

Dull and bright: cryptic diversity within the *Hipposideros larvatus* group in Indochina (Chiroptera: Hipposideridae)

Temní a zářiví: kryptická diversita pavrápenců skupiny *Hipposideros larvatus* ze Zadní Indie (Chiroptera: Hipposideridae)

Sergei V. KRUSKOP

Zoological Museum, Moscow State University, Bolshaya Nikitskaya, 6, 125009 Moscow, Russia;
kruskop@zmmu.msu.ru

received on 14 November 2015

Abstract. Leaf-nosed bats of the *Hipposideros larvatus* species complex are widespread throughout South-East Asia; however, their taxonomic diversity is strongly underestimated. Our analysis of the genetic and morphological diversity within this complex in Indochina and our comparison of this with samples from Myanmar, Thailand and the Sunda Islands demonstrate that the diversity of these bats cannot simply be described as two species, *H. larvatus* and *H. grandis*, as many experts do today. We came to the conclusion that there are at least four species of *larvatus*-like *Hipposideros* in the Vietnamese fauna alone, none of which can be associated with *H. larvatus* s.str. In the meantime, populations from Southern Vietnam may be treated as *H. grandis* until the alternate versions get support from new genetic data. Small animals inhabiting the Con Dao archipelago possess cranial proportions similar to those of insular populations from North Vietnam. However, based on genetic data and baculum proportions, they also belong to *H. grandis*. Their differences from their conspecifics from South-East Asia lowlands let us suggest a new subspecies, probably endemic to the Con Dao Islands.

Key words. *Hipposideros larvatus*, *Hipposideros grandis*, South-East Asia, Indochina, taxonomy, new subspecies.

INTRODUCTION

Hipposideros is a core genus in the family Hipposideridae. It is one of the largest and most diverse mammalian genera. *Hipposideros* is widely distributed in the Palaeotropics and Australia and includes more than 70 recent species (SIMMONS 2005). Its taxonomic diversity is still understudied, which is predictable for a widely distributed tropical genus; articles containing descriptions of new (or revisions of previously described) taxa are published regularly (ROBINSON et al. 2003; GUILLEN-SERVENT & FRANCIS 2006, THABAH et al. 2006, DOUANGBOUPHA et al. 2010a, b, 2011, VU DINH THONG et al. 2012a, b).

The *H. larvatus* species complex occupies one of the key sites in the diversity of the genus. It is widely distributed across most of South-East Asia, from North-East India to Hainan and the Sunda Islands (CORBET & HILL 1992) and within this huge range it displays a number of forms with uncertain taxonomic ranks (KITCHENER & MARYANTO 1993, THABAH et al. 2006, FRANCIS et al. 2010).

Until recently, all of the forms within this species complex were assigned, following TATE's opinion (TATE 1941), to the single polymorphic species *H. larvatus* s.l. (HILL 1963, CORBET & HILL 1992, KOOPMAN 1993). Across its distribution area, up to eight subspecies were accepted (e.g., KOOPMAN 1994); its geographical diversity was (in general) described as gradual decrease in mean body size from north-west to south-east (from Assam and Upper Burma to the Sunda Islands; see: CORBET & HILL 1992). It is noteworthy that these eight subspecies (ibid.) also included the form *alongensis* (which was said to be distributed throughout Northern Vietnam). However, it was cogently shown by TOPÁL (1993) that *H. alongensis* was definitely not a part of *H. larvatus*. The distribution of the subspecies *H. l. grandis* (described from Upper Burma, the Chindwin valley; ALLEN 1936) was treated as a distribution of the mainland Asian population with a relatively large mean size that covered Myanmar, Thailand and South Indochina (HILL 1963, CORBET & HILL 1992).

KITCHENER & MARYANTO (1993), who undertook a detailed study of the Sunda material, came to the conclusion that there was a high cryptic diversity within the *H. larvatus* group (even within the borders of the Sunda region) and described a few new species and subspecies. They expressed an opinion that the taxonomic diversity of the *H. larvatus* group in mainland Asia could also be higher than accepted traditionally; in particular, *H. grandis* might be a separate species. It is noteworthy that the authors possessed only one specimen from Thailand, which they assigned to *H. grandis* only presumably, because of its geographic origin. Nonetheless, *H. grandis* was later treated as a separate species, referring to the KITCHENER & MARYANTO's publication (e.g., SIMMONS 2005). TATE (1941) supposed a synonymy of the forms *leptophyllus* Dobson, 1874 and *grandis* Allen, 1936, which automatically makes *grandis* a junior synonym. Nevertheless, when the species complex was later divided into two species, *leptophyllus* was left as a subspecies of *H. larvatus* (SIMMONS 2005). In 2006, on the basis of bioacoustic data, a sympatric occurrence of the two forms of the *H. larvatus* species complex was shown in India (THABAH et al. 2006). One of those forms was designated as *H. grandis*, despite its aforementioned possible synonymy with *leptophyllus*; a new name, *H. khasiana*, was suggested for the other. Unfortunately, the taxonomic and nomenclatural conclusions of the authors of the aforementioned publication are not quite accurate.

Previously, we made an attempt to systemize the diversity of the *H. larvatus* group in the Vietnamese fauna (KRUSKOP 2003); however, that study was based on a material that was insufficient to make proper taxonomic conclusions. It is currently accepted that there are up to three different species from the *H. larvatus* group in the territory of Vietnam, including *H. larvatus* itself and *H. grandis*; the northern populations are traditionally treated as *H. larvatus*, and the southern as *H. grandis* (KRUSKOP 2013). The third form (from Central Vietnam) probably represents a yet undescribed species that has been designated as *Hipposideros* CMF sp. C (FRANCIS et al. 2010). However, neither the number of forms inhabiting Vietnam nor their association with valid names is clear.

MATERIAL AND METHODS

This study was conducted on scientific material collected in Vietnam over a number of different years of field work by Russian specialists. Beginning in 1989, these works were organized under the guidance and support of the Vietnamese-Russian Science and Technological Tropical Center. Specimens from scientific collections were used for comparison, which are preserved in the Zoological Museum of the Moscow State University, Moscow (ZMMU), the Zoological Museum, Berlin (ZMB.), the Natural History Museum, London (BMNH), the National Museum of Natural History, Paris (MNHN) and the Natural

History Museum, Vienna (NMW, Vienna). Altogether 122 specimens (skulls with skin/alcohol preserved bodies) were examined, which originated from Vietnam, China, Thailand, Cambodia, Malaysia, Myanmar (Burma) and the Sunda Islands (see Appendix). Unfortunately, no type material was studied except for the type of *Rhinolophus vulgaris* Horsfield, 1823 described from Java and represented by a highly damaged skull. Information about the above mentioned forms was taken from literature. For the examination of baculum morphology, 13 penial bones from different parts of Vietnam were prepared, using a standard method with coloration by alizarin red (WHITE 1951).

