted closely. This result does not support the existence

of two distinct species. I, therefore, suggest that the observed morphological variation is intraspecific variation found in *M. harrisoni* and involves strong sexual dimorphism; consequently, I regarded *M. tiensa* as a junior synonym of *M. harrisoni*. Because the number of specimens was not sufficient at each locality, I cannot surely indicate about the geographic variation and the possible intraspecific divergence within *M. harrisoni*.

Representative skulls of males and females are presented in Fig. 4. 8. Difference in the braincase region between males and females was relatively small, as shown in the area connecting the posterior end of the interorbital region, outer margin of the braincase and the posterior end of the skull in dorsal view (Fig. 4. 8). On the other hand, the area of the nasal capsule was expanded laterally and anteriorly in females than males, as shown in Fig. 4. 8 with line connecting the anterior end of the interorbital region, the anterior of the zygomata, the posterior margin of the canines, and the anterior tip of the skull. In addition, females have well-developed canines (C) and a robust rostrum as compared to males (Fig. 4. 8).

Size and shape of the braincase and nasal capsule may be related to functional limitation for size and shape change throughout various regions. Therefore, sexual dimorphism may be morphologically established under these functional limitations different among skull regions such as braincase and nasal capsule, and not related with overall size and shape changes. As a result, sexual dimorphoism shows complicated pattern. Previously observed profile variation in *M. harrisoni* and *M. tiensa* should be re-evaluated with consideration of these complicated morphological variations among the sexes (Fig. 4. 8). In addition, the difference in length of the interorbital region (elongated in females) likely results in a difference in bite force between sexes. To understand the sexual dimorphism, three-dimensional geometric morphometric or CT scanning reconstruction methods are needed.

Francis and Eger (2012, Fig. 9) provided photos of five individuals of *M. harrisoni* and *M. tiensa*. The smallest depicted female specimen (HZM 1.31525) has caused confusion, suggesting that females and males widely overlap in overall size. My present STOTL measurement of the same specimen (19.33 mm), however, is actually closer to the two larger female specimens, EGD 24974 (19.87 mm) and HZM 1.36316 (18.39 mm; erroneously labelled as “1.36136” in the caption). I assume that scaling or size adjustment error might occurred during the preparation of the figure in Francis and Eger (2012).

Murina fionae Francis and Eger, 2012

Murina CMF sp. B: Francis *et al.*, 2010: 6.

Murina peninsularis: Matveev and Csorba, 2007: 100.

Murina fionae Francis and Eger, 2012: 32; Type locality: Pha Deng, 8 km E of Ban Navang, Khammouan Province, Laos, 1,140 m above sea level; Thomas *et al.*, 2013: 231.

Distribution

Vietnam, Laos, and Cambodia (Francis and Eger, 2012; Soisook *et al.*, 2013b).

In Vietnam (Fig. 4. 1): Quang Binh (Phong Nha-Ke Bang NP) [24], Quang Tri (Bac Huong Hoa NR) [25], Quang Nam (Ngoc Linh NR, Song Thanh NR) [27, 28], Quang Ngai (Ba To area) [30], Kon Tum (Chu Mom Ray NP) [31], Gia Lai (Kon Cha Rang NR, Kon Ka Kinh NP) [32], Dong Nai (Cat Tien NP) [39] (Francis and Eger, 2012; Soisook *et al.*, 2013b; This study).

Description

Large species with "*cyclotis*–type" dentition (Table 4. 2, 4. 4; Fig. 4. 3). Ears are moderately large and rounded. The fur of the dorsum is long with pale buff bases and orange-brown tips. Scattered longer guard hairs are pale to the tip, creating a frosted appearance. The hairs of the ventrum are unicoloured, pale buff orange over most of the venter, but more whitish near the chin. The interfemoral membrane, legs, feet and tail are covered with long orange-brown hairs, which are relatively dense on the legs and feet. Plagiopatagium is attached to the base of the toe claw.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is well domed. Sagittal crest is strong and the lambdoid crest is weakly developed. I2 is lateral to I3, C is much higher than P4. C basal area is slightly larger or equal to P4. P2 height is subequal to P4, its basal area is two-thirds to nearly equal to P4. No mesostyles are on M1 and M2. In the mandible, talonids of m1 and m2 are reduced relative to trigonid. In the lateral view, posterior cusps are slightly more than half the height of the anterior cusps. When viewing from above, the length of the talonid is less than half the length of trigonid.

Taxonomic note

Francis and Eger (2012) described this species based on specimens from Laos and

Vietnam.

Murina huttoni (Peters, 1872)

Harpiocephalus huttoni Peters, 1872: 257; Type locality: Dehra Dun, Kumaon, northwestern India.

Murina huttoni: Hendrichsen *et al.*, 2001: 103; Francis and Eger, 2012: 20; Thomas *et al.*, 2013: 231.

Distribution

Northwest India, Tibet to Thailand, Vietnam, northeastern and southern China, and west Malaysia (Tate, 1941; Hill, 1964; Corbet and Hill, 1992; Bates and Harrison, 1997; Simmons, 2005; Smith and Xie, 2008; Zhou *et al.*, 2011).

In Vietnam (Fig. 4. 1): Lao Cai (Hoang Lien NP) [1], Cao Bang (Phia Oac-Phia Den NR) [5], Nghe An (Pu Mat NP) [22], Quang Tri (Bac Huong Hoa NR) [25], Quang Nam (Ngoc Linh NR) [28], Kon Tum (Ngoc Linh NR) [29], Dak Lak (Chu Yang Sin NP) [35], Lam Dong (Bi Dup-Nui Ba NP) [36], Khanh Hoa (Hon Ba NR) [37] (Can *et al.*, 2008; Kruskop, 2013; This study).

Description

Medium-sized species with "*cyclotis*–type" dentition (Table 4. 2, 4. 4; Fig. 4. 3). Both dorsum and ventral fur are dark. The fur of the dorsum is long and fluffy, and is slate grey with a pale buffy band which darkens gradually into a darker orange-brown band. The ventral fur is similar but somewhat paler. The interfemoral membrane is extensively covered with reddish-brown hairs, which are longer near the body and shorter near the edge. Plagiopatagium is attached to base of the toe claw.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is flat. Sagittal and lambdoid crests are weakly developed. I2 is lateral or partly anterior to I3. C is much higher than P4. C basal area equals that of P4. P2 height is subequal to P4, and its basal area is two-thirds that of P4. M1 and M2 mesostyles are well developed. In the mandible, talonids of m1 and m2 are well developed; viewed from above, the length of talonids on the lingual side is only slightly less than that of trigonid; in lateral view, the posterior cusps are about two-thirds the height of the anterior cusps.

Karyotype

Karyotype (Fig. 4. 6A, Table 4. 5, Appendix 4. 4) (IEBR-M5407) is 2n=44, FN=50. Autosomes consist of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome pair can be identified as a medium-sized metacentric element.

Taxonomic note

Hill (1964) and Corbet and Hill (1992) recognised two subspecies: *M. huttoni rubella* (Thomas, 1914) (from southeast China and probably in north Thailand) and *M. h. huttoni* (Peters, 1872) (from the rest of the area) in having different colour patterns. In Vietnam, I found variations in colour among two specimens from Hoang Lien National Park (Lao Cai province): a more reddish orange specimen that is most similar to *M. huttoni rubella* (Hill, 1964; Hendrichsen *et al.*, 2001; Francis and Eger, 2012), and a more greyish brown individual in concordance with the description of *M. h. huttoni*. Additional studies covering the whole distribution range are needed to understand the possible cryptic diversity.

Murina cyclotis Dobson, 1872

Murina cyclotis Dobson, 1872: 210; Type locality: Darjeeling, NE India; Hendrichsen *et al.*, 2001: 104; Ith *et al.*, 2011: 97; Francis and Eger, 2012: 17; Thomas *et al.*, 2013: 230; Soisook *et al.*, 2013b: 274.

Distribution

Sri Lanka, India, Myanmar, Laos, Vietnam, the southern China in Guangdong Province and Hainan Island, south to West Malaysia, Borneo, Sumatra, Philippines, and Lesser Sunda (Tate, 1941; Ellerman and Morrison-Scott, 1951; Hill, 1964; Corbet and Hill, 1992; Bates and Harrison, 1997; Francis *et al.*, 1999; Simmons, 2005; Francis, 2008; Smith and Xie, 2008, Ith *et al.*, 2011; Francis and Eger, 2012; Thomas *et al.*, 2013; Soisook *et al.*, 2013b).

In Vietnam (Fig. 4. 1): Son La (Xuan Nha NR) [15], Phu Tho (Xuan Son NP) [12], Cao Bang (Phia Oac-Phia Den NR) [5], Vinh Phuc (Tam Dao NP) [11], Quang Ninh (Bai Tu Long NP) [9], Hai Phong (Cat Ba NP) [10], Ninh Binh (Cuc Phuong NP) [18], Thanh Hoa (Pu Hu NR, Pu Luong NR, and Xuan Lien NR) [16, 17, 19], Nghe An (Pu Huong NR, Pu Mat NP) [21, 22], Quang Binh (Phong Nha-Ke Bang NP) [24], Quang Tri (Dakrong NR) [25], Thua Thien-

Hue (Bach Ma NP) [26], Kon Tum (Ngoc Linh NR) [29], Quang Ngai (Ba To area) [30], Gia Lai (Kon Ka Kinh NP) [32], Binh Dinh (Phu Yen district) [33], Lam Dong [36], Binh Phuoc [41], Ba Ria-Vung Tau [42] (Can *et al.*, 2008; Kruskop, 2013; This study).

Description

Medium-sized species with "*cyclotis*–type" dentition (Tables 4. 2, 4. 4; Fig. 4. 3). The ears are relatively long. The hairs of the dorsum have grey to dark grey bases, and a buffy area that gradually darkens to orange near the tips, but does not create strongly contrasting bands of colour. The hairs on the ventral surface show dark grey bases with buffy white tips, which may have a slight orange colouration. However, orange covers most of the venter, and is more whitish near the tips for specimens in the south. Plagiopatagium is attached to the base of the toe claw.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum not inflated and the braincase is slightly domed in females, and more domed in males. Sagittal and lambdoid crests are weak. I2 is lateral to I3, but I3 partly anterior to I2. C is much higher than P4. The C basal area is equal or is slightly larger than P4. P2 height is subequal to or slightly shorter than P4, and its basal area is two-third that of P4. No mesostyle is found on M1 and M2. In the mandible, the talonid of m1 and m2 is greatly reduced relative to the trigonid. Viewed from above, the length of the talonid is less than half the length of the trigonid. In the lateral view, the posterior cusps are no more than half the height of the anterior cusps. In the mandible, both premolars are similar in height.

Karyotype

Karyotype (Fig. 4. 6B, Table 4. 5, Appendix 4. 4) (IEBR-M4071) is 2n=44, FN=50. Autosomes consist of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome is a medium-sized metacentric element, and the Y chromosome is a small acrocentric element.

Taxonomic note

Ellerman and Morrison-Scott (1951), Hill (1964), Eisenberg and McKay (1970), Corbet and Hill (1992), Koopman (1994), Simmons (2005) recognized three subspecies: *M. cyclotis eileenae* (Ceylon), *M. cyclotis cyclotis* (Northeastern India to Hainan and Vietnam), and *M. cyclotis peninsularis* (Malaysia). Francis and Eger (2012) elevated *M. peninsularis* to full species, and suggested that *M. cyclotis sensu stricto* is a complex of cryptic taxa; therefore,

future taxonomic studies covering its wide distribution are desired. Soisook *et al.* (2013b) studied this species' complex and considered *eileenae* to be a synonym of *M. cyclotis*, and *M. peninsularis* to be a valid species. In addition, Soisook *et al.* (2013b) described a new species, *M. guilleni,* from Thailand and further discussed the taxonomic problems in *M. cyclotis* that should be addressed in future studies.

Murina lorelieae Eger and Lim, 2011

Murina lorelieae Eger and Lim, 2011: 234; Type locality: Diding Headwater Forest Nature Reserve, Jing Xi County, Guangxi Zhuang Autonomous Region, China.

Murina lorelieae ngoclinhensis Tu, Cornette, Utge and Hassanin, 2015: 209; Type locality: Ngoc Linh Nature Reserve, Vietnam.

Distribution

Southern China, Vietnam (Tu *et al.*, 2015).

In Vietnam (Fig. 4. 1): Kon Tum (Ngoc Linh NR) [29] (Tu *et al.*, 2015; This study).

Description

Medium-sized species with "*suilla*–type" dentition (Tables 4. 2, 4. 3, 4. 4; Fig. 4. 3). The ear is round and both sides of the muzzle are dark brown. The pelage is characterized by long shiny hairs (8 mm ventrally and 13–15 mm dorsally), with distinct copper reddish-brown and dirty white colourations on dorsal and ventral surfaces. Dorsal hairs are dark grey basally, pale in the middle and reddish brown at the tip. Ventral hairs are dark grey to about two-thirds of the length and whitish at the tip.

Skull and dentition (Figs. 4. 4, 4. 5). The skull is domed. The lateral profile of the anterior part of the skull gradually rises from the rostrum to the forehead. The sagittal crest is lacking; lambdoid crest is visible but weak. Maxillary toothrows are convergent anteriorly. The dentition is quite robust. I2 is anterior to I3, and I2 is visible laterally. I2 and I3 are subequal in height and are much less than half the height of upper C. Upper C slightly but clearly exceeds the height of P4, the basal area of C is less than that of P4. The crown area of P2 is slightly more than half that of P4. M1 and M2 have well developed mesostyles and curved labial faces. Paracone, metacone, and protocone of M1 and M2 are distinctly defined.

Karyotype

Karyotype (Fig. 4. 6C, Table 4. 5, Appendix 4. 4) based on a specimen from Kon Tum province (Ngoc Linh Nature Reserve) (HNHM B20140915.7) is 2n = 44, FN = 50. Autosomes consist of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome is a medium-sized submetacentric, and the Y chromosome is a small acrocentric element.

Taxonomic note

Eger and Lim (2011) described *M. lorelieae* based on a single specimen from Diding Headwater Forest Nature Reserve, Jing Xi County, Guangxi Zhuang Autonomous Region, China; close to the border with northeast Vietnam. Tu *et al.* (2015) recorded this species from Ngoc Linh Mountain in the Central Highlands of Vietnam at over 1,600 m elevation (Tu *et al.*, 2015). Based on DNA barcoding and morphological data, Tu *et al.* (2015) described a new subspecies *M. lorelieae ngoclinhensis*. This species has been recorded only from two localities at high elevations in southern China and Vietnam, but additional surveys are expected to find new localities and to further describe the geographic boundary of the two subspecies.

Although Tu *et al.* (2015) regarded *M. lorelieae* as a member of the *M. cyclotis*–group (on the basis of three specimens from Vietnam), a closer examination of additional specimens proved that *M. lorelieae* shows "*suilla*–type" dentition.

Murina annamitica Francis and Eger, 2012

Murina CMF sp. D: Francis *et al.*, 2010: 6.

Murina annamitica Francis and Eger, 2012: Type locality: near Nam Pan in the Annamite Mountains, Bolikhamxai Province, Laos, about 1,300 m above sea level; Thomas *et al.*, 2013: 231.

Distribution

Vietnam and Laos (Francis and Eger, 2012).

In Vietnam (Fig. 4. 1): Son La (Xuan Nha NR) [15], Lao Cai (Hoang Lien NP) [1], Tuyen Quang (Na Hang NR) [3], Thanh Hoa (Pu Luong NR) [17], Nghe An (Pu Huong NR and Pu Mat NP) [22], Quang Tri (Bac Huong Hoa NR) [25], Quang Nam (Ngoc Linh) [28], Kon Tum (Ngoc Linh) [29], Quang Ngai (Ba To area) [30], Binh Phuoc (Bu Gia Map NR) [41] (Francis and Eger, 2012; Kruskop, 2013; This study).

Description

Medium-sized species with "*cyclotis*–type" dentition (Tables 4. 2, 4. 4; Fig. 4. 3). The interfemoral membrane is extensively covered with hairs. There are short hairs on the forearm and leading edge of the wing. Plagiopatagium is attached to the base of the toe claw. The ear is round without a notch on its posterior border. Dark bases extend to the fur of the dorsum. The fur of the dorsum is long and fluffy. The hairs have slate grey bases followed by a buffy band, then darker brown to orange-brown tips. The overall appearance is orange-brown to brown. The fur of the underside has slate grey bases followed by buffy tips, giving an overall greyish buff appearance.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum not inflated and the braincase is domed. Sagittal and lambdoid crests are weak. I2 is lateral to I3. C basal area equals that of P4. P2 is less in height than P4 and its basal area is two-thirds that of P4. M1 and M2 mesostyles are well developed, comparable in height to the metastyle and parastyle, giving a distinct W-shape to the surface. In the mandible, both premolars are similar in height, and lower molars have well-developed talonids.

Taxonomic note

Francis and Eger (2012) described *M. annamitica* as a new species from Laos; and also referred material from the centre of Vietnam.

Murina beelzebub Son, Furey and Csorba 2011

Murina tubinaris: Hendrichsen *et al.* 2001: 103 (part)

Murina beelzebub Son, Furey and Csorba, 2011 in Csorba *et al.*, 2011: 899; Type locality: Bac Huong Hoa Nature Reserve, Huong Hoa District, Quang Tri Province, Vietnam, 400 m above sea level.

Distribution

Recorded only from Vietnam.

In Vietnam (Fig. 4. 1): Quang Tri (Bac Huong Hoa NR) [25], Kon Tum (Ngoc Linh NR) [29], Quang Ngai (Ba To area) [30], Gia Lai (Kon Ka Kinh NP) [32] (Csorba *et al.*, 2011; This study).

Description

Medium-sized species with "*suilla*–type" dentition (Tables 4. 2, 4. 4; Fig. 4. 3). On the dorsal surface, the proximal sixth of individual hairs is dark brown, whereas the remaining distal portion is initially light grey and terminates in a distinctly darker tip. Longer silver guard hairs are scattered over all of the dorsum. The upper surface of the hind limbs, feet, and uropatagium are densely covered in long, uniformly dark brown hairs. Ventrally, hairs are dark brown for the proximal two-thirds, whereas the remaining upper portion is white. Ventral surface of the uropatagium is covered in uniformly white hairs, some of which are also present on the plagiopatagium adjacent to the body. The ear has a slight emargination along its posterior border, and the plagiopatagium is attached to the base of the claw on the outer toe.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is domed. No sagittal crest, and the lambdoid crest is weak. Rostrum is slightly elongated but is not inflated. The depth of the narial emargination exceeds its width. The zygoma is strong and possesses a slight dorsal process. A medial process is present in the posterior palatal region. The medial ridge separating the basioccipital pits is relatively narrow, and the anterior borders of the pits are weakly defined. I2 is partly anterior to I3. C is slightly higher than P4. C has a basal area smaller than that of P4. P2 is much shorter than P4; its basal area is half that of P4. M1 and M2 mesostyles are weakly developed. In the mandible, p2 has less than one-half the basal area of p4 and attains more than two-thirds its height. Talonids of m1 and m2 equal their trigonids in the crown area and entoconids of the teeth distinctly exceed their hypoconids in height.

Karyotype

Karyotype (Fig. 4. 6D, Table 4. 5, Appendix 4. 4) based on a female specimen from Quang Tri province (Bac Huong Hoa Nature Reserve) (IEBR-M4842) is 2n = 44, FN = 50. Autosomes consist of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome pair can be identified as a medium-sized submetacentric element.

Taxonomic note

The first specimen (HZM) was collected around Kon Cha Rang and Kon Ka Kinh Nature Reserve (Gia Lai province) (1,600 m above sea level) by Benjamin Hayes (Trai *et al.*, 2000), which Hendrichsen *et al.* (2001) identified as *M. tubinaris*. Thereafter, Csorba *et al.* (2011) described *M. beelzebub* based on specimens from central Vietnam (Quang Tri province) and the HZM specimen from Kon Ka Kinh Nature Reserve.

Murina walstoni Furey, Csorba and Son, 2011

Murina walstoni Furey, Csorba and Son, 2011 in Csorba *et al.*, 2011: 900; Type locality: Veun Sai Protected Forest, Veun Sai District, Cambodia, 110 m above sea level; Francis and Eger, 2012: 29; Thomas *et al.*, 2013: 232.

Distribution

Vietnam, Laos, and Cambodia (Csorba *et al.*, 2011; Francis and Eger, 2012; Kruskop, 2013; Thomas *et al.*, 2013).

In Vietnam (Fig. 4. 1): Dak Lak (Yok Don NP) [34], Ninh Thuan (Nui Chua NP) [38], Dong Nai (Vinh Cuu NR) [39], Kien Giang (Phu Quoc NP) [43] (Csorba *et al.*, 2011; Kruskop, 2013; This study).

Description

Medium-sized species with "*suilla*–type" dentition (Tables 4. 2, 4. 4; Fig. 4. 3). On the dorsal surface, the fur is warm brown. Ventrally, basal two-thirds of the hairs are uniformly white, the tips are brown or orange-brown, and the ventral surface is pure white. The plagiopatagium is attached to the base of the first toe claw.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is domed. Sagittal and lambdoid crests are well developed. I2 is partly anterior to I3. Upper C is higher than P4. C basal area is smaller than that of P4. P2 is much less in height than P4, and its basal area is half that of P4. M1 and M2 mesostyles are moderaterly developed. In the mandible, c exceeds p4 in height and basal area. The basal area of p2 varies from one-half to less than that of p4 and attains more than two-thirds its height. The talonids of m1 and m2 exceed their trigonids in crown area, and their entoconids are equal to or slightly higher than their respective hypoconids.

Taxonomic note

Csorba *et al*. (2011) described *M. walstoni* as a new species from Cambodia; and also referred material from the Central Highlands of Vietnam, but these specimens collected in low elevation at 360 m of above sea level, near the border of Vietnam and Cambodia.

Murina feae (Thomas, 1891)

Harpiocephalus feae Thomas, 1891: 884; Type locality: Biapo, Karin Hills, Burma.

Murina tubinaris: Corbet and Hill, 1992: 151 (part); Koopman, 1994: 132 (part); Simmons, 2005 (part); Francis *et al.*, 1999: 233 (part); Francis, 2008: 253 (part).

Murina cineracea Csorba and Furey, 2011:896; Type locality: Cambodia, Mondulkiri Province, Seima Biodiversity Conservation Area.

Distribution

Myanmar, Thailand, Vietnam, Laos, and Cambodia (Thomas, 1891; Osgood, 1932; Francis *et al.*, 1999, Can *et al.*, 2008; Csorba *et al.*, 2011, Francis and Eger, 2012; Kruskop, 2013).

