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Description of a new species of *Myotis* (Vespertilionidae) from Vietnam

Nguyen Truong Son[1], Tamás Görföl[2, 3], Charles M. Francis[4], Masaharu Motokawa[5], Péter Estók[6], Hideki Endo[7], Vu Dinh Thong[1], Nguyen Xuan Dang[1], Tatsuo Oshida[8], and Gábor Csorba[2, 9]

[1]*Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam*
[2]*Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary*
[3]*Institute for Veterinary Medical Research, Centre for Agricultural Research, Hungarian Academy of Sciences, Budapest, Hungary*
[4]*Canadian Wildlife Service, Environment Canada, Ottawa, Canada*
[5]*The Kyoto University Museum, Kyoto University, Kyoto, Japan*
[6]*Department of Zoology, Eszterházy Károly College, Eger, Hungary*
[7]*The University Museum, University of Tokyo, Tokyo, Japan*
[8]*Laboratory of Wildlife Ecology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Japan*
[9]*Corresponding author: E-mail: csorba@nhmus.hu*

During the examination of a series of specimens, formerly referred to *Myotis montivagus*, recently collected in Vietnam and Lao PDR, we found that they differ in several important ways from any species formerly included in *M. montivagus*. We describe them as a new species characterised by a relatively long forearm, moderately long ears, flat cranial profile and wide anteorbital bridge. Based on characters classically used to separate the 'subgenera' of *Myotis* the new species shows affinities to both the nominate subgenus '*Myotis*' and '*Selysius*'. Our morphological investigations support recent phylogenetic analyses showing that the former 'subgenera' of *Myotis* are in fact paraphyletic groups, even within Southeast Asia. Nevertheless, many of the external and craniodental features formerly used to separate these subgenera provide a practical means of grouping species. Using these characters we provide an identification key to identify the new species, as well as other currently recognized medium and large sized, small-footed *Myotis* species from the Indomalayan Region.

*Key word*s: identification key, Indochina, Indomalayan Region, morphology, Myotinae, taxonomy

Introduction

Myotis is the most speciose genus of bats, and the only one that can be found in all continents except Antarctica (Simmons, 2005). From the high diversity of this group we can predict a great number of morphologically similar species and taxonomic challenges in identifying both individual species and their relationships (Datzman *et al*., 2012; Kruskop *et al.*, 2012). Tate (1941) divided the genus into seven subgenera (*Selysius*, *Isotus*, *Paramyotis*, *Chrysopteron*, *Myotis*, *Leuconoe* and *Rickettia*). Findley (1972) recognized only three (*Myotis*, *Selysius* and *Leuconoe*) in his numerical taxonomic study based on phenetic characters. In the Indomalayan Region these three taxa and *Chrysopteron* have been accepted as subgeneric divisions by many comprehensive works (Corbet and Hill, 1992; Koopman, 1994; Francis, 2008). However, recent phylogenetic analyses suggest that these widely used subgenera are paraphyletic groups of species which have evolved similar morphology through convergent evolution to particular ecological roles (Ruedi and Mayer, 2001; Kawai *et al.*, 2003; Stadelmann *et al.*, 2004*a*, 2004*b*, 2007; Francis *et al*., 2010). To complement the genetic results, we investigated a wide range of species to check the external and craniodental morphological traits on which the earlier systematic arrangement was based.

In connection with this large-scale morphological comparison, when examining newly vouchered *Myotis* material from Vietnam stored in the collections of the Institution of Ecology and Biological Resources, Vietnam and the Hungarian Natural History Museum, Hungary, we found 13 specimens of a relatively large form of *Myotis*. This species, characterised by moderately long ears and a relatively flat cranial profile, does not match any currently recognized species. Based on morphological and genetic analyses, it appears to be related to members

of the *M. montivagus* group which were formerly considered subspecies (Corbet and Hill, 1992) but are now recognized as distinct species: *M. borneoensis*, *M. federatus*, *M. montivagus* s. str. and *M. peytoni* (Görföl *et al.*, 2013). Collectively the *M. montivagus* group is characterised by a forearm length between 39–49 mm, relatively short ears, flattened to moderately domed braincase, wide anteorbital bridge and displaced middle premolars. The new species matches additional specimens from Lao PDR and China which were previously published under the name *M. montivagus* (Francis *et al*., 1999, 2010; Francis, 2008). Collectively they differ from *montivagus* in a strict sense and other known taxa in several morphological traits and we describe them herewith as a species new to the science. To help field and museum researchers with the identification of vouchered material of this difficult group, we also provide an identification key to all presently known species of medium and large sized, small-footed *Myotis* from the Indomalayan Region.

Materials and Methods

Bats were captured and handled in the field with methods conforming to the guidelines approved by the American Society of Mammalogists for the use of wild mammals in research (Gannon *et al*., 2007). External measurements were taken from alcohol-preserved museum specimens or in the field (Lao specimens) to the nearest 0.1 mm. Craniodental measurements were taken to the nearest 0.01 mm using digital calipers and a stereomicroscope. Measurements include only those taken from full-grown individuals as indicated by the presence of fully ossified metacarpal-phalangeal joints.

Museum Acronyms

AMNH: American Museum of Natural History, New York, USA; BM(NH): The Natural History Museum, London, United Kingdom, formerly British Museum (Natural History); BNHS: Bombay Natural History Society, Mumbai, India; CDZTU: Central Department of Zoology, Tribhuvan University, Kathmandu, Nepal; HNHM: Hungarian Natural History Museum, Budapest, Hungary; HZM: Harrison Institute, Sevenoaks, United Kingdom, formerly Harrison Zoological Museum; IEBR: Institute of Ecology and Biological Resources, Hanoi, Vietnam; MNHN: Muséum national d'Histoire naturelle, Paris, France; NSMT: National Museum of Nature and Science, formerly National Science Museum, Tokyo, Japan; PSUZC: Prince of Songkla University Zoological Collection, Hat Yai, Thailand; RMNH: Naturalis Biodiversity Center, Leiden, The Netherlands, formerly Rijksmuseum van Natuurlijke Historie; ROM: Royal Ontario Museum, Toronto, Canada; SMF: Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt am Main, Germany; ZMB: Museum für Naturkunde, Berlin, Germany, formerly Zoological Museum Berlin; ZMMU: Zoological Museum of Moscow University, Moscow, Russia; ZSI: Zoological Survey of India, Kolkata, India.

