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New insights into the taxonomy of the marmoset rats *Hapalomys* (Rodentia: Muridae)

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Abstract. A new species of marmoset rat, *Hapalomys suntsovi*, is described from Binh Phuoc Province, southern Vietnam. The species seems to be endemic to Vietnam. It is diagnosed on the basis of cranial morphology, the diversity of COI gene sequences and karyotypic peculiarities. A comparison with the two currently recognised *Hapalomys* species is provided. This finding represents the southernmost record of marmoset rats in Vietnam.

Key words. rodents, skull morphology, genetic diversity, Southeast Asia, new species

INTRODUCTION

The genus *Hapalomys* Blyth, 1859 includes medium-sized rodents, the so-called marmoset rats that are well-adapted for arboreal life and inhabit the bamboo forests of Southeast Asia (Musser & Newcomb, 1983). Marmoset rats are one of the less-investigated groups within recent rodents due to their rarity, scattered natural range, and specific ecology, because these species are highly arboreal and restricted to bamboo habitats (Lunde & Aplin, 2008; Clayton, 2008). There are no more than two dozen specimens currently available at scientific collections worldwide, few of which are genetically sampled. Evolutionary relationships of the marmoset rats have been debated until it was revealed in a molecular phylogenetic study that the group has no close relatives among the Murinae and represents a basal branch within the subfamily (Meschersky et al., 2016). Up to today, actual scarcity of comparative materials has hampered investigating their natural history and taxonomy.

According to the taxonomic study of Musser (1972), two *Hapalomys* species are currently recognised: *H. longicaudatus* Blyth, 1859 and *H. delacouri* Thomas, 1927. The former is distributed in Southeastern China, Southeastern Myanmar, Western and Peninsular Thailand and the Malay Peninsula, whereas the latter is known from Southern China (Hainan and Guangxi), Northern Laos and Central Vietnam (Musser & Carleton, 2005; Lunde & Aplin, 2008). Three subspecies have been recognised by Musser (1972) within *H. delacouri*: *H. d. delacouri* from Central Vietnam, *H. d. pasquieri* Thomas, 1927 from Northern Laos, and *H. d. marmosa* Allen, 1927 from Hainan. Previous classifications of this genus have been based on external morphology and cranial characters and have cast debates for many years (Musser & Carleton, 1993, 2005; Nowak, 1999).

Recent chromosomal studies revealed a high karyotypic diversity in *Hapalomys*. Yong et al. (1982) described the karyotype of *H. longicaudatus* from Malaysia with diploid number 2n=50. Badenhorst et al. (2009) reported on the karyotype of *H. delacouri* from Loei, Northern Thailand, as having 2n=48 and NFa=92. A karyotype of a *Hapalomys* specimen from Bu Gia Map, Southern Vietnam, was reported as 2n=38 and NFa=48 (Abramov et al., 2012). Strong karyological differences between Vietnamese and Thai specimens seem to be indicative of a species level divergence. Based on the distributional patterns, Abramov et al. (2012) proposed to treat the marmoset rat from Northern Thailand as *H. pasquieri* (described from northern Laos), whereas those from Southern Vietnam as *H. delacouri* (described from Kon Tum Province, Vietnam).

The aims of this study are (1) to address the taxonomic status of different populations of *Hapalomys* from Indochina based on the molecular and morphological analyses of original and museum specimens, and (2) to describe a new species from Southern Vietnam.

MATERIALS AND METHODS

Specimen sampling. Field works were conducted by the Joint Russian-Vietnamese Tropical Research and Technological Centre in Southern and Central Vietnam from 2009–2015. In total, 10 specimens of *Hapalomys* were collected in Binh Phuoc and Ha Tinh provinces (Fig. 1, Appendix 1). The specimens (skulls and skins) are kept in the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia (ZIN) and the Zoological Museum, Moscow State