In Vietnam (Fig. 4. 1): Lai Chau (Co Ma) [13], Son La (Phu Yen) [13], Phu Tho (Xuan Son NR) [12], Ha Giang (Duc Xuan area) [2], Tuyen Quang (Na Hang NR) [3], Bac Kan (Ba Be NP, Kim Hy NR) [4, 6], Thai Nguyen (Than Sa NR) [7], Vinh Phuc (Tam Dao NP) [1], Thanh Hoa (Pu Luong NR, Pu Hu NR, Xuan Lien NR) [16, 17, 19], Ninh Binh (Cuc Phuong NP) [18], Nghe An (Pu Hoat NR, Pu Mat NP, Pu Huong NR) [19, 21, 22], Ha Tinh (Vu Quang NP) [23], Quang Binh (Phong Nha-Ke Bang NP) [24], Quang Tri (Bac Huong Hoa NR, Dakrong NR) [25], Thua Thien-Hue (Bach Ma NP) [26], Quang Nam (Ngoc Linh NR) [28], Kon Tum (Ngoc Linh NR) [29], Gia Lai (Kon Ka Kinh NP) [32], and Dong Nai (Cat Tien NP) [40] (Can *et al.*, 2008; Csorba *et al.*, 2011; Kruskop, 2013; This study).

Description

Small to medium-sized species with "*suilla*–type" dentition (Tables 4. 2, 4. 4; Fig. 4. 3). The ear is evenly rounded and without an emargination. On the dorsal surface, the lower portion of individual hairs is dark brown, whereas the upper portion is light grey and terminates in a distinctly darker tip. Darkening of hair tips is more evident on the nape and the head, with an overall impression of dark greyish-brown and darker brown toward the head. The upper surface of the hind limbs, feet, and uropatagium are sparsely covered in short, uniformly dark brown hairs. On the ventral surface of the body, hairs are dark brown basally, whereas the upper portion is white. The ventral surface of the uropatagium is covered in relatively short uniformly white hairs, which are also present on the plagiopatagium adjacent to the body. The plagiopatagium is attached to the base of the toe claw.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is domed. There is no sagittal crest and the lambdoid crest is weak. I2 is partly anterior to I3. C is slightly

but evidently higher than P4. P2 is much less in height than P4. C basal area is smaller that of P4. M1 and M2 mesostyles are weak. In the mandible, c slightly exceeds p4 in height and is equal or greater in basal area; p2 has less than one-half the basal area of p4 and attains more than two-thirds its height. The talonids of m1 and m2 equal their respective trigonids in crown area, and the entoconids of these teeth exceed their hypoconids in height. The postristid connects the hypoconid with the tip of the entoconid.

Karyotype

Karyotype (Fig. 4. 6E, Table 4. 5, Appendix 4. 4) based on a specimen from Thanh Hoa Province (Xuan Lien Nature Reserve) (IEBR-M4214) is 2n = 44, FN = 50. Autosomes consist of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome is identified as a medium-sized metacentric element.

Taxonomic note

Thomas (1891) described *Harpiocephalus feae* from Burma (Myanmar), but the species was considered a synonym of *M. aurata* since then (Tate 1941, Maeda, 1980; Corbet and Hill, 1992). Recently, Csorba *et al.* (2011) split *M. tubinaris* (Scully, 1881) into two species and restricted the distribution of *M. tubinaris* sensu stricto to Pakistan and northwest India. They described a new species, *M. cineracea,* that occurred from West Bengal and Arunachal Pradesh in India through Myanmar, Thailand, Laos to Vietnam. Francis and Eger (2012), however, based on the morphological study of the holotype, concluded that *M. feae* is actually a conspecific with *M. cineracea,* and therefore the name *M. feae* has priority over *M. cineracea*.

Murina eleryi Furey, Thong, Bates and Csorba, 2009

Murina aurata: Francis *et al.*, 1999: 233 (part); Francis, 2008: 253 (part); Francis *et al.*, 2010: 6 (part).

Murina eleryi Furey, Thong, Bates and Csorba, 2009: 226; Type locality: Kim Hy Commune, Na Ri district of Kim Hy Nature Reserve, Bac Kan province, Vietnam, 525 m above sea level; Francis and Eger, 2012: 28; Thomas *et al.*, 2013: 231.

Distribution

Vietnam, Laos, and southern China in the provinces of Guizhou, Hunan, Guangdong,

Guangxi (Furey *et al.*, 2009; Francis and Eger, 2012; Liu *et al.*, 2014; Xu *et al.*, 2014).

In Vietnam (Fig. 4. 1): Ha Giang [2], Cao Bang (Phia Oac-Phia Den NR) [5], Bac Kan (Kim Hy NR) [6], Phu Tho (Xuan Son NP) [12], Son La (Muong Do area) [13], Thanh Hoa (Xuan Lien NR) [19], Quang Binh (Phong Nha-Ke Bang NP) [24]; Quang Nam (Ngoc Linh NR) [28]; Kon Tum (Ngoc Linh NR) [29], Quang Ngai (Ba To area) [30] (Furey *et al.*, 2009; Francis and Eger, 2012; Kruskop, 2013; This study).

Description

Small species with "*suilla*–type" dentition (Tables 4. 2, 4. 4; Fig. 4. 3). Longer, shiny golden hairs with darker bases are scattered over the back, nape and head. On the dorsal surface, the lower portion of under hairs are dark brown and are followed by a pale grey-yellow mid-section which progressively darkens to copper-reddish before terminating in a distinctly darker tip. The superficial impression is copper-reddish mottled with underlying dark brown and overlain by individual shiny gold hairs. Ventrally, the fur is black on the basal half and creamy white on the remainder, except the sides of the ventrum and upper chest, where hair tips graduate toward light brown. The plagiopatagium is attached to the base of the first claw.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is moderately domed. No sagittal crest and the lambdoid crest is weak, but present. I2 is anterior to I3. C is higher than P4. C basal area is much smaller than that of P4. P2 basal area is less than half that of P4. M1 and M2 mesostyles are well developed. In the mandible, c distinctly exceeds p4 in height and is equal or slightly greater in basal area. The talonids of m1 and m2 are clearly separated from their trigonids and exceed these in crown area, and the entoconid clearly exceeds the hypoconid in height.

Taxonomic note

Francis *et al.* (1999), Furey and Tu (2006) and Francis (2008) reported specimens of *M. aurata* Milne-Edwards, 1872 from and around Vietnam. Furey *et al.* (2009), based on many specimens from northern Vietnam, described a new species, *M. eleryi*, and provided diagnostic characters to separate it from *M. aurata*. Thereafter, Francis and Eger (2012) suggested that all specimens from Laos and Vietnam formerly identified as *M. aurata*, to be referred to as *M. eleryi* or *M. harpioloides*. Therefore, I conclude that *M. aurata* does not occur in Vietnam and Laos. Xu *et al.* (2014) studied the genetic structure among specimens from southern China,

Vietnam, and Laos, and suggested that a complicated phylogeographic pattern may exist.

Murina harpioloides Kruskop and Eger, 2008

Murina harpioloides Kruskop and Eger, 2008: 215; Type locality: Da Lat plateau, 30 km north-east from Da Lat, Lam Dong Province, Vietnam, about 1800 m above sea level.

Distribution

Known only from Vietnam (Kruskop and Eger, 2008).

In Vietnam (Fig. 4. 1): Lam Dong (Bi Dup-Nui Ba NP and Da Lat plateau) [36] (Kruskop and Eger, 2008; Abramov *et al.*, 2009; This study).

Description

Small species with "*suilla*–type" dentition (Tables 4. 2, 4. 3, 4. 4; Fig. 4. 3). The fur of the dorsum is bicoloured in having dark brown under fur and a bright golden tip on the guard hairs. The dorsal guard hairs are dark brown at the base. The distal halves are tricoloured, with pale brown and darker brown rings and bright orange gold tips. Hair on the ventrum is dark brown at the base and tipped with pale silver grey. The entire tail membrane from the proximal to distal edge, and about one-third of the plagiopatagium next to the body, are covered dorsally with fur similar to guard hairs covering the body. Toes (up to the bases of claws), thumb, the upper side of the forearm and proximal part of the fifth metacarpal are covered with bright golden hairs.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is gradually sloped and the braincase is moderately rounded and domed. No sagittal crest and the lambdoid crest is weak, but present. I2 is anterior to I3; C is similar in height as P4. C basal area is much smaller than that of P4. P2 much less in height than P4, and its basal area is less than half that of P4. M1 and M2 mesostyles are weak. In the mandible, the lower canine possesses a small but distinct additional anterior cusp; c distinctly equals p4 in height and is equal or slightly greater in the basal area. The talonids of m1 and m2 are moderately separated from their trigonids, and the hypoconid distinctly exceeds the entoconid in height.

Taxonomic note

Kruskop and Eger (2008) described this species from Lam Dong province. Subsequently, Kruskop and Shchinov (2010) recorded *M*. cf. *harpioloides* from the Hoang Lien mountain range in northern Vietnam, far from the only previously known location of the species.

Recently, Kruskop (2013) re-identified this specimen as *M. chrysochaetes*, and indicated that *M. harpioloides* has more orange colouration of the guard hairs and a less domed braincase as compared to *M. chrysochaetes*. During the present study, two specimens were collected from Bi Dup-Nui Ba National Park in Lam Dong province, extending the known distribution of this species.

Murina chrysochaetes Eger and Lim, 2011

Murina chrysochaetes Eger and Lim, 2011: 228; Type locality: Diding Headwater Forest Nature Preserve, Jing Xi County, Guangxi Zhuang Autonomous Region, China, 978 m above sea level.

Distribution

Known to occur in Vietnam and the Guangxi Zhuang Autonomous Region of southern China (Eger and Lim, 2011; Kruskop, 2013).

In Vietnam (Fig. 4. 1): Lao Cai (Hoang Lien NP) [1] (Kruskop, 2013), Cao Bang (Phia Oac-Phia Den NR) [5] (This study).

Description

Small species with "*suilla*–type" dentition (Tables 4. 2, 4. 3, 4. 4; Fig. 4. 3). Ear is small, broad and round with little emargination on it is posterior edge. Tubular nostrils are proportionally long and the nostrils and the tip of the muzzle have a mid-brown pigmentation. The dorsum is a mix of black and gold bands, with gold mid-bands and dark tips, overlaid by long, gold-tipped guard hairs. The ventral pelage is dark at the base and the tips of the guard hairs are golden in colour.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is short and narrow. Braincase is highly domed, the slope of the forehead is abrupt. No sagittal crest and the lambdoid crest is weak, but present. I2 is anterior to I3; C equals P4 in height, and only half of it in basal dimensions; P2 is small, about half the height and one-third the crown area of P4. M1 and M2 mesostyles are reduced. The lower canine is the same height as p2, but exceeds it in basal area; p2 is small.

Taxonomic note

Eger and Lim (2011) described *M. chrysochaetes* from China, close to the border of northeast Vietnam. Kruskop (2013) recorded a single specimen from Hoang Lien Mountain

(Lao Cai province) in northern Vietnam. During the present study, a single specimen was collected from Pia Oac-Phia Den Nature Reserve, Cao Bang province. These known localities are restricted to high mountains around the borders of Vietnam and China. Based on this study and Son *et al*. (2015b) from the comparison with Eger and Lim (2011), I concluded that the females larger than males.

4. 3. 2. Genus *Harpiocephalus* Gray, 1842

Diagnostic characters

A medium-sized vespertilionid bat with tubular nostrils. Total length of skull is over 20.0 mm. Dental formula: I2/3 C1/1 P2/2 M3/3 = 34. M3 is reduced and peg-like. The incisors are shorter than the first upper premolar.

Harpiocephalus harpia (Temminck, 1840)

Vespertilio harpia Temminck, 1840: 219; Type locality: Mt. Gede, Java.

Harpiocephalus mordax Thomas, 1923: 88; Type locality: Mogok, N Burma.

Harpiocephalus harpia: Hendrichsen *et al.*, 2001: 105; Lunde *et al.*, 2007: 160; Abramov *et al.*, 2009: 67.

Distribution

Known to occur in India, Vietnam, Cambodia, Myanmar, Thailand, China, Malaysia, and Indonesia (Corbet and Hill, 1992; Koopman, 1994; Hendrichsen *et al.*, 2001; Matveev, 2005; Kruskop, 2013).

In Vietnam (Fig. 4. 1): Lao Cai (Hoang Lien NP) [1], Tuyen Quang (Na Hang NR) [3], Bac Kan (Ba Be NP) [4], Cao Bang (Pia Oac-Phia Den NR) [5], Lang Son (Huu Lien NR) [8], Hai Phong (Cat Ba NP) [10], Nghe An (Pu Huong NR) [21], Quang Binh (Phong Nha–Ke Bang NP) [24], Kon Tum (Ngoc Linh NR) [29], Lam Dong (Bi Dup-Nui Ba NP) [36] (Hendrichsen *et al.*, 2001; Lunde *et al.* 2007; Thong and Furey. 2008; Abramov *et al.* 2009; Kruskop and Shchinov. 2010; This study).

Description

A medium-sized vespertilionid bat, but the largest species of the subfamily Murininae (Tables 4. 2, 4. 3, 4. 4; Fig. 4. 3). The dorsal pelage has dark grey bases with a light reddish buff,

and a rich, dark red tip. The ventral pelage is pale grey or reddish with dark bases. The wings are dark brown.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is short and broad and the braincase is domed. Sagittal and lambdoid crests are well developed. The dentition is robust. Upper canines are strong. I2 height clearly exceeds that of I3. Both upper incisors are much lower in height than C. P2 smaller than P4 in basal dimensions, and are subequal in height. M1 and M2 have no mesostyle. M3 is reduced. In the mandible, the coronoid process is prominent, c is well developed; p2 is less than p4 basally but equal in height.

Karyotype

The karyotype (Fig. 4. 6F, Table 4. 5, Appendix 4. 4) of the specimen from Kon Tum Province (Ngoc Linh Nature Reserve) (IEBR-M5661) is 2n = 44, FN = 52. Autosomes consist of three large and one small metacentric pairs, one submetacentric pair, and 16 medium-sized to small acrocentric pairs, gradually decreasing in size. The X chromosome is a medium-sized metacentric, and the Y chromosome is a small acrocentric.

Taxonomic note

Harpiocephalus had been considered to include two species, *H. harpia* and *H. mordax* (Thomas, 1923; Hill and Francis, 1984; Corbet and Hill, 1992; Hendrichsen *et al.* 2001, Simmons, 2005), where *H. mordax* is greater and more robust in skull size and shape than *H. harpia*. Matveev (2005) reviewed the literature and specimens from Cambodia and indicated that male and female specimens differed in size and shape. These specimens purely fit with the view of Hill and Francis (1984) on *H. harpia* (male) and *H, mordax* (female), and molecular markers (Inter-SINE-PCR) clearly demonstrated that the two populations could not be separated as a species level (Matveev, 2004). Lin *et al.* (2006) reported the genus from Taiwan for the first time and considered *Harpiocephalus* a monotypic genus and *H. mordax* to be a synonym of *H. harpia* in reference to size differences between sexes. Sexual dimorphisms were also confirmed in the population in China (Zhou *et al.*, 2014; Chen *et al.*, 2015), and it is currently thought that only *H. harpia* exists.

There is no study on geographic variation of the widely distributed *H. harpia*. The karyotype of "*H. mordax*" from Thailand (McBee *et al.*, 1986) is 2n=40. This is different from karyotypes reported in Taiwan and Guangdong Province, China (Lin *et al.*, 2006; Zhou *et al.*,

2014). Further morphological and molecular biological studies throughout the whole distribution area of *Harpiocephalus* should be performed.

4. 3. 3. Genus *Harpiola* Thomas, 1915

Diagnostic character

Small-sized vespertilionid bats with tubular nostrils: STOTL < 18.0 mm. The dental formula is I2/3 C1/1 P2/2 M3/3=34. Both upper premolars (P2 and P4) and canine are similar in shape and size. I3 is large, robust and in contact with the upper canine. I3 is slightly larger than I2. The upper incisors exceed the half of the height of the corresponding canines. P2 height is more than that of P4, and the lower canine is bicuspid.

Taxonomic note

Harpiola was described by Thomas (1915) based on *Murina grisea* Peters, 1872 as type species. Although, Ellerman and Morrison-Scott (1951), Corbet and Hill (1992), Koopman (1994) and Simmons (2005) treated *Harpiola* as a subgenus of *Murina*, Tate (1941), Bhattacharyya (2002), Kuo *et al.* (2006) and Kruskop *et al.* (2006) emphasized the considerable differences in skull and dentition between *Murina* and *Harpiola*, and accepted the valid generic status of *Harpiola*, which view is followed herewith.

Harpiola isodon Kuo, Fang, Csorba and Lee, 2006

Harpiola isodon Kuo, Fang, Csorba and Lee, 2006: 13; Type locality: Hualien County, Jhuosi Township, Yuli Wildlife Refuge, Taiwan, 23°32'N, 121°15'E, 2,000 m elevation; Kruskop, 2013: 176.

Harpiola cf. *isodon*; Kruskop *et al.*, 2006: 14.

Distribution

Vietnam and Taiwan (Kuo *et al.*, 2006; Kruskop *et al.*, 2006; Kruskop and Shchinov, 2010; Kruskop, 2013).

In Vietnam: (Fig. 4. 1). Lao Cai (Hoang Lien NP) [1] and Kon Tum (Ngoc Linh NR) [29] (Kruskop *et al.*, 2006, Kruskop and Shchinov, 2010; Kruskop, 2013; This study).

Description

Medium-sized species of the subfamily (Tables 4. 2, 4. 3, 4. 4; Fig. 4. 3). On the dorsal

surface, hairs are long and woolly; the basal part of underfur is dark brown with a bright yellow subterminal band and a dark brown tip. Guard hairs scattered all over the back are dark brown at the basal four-fifths with shiny golden yellow tips. From the ventral aspect, the fur is shorter, dark brown at the base and light brown in the terminal one-third. The dorsal side of the tail membrane, the tibia and the foot are all densely and evenly furred, including the last caudal vertebra, which is free from the uropatagium. The whole area of the tail membrane is also covered with dense, stiff, silvery grey hairs. The ear conch is possesses a distinct emargination at the upper third of its posterior border. The tragus is moderately long (7.60 mm around), but wide at its base and gradually tapering to the backward-curved tip, which just reaches the level of the notch. The base of the tragus is with a small tooth-like projection at its outer margin.

Skull and dentition (Figs. 4. 4, 4. 5). Rostrum is not inflated and the braincase is moderately domed. No sagittal crest and the lambdoid crest is weakly developed. Narial emargination is much longer than wide. Basioccipital pits are well-defined, usually elongated and especially narrower posteriorly. I2 is a bit longer than the outer upper incisor (I3). Both upper incisors are about two-thirds that of C in height, and the basal area of the second upper incisor is more than two-thirds that of C. The basal area of C, P2, P4 are subequal and they are gradually decreasing in height. The mesostyle of M1 and M2 is weak, but recognizable. In the mandible, the lower canine has a well-developed additional cusp. The lower canines and premolar teeth are similar in bulk, and c is slightly less than p2 in height. Entoconid in m1 and m2 is lower than hypoconid, and formed a distinct cusp widely separated from metaconid.

Karyotype

Karyotype (Fig. 4. 6G, Table 4. 5, Appendix 4. 4) based on one specimen from Lao Cai province (Hoang Lien National Park) (IEBR-M5436) is 2n = 44, FN = 50. Autosomes consist of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs gradually decreasing in size. The X chromosome is a medium-sized metacentric.

Taxonomic note

This species was described as a second species of the genus *Harpiola* from Taiwan by Kuo *et al.* (2006). Kruskop *et al.* (2006) and Kruskop and Shchinov (2010) reported this species from Vietnam, and considered it to be conspecific with the population in Taiwan.

4. 4. Discussion

Present and previous studies for karyotypes of the subfamily Murininae (Table 4. 5; Harada, 1973; Ando *et al.*, 1977; McBee, 1981; Harada *et al.*, 1987; Ono and Obara, 1994; Lin *et al.*, 2002, 2006; Volleth, 2006; Gu, 2006; Wu *et al.*, 2010; Zhou *et al.*, 2011, 2014) emphatically indicated that all species karyotyped had 2n=44, except for *Harpiocephalus harpia* (as *H. mordax*) reported by McBee (1981) from Thailand. Species of *Murina* and *Harpiola* share similar karyotypes, characterized by three large metacentric and one small submetacentric autosomal pairs, while *Harpiocephalus* differs in having an additional small submetacentric pair (no. 5). This feature is also shared with *H. harpia* populations in Taiwan and Guangdong, southern China (Lin *et al.*, 2006; Zhou *et al.*, 2014), and is suggested to have evolved by the inversion of the largest acrocentric pair in the *Murina* karyotype during the evolution of the genus *Harpiocephalus*. Except for *H. harpia*, conservative trends in chromosome rearrangements in the subfamily Murininae have been confirmed in this study, including additional species in the genus *Murina*. Cytological isolation mechanism may not be responsible for the diversification of the genus *Murina*. Molecular data did not suggest clear relationships among lineages, but this may be interpreted as many lineages of the subfamily Murininae having been separated simultaneously and diverged thereafter. Future studies to examine the evolutionary history and mechanisms that enable such diversification within a short time period are needed.

Son *et al.* (2015b) suggested that the important role of morphological diversification among the species of *Murina* in Vietnam is in the interaction among sympatric species pairs and between sexes. This is due to the observations from species that have diverged in the combination of size and shape of skulls, and sexual size dimorphism (i.e., larger females) with different dimorphic characteristics among species. Detailed analyses in this study of the sexual differences in *M. harrisoni* showed more complicated patterns of diversification. Sexual size dimorphism has not simply been established through differences in size and allometric-based shape, but through complicated size and shape differentiation due to the functional limitations and compensation of the skull. Continued observations of skulls (Fig. 4. 8) may suggest that limiting factors for morphological variability exist in the nasal capsule or braincase, possibly in relation to echolocation function.

Distribution data and overall body size provide another interesting view for the interaction

among sympatric species pairs. In each locality (Table 4. 1), there were from 1 to 7 species, except in the Kon Tum where 10 species were recorded, indicating a high species diversity among localities. This is probably because high mountains and primary forests enable the co-occurrence of multiple species through altitudinal distribution (Fig. 4. 10).

Among the 15 Murininae species in Vietnam, *Harpiocephalus harpia*, *M. cyclotis*, *M. annamitica*, *M. feae*, and *M. eleryi* were recorded from more than 10 localities (Table 4. 1). Similar-sized species tend to separate by elevation as shown in Table 4. 1 and Fig. 4. 10. On the other hand, two medium-sized species, *M. cyclotis* and *M. feae,* are both found in lowland and overlap localities (Table 4. 1, Fig. 4. 10). They provide an interesting example in that these two species clearly separate by STOTL in spite of overlapping FA (Fig. 4. 9). I suggest that a morphological shift in skull size contributed to decreased interspecific competition among similar-sized species with overlapping FA. FA–STOTL plots (Fig. 4. 9) also indicate that other species are well separated and only overlap in FA or STOTL among similar-sized species. In addition, the patterns of FA–STOTL shift for each species might not be parallel to the relationships between males and females.