Specimens Examined

Myotis altarium: CHINA: BM(NH) 11.2.1.9 (holotype), BM(NH) 11.2.1.7-8, BM(NH) 11.2.1.11-12, HNHM 2011.13.3. *Myotis annectans*: INDIA: BM(NH) 16.3.25.30 (*primula* holotype), BM(NH) 20.7.27.2-3; CAMBODIA: HNHM 2005.82.8.; THAILAND: BM(NH) 78.2355; VIETNAM: HNHM 2008.23.10. *Myotis ater*: INDONESIA: ZMB 2956 (syntype); CAMBODIA: HZM 10.324188; VIETNAM: HNHM 2008.23.13-14., IEBR PL16, PL18. *Myotis borneoensis*: BORNEO: BM(NH) 83.349 (holotype), BM(NH) 83.345-348, BM(NH) 83.350, BM(NH) 83.74. *Myotis chinensis*: VIETNAM: HNHM 93.55.1-2., 99.3.1. *Myotis csorbai*: NEPAL: HNHM 97.2.4. (holotype). *Myotis federatus*: PENINSULAR MALAYSIA: BM(NH) 16.4.20.5 (holotype), HNHM 98.14.31. *Myotis fimbriatus*: China: ZMB 4148 (holotype). *Myotis formosus*: NEPAL: HNHM 98.8.22. *Myotis frater*: CHINA: AMNH 48039 (holotype). *Myotis hasseltii*: INDONESIA: ZMB 66930 (topotype). *Myotis hermani*: INDONESIA: BM(NH) 23.1.2.13 (holotype). *Myotis horsfieldii*: INDONESIA: ZMB 2558 (syntype). *Myotis longipes*: INDIA: HNHM 92.104.45-48. *Myotis macrotarsus*: PHILIPPINES: MNHN 1977-557. *Myotis montivagus*: CHINA: BM(NH) 76.3.10.5 (holotype); MYANMAR: BM(NH) 32.11.1.4-5. *Myotis muricola*: NEPAL: BM(NH) 45.1.8.143 (holotype). *Myotis pequinius*: CHINA: BM(NH) 8.8.7.2 (holotype), BM(NH) 8.8.7.3, BM(NH) 26.2.3.4. *Myotis peytoni*: INDIA: BM(NH) 12.8.25.1 (holotype), BM(NH) 12.11.28.55-61. *Myotis pilosus*: CHINA: HNHM 2005.40.3. *Myotis pruinosus*: JAPAN: NSMT 14842 (holotype), NSMT 28245. *Myotis ridleyi*: MALAYSIA: BM(NH) 98.3.13.6. *Myotis rosseti*: CAMBODIA: RMNH 19629 (holotype). *Myotis sicarius*: INDIA: BNHS 3784; NEPAL: BM(NH) 23.1.9.4-5, BNHS 3783, CDZTU BAT24-25, HZM 1.16284, ZMMU 164493-164495, ZSI 17429; SIKKIM: BM(NH) 91.10.7.56 (holotype). *Myotis siligorensis*: INDIA: BM(NH) 79.11.21.125 (holotype). *Myotis taiwanensis*: TAIWAN: HNHM 2005.65.43. *Myotis yanbarensis*: JAPAN: NSMT 31306 (holotype).

Measurements

Abbreviations and definitions for external measurements include FA: forearm length — from the extremity of the elbow to the extremity of the carpus with the wings folded; EAR: ear length — from the lower border of the external auditory meatus where it joins with the body to the tip of the pinna; TIB: tibia length — from the knee joint to the ankle; and HF: hind foot — from the tip of the longest digit, excluding the claw, to the extremity of the heel, behind the os calcis. 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; C^1C^1W: width across the upper canines — greatest width across the outer borders of the upper canines; M^3M^3W: 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; CM^3L: maxillary toothrow length — from the front of the upper canine to the back of the crown of the third molar; CP^4L: 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; CM_3L: 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^1 versus P^4).

All statistical analyses were carried out with R 2.13.2 (R Development Core Team, 2012). Principal component analysis (PCA) on the correlation matrix was used for multivariate comparisons of craniodental data. One-way ANOVA was used for multiple comparisons of different external and craniodental measurements. DNA barcode data for the specimens from Lao PDR were taken from existing published data (Francis *et al*., 2010).

Results

Myotis indochinensis sp. n.
(Figs. 1–5, Tables 1–3)

Myotis montivagus: Francis *et al*. (1999, 2010), Francis (2008; in part).

Type material

Holotype: IEBR M-839-2 (collector number # AL02), adult female, in alcohol, skull removed. Collected by Nguyen Truong Son and Ho Thu Cuc on 15 August, 2001. Measurements (in mm) are as follows: FA = 44.1, TIB = 18.9, HF = 8.9, GTL = 18.13, CCL = 16.38, C^1C^1W = 4.93, M^3M^3W = 7.86, ZYW = 12.15, MAW = 9.39, IOW = 4.54, BCW = 8.33, BCH = 6.08, AOB = 1.49, CM^3L = 7.39, CP^4L = 3.45, ML = 13.74, CM_3L = 7.83, CPH = 4.52, body mass (g) = 13.0.

Type locality

16°06’N, 107°19’E, Loa village, Dong Son commune, A Luoi District, Thua Thien-Hue Province, Vietnam, 970 m a.s.l. (above sea level).

Paratypes

HNHM 24210 (# AL07), dry skin, skull removed; HZM 1.40167 (# AL06), IEBR M-839-3 (# AL03, to be deposited in ROM), IEBR M-839-4 (# AL04), IEBR M-839-5 (# AL05), IEBR M-839-8 (# AL08), IEBR M-839-9 (# AL09), PSUZC MM 2011.57 (# AL01), bodies in alcohol, skulls removed. All paratypes are adult females and were collected in the same locality and the same day as the holotype specimen.