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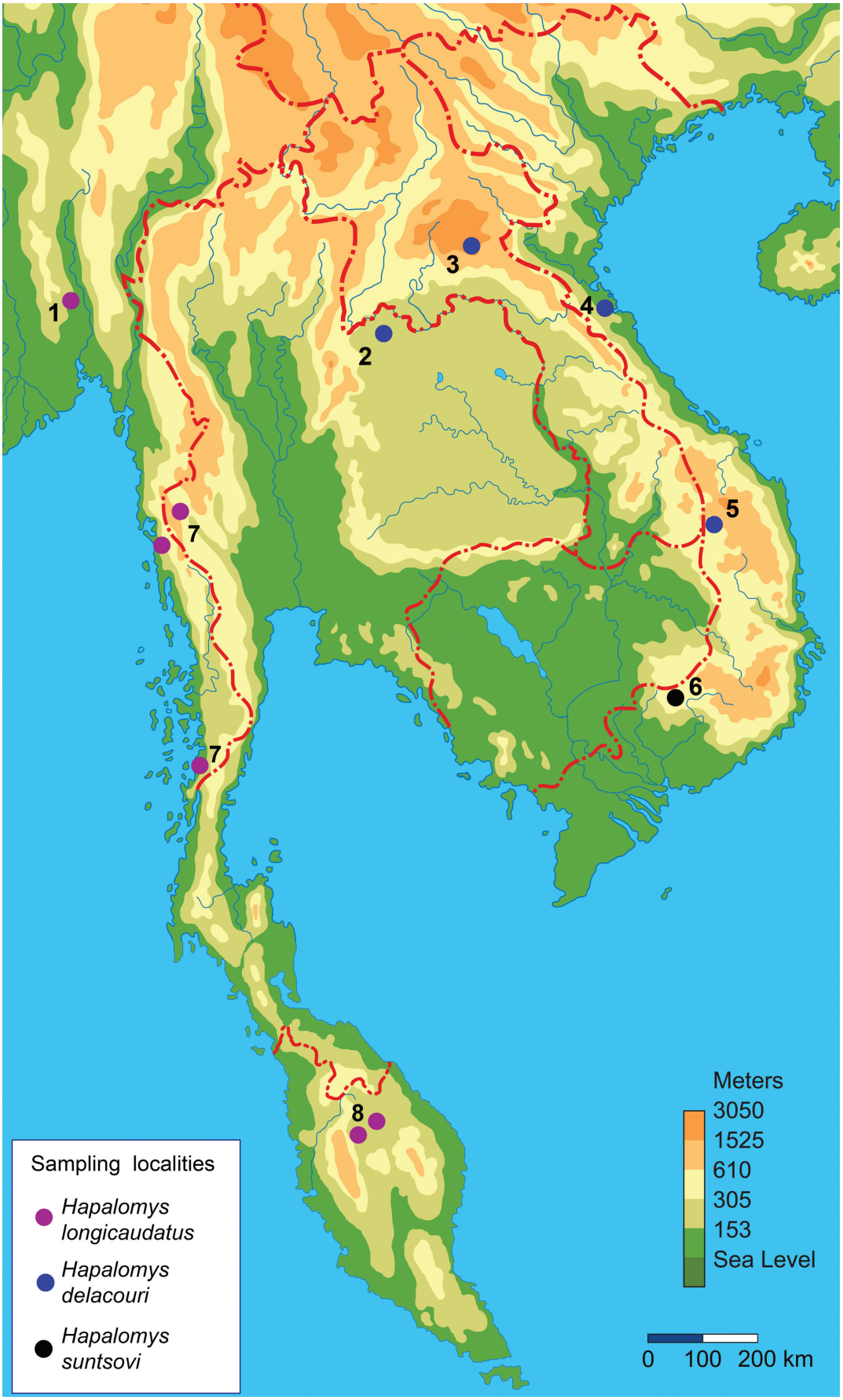

Fig. 1. Map of localities. 1 – Myanmar, the type locality of *Hapalomys longicaudatus*; 2 – Thailand, locality of R5237 (Badenhorst et al., 2009); 3 – Laos, the type locality of *Hapalomys pasquieri*; 4 – Vietnam, Ha Tinh Province, Ke Go NR, locality of ZIN 103040; 5 – Vietnam, Kon Tum Province, Dakto, the type locality of *Hapalomys delacouri*; 6 – Vietnam, Binh Phuoc Province, Bu Gia Map NP; 7 – records of *Hapalomys longicaudatus* (after Musser, 1972); 8 – Malaysia, an approximate locality of the *Hapalomys longicaudatus* record from Yong et al. (1982).

