

THE SUBSPECIES OF *MYOTIS MONTIVAGUS* –
TAXONOMIC REVISION AND SPECIES LIMITS
(MAMMALIA: CHIROPTERA: VESPERTILIONIDAE)

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A morphological evaluation of different *Myotis montivagus* subspecies and *M. annectans* is presented. Using evidence provided by cranial and dental features and multivariate statistical analyses, we raise the four *montivagus* subspecies to species level, recognizing *M. borneoensis*, *M. federatus*, *M. montivagus* and *M. peytoni* as distinct species. Diagnoses, distribution and ecological data are given for each of these species and the morphologically very similar *M. annectans*. The conservation status of *M. montivagus* *sensu lato* should be reconsidered as our elevation of these subspecies to species results in a significantly smaller distribution range for each taxon.

Key words: Indomalayan Region, *Myotis annectans*, species identification, taxonomy.

INTRODUCTION

Bats are a highly diverse group of mammals with 1259 species presently known (FENTON 2012), a number which continues to grow as new taxa are described every year (e.g. VELAZCO *et al.* 2010, CSORBA *et al.* 2011, FRANCIS & EGER 2012). These discoveries are based not only on specimens collected during contemporary field expeditions but also on studies of museum specimens sometimes over a hundred years old. Correct recognition and classification of taxonomic units is essential for studies in biogeography, ecology and conservation. Conservation mainly focuses on species level taxonomic units; hence failure to recognize these correctly could lead to vulnerable species being overlooked. Re-evaluation of different taxonomic units, investigation of type material and description of cryptic taxa based on morphology and morphometrics are consequently essential even in the age of genetics.

Myotis is the most speciose genus of bats and includes a large number of morphologically similar species. *M. montivagus* (as *Vesptilio montivagus*) was described by DOBSON (1874) from Yunnan, China and is characterised by its relatively small size (forearm 39.2–41.5 mm), small foot, and displaced middle

upper premolar (P3) and lower middle premolar (p3) in the toothrow. Four subspecies are currently recognised. WROUGHTON and RYLEY (1913) described *M. peytoni* from Kanara, India as a new species of the "small-footed section" of *Myotis* on account of its much larger size compared to *mystacinus* and *nipalen-sis*. THOMAS (1916) distinguished a Malaysian bat as *M. peytoni federatus* by its smaller forearm, metacarpals and hind legs. Based on dental characters, both *peytoni* and *federatus* were regarded as closely allied to and synonymised with *M. montivagus* by HILL (1962), the latter being regarded by him as a member of the *Selysius* subgenus. Another subspecies, *M. montivagus borneoensis*, was proposed by HILL and FRANCIS (1984). These authors postulated that this form is cranially the largest of the species whereas the nominotypical subspecies from south China and north Myanmar is the smallest.

M. annectans was originally described (DOBSON 1871) as a species of *Pipistrellus* due to its missing upper and lower middle premolars but was later transferred to *Myotis* by TOPÁL (1970) who (after investigating the type specimen of *M. annectans* held in the collection of Zoological Survey of India, Kolkata) also viewed *M. primula* Thomas, 1920 as a synonym of *M. annectans*. The dentition of the type specimen of *M. primula* is complete with three premolars in the upper and lower toothrows but the presence or absence of the minute middle premolars within the species is variable. This is demonstrated, for example, by the presence of P3 and absence of p3 in a specimen from Cambodia (HNHM 2005.82.8.). HILL and THONGLONGYA (1972) also provided a detailed description of a *M. annectans* specimen (reportedly housed in the Thai National Reference Collection) and compared it with the type of *M. primula*. The specific distinctiveness of *M. annectans* and *M. montivagus* was, however, questioned by BORISENKO and KRUSKOP (2003: 125) in view of "the wide intraspecific variation of *M. montivagus*... and that both species are known from very few specimens".

M. montivagus, *peytoni*, *federatus* and *primula* (*annectans*) were analysed using numerical taxonomic methods by FINDLEY (1972). He placed *primula* in the *muricola*-group of the *Selysius* subgenus; *montivagus* in the *montivagus*-group and *peytoni* together with *federatus* in the *peytoni*-group. The two latter groups were placed in the subgenus *Leuconoe*. He regarded the *montivagus* and *peytoni* groups as comprising seemingly quite distinct taxa and further noted that "the collocation of *peytoni* with *montivagus*, as suggested by HILL (1962) is not strongly supported".

HILL (1962) and CORBET and HILL (1992) distinguished *montivagus* and *annectans* by the widely or narrowly separated anteorbital foramen but neither defined the measuring points or provided metric data. The anterior point of the "anteorbital bridge" (AOB, the distance by which the anteorbital foramen is separated from the orbit) is evident but the posterior end is weakly

determined. In fact, two foramens (their visibility varies) open from the orbit, namely the foramen lachrymale and the caudal opening of the infraorbital canal. The anterior rim of the zygoma can extend to either of these and, depending on the taxon and age of the individual, can be developed to a different extent. The posterior point of AOB therefore requires precise definition. In this paper, we consequently define the foramen infraorbitale and the foramen lachrymale as landmark measurement points for AOB (Fig. 1).

We critically evaluate the morphological characters of all these taxa and provide skull diagrams of their type specimens, in addition to craniodental measurements and statistical comparisons. The four *montivagus* subspecies are consequently raised to species level. An amended diagnosis of *M. annectans* (morphologically the closest species to the *montivagus*-group) and a character matrix to compare and discriminate these five species are also given.

MATERIALS AND METHODS

Specimens used for comparisons and statistical analyses are listed under the corresponding taxa in the results section.