Referred material

LAO PDR: ROM 106525, adult male, body in alcohol, skull removed, ROM 106526, adult female, body in alcohol, skull removed, ROM 117924 adult female in alcohol, SMF 94079 adult female, body in alcohol, skull removed, all four from Nam Pakkatan, Nakai Plateau, Khammouane Province; SMF 94080, adult male, body in alcohol, skull removed, Nam Pan, Bolikhamsai Province. VIETNAM: HNHM 2008.23.6., adult female, body in alcohol, skull removed, Tam Dao National Park, Vinh Phuc Province; IEBR M-57 (# SL43), adult female, dry skin, skull removed, Phieng Dung cave, Na Hang Nature Reserve, Tuyen Quang Province; IEBR TX05 and TX07, both adult males, bodies in alcohol, skulls removed, Lung Khoai village, Ta Xua Nature Reserve, Son La Province.

Etymology

The name refers to the biogeographical unit where the specimens of the new species were collected. The proposed English name is Indochinese mouse-eared bat.

Diagnosis

A medium-sized *Myotis* (FA 43.7–45.6 mm, GTL 17.70–18.37 mm; Table 1), with moderately long ears, four-lobed lower incisors, flat cranial profile, well developed sagittal and lambdoid crests, middle premolars intruded lingually in both the upper and the lower toothrows.

Description

Medium sized *Myotis* (Table 1), external measurements (in mm) are as follows (sample size is given in parentheses): FA = 43.3–45.6 (18); EAR = 13.8–16.1 (13); TIB = 18.5–20.2 (12); HF = 8.8–10.6 (17). The fur (description is based on the HNHM 24210 paratype dry skin) on the dorsum is relatively long and uniformly dark brown; some crown hairs with lighter tips. On the ventral surface the fur is dark brown (as on the dorsum) basally, but the distal half is lighter yellowish-brown, so the collective impression of the ventral side is lighter than on the dorsum (Fig. 1). The ears are relatively long and narrow, but do not reach the tip of the nostrils when laid forward. The anterior margin of the ears is convex with the tip rounded, posterior margin concave and with a shallow emargination. The tragus has a well-developed lobe at the base and reaches about half the length of the ear pinna (Fig. 2). Wings attach at the base of the first toe; the calcar extends to half of the free edge of the uropatagium.

TABLE 1. Selected external and craniodental measurements (in mm) of *M. indochinensis*, *M. annectans*, *M. borneoensis*, *M. federatus*, *M. peytoni* and *M. sicarius*. Values are given as $\bar{x}$ ± SD ($n \geq 3$), min–max, (n). Acronyms and definitions for measurements are given in the text

Character	*indochinensis*	*annectans*	*borneoensis*	*federatus*	*peytoni*	*sicarius*
FA	44.75 ± 0.63	46.11 ± 1.17	43.60 ± 1.07	41.01 ± 0.99	45.50 ± 0.71	50.12 ± 1.83
	43.7–45.6 (13)	44.9–48.4 (8)	42.1–44.8 (8)	39.5–42.5 (9)	45.0–47.0 (7)	48.20–54.5 (11)
GTL	17.96 ± 0.22	17.41 ± 0.34	18.03 ± 0.28	16.97	17.14 ± 0.38	18.78 ± 0.16
	17.70–18.37 (13)	16.96–17.77 (6)	17.65–18.57 (7)	16.79–17.14 (2)	16.19–17.60 (10)	18.68–18.96 (3)
CCL	16.00 ± 0.24	15.31 ± 0.27	15.76 ± 0.25	15.02	15.25 ± 0.19	16.61 ± 0.41
	15.66–16.44 (13)	14.86–15.65 (7)	15.43–16.10 (7)	15.01–15.03 (2)	14.95–15.52 (8)	16.19–17.10 (5)
C^1C^1W	4.98 ± 0.13	4.74 ± 0.16	4.74 ± 0.11	4.62	4.69 ± 0.19	5.12 ± 0.22
	4.74–5.20 (13)	4.45–4.91 (7)	4.63–4.93 (7)	4.41–4.82 (2)	4.24–4.92	(10) 4.89–5.50 (7)
M^3M^3W	7.72 ± 0.16	7.31 ± 0.19	7.54 ± 0.12	7.10	7.19 ± 0.17	7.92 ± 0.22
	7.50–7.99 (13)	7.02–7.61 (7)	7.37–7.69 (7)	6.99–7.20 (2)	6.73–7.34 (10)	7.59–8.20 (7)
ZYW	11.91 ± 0.25	11.41 ± 0.15	11.98 ± 0.09	–	11.45 (1)	12.06 ± 0.26
	11.60–12.38 (11)	11.30–11.51 (2)	11.82–12.09 (6)	–	–	11.78–12.30 (3)
MAW	9.16 ± 0.12	8.55 ± 0.03	8.70 ± 0.13	8.49 (1)	8.53 ± 0.13	9.13 ± 0.24
	9.04–9.39 (12)	8.53–8.57 (2)	8.48–8.88 (7)	–	8.33–8.78 (8)	8.80–9.50 (7)
IOW	4.48 ± 0.11	4.27 ± 0.15	4.02 ± 0.10	3.97	4.08 ± 0.17	4.42 ± 0.23
	4.24–4.69 (13)	4.01–4.46 (7)	3.85–4.15 (7)	3.96–3.98 (2)	3.78–4.37 (10)	4.10–4.70 (6)
BCW	8.14 ± 0.15	8.11 ± 0.35	7.77 ± 0.11	7.64 (1)	7.84 ± 0.19	8.14 ± 0.15
	7.87–8.33 (12)	7.86–8.36 (2)	7.62–7.91 (7)	–	7.62–8.10 (8)	8.01–8.31 (3)
BCH	6.23 ± 0.16	5.78 ± 0.00	6.73 ± 0.17	5.95 (1)	5.93 ± 0.15	6.39 ± 0.23
	5.94–6.49 (12)	5.78–5.78 (2)	6.51–6.98 (7)	–	5.65–6.09 (7)	6.14–6–60 (3)
AOB	1.41 ± 0.15	0.56 ± 0.07	1.42 ± 0.12	1.38	1.43 ± 0.07	0.99 ± 0.12
	1.20–1.73 (13)	0.47–0.67 (7)	1.25–1.65 (7)	1.35–1.40 (2)	1.34–1.49 (10)	0.90–1.16 (4)
CM^3L	7.16 ± 0.15	6.76 ± 0.10	6.95 ± 0.12	6.61	6.69 ± 0.11	7.36 ± 0.16
	6.99–7.44 (13)	6.60–6.88 (7)	6.71–7.10 (7)	6.44–6.78 (2)	6.50–6.90 (10)	7.18–7.66 (9)
CP^4L	3.32 ± 0.08	3.21 ± 0.16	3.15 ± 0.06	3.04 (1)	3.12 ± 0.07	3.61 ± 0.11
	3.20–3.45 (13)	3.09–3.32 (2)	3.07–3.24 (7)	–	3.06–3.22 (8)	3.49–3.76 (4)
ML	13.55 ± 0.26	12.81 ± 0.23	13.57 ± 0.22	12.62	12.78 ± 0.28	14.10 ± 0.32
	13.05–14.04 (13)	12.60–13.21 (7)	13.33–14.03 (7)	12.41–12.82 (2)	12.16–13.16 (10)	13.60–14.69 (8)
CM_3L	7.65 ± 0.15	7.25 ± 0.13	7.32 ± 0.11	7.03	7.15 ± 0.11	7.89 ± 0.33
	7.46–7.94 (13)	7.04–7.44 (7)	7.15–7.46 (7)	6.93–7.12 (2)	6.93–7.35 (10)	7.20–8.40 (9)
CPH	4.47 ± 0.12	4.04 ± 0.39	4.76 ± 0.16	4.14 (1)	4.12 ± 0.13	4.76 ± 0.25
	4.27–4.71 (12)	3.76–4.31 (2)	4.49–4.92 (7)	–	3.85–4.24 (8)	4.52–5.01 (3)