Forearm length and overall skull size have often been considered as an indicator of overall size of bats, however, I suggest that these two characteristics are related with completely different adaptations among species and between sexes. Wu *et al.* (2015) reported that echolocation call frequencies in *Rhinolophus* bats correlates with nasal capsule size in the skull, but did not relate to forearm length. In concordance with Son *et al.* (2015b), I suggest that skull size and shape factors are affected by food habits and the echolocation function, whereas the FA and external morphology are more strongly related to flight behaviour and aerial niche use.

Vietnam possesses the highest number of species of the subfamily Murininae in the world. Although this diversity may be a result of greater sampling effort within Vietnam, the complex geological history and biogeographic features of the country suggest a greater likelihood of complex speciation within this group of bats than perhaps exists in other countries of mainland Southeast Asia. My study also suggests that ecological adaptations, such as interactions among sympatric species pairs and intraspecific relationships between males and females, played important roles in the formation of taxonomic and morphological diversity. Understanding the reasons for the high species diversity as well as the evolutionary processes of the subfamily will

require additional study on the taxonomy, distribution, ecology, and behavior of this group in Vietnam, and in Southeast Asia in general.

Table 4. 1. Distribution of the subfamily Murininae from Vietnam. Locality numbers correspond to Fig. 4. 1 and Appendix 4. 4. Species are arranged following overall size of skull (in decreasing order) (abbreviated name with first 3-4 characters of species name).

Number of Locality	Province	Number of Species	Species / Number of provinces where the species occurs														
			H. har	M. harr	M. leu	M. fio	M. hut	M. cyc	H. iso	M. lor	M. ann	M. bee	M. wal	M. fea	M. ele	M. harp	M. chr
			10	8	1	7	9	23	2	1	10	3	4	18	10	1	2
1	Lao Cai	5	o				o		o		o						o
2	Ha Giang	3						o						o	o		
3	Tuyen Quang	4	o					o			o			o			
4, 6	Bac Kan	5	o	o				o						o	o		
5	Cao Bang	5	o				o	o							o		o
7	Thai Nguyen	1												o			
8	Lang Son	1	o														
9	Quang Ninh	1						o									
10	Hai Phong	2		o				o									
11	Vinh Phuc	4	o	o				o						o			
12	Phu Tho	4		o				o						o	o		
13, 14, 15	Son La	5		o				o			o			o	o		
18	Ninh Binh	2						o						o			
16, 17, 19, 20	Thanh Hoa	5		o				o			o			o	o		
21, 22	Nghe An	7	o	o	o		o	o			o			o			
23	Ha Tinh	1												o			
24	Quang Binh	5	o			o		o						o	o		
25	Quang Tri	6				o	o	o			o	o		o			
26	Thua Thien-Hue	2						o						o			
27, 28	Quang Nam	5				o	o				o			o	o		
29, 31	Kon Tum	10	o			o	o	o	o	o	o	o		o	o		
30	Quang Ngai	5				o		o			o	o			o		
32	Gia Lai	3				o		o						o			
33	Binh Dinh and Phu Yen	1						o									
34, 35	Dak Lak	3		o			o						o				
36	Lam Dong	4	o				o	o								o	
37	Khanh Hoa	1					o										
38	Ninh Thuan	1											o				
39, 40	Dong Nai	4				o		o					o	o			
41	Binh Phuoc	2						o			o						
42	Ba Ria-Vung Tau	1						o									
43	Kien Giang	1											o				

Table 4. 2. Mean, range, and sample size for external measurements (mm) and body mass (gram) of bats of the subfamily Murininae from Vietnam.

Species		FA	HB	T	HF	E	TIB	Body mass
M. leucogaster [1]	♀	41.80	-	40.00	9.80	14.2	18.80	8.8
M. harrisoni	♂	35.30 (34.0–36.7) 11	44.27 (38.9–50.0) 3	39.50 (35.8–45.5) 3	8.2 (7.4–9.0) 3	14.60 (13.5–15.5) 3	19.33 (19.0–19.5) 3	8.4
	♀	38.18 (35.6–40.1) 10	40.3, 44.9	40.1, 41.7	8.1, 10.2	15.4, 18.8	18.6, 21.0	10.5
M. fionae	♂	35.32 (34.2–36.4) 6	45.62 (42.1–48.2) 6	39.95 (37.0–44.5) 6	8.17 (6.8–9.3) 6	14.32 (13.7–14.6) 6	19.20 (18.5–20.8) 6	7.87 (7.5–9.0) 6
	♀	37.9	51.3	41.7	9.1	16.0	20.7	12.0
M. huttoni	♂	33.36 (32.0–36.0) 8	46.21 (44.0–50.0) 7	37.57 (31.0–41.5) 7	7.30 (6.6–8.6) 7	16.32 (14.0–17.0) 8	16.71 (16.7–16.7) 8	5.89 (5.3–6.3) 5
	♀	34.34 (33.1–35.5) 10	46.26 (40.0–53.0) 10	36.02 (32.0–42.5) 10	7.89 (7.0–8.9) 10	16.30 (15.9–17.0) 10	16.74 (16.0–17.7) 10	6.36 (5.3–8.0) 10
M. cyclotis	♂	30.33 (28.9–32.0) 33	40.98 (38.0–48.0) 33	35.13 (31.8–38.7) 33	7.27 (6.3–8.5) 33	14.55 (12.3–17.0) 33	17.01 (15.9–17.8) 36	5.01 (4.1–6.0) 19
	♀	34.37 (32.1–36.3) 26	44.07 (40.0–51.0) 26	38.33 (32.1–43.5) 26	7.53 (6.3–8.60) 26	15.01 (12.5–18.6) 26	18.27 (15.0–20.1) 26	6.82 (4.7–8.2) 16
M. lorelieae	♂	33.72 (33.0–34.5) 7	39.14 (37.0–41.0) 7	35.00 (31.0–38.0) 7	6.71 (6.0–7.5) 7	15.10 (14.0–16.0) 7	33.72 (33.0–34.5) 7	4.87 (4.2–6.6) x
	♀	35.25 (34-9–35.6) 3	44.40 (43.3–45.5) 3	39.70 (38.4–41.0) 3	8.45 (8.4–8.5) 3	15.80 (15.6–16.0) 3	19.20 (19.1–19.3) 3	6.00 (5.5–6.5) 3
M. annamitica	♂	30.91 (29.4–32.1) 11	40.32 (36.2–48.0) 10	35.72 (32.5–38.8) 10	6.74 (5.9–8.1) 10	12.86 (11.9–14.2) 10	16.58 (15.4–17.4) 11	5.66 (4.3–7.0) 8
	♀	32.12 (27.0–34.6) 10	43.70 (38.2–55.0) 10	36.80 (32.4–40.3) 10	7.15 (6.2–8.1) 10	13.09 (11.9–15.0) 10	17.19 (16.0–18.0) 10	6.75 (5.3–8.0) 10
M. beelzebub	♂	34.43 (34.4–34.5) 3	42.67 (40.0–44.0) 3	38.90 (36.8–41.4) 3	7.13 (6.6–8.6) 3	14.13 (14.1–14.2) 3	18.57 (18.1–19.4) 3	3.0, 5.5
	♀	36.45 (36.0–37.3) 5	44.37 (41.6–49.0) 5	39.60 (33.0–44.8) 5	6.80 (5.5–8.0) 5	13.73 (13.2–14.0) 5	18.84 (18.0–19.6) 5	3.0, 5.5
M. walstoni	♂	33.16 (32.7–34.1) 3	35.41 (34.8–35.9) 3	30.93 (29.8–32.5) 3	6.52 (6.1–7.0) 3	13.01 (12.5–14.0) 3	14.08 (13.4–15.0) 3	4.40 (4.2–4.6) 3
	♀	33.40 (32.6–33.5) 3	40.22 (35.2–43.5) 3	28.79 (26.6–30.0) 3	6.36 (6.1–6.5) 3	12.90 (12.1–14.1) 3	14.66 (13.9–15.6) 3	4.6
M. feae	♂	30.12 (27.5–33.4) 17	38.29 (33.7–43.0) 13	34.89 (31.4–39.5) 13	6.86 (6.0–8.4) 14	12.99 (11.5–14.3) 14	16.57 (15.7–18.1) 17	4.22 (3.5–5.3) 8
	♀	31.40 (28.1–34.3) 16	38.69 (32.8–43.5) 16	35.46 (30.0–41.6) 16	6.83 (6.1–8.0) 16	12.90 (11.0–15.0) 16	16.95 (15.6–17.8) 16	4.20 (3.9–4.4) 6
M. eleryi	♂	28.23 (27.3–29.4) 7	33.19 (31.5–36.2) 3	29.52 (26.5–32.3) 7	6.40 (5.2–7.7) 7	12.20 (11.5–13.3) 7	14.05 (13.0–15.1) 7	4.03 (2.5–5.0) 6
	♀	29.87 (28.6–31.3) 8	35.8, 39.0	29.87 (27.3–32.1) 8	6.75 (6.0–7.4) 8	12.57 (11.7–13.3) 8	13.96 (13.2–15.0) 8	4.79 (4.0–5.5) 7
M. harpioloides	♂	28.8	40	26.0	6.4	12.5	14.4	4.0
	♀	29.7[2], 29.8	34.5, 35.0[2]	27.0, 30.5[2]	6.0, 6.5[2]	11.0, 12.3[2]	13.3	4.2[2], 5.5
M. chrysochaetes	♂	-	-	-	-	-	-	
	♀	28.6[3], 29.8	40.0[3], 41.0	24.0[3], 26.0	5.5[3], 5.6	12.0[3], 12.6	12.6[3], 12.7	4.0[3], 4.4
Harpiocephalus harpia	♂	49.4, 49.5	55.0, 57.0	40.0, 50.0	11.0, 11.2	17.0, 18.0	22.0, 24.0	16.0, 24.0
	♀	52.8 (50.9–54.9) 3	59.7 (59.0 –61.0) 3	48.6 (47.7–50.0) 3	11.5 (11.0–12.0) 3	17.7 (17.0–18.0) 3	22.7 (22.0–23.5) 3	27.1 (25.0–30.2) 3
Harpiola isodon	♂	-	-	-	-	-	-	-
	♀	37.3	44.0	36.0	7.5	15.0	15.0	7.0

[1]: The measurements follow Hendrichsen *et al*. (2001) [2]: The measurements follow Kruskop and Eger (2008) [3]: Eger and Lim (2011)

Table 4. 3. Updated craniodental measurements (mm) of *M. chrysochaetes*, *M. harpioloides*, *M. lorelieae*, *M. harrisoni*, *Harpiocephalus harpia*, and *Harpiola isodon* (specimens of *M. harrisoni* from Vietnam, Cambodia, China, and Thailand, and those for other species from Vietnam).

Measuremeants	*M. chrysochaetes*	*M. harpioloides*		*M. lorelieae*		*M. harrisoni*		*Harpioc. harpia*		*Harpiola isodon*
	♀ (n=2)	♂ (n=1)	♀ (n=2)	♂ (n=7)	♀ (n=3)	♂ (n=12)	♀ (n=10)	♂ (n=3)	♀ (n=2)	♀ (n=1)
STOTL	14.57–14.72	14.90	14.53–14.62	15.83–16.39 16.12±0.19	16.33–16.74 16.54±0.29	16.95–118.39 17.85±0.46	17.46–19.43 18.64±0.63	21.45–23.07 22.26±0.07	22.82–23.25	17.09
CCL	12.19–12.82	12.59	12.34–12.40	13.55–14.14 13.96±0.20	13.55–14.14 13.96±0.20	15.46–16.25 15.92±0.25	15.96–17.16 16.62±0.49	18.90–19.42 19.42±0.73	20.01–20.26	14.95
C1C1W	3.42–3.63	3.46	3.41–3.42	3.74–3.92 3.86±0.06	3.74–3.92 3.86±0.06	4.16–4.94 4.64±0.21	4.66–5.31 5.00±0.19	6.45–7.03 6.74±0.41	6.74–7.17	4.26
M3M3W	4.89–4.93	4.95	4.86–4.90	5.29–5.58 5.43±0.09	5.28–5.58 5.43±0.09	5.63–5.98 5.81±0.18	5.78–6.44 6.12±0.21	6.24–6.89 6.57±0.46	7.23–7.75	5.65
ZYW	8.16–8.41	8.48	8.13–8.32	8.78–9.17 8.97±0.14	9.05–9.45 9.25±0.28	9.97–10.62 10.32±0.25	10.13–11.47 9.29±0.38	12.92–14.54 13.73±1.15	14.48–15.09	9.61
MAW	7.26–7.62	7.45	7.35–7.37	7.76–7.89 7.68±0.10	7.76–8.07 7.92±0.22	8.31–9.31 8.85±0.29	8.34–9.61 9.29±0.38	10.70–11.75 11.23±0.74	11.45–11.98	8.12
IOW	4.17–4.24	4.35	4.11–4.16	4.17–4.29 4.21±0.04	4.17–4.39 4.29±0.15	4.23–4.58 4.36±0.12	4.30–4.58 4.48±0.09	5.42–5.72 5.57±0.21	5.57–6.05	5.12
BCW	7.12–7.27	7.47	7.10–7.21	7.33–7.62 7.46±0.11	7.45–7.90 7.68±0.32	7.46–8.11 7.81±0.22	7.76–8.22 7.94±0.29	9.18–9.66 9.42±0.34	9.60–10.23	7.72
BCH	6.33–6.34	6.50	6.36–6.41	6.20–6.94 6.65±0.26	6.45–6.54 6.53±0.08	6.16–6.78 6.49±0.18	6.22–7.23 6.74±0.29	9.25–9.76 9.51±0.36	9.74–10.12	7.77
CM3L	4.55–4.66	4.68	4.68–4.70	5.21–5.40 5.30±0.06	5.46–5.64 5.55±0.13	5.82–6.31 6.11±0.17	6.29–7.14 6.53±0.25	6.81–7.08 6.95±0.19	7.08–7.12	5.61
CP4L	1.97–2.02	2.03	1.95–1.96	2.40–2.56 2.52±0.06	2.78–2.85 2.82±0.05	2.84–3.19 3.04±0.11	3.16–3.37 3.25±0.08	4.12–4.25 4.19±0.09	4.05–4.33	2.74
ML	9.30–9.94	9.76	9.31–9.52	10.21–10.78 10.53±0.18	10.87–11.32 11.10±0.13	11.95–12.89 12.44±0.34	12.55–13.62 13.08±0.37	15.11–15.74 15.43±0.45	16.28–16.45	11.63
cm3L	5.00–5.08	5.12	5.13–5.14	5.62–5.81 5.74±0.06	5.88–6.19 6.04±0.22	6.30–6.95 6.69±0.21	6.81–7.43 7.07±0.19	7.65–8.02 7.84±0.26	7.83–8.10	5.91
cp4L	1.80–1.83	1.90	1.75–1.86	2.31–2.42 2.37±0.04	2.50–2.68 2.59±0.13	2.84–3.22 3.03±0.13	3.07–3.36 3.19±0.09	4.08–4.331 4.20±0.16	4.13–4.24	2.47
CPH	3.29–3.51	3.30	3.25–3.34	3.50–4.00 3.67±0.17	3.94–3.96 3.95±0.01	4.26–5.04 4.70±0.28	4.61–5.52 5.14±0.27	8.07–8.78 8.43±0.50	8.80–9.66	3.74

Value given as mean ± standard deviation (if n≥3) and minimum-maximum

Table 4. 4. Morphological comparison among species of the subfamily Murininae

Species	Sex	STOTL (mm)	CM3L (mm)	ML (mm)	BCH/BCW (%)	Dentition	Braincase	Sagittal crest	Lambdoid crest	M1/M2 mesostyles
M. leucogaster	♂	19.27 (1)	6.27 (1)	13.17 (1)	84.7	*suilla*–type	Domed	Weakly developed	Weak	Weakly developed
	♀	18.49 (1)	6.33 (1)	13.32 (1)	80.8					
M. harrisoni	♂	16.95–18.39 (12)	5.82–6.31 (12)	11.95–12.89 (12)	77.9–89.1	*cyclotis*–type	Flat	Well developed	Well developed	Weakly developed
	♀	17.46–19.72 (11)	6.29–7.14 (11)	12.55-13.75 (11)	79.0–92.9					
M. fionae	♂	17.86–18.23 (6)	6.10–6.38 (6)	12.05–12.44 (6)	84.1–94.4	*cyclotis*–type	Well domed	Well developed	Weakly developed	Absent
	♀	19.08 (1)	6.39 (1)	12.85 (1)	91.5					
M. huttoni	♂	16.61–18.52 (14)	5.56–6.23 (14)	11.35–12.30 (14)	80.1–93.1	*cyclotis*–type	Flat	Weakly developed	Weakly developed	Well developed
	♀	16.61–18.81 (14)	5.66–6.30 (14)	11.59–12.70 (14)	79.8–87.9					
M. cyclotis	♂	16.08–17.66 (40)	5.16–5.59 (40)	10.44–11.87	77.7–96.2	*cyclotis*–type	Domed	Weakly developed	Weakly developed	Absent
	♀	16.70–18.08 (33)	5.55–5.89 (33)	10.90–12.34 (33)	80.5–96.4					
M. lorelieae	♂	15.83–16.39 (7)	5.21–5.40 (7)	10.21–10.78 (7)	86.8–94.1	*suilla*–type	Domed	Absent	Weak	Well developed
	♀	16.33–16.74 (3)	5.46–5.64 (3)	10.79–11.32 (3)	82.8–89.8					
M. annamitica	♂	15.63–16.47 (11)	5.19–5.60 (11)	10.13–10.98 (11)	82.4–91.6	*cyclotis*–type	Domed	Weakly developed	Weak	Well developed
	♀	16.40–17.16 (11)	5.23–5.69 (11)	10.69–11.47 (11)	80.5–90.5					
M. beelzebub	♂	16.40–16.69 (4)	5.27–5.54 (4)	10.73–11.11 (4)	80.8–83.3	*suilla*–type	Domed	Absent	Weak	Weakly developed
	♀	16.73–16.99 (6)	5.40–5.70 (6)	10.88–11.48 (6)	79.8–83.7					
M. walstoni	♂	15.39–15.73 (3)	5.34–5.39 (3)	10.62–10.74 (3)	79.3–90.9	*suilla*–type	Domed	Well developed	Well developed	Developed
	♀	15.15–15.92 (6)	5.27–5.48 (6)	10.40–10.95 (6)	86.1–94.5					
M. feae	♂	14.91–16.30 (20)	4.62–5.25 (20)	9.63–10.64 (20)	76.4–91.1	*suilla*–type	Domed	Absent	Weak	Weak
	♀	15.13–16.11 (18)	4.89–5.47 (18)	9.80–10.86 (18)	76.4–88.0					
M. eleryi	♂	13.79–15.18 (9)	4.53–4.79 (8)	9.25–9.60 (8)	79.5–84.2	*suilla*–type	Domed	Absent	Weak	Well developed
	♀	14.21–15.15 (10)	4.48–4.89 (10)	9.28–9.97 (10)	76.6–87.8					
M. harpioloides	♂	14.90 (1)	4.68 (1)	9.76 (1)	87.0	*suilla*–type	Domed	Absent	Weak	Weak
	♀	14.53–14.62 (2)	4.68–4.70 (2)	9.31–9.52	88.2–90.3					
M. chrysochaetes	♂	–	–	–	–	*suilla*–type	Domed	Absent	Weak	Reduced
	♀	14.57–14.72 (2)	4.55– 4.66 (2)	9.30–9.94(2)	87.0, 89.0					
Harpioc. harpia	♂	21.45–23.07 (2)	6.81–7.09 (2)	15.11–15.74	100.8, 101.0	–	Domed	Well developed	Well developed	Absent
	♀	22.82–23.25 (3)	7.08–7.12 (3)	16.28–16.45 (3)	97.6–105.4					
Harpiol. isodon	♂	–	–	–	–	–	Domed	Absent	Weakly developed	Weak
	♀	17.09 (1)	5.61 (1)	11.63 (1)	100.6					

Value given as minimum-maximum and quantity of specimen

Table 4. 5. Comparison of karyotypes of the subfamily Murininae.

Species	Locality	2n	FN	M	SM	ST	A	X	Y	References
M. leucogaster	China	44	58	3	1	4	13	M	A	Gu (2006)
M. hilgendorfi	Japan	44	56	3	1	3	14	SM	A	Harada (1973); Harada *et al*. (1987), Ando *et al*. (1977)
M. harrisoni	China	44	50	3	1	0	17	M	–	Wu et al. (2010)
M. harrisoni	Thailand	44	50	3	1	0	17	M	A	McBee *et al*. 1986 (see Francis and Eger [2012])
M. huttoni	Vietnam	44	50	3	1	0	17	M	A	This study (n=5)
M. cyclotis	Vietnam	44	50	3	1	0	17	M	A	This study (n=5)
M. lorelieae	Vietnam	44	50	3	1	0	17	SM	A	This study (n=2)
M. beelzebub	Vietnam	44	50	3	1	0	17	M	–	This study (n=1)
M. feae	Vietnam	44	50	3	1	0	17	M	–	This study (n=1)
M. feae	China	44	50	3	1	0	17	M	A	Zhou *et al*. (2011)
M. puta	Taiwan	44	50	3	1	0	17	M	A	Lin *et al*. (2002)
M. suilla	Malaysia	44	58	3	1	4	13	SM	ST	Volleth (2006)
M. ussuriensis	Japan	44	56	3	0	4	14	M	A	Ono and Obara (1994)
M. ussuriensis	Japan	44	56	3	1	3	14	SM	A	Harada *et al*. (1987), Ando *et al*. (1977)
Harpiocephalus harpia	Vietnam	44	52	4	1	0	16	M	A	This study (n=1)
H. harpia	Taiwan	44	52	4	1	0	16	M	–	Lin *et al*. (2006)
H. harpia	China	44	52	4	1	0	16	M	A	Zhou *et al*. (2014)
H. harpia	Thailand	40	–	–	–	–	–	–	–	McBee *et al*. (1986)
Harpiola isodon	Vietnam	44	50	3	1	0	17	M	–	This study (n=1)

M: Metacentrics; SM: Submetacentrics; ST: Subtelocentrics; A: Acrocentrics

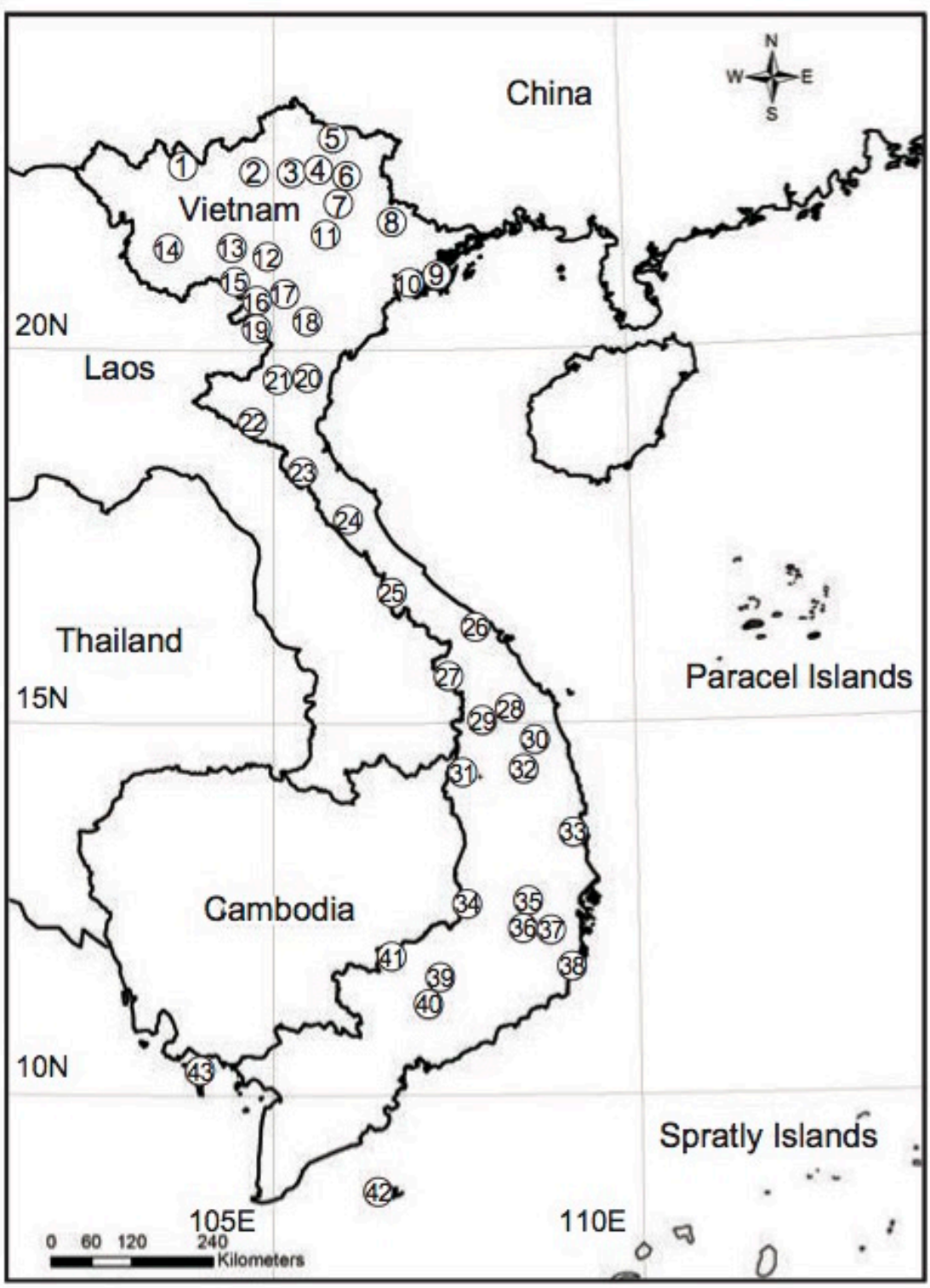

Figure 4. 1. Map of localities for specimens of the subfamily Murininae from Vietnam. Locality names are given in Appendix 1.