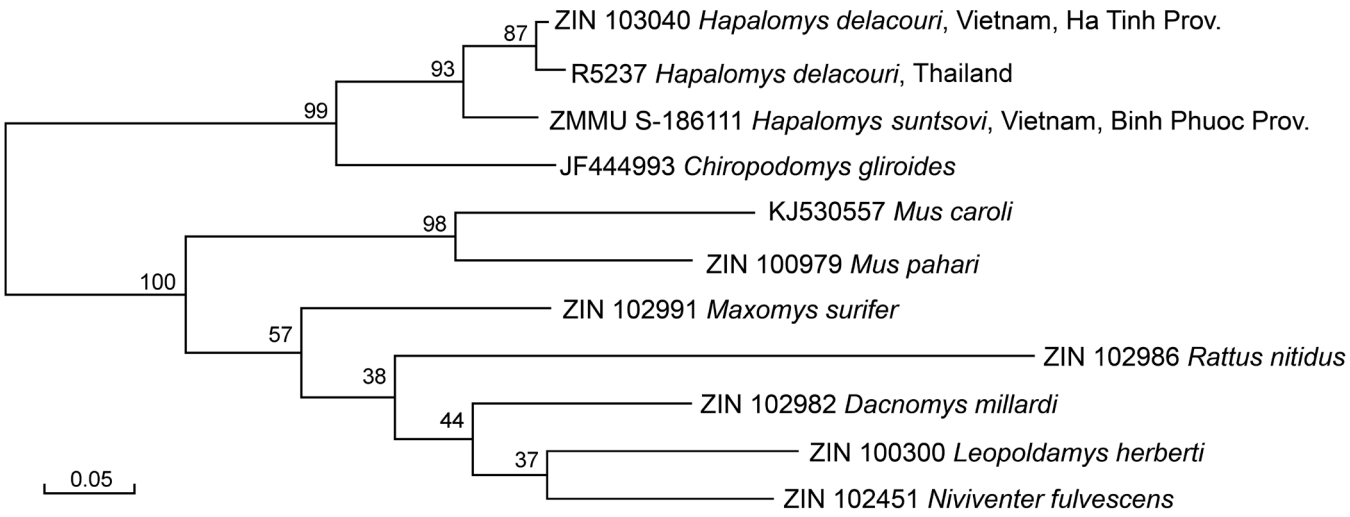

Fig. 2. Maximum Likelihood phylogenetic tree (GTR+G+I) of *Hapalomys* spp. and relative murid taxa as inferred from the COI gene sequence. Posterior probabilities are indicated above the corresponding nodes.

University, Moscow, Russia (ZMMU). Tissue samples are preserved in 96% ethanol.

Morphological analysis. Twenty measurements were taken from each skull by means of digital calipers to the nearest 0.01 mm: occipitonasal length (ONL), zygomatic breadth (ZB), length of rostrum (LR), breadth of rostrum (BR), breadth of braincase (BBC), height of braincase (HBC), breadth of zygomatic plate (BZP), length of diastema (LD), length of incisive foramina (LIF), breadth of incisive foramina (BIF), length of bony palate (LBP), breadth across bony palate at first molars (BBP), postpalatal length (PPL), breadth of mesopterygoid fossa (BMF), length of bulla (LB), crown length of upper molar row (CLM 1-3), breadth of first upper molar (BM1), crown length of lower molar row (CLm 1-3), breadth of first lower molar (Bm1), interorbital breadth (IB). The cranial measurements follow Musser & Newcomb (1983) and Musser et al. (2006). Standard external body measurements (head and body length, tail length, hind foot length, and ear length) were taken in the field. For a comparison, we used the external measurements available on museum tags, apparently representing those taken by original collectors in the field.

Skulls and skins from Vietnam were compared with the specimens kept in the collection of the Natural History Museum, London, UK (BMNH) (see Appendix 1). The specimen of *H. delacouri* from Thailand (R5237 CERoPath collection, available at open access at http://www.ceropath.org), which was discussed by Badenhorst et al. (2009) and Abramov et al. (2012), has also been included in the comparison.

The principal components analysis (PCA) was conducted to evaluate morphological variation among these samples. A one-way analysis of variance (ANOVA) was performed to test the differences among groups based on all cranial variables. The software program Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA) was used for all analytical procedures.