Institutional abbreviations include BM(NH): Natural History Museum, London, United Kingdom, formerly British Museum (Natural History); HNHM: Hungarian Natural History Museum, Budapest, Hungary; HZM: Harrison Institute, Sevenoaks, United Kingdom, formerly Harrison Zoological Museum.

Forearm length data were compiled from the literature (HILL 1962, TOPÁL 1970, HILL & FRANCIS 1984, DAS 1987, HELLER & VOLLETH 1988, MANDAL *et al.* 2000, LUNDE *et al.* 2003, BATES *et al.* 2005, WILSON *et al.* 2006, SUYANTO & STRUEBIG 2007) and taken by the authors from alcohol-preserved museum specimens to the nearest 0.1 mm. Among the *montivagus* material from Malaysia listed by HELLER and VOLLETH (1988), two specimens were excluded from statistical analyses as they exhibit excessively large forearm measurements which cannot be explained by intraspecific variability and most probably represent a different taxon.

Craniodental measurements were taken by the authors to the nearest 0.01 mm using digital calipers and a stereomicroscope. Measurements include only those taken from adults. Abbreviations and definitions for craniodental measurements are GTL: greatest length of skull – from the front of the 1st upper incisor to the most projecting point of the occipital region; CCL: condylo-canine length – from the exoccipital condyle to the most anterior part of the canine; 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); AOB: anteorbital width – the distance by which the anteorbital foramen is separated from orbit, measured from the foramen infraorbitale to the foramen lachrymale; CM3L: maxillary toothrow length – from the front of the 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 last premolar; ML: mandible length – from the anterior rim of the alveolus of the 1st 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 3rd lower molar; and 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. Absolute crown height was used in all height comparisons for individual teeth (e.g. C versus P4).

Statistical analyses were carried out with R (R CORE TEAM 2012). Measurements were compared using Welch two sample t-tests. All tests were two-tailed. Principal Component Analysis (PCA) on the correlation matrix was used for multivariate comparisons. The data were also analysed using conditional inference trees, which estimate regression relationships by binary recursive partitioning in a conditional inference framework (HOTHORN *et al.* 2006). We treated species as the response variable and morphological measurements as explanatory variables. Due to incomplete datasets, external (forearm) and craniodental data were analysed separately.

RESULTS

Morphology and morphometrics

The skull profile of *M. annectans* is characterised by a weak rostral depression; the skull is more domed in *M. montivagus sensu lato* although to a variable extent among the subspecies (Fig. 2). There are significant differences in AOB values (Welch two-sample t-test, $t = -19.81$, $p < 0.0001$) which are considerably smaller in *M. annectans* and greater in all subspecies of *M. montivagus* (Table 1, Fig. 3). The second upper premolar is often lacking or excessively reduced in *M. annectans* whereas in all *M. montivagus* subspecies it is always present and usually larger in relation to P4 (Fig. 4).

Within *montivagus*, subspecies can be separated by a combination of their external and craniodental features. The subspecies *borneoensis* (from Borneo) and *peytoni* (from south and east-central India) have the largest forearm while

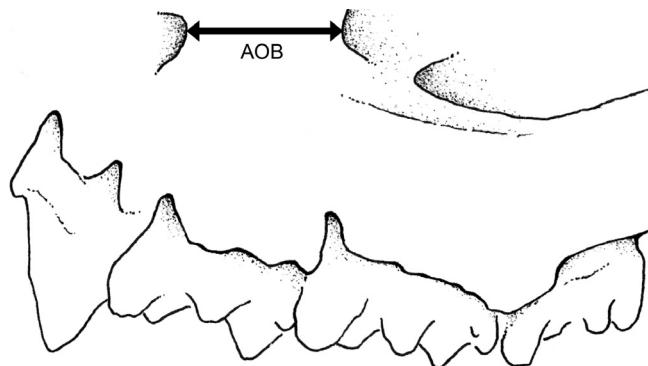


Fig. 1. Measuring points of the anteorbital bridge (AOB).

montivagus (from south China, north Myanmar) and *federatus* (from Peninsular Malaysia) are smaller externally. Cranially, Bornean specimens are the largest, whereas bats from south China and north Myanmar are the smallest. Cranial dimensions overlap in Peninsular Malaysian and Indian bats. Bornean specimens have the highest sagittal and lambdoid crests; in other subspecies these are poorly developed. The upper middle premolars (P3) of Bornean and Peninsular Malaysian specimens are much smaller than those of specimens from south China, north Myanmar or south and east-central India, hence P2 and P4 are fully or nearly in contact with each other in Bornean and Peninsular Malaysian bats. The upper premolars stand loosely in Indian specimens whereas in Peninsular Malaysian specimens these are crowded and P2 and P4 are in full contact. The lower middle premolar of Bornean and Peninsular Malaysian bats is fully intruded from the toothrow but remains within the toothrow in south China, north Myanmar and south and east-central India specimens.

Multivariate statistical methods were employed alongside classical morphological comparisons to broadly elucidate relationships within *montivagus*.