The skull is massive with a broad and short rostrum; the cranial profile is flattened, the depression between the rostrum and the braincase is shallow. Zygomata are strong, the sagittal and lambdoid crests are well pronounced; the anteorbital bridge is relatively wide (Fig. 3). The upper incisors are bicuspid, with no cingular cusps. The inner upper incisor (I^2) is slightly longer than the outer upper incisor (I^3) which exceeds the secondary cusp of I^2. The upper canine (C^1) is heavy and higher than the third upper premolar (P^4). There is a definite gap between I^3 and C^1. The middle upper premolar (P^3) is small, not visible when viewed laterally, totally intruded from the toothrow. The basal dimension of the anterior upper premolar (P^2) is one-quarter that of P^4 and is approximately twice the size of P^3 (Fig. 4). M^1 and M^2 have a very reduced paraconule and paraloph but other cusps are not reduced. The lower canine (C_1) is about as high as the third lower premolar (P_4). The first lower premolar (P_2) is about half the height of the corresponding canine and last premolar. The middle lower premolar (P_3) is small, partly intruded from the toothrow but visible laterally; P_2 and P_4 are not in contact. The lower molars are myotodont.

Comparisons

The relatively small feet, wing membrane attached at toe, and calcar reaching only half of the free edge of the interfemoral membrane collectively separate *M. indochinensis* from the large-footed species in the Indomalayan Region including *M. adversus*, *M. annamiticus*, *M. fimbriatus*, *M. hasseltii*, *M. horsfieldii*, *M. laniger*, *M. longipes*, *M. macrotarsus*, *M. pilosus* and *M. stalkeri* (Corbet and Hill, 1992; Francis, 2008). The wing membranes of *M. indochinensis* are unicoloured, which character unequivocally distinguishes it from *M. formosus* and *M. hermani.*

Among the remaining Indomalayan species, as *M. indochinensis* has a forearm length of over

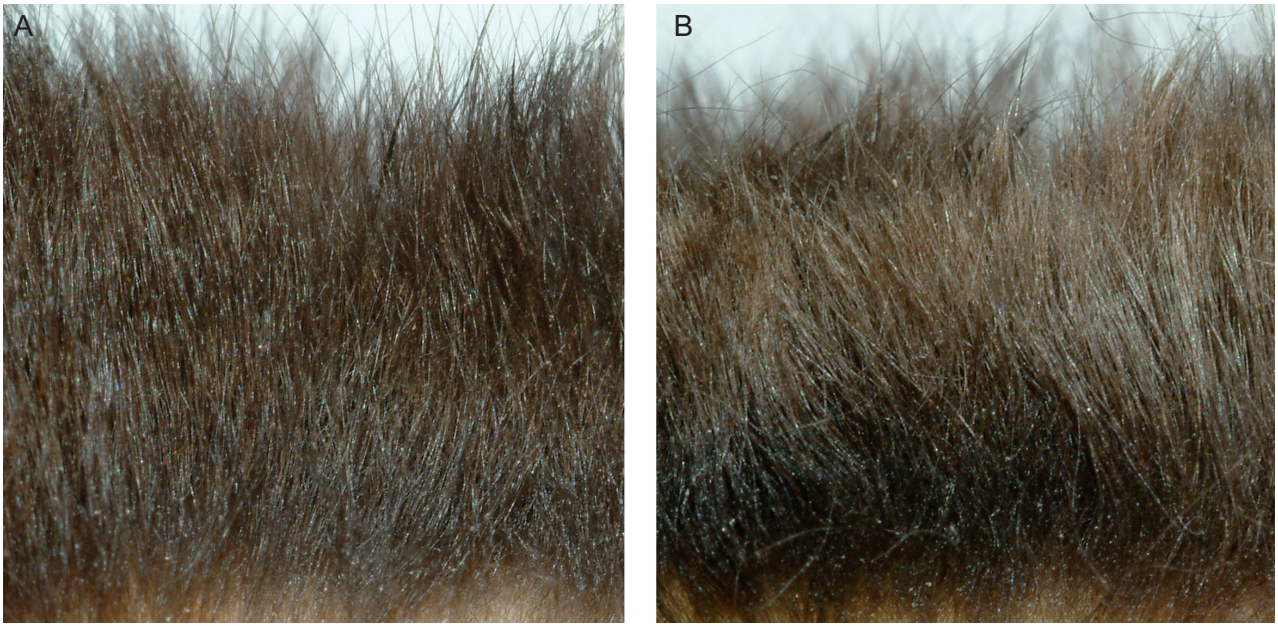

FIG. 1. Photographs showing (A) dorsal and (B) ventral hairs of *M. indochinensis* (HNHM 24210 paratype)