Cranial and dental measurements were made (under binoculars) with digital calipers to the nearest 0.01 mm. Eighteen measurements were taken: greatest skull length (TL), condylo-canine length (CCL), skull width at mastoid (MW), brain case width above mastoids (BCW), occiput height (height from the lower margins of the occipital condyles to the highest point just above them; OH), zygomatic width (ZW), width of postorbital constriction (POC), rostral width at the level of anteorbital foramina (RW), length of rostrum in front of anteorbital foramen (RL), width across upper canines (CC), width across posterior upper molars (MM), length of the upper tooth row (CM), length of the upper molariform row, distance from P⁴ to posterior molar (PM), longitudinal length of the upper canine (C), width of nasal opening (NO), lower tooth row length (cm), articular length of mandible (MdL), and height of mandible (MdH). To evaluate the pattern of distribution of qualitative traits, principal component (PC) and discriminant analyses (DF) were carried out on the basis of cranio-dental measurements with the use of appropriate modules of the STATISTICA for Windows 7.0 package. Discriminant Function Analysis was performed on six sample sets (each consisting of nine specimens or more) from: the lowland forests of Southern Vietnam (material from the Cat Tien National Park), the Con Dao Islands (Southern Vietnam), Halong Bay (Northern Vietnam), Java, Myanmar and Thailand.

Molecular data were taken from published online datasets housed by the Barcode of Life Data Systems (BOLD; www.boldsystems.org). The standard DNA barcode region – 657 base pair 5' segment of the mitochondrial cytochrome oxidase subunit I (COI) gene was sequenced bidirectionally using standard DNA barcoding protocols for mammals (CLARE et al. 2007, BORISENKO et al. 2008, IVANOVA et al. 2012). Altogether 71 COI sequences of Indochinese specimens belonging to the *larvatus* species complex were used, together with 86 sequences of another ten South-East Asian *Hipposideros* species, all taken from BM, ABBCI and BCDI projects of BOLD. A list of BOLD Process ID numbers is provided below:

Hipposideros cf. larvatus

Laos: ABBM 253-05, ABBM 343-05. **Vietnam, Halong Bay Islands:** SKMZM 1087-12, SKMZM 1106-12, SKMZM 1109-12. **Southern China:** ABCMA 488-06, ABCMA 629-07, ABCMA 632-07. **North Vietnam:** ABRVN 083-06, ABRVN 084-06, ABRVN 087-06, ABRVN 088-06, ABRVN 093-06, ABRVN 098-06, ABRVN 100-06, ABRVN 101-06, ABRVN 266-06, ABRVN 270-06, ABRVN 273-06, ABRVN 276-06, ABRVN 280-06, ABRVN 281-06, ABRVN 286-06, ABRVN 332-06, ABRVN 602-06, ABRVN 607-06, ABRVN 615-06, ABRVN 617-06, ABRVN 618-06, ABRVN 619-06, ABRVN 620-06, ABRVN 623-06, ABRVN 625-06, ABRVN 626-06, ABRVN 627-06, BMNH 321-04.

***Hipposideros aff. larvatus* (“*H. CMF* sp. C”)**

Laos: BMNH 135-03. **Central Vietnam:** BMNH 588-04;

Hipposideros grandis

South Vietnam: ABBSI 245-10, ABBSI 255-10, ABBSI 256-10, ABBSI 398-11, ABRLA 143-06, ABRVN 314-06, ABRVN 315-06, ABRVN 318-06, ABRVN 319-06, ABRVN 320-06, ABRVN 321-06, ABRVN 324-06, ABRVN 333-06, ABRVN 335-06, ABRVN 366-06, ABRVN 368-06, ABRVN 369-06, ABRVN 389-06, ABRVN 399-06, ABRVN 400-06, ABRVN 401-06, ABRVN 402-06, ABRVN 403-06, ABRVN 493-06, ABRVN 533-06, ABRVN 550-06, BMNH 179-03, BMNH 598-04.

Hipposideros cf. grandis

Vietnam, Con Dao Islands: ABBSI 315-11, ABBSI 316-11, ABBSI 317-11, ABBSI 319-11, ABBSI 337-11.

Hipposideros alongensis

SKMZM 1088-12, SKMZM 1094-12, SKMZM 1100-12;

Hipposideros armiger

Laos: ABBM 191-05, BMNH 044-03, BMNH 068-03. **South China:** ABCMA 052-06, ABCMA 053-06, ABCMA 054-06, ABCMA 055-06, ABCMA 349-06, ABCMA 350-06, ABCMA 351-06, ABCMA 352-06, ABCMA 353-06, ABCMA 354-06, ABCMA 363-06, ABCMA 613-07, ABCMA 811-07, ABCMA 830-07, ABCMA 856-07, BMNH 377-04. **North Vietnam:** ABRVN 642-06, ABRVN 643-06, ABRVN 644-06, ABRVN 645-06, ABRVN 646-06, ABRVN 647-06, ABRVN 649-06, ABRVN 650-06, ABRVN 677-06, ABRVN 678-06, ABRVN 679-06, ABRVN697-06, SKMZM 1233-13, SKMZM 1234-13, SKMZM 1236-13. **Central Vietnam:** BMNH 657-05. **South Vietnam:** BMNH 622-04.

Hipposideros cineraceus

South Vietnam: ABBSI 262-10, ABBSI 305-11, ABBSI 307-11, ABBSI 308-11, ABBSI 309-11;

Hipposideros diadema

South Vietnam: ABBSI 219-10, ABBSI 223-10. **Malaysia:** ABRSS 330-06, ABRSS 331-06, ABRSS 350-06, ABRSS 351-06, ABRSS 357-06, BMNH 419-04. **Laos:** BMNH 182-03.

Hipposideros galeritus

South Vietnam: ABBSI 236-10, ABBSI 310-11, ABBSI 311-11, ABBSI 312-11, ABBSI 313-11, ABBSI 314-11, BMNH 597-04, SKMZM 1126-12, SKMZM 1130-12, SKMZM 1131-12, SKMZM 1176-13, SKMZM 1198-13.

Hipposideros cf. griffini

South and Central Vietnam: BMNH 554-04, SKBPA 498-08, SKMZM 1148-12, SKMZM 1152-12, SKMZM 1190-13, SKMZM 1191-13, SKMZM 1194-13, SKMZM 1210-13.