DNA sequencing. Two *Hapalomys* specimens from Vietnam (ZMMU S-186111 from Binh Phuoc Province and ZIN 103040 from Ha Tinh Province) were sampled for the genetic analysis. A small quantity of liver preserved in 96% alcohol was used for DNA extraction. Total genomic DNA was extracted using the routine phenol/chloroform/proteinase K protocol (Kocher et al., 1989; Sambrook et al., 1989). The DNA was further purified by double ethanol precipitation. The COI gene (5'-proximal 680 bp portion of subunit I) was amplified using the universal conservative primers BatL 5310 and R6036R under the protocol described by Ivanova et al. (2012). This method is used for DNA-barcoding in a number of mammals (Hebert et al., 2003a) in Barcoding of The Life Program (www.barcodinglife.org). For comparative analysis we used genetic data for the Thai specimen R5237 of *H. delacouri* which is available at the CERoPath project site in open access. ABI PRISM 3730xl Genetic Analyzer (Applied Biosystems, USA) has been used for bidirectional sequencing with BigDye® Terminator v3.1 Cycle Sequencing Kit in the agreement with the manufacturer's protocol.

Genetic data alignment and analysis. All COI gene fragments obtained were replicable by routine PCR under different initial DNA matrix concentration and amplification conditions (2–500 ng of total DNA template and within limits of annealing temperatures 49–58°C). Resulted fragments were abundant, predicted length and without any appreciable co-amplified products. They were run two times with the same resulted sequence obtained. These precautions allow us to avoid erroneous conclusions due to sequencing error or samples contamination. As a rule, COI gene taken alone is shown not to be the best genetic marker for profound phylogenetic reconstructions (Meyer & Paulay, 2005; Vences et al., 2005; Wiemers & Fiedler, 2007) due to the high level of accumulated homoplasy. Nevertheless, this gene is appropriate for the evaluation of genetic distances between closely related taxa and for the species delimitation by pairwise comparisons for a number of taxa (Hebert et al., 2003a, b; Hebert & Gregory, 2005; Ward et al., 2005). Six original murid specimens (*Mus pahari*, *Rattus nitidus*, *Maxomys surifer*, *Niviventer fulvescens*, *Leopoldamys*

Table 1. Factor loadings and cumulative variance for the principal components PC 1–PC 3 in the principal components analysis illustrated in Fig. 3.

Characters	PC 1	PC 2	PC 3
ONL	-0.977	-0.077	-0.104
ZB	-0.938	-0.098	-0.072
LR	-0.630	-0.400	-0.474
BR	-0.856	-0.232	-0.304
BBC	-0.835	0.086	0.019
HBC	-0.968	0.054	0.011
BZP	-0.966	0.036	0.030
LD	-0.900	-0.070	-0.224
LIF	-0.405	0.765	-0.162
BIF	0.727	-0.171	0.250
LBP	-0.947	-0.143	0.076
BBP	0.266	-0.799	-0.021
PPL	-0.947	-0.029	-0.169
BMF	-0.524	-0.175	0.677
LB	-0.790	-0.150	0.290
CLM 1-3	-0.950	0.011	0.173
BM 1	-0.926	0.060	0.224
CLm 1-3	-0.927	-0.027	0.183
Bm 1	-0.944	0.128	0.172
IB	-0.893	0.096	-0.092
Variance explained	70.5%	8.0%	6.0%

herberti and *Dacnomys millardi*) collected from Vietnam and two taxa (*Chiropodomys gliroides* and *Mus caroli*) from GenBank have been used in the study as outgroups to test the characteristic level of diversity. All new sequences were deposited in GenBank under the accession numbers: KU958011 to KU958018.

All sequences (608 bp for final analysis) were aligned using BioEdit (Hall, 1999) and Clustal W incorporated into BioEdit and MEGA6 software and were verified manually. No additional stop codons, indel mutations, reading frame shifts or significant base composition biases were detected in search for possible nuclear mitochondrial (NUMT) pseudogenes included into analyses. The basic sequences parameter calculations (i.e., variable sites, parsimony informative sites, base composition biases, nucleotide frequencies and nucleotide substitution tables), codon evolution model testing, as well as inter- and intrapopulation divergence/distances evaluations (*d*, Tamura 3 parameters model) were performed using MEGA6 software (Tamura et al., 2013). We used the Maximum Likelihood (ML) algorithms (GTR+G+I model, *G* parameter=1.02 based on Bayesian Information Criterion (BIC) and Akaike Information Criterion (AIC) as implemented at MEGA6 software (Tamura et al., 2013). 1,000 independent replicates were performed to evaluate bootstrap level for branching nodes.