43 mm, species with FA value always smaller than 40 mm (*M. ater*, *M. frater*, *M. muricola*, *M. oreias*, *M. ridleyi*, *M. rosseti* and *M. siligorensis*) are clearly separable. Similarly, *M. blythii* and *M. chinensis* are distinguished from *M. indochinensis* by their much larger external (FA > 55.5 mm) and craniodental measurements (CM^3L > 8.0 mm) (Corbet and Hill, 1992; Bates and Harrison, 1997).

Indomalayan species with comparable forearm and craniodental values are: *M. altarium*, *M. annectans*, *M. borneoensis*, *M. federatus*, *M. montivagus*, *M. pequinius*, *M. peytoni* and *M. sicarius* (Corbet and Hill, 1992; Francis, 2008; Görföl *et al.*, 2013). *Myotis altarium* has a skull with a short and distinctly upturned rostrum and upper and lower middle premolars which are not displaced inwards. *Myotis montivagus* is smaller with no overlap in all measured characters (except AOB) and has a distinctively domed braincase. *Myotis pequinius* has a fringe of stiff hairs on the free edge of the uropatagium (lacking in *M. indochinensis*) and is distinctly larger (FA 49.6–52.7 mm) (Jones *et al.*, 2006).

The remaining species (*M. annectans*, *M. borneoensis*, *M. federatus*, *M. peytoni* and *M. sicarius*) overlap with *M. indochinensis* in external and/or craniodental measurements. To compare these, we used a Principal Component Analysis in addition to morphological comparisons and univariate statistical analyses. The PCA on the 15 craniodental measurements showed good divergence between *M. indochinensis* and four of the other species, but not *M. sicarius* (Fig. 5 and Table 2). However, *M. sicarius* can be readily distinguished from *M. indochinensis* by its measurements and skull shape (see below).

Myotis annectans approaches the forearm length of *M. indochinensis*, but many of its cranial and dental dimensions are smaller than that of the latter species (Table 3). *Myotis annectans* is further distinguishable from *M. indochinensis* by its more

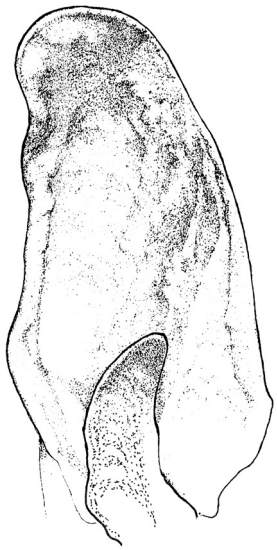

FIG. 2. Right ear and tragus of *M. indochinensis* (IEBR TX05) from Vietnam

reduced (frequently missing) anterior upper and lower premolars and narrower anteorbital bridge which does not exceed 0.7 mm (Table 3). Moreover, the sagittal and lambdoid crests of *M. annectans* are less developed than in *M. indochinensis*, and *M. annectans* has longer, distinctly coloured fur with pale tips to the hairs and usually an orange-brown patch in the centre of the underparts (Francis, 2008).

Myotis borneoensis is similar to *M. indochinensis* in many morphometric characters (Table 3), but is significantly smaller ($P < 0.01$) in the following measurements: MAW, IOW, BCW, BCH, CP^4L, CM_3L and CPH. The anterior upper premolar (P^2) of *M. borneoensis* is smaller in proportion to P^4 than in *M. indochinensis*, while P^3 of *M. borneoensis* is much smaller than that of *M. indochinensis* and totally intruded from the toothrow.

Myotis federatus is significantly smaller ($P < 0.01$) in the FA, GTL, CCL, M^3M^3W, MAW, IOW, CM^3L, ML and CM_3L values than *M. indochinensis*; its skull is more domed and it has a clearly less developed sagittal crest. *Myotis federatus* also has a darker, almost blackish-brown dorsal fur.

Myotis peytoni is significantly smaller ($P < 0.01$) in the GTL, CCL, C^1C^1W, M^3M^3W, MAW, IOW, BCW, BCH, CM^3L, CP^4L, ML, CM_3L and CPH measurements. The cranial profile of this species is more elevated than in *M. indochinensis*. The middle upper premolar of *M. peytoni* is in the toothrow, while it is displaced in *M. indochinensis*.

Myotis indochinensis is most similar to *M. sicarius* in general skull shape and dental features (including the relative size and position of premolars in both toothrows), but is significantly smaller with no overlap in the following measurements: FA, GTL, CCL, AOB, CP^4L and ML (Table 2). The new species is further separable from *M. sicarius* by its even more flattened cranial profile and more developed sagittal and lambdoid crests.

Genetic relationships

DNA barcodes for all five specimens of *M. indochinensis* sp.n. from Laos, as well as one specimen from Ha Tinh, Vietnam and six specimens from Guangxi, China (these additional specimens were not examined as part of this study) were published by Francis *et al*. (2010) as '*M. montivagus*'. Only minor intraspecific variation was detected within the series suggesting that all of these specimens represent the same species. The sequences differed by approximately 10% from the next nearest neighbour for which DNA barcodes were available, which was an unidentified species called 'CMF sp.