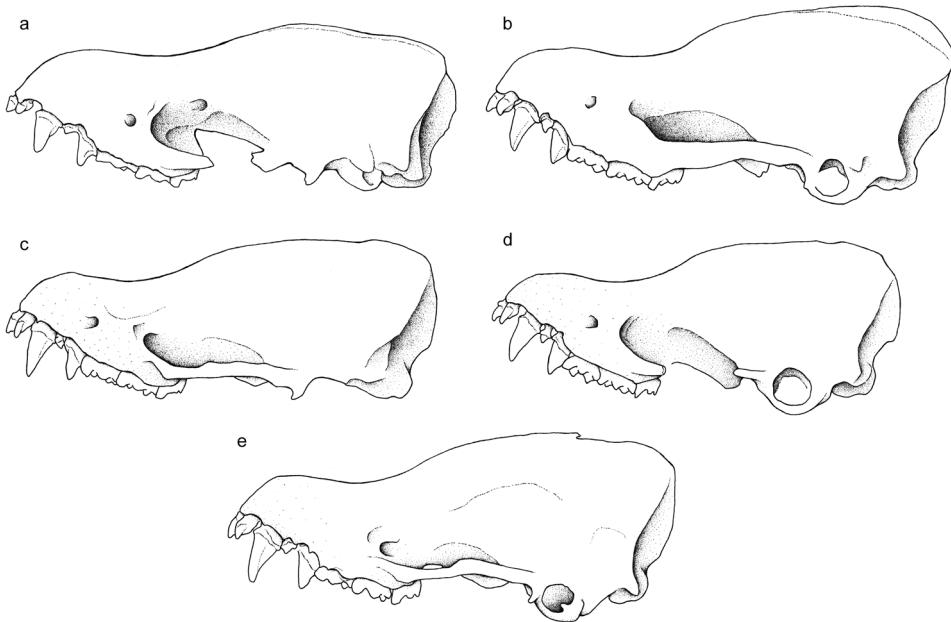


Fig. 2. Lateral view of skulls: a = *M. annectans* BM(NH) 78.2355 from Thailand, b = *M. borneoensis* BM(NH) 83.349 (holotype), c = *M. federatus* BM(NH) 16.4.20.5 (holotype), d = *M. montivagus* BM(NH) 76.3.10.5 (holotype), e = *M. peytoni* BM(NH) 12.8.25.1 (holotype).

Scale = 5 mm.

Table 1. Selected external and craniodental measurements (in mm) of *Myotis annectans*, *borneoensis*, *federatus*, *montivagus* and *peytoni*. Values are given as mean, \pm SD ($n \geq 2$), min-max, (n). Acronyms and definitions for measurements are given in the text.

character	<i>annectans</i>	<i>bornoensis</i>	<i>federatus</i>	<i>montivagus</i>	<i>peytoni</i>
FA	46.11 \pm 1.17	43.6 \pm 1.07	41.01 \pm 0.99	40.28 \pm 0.78	45.50 \pm 0.71
	44.9–48.4 (8)	42.1–44.8 (8)	39.5–42.5 (9)	39.2–41.5 (6)	45.0–47.0 (7)
GTL	17.41 \pm 0.34	18.03 \pm 0.28	16.97	15.69	17.09 \pm 0.41
	16.96–17.77 (6)	17.65–18.57 (7)	16.79–17.14 (2)	15.62–15.76 (2)	16.19–17.60 (11)
CCL	15.31 \pm 0.27	15.76 \pm 0.25	15.02	14.09	15.16 \pm 0.30
	14.86–15.65 (7)	15.43–16.10 (7)	15.01–15.03 (2)	14.07–14.10 (2)	14.50–15.52 (9)
C1C1W	4.74 \pm 0.16	4.74 \pm 0.11	4.62	4.45 \pm 0.06	4.68 \pm 0.19
	4.45–4.91 (7)	4.63–4.93 (7)	4.41–4.82 (2)	4.39–4.51 (3)	4.24–4.92 (11)
M3M3W	7.31 \pm 0.19	7.54 \pm 0.12	7.10 \pm 0.15	6.67 \pm 0.15	7.18 \pm 0.17
	7.02–7.61 (7)	7.37–7.69 (7)	6.99–7.20 (2)	6.50–6.79 (3)	6.73–7.34 (11)
ZYW	11.41	11.98 \pm 0.09	–	–	11.45 (1)
	11.30–11.51 (2)	11.82–12.09 (6)			
MAW	8.55	8.70 \pm 0.13	8.49 (1)	7.97	8.49 \pm 0.19
	8.53–8.57 (2)	8.48–8.88 (7)		7.93–8.01 (2)	8.12–8.78 (9)
IOW	4.27 \pm 0.15	4.02 \pm 0.10	3.97	3.81	4.08 \pm 0.16
	4.01–4.46 (7)	3.85–4.15 (7)	3.96–3.98 (2)	3.74–3.88 (2)	3.78–4.37 (11)
BCW	8.11	7.77 \pm 0.11	7.64 (1)	7.17	7.80 \pm 0.21
	7.86–8.36 (2)	7.62–7.91 (7)		7.15–7.19 (2)	7.54–8.10 (9)
BCH	5.78 (2)	6.73 \pm 0.17	5.95 (1)	5.75	5.91 \pm 0.15
		6.51–6.98 (7)		5.73–5.76 (2)	5.65–6.09 (8)
AOB	0.56 \pm 0.07	1.42 \pm 0.12	1.38	1.06 \pm 0.03	1.41 \pm 0.08
	0.47–0.67 (7)	1.25–1.65 (7)	1.35–1.40 (2)	1.03–1.08 (3)	1.24–1.49 (11)
CM3L	6.76 \pm 0.10	6.95 \pm 0.12	6.61	6.14 \pm 0.04	6.68 \pm 0.11
	6.60–6.88 (7)	6.71–7.10 (7)	6.44–6.78 (2)	6.09–6.17 (3)	6.50–6.90 (11)
CP4L	3.21	3.15 \pm 0.06	3.04 (1)	2.91 \pm 0.03	3.10 \pm 0.08
	3.09–3.32 (2)	3.07–3.24 (7)		2.89–2.94 (3)	2.98–3.22 (9)
ML	12.81 \pm 0.23	13.57 \pm 0.22	12.62	11.66 \pm 0.19	12.72 \pm 0.32
	12.60–13.21 (7)	13.33–14.03 (7)	12.41–12.82 (2)	11.48–11.85 (3)	12.16–13.16 (11)
cm3L	7.25 \pm 0.13	7.32 \pm 0.11	7.03	6.43 \pm 0.07	7.13 \pm 0.13
	7.04–7.44 (7)	7.15–7.46 (7)	6.93–7.12 (2)	6.35–6.47 (3)	6.91–7.35 (11)
CPH	4.04	4.76 \pm 0.16	4.14 (1)	3.76 \pm 0.08	4.10 \pm 0.13
	3.76–4.31 (2)	4.49–4.92 (7)		3.67–3.83 (3)	3.85–4.24 (9)