Hipposideros khaokhouaensis

North Vietnam: SKMZM 1108-12.

Hipposideros pendelburyi

Thailand: ABBM 064-05.

Hipposideros pomona

North Vietnam: SKMZM 1097-12, SKMZM 1098-12. **Central Vietnam:** BMNH 659-05. **South Vietnam:** ABBSI 346-11, BMNH 618-04, BMNH 681-05, SKMZM 1111-12, SKMZM 1199-13.

Hipposideros swinhoei / *H. scutinares*

North and Central Vietnam: BMNH 398-04, BMNH 587-04, BMNH 658-05.

Analyses of these data were performed by the staff of the Canadian Centre for DNA Barcoding (CCDB), University of Guelph, Canada. Analysis of molecular COI data was performed using MEGA ver. 5 molecular genetic analysis software (TAMURA et al. 2011). A distance-based tree was built with the Neighbour-Joining algorithm using the maximum composite likelihood model (TAMURA et al. 2007) and pairwise deletion of missing data. The rate variation among sites was modeled with a gamma distribution (shape parameter = 1). Branch support was assessed by bootstrapping with 1000 replicates.

RESULTS

The traditionally accepted differences between *Hipposideros larvatus* and *H. grandis* are usually described as differences in body size and coloration. *Hipposideros grandis* (at least in general)

is larger and has a richer and brighter fur coloration than *H. larvatus* (KRUSKOP 2013). In his original description, ALLEN (1936) specified that *H. grandis* differed from the typical Javanese form in its larger size and paler coloration, and had a characteristic contrast between its underfur and guard hairs. That was in part the reason for allocating smaller individuals from the Con Dao islands not to the mainland race of *H. larvatus* s. lato, but to the Bornean subspecies *H. l. neglectus* (VAN PEENEN et al. 1970).

Within the Vietnamese territory, the coloration diversity of *H. larvatus* s. lato is not too large, except for animals from southern lowland forests. Most specimens have a brownish or grayish coloration. The underfur on their backs is distinctly paler than their guard hairs; underfur on their bellies, which are paler in general, are somewhat darker than the guard hairs. In animals from the Halong Bay, the belly and underfur are grayish, almost without yellowish tints. Animals from Southern Indochina are much brighter and have two distinct color phases: a darker one with brown (even blackish-brown) guard hairs and pale underfur; and a lighter one with golden-reddish bellies and underfur. We have found two similar color phases in samples from Thailand (“larger” form; see below), although in this case the darker phase had almost no brownish tints; it possessed blackish guard hairs and a whitish underfur. This difference probably reflects just individual variability. Although the coloration of Vietnamese, Cambodian and Thai animals is not entirely identical to Allen’s description of *H. grandis*, it matches the trend towards brighter coloration than found in insular populations and the presence of two color phases.

The results of our principal component analysis, although they did not divide the samples discretely, definitely demonstrate morphometric heterogeneity within the *H. larvatus* group (Fig. 1). In the space of the first and third PCs (maximum correlation with PM and C, and with BCW,

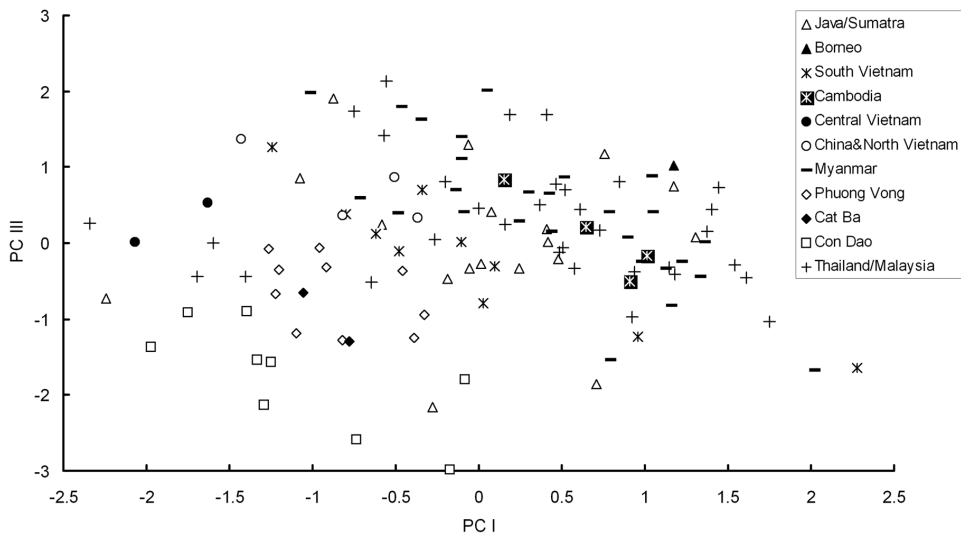


Fig. 1. Bivariate scatterplot for the two first principal components, calculated for 18 cranial and dental measurements of 121 specimens of leaf-nosed bats from the *Hipposideros larvatus* species complex.

Obr. 1. Bivariátní graf první a druhé hlavní proměnné, spočtené z 18 lebečních a dentálních rozměrů 121 jedinců pavrápenců komplexu *Hipposideros larvatus*.

Table 1. Squared Mahalanobis distances between group centroids (six studied sample sets, see text) and from group centroids to selected outlying specimens from Borneo (*Hipposideros [larvatus] neglectus*), Tonkin (inner regions of Northern Vietnam; possible unnamed species), Chinese province Guanxi, Kebang (Quang Binh province of Vietnam; *Hipposideros* SMF sp. C) and Thailand (“smaller” form)
 Tab. 1. Mahalanobisovy čtvercové vzdálenosti mezi centroidy skupin (šest studovaných souborů jedinců) a mezi centroidy skupin k vybraným jedincům z Bornea (*Hipposideros [larvatus] neglectus*), Tonkinu (vnitřní oblast severního Vietnamu; možná neznámý druh), čínské provincie Kuang-si a vietnamské provincie Quang Binh; *Hipposideros* SMF sp. C) a Thajska (“menší” forma)