RESULTS

Morphometric analysis. Nineteen skulls were used for the morphometric analysis, including the holotype of *H. delacouri*

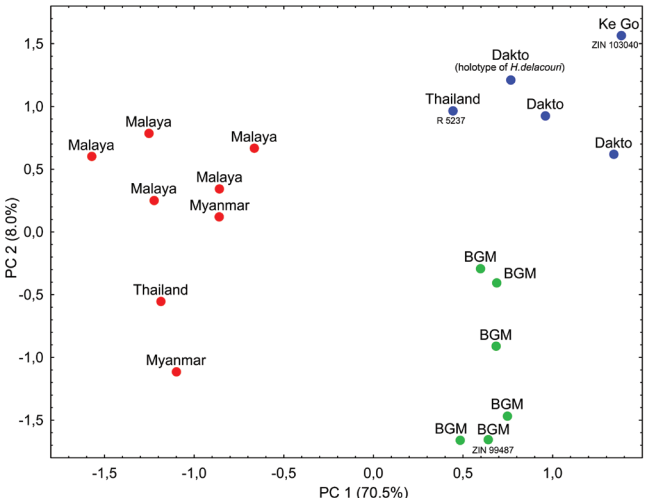

Fig. 3. Ungrouped morphometric separation (principal components analysis) drawn from the 19 specimens of *Hapalomys* spp. Red dots – *H. longicaudatus*; blue dots – *H. delacouri*; green dots – *H. suntsovi* from the Bu Gia Map NP (BGM), Binh Phuoc Province, Vietnam.

(BMNH 26.10.4.183). The principal component analysis drawing on 20 craniodental measurements has revealed three discrete groupings: *H. longicaudatus*, the type series of *H. delacouri* and the specimens from Bu Gia Map (Fig. 3, Table 1). *H. longicaudatus* and two Vietnamese groups diverge along the first principal component PC 1, reflecting the differences in overall cranial size. Bu Gia Map group diverges from *H. delacouri* along the second principal component PC 2 in particular, reflecting their more extended palate and the shortened incisive foramina. The specimen ZIN 103040 from Ke Go NR and the specimen R5237 from Thailand cluster with typical *H. delacouri* from Dakto.

A summary of the descriptive statistics of morphometric variables is given in Table 2. The skull of Southern Vietnamese *Hapalomys* is significantly larger than that of *H. delacouri* in most of the characters (ONL, ZB, BR, HBC, BZP, LBP, BBP, LB), except for the shortened incisive foramina (LIF).

Genetic analysis. All three *Hapalomys* samples are clustered together, forming the most basal clade within the dataset that appear to be even more distant than the *Mus* branch (Fig. 2). The mean intragroup diversity (d, T3P) calculated between *Hapalomys* samples is 0.053 ± 0.009, which is characteristic interspecies divergence level for most mammalian genera (Hebert et al., 2003a, b; Jansa et al., 2006, 2009). An identity level calculated for the sequences R5237 from Thailand and ZIN 103040 from Ke Go NR is 0.983, which correspond to genetic distance (d, T3P) 0.022 ± 0.007. Corresponding values for ZMMU S-186111 and ZIN 103040 reach 0.936 and 0.069 ± 0.013; values for ZMMU S-186111 and R5237 are 0.936 and 0.064 ± 0.012 respectively. The former distance level is typical for geographical populations within many rodent species (see Liu et al., 2004; Robins et al., 2007; Rowe et al., 2008; Balakirev et al., 2011; Lu et al., 2015), whereas the latter unconditionally indicates the status of a different species (Hebert et al., 2003a, b). Thus, it is safe to conclude

Table 2. Cranial and external measurements (means and range, in mm) of *Hapalomys* spp.