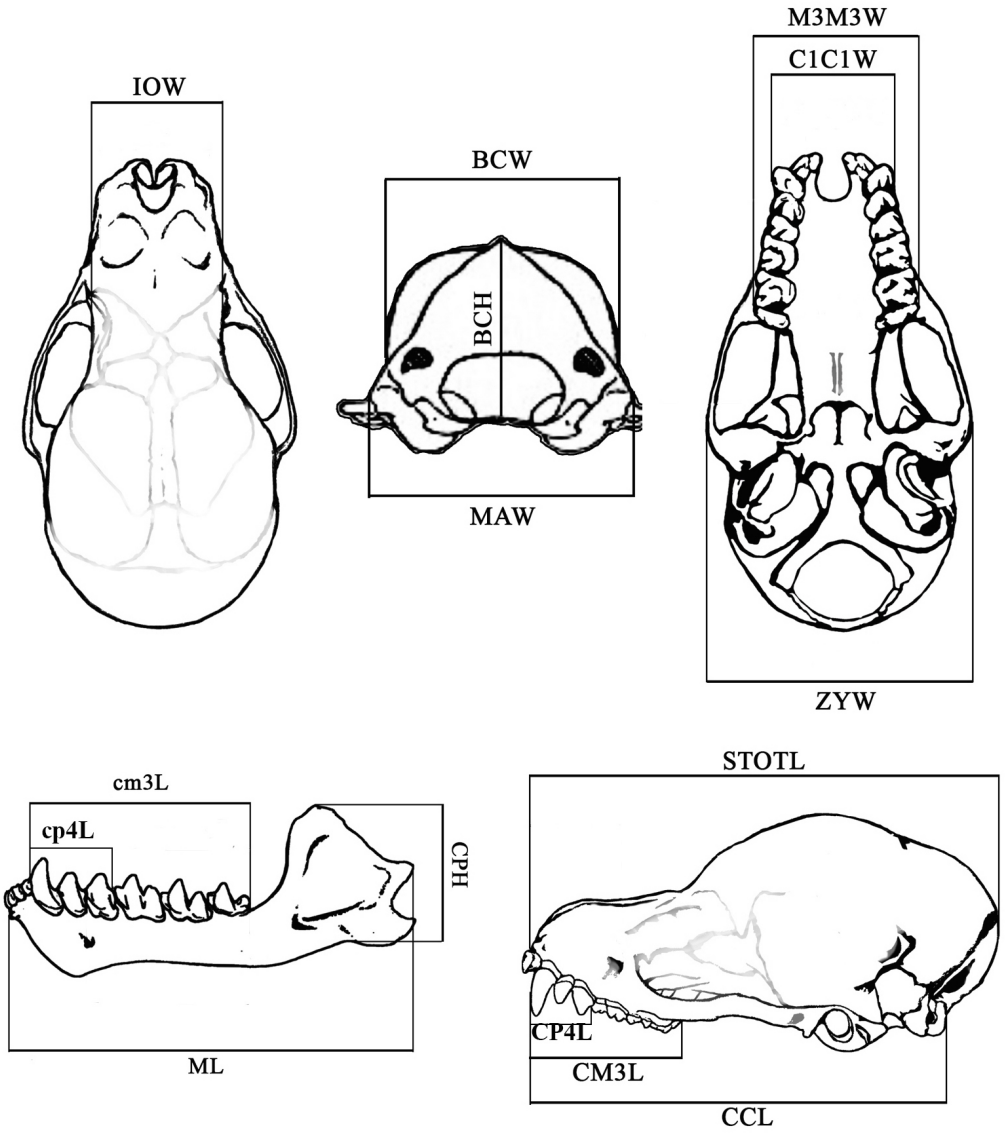

Figure 4. 2. Craniodental measurements of Murininae used in this study.

Figure 4. 3. Face (left), ventral fur (middle), and dorsal fur (right) of the subfamily Murininae from Vietnam: A, *M. harrisoni* (IEBR-M3299); B, *M. fionae* (IEBR-M3080); C, *M. huttoni* (IEBR-M5693); D, *M. cyclotis* (IEBR-M4223); E, *M. lorelieae* (IEBR-M5656); F, *M. annamitica* (IEBR-M3034); G, *M. beelzebub (*IEBR-M3904); H, *M. walstoni* (IEBR-M4592); I, *M. feae* (IEBR-M3264)); J, *M. eleryi* (IEBR-M4070); K, *M. harpioloides* (IEBR-M5806); L, *M. chrysochaetes (*ROM MAM 116181); M, *Harpiocephalus harpia* (IEBR-M6037 left, IEBR-M5661 middle and right); N, *Harpiola isodon* (IEBR-M5436).

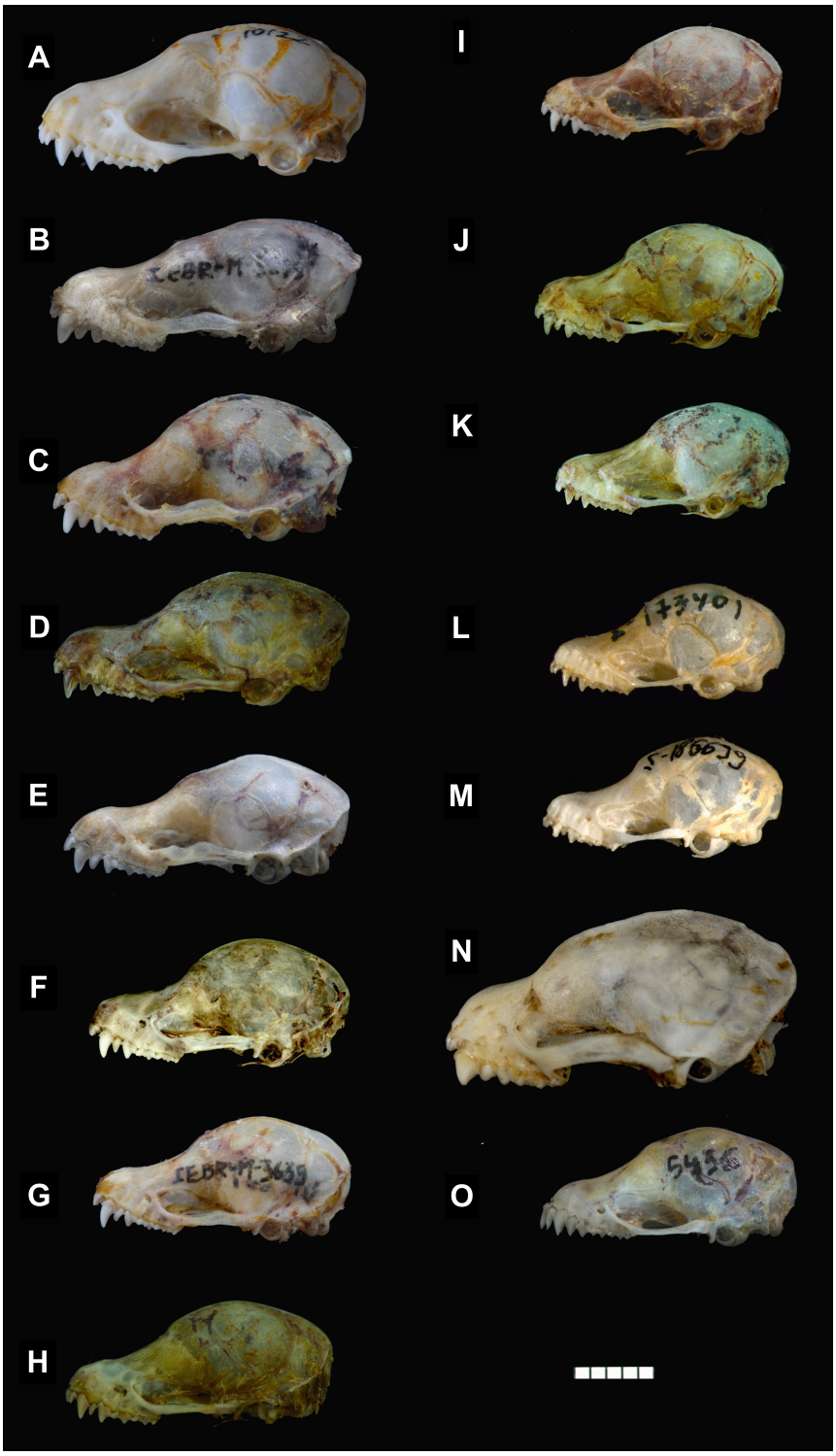

Figure 4. 4. Left lateral view of skull of the subfamily Murininae in Vietnam: A, *M. leucogaster* (GZU 10122); B, *M. harrisoni* (IEBR-M3299); C, *M. fionae* (IEBR-M3635); D, *M. huttoni* (IEBR-M5693); E, *M. cyclotis* (IEBR-M4223); F, *M. lorelieae* (IEBR-M5656); G, *M. annamitica* (IEBR-M3639); H, *M. beelzebub* (IEBR-M5645); I, *M. walstoni* (IEBR-VTTu 15-0033); J, *M. feae* (IEBR-M5719); K, *M. eleryi* (IEBR-M5718); L, *M. harpioloides* (ZMMU S173401); M, *M. chrysochaetes* (ZMMU S186699); N, *Harpiocephalus harpia* (IEBR-M422); O, *Harpiola isodon* (IEBR-M5436).

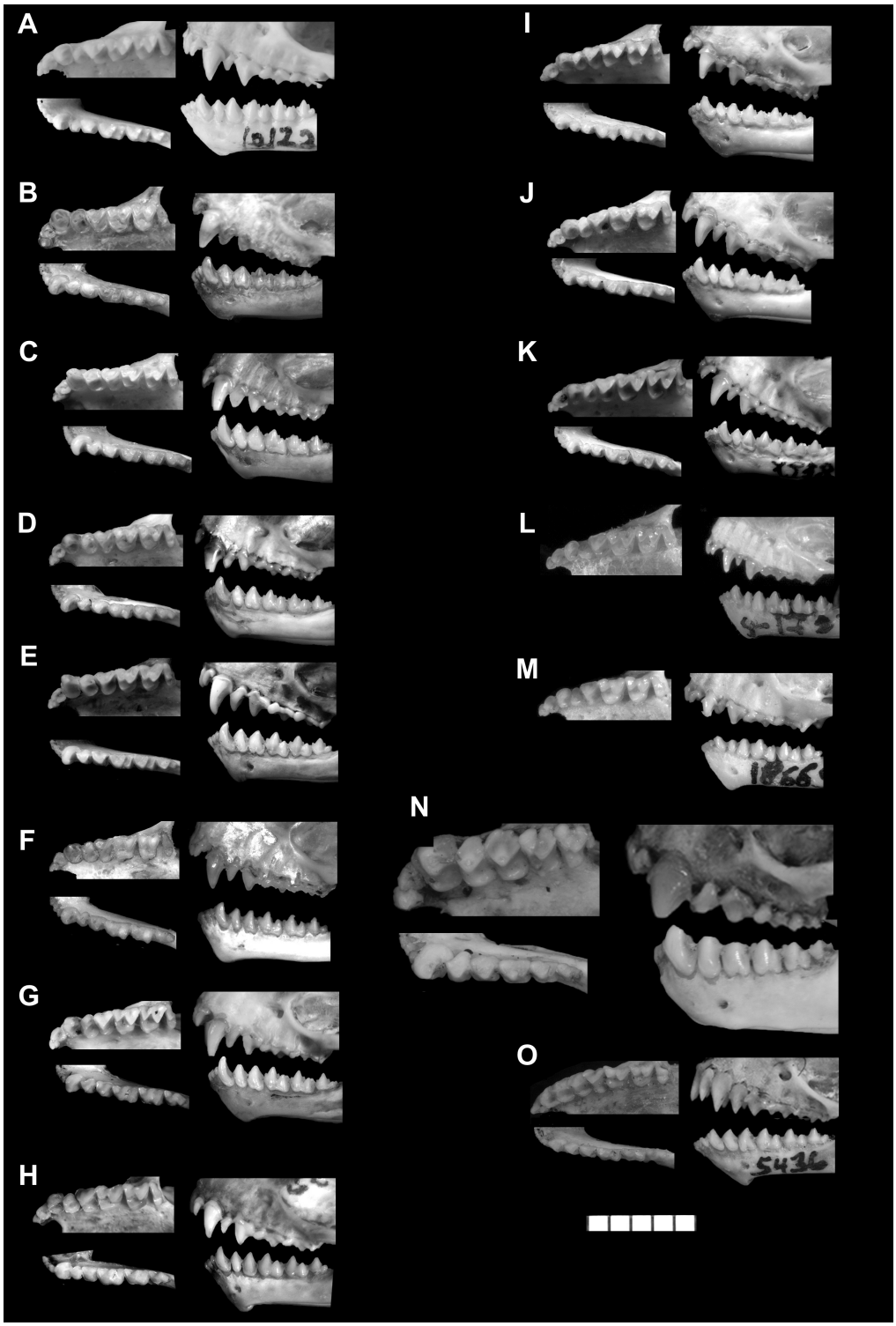

Figure 4. 5. Lateral and crown view of upper (left) and lower (right) dentition of the subfamily Murininae in Vietnam: A, *M. leucogaster* (IBHG 10122); B, *M. harrisoni* (IEBR-M3299); C, *M. fionae* (IEBR-M3635); D, *M. huttoni* (IEBR-M5693); E, *M. cyclotis* (IEBR-M4223); F, *M. lorelieae* (IEBR M5656); G, *M. annamitica* (IEBR-M3639); H, *M. beelzebub* (IEBR-M5645); I, *M. walstoni* (IEBR VTTu 15-00033); J, *M. feae* (IEBR-M5719); K, *M. eleryi* (IEBR-M4070); L, *M. harpioloides* (ZMMU S173401); M, *M. chrysochaetes* (ZMMU S186699); N, *Harpiocephalus harpia* (IEBR-M422); O, *Harpiola isodon* (IEBR-M5436).

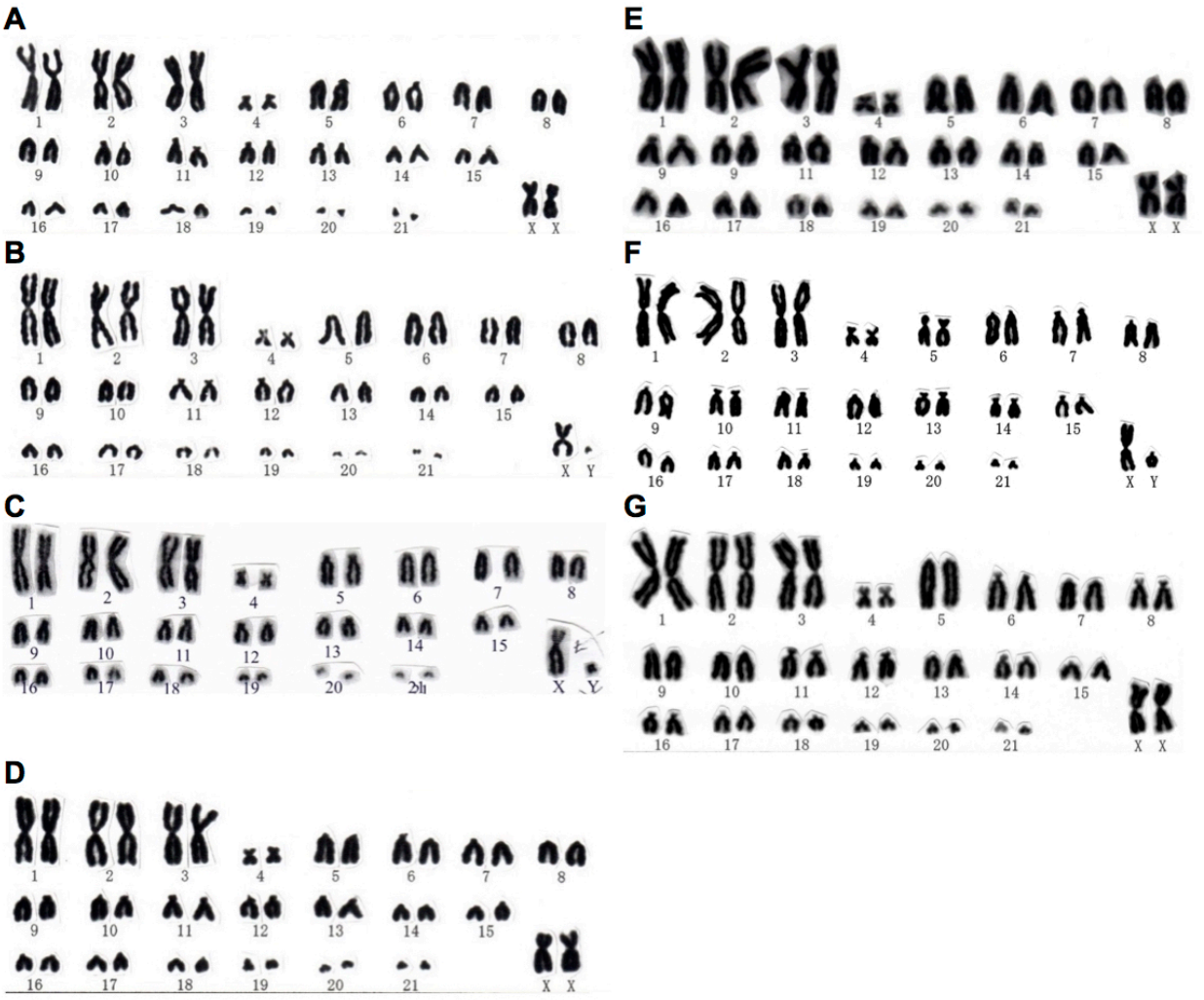

Figure 4. 6. Karyotypes of the subfamily Murininae from Vietnam: A, *M. huttoni* (IEBR-M5407); B, *M. cyclotis* (IEBR-M4071); C, *M. lorelieae* (HNHM B20140915.7); D, *M. beelzebub* (IEBR-M4842); E, *M. feae* (IEBR-M4214); F, *Harpiocephalus harpia* (IEBR-M5661); G, *Harpiola isodon* (IEBR-M5436).

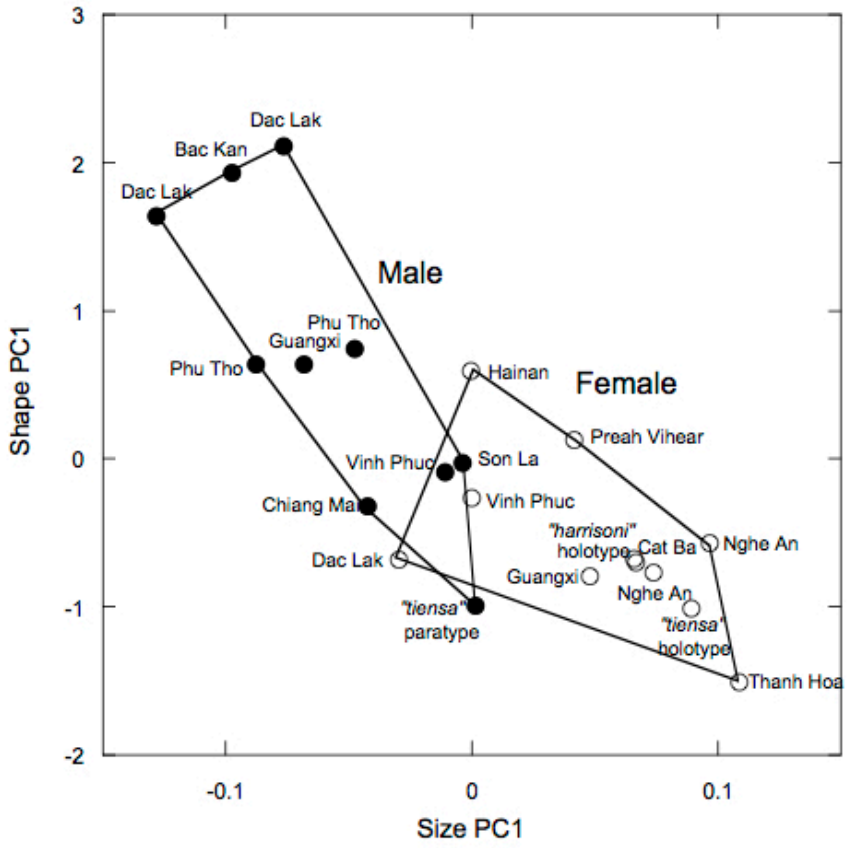

Figure 4. 7. Scatter plots between size PC1 and shape PC1 based on craniodental measurements of *Murina harrisoni* and "*M. tiensa*" specimens. Open and closed circles represent females and males, respectively.