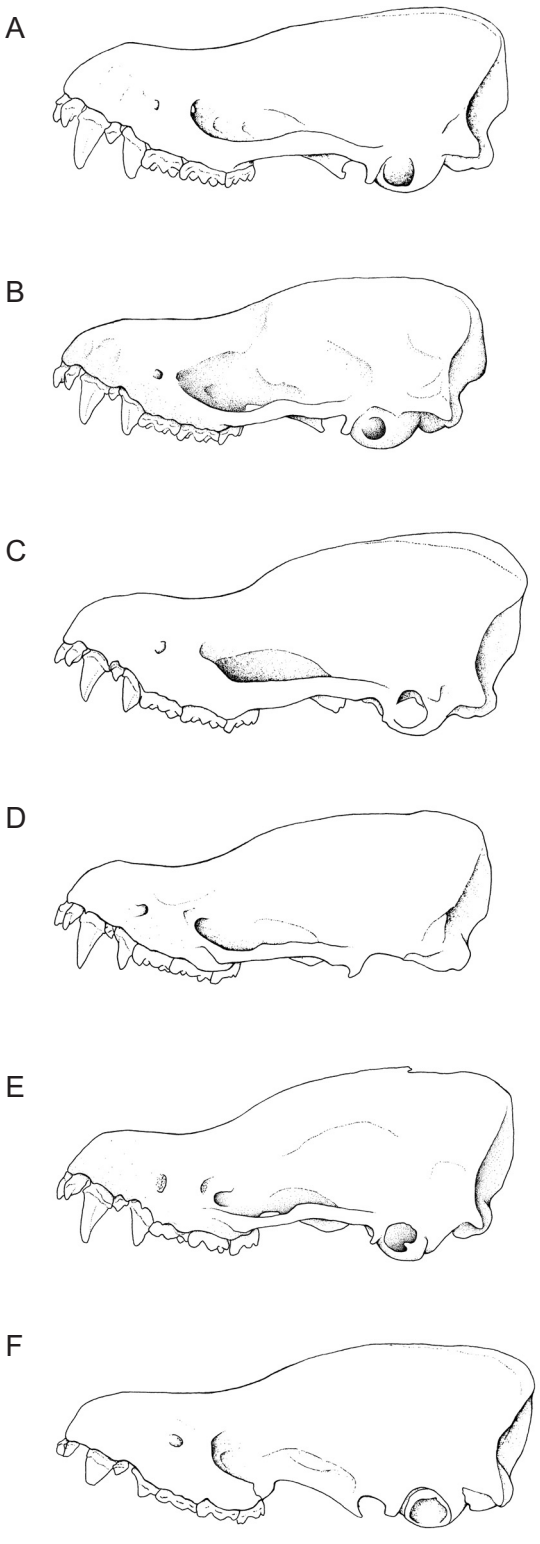

FIG. 3. Lateral view of skulls of (A) *M. indochinensis* IEBR M-839-2 (holotype), (B) *M. annectans* HNHM 2008.23.10. from Vietnam, (C) *M. borneoensis* BM(NH) 83.349 (holotype), (D) *M. federatus* BM(NH) 16.4.20.5 (holotype), (E) *M. peytoni* BM(NH) 12.8.25.1 (holotype), (F) *M. sicarius* BM(NH) 23.1.9.4 from Nepal. Scale = 5 mm

E' in Francis *et al*. (2010). This level of divergence clearly indicates a distinct species. Recent analyses of cytochrome *b* data from one specimen of CMF sp. E (ROM 106389) suggest that it may be closely related to, or even conspecific with, specimens referred to *M. federatus* from peninsular Malaysia (SMF 69341; all labelled as *M.* cf. *montivagus* in figure 1 of Ruedi *et al*., 2013). This suggests that at least some of the species formerly grouped under the name *M. montivagus* (Görföl *et al.*, 2013) may form a natural grouping of related species. However, DNA sequences are not yet available for other species in this group (*M. borneoensis*, *M. peytoni* and *M. montivagus* itself) to test this hypothesis.

Distribution and ecological notes

The type locality was in a secondary forest in the vicinity of the village of Loa, situated near the newly established Saola Nature Reserve. The type series was collected in mist-nets set across a large stream with exposed rocks. No further bat species was collected during the two-day rapid survey.

Tam Dao National Park is an area of some 36,883 ha, of which about one third is relatively undisturbed subtropical rainforest. The park consists of a series of mountain peaks of heights between 1200–1600 m a.s.l. that are covered with forests. The rainforest extends from about 300 m a.s.l. to the peaks, although in some areas rainforest cover does not start below 600 m a.s.l. The lower slopes of the range are either bare, having been cleared of

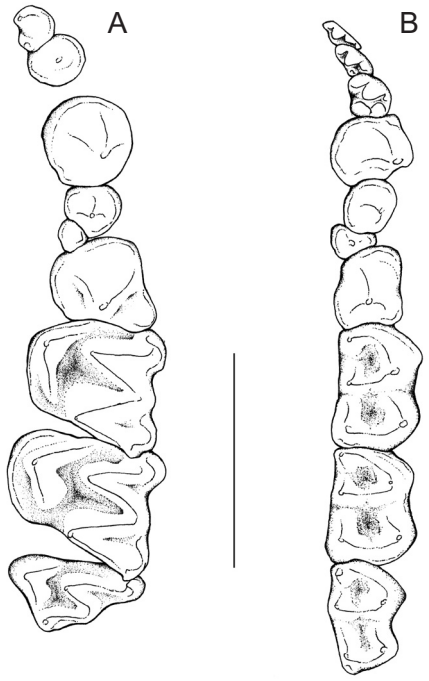

FIG. 4. Occlusal view of (A) left upper and (B) right lower dentition of *M. indochinensis* (IEBR M-839-2, holotype). Scale = 3 mm