Characters	*H. suntsovi*, *n*=6	*H. delacouri*, *n*=4–5	*H. longicaudatus*, *n*=8
ONL	34.66 (33.49–35.54)	33.11 (31.81–34.15)	39.20 (37.63–41.48)
ZB	18.55 (17.73–19.62)	17.45 (16.75–17.90)	20.90 (19.85–22.02)
LR	10.15 (9.90–10.57)	9.63 (9.25–10.32)*	10.35 (9.45–10.90)
BR	6.71 (6.31–7.09)	5.95 (5.08–6.70)	7.54 (6.72–8.10)
BBC	15.17 (14.60–15.90)	15.33 (14.72–16.70)	16.62 (16.10–17.28)
HBC	9.50 (9.23–9.82)	9.14 (9.05–9.26)*	11.16 (10.74–11.74)
BZP	3.90 (3.49–4.05)	3.56 (3.31–3.75)*	5.40 (5.08–5.80)
LD	8.99 (8.65–9.37)	8.57 (7.91–8.90)	10.08 (9.23–11.00)
LIF	5.32 (4.98–5.92)	5.95 (5.70–6.24)	6.02 (5.39–6.50)
BIF	1.97 (1.90–2.15)	1.95 (1.80–2.10)	1.76 (1.63–2.10)
LBP	7.51 (7.30–7.71)	6.77 (6.40–7.04)	9.42 (8.68–10.09)
BBP	2.81 (2.63–3.00)	2.51 (2.39–2.67)	2.55 (2.40–2.76)
PPL	12.27 (11.84–12.60)	11.86 (10.91–13.00)	14.07 (13.20–14.90)
BMF	1.94 (1.86–2.00)	1.91 (1.76–2.00)	2.02 (1.93–2.14)
LB	7.00 (6.56–7.50)	6.59 (6.40–6.86)	7.96 (7.40–8.70)
CLM 1-3	6.28 (6.11–6.52)	6.06 (5.50–6.42)	7.77 (7.55–7.95)
BM 1	1.83 (1.76–1.87)	1.76 (1.66–1.82)	2.32 (2.15–2.50)
CLm 1-3	6.40 (6.24–6.73)	5.95 (5.50–6.38)	8.06 (7.80–8.30)
Bm 1	1.81 (1.70–1.87)	1.75 (1.62–1.82)*	2.25 (2.16–2.40)
IB	5.15 (5.00–5.30)	5.07 (4.62–5.44)	5.72 (5.45–5.95)
Length of head and body	135.6 (127.0–146.0)	129.3 (115.0–136.0)	157.0 (140.0–165.0)
Length of tail	157.1 (150.0–165.0)	148.6 (140.0-160.0)	197.8 (176.0–215.0)

Note: Characters marked by * consist data for four specimens of *H. delacouri*, others – for five specimens.

that the populations from Southern and Central Vietnam that were previously attributed to *Hapalomys delacouri* actually belong to two different, genetically distinct *Hapalomys* species that can be undoubtedly diagnosed by the genetic barcode procedure.

SYSTEMATICS

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

Hapalomys Blyth, 1859

Hapalomys suntsovi, new species

Holotype. ZIN 99487, field no.26, male, skin, skull, collected 14 January 2010 by A.V. Abramov and A.V. Shchinov.

Type locality. Vietnam, c. 13 km NE of Bu Gia Map Village, Bu Gia Map National Park, Binh Phuoc Province, 12°12′N, 107°12′E, elevation 540 m above sea level.

Paratypes. ZIN 98922, field no.11, male, body in ethanol, skull extracted, collected 25 April 2009; ZIN 99483, field no.6, male, skin, skull, skeleton, collected 11 January 2010; ZIN 99484, field no.11, male, skin, skull, skeleton, collected 12 January 2010; ZIN 99485, field no.17, female, specimen in ethanol, collected 13 January 2010; ZIN 99486, field no.18, female, skin, skull, collected 13 January 2010; ZIN 99488, field no.31, male, skin, skull, collected 16 January 2010; ZIN 100410, male, specimen in ethanol, collected 16 January 2010 (karyotyped, see Abramov et al., 2012); collected by A.V. Abramov and A.V. Shchinov from the same locality as the holotype; ZMMU S-186111, field no. BZM-18, GenBank accession number (COI) KU958011, female, skull, skin, body in ethanol, collected 6 November 2009 by A.V. Shchinov and A.E. Balakirev from the same locality as the holotype.

Fig. 4. General appearance of *Hapalomys suntsovi* based on a specimen ZIN 99484, collected from the Bu Gia Map NP, Vietnam, on 12 January 2010.