		Cat Tien NP	Con Dao	Halong Bay	Java	Myanmar	Thailand
Vietnam, Cat Tien NP		0	63.397	43.832	29.470	17.757	21.278
Vietnam, Con Dao Islands			0	15.527	29.125	83.691	67.810
Vietnam, Halong Bay				0	22.394	60.957	52.045
Java (<i>H. larvatus ?larvatus</i>)					0	37.300	34.958
Myanmar						0	17.112
Thailand (“large” form)							0
Borneo	ZMB 49204	53.606	113.815	108.825	59.870	31.957	36.363
Tonkin	ZMB 54084	53.574	57.647	58.138	31.746	59.979	68.752
	ZMB 67794	38.129	54.248	45.578	31.365	33.365	45.113
Guanxi	ZMMU S103720	72.699	64.709	37.870	51.922	70.872	60.978
Kebang	ZMMU S167177	128.821	76.717	100.336	74.945	161.432	154.569
Thailand	NMW 42879	30.988	45.588	42.418	38.026	47.019	53.880
	NMW 65569	76.387	45.826	36.260	60.308	73.069	62.265
	NMW 65570	56.420	45.658	35.301	55.403	58.119	59.449
	NMW 65571	67.980	26.389	26.787	35.392	69.117	66.195

respectively, eigenvalues 13.111 and 0.792, percentage of total variety – 72.84% and 4.40%) two groups may be distinguished. One includes animals from southern Indochina, Myanmar, Thailand, Malaysia, and the Sunda Islands (Java, Sumatra, Borneo and Labuan). The second one consists of animals from the Halong Bay islands and the Con Dao islands, as well as specimens from Central Vietnam, a smaller part of the Sunda sample, and five individuals from Thailand.

The differences between sample sets used in the DF analysis are significant ($p < 0.0001$); the association of these specimens with a particular sample (in most cases) matched the expected level. The smallest values of the squared Mahalanobis distances between sample centroids (less than 20, which is close to higher values of variability within samples) were found between samples from Myanmar, Thailand and Cat Tien, and also between insular samples from Con Dao and Halong Bay (Table 1). The largest distance values were between the Con Dao samples and samples from Cat Tien, Myanmar and Thailand. An absence of similarity to any of the sample sets was found in specimens from Borneo, Sumatra, Malaysia, the inner parts of Northern Vietnam and Central Vietnam. The specimen from Central Vietnam, allocated to *Hipposideros* CMF sp. C, expectedly demonstrated the largest difference from the sample sets (squared Mahalanobis distances approximately two times greater than the largest distances between group centroids). Five Thai specimens definitely did not belong to the same sample as the others; four of them demonstrated no strict similarity to any other analyzed sample.

Specimens from different Sunda Islands do not belong to a single sample as it was shown by both morphometric analyses. We expected that, taking into account the cryptic diversity described by KITCHENER & MARYANTO (1993). According to our results, there are at least two different taxa of the *larvatus* species complex inhabiting the inner parts of Thailand (which can be named formally as “larger” and “smaller” forms) and most probably sympatric in at least one locality.

Unfortunately, no penial bone material was available for the animals from Central Vietnam and the inner regions of Northern Vietnam. Penial bones of animals from the coastal parts of Northern Vietnam and from the south of the country are distinct from each other in terms of their shape (Fig. 2); none of them definitely match the bacula described by KITCHENER & MARYANTO (1993) as that of *H. cf. grandis* or typical *H. larvatus* (KRUSKOP 2014). Penial bones of animals from Halong Bay are elongated and proportionally narrow, with somewhat angular bases, shallow basal cavities, and poorly developed septa; their lower basal lobes are short. In contrast to the penial bone of a typical Javanese *H. larvatus* (KITCHENER & MARYANTO 1993), there are no noticeable lateral projections in the widest part of the bone. Penial bones of mainland North Vietnam specimens were described by TOPÁL (1975). They differ from those of Halong Bay animals only slightly in size and shape; however, it is not clear to which genetic

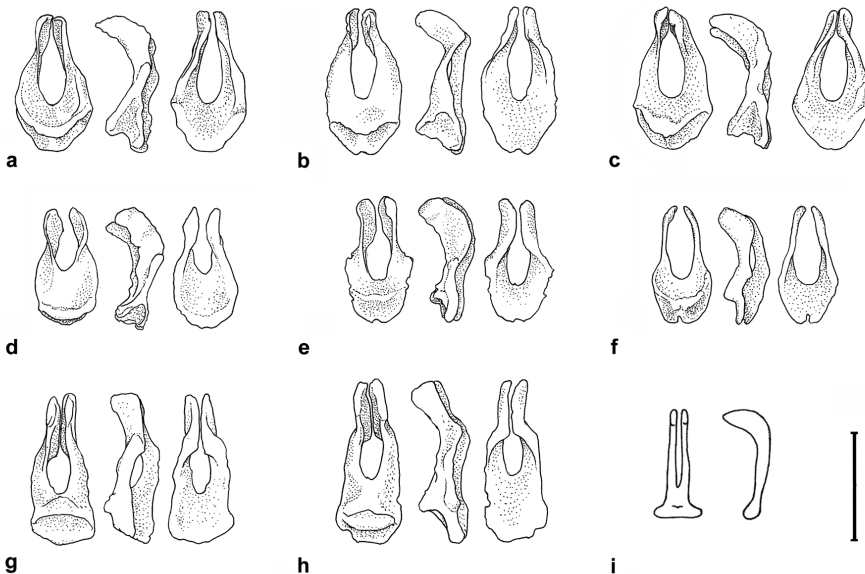


Fig. 2. Penial bones (dorsal and lateral views) of the *Hipposideros larvatus* species complex. Scale bar = 1 mm. Explanations: a–c – *H. grandis* from Dong Nai and Lam Dong provinces of S. Vietnam; d–f – *H. cf. grandis* from Con Dao archipelago (South Vietnam); g–h – *H. cf. larvatus* from Halong Bay Islands (North Vietnam); i – *H. larvatus larvatus* (after KITCHENER & MARYANTO 1993).

Obr. 2. Penisové kosti (dorsální a laterální pohled) pavůpávců skupiny *Hipposideros larvatus*. Měřítko = 1 mm. Vysvětlivky: a–c – *H. grandis* ze severovietnamských provincií Dong Nai a Lam Dong; d–f – *H. cf. grandis* ze souostroví Con Dao (jižní Vietnam); g–h – *H. cf. larvatus* z ostrovů Halong Bay (severní Vietnam); i – *H. larvatus larvatus* (podle KITCHENERA & MARYANTA 1993).

lineage the animals studied by Topal belong. The penial bones of Southern Vietnam individuals are distinctly shorter in proportion and generally have oval or roundish-diamond shapes. Their bases usually possess definite basal concavities with well-developed medial septa and elongated lower lobes. The bacula of animals from Con Dao are quite similar in their overall shape and proportion to those of mainland specimens, from which they are distinguished by their somewhat smaller size. They are quite different from penial bones of Bornean *H. larvatus neglectus* (as described in ZUBAID & DAVISON 1987).