Principal Component Analysis (based on craniodental characters listed in Table 1) resulted in good separation of two groups representing specimens from Borneo and from south China and north Myanmar, respectively (Fig. 5 and Table 2). The third group contained specimens from south and east-central India and Peninsular Malaysia. The latter bats differ, however, in the length of their forearm: individuals from India have significantly longer forearms than bats from Peninsular Malaysia (Welch two-sample t-test, $t = -10.54$, $p < 0.0001$).

The full cranial and dental metric datasets were also analysed using conditional interference trees. Fig. 6 provides statistical support for four groups: *M. annectans*, south Chinese and north Myanmar *montivagus* *sensu stricto*, *boreoensis*, and a fourth comprising *federatus* and *peytoni*. However, individuals within the latter group can be readily separated by their dental characters and forearm measurements (see above).

Systematic descriptions

The presence of morphologically distinct and geographically separate taxa within *M. montivagus* *sensu lato* is supported by morphometric statistical analyses. These can be assigned to the four named forms of *M. montivagus*

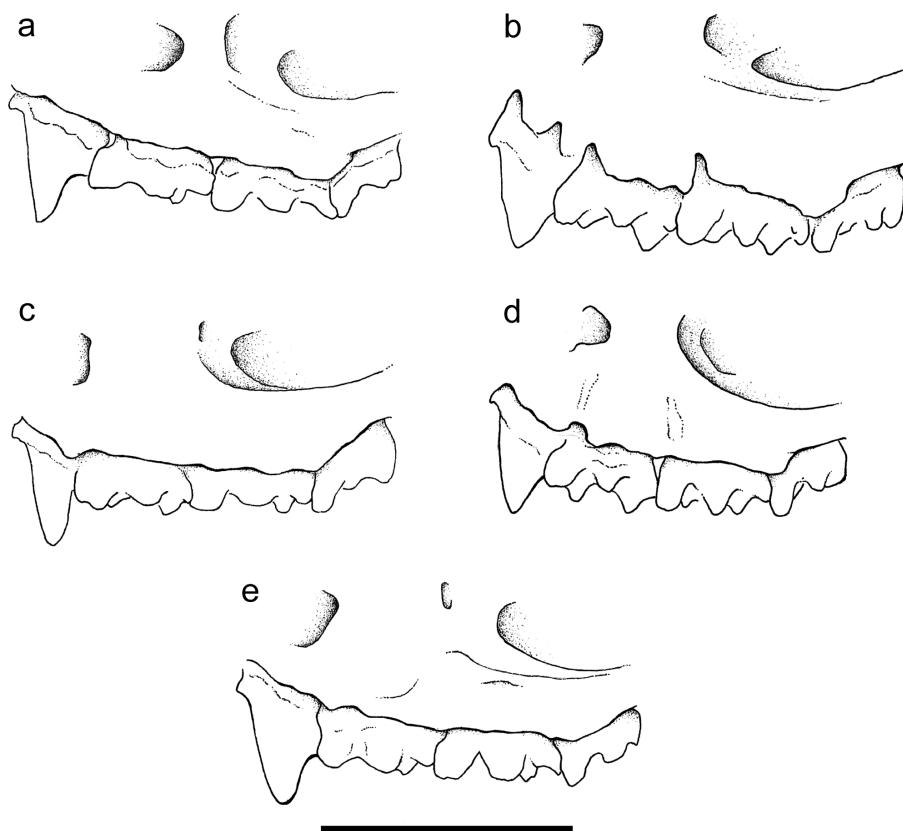


Fig. 3. Detail of the rostral part of skulls: a = *M. annectans* BM(NH) 78.2355 from Thailand, b = *M. boreoensis* BM(NH) 83.349 (holotype), c = *M. federatus* BM(NH) 16.4.20.5 (holotype), d = *M. montivagus* BM(NH) 76.3.10.5 (holotype), e = *M. peytoni* BM(NH) 12.8.25.1 (holotype). Scale = 3 mm.

(previously generally regarded as subspecies), and based on the differences above, are recognized here as valid species.