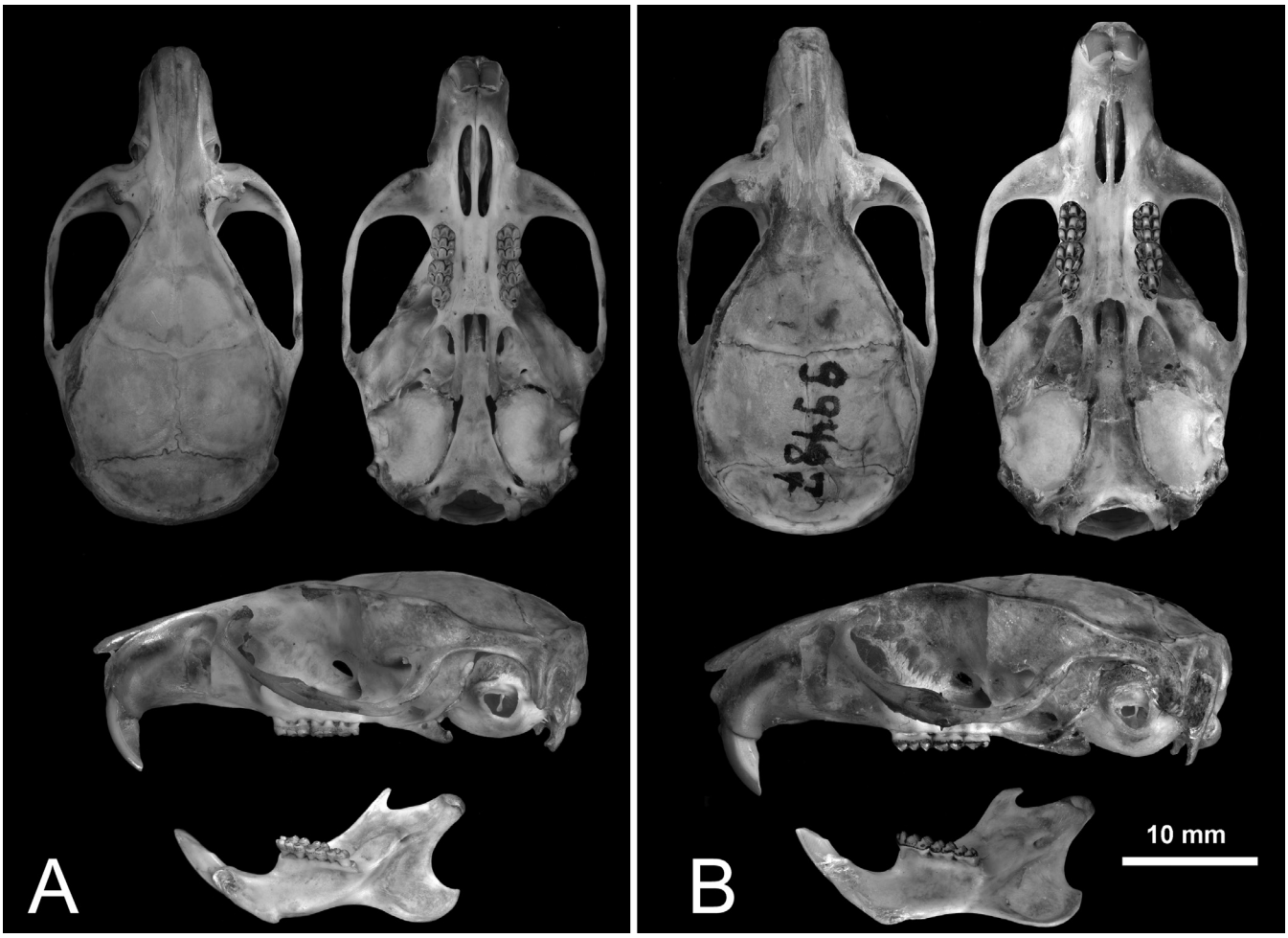

Fig. 5. Ventral, dorsal and lateral views of skull and lingual side of mandibles: A – *Hapalomys suntsovi* (holotype, ZIN 99487, Binh Phuoc Province, Vietnam); B – *Hapalomys delacouri* (ZIN 103040, Ha Tinh Province, Vietnam). Scale bar =10 mm.

Diagnosis. A medium-sized *Hapalomys* that on the average is smaller in its external and cranial measurements than *H. longicaudatus*. It is comparable to *H. delacouri* in its body and cranium size, but can be distinguished by the longer tail, the relatively short incisive foramina, and the cytochrome oxidase *c* subunit I (COI). Distinguished from both known species by the karyotype composition.