In the tree obtained from the analysis of the COI gene of South-East Asian leaf-nosed bats (Fig. 3), four clades, associated with the *H. larvatus* species complex, are easily seen with a high bootstrap support (99–100) and a nearly species level of divergence. The most divergent clade is represented by the undescribed form *H. CMF* sp. C, which is distinct from other *H. larvatus* s. lato at approximately the same level as the definitely distinct *H. armiger* (about 7–10% of divergence). The difference level between the other haplogroups is lower. Two clades with about 5% of divergence are formed by animals from northern Indochina, which are traditionally included into *H. larvatus* s. str. One of these two clades is composed of haplotypes from northern Laos and from Halong Bay; on their turn they appeared to be divided by ca. 1.5% of divergence. Animals from Southern Vietnam, usually allocated to *H. grandis*, are distinct from Northern Vietnamese animals by ca. 5–5.5%. The haplogroup from the Con Dao Islands is also nested within this clade, showing ca. 1% of divergence from the mainland haplotypes (which has already been mentioned in the literature: KRUSKOP 2011). The divergence level between the

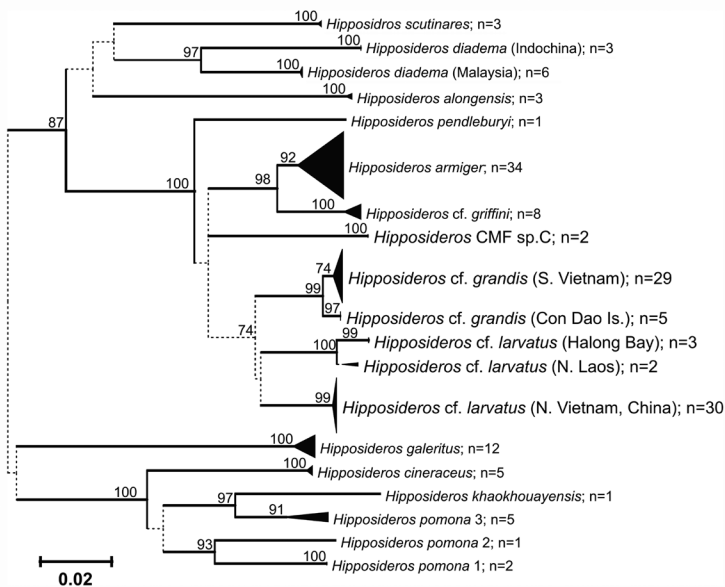


Fig. 3. Kimura-2-parameter tree for COI mt-gene sequences of 153 South-East Asian leaf-nosed bats. Only bootstrap supports over 70 are shown.

Obr. 3. Strom Kimura-2-parametru spočtený ze sekvencí mitochondriálního genu COI získaných ze 153 jedinců pavrápenců jihovýchodní Asie. Ukázána je pouze bootstrapová podpora vyšší než 70.

above mentioned main clades is comparatively low, though it definitely exceeds the diversity within each cluster and also exceeds the intraspecific diversity of most of other species involved in this analysis (except for *H. diadema* and *H. pomona*, which were definitely representative of multispecies complexes; e.g., FRANCIS et al. 2010).

DISCUSSION

Both the number of species within the *Hipposideros larvatus* group and their valid names are subjects for discussion. For instance, some doubts have been expressed about the use of the name *H. grandis* for Indochinese animals (FRANCIS 2008).

Nonetheless, there are no doubts that the Indochinese territory is inhabited by several species of the *larvatus* complex. According to our data, there might be no less than four such forms; however, the use of only one gene marker is insufficient to make a final decision. At least, animals from Halong Bay differ from their South Vietnamese cousins in their size, coloration and baculum morphology; they undoubtedly belong to a different species. There are no grounds to think that Halong Bay animals are closer to the typical *H. larvatus*; this cannot be implied from their skull morphometry or penial bone morphology. With high probability, the race inhabiting the coastal areas of North Vietnam represents a distinct species. Of the available names suggested for the *larvatus* group, the name *H. poutensis* Allen, 1906 (described from the Island of Hainan) is probably acceptable for this species; however, comparative material from its terra typica is needed to formulate a final conclusion.

Animals from the inner regions of North Vietnam were unfortunately very poorly represented in our studied material. Besides their genetic differences, their distinct morphometric positions should be mentioned. Their size is similar to that of South Vietnam individuals.

Though the animals from Southern Vietnam are not identical to those from Myanmar, they are definitely similar in morphology and demonstrate common trends in fur coloration. Until opposite results are obtained (e.g., from a molecular genetic analysis) and the taxonomic position of the form *leptophyllus* is clarified, we may consider that the animals from southern Indochina actually belong to *H. grandis*. As mentioned above, there are two different forms of *H. larvatus* s.l. in Thailand. KITCHENER & MARYANTO, judging by the published dimensions, disposed the specimen of the “smaller” form (KITCHENER & MARYANTO 1993: 126). This can explain differences in baculum shape between Vietnamese *H. grandis* and “*H. cf. grandis*” from Thailand.

Animals from the Con Dao Islands represent a special subject for discussion. According to their craniometry, they occupy a distinct position: they demonstrate some similarities with Halong Bay individuals, from which they are very distinct both in genetics and baculum morphology. In contrast, though quite different from South Vietnamese animals in cranial morphometry, Con Dao individuals are very similar to them in penial bone shape and belong to the same genetic lineage. Thus, we may consider that we are dealing with a subspecies that has recently divided from the mainland population and has quickly gained some valuable morphological differences in these insular conditions. Since no valid name could be applied to this subspecies, we offer its formal description below.

***Hipposideros grandis consonensis* subsp. nov.**

HOLOTYPE. ZMMU S-186749, adult male, (body in alcohol, with extracted skull), collected: Vietnam, Ba Ria-Vung Tau Province, Con Son Island (largest island of the Con Dao archipelago), vicinity of the Con

Dao populated place, May 2010, collected by S.V. KRUSKOP (within a complex expedition organized by the Vietnamese-Russian Tropical Center).