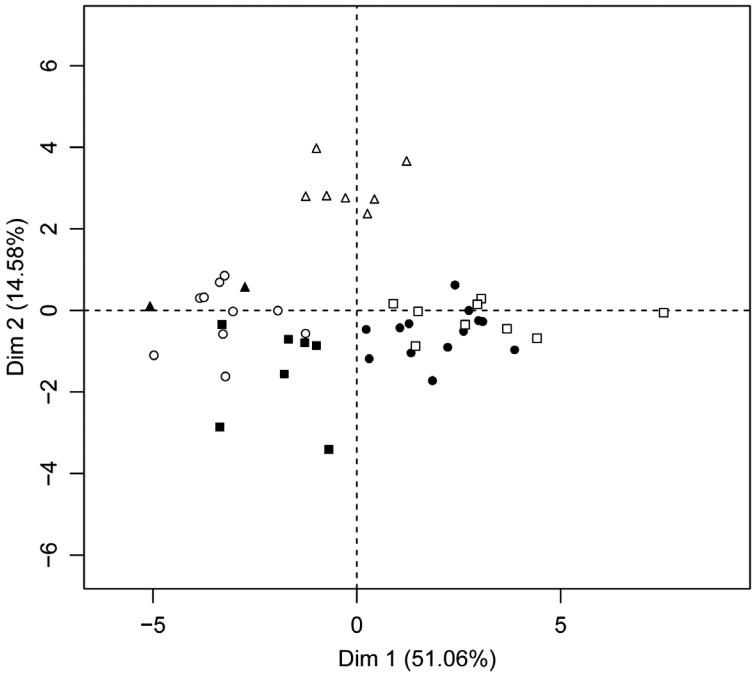

FIG. 5. Principal component analysis based on 15 craniodental characters of *M. indochinensis* (black circles), *M. annectans* (black squares), *M. borneoensis* (empty triangles), *M. federatus* (black triangles), *M. peytoni* (empty circles) and *M. sicarius* (empty squares)

TABLE 2. Factor loadings of craniodental characters obtained by the PCA

Character	PC1	PC2	PC3
GTL	0.821	–	-0.310
CCL	0.820	–	-0.300
C^1C^1W	0.735	–	0.322
M^3M^3W	0.856	–	0.306
IOW	0.650	-0.520	–
ZYW		0.383	0.732
MAW	0.793		0.365
BCW	0.588	-0.560	–
BCH	0.358	0.761	–
AOB	–	0.477	–
CM^3L	0.933	–	–
CP^4L	0.740	–	-0.314
ML	0.891	–	–
CM_3L	0.908	–	–
CPH	0.627	0.584	–
Eigenvalue	7.659	2.187	1.382
Percentage of variance	51.06	14.58	9.21

forest, or have been replanted with conifers (Frontier Vietnam, 1994). The heavily pregnant *M. indochinesis* specimen was mist-netted in a primary forest at an elevation of 450 m a.s.l.

Na Hang Nature Reserve with an area of 42,000 ha is made up of steep limestone hills mainly between 300 and 800 m a.s.l. Evergreen lowland forests (primary and secondary) are present on the limestone slopes of the reserve, and montane and sub-montane forests on the higher terrains over 700 m a.s.l. Karst processes have produced several extensive cave systems (Frontier Vietnam, 1997). Phieng Dung cave (22°30'N, 105°24'E), where one of the referred specimens was caught, is located at 990 m a.s.l. In addition to the new species, it also provides shelter for the following bat species: *Rhinolophus affinis*, *R. pearsoni*, *Aselliscus stoliczkanus*, *Hipposideros armiger*, *H. larvatus* and *H. lylei*.

Ta Xua Nature Reserve is situated in the catchment of the Black River and has an area of approximately 18,000 ha. The topography of the reserve is dominated by a ridge of high mountains that runs along the north of the site. This ridge is a southerly extension of the Hoang Lien Mountains and forms the border between Son La and Yen Bai provinces. There are many peaks above 2,000 m a.s.l. along this ridge (Tordoff *et al*., 2004). The vegetation at higher elevations is forest on limestone which is replaced by disturbed secondary forest below 400 m a.s.l. The two *M. indochinensis* specimens were caught in a secondary forest at the elevation of 370 m a.s.l.

DISCUSSION

The large series of specimens of *M. indochinensis* sp. n. allowed a detailed morphological and statistical analysis and provided a solid base for taxonomic conclusions. The available DNA evidence supports the morphological conclusions, although DNA data are not yet available for some of the potentially most closely related species. Our data found the new species at four localities in different parts of Vietnam suggesting it may have a wide distribution in the country. Bates *et al.* (1999) and Hendrichsen *et al.* (2001) reported *M. montivagus* specimens from two further localities in Vietnam that were described as intermediate in size between the

TABLE 3. The results (*P*-values) of one-way ANOVA comparing selected external and craniodental measurements of *M. indochinensis* with *M. annectans*, *M. borneoensis*, *M. federatus*, *M. peytoni* and *M. sicarius*

Character	*annectans*	*borneoensis*	*federatus*	*peytoni*	*sicarius*
FA	0.108	0.251	< 0.001	0.730	< 0.001
GTL	0.007	0.994	0.001	< 0.001	0.002
CCL	< 0.001	0.349	< 0.001	< 0.001	< 0.001
C^1C^1W	0.044	0.042	0.069	0.002	0.468
M^3M^3W	< 0.001	0.244	< 0.001	< 0.001	0.185
ZYW	0.047	0.954	–	0.280	0.805
MAW	< 0.001	< 0.001	0.003	< 0.001	0.999
IOW	0.049	< 0.001	< 0.001	< 0.001	0.958
BCW	1.000	0.001	0.070	0.005	1.000
BCH	0.014	< 0.001	0.562	0.007	0.642
AOB	< 0.001	1.000	0.999	0.998	< 0.001
CM^3L	< 0.001	0.024	< 0.001	< 0.001	0.014
CP^4L	0.451	0.002	0.030	< 0.001	< 0.001
ML	< 0.001	1.000	< 0.001	< 0.001	< 0.001
CM_3L	< 0.001	0.005	< 0.001	< 0.001	0.054
CPH	0.017	0.007	0.380	< 0.001	0.079

two former subspecies, *M. montivagus federatus* and *M. montivagus borneoensis*. Based on the forearm length and the craniodental description of these specimens, they may also represent *M. indochinensis*, although further investigation is needed to clarify their proper taxonomic status. The Lao specimens came from two localities in central Laos, while evidence from DNA barcodes of specimens in the Royal Ontario Museum indicates the species also occurs in Guangxi province in China.