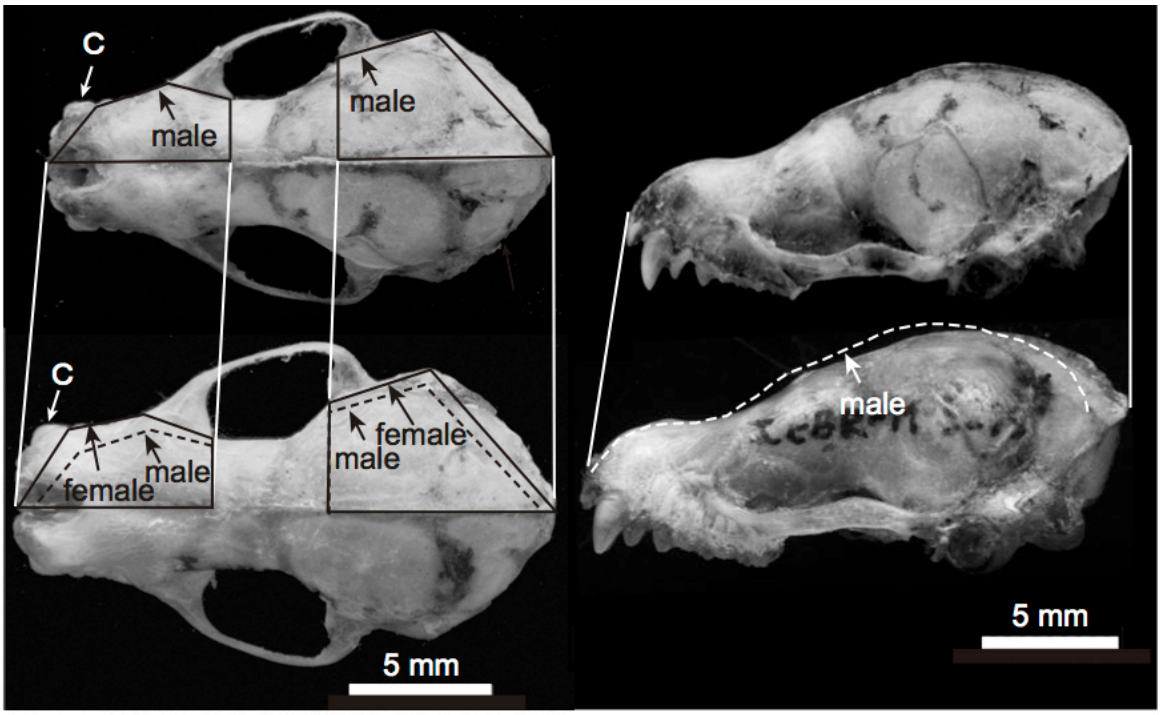

Figure 4. 8. Dorsal and left lateral views of mandibles from male (IEBR-M4998/B190913.7) and female (IEBR-M3299/PM28) specimens of *Murina harrisoni*.

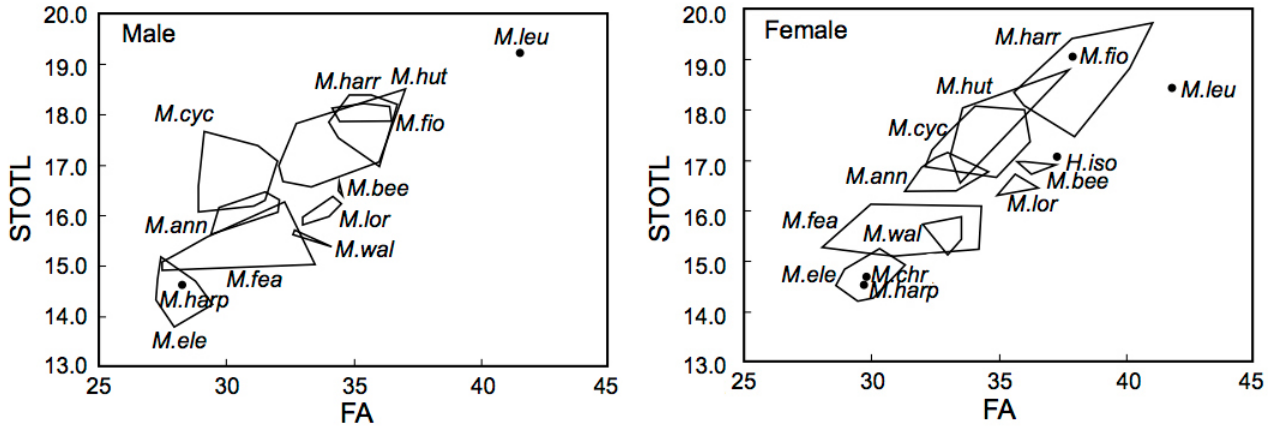

Figure 4. 9. Scatter plots between FA and STOTL of the genus *Murina* and *Harpiola* from Vietnam: male and female (abbreviated name with first 3-4 characters of species name).

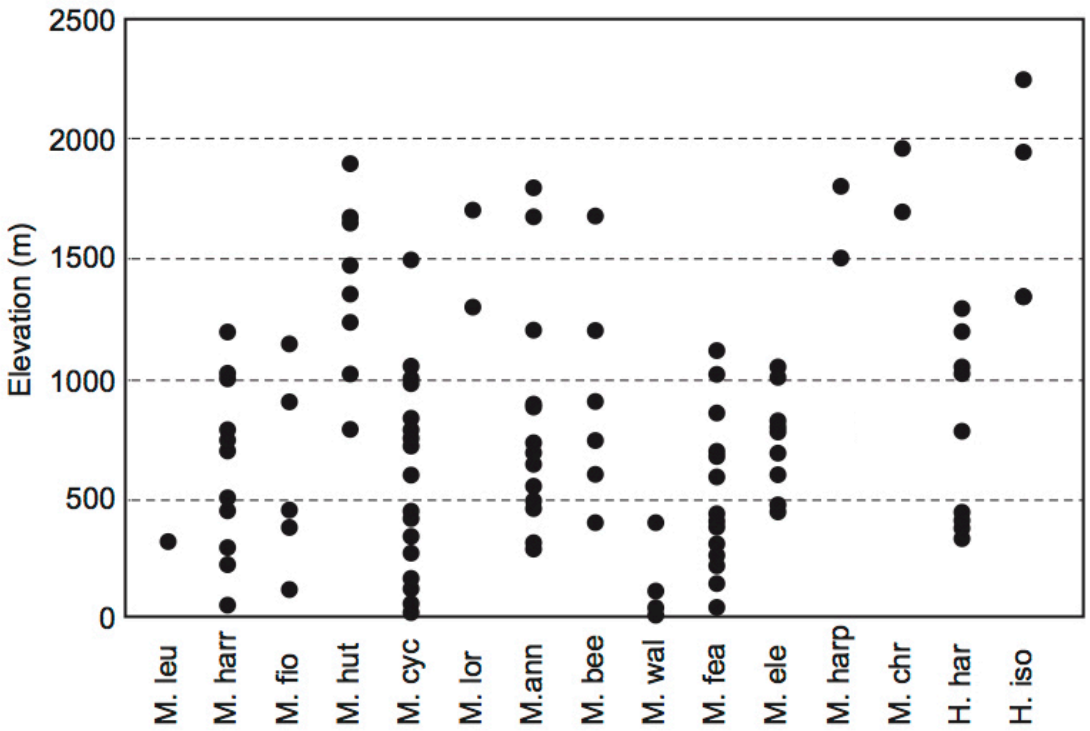

Figure 4. 10. Elevation distribution of the subfamily Murininae from Vietnam. Species are arranged following the overall size of skull (in decreasing order) (abbreviated name with first 3-4 characters of species name).

CHAPTER V

General Discussion and Conclusions

The knowledge of the morphological variations and systematics of tube-nosed and woolly bats in Vietnam has been limited, mainly due to the difficulty of collecting them in the field and lacking specimens. In particular, the taxonomy, distribution, and behaviors within and between the taxa representing different lifestyles have remained unclear. The skull morphometric variations of size and shape in Murininae and Kerivoulinae have been expected to detail to develop the morphological identification key for the species from Vietnam and surrounding regions.

In this thesis, I addressed the morphological analysis of the skull size and shape of genus *Murina* (Chapter II), Kerivoulinae (Chapter III), and comprehensive studies of taxonomy, distribution, and status of tube-nosed bats of subfamily Murininae in Vietnam (Chapter IV). As the results, my conclusions are follows:

5. 1. Morphological diversification among the species of tube-nosed and woolly bats from Vietnam

Recent publications divided the tube-nosed and woolly bats into several groups: the large-sized group comprising *K. papillosa* (Temminck, 1840), *Kerivoula kachinensis* (Bates *et al*., 2005), *Murina tiensa* (Csorba *et al*., 2007), *M. fionae* (Francis and Eger, 2012); the medium-sized group consisting of *M. harrisoni* (Csorba and Bates, 2005), *Harpiola isodon* (Kuo *et al*. 2006), *K. titania* (Bates *et al*., 2007), *M. beelzebub* (Csorba *et al*., 2011), and *M. pluvialis* (Ruedi *et al*. 2012); the small-medium sized species group containing *M. guilleni* (Soisook *et al*., 2013b); the relatively small-sized group: *M. walstoni* (Csorba *et al*., 2011), *M. annamitica* (Francis and Eger, 2012); and very small-sized group as *K. krauensis* (Francis *et al*., 2007), *M. harpioloides* (Kruskop and Eger, 2008), *M. eleryi* (Furey *et al*. 2009), *M. chrysochaetes, M. lorelieae*, *M. shuipuensis* (Eger and Lim, 2011), *M. jaintiana* (Ruedi *et al*. 2012), and *M. balaensis* (Soisook *et al*., 2013a). However, these findings have been only based on few external morphological differences among species, such as fur color, forearm length, head and body length, and body weight. Nevertheless, a comprehensive skull morphometric analysis based on voucher specimens of various species has never been carried out for the subfamily Murininae and Kerivoulinae.

In this study, based on the morphological data of genus *Murina* in Chapter I and the biodiversity data of Murininae in chapter IV, the size of three genus (*Harpiocephalus*, *Harpiola*,

and *Murina*) was compared. The skull of *Harpiocephalus* species was largest (Table 4. 4). The member of *Murina* was assigned to three groups (Fig. 2. 2, Tables 2. 3 and 4. 4): the large-sized group (*M. leucogaster*, *M. harrisoni*, *M. fionae*), the medium-sized group (*M. huttoni*, *M. cyclotis*, *M. lorelieae*, *M. walstoni*, *M. feae*) overlapping with *Harpiola isodon*, and the small-sized group (*M. eleryi*, *M. harpioloides*, *M. chrysochaetes*) (Fig. 2. 2 and Table 2. 2). My results also showed that the species of Murininae does not overlap with other species (Fig. 2. 3) and could be divided into three groups based on the shape of skull (Fig. 4. 4 and Table 4. 4): the flattened braincase group (*M. harrisoni*, *M. huttoni*); the domed braincase group (*M. leucogaster*, *M. cyclotis*, *M. lorelieae*, *M. annamitica*, *M. beelzebub*, *M. walstoni*, *M. feae*, *M. eleryi*, *M. harpioloides*, *M. chrysochaetes*, *Harpiocephalus harpia* and *Harpiola isodon*), and highly domed braincase group (*M. fionae*).

Recent results showed the sexual dimorphism in Murininae species as *Harpiocephalus harpia* (Matveev, 2005; Lin *et al*., 2006, Zhou *et al*., 2014; Chen *et al*., 2015) and *Murina cyclotis* (Francis and Eger, 2012). My results indicated that the sexual dimorphism of skull size is various in the species: the females significantly larger than the males in *M. cyclotis* (Son *et al*., 2015b) and *M. harrisoni* (Son *et al*., 2015a, Fig. 4. 7) or the females slightly larger than the males in *M. beelzebub*, *M. lorelieae* (Table 4. 4), *M. annamitica* (Son *et al*., 2015b), but similar in skull size in *M. walstoni* (Table 4. 4) and *M. feae* (Son *et al*., 2015b). Detail sexual differences in *M. harrisoni* (Son *et al*., 2015a, Figs. 4. 7 and 4. 8) and as well as Son *et al*. (2015b) and Wu *et al*. (2015), I suggest that limiting factors for morphological variability exists in the nasal capsule or braincase, possibly in relation with the echolocation function.

My results suggested that the genus *Murina* are separated into two types, namely "*suilla*-type" dentition and "*cyclotis*-type" dentition by significantly differing in the relative ratio of the upper teeth of canines and second upper premolars (Son *et al*. 2015b). The results also indicated that the forearm length and overall skull size are related with completely different adaptational strategies among sympatric species pairs and intraspecific differences between sexes (Son *et al*., 2015a, Fig. 4. 9). Thus, the ecological adaptations for food habit might have produced morphological diversifications among species and sexes of the subfamily Murininae in Vietnam. For example, *M. cyclotis* and *M. feae* are similar in forearm length but they could be separated by skull size (Son *et al*., 2015a, Fig. 4. 9), whereas *M. fionae* clearly differs from *M. harrisoni* by the shape of skull (Figs. 2. 3, 4. 4).

The sexual dimorphism was indistinct in the species of Kerivoulinae (Chapter III). I found the significant differences in the skull size and shape of six species of Kerivoulinae from

Vietnam, of which, the largest-sized species is *K. papillosa*, which is larger than *K. kachinensis*; medium-sized species are *P. jagorii*, *K. titania*, and small-sized species are *K. picta, K. hardwickii* populations (Figs. 3. 3, 3. 4, 3. 5). In addition, my results suggested that the genus *Phoniscus* is clearly separated from *Kerivoula* by the difference in the size and shape of skull, nasal sinus, anterior palatal, canines, and second upper and lower premolars. These two genus can also be osteometrically separated by measurements of the braincase height and the interorbital width (Fig. 3. 8A, B). Remarkably, the morphological variations in the skull shape of *K. hardwickii* in Vietnam suggested a possible separation into three morphotypes: the north and the south populations may be representative of two distinct taxa, whereas the central population showed variation in skull shape and has a wide distribution from northern to southern Vietnam (Figs. 3. 8D, 3. 9).

5. 2. Diversity of tube-nosed and woolly bats in Vietnam

At present 15 species of Murininae have been recognized from Vietnam. In this study, I examined the species biodiversity of the subfamily Murininae in Vietnam which harbors the highest diversity of tube-nosed bats from South and Southeast Asia including about 40% of total species of Murininae when compared to other countries in Southeast Asia: Myanmar (4 species: Bates *et al.*, 2000), Thailand (10 species: Bumrungsri *et al*., 2006; Soisook, 2011; Soisook *et al*., 2013a, b), Laos (8 species: Francis and Eger, 2012), Cambodia (6 species: Csorba and Bates, 2005; Matveev and Csorba, 2007; Csorba *et al*., 2011; Ith *et al*., 2011).

In Southeast Asia, the subfamily Kerivoulinae currently contains 12 species of *Kerivoula* and two species of *Phoniscus* (Corbet and Hill, 1992; Vanitharani *et al*., 2003; Bates *et al*., 2004, 2007; Simmons, 2005; Thong *et al*., 2006; Francis et al., 2007; Douangboubpha *et al*., 2015). In this study, I accounted six species of the subfamily Kerivoulinae in Vietnam based the result from Hendrichsen *et al*. (2001), Bates *et al*. (2007), Can *et al*. (2008), and Kruskop (2013). The species richness of Kerivoulinae in Vietnam is higher than that of Myanmar (4 species) (Bates et al., 2000, 2004), Cambodia (4 species: Bates *et al*., 2007, Kingsada *et al*., 2011, Phauk *et al*., 2013), similar in Laos (6 species: Francis *et al*., 1999, Soisock *et al*., 2007; Thomas *et al*., 2013), but less Thailand (11 species) (Bates *et al*., 2007; Soisook, 2011; Douangboupha *et al*., 2014; Douangboubpha *et al*., 2015) and *K. hardwickii* can be separated into the three distinct species (Son *et al*., 2016).

In summary, Vietnam is surely considered as a hotspot of biodiversity in Asia. This idea has been proposed (Myers *et al*., 2000; Sterling *et al.* 2006; Tordoff *et al*., 2012). In addition to this current situation, future discoveries of new species and new records of species occurring in adjacent regions will surely comprehensively demonstrate further rich fauna of bats in this

country.

5. 3. Distribution status of tube-nosed and woolly bats in Vietnam

The distribution of several common species, e.g., *M. cyclotis*, *M. annamitica*, *M. feae*, *M. eleryi*, and *Harpiocephalus harpia* is shown in Table 4. 1, Fig. 4. 1, and Table 3. 2 for *K. kachinensis* and *K. titania*. These species have a wide distribution from north to central highlands, and southern Vietnam, and from low to the elevation of 1000 m above sea level. Other species, *M. lorelieae*, *M. harpioloides*, *M. chrysochaetes*, and *H. isodon* were found only at elevation above 1000 m above sea level in the north (Hoang Lien mountain), and high mountain in central part of Vietnam. These species have overlapped distribution with a common species, *M. huttoni*. *M. leucogaster*, a rare species, and has been known only from a single specimen collected in lowland area of Nghe An province (Fig. 1. 3, [22]). *M. fionae* has been found in the central Vietnam at elevation from 300 to 1200 m above sea level, whereas *M. beelzebub* has been known from north central, central highlands and south central Vietnam at elevations from 400 to 1600 m above sea level (Table 4. 1; Fig. 4. 10). In contrast, *M. walstoni* is a common species and distributed only in low areas (less 400 m above sea level.) in the central highland and south of Vietnam (Table 4. 1; Fig. 4. 10).

The fragmentation, complexity of the topography and the climatic conditions as well as a diversity of vegetation types in Vietnam (Rundel, 1999; Averyanov *et al*. 2003, Sterling *et al*., 2006, Can *et al*., 2008, Sang *et al*., 2009) may lead the high diversity of Vietnamese tube-nosed and woolly bats. The species richness of tube-nosed bats is usually in mountain forest over 500 m to higher elevations and primary forest (Table 4. 1; Figs. 4. 1, 4. 10): Hoang Lien Mountain in Lao Cai province (5 species) [1], Ngoc Linh Mountain in Kon Tum province (10 species) [29], and Ammatite Mountain Range from Nghe An province (7 species) [21, 22] to Quang Binh province (5 species) [24], and Quang Tri province (6 species) [25]. *K. hardwickii* is a widespread species in Vietnam (Can *et al*., 2008; Hendrichsen *et al*., 2001; Kruskop, 2013; Kuznetsov, 2006). However, Son *et al*. (2016) indicated that the populations of *K. hardwickii* from northern, central, and southern Vietnam should be considered as three distinct taxa [Figs. 3. 2; 3. 8D, E]. Based on the variations of skull size and shape in *K. hardwickii*, Thanh Hoa [16, 17, 19, 20] and Dong Nai [40] provinces (Figs. 1. 1, 1. 2, 3. 2) could be considered as the transition zones of the northern, central and southern population of this species.

5. 4. Karyotype diversification of tube-nosed bats

This study provided the data about karyotype of seven species of Murininae from Vietnam,

of which karyotype of five species have been reported for the first recorded (*M. huttoni, M. cyclotis*, *M. beelzebub*, *M. lorelieae*, and *Harpiola isodon*). The results indicated that the species of *Murina* and *Harpiola* have the same karyotype (n=44) and the morphological characteristics of chromosome are similar, whereas it is fewer differs from the number in *Harpiocephalus harpia* in Thailand (n=40) (McBee *et al*., 1986). In additional, I also investigated the karyotype of *H. harpia* from Taiwan and Guangdong province in southern China, which have an additional small submetacentric pair.

5. 5. Taxonomic assignment

Subfamily Murininae

There are few usable external, craniodental measurements, teeth character, shape skull, and the fur color (or color pattern) for species identification in the subfamily Murininae. Murininae contains two genus, *Harpiocephalus* and *Murina* (Corbet and Hill, 1992; Koopman, 1993; 1994; and Simmons, 2005). Actually *Murina* had been synonymized with *Harpiola* (Thomas, 1915; Tate, 1941), and Ellerman and Morrison-Scott (1951) assigned *Harpiola* as a subgenus of *Murina*. However, Bhattacharyya (2002) re-evaluated *Harpiola* as full generic rank. Kou *et al*. (2006) reconfirmed that genus *Harpiola* is separated from *Murina* and described the second species *Harpiola isodon* from Taiwan. Subsequently, Kruskop *et al*. (2006) and Kruskop and Shchinov (2010) reported *H. isodon* from Vietnam. These authors also showed that *Harpiola* can be distinguided from *Murina* by having the first upper premolar higher than that of the second upper premolar.

The skull size of *Harpiocephalus* is significantly larger than those of *Murina* and *Harpiola* (Son *et al*., 2015a). *Harpiola* can be clearly separated from *Murina*. The both upper premolars and canine are similar in size and shape and the upper incisors exceed the half of the height of the corresponding canines in *Harpiola* (Kuo *et al*., 2006; Kruskop *et al*., 2006; Son *et al*., 2015a).

M. harrisoni can be clearly separated from the other species of subfamily Murininae by having the flattened skull and difference in color pattern (Csorba and Bates, 2005; Csorba *et al*., 2007; Son *et al*., 2015a). Son *et al*. (2015a, b) showed significant differences of "*suilla*-type" and "*cyclotis*-type" dentition by the ratio of canine and second upper premolar. The largest species of "*suilla*-type" dentition, *M. leucogaster* is different from the other species of *"cyclotis*-type" dentition. Moreover, *M. walstoni* and *M. fionae* are distinguishable from the other species of Murininae by color pattern (Csorba *et al*., 2011; Francis and Eger, 2012; Son *et al*., 2015a).

In terms of color pattern, *M. feae* is similar to *M. beelzebub* (Csorbat *et al*. 2011; Francis and Eger 2012) but the skull size of *M. beelzebub* is distinctly larger that of *M. feae* (Son *et al*., 2015b) as well as FA and TIB (Son *et al*. 2015a). The color pattern is also similar in *M. huttoni*, *M. cyclotis*, *M. lorelieae*, and *M. annamitica,* (Francis and Eger, 2012, Tu *et al*., 2015), however, *M. cyclotis* differs from other species in having a reduced mesostyle on the upper molars (Francis and Eger, 2012; Son *et al*., 2015a), whereas the skull size of *M. huttoni* is distinctly larger than that of *M lorelieae*, *M. annamitica*, and the braincase is flattened (Son *et al*., 2015a), and *M lorelieae* differs from and *M. annamitica* by the differences in fur color of ventral surface (Eger and Lim, 2011; Tu *el al*., 2015; Son *et al*., 2015a) and "type" of dentition (Son *et al*., 2015a).