Widely accepted species of *Myotis* from the region are also separated from each other by similar quantitative features and magnitude of mensural differences (CORBET & HILL 1992, BORISENKO & KRUSKOP 2003). Recently described species e.g. *M. gomantongensis* (Francis et Hill, 1998), *M. annamiticus* (Kruskop et Tsytulina, 2001), *M. phanluongi* (Borisenko et al., 2008) also exhibit similar differences compared to their morphologically closest relatives and once analysed

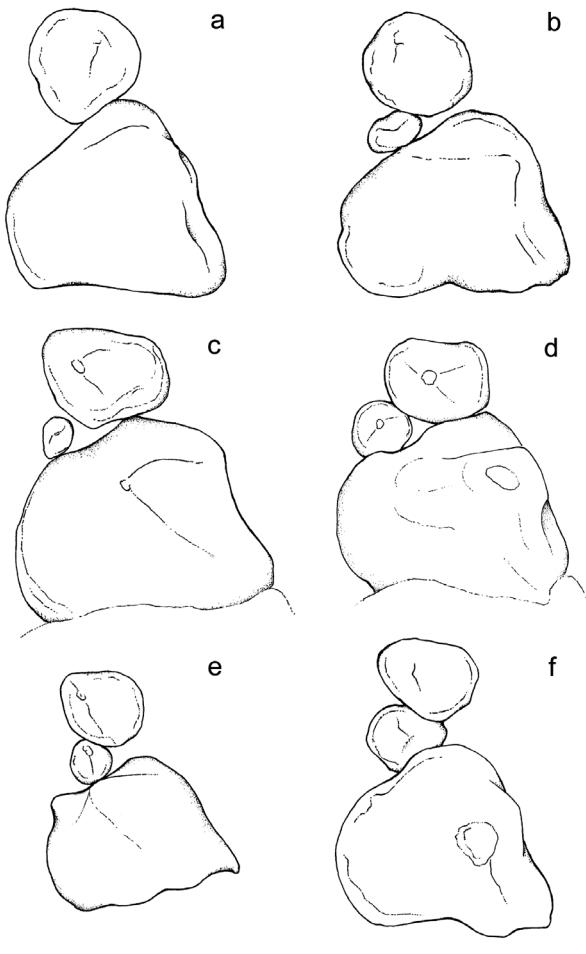


Fig. 4. Occlusal view of left upper premolar rows: a = *M. annectans* BM(NH) 78.2355 from Thailand, b = *M. annectans* BM(NH) 16.3.25.30 (holotype of *M. primula*), c = *M. borneoensis* BM(NH) 83.349 (holotype), d = *M. federatus* BM(NH) 16.4.20.5 (holotype), e = *M. montivagus* BM(NH) 76.3.10.5 (holotype), f = *M. peytoni* BM(NH) 12.8.25.1 (holotype). Scale = 3 mm.

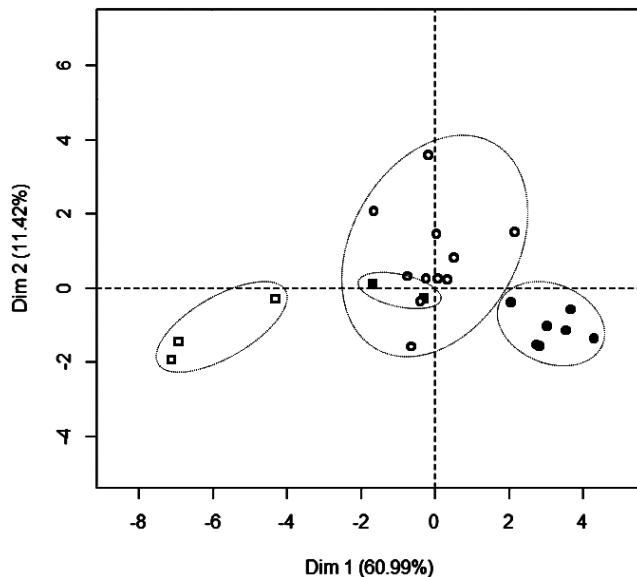


Fig. 5. Principal Component Analysis based on 15 craniodental characters of *M. borneoensis* (black circles), *M. federatus* (black squares), *M. montivagus* (empty squares) and *M. peytoni* (empty circles) specimens.

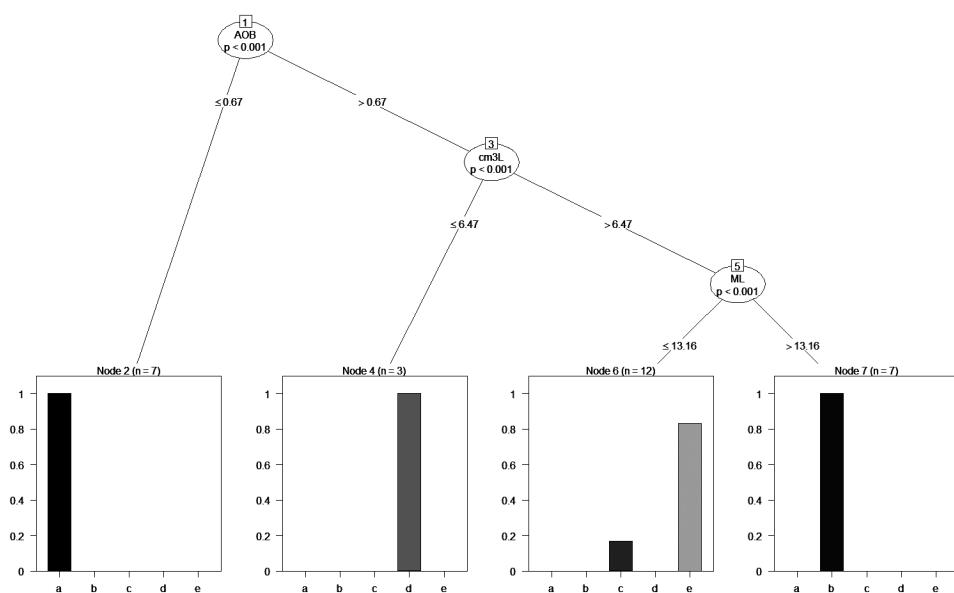


Fig. 6. Conditional interference tree based on 15 cranial characters of 29 specimens (a = *Myotis annectans*, b = *M. borneoensis*, c = *M. federatus*, d = *M. montivagus* and e = *M. peytoni*).