Thanks to the intensive research efforts in recent years the number of bat species recorded from Vietnam continuously increases. In the latest compilation of the mammals of Vietnam, Can *et al.* (2008) listed 111 bat species and since then, within a few years, seven more species new to science have been reported from the country (Borisenko *et al.*, 2008; Furey *et al.*, 2009; Csorba *et al.*, 2011; Francis and Eger, 2012; Thong *et al.*, 2012), although one other species was reduced to a synonym (Francis and Eger, 2012). Based on published literature, the following *Myotis* species are presently known from Vietnam: *M. annamiticus*, *M. annectans*, *M. ater*, *M. chinensis*, *M. hasseltii*, *M. horsfieldii*, *M. indochinensis*, *M. laniger*, *M. muricola*, *M. phanluongi*, *M. pilosus*, *M. rosseti* and *M. siligorensis*. *Myotis montivagus* has also been reported (Bates *et al.*, 1999; Hendrichsen *et al.*, 2001; Kuznetsov *et al.*, 2001; Kruskop and Schinov, 2010), but no measurements were published, so these specimens need to be re-examined to determine whether they represent true *M. montivagus* or what we have now described as *M. indochinensis* (see remarks above).

The characters of this new species support our assertion that the anatomical traits formerly used to discriminate the subgenera of *Myotis* are not consistent across species. As defined by Tate (1941), Corbet and Hill (1992) and Francis (2008) the *Myotis* subgenus is characterised by relatively long ears, small feet, low braincase, gradually sloping skull profile and four-lobed first and second lower incisors, whereas the *Selysius* subgenus is characterized as having relatively small feet, wing membrane attached at base of toes, ears not enlarged, and middle lower incisors usually with only three lobes. *Myotis montivagus* and its allies have traditionally been included in *Selysius*, but the flattened skull more closely matches *Myotis*. Among other species regarded as belonging to the *Myotis* subgenus the ear is not always enlarged (e.g., *M. sicarius*) and the skull is not always flattened (e.g., *M. altarium*). Some other species allocated to *Selysius* (e.g., *M. ater* and *M. annectans*) have relatively flattened skulls. In general, the number of the lobes on the lower incisors is variable and the lobes themselves are not always evidently separable. Similarly, some features thought to be exclusively typical for *Leuconoe* (plagiopatagium attached at metatarsus or above, developed protoconuli on upper molars) can also be found in some other species. *Myotis siligorensis* has the wing attached near the middle of the metatarsi; and both *pruinosus* and *siligorensis* have well defined protoconuli on M^1 and M^2. However, these latter species do not possess other features characteristically found in *Leuconoe* (i.e., hindfoot more than half of tibia length and calcar extending to over half of the free edge of the interfemoral membrane).

As a consequence, we do not consider the suites of characters formerly used to discriminate subgenera to be useful even for distinguishing ecomorphs. Nevertheless, several of these characters are useful for differentiating individual species. In particular, the term ‘large-footed’ is used to designate species with hindfoot more than half of tibia length, long calcar and high attachment point of wing as a convenient character for field identification. This includes several groups of apparently unrelated species that may use ‘trawling’ on the surface of the water to catch food.

Identification key to selected South-east Asian *Myotis*

Barcoding and phylogenetic results provide evidence that some widely distributed small-sized species e.g. *M. ater* and *M. muricola* form divergent clades suggesting that further undescribed cryptic species are present (Francis *et al.*, 2010; Wiantoro *et al.*, 2012). The species level taxonomy of some of the large-footed *Myotis* is also confusing (Francis *et al.*, 2010; own unpublished data) and requires revision. To facilitate research in the wider geographical area, an identification key is herewith provided for the medium and large-sized (FA over 40 mm) *Myotis* species with small feet from the Indomalayan Region which includes the new species.

1a. Wing membrane with conspicuous black and orange coloration 2
1b. Wing membrane unicoloured 3
2a. FA over 55 mm, CM^3L over 8 mm ... *hermani*
2b. FA less than 55 mm, CM^3L less than 8 mm .... *formosus*
3a. Edge of interfemoral membrane with dense, stiff hairs (FA 43.7–45.6 mm, CM^3L over 7.5 mm) ..... *pequinius*
3b. Interfemoral membrane without such hairs ... 4

4a. FA over 55.5 mm, CM^3L over 8.0 mm..... 5
4b. FA less than 55.5 mm, CM^3L less than 8.0 mm 6
5a. FA over 60 mm, I^3 less than twice I^2 in crown area ..... *chinensis*
5b. FA usually less than 60 mm, I^3 more than twice I^2 in crown area ..... *blythii*
6a. Ear extends approx. 5 mm over tip of nose when laid forward; anterior part of rostrum upturned ..... *altarium*
6b. Ear at most just reaches tip of nose; rostrum not upturned 7
7a. FA 39–42 mm ..... *montivagus*
7b. FA over 42 mm 8
8a. Anteorbital bridge very narrow, < 0.7 mm (P^3 absent or minute) ..... *annectans*
8b. Anteorbital bridge wider (P^3 always present) 9
9a. FA ≥ 48 mm (CCL > 16 mm) ..... *sicarius*
9b. FA ≤ 47 mm (CCL < 17 mm) 10
10a. P^3 rudimentary, fully out of toothrow (FA 42–45 mm) ..... *borneoensis*
10b. P^3 basally at least one-quarter of P^2..... 11
11a. FA < 43 mm (CCL 15.01–15.02 mm, sagittal and lambdoid crests less developed) .... *federatus*
11b. FA > 43 mm 12
12a. Cranial profile with distinct frontal depression and elevated frontal region, sagittal and lambdoid crests less developed..... *peytoni*
12b. Cranial profile almost straight, frontal part flattened, sagittal and lambdoid crests well developed ..... *indochinensis*

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