DIAGNOSIS. Medium sized *Hipposideros*, a member of the *larvatus* species complex, possessing all of its typical traits. It differs from other forms assigned to *H. grandis* in its smaller mean values of external and cranial measurements. Forearm of Con Dao subspecies is 53.8–57.6 mm vs. 56.5–63.2 mm in Cat Tien animals and 57.5–65.9 mm in Cambodian specimens (MATEVEEV 2005); ALLEN (1936) provides a forearm length of 62.6 mm for the *H. grandis* holotype. Skulls of Con Dao bats are distinctly smaller than those in mainland specimens: TL 20.6–21.4 mm, CC 4.89–5.06 mm; in other South Indochina specimens and animals from Myanmar — no less than 22.3 and 5.4 mm, respectively. The fur on the dorsal part of the body has three coloration zones: grayish-pale hair bases, a dark-brown zone and pale tips. This coloration resembles that of the darker mainland form, but the dark-brown zone is narrower, with a less abrupt contrast

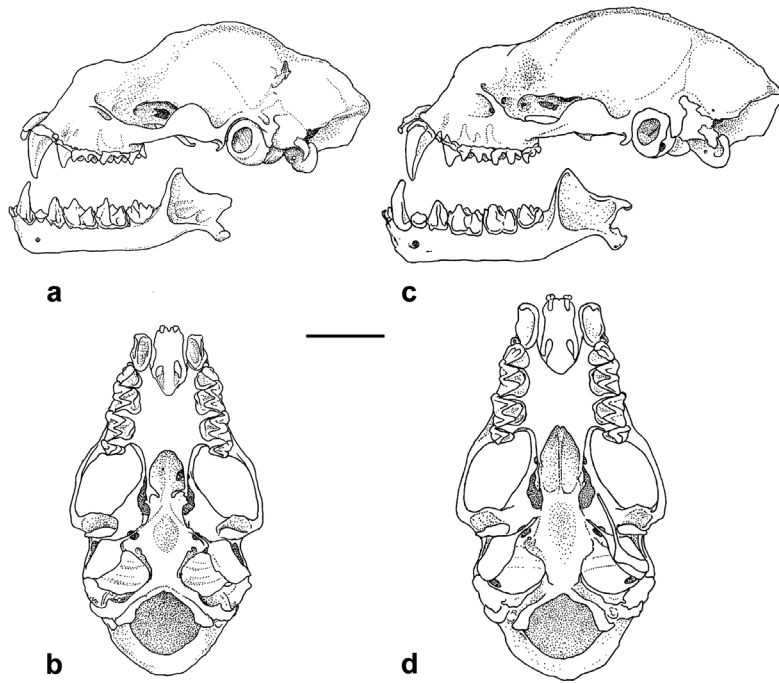


Fig. 4. Skull of *Hipposideros grandis consonensis* ssp. nov. (holotype ZMMU S-186749, ventral and lateral views) in comparison with the skull of *H. grandis* from mainland Southern Vietnam (specimen ZMMU S-18920, close to average size within the sample set). Difference in shape of the parietal region represents individual variation, not a feature of a new taxon. Scale bar = 5 mm.

Fig. 4. Lebka poddruhu *Hipposideros grandis consonensis* ssp. nov. (holotyp ZMMU S-186749, ventralní a laterální pohled) ve srovnání s lebkou *H. grandis* s pevniny jižního Vietnamu (ZMMU S-18920, jedinec rozměry blížký průměrům hodnotám všech šetřených jedinců). Rozdílný tvar spánkové oblasti představuje individuální variabilitu, nikoli znak nového taxonu. Měřitko = 5 mm



Fig. 5. Photo of a live individual of *Hipposideros grandis consonensis* ssp. nov., demonstrating facial structures and proportions typical of the *H. larvatus* species group.

Fig. 5. Fotografie živého jedince *Hipposideros grandis consonensis* ssp. nov., ukazující strukturu a tvar nosního listku typický pro komplex *H. larvatus*.

with the pale bases. The pale tips are very short, and are barely observable on stuffed skins. This provides a duller impression of the animal's overall coloration. Its ventral fur is monotonously grayish-pale. Adult females seem to be more yellowish, but a definite reddish color phase was not revealed amongst the specimens under study. The baculum shape is similar to that of South Vietnam specimens but is a little bit smaller (length 1.08–1.14 mm in Condao specimens vs. 1.14–1.34 mm in mainland individuals).

This subspecies is probably endemic to the Con Dao Islands, where it inhabits sparse forests and forest edges (and also peripheries of settlements). It apparently represents the most numerous bat species in the archipelago. However, no individuals from the coastal regions of Southern Vietnam were available for comparison. If such a population exists, its representatives might be more similar to Con Dao individuals than to animals from the inner parts of the country.

In summary, the *larvatus* species complex demonstrates a tendency common in other tropical bats with wide distribution ranges: a multivariate study of the available material reveals a large number of cryptic forms instead of a single polymorphic species. Occupying analogous ecological niches in different parts of tropical Asia, these species are quite similar morphologically. The level of genetic divergence may noticeably differ from morphological variability. Though a representation of characteristics of cryptic diversity within *H. larvatus* s. lato has already been shown, further multivariate studies are needed to make final decisions about the taxonomic content and structure of this complex, involving new material (particularly molecular genetics) from India, Myanmar, China and the Sunda Islands.

SOUHRN

Paprárenci komplexu *Hipposideros larvatus* jsou široce rozšířeni v jihovýchodní Asii, ovšem jejich skutečná diversita se odráží v taxonomii skupiny jen nedostatečně. Naše analýsa genetické a morfologické

proměnlivosti komplexu v Zadní Indii a její srovnání s jedinci z Barmy, Thajska a Sundských ostrovů ukázala, že diversitu těchto netopýrů nelze jednoduše vyjádřit jen vymezením dvou druhů, *H. larvatus* a *H. grandis*, jak bylo dosud činěno. Dospěli jsme k závěru, že nejméně čtyři druhy pavrápenců skupiny *H. larvatus* jsou přítomny jen ve fauně Vietnamu, přičemž žádný z nich nepředstavuje samotný druh *H. larvatus* s.str. Populace jižního Vietnamu mohou být identifikovány jako *H. grandis* dokud se neukáže nutnost jiného pojmenování, jak naznačují genetická data. Rozměrově malí pavrápenci obývající souostroví Con Dao mají lebeční proporce podobné ostrovním jedincům ze severního Vietnamu. Ovšem podle výsledků genetické analýzy a tvaru a velikosti penisové kosti náležejí nepochybně také druhu *H. grandis*. Nápadné rozdílů mezi těmito ostrovními populacemi a populacemi nížin jihovýchodní Asie nás vedly k vymezení nového poddruhu, zřejmě endemického ostrovům Con Dao.

A c k n o w l e d g e m e n t s

I am sincerely grateful to Dr. Frieder MAYER and Mrs. Nora LANGE for access to the bat collections of the Berlin Zoological Museum and for their kind help and hospitality; to Dr. Roberto Portela MIGUEZ for access to the bat collection of the Natural History Museum in London; to Dr. Jean-Marc PONS for access to the collections of the National Museum of Natural History in Paris; and to Dr. Frank Emmanuel ZACHOS and Mr. Alexander BIBL for access to the collection of the Natural History Museum in Vienna. Original material was collected with the support from and under the supervision of the Vietnamese-Russian Tropical Center for Science and Technology. The extraction and sequencing of DNA material were performed by the Canadian Barcoding Center. This study was financially supported by the Russian Foundation for Basic Research (grant No 13-04-00439-a).