Table 2. Factor loadings of craniodental characters of *M. montivagus*-group obtained by the PCA.

Character	Dim.1	Dim.2
GTL	0.9079	
CCL	0.9054	
UCCW	0.5712	
UM3M3W	0.9095	
IOW		0.5312
ZYW		-0.6942
MAW	0.8613	
BCW	0.6508	0.6337
BCH	0.7101	-0.4605
AOB	0.6885	
UCM3L	0.9424	
UCP4L	0.8135	
MANL	0.9478	
LCM3L	0.9277	
PCH	0.8802	
Eigenvalue	9.1483	1.7133
Percentage of variance	60.9883	11.4218

genetically turn out to be quite distinct (BORISENKO *et al.* 2008, FRANCIS *et al.* 2010).

Diagnoses, distribution (Fig. 7) and ecological data for these species and *M. annectans* are given below.

Myotis annectans (Dobson, 1871) Hairy-faced Myotis

Pipistrellus annectans DOBSON, 1871: 213
Myotis primula THOMAS, 1920: 248
Pipistrellus annectens (sic!): TATE 1942: 251
Myotis annectans: TOPÁL 1970: 374
 (first use of current name combination)
Myotis annectans: CORBET *et al.* 1992: 124
Myotis annectans: KOOPMAN 1994: 104

Material investigated: INDIA (West Bengal) – BM(NH) 16.3.25.30 (*primula* holotype), BM(NH) 20.7.27.2, 20.7.27.3; CAMBODIA – HZM 1.32758; HNHM 2005.82.8; THAILAND – BM(NH) 78.2355; VIETNAM – HNHM 2008.23.10.

Table 3. Character matrix of *M. annectans*, *borneoensis*, *federatus*, *montivagus* and *peytoni*.

Species	FA	AOB	P3 size	P3 position	P2 / P4	p3 position
<i>annectans</i>	44.9–48.4	0.47–0.67	missing / minute	missing / fully intruded	in contact	fully intruded
<i>bornoensis</i>	42.1–44.8	1.25–1.65	minute	fully intruded	in contact / narrowly separated	fully intruded
<i>federatus</i>	39.5–42.5	1.35–1.40	reduced	intruded	in contact	fully / partly intruded
<i>montivagus</i>	39.2–41.5	1.03–1.08	reduced	in toothrow	well separated	in toothrow
<i>peytoni</i>	45.0–47.0	1.24–1.49	developed	in toothrow	well separated	fully / partly in toothrow

Amended diagnosis

Forearm 44.9–48.4 mm, CCL 14.86–15.65 mm (Table 1). Dorsal hairs with long, dark brown bases and paler tips, creating a frosted effect. Ventral hairs with dark brown bases and silvery-white tips, except for middle of belly where tips are orange-brown. Ears moderately large, tragus long and narrow with a rounded tip (DOBSON 1871, FRANCIS 2008).

Cranial profile flattened, the depression between rostrum and braincase is shallow. Only a weak sagittal crest present; the antorbital bridge is narrow. Basal dimension of the anterior upper premolar (P2) is one-quarter or one-third that of P4. Middle upper premolar minute or often lacking; when present, completely displaced from toothrow. Middle lower premolar (p3) very small, totally intruded from the toothrow, not visible laterally; p2 and p4 are not in contact.

Distribution and ecological notes

M. annectans has a relatively wide distribution ranging from northeast India (DOBSON 1871, THOMAS 1920, BATES & HARRISON 1997) to north Thailand

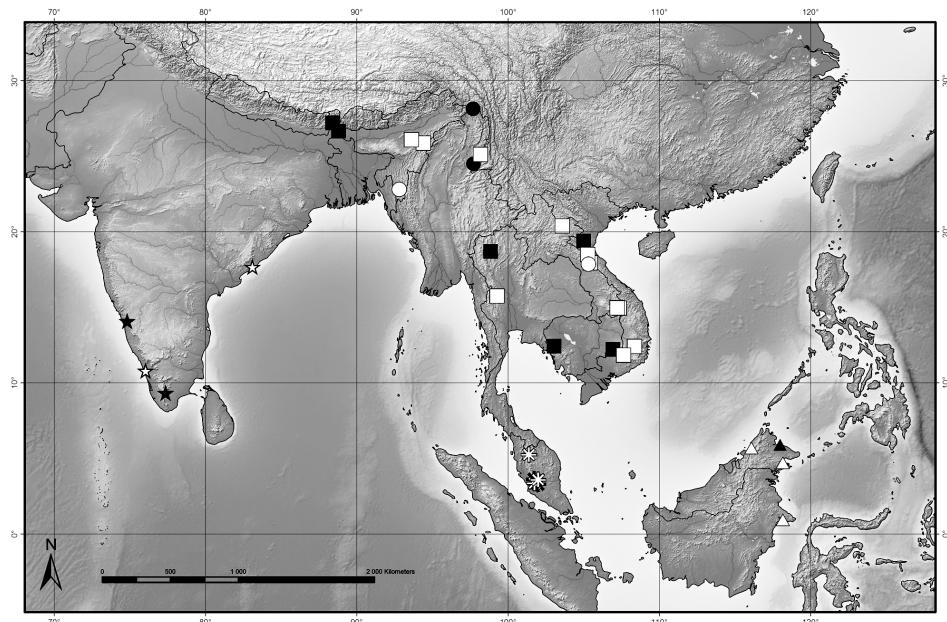


Fig. 7. Distribution map of *M. annectans* (squares), *M. borneoensis* (triangles), *M. federatus* (asterisks), *M. montivagus* (circles) and *M. peytoni* (stars). Full symbols represent investigated specimens whereas empty symbols denote literature data.