The color pattern is various in *M. eleryi* (Furey *et al*., 2009) to compare with *M. harpioloides* (Kruskop and Eger, 2008), and *M. chrysochaetes* (Eger and Lim, 2011). The skull size of *M. chrysochaetes* is smaller than that of *M. eleryi* and they also differs from each other in other skull features and fur color (Eger and Lim, 2011). However, Son *et al*. (2015a, b) indicated that the external and craniodental measurement are overlapped in *M. eleryi*, *M. harpioloides* and *M. chrysochaetes* but *M. chrysochaetes* differs from *M. eleryi* and *M. harpioloides* by the difference in skull shape (Fig. 4. 4) and reduced mesostyle on the first and second upper molars. Whereas *M. harpioloides* has more orange colouration of the guard hairs (Fig. 4. 3) and a slightly reduced mesostyle on the first and second upper molars, but well developed in *M. eleryi*.

Subfamily Kerivoulinae

Thomas (1914), Troughton (1929), Hill (1965), Corbet and Hill (1992) indicated that the subfamily Kerivoulinae includes two genus, *Phoniscus* and *Kerivoula*, but Tate (1941), Laurie and Hill (1954), Ryan (1965), Koopman (1993, 1994) considered *Phoniscus* as a subgenus of *Kerivoula*. Taxonomy of the Kerivoulinae in Southeast Asia including Vietnam remains unclear with highly problematic (Thong *et al*., 2006) and a large number of cryptic forms (Mayer and Helversen, 2001, Helversen *et al*., 2001) and an unresolved taxonomy (Francis *et al*., 2007, 2010, Dounangboubpha *et al*., 2015) and these is a lack of material for comparisons (Faisal *et al*., 2010). Recently publication also indicated with highly problematic in *Kerivoula* species in Vietnam, in which Bates *et al*. (2007) described a new species, *K. titania* from Cambodia and Vietnam. These authors also verified that the previous record of *M. flora* from Vietnam by Hendrichsen *et al*. (2001) is a misidentification and it should be treated as *K. titania.*

The study indicated *Phoniscus* can be clearly distinct from *Kerivoula* by the differences size and shape of braincase, interorbital, and anterior palatal emargination (Son *et al*., 2016).

The size and skull shape are also different among the species of Kerivoulinae. The large-sized group consists of *K. kachinensis* and *K. papillosa*, and the two species are similar in large size but differs from each other in braincase height (Son *et al*., 2016). The two species are clearly different from *K. kachinensis* by flatted skull (Bates *et al*., 2004, Thong *et al*., 2006; Soisook et al., 2007). Recent results also indicated the variation in shape skull of *K pipillosa* (Hansan and Abdullah, 2011; Dounangboubpha *et al*., 2015) and *K. hardwickii* (Dounangboubpha *et al*., 2015) in Southeast Asia. There appear to be three morphotypes of *K. hardwickii* in Vietnam (Son *et al*. 2016), and *K. papillosa* is smaller to compare with *K. papollosa* in Malaysia's population (Kingston *et al*., 1999; Hansan and Abdullah, 2011) and distributed only in southern of Vietnam (Son *et al*. 2016).

The genus *Kerivoula* from Vietnam are taxonomically complex including a number of cryptic species. The results also revealed the morphological variations in the skull shape of *K. hardwickii* in Vietnam. This suggests a possible separation of the species into three morphotypes, representing cryptic species supported by statistical differences with wide variation in skull shape, size and teeth.

Conclusions

This is the first study on the multivariate analysis of comprehensive assesses of interspecific and intraspecific variation patterns related to species discrimination, species taxonomy, diversification, and sexual dimorphism of subfamily Murininae and Kerivoulinae from Vietnam. The important contributions are shown as follows:

1) Accounted fifteen Murininae species of three genus in Vietnam, the subfamily indicated the highest diversity in Southeast Asia and the world. The results regarded Vietnam as the species center of the subfamily Murininae in the world. The high species diversity of the subfamily Murininae reflects the complicated geomorphology and caused allopatric speciation, as well as ecological interactions and adaptations between sympatric species pairs and intraspecific differences between sexes. The results also updated locality records and karyotypes of four *Murina* species (*M. huttoni*, *M. cyclotis*, *M. lorelieae*, and *M. beelzebub*), and one *Harpiola* species (*Harpiola isodon*) from Vietnam. The karyotypes of all species had similar in chromosome number, but *Harpiocephalus* is different from the other taxa in having an additional small submetacentric.

2) According to the overall skull size, the studied species could be clearly divided the two subfamilies Murininae and Kerivoulinae as following: largest species (*Harpiocephalus harpia*), large species (*M. leucogaster, M. tiensa, M. fionae, K. kachinensis*, and *K. papillosa*), medium species (*M. huttoni*, *Harpiola isodon*, *M. cyclotis*, *M. lorelieae*, *M. annamitica*, *M. beelzebub*, *M. walstoni*, *M. feae*, *Phoniscus jagorii*, and *K. titania*), and small species (*M. eleryi*, *M. chrysochaetes*, *M. harpioloides, K. picta*, and *K. hardwickii*).

3) The study provided the key of taxonomic relationships among *Murina* species from Vietnam. The morphological characteristics related to skull size, skull shape, and pelage characteristics revealed by this study are essential and substantial for the species identification of this groups from Vietnam.

4) The results clearly revealed the morphological variations in the skull shape of *K. hardwickii* in Vietnam. The results demonstrated *K. hardwickii* can be separated into the three morphotypes by differences in variations of skull size, shape, and teeth. This results will serve as the basis for the future assessment and classification of this group in Southeast Asia.

5) The food habits, zoogeographic barrier, elevation pattern can be related to significant differences size, shape of skull, distribution pattern of each species. The sexual dimorphism depends on each species in Murininae. In some species *Harpiocephalus harpia*, *M. harrisoni*, *M.*

cyclotis females are significantly larger than males. Distribution pattern are shown in *M. beelzebub, M. walsotni, M. harpioloides, M. chrysochaetes*, and *K. hardwickii* populations.

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References

Abramov, A. V. and Kruskop, S. V. **2012**. The mammal fauna of Cat Ba Island, northern Vietnam. *Russian Journal of Thesiology*, 11: 57–72.

Abramov, A. V., Rozhnov, V. V., and Morozov, P. N. **2006**. Notes on mammals of the Ngoc Linh Nature Reserve (Vietnam, Kon Tum province). *Russian Journal of Theriology*, 5: 85–92.

Abramov, A. V., Kalinin, A. A., and Morozov, P. N. **2007**. Mammal survey on Phu Quoc Island, southern Vietnam. *Mammalia*: 40–46.

Abramov, A. V., Kruskop, S. V., and Shchinov, A. V. **2009**. Small mammals of the Dalat Plateau, Southern Vietnam. *Russian Journal of Theriology*, 8: 61–73.

Ando, K., Tagawa, T., and Uchida, T. A. **1977**. Considerations of karyotypic evolution within Vespertilionidae. *Experientia*, 33: 877–879.

Anthony, E. L. P. **1988**. Age determination in bats. Pp. 47–58, *in* Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington D. C., 479 pp.

Averyanov, L. V., Loc, P. K., Hiep, N. T., and Harder, D. K. **2003**. Phytogeographic review of Vietnam and adjacent areas of Eastern Indochina. *Komarovia*, 3: 1–83.

Bain, R. H. and Hurley, M. M. **2011**. A Biogeographic synthesis of the amphibians and reptiles of Indochina. Bulletin of the American Museum of Natural History. 138 pp.

Barlow, K. E., Jones, G., and Barratt, E. M. **1995**. Can skull morphology be used to predict ecological relationships between bat species? A test using two cryptic species of pipistrelle. Proceedings of the Royal Society of London B, 264: 1695–1700.

Bates, P. J. J. and Harrison, D. L. **1997**. Bats of the Indian subcontinent. Harrison Zoological Museum, Sevenoaks, UK, 258 pp.

Bates, P. J. J., Harrison, D. L., Jenkins, P. D., and Walston, J. L. **1997**. Three rare species of *Pipistrellus* (Chiroptera: Vespertilionidae) new to Vietnam. *Acta Zoologica Academiae Scientiarum Hungaricae,* 43: 359–374.

Bates, P. J. J., New, T., Pearch, M. J., Swe, K. M., Bu, S. S. H., and Tun, T. **2000**. A review of bat research in Myanmar (Burma) and results of a recent survey. *Acta Chiropterologica*, 2: 53–82.

Bates, P. J. J., Struebig, M. J., Rossiter, S. J., Kingston, T., Oo, S. S. L., and Mya, K. M. **2004**. A new species of *Kerivoula* (Chiroptera: Vespertilionidae) from Myanmar (Burma). *Acta Chiropterologica*, 6: 219–226.

Bates, P. J. J., Struebig, M. J., Hayes, B. D., Furey, N. M., Mya, K. M., Thong, D. V., Tien, D. P., Son, T. N., Harrison, D. L., Francis, C. M., and Gabor, C. **2007**. A new species of *Kerivoula* (Chiroptera: Vespertilionidae) from Southeast Asia. *Acta Chiropterologica*, 9: 323–337.

Bhattacharyya, T. P. **2002**. Taxonomic status of the genus *Harpiola* Thomas, 1915 (Mammalia: Chiroptera: Vespertilionidae), with a report of the occurrence of *Harpiola grisea* (Peters, 1872) in Mizoram, India. Proceedings of the Zoological Society, Calcutta, 55: 73–76.

Blackith, R. E. and Reyment, R. A. **1971**. Multivariate Morphometric. London, New York, Academic Press, 412 pp.

Borissenko, A. V. and Kruskop, S. V. **2003**. Bat of Vietnam and Adjacent manual. Zoological Museum of Moscow M.V. Lomonosov State University. Moscow, 203 pp.

Borissenko, A. V., Kruskop, S. V., and Ivanova, N. V. **2008**. A new mouse-eared bat (Mammalia: Chiroptera: Vespertilionidae) from Vietnam. *Russian Journal of Theriology*, 7: 57– 69.

Bourret, R. **1942**. Les mammifères de la collection du laboratoire de Zoologie de l'Ecole supérieure des sciences. Notes et Travaux de l'Ecole Supérieure, Université Indochinoise No. 1: 1–44.

Bumrungsri, S., Harrison, D. L., Satasook, C., Prajukjitr, A., Thong-Aree, S., and Bates, P. J. J. **2006**. A review of bat research in Thailand with eight new species records for the country. *Acta Chiropterologica*, 8: 325–359.

Can, N. D, Endo, H., Son, T. N., Oshida, T., Canh, X. L., Phuong, H. D., Lunde, P. D., Kawada, I. S., Hayashida, A., and Sasaki, M. **2008**. Checklist of wild mammal species of Vietnam. Primate Research Institute, Inuyama, Japan. 400 pp. [in English and Vietnamese].

Chen, B., Yu, W., Wu, Y., Li F., Xu, Z., Zhang, Q., Harada, M., Motokawa, M., Peng, H., Wang, Y., and Li, Y. **2015**. New record and sexual dimorphism of *Harpiocephalus harpia* in Guangxi and Jiangxi, China. *Sichuan Journal of Zoology*, 34: 211–215. [in Chinese with English abstract].

Corbet, G. B. and Hill, J. E. **1992**. The Mammals of the Indomalayan Region: A Systematic Review. Oxford University Press, Oxford, 488 pp.

Csorba, G. and Bates, P. J. J. **2005**. Description of a new species of *Murina* from Cambodia (Chiroptera: Vespertilionidae: Murininae). *Acta Chiropterologica*, 7: 1–7.

Csorba, G., Thong, D. V., Bates, P. J. J., and Furey, N. M. **2007**. Description of a new species of

Murina from Vietnam (Chiroptera: Vespertilionidae: Murininae). Occasional Papers, Museum of Texas Tech University, 268: 1–12.

Csorba, G., Son, T. N., Ith, S., and Furey, N. M. **2011**. Revealing cryptic bat diversity: Three new *Murina* and redescription of *M. tubinaris* from Southeast Asia. *Journal of Mammalogy*, 92: 891–904.

Csorba, G., Chou, C-H., Ruedi, M., Görföl, T., Motokawa, M., Wiantoro, S., Thong, D. V., Son, T. N., Lin L-K., and Furey, N. **2014**. The reds and the yellows: A review of Asian *Chrysopteron* (Chiroptera: Vespertilionidae: *Myotis*). *Journal of Mammalogy*, 95: 663–678.

Dang, X. N. and Canh, X. L. **2009**. Taxonomy of Mammals and Characteristics of Mammal fauna of Vietnam. Publishing House for Sciences and Technology. Hanoi, 149 pp. [In Vietnamese].

Dang, X. N., Son, T. N., and Ha, M. N. **2000**. The bats of fauna of Phong Nha-Ke Bang. *Journal of Forestry*, Hanoi, 12: 40–42. [in Vietnamese with English abstract].

Dang, X. N., Nghia, X. N., Son, T. N., and Hai, H. T. **2012**. Study of mammal diversity in Xuan Nha and Muong Do Nature Reserve, Son La province, Northwestern Vietnam. *Mammal Study*, 37: 55–62.

Dobson, G. E. **1872**. Notes on some bats collected by Captain W. G. Murray, in the North-Western Himalaya, with description of new species. *Proceedings of the Asiatic Society of Bengal*, 1872: 208–210.

Douangboubpha, B., Bumrungsri, S., Soisook, P., Karapan, S., and Bates, P. J. J. **2014**. The discovery of *Kerivoula krauensis* (Chiroptera: Vespertilionidae) in southern peninsular Thailand provindes new information on the distribution and conservation of this data deficient species. *Songklanakarin Journal of Sciences Technology*, 36: 577–582.

Douangboubpha, B., Bumrungsri, S., Satasook, C., Wanna W., Soisook P., and Bates, P. J. J. **2015**. Morphology, genetics and echolocation calls of the genus *Kerivoula* (Chiroptera, Vespertilionidae: Kerivoulinae) in Thailand. *Mammalia*. ISSN (Online) 1864-1547, ISSN (Print) 0025–1461.

Eger, J. L. and Lim, B. K. **2011**. Three new species of *Murina* from Southern China (Chiroptera: Vespertilionidae). *Acta Chiropterologica*, 13: 227–243.

Eisenberg, J. F. and Mckay, G. M. **1970**. An annotated checklist of the recent mammals of Ceylon with keys to the species. *Ceylon Journal of Scienc*e (*Biological Sciences*), 8: 69–99.

Elizabeth G. M. **2006**. Statistics in Psychosocial Research. Lecture 8. Factor Analysis I. The Johns Hopkins University and Elizabeth Garrett-Mayer. 2–56.

Ellerman, J. R. and Morrison-Scott, T. C. S. **1951**. Checklist of Palaearctic and Indian mammals 1758 to 1946. Trustees of the British Museum (Natural History), London. 810 pp.

Endo, H., Hikida, T., Motokawa, M., Chou, L. M., Fukuta, K., and Stafford, B. J. **2003a**. Morphological adaptation of the skull for various behaviors in the tree shrews. *The Journal of Veterinary Medical Science*, 65: 873–879.

Endo, H., Kimura, J., Oshida, T., Stafford, B. J., Rerkamnuaychoke, W., Nishida, T., Sasaki, M., Hayashida, A., and Hayashi, Y. **2003b**. Geographical variation of skull morphology and its functional significances in the red-checked squirrel. *The Journal of Veterinary Medical Science*, 65: 1179–1183.

Endo, H., Kimura, J., Oshida, T., Stafford, B. J., Rerkamnuaychoke, W., Nishida, T., Sasaki, M., Hayashida, A., and Hayashi, Y. **2004**. Geographical variation of skull size and shape in various populations in the black giant squirrel. *The Journal of Veterinary Medical Science*, 66: 1213–1218.

Endo, H., Hayashida, A., and Fukuta, K. **2007**. Multivariate analyses of the skull size and shape in the five geographical populations of the lesser false vampire. *Mammal Study*, 32: 23–31.

Faisal, A. A. K., Solari, S., Swier, V. J., Larsen, P. A., Abdullah, M. T., and Baker, R. J. **2010**. Systematics of Malaysian woolly bats (Vespertilionidae: *Kerivoula*) inferred from mitochondrial, nuclear, karyotypic and morphological data. *Journal of Mammalogy*, 91: 1058–1072.

Fooden, J. **1996**. Zoogeography of Vietnam primates. *International Journal of Primatololy*, 17: 845–899.

Francis, C. M. **2008**. A guide to the mammals of Southeast Asia. Princeton University Press, Princeton. 392 pp.

Francis, C. M. and Eger, J. **2012**. A review of tube-nosed bats *(Murina)* from Laos with a description of two new species. *Acta Chiropterologica*, 14: 15–38.

Francis, C. M., Guillén, A., and Robinson, M. F. **1999**. Order Chiroptera: Bats. *In* Wildlife in Lao PDR: 1999 status report Duckworth, J. W., R. E. Salter and K. Khounboline, editors. IUCN/WCS/CPAWM. Vientiane. 225–235.

Francis, C. M., Kingston, T., and Zubaid, A. **2007**. A new species of *Kerivoula* (Chiroptera: Vespertilionidae) from peninsular Malaysia. *Acta Chiropterologica*, 9: 1–12.

Francis, C. M., Borisenko, A. V., Ivanova, N. V., Eger, J. L., Lim, B. K., Servent, A. G., Kruskop, S. V., Mackie, L., and Hebert, P. D. N. **2010**. The role of DNA barcodes in understanding and conservation of mammal diversity in Southeast Asia. *Plos One. Asian Mammals and DNA barcodes*, 5 e12575: 1–12.

Fukui, D., Maeda, K., and Hill, A. D. **2005**. Geographical variation in the cranial external characters of the little tube-nosed bat, *Murina silvatica*, in the Japanese archipelago. *Acta Theriologica*, 50: 309–322.

Furey, N. M. and Tu, T. V. **2006**. The bat fauna of Khau Ca area, Vi Xuyen and Bac Me district, Ha Giang province, northern Vietnam. Report to the Fauna and Flora International Vietnam Programme, 18 pp.

Furey, N. M., Thong, D. V., Bates, P. J. J., and Csorba, G. **2009**. Description of a new species belonging to the *Murina* "*suilla*-group" (Chiroptera: Vespertilionidae: Murininae) from north Vietnam. *Acta Chiropterologica*, 11: 225–236.

Gannon W. L. and G. R. Rácz. **2006**. Character displacement and ecomorphological analysis of two long-eared *Myotis* (*M. auriculus* and *M. evotis*). *Journal of Mammalogy*, 87: 171–179.

Gray, J. E. **1842**. Description of some new genus and fifty unrecorded species of Mammalia. *Annals and Magazine of Natural History*, 10: 255–267.

Görföl, T., Csorba, G., Eger, J. L., Son, T. N., and Francis, C. **2014**. Canines make the difference: a new species of *Hypsugo* (Chiroptera: Vespertionidae) from Laos and Vietnam. *Zootaxa*, 3887: 239–250.

Gu, X. **2006**. The Karyotypes of six species of bats from Guizhou. *Chinese Journal of Zoology*, 41: 112–116. [in Chinese with English abstract].

Hammer, Ø., Harper, D. A. T., and Ryan, P. D. **2001**. *Palaeontologica Electronica* 4 (1): pp. 9. *In* PAST: Paleontological statistics software package for education and data analysis. <http://palaeo-electronica.org/20011/past/issue101.htm> (download on 10 September 2012).

Harada, M. **1973**. Chromosomes of nine Chiroptera species in Japan (Chiroptera). *La Kromosoma*, 91: 2885–2895.

Harada, M. and Yosida, T. H. **1978**. Karyological study of four Japanese *Myotis* bats (Chiroptera, Mammalia). *Chromosoma*, 5: 283–291.

Harada, M., Ando, K., Uchida, T. A., and Takada, S. **1987**. A karyological study on two Japanese species of *Murina* (Mammalia: Chiroptera). *Journal of the Mammalogical*

Society of Japan, 12: 15–23.

Hasan, N. H. and Abdullah, M. T. **2011**. A morphological analysis of Malaysian *Kerivoula* (Chiroptera, Vespertilionidae). *Mammal Study*, 36: 87–97.

Helversen, O. von, Heller, K. G., Mayer, F., Nemeth, A., Volleth, M., and Gombkötö, P. **2001**. Cryptic mammalian species: a new species of whisker bat (*Myotis alcathoe* n. sp.) in Europe. *Naturwissenschaften*, 88: 217–223.

Hendrichsen, D. K., Bates, P. J. J, Hayes, B., and Walston, J. L. **2001**. Recent records of bats (Mammalia: Chiroptera) from Vietnam with six species new to the country. *Myotis*, 39: 35–122.

Hill, J. E. **1964**. Notes on some tube-nosed bats, genus *Murina*, from Southeastern Asia, with descriptions of a new species and a new subspecies. *Federation Museums Journal*, 8: 48– 59.

Hill, J. E. **1965**. Asiatic bats of the genus *Kerivoula* and *Phoniscus* (Vespertilionidae) with a note on *Kerivoula aerosa* Tomes. *Mammalia*, 29: 524–556.

Hill, J. E. **1983**. Bats (Mammalia: Chiroptera) from Indo-Australia. *Bulletin of the British Museum Natural History*, Zoology, 45: 103–208.

Hill, J. E. and Francis, C. M. **1984**. New bats (Mammalia: Chiroptera) and new records of bats from Borneo and Malaya. *Bulletin of the British Museum Natural History*, Zoology, 47: 305–329.

Hill, J. E. and Rozendaal, F. G. **1989**. Records of bats (Microchiroptera) from Wallacea. *Zoologische Mededelingen* (Leiden), 63: 97–122.

Hong, M. P. **2001**. Bats of Vietnam bats and their production in economic and agricultural. Agricultural Publish House. Hanoi. 147 pp. [in Vietnamese].

Horsfield, T. **1821–24**. Zoological researches in Java and the neighboring islands Kingbury, Parbury & Allen. London. unpaginated.

Husar, S. L. **1976**. Behavioral character displacement: evidence of food partitioning in insectivorous bats. *Journal of Mammalogy*, 57: 331–338.

Huynh, H. D., Tien, V. D., Sung V. C., Anh, T. P., and Khien, M. H. **1994**. Checklist of Mammalia of Vietnam. Science and Technics Publishing House, Ha Noi, 168 pp. [in Vietnamese].

Ith, S., Csorba, G., Bates, P. J. J., and Furey, N. M. **2011**. Confirmation of seven bat species for Cambodia. *Cambodian Journal of Natural History*, 2: 92–103.

James D. B. **2009**. Choosing the right number of components or factor in PCA and EFA. Shiken: *JALT testing and Evaluation SIG Newletter*, 13: 19–23.

Jungers, W. L., Falsetti, A. B., and Wall, C. E. **1995**. Shape, relative size, and size-adjustments in morphometrics. *Yearbook of Physical Anthropology*, 38: 137–161.