Description. A medium-sized marmoset rat with the head and body length of 135.6 mm (127.0–146.0 mm) and the tail length of 157.1 mm (150.0–165.0 mm). Pelage is soft and dense, dorsum grayish brown, ventral surface white, demarcation between upper parts and under parts colouration coloration is apparent (Fig. 4; see also fig. 2 in Abramov et al., 2012). The tail is longer than the head and body length (~116%), its distal part covered with long hairs. The hallux is fully opposable, bearing a nail instead of a claw. Skull with short and broad rostrum. The braincase with prominent postorbital and temporal ridges. Incisive foramina relatively short. The upper and lower molars have three longitudinal cusp rows.

Comparisons. As compared with *H. longicaudatus*, *H. suntsovi* can be readily separated by its smaller size. By its size, the new species is most similar to *H. delacouri*, but has a longer tail. In *H. suntsovi*, the incisive foramina are absolutely shorter and shorter relative to the overall skull size in comparison to those of *H. delacouri* and *H. longicaudatus*. *H. delacouri* and *H. suntsovi* do not have additional cusps on the anterior margin of each upper first molar, *H. longicaudatus* has two small, but well developed and conspicuous cusps on the anterior margin (see Musser, 1972: fig. 10). In *H. suntsovi* and *H. delacouri*, the lingual row of cusps of each first upper molar are smaller in comparison with other cusps of the tooth (Fig. 5), in contrast to *H. longicaudatus* has similar-sized cusps (Musser, 1972: fig. 10).

H. suntsovi and *H. delacouri* are distinguished by the differences in COI gene sequences. *H. suntsovi* differs from *H. delacouri* and *H. longicaudatus* in the diploid number of chromosomes: 2n=38 (specimen ZIN 100410, Abramov et al., 2012), 2n=48 and 2n=50, respectively.

Etymology. The new species is dedicated to Dr Viktor V. Suntsov (A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow), in recognition of his many contributions to the study of rodents of Vietnam. During 1992–2010, Dr Suntsov headed the Southern Division of the Joint Russian-Vietnamese Tropical Research and Technological Centre in Ho Chi Minh City.

Distribution. Currently known from the type locality, the Bu Gia Map National Park, Binh Phuoc Province, Southern Vietnam. It is likely to occur in the adjacent forest regions of Eastern Cambodia.

Natural history. The series of type specimens was collected in old, mature, thick trunk bamboo thickets growing along a forest road (Abramov et al., 2011). All specimens were taken by traps set 5–7 m over the ground surface. Two females caught on 13 January 2010 were pregnant (at early stage) bearing four and five small embryos.

DISCUSSION

The intraspecific variation in *Hapalomys* spp. is poorly studied because of the scarcity of studied specimens (see Musser, 1972). Indeed, only few specimens of the marmoset rats, especially those of *H. delacouri* s. lato, are known in scientific collections. The actual scarcity of samples available does not allow us to perform the most profound phylogenetic analyses that demonstrate its best potential for large sample sets and complicated multitaxa evolution. In spite of that, even the techniques applied demonstrated a drastic phylogenetic pattern that arises the question about taxonomical application of taxa of study. Our data provides new insights into the taxonomy and distribution of *Hapalomys* in Indochina. The discovery of new morphologically and genetically distant species in Southern Vietnam is in good concordance with other records of unique taxa of small mammals in the region (Abramov et al., 2010; Bannikova et al., 2011; Balakirev et al., 2013). The occurrence of endemic and genetically distinct forms in the mountainous areas of Southern Vietnam also suggests that this "Indochinese pocket" of biodiversity seemed to be a potential refuge during the last Ice Age (Bannikova et al., 2014; Meschersky et al., 2016; Zemlemerova et al., 2016).

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APPENDIX

Appendix 1. Specimens included in the study. The following are acronyms prefacing specimen numbers: BMNH, the Natural History Museum, London, UK; ZIN, the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia; ZMMU, the Zoological Museum of Moscow State University, Moscow, Russia.

Hapalomys suntsovi, new species (n=9).
Vietnam, Binh Phuoc Province, Bu Gia Map National Park, 13 km NE of Bu Gia Map Village (12°12′N, 107°12′E): ZIN 98922, ZIN 99483, ZIN 99484, ZIN 99485, ZIN 99486, ZIN 99487 (holotype), ZIN 99488, ZIN 100410, ZMMU S-186111.

Hapalomys delacouri (n=6).
Vietnam, Kon Tum Province, Dakto: BMNH 26.10.4.182, BMNH 26.10.4.183 (holotype of *H. delacouri*), BMNH 