(HILL & THONGLONGYA 1972, BICKHAM *et al.* 1986), Laos (FRANCIS *et al.* 1999, FRANCIS *et al.* 2010), Vietnam (FRANCIS *et al.* 2010, LUNDE 2003) and Cambodia (HENDRICHSEN *et al.* 2001a). It is also recorded from Yunnan, China (WANG 2003). Specimens were found mainly in hill forest habitats at 1077 and 923 metre elevations (THOMAS 1920) and at 1250 metres in Doi Pui, Chiang Mai, Thailand (HILL & THONGLONGYA 1972).

Myotis borneoensis Hill et Francis, 1984
Bornean Whiskered Myotis

Myotis montivagus borneoensis HILL & FRANCIS, 1984: 309

Myotis montivagus borneoensis: CORBET & HILL 1992: 123

Myotis montivagus borneoensis: KOOPMAN 1994: 106

Material investigated: MALAYSIA (Sabah) – BM(NH) 83.349 (holotype), BM(NH) 83.74, 83.345, 83.346, 83.347, 83.348, 83.350.

Amended diagnosis

Forearm 42.1–44.8 mm, CCL 15.43–16.10 mm (Table 1). Upperparts with rather long and dense fur, with blackish brown bases and dark brown tips. Fur on underparts with similar blackish brown bases and buffy brown tips. Ears long and narrow, with a long tragus, which reaches half the length of the ear and bends slightly forward (HILL & FRANCIS 1984).

Cranial profile relatively flat, the depression between the rostrum and braincase is rather shallow. Sagittal and lambdoid crests are well developed; the anteorbital bridge is wide. Basal dimension of the anterior upper premolar (P2) is one-third that of P4. Middle upper premolar (P3) very small and completely displaced from the toothrow so that the first (P2) and third upper premolar (P4) are usually in tight contact. Lower middle premolar (p3) is intruded from the toothrow and not visible laterally; p2 and p4 are not in contact.

Distribution and ecological notes

M. borneoensis is confined to Borneo. It occurs in Sabah, Malaysia (HILL & FRANCIS 1984, PAYNE *et al.* 1985, YASUMA & ANDAU 2000 in FRANCIS *et al.* 2008), Sarawak (WILSON *et al.* 2006), and also in Kalimantan, Indonesia (SUYANTO & STRUEBIG 2007). PAYNE *et al.* (1985) and WILSON *et al.* (2006) recorded the species alongside forest streams, whereas specimens collected in Kalimantan emerged from a cave in a karst area.

Myotis federatus Thomas, 1916
Malayan Whiskered Myotis

Myotis peytoni federatus THOMAS, 1916: 3
Myotis federatus: TATE 1941: 557
Myotis federatus: FINDLEY 1972: 33
Myotis montivagus federatus: CORBET & HILL 1992: 123
Myotis montivagus federatus: KOOPMAN 1994: 106
Myotis montivagus federatus: FRANCIS 2008: 232

Material investigated: MALAYSIA (Peninsular Malaysia) – BM(NH) 16.4.20.5 (holotype), HNHM 98.14.31.

Amended diagnosis

Forearm 39.5–42.5 mm, CCL 15.01–15.03 mm (Table 1). Fur is uniform dark brown, usually without paler tips (THOMAS 1916). Ears moderately large and narrow. Tragus bends forward and reaches half the height of the ear.

Braincase slightly domed. Sagittal and lambdoid crests are poorly developed; the antorbital bridge is wide. Basal dimension of the anterior upper premolar (P2) is one-quarter that of P4. Middle upper premolar (P3) small and completely displaced from the toothrow so that the first (P2) and third upper premolar (P4) are in contact. Middle lower premolar (p3) small, intruded from the toothrow and not visible laterally; p2 and p4 are not in contact.

Distribution and ecological notes

M. federatus is restricted to Peninsular Malaysia. Besides the type locality at the border of Selangor and Pahang, it has been recorded at 900 metres in Ulu Gombak and Genting Highlands (HELLER & VOLLETH 1988), and in the Temengor Forest Reserve, Hulu Perak (FRANCIS 1995). One other specimen was caught at the Batu Caves, near Kuala Lumpur (HNHM).

Myotis montivagus (Dobson, 1874)
Burmese Whiskered Myotis

Vespertilio montivagus DOBSON, 1874: 237
Myotis mystacinus mystacinus (part): ALLEN 1938: 215
Myotis montivagus: TATE 1941: 560
Myotis mystacinus montivagus: ELLERMANN & MORRISON-SCOTT 1951: 140
Myotis montivagus: FINDLEY 1972: 32
Myotis montivagus montivagus: CORBET & HILL 1992: 123

Myotis montivagus montivagus: KOOPMAN 1994: 106
Myotis montivagus montivagus: FRANCIS 2008: 232

Material investigated: CHINA (Yunnan) – BM(NH) 76.3.10.5 (holotype); MYANMAR – BM(NH) 32.11.1.4, 32.11.1.5

Amended diagnosis

Forearm 39.2–41.5 mm, CCL 14.07–14.10 mm (Table 1). Fur is long and dense on both the upperparts and underparts. Dorsal hairs are dark brown overall, with blackish brown bases and paler chocolate brown tips. Ventrally, hair bases are the same blackish brown but with paler tips (HILL 1962). Ears are narrow, tapering, with rounded tips. Tragus long, narrow, and its inner margin straight (DOBSON 1874).