Khoi, V. L. **2000**. List of Mammal of Vietnam. Agricultural Publish House. Hanoi. 139pp. [in Vietnamese].

Khoi, V. L., Tien, D. P., Son, T. N., and Hung, M. T. **2007**. Preliminary result on bat survey in Chu Yang Sin, Yok Don National Park (Dak Lak province) and Pu Huong Nature Reserve (Nghe An province). *Proceedings of the 2nd National Scientific Conference on Ecology and Biological Resources Hanoi.* Agricultural Publish House: 373–379. [in Vietnamese with English abstract].

Kingsada, P., Douangboubpha, B., Ith, S., Furey, N., Soisook, P., Bumrungsri, S., Satasook C., Thong, V. D., Csorba, G., Harrison, D., Pearch, M., Bates, P., and Thomas, N. **2011**. A checklist of bats from Cambodia, including the first record of the intermediate horseshoe bat *Rhinolophus affinis* (Chiroptera: Rhinolophidae), with additional information from Thailand and Vietnam. *Cambodian Journal of Natural History*, 1: 49–58.

Kingston, T., Jones, G., Akbar, Z., and Kunz, T. H. **1999**. Echolocation signal design in Kerivoulinae and Murininae (Chiroptera: Vespertilionidae) from Malaysia. *Journal of Zoology,* (*London*), 249: 359–374.

Koopman, K. F. **1989**. Distributional Patterns of Indo-Malayan Bats (Mammalia: Chiroptera). *American Museum Novitates*, 2942: 19p.

Koopman, K. F. **1993**. Order Chiroptera. *In* Mammal species of the World. 2nd New records of Microchiroptera from Vietnam and Thailand 93 edition (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington D. C. 137–241.

Koopman, K. F. **1994**. Chiroptera: systematics. *In* Handbook of Zoology. Vol. 8, Part 60: Mammalia. Walter de Gruyter, Berlin, 217 pp.

Kruskop, S. V. **2013**. Bats of Vietnam. Checklist and an Identification Manual. Joint Russian-Vietnamese Sciences and Technological Centre and Zoological Museum of Moscow M. V. Lomolosov State University, 299 pp.

Kruskop, S. V. and Eger, J. L. **2008**. A new species of Tube-nosed bat *Murina* (Vespertilionidae, Chiroptera) from Vietnam. *Acta Chiropterologica*, 10: 213–220.

Kruskop, S.V. and Shchinov, A. V. **2010**. New remarkable bat records in Hoang Lien Son mountain range, northern Vietnam. *Russian Journal of Theriology*, 9: 1–8.

Kruskop, S. V., Kalyakin, M. V., and Abramov, A. V. **2006**. First record of *Harpiola*

(Chiroptera, Vespertilionidae) from Vietnam. *Russian Journal of Theriology*, 5: 13–16.

Kuo, H.-C., Fang, Y.-P., Csorba, G., and Lee, L.-L. **2006**. The definition of *Harpiola* (Vespertilionidae: Murininae) and the description of a new species from Taiwan. *Acta Chiropterologica*, 8: 11–19.

Kuo, H.-C., Fang, Y.-P., Csorba, G., and Lee, L. L. **2009**. Three new species of *Murina* (Chiroptera: Vespertilionidae) from Taiwan. *Journal of Mammalogy*, 90: 980–991.

Kuznetsov, G. V. **2006**. Mammals of Vietnam. KMK Scientific Press Ltd., Moscow, 420 pp. [In Russian].

Laurie, E. M. and Hill, J. E. **1954**. List of Land Mammals of New Guinea, Celebes and adjacent islands. British Museum (Natural History) Publications. London. 1758–1952.

Lin, L. K., Motokawa, M., and Harada, M. **2002**. Karyology of ten vespertilionid bats (Chiroptera: Vespertilionidae) from Taiwan. *Zoological Studies*, 41: 347–354.

Lin, L. K., Harada, M., Motokawa, M., and Lee, L. L. **2006**. Updating the occurrence of *Harpiocephalus harpia* (Chiroptera: Vespertilionidae) and its karyology in Taiwan. *Mammalia*, 70: 170–172.

Lindenfors, P., Gittleman, J. L., and Jones, K. E. **2007**. Sexual size dimorphism in mammals. *In* (D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, eds.). Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford. 16–26.

Lisón, F., Haz, A., Revelles, C. G., and Calvo, J. F. **2014**. Sexual size dimorphism in greater mouse-eared bat *Myotis myotis* (Chiroptera: Vespertilionidae) from a Mediterranean region. *Acta Zoologica*, 95: 137–142.

Liu, Z., Zhang, Y., Zhang, J., and Zhang, L. **2014**. *Murina eleryi* discovered in Hunan province. *Chinese Journal of Zoology*, 49 (1): 132–135. [in Chinese with English abstract].

Lunde, D. P., Musser, G. G., and Tien, D. P. 2003a. Records of some little known bats (Chiroptera: Vespertilionidae) from Vietnam. *Mammalia*, 67: 459–461.

Lunde, D., Musser, G. G., and Son, T. N. **2003b**. A survey of small mammals from Mt. Tay Con Linh II, Vietnam, with the description of a new species of *Chodsigoa* (Insectivora: Soricidae). *Mammals Study*, 28: 31–46.

Lunde, D. P., Son, T. N., and Musser, G. G. **2007**. A survey of small mammals from Huu Lien Nature Reserve, Lang Son Province, Vietnam. *Mammal Study*, 32: 155–168.

Maeda, K. **1980**. Review on the classification of little Tube-nosed bats, *Murina aurata* group. *Mammalia*, 44: 531–551.

Matthew, J. S., Rossiter, S. J., Bates, P. J. J., Kingston, T., Oo, S. S. L , New, A. A., Aung, M. M., Win, S. S., and Mya, K. M . **2005**. Results of a recent bat survey in upper Myanmar including new records from the Kachin forests. *Acta Chiropterologica*, 7: 147–163.

Matveev, V. A. **2004**. Systematics of Old World Chiroptera Derived from the Insertions of DNA Interspersed Repeats. PhD thesis. Moscow: Moscow State University. 293 pp.

Matveev, V. A. **2005**. Checklist of Cambodian bats (Chiroptera), with new records and remarks on taxonomy. *Russian Journal of Theriology,* 4: 43–62.

Matveev, V. A. and Csorba, G. **2007**. Bat fauna of Cambodia. *Bat Research News*, 48: 100–101.

Mayer, F. and Helversen, O. von. **2001**. Cryptic diversity in European bats. *Proceeding of the Royal Society London*. *Biological Sciences*, 268: 1825–1832.

McBee, K., Bickham, J. W., Yenbutra, S., Nabhitabhata, J., and Schlitter, D. **1986**. Standard karyology of nine species of vespertilionid bats (Chiroptera: Vespertilionidae) from Thailand. *Annals of Carnegie Museum* 55: 95–116.

Miller, G. S. **1905**. A new genus of bats from Sumatra. *Proceedings of the Biological Society Washington*, 48: 229–230.

Miller, G. S. **1907**. The families and genus of bat. United States of National Museum. *Bulletin*, 57: I-XVII, 1–282.

Milne-Edwards, A. **1868–74**. Mémoire sur la faune mammalogique du Tibet oriental et principalement de la principauté de Moupin. *In*: Recherches pour servir à l'histoire naturelle des mammifères: comprenant des considérations sur la classification de ces animaux (Minle. H-Edwards), 2 volumes. G. Masson, Paris. 231–379.

Minh, D. L., Ha, M. N., and Son, T. N. **2011**. Biodiversity and conservation status of the bat fauna at Pu Mat National Park. *Proceedings of the 4th National Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 737–743. [in Vietnamese with English abstract].

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. **2000**. Biodiversity hotpots for conservation priorities. *Nature*, 403: 853–858.

Myers, P. P. **1978**. Sexual dimorphism in size of vespertilionid bats. *The American Naturalist*, 112: 701–711.

Ono, T. and Obara, Y. **1994**. Karyotypes and Ag-NOR variations in Japanese vespertilionid bats (Mammalia: Chiroptera). *Zoological Science*, 11: 473–484.

Osgood, W. H. **1932**. Mammals of the Kelley-Roosevelts and Delacour Asiatic Expeditions.

Publications of Field Museum of Natural History, Zoological Series, 18: 193–339.

Payner, R. W. **1987**. Genstat 5 reference manual. Clarendon Press, Oxford, 749 pp.

Peters, W. **1872**. Mittheilung über neue Flederthiere. *Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1872: 256–264.

Phauk, S., Sarith, P., and Furey, N. M. **2013**. Cambodian bat echolocation: a first description of assemblage call parameters and assessment of their utility for species identification. *Cambodia Journal of Natural History*, 1: 16–26.

Phuong, H. D. and Son, T. N. **2011**. Value of mammal species of Northwest Vietnam. *Proceedings of the 4th National Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 1241–1248. [in Vietnamese with English abstract].

Postawa T., Zagorodniuk, I., and Bachnek, J. **2012**. Patterns of cranial size variation of two sibling species *Plecotus auritus* and *P. austriacus* (Chiroptera: Vespertilionidae) in a contact zone. *Journal of Zoology*, 288: 294–302.

Racey, P. A. **1990**. Reproductive assessment. *In* (T. H. Kunz, ed.). Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, D. C. 31–45.

Reyment, R. A. **1971**. Multivariate normality in morphometric analysis. *Mathematical Geology*, 3: 357–368.

Ruedi, M., Biswas, J., and Csorba, G. **2012**. Bats from the wet: two new species of tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India. *Revue Suisse de Zoologie*, 119: 111–135.

Rundel, P. W. **1999**. Forest habitats and flora in Laos, Cambodia, and Vietnam. Conservation Priorities in Indochina-WWF Desk Study. 85–157.

Ryan, R. M. **1965**. Taxonomic status of the vespertilionid genus *Kerivoula* and *Phoniscus*. *Journal of Mammalogy*, 46: 517–518.

Scully, J. **1881**. On the mammals of Gilgit. *Proceedings of the Zoological Society of London,* 1881: 197–209.

Sang, V. N., Cuc, T. H., and Truong, Q. N. **2009**. Herpestofauna of Vietnam. Frankfurt am Main. 768 pp.

Simmons, N. B. **2005**. Order Chiroptera. *In* (D. E Wilson and D. M. Reeder, eds.). Mammal Species of the World: A Taxonomic and Geographic Reference 3rd ed. Johns Hopkins University Press, Baltimore, Maryland. 312–529.

Smith, A. T. and Xie, Y. **2008**. A Guide to the Mammals of China. Princeton University Press, Princeton, 544 pp.

Soisook, P. **2011**. A checklist of bats (Mammalia: Chiroptera) in Thailand. *Journal of Wildlife in Thailand*, 18: 121–151.

Soisook P., Bumrungsri, S., Dejtaradol, A., Francis, C. M., Csorba, G., Servent, A. G., and Bates P. J. J. **2007**. First records of *Kerivoula kachinensis* (Chiroptera: Vespertilionidae) from Cambodia, Lao PDR and Thailand. *Acta Chiropterologica*, 9: 339–345.

Soisook, P., Karapan, S., Satasook, C., and Bates, P. J. J. **2013a**. A new species of *Murina* (Mammalia: Chiroptera: Vespertilionidae) from peninsular Thailand. *Zootaxa*, 3746: 567–579.

Soisook, P., Karapan, S., Satasook, C., Thong, V. D., Khan, F. A. A., Maryanto, I., Csorba, G., Furey, N., Aul, B., and Bates, P. J. J. **2013b**. A review of the *Murina cyclotis* complex (Chiroptera: Vespertilionidae) with description of a new species and subspecies. *Acta Chiropterologica*, 15: 271–292.

Son, T. N. **2001**. Biodiversity of mammalian fauna in Luc Son, Bac Giang. Workshop Biology International in Vietnam. Agriculture Publishing House. 45–50. [in Vietnamese with English abstract].

Son, T. N. **2005**. Bat diversity in Ba Be National Park and Na Hang Natural Reserve. Propose solutions for management and conservation. Master thesis. Hanoi: Institute of Ecology and Biological Resources (Vietnam Academy of Sciences and Technology) and Thai Nguyen University. 74 pp.

Son, T. N. and Thong, D. V. **2004**. Results of the bat survey in the Dong Phuc, Ban Thi-Xuan Lac areas (Bac Can province) and the Sinh Long, Ban Lam areas (Tuyen Quang province). *Journal of Biology*, 26: 25–30. [in Vietnamese with English abstract].

Son, T. N. and Thong, D. V. **2005**. The biodiversity of bat fauna in Ba Be National Park and Na Hang Nature Reserve area. Issues of Basic Research in Life Sciences. Science and Techniques Publishing House. 272–275. [in Vietnamese with English abstract].

Son, T. N. and Csorba G. **2007**. Preliminary result on bat survey in Bac Huong Hoa protected area and Dakrong Nature Reserve, Quang Tri province. *Proceedings of the 2nd National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 532–536. [in Vietnamese with English abstract].

Son, T. N. and Nghia, X. N. **2007**. Results of the survey of the bat fauna in the Tam Dao National Park, Vinh Phuc province and characteristic of biological and ecological of some species. *Proceedings of the 2nd National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 522–531. [in Vietnamese with English abstract].

Son, T. N. and Thong, D. V. **2011**. Recent bat survey in Chu Mom Ray National Park (Kon Tum province) and Song Thanh Nature Reserve (Quang Nam Province). *Proceedings of the 4th National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 314–318. [in Vietnamese with English abstract].

Son, T. N., Dang, X. N., and Hendrichsen, D. **2000**. Preliminary results of surveys of bats (Chiroptera) in Phong Nha–Ke Bang (Quang Binh province) and Huu Lien (Lang Son province). *Journal of Biology*, 22: 145–150. [in Vietnamese with English abstract].

Son, T. N., Can, N. D., and Thong, D. V. **2003**. The fauna of bat in Na Hang Nature Reserve, Tuyen Quang province. Issues of Basic Research in Life Sciences. Science and Technics Publishing House. 721–725. [in Vietnamese with English abstract].

Son, T. N., Tien, D. P., Can, N. D., Lunde, D., Musser, G., and Dung, A. D. **2004**. Species diversity of the bat in Huu Lien Nature Reserve and the threaten factors to the population Ha Noi. Issues of Basic Research in Life Sciences. Science and Techniques Publishing House. 214–218. [in Vietnamese with English abstract].

Son, T. N., Kawada, I. S., Moribe, J., and Abramov. V. A. **2009a**. The recorded results on small mammal in Hoang Lien National Park and Van Ban area, Lao Cai province. *Proceedings of the 3rd National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 784–789. [in Vietnamese with English abstract].

Son, T. N., Phuong, H. D., Cuong, V. T., Thong, D. V., and Csorba, G. **2009b**. Preliminary results about bats and rodent in Vinh Cuu Nature Reserve and Historical Monument, Dong Nai province. *Proceedings of the 3rd National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 776–783. [in Vietnamese with English abstract].

Son, T. N., Thong, D. V., Tien, D. P., and Khoi, V. L. **2009c**. Status of Flying Fox Bat (*Pteropus* spp.) in Vietnam. *Journal of Biology*, 31: 52–57. [in Vietnamese with English abstract].

Son, T. N., Thong, D. V., and Dang, X. N. **2010**. Status and distribution of some bats of the families Hipposideridae and Rhinolophidae in Vietnam. Issues of Basic Research in Life Sciences. *Journal of Biotechnology*, 8: 981–990. [in Vietnamese with English abstract].

Son, T. N., Dang, X. N., and Can, N. D. **2011**. Fauna (Mammalia) diversity of northeast region of Vietnam. 2011. *Proceedings of the 4th National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 865–875. [in Vietnamese with English abstract].

Son, T. N., Görföl, T., Francis, C., Motokawa, M., Estók, P., Endo, H., Thong, D. V., Dang, X. N., Oshida, T., and Csorba, G. **2013**. Description of a new species of *Myotis* (Vespertilionidae) from Vietnam. *Acta Chiropterologica*, 15: 473–483.

Son, T. N., Csorba, G., Tu, T. V., Thong, D. V., Wu, Y., Harada, M., Oshida, T., Endo, H., and Motokawa, M. **2015a**. A new species of the genus *Murina* (Chiroptera: Vespertilionidae) from the Central Highlands of Vietnam with a review of the subfamily Murininae in Vietnam. *Acta Chiropterologica*, 17. (in press).

Son, T. N., Motokawa, M., Oshida, T., Thong, D. V., Csorba, G., and Endo, H. **2015b**. Multivariate analysis of the skull size and shape in tube-nosed bats of the genus *Murina* (Chiroptera: Vespertilionidae) from Vietnam. *Mammal Study*, 40: 79–94.

Son, T. N., Motokawa, M,. Oshida, T., and Endo, H. **2016**. A morphological analysis of the skull size and shape of Kerivoulinae (Chiroptera: Vespertilionidae) from Vietnam. *The Journal of Veterinary Medical Science*, 78. (in press).

Sterling, E. J., Hurley, M. M., and Minh, L. D. **2006**. Vietnam a Natural History. Yale University Press. 420 pp.

Tate, G. H. H. **1941**. Results of the Archbold epeditions No. 40. Notes on Vespertilionid bats. American Museum of Natural History, *Bulletin*, LXXVIII, Art. IX, 567–597.

Temminck, C. J. **1835–1841**. Monographies de Mammalogie ou description de quelques genres de mammifères, ont les espèces ont été observées dans les différents musées de l'Europe.Vol. 2. C. C. van der Hoek, Leiden, 392 pp.

Thanh, T. H., Fukui, D., Son, T. N., Huan, X. N., and Thong, D. V. **2014**. The currently known bat species composition of Khau Ca species and habitat conservation area, Ha Giang province. Vietnam National University. *Journal of Sciences*, 30: 103–110. [in Vietnamese with English abstract].

Thanh, T. H., Son, T. N., Khoi, V. N., and Thong, D. V. **2015**. Bat species composition in Ba Hon area, Hon Dat district, Kien Giang province. *Proceedings of the 6th National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 865–871. [in Vietnamese with English abstract].

Thomas, M. N., Duckworth, J. W., Douangboubpha, B., Williams, M., and Francis, C. M. **2013**. A checklist of bats (Mammalia: Chiroptera) from Lao PDR. *Acta Chiropterologica*, 15: 193–260.

Thomas, O. **1891**. Diagnoses of three new mammals collected by Signor L. Fea in the Carin Hills, Burma. *Annali del Museo Civico di Storia Naturale di Genova* (ser. 2), 10: 884.

Thomas, O. **1914**. New Asiatic and Australian bats and a new bandicoot. *Annals of the Magazine of Natural History*, 13: 439–444.

Thomas, O. **1915**. A special genus for the Himalayan bat known as *Murina grisea*. *Annals and Magazine of Natural History*, 8, 16: 309–310.

Thomas, O. **1923**. Scientific results from the mammal survey. XLI. On the forms contained in the genus *Harpiocephalus*. *Journal of the Bombay Natural History Society*, 29: 8889.

Thong, D. V. **2011**. Systematics and Echolocation of Rhinolophoid Bats (Mammalia: Chiroptera) in Vietnam. PhD thesis. University of Tübingen, Tübingen, Germany: 250 pp.

Thong, D. V. **2014a**. Taxonomic and distributional assessments of *Chaerephon plicatus* (Chiroptera: Molossidae) from Vietnam. *Journal of Biology*, 36: 479–486.

Thong, D. V. **2014b**. Acoustic identification and taxonomic remarks of Hipposiderids and Rhinolophids (Chiroptera: Hipposideridae, Rhinolophidae) in Tam Dao National Park, northeastern Vietnam. *Journal of Biology*, 36: 487–493.

Thong, D. V. **2014c**. Taxonomy and ecology of *Cynopterus horsfieldi* (Chiroptera: Pteropodidae) from Vietnam. *Biodiversity and Biological active substances*. 329–334.

Thong, D. V. and Viet, H. T. **2004**. Key to Chiropterans of Pu Hoat Nature Reserve and Bach Ma National Park. Ha Noi University of Education. *Journal of Science*, 4: 127–130. [in Vietnamese with English abstract].

Thong, D. V. and Furey, M. N. **2008**. The bat fauna of Cat Ba Biosphere Reserve. *Journal of Biology*, 30: 73–77. [in Vietnamese with English abstract].

Thong, D. V., Tien, P. D., and Sung, C.V. **2001**. Mountain Fruit Bat (*Sphaerias blanfordi*) first recorded in Vietnam. *Journal of Biology*, 23: 17–30. [in Vietnamese with English abstract].

Thong, D. V., Tien, D. P., and Son, T. N. **2003**. The fauna of bat recorded in Ba Be NP and Na Hang NR. Laboring Publishing House. 109–114. [in Vietnamese with English abstract].

Thong, D. V., Tien, D. P., Viet, H. T., and Furey, N. **2004**. Bats in Vietnam and their Vietnamese name. Ha Noi University of Education. *Journal of Science*, 4. 120–126.

Thong, D. V., Huynh, H. D., and Khoi, V. L. **2005**. Two bat species new to Vietnam. *Journal of Biology*, 27: 7–10. [in Vietnamese with English abstract].

Thong, D. V., Bumrungsri, S., Harrison, D. L., Pearch, M., Helgen, K.M., and Bates, P. J. J. **2006**. New records of Microchiroptera (Rhinolophidae and Kerivoulinae) from Vietnam and Thailand. *Acta Chiropterologica,* 8: 83–93.

Thong, D. V., Tu, T. V, Tien, D. P., Chu, C-W, Senawi, J., Bates, P. J. J., and Furey, N. **2007**. Echolocation call frequency of Marshall's Horseshoe Bat *Rhinolophus marshalli* from Cat Ba National Park and its current status in Vietnam. *Proceedings of the 2nd National Scientific Conference on Ecology and Biological Resources Hanoi.* Agricultural Publish House Hanoi. 274–277. [in Vietnamese with English abstract].

Thong, D. V., Dietz, C., Schnitzler, H.-U., Denzinger, A., Furey, N. M., Borissenko, A., and Bates, P. J. J. **2008**. First record of *Hipposideros khaokhouayensis* from Vietnam. Hanoi National University of Education. *Journal of Sciences*: 23–28.

Thong, D. V., Son, T. N., Hai, H. T., and Nha, V. P. **2009**. Current status of bats at Muong Do area, Phu Yen district, Son La province. *Proceedings of the 3rd National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 818–822. [in Vietnamese with English abstract].

Thong, D. V., Son, T. N., and Tien, D. P. **2010**. An overview of bat research in Bai Tu Long and Con Dao National Park, with results from recent surveys. Issues of Basic Research in Life Sciences. *Journal of Biotechnology*, 8: 999–1005. [in Vietnamese with English abstract].

Thong, D. V., Dietz, C., A. Denzinger, A., Bates, P. J. J., Furey, N. M., Csorba, G., Hoye, G., Thuy, D. L., and Schnitzler. H.-U. **2011**. Further records of *Murina tiensa* from Vietnam with first information on its echolocation calls. *Hystrix–Italian Journal of Mammalogy*, 22: 129–138.