REFERENCES

- ALLEN G. M., 1936: Two new races of Indian bats. *Records of the Indian Museum*, **38**: 343–346.
- ALLEN G. M., 1938: *The Mammals of China and Mongolia*. American Museum of Natural History, New York, 620 pp.
- BORISENKO A. V., LIM B. K., IVANOVA N. V., HANNER R. H. & HEBERT P. D. N., 2008: DNA barcoding in surveys of small mammal communities: A field study in Suriname. *Molecular Ecology Resources*, **8**(3): 471–479.
- CLARE E. L., LIM B. K., ENGSTROM M. D., EGER J. L. & HEBERT P. D. N., 2007: DNA barcoding of Neotropical bats: species identification and discovery within Guyana. *Molecular Ecology Notes*, **7**: 184–190.
- CORBET G. B. & HILL J. E., 1992: *The Mammals of the Indomalayan Region*. Oxford University Press, Oxford, 488 pp.
- DOUANGBOUBPHA B., BUMRUNGSI S., SOISOOK P., MURRAY S. W., PUECHMAILLE S. J., SATASOOK C., BU S. S. H., HARRISON D. L. & BATES P. J. J., 2010a: A taxonomic review of *Hipposideros halophyllus*, with additional information on *H. ater* and *H. cineraceus* (Chiroptera: Hipposideridae) from Thailand and Myanmar. *Acta Chiropterologica*, **12**: 29–50.
- DOUANGBOUBPHA B., BUMRUNGSI S., SOISOOK P., SATASOOK C., THOMAS N. M. & BATES P. J. J., 2010b: A taxonomic review of the *Hipposideros bicolor* species complex and *H. pomona* (Chiroptera: Hipposideridae) in Thailand. *Acta Chiropterologica*, **12**: 415–438.
- DOUANGBOUBPHA B., BUMRUNGSI S., SATASOOK C., SOISOOK P., BU S. S. H., AUL B., HARRISON D. L., PEARCH M., THOMAS N. M. & BATES P. J. J., 2011: A new species of small *Hipposideros* (Chiroptera: Hipposideridae) from Myanmar and a revaluation of the taxon *H. nicobarulae* Miller, 1902 from the Nicobar Islands. *Acta Chiropterologica*, **13**: 61–78.
- FRANCIS C. M. 2008: *A Field Guide to the Mammals of South-East Asia*. New Holland, London, 392 pp.
- FRANCIS C. M., BORISENKO A. V., IVANOVA N. V., EGER J. L., LIM B. K., GUILLEN-SERVENT A., KRUSKOP S. V., MACKIE I. & HEBERT P. D., 2010: The role of DNA barcodes in understanding and conservation of mammal diversity in Southeast Asia. *Public Library of Science One*, **5**(9): 1–12.

- GUILLEN-SERVENT A. & FRANCIS C. M., 2006: A new species of bat of the *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from Central Laos, with evidence of convergent evolution with Sundaic taxa. *Acta Chiropterologica*, **8**: 39–61.
- HILL J. E., 1963: A revision of the genus *Hipposideros*. *Bulletin of the British Museum (Natural History), Zoology*, **11**: 3–129.
- IVANOVA N. V., CLARE E. L. & BORISENKO A. V., 2012: Mammalian DNA barcoding. Pp.: 153–182. In: KRESS W. J. & ERICKSON D. L. (eds.): *DNA Barcodes: Methods and Protocols. Methods in Molecular Biology. Volume 858*. Springer Science & Business Media.
- KITCHENER D. J. & MARYANTO I., 1993: Taxonomic reappraisal of the *Hipposideros larvatus* species complex (Chiroptera: Hipposideridae) in the Greater and Lesser Sunda Islands, Indonesia. *Records of the Western Australian Museum*, **16**: 119–173.
- KOOPMAN K. F., 1993: Order Chiroptera. Pp.: 137–241. In: WILSON D. E. & REEDER D. M. (eds.): *Mammal Species of the World. A Taxonomic and Geographic Reference. Second Edition*. Smithsonian Institution Press, Washington, 1206 pp.
- KOOPMAN K. F., 1994: *Chiroptera: Systematics. Handbook of Zoology. Volume VIII, Mammalia, Part 60*. Walter de Gruyter, New York, 217 pp.
- KRUSKOP S. V., 2003: [On the subspecies content of the leaf-nosed bat *Hipposideros larvatus* (Chiroptera: Rhinolophidae) in Central Vietnam]. Pp.: 110–113. In: AVERIYANOV A. O. & ABRAMSON N. I. (eds.): *Systematics, Phylogeny and Paleontology of Small Mammals. Materials of the International Conference*. Zoological Institute of the Russian Academy of Science, St. Petersburg (in Russian, with a summary in English).
- KRUSKOP S. V., 2013: *Bats of Vietnam. Checklist and an Identification Manual*. KMK Scientific Press, Moscow, 300 pp.
- KRUSKOP S. V., 2014: [The bacula of bats from Indochina: Rhinolophoids (Rhinolophidae, Hipposideridae)]. *Plecotus et al.*, **17**: 3–17 (in Russian, with a summary in English).
- MATVEEV V. A., 2005: Checklist of Cambodian bats (Chiroptera), with new records and remarks on taxonomy. *Russian Journal of Theriology*, **4**(1): 43–62.
- ROBINSON M. F., JENKINS P. D., FRANCIS C. M. & FULFORD A. J. C., 2003: A new species of the *Hipposideros pratti* group (Chiroptera, Hipposideridae) from Lao PDR and Vietnam. *Acta Chiropterologica*, **5**: 31–48.
- SIMMONS N. B., 2005: Order Chiroptera. Pp.: 312–529. In: WILSON D. E. & REEDER D. M. (eds.): *Mammal Species of the World. A Taxonomic and Geographic Reference. Third Edition. Volume 1*. Johns Hopkins University Press, Baltimore, 743 pp.
- TAMURA K., PETERSON D., PETERSON N., STECHER G., NEI M. & KUMAR S., 2011: MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, **28**: 2731–2739.
- TATE G. H. H., 1941: A review of the genus *Hipposideros* with special reference to Indo-Australian species. *Bulletin of the American Museum of Natural History*, **78**: 353–393.
- THABAH A., ROSSITER S. J., KINGSTON T., ZHANG S., PARSONS S., MYA K. M., AKBAR Z. & JONES G., 2006: Genetic divergence and echolocation call frequency in cryptic species of *Hipposideros larvatus* s.l. (Chiroptera: Hipposideridae) from the Indo-Malayan region. *Biological Journal of the Linnean Society*, **88**: 119–130.
- THONG V. D., PUECHMAILLE S. J., DENGINGER A., DIETZ C., CSORBA G., BATES P., TEELING E. C. & SCHNITZLER H.-U., 2012a: A new species of *Hipposideros* (Chiroptera: Hipposideridae) from Vietnam. *Journal of Mammalogy*, **93**: 1–11.
- THONG V. D., PUECHMAILLE S. J., DENZINGER A., BATES P., DIETZ C., CSORBA G., SOISOOK P., TEELING E. C., MATSUMURA S., FUREY N. & SCHNITZLER H.-U., 2012b: Systematics of the *Hipposideros turpis* complex and a description of a new subspecies from Vietnam. *Mammal Review*, **42**: 166–192.
- TOPÁL G., 1993: Taxonomic status of the *Hipposideros larvatus alongensis* Bourret, 1942 and occurrence of *Hipposideros turpis* Bangs, 1904 in Vietnam (Mammalia, Chiroptera). *Acta Zoologica Hungarica*, **39**: 267–288.