Braincase distinctly domed, frontal depression well-expressed. The sagittal and lambdoid crests are weakly developed. The antorbital bridge is wide. Basal dimensions of the anterior upper premolar (P2) about one-third that of P4. Middle upper premolar (P3) relatively well developed and almost in the toothrow, separating the first (P2) and third upper premolar (P4). Lower middle premolar (p3) developed and placed in the toothrow.

Distribution and ecological notes

According to published records, *M. montivagus* has the widest distribution of its group. The holotype was collected in Yunnan, south China (DOBSON 1871). The species also occurs in northern Myanmar (BM(NH)) and Laos (FRANCIS *et al.* 1999) where it was found in a hill forest at 1000 m and in an open forest at 500 m elevation on the Nakai Plateau. KUZNETSOV *et al.* (2001) recorded it from Vu Quang, Vietnam and MANDAL *et al.* (2000) collected four specimens at 1500 m in Mizoram, north-east India.

Myotis peytoni Wroughton et Ryley, 1913 Peyton's Whiskered Myotis

Myotis peytoni WROUGHTON & RYLEY, 1913: 13
Myotis peytoni: TATE 1941:562
Myotis peytoni: FINDLEY 1972: 33
Myotis montivagus peytoni: CORBET & HILL 1992: 123
Myotis montivagus peytoni: KOOPMAN 1994: 106

Material investigated: INDIA (Karnataka) – BM(NH) 12.8.25.1 (holotype), BM(NH) 12.11.28.55, 12.11.28.56, 12.11.28.57, 12.11.28.58, 12.11.28.59, 12.11.28.60, 12.11.28.61; (Tamil Nadu) HZM 3.36354, 4.36355

Amended diagnosis

Forearm 45.0–47.0 mm, CCL 14.50–15.52 mm (Table 1). Fur fairly long and loose. Dorsal surface uniform dark “vandyke brown” with chocolate brown tips; ventrally hair bases are dark, the tips paler brown to fawn. Tragus is medium length, less than half the height of pinna; inner edge straight (WROUGHTON & RYLEY 1913, BATES & HARRISON 1997).

Cranial profile moderately domed, with a depression between the rostrum and braincase. Sagittal and lambdoid crests are less developed; the anteorbital bridge is wide. Basal dimension of the anterior upper premolar (P2) is one-quarter that of P4. Middle upper premolar (P3) is well-developed and only partly displaced from the toothrow, so the first (P2) and third upper premolar (P4) are not in contact. Lower middle premolar (p3) partly or fully lies in the toothrow, p2 and p4 are separated.

Distribution and ecological notes

The type series was collected at Gersoppa (now Jog) Falls in southwest India. The distribution of the species is limited to the east-central and southern part of the Indian Subcontinent (WROUGHTON & RYLEY 1913, GHOSH 1989, BATES & HARRISON 1997, VANITHARANI *et al.* 2005, VANITHARANI 2006).

DISCUSSION

Molecular investigations frequently present un-named lineages on phylogenetic trees for different chiropteran families (e.g. CLARE *et al.* 2006, FRANCIS *et al.* 2010) because of questionable taxonomic assignment of studied specimens due to the lack of thorough revisions. Needless to say, the results of such studies must be harmonised with existing scientific names, which is hardly possible without re-examination – and frequently re-description – of type materials for less known taxa. The present work re-evaluated the taxonomic status of four formerly accepted subspecies of *M. montivagus* and elevated them to species rank using cranial and dental characters and multivariate statistical analyses. To assist determination of species within the *montivagus*-group and the morphologically similar *M. annectans*, a character matrix is provided in Table 3.

It is worth noting that two Vietnamese specimens of *M. montivagus* collected in Pu Mat Nature Reserve, Nghe An Province and in Kon Cha Rang, Gia Lai Province (BATES *et al.* 1999, HENDRICHSEN *et al.* 2001b) could not be definitely assigned to subspecies by the authors as they shared characters “considered diagnostic for two of the geographically adjacent races” namely

montivagus montivagus and *montivagus borneoensis*. Although the authors did not provide comparisons with *annectans* or details of anteorbital bridge development, mensural data and accompanying skull and dentition drawings suggest a species other than *annectans*, *montivagus* and *bornoensis*.

The Barcodes of Life database includes mtDNA sequences for specimens referred to *M. montivagus* (in a broad sense) from China, Laos and Vietnam some of which were analysed in FRANCIS *et al.* (2010). However, without proper descriptions of skull characters and mensural data, determination of these specimens is not possible (see also remarks above on the questionable identity of some Vietnamese specimens); therefore these records are not depicted in Fig. 7.

Besides mapping the holotype specimen from Yunnan, SMITH and XIE (2008) also included *M. montivagus montivagus* in range maps for central-east China without explanation. As approximately 1600 km lies between these localities and the closest substantiated record of any of the former *montivagus* subspecies, these data are considered here as unconfirmed.

M. montivagus (*sensu lato*, including all its former subspecies) is currently considered Least Concern in the IUCN Red List of Threatened Species (FRANCIS *et al.* 2008) because of "its wide distribution, presumed large population, it occurs in a number of protected areas, has a tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category". However, since the taxa elevated to species rank herein have significantly smaller distribution ranges, this categorisation should be reconsidered.

*

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