Thong, D. V., Puechmaille, S. J., Bates, P. J. J., Csorba, G., Denginger, A., Dietz, C., Soisook, P., Furey, N. M., and Schnitzler, H.-U. **2012a**. Systematics of the *Hipposideros turpis* species complex (Chiroptera: Hipposideridae), with description of a new subspecies from Vietnam. *Mammal Review*, 42: 166–192.

Thong, D. V., Puechmaille, S. J., Denzinger, A., Dietz, C., Csorba, G., Bates, P. J. J., Teeling, E. C., and Schnitzler, H.-U. **2012b**. A new species of *Hipposideros* (Chiroptera: Hipposideridae) from Vietnam. *Journal of Mammalogy*, 93: 1–11.

Tien, D. P., Hoi, M. T., Son, T. N., and Thong, D. V. **2004**. Results of a bat survey in Xuan Son National Park. Issues of Basic Research in Life Sciences. Science and Technics Publishing House. 267–270. [in Vietnamese with English abstract].

Tordoff, A. W., Hieu, T. M., Ngoc, T. Q., Sterling, E., Sweet, P., Chesser, T., Kevin, B., Eger, J., Lim, B., Harder, D., Hiep, N. T., Anh, P. T., Thuy, L. D., Tien, P. D., Do, N. T., Hien, N. H., Truong, N. Q., and Loc, P. K. **2000**. A feasibility study for the establishment of Ngoc Linh Nature Reserve, Quang Nam province, Vietnam. Birdlife International

Vietnam Programme, Hanoi, 74 pp.

Tordoff, A. W., Bao, T. Q., Tu, N. D., and Hung, L. M. **2004**. Sourcebook of existing and proposed protected areas in Vietnam. Second edition. Hanoi: BirdLife International in Indochina and the Ministry of Agriculture and Rural Development.

Tordoff, A. W., Baltzer, M. C., Fellowes, J. R., Pilgrim, J. D., and Langhammer, P. F. **2012**. Key biodiversity areas in the Indo-Burma hotspot: Process, progress and future directions. *Journal of Threatened Taxa*, 4: 2779–2787.

Trai, L. T., Richardson, W. J., Tuyen, B. D., Cham, L. V., Dung, N. H., Hoach, H. V., Monastyrskii, A. L., and Eames, J. C. **1999**. An investment plan for Ngoc Linh Nature Reserve, Kon Tum province, Vietnam: A contribution to the management plan. BirdLife International Vietnam Programme, Hanoi, 106 pp.

Trai, L. T., Cham, L. V., Ngoc, T. Q., Hieu, T. M., Sang, N. V., Monastyrskii, A. L., Hayes, B. D., and Eames, J. C. **2000**. An investment plan for Kon Ka Kinh Nature Reserve, Gia Lai province, Vietnam: A contribution to the management plan. BirdLife International Vietnam Programme, Hanoi, 77 pp.

Troughton, E. G. **1929**. A new genus and species of bat (Kerivoulinae) from the. Solomons, with a review of the genus of the subfamily. *Australia Mas*, 17: 85–99.

Tu, T. V., Cornette, R., Utge, J., and Hassanin, A. **2015a**. First records of *Murina lorelieae* (Chiroptera: Vespertilionidae) from Vietnam. *Mammalia,* 79: 201–213.

Tu, T. V., Son, T. N., and Anh, H. L. **2015b**. First record of Japanese pipistrelle, *Pipistrellus abramus* (Temminck, 1838) on Bach Long Vi island, Hai Phong city. *Proceedings of the 6th National Scientific Conference on Ecology and Biological Resources Hanoi*. Agricultural Publish House. 383–386. [in Vietnamese with English abstract].

Van Peenen, P. F. D., Ryan, P. F., and Light, R. H. **1969**. Preliminary Identification Manual for Mammals of South Vietnam. Smithsonian Institution, 310 pp.

Vanitharani, J., Rajendran, A., Bates, P. J J., Harrison, D. L., and Pearch, M. J. **2003**. A taxonomic reassessment of *Kerivoula lenis* Thomas, 1916 (Chiroptera: Vespertilionidae) including a first record from peninsular India. *Acta Chiropterologica*, 5: 49–60.

Vishakha, K., Yardi, K., and Raut, R. **2007**. Diversity and distribution of bats in the eastern Ghats of India. *Zoo's Print Journal*, 22: 2752–2758.

Volleth, M. **2006**. Karyotype analysis of *Murina suilla* and *Phoniscus atrox* from Malaysia (Chiroptera: Murininae, Kerivoulinae). *Lynx (Praha)*, 37: 275–284.

Wang, Y. X. **2003**. A complete checklist of mammal species and subspecies in China: a

taxonomic and geographic reference. Beijing, China: China Forestry Publishing House. 59–60 (in Chinese).

Wu, H., Jiang, T. L., Muller, R., and Feng, J. **2015**. The allometry of echolocation call frequencies in horseshoe bats: nasal capsule and pinna size are the better predictors than forearm length. *Journal of Zoology*, 297: 211–219.

Wu, Y., Li Y., Lin, L. K., Harada, M., Chen, Z., and Motokawa, M. **2012**. New records of *Kerivoula titania* (Chiroptera: Vespertilionidae) from Hainan Island and Taiwan. *Mammal Study*, 37: 69–72.

Wu, Y., Motokawa, M., Li, Y., Harada, M., Chen, Z., and Yu, W. **2010**. Karyotype of Harrison's tube-nosed bat *Murina harrisoni* (Chiroptera: Vespertilionidae: Murininae) based on the second specimen recorded from Hainan Island, China. *Mammal Study*, 35: 277–279.

Xu, Z., Yu, W., Wu, Y., Li, F., Chen, B., Harada, M., Motokawa, M., Gong, Y., and Li, Y. **2014**. Preliminary study on population genetic structure and taxonomy of Elery's Tube-nosed bat (*Murina eleryi*). *Acta Theriologica Sinica*, 34: 270–277 (Chinese). [in Chinese with English abstract].

Zhou, Q., Zhang, Y., Motokawa, M., Harada, M., Gong, Y., Li, Y., and Wu, Y. **2011**. A new record bat *Murina huttoni* from Guangdong, China and its morphology, karyotypes, echolocation calls. *Chinese Journal of Zoology*, 41: 109–114. [in Chinese with English abstract].

Zhou, Q., Xu, Z., Yu, W., Li, F., Chen, B., Gong, Y., Harada, M., Motokawa, M., Li, Y., and Wu, Y. **2014**. The occurrence of bat *Harpiocephalus harpia* from Nanlin, Guangdong and its karyotypes, echolocation calls. *Chinese Journal of Zoology* 49: 41–45. [in Chinese with English abstract].

Appendix:

Appendix 1. 1. Localities for the specimens of the subfamily Murininae from Vietnam used in this study. Locality numbers correspond with Fig. 1. 3.

1. Lao Cai (Hoang Lien NP); 2. Ha Giang (Duc Xuan area; Vi Xuyen area; Khau Ca NR); 3. Tuyen Quang (Na Hang NR); 4. Bac Kan (Ba Be NP); 5. Cao Bang (Pia Oac NR); 6. Bac Kan (Kim Hy NR); 7. Thai Nguyen (Than Sa NR); 8. Lang Son (Huu Lien NP); 9. Quang Ninh (Bai Tu Long NP); 10. Hai Phong (Cat Ba NP); 11. Vinh Phuc (Tam Dao NP; Me Linh and Tam Dao NP); 12. Phu Tho (Xuan Son NP); 13. Son La (Co Ma area; Ta Sua NR); 14. Son La (Thuan Chau); 15. Son La (Xuan Nha NR); 16. Thanh Hoa (Pu Hu NR); 17. Thanh Hoa (Pu Luong NR); 18. Ninh Binh (Cucc Phuong NP); 19. Thanh Hoa (Xuan Lien NR); 20. Thanh Hoa (Ben En NP); 21. Nghe An (Pu Huong NR); 22. Nghe An (Pu Mat NP); 23. Ha Tinh (Vu Quang NP); 24. Quang Binh (Phong Nha-Ke Bang NP); 25. Quang Tri (Bac Huong Hoa NR; Dak Rong NR); 26. Thua Thien-Hue (Bach Ma NP); 27. Quang Nam (Song Thanh NR); 28. Quang Nam (Ngoc Linh NR); 29. Kon Tum (Ngoc Linh NR); 30. Quang Ngai (Ba To area); 31. Kon Tum (Chu Mom Ray NP); 32. Gia Lai (Kon Ka Kinh NP); 33. Binh Dinh and Phu Yen (Hoa Son area); 34. Dak Lak (Yok Don NP); 35. Dak Lak (Chu Yang Sin NP); 36. Lam Dong (Bi Dup-Nui Ba NP); 37. Khanh Hoa (Hon Ba NR); 38. Ninh Thuan (Nui Chua NP); 39. Dong Nai (Cat Tien NP); 40. Dong Nai (Vinh Cuu NR); 41. Binh Phuoc (Bu Gia Map NP); 42. Ba Ria-Vung Tau (Con Dao NP); 43. Kien Giang (Phu Quoc NP).

Appendix 2. 2. Specimens examined for study of the skull size and shape in tube-nosed bats of the genus *Murina*

Murina chrysochaetes (*n* = 1). Female (1): S186699. ***Murina harpioloides*** (*n* = 1). Female (1): ZMMU S-173401. ***Murina eleryi*** (*n* = 6). Male (3): IEBR-M-3644, 4070, HNHM 2007.51.1; Female (3): IEBR-M-3866, 4511, HNHM 2007.28.2. ***Murina feae*** (*n* = 33). Male (17): IEBR-M-1363, 1364, 3068, 3154, 3264, 3722, 3869, 3873, 4116, 4121, 4125, 4510, 4991, 5055, HNHM 22860, 22823, 2000.84.7; Female (16): IEBR-M-0495, 1360, 3718, 3728, 3867, 3870, 3871, 4214, 4127, 4123, 4563, 4679, 5054, HNHM 22868, 2000.84.4, 2010.42.2. ***Murina walstoni*** (*n* = 6). Male: IEBR-M-1481, 2479, 2920; Female: IEBR-M-1480, 4592, HNHM 22933. ***Murina annamitica*** (*n* = 21). Male (11): HNHM 22929, IEBR-M-1600, 2997, 3327, 3633, 3650, 3652, 4122, 4124, 4508, ZMMU S184673; Female (10): IEBR-M 2181, 3034, 3148, 3167, 3630, 3640, 3642, 3639, 4131, 4718. ***Murina beelzebub*** (*n* = 7). Male (3): HNHM 2007.50.24, IEBR-M-3904, 4149; Female (4): IEBR-M-4842, 3636, HNHM 2007.50.7, 2007.50.6. ***Murina cyclotis*** (*n* = 57). Male (32): IEBR-M-0505, 1390, 1887, 1891, 2180, 3046, 3054, 3069, 3129, 3132, 3133, 3134, 3320, 3607, 3632, 3736, 3738, 3874, 3875, 4052, 4071, 4119, 4120, 4126, 4172, 4187, 4562, 4591, 4678, 4753, 4942, 4976; Female (25): IEBR-M-0492, 1210, 1359, 1632, 2855, 3128, 3131, 3316, 3330, 3643, 3646, 3645, 3651, 3725, 37263868, 3872, 3876, 4223, 4560, 4561, 4953, HNHM 22919, 22925, S-184674. ***Murina huttoni*** (*n* = 7). Male (4): IEBR-M-4718, S-175150, 175151, 186700; Female (3): ZMMU S-186525, IEBR-M-3153, HNHM 22885. ***Murina fionae*** (*n* = 6). Male (5): IEBR-M-3080, 3588, 3902, 3917, HNHM 22858; Female (1): IEBR-M-4115. ***Murina tiensa*** (*n* = 5). Male (3): HNHM 2007.28.1, 2010.42.1, IEBR-M-4998; Female (2): IEBR-M-3299, HNHM 2009.6.2.

Appendix 3. 3. Specimens examined for study of the skull size and shape of Kerivoulinae (Chiroptera: Vespertilionidae) from Vietnam

K. hardwickii*-N** (n=39). Female (21): IEBR-M1950, 2937, 2938, 2940, 2941, 3048, 3933, 4982, 4999, 5003, 5005, 5027, 5485, 5548, 5621, 5635, 5637, T.050412.12, 050412.6, 050412.8, 050412.13, 050412.15. Male (18): IEBR-M2164, 2170, 2937, 3719, 3731, 3737, 4744, 4755, 5023, 5022, 5633, 5634, 5636, T.050412.3, 050412.7, 050412.17. ***K. hardwickii*-C** (n=17). Female (n=13): IEBR-M2163, 2168, 2166, 2169, 2217, 3074, 3075, 3286, 3432, 3438, 3590, 3878, 3879, 5057, 5734, IEBR-B240813.6. Male (n = 4): IEBR M2166, 2169, 2217, 5734. ***Kerivoula hardwickii*-S** (n=18). Female (8): IEBR-M1809, 2378, 2392, 2819, 2907, 2824, 2910, 4410. Male (10): IEBR-M2755, 2808, 2812, 2817, 2821, 2823, 2831, 2931, 4364, 4621. ***K. kachinensis (n=38). Female (30): IEBR-M498, 499, 500, 503, 1289, 1365, 1888, 1890, 1913, 1914, 1934, 1949, 1954, 1956, 2568, 2575, 3268, 3271, 3298, 3455, 3585, 3710, 5310, 5337, 5339, 5623, 5626, 5632, IEBR-B310414.14, VN11-1831. Male (8): IEBR-M-900, 1310, 2569, 3265, 5022, LV 05, VN11-0948, 0940. ***K. papillosa*** (n=5). Female (3): IEBR-M4620, 4625, 4363. Male (2): IEBR-M4365, 4417. ***K. picta*** (n=2). Female (1): IEBR-M12. Male (1): IEBR-M14. ***K. titania*** (n=49): Female (35): IEBR-M493, 494, 1314, 1366, 1379, 1380, 1929, 2468, 2470, 2471, 3062, 3064, 3077, 3091, 3179, 3189, 3304, 3305, 3314, 3317, 3903, 4153, 4227, 4622, 4623, 5311, 5312, 5372, 5403, 5404, 5753, VN11-0002, 0939, 0944, 0945. Male (14): IEBR-M490, 502, 3060, 3061, 3301, 3318, 3953, 5359, 5638, NH-2008, T.050412.10, 050412.14, VN11-0044, 1832. ***Phoniscus jagorii*** (n=4): Female (2): IEBR-M5418, VN14-0190. Male (2): IEBR-M4458, 5308.

Appendix 4. 4. Specimens of the subfamily Murininae used to review of the subfamily Murininae in Vietnam. Asterisk (*) indicates specimens examined for karyotype. Locality numbers correspond with Fig. 4. 1.

(F). ***M. leucogaster*** (n=2): Nghe An (Pu Mat NP) [22]: HZM1.31758 (F). China: Sichuan: IBHG10122 (M). ***M. harrisoni*** (n=21): Son La [15]: HNHM 2010.42.1 (M); Phu Tho [12]: Thong Coll.T2, IEBR T.290708.7 (M); Bac Kan [6]: HZM.2.38178 (holotype of *tiensa*) (F), HNHM 2007.28.1 (paratype of *tiensa*), HZM NF 301006.1 (M); Vinh Phuc [11]: HNHM 2009.6.2 (F), IEBR-M4998 (M); Hai Phong [10]: IEBR T.220408.2 (F); Thanh Hoa [19]: IEBR-M6033 (F), Nghe An [22]: IEBR-M3299; HZM 1.31525 (F); Dak Lak [34]: ROM 107750 (F), 107739, 107749 (M); Cambodia: HZM 1.36316 (holotype), CBC 01290 (F); China: Hainan: IBGH 8295 (F); China: Guangxi: ROM 116463 (F), ROM 116468 (M); Thailand: SMF 53218 (M). ***M. fionae*** (n=7): Quang Nam [27]: IEBR-M3080 (M); Kon Tum [31]: IEBR-M5075 (M); Gia Lai [32]: IEBR-M3588 (M); Quang Ngai [30]: IEBR-M3635 (F), M3902, M3917 (M); Dong Nai [40]: HNHM 22858 (M). ***M. huttoni*** (n=27): Lao Cai [1]: ZMMU S186525, IEBR-M5434, M5435*, M5437* (F), ZMMU S186700, IEBR-M5428*, M5480*, M5482 (M); Cao Bang [5]: IEBR-M6023; Quang Tri [25]: IEBR-M3153 (F); Kon Tum [29]: IEBR-M5644, M5693* (F), VN11 1543, M5640*, M5641, M5643, M5653, M5696 (M); Dak Lak [35]: HNHM 22885 (F); Lam Dong [36]: IEBR-M5407*, M5413, M5415*, M5416 (F), M4718, M5419 (M); Khanh Hoa [37]: ZMMU S175150, ZMMU S175151 (M). ***M. cyclotis*** (n=75): Son La [14, 15]: IEBR-M3046, M4678 (M); Phu Tho [12] IEBR-M4052*, M4071* (M); Ha Giang [2]: IEBR-M4753* (M); Cao Bang [5]: IEBR M5631, M5630, M6001 (F); IEBR M5627, M5628, M5629, M6000 (M); Bac Kan [4] IEBR-M1210, M4561 (F), M4562 (M); Tuyen Quang [3]: IEBR-M0492, M5394 (F), M0505, M1887, M1891, M4976, M5296, M5309, IEBR VN11-1562 (M); Vinh Phuc [11]: IEBR-M4560 (F); Quang Ninh [9]: IEBR-M2855, M3128, M3131 (F), M3129, M3132, M3133, M3134 (M); Ninh Binh [18]: HNHM22919/2008.23.1 (F); Thanh Hoa [16, 17, 19] IEBR-M3725, M3726, M4223*, M6034, M6039, M6040 (F), M3736, M3738, M4126, M6036, M6038, M4172 (M); Nghe An [21, 22]: HNHM 22925, IEBR-M1359, M1632, M3316, M3330 (F), M1390, M2180, M4119, M4120, M3054, M3069, M3320 (M); Quang Binh [24]: IEBR-M3868, M3872, M3876 (F), M3874, M3875, M5333 (M); Quang Tri [25]: IEBR-M4953 (F), M4942* (M); Kon Tum [29]: IEBR-M5338 (M); Gia Lai [32]: IEBR-M3607 (M); Lam Dong [36]: IEBR-M5776 (M); Quang Ngai [30]: IEBR-M3645, M3646, M3651 (F), M3632 (M); Phu Yen [33]: IEBR-M4187 (M); Dong Nai [40]: IEBR-M4591 (M); Binh Phuoc [41]: ZMMU S184674 (F). ***M. lorelieae*** (n=10): Kon Tum [29]: VN11-1161, 1223, IEBR-M5656 (F); VN11-1220, IEBR-M5648*, M5651, M5662, M5663, HNHM B20140915.5,

20140915.7* (M). ***M. annamitica*** (n=22): Son La [15]: IEBR-M3034 (F), M2997 (M); Lao Cai [1] IEBR-M5429 (F), ZMMU S184673 (M); Tuyen Quang [3] IEBR-M4508 (M); Thanh Hoa [17] IEBR-M4122, M4124 (M); Nghe An [21, 22] IEBR-M2181 (F), HNHM 22929, IEBR-M1600, M3327 (M); Quang Tri [25] IEBR-M3148, M3167 (F); Kon Tum [29] IEBR-M4131 (F); Quang Ngai [30] IEBR-M3630, M3639, M3640, M3643, M4718 (F), M3633, M3650, M3652 (M). ***M. beelzebub*** (n=10): Quang Tri [25]: IEBR-M3636, M4842*, M5645, M5760 (paratype), VN11-1586, HNHM 2007.50.7 (paratype) (F), HNHM 2007.50.24 (holotype) (M); Kon Tum [29]: IEBR Tu071211.1, M5645 (F), IEBR-M4149, M5646 (M); Quang Ngai [30] IEBR-M3636 (F), M3904 (M). ***M. walstoni*** (n=9): Yok Don [34]: IEBR-M1480, HNHM 22933 (F), IEBR-M1481 (M); Ninh Thuan [38]: IEBR-M6030, M6031, M6032 (F); Dong Nai [40]: IEBR-M4592 [F); Kien Giang: IEBR-M2479, M2920 (M). ***M. feae*** (n=38): Son La [14]: HNHM 2010.42.2, IEBR-M4679 (F); Ha Giang [2] IEBR-M3264 (M); Tuyen Quang [3]: IEBR-M0495 (F), IEBR-M504, M5350, (M); Bac Kan [4]: IEBR-M4563 (F); IEBR-M323, M4510, HNHM 2000.84.7 (M); Vinh Phuc [11]: IEBR-M4991, M5056 (M); Ninh Binh [18]: IEBR-M5054 (F); Thanh Hoa [16, 17, 19]: HNHM 2000.84.4, IEBR-M3718, M3728, M4123, M4127, M4214*, VN110495 (F), HNHM 2000.84.7, IEBR-M3722, M4121, M4125 (M); Nghe An [21, 22]: IEBR-M1360, M1387.1/22868 (F), IEBR-M1363, M1364, M3068 (M); Ha Tinh [23]: IEBR-VN110001, 0007; Quang Binh [24]: IEBR-M3867, M3870, M3871 (F), M3869, M3873 (M); Quang Tri [25] IEBR-M3154, M4116 (M); Kon Tum [29]: IEBR-M5719 (M); Dong Nai [39]: IEBR-M323/22860 (M). ***M. eleryi*** (n=19): Son La [14]: IEBR-T.241107.1 (M); Phu Tho [12] IEBR-M4070 (M); Ha Giang [2]: NF.250506.1 (M); Cao Bang [5]: IEBR-M5622 (F); M6024 (M); Bac Kan [6]: BMNH 2008.25, ROM-NF.240507.1, HZM.1.39006, NF.230707.1, 240707.2, HNHM 2007.28.2 (paratype) (F), HNHM 2007.51.1 (holotype), NF.170906.3, 030707.1 (M); Thanh Hoa [19]: IEBR-M6035 (M); Quang Binh [30]: IEBR-M3866 (F); Kon Tum [29]: IEBR-M5718 (F); Quang Ngai [35]: IEBR-M4511 (F), IEBR-M3644 (M). ***M. harpioloides*** (n=3): Lam Dong [44]: ZMMU S173401 (F), IEBR-M5806 (F), IEBR-M5860 (M). ***M. chrysochaetes*** (n=2): Cao Bang [5]: IEBR-M-6020 (F), Lao Cai [13]: ZMMU S186699 (F). ***Harpiocephalus harpia*** (n=5): Cao Bang [5]: IEBR-M6037 (M); Tuyen Quang [3]: IEBR-M422 (F); Nghe An [21]: IEBR-M1362, M1391 (F); Kon Tum (Ngoc Linh NR): IEBR-M5661* (M). ***Harpiola isodon*** (n=1): Lao Cai [1]: IEBR-M5436* (F).