- VAN PEENEN P. F. D., CUNNINGHAM M. L. & DUNCAN J. F., 1970: A collection of mammals from Con Son island, Vietnam. *Journal of Mammalogy*, **51**: 419–424.
- WHITE J., 1951: A practical method for mounting the bacula of small mammals. *Journal of Mammalogy*, **32**: 125.
- ZUBAID A. & DAVIDSON G. W. H., 1987: A comparative study of the baculum in Peninsular Malaysian hipposiderines. *Mammalia*, **51**: 139–144.

APPENDIX

List of specimens measured for cranial morphometry. Specimens which were also used in the genetic study are underlined.

Hipposideros cf. grandis

Myanmar: MNHN 21.1.17.117 ♀; MNHN 21.1.17.119 ♀; MNHN 21.1.17.115 ♂; MNHN 21.1.17.116 ♂; NMW 28192 ♀; ZMB 40521 ♀; ZMB 40529 ♀; ZMB 45518 ♀; ZMB 49204 ♀; ZMB 49519 ♀; ZMB 49520 ♀; ZMB 49522 ♀; ZMB 49523 ♀; ZMB 49524 ♀; ZMB 49527 ♀; ZMB 49528 ♀; NMW 28390 ♂; ZMB 49502 ♂; ZMB 49503 ♂; ZMB 49504 ♂; ZMB 49505 ♂; ZMB 49506 ♂; ZMB 49509 ♂; ZMB 49511 ♂; ZMB 49512 ♂; ZMB 49513 ♂; ZMB 49514 ♂; ZMB 49516 ♂. **Cambodia:** ZMMU S-126131 ♀; ZMMU S-166125 ♀; ZMMU S-166128 ♀; ZMMU S-166126 ♂. **Thailand** (“larger” Thai form): NMW 65477 ♀; NMW 65478 ♀; NMW 65482 ♀; NMW 65485 ♀; NMW 65486 ♀; NMW 65488 ♀; NMW 65491 ♀; NMW 65494 ♀; NMW 65496 ♀; NMW 65499 ♀; NMW 42881 ♂; NMW 42882 ♂; NMW 42883 ♂; NMW 65479 ♂; NMW 65480 ♂; NMW 65483 ♂; NMW 65487 ♂; NMW 65489 ♂; NMW 65490 ♂; NMW 65492 ♂; NMW 65493 ♂; NMW 65495 ♂; NMW 65497 ♂; NMW 65498 ♂; NMW 65500 ♂; NMW 65501 ♂; NMW 65569 ♂. **Mainland South Vietnam:** ZMMU S-172572 ♀; ZMMU S-172575 ♀; ZMMU S-172576 ♀; ZMMU S-172569 ♂; ZMMU S-172571 ♂; ZMMU S-186569 ♂; ZMMU S-186570 ♂; ZMMU S-186571 ♂; ZMMU S-189220 ♂; ZMMU S-189221 ♂. **South Vietnam, Con Dao Islands:** ZMMU S-164636 ♀; ZMMU S-164637 ♀; ZMMU S-186740 ♀; ZMMU S-186744 ♀; ZMMU S-186748 ♀; ZMMU S-186736 ♂; ZMMU S-186738 ♂; ZMMU S-186749 ♂; ZMMU S-186750 ♂.

Hipposideros [larvatus] neglectus

Borneo: ZMB 49204 ♀.

Hipposideros cf. larvatus

Java: ZMB 2505 sex?; ZMB 8935 sex?; ZMB 8937 sex?; ZMB 8938 sex?; MNHN 79.11.21.93 sex? (type of *vulgaris* Horsfield, 1823); MNHN 9.1.5.217 ♀; ZMB 8497 ♀; MNHN 61.1777 ♂; MNHN 9.1.5.203 ♂; MNHN 9.1.5.213 ♂; NMW 28195 ♂; ZMB 2572 ♂; ZMB 67647 ♂. **Labuan Island:** ZMB 11363 sex?; ZMB 15734 sex?; ZMB 2978 ♂. **Sumatra:** NMW 28194 ♂; NMW 39970 ♂. **Undetermined Sunda island:** NMW 62919 sex?. **Peninsular (?) Malaysia:** NMW 28388 ♀. **Thailand** (“smaller” Thai form): NMW 42880 ♀; NMW 65570 ♀; NMW 65571 ♀; NMW 42879 ♂; NMW 65484 ♂. **China, Guanxi:** ZMMU S-103720 ♀. **North Vietnam, Halong Bay Islands:** ZMMU S-190295 ♀; ZMMU S-190296 ♂; ZMMU S-164642 ♀; ZMMU S-164644 ♀; ZMMU S-164645 ♀; ZMMU S-164695 ♀; ZMMU S-164707 ♀; ZMMU S-164710 ♀; ZMMU S-164661 ♂; ZMMU S-164666 ♂; ZMMU S-164668 ♂; ZMMU S-164670 ♂. **Mainland North Vietnam:** ZMB 54031 sex?; ZMB 54084 sex?; ZMB 67794 sex?; **South-Central Vietnam, Nha Trang:** ZMMU S-60782 ♀.

Hipposideros CMF sp. C

Central Vietnam: ZMMU S-167177 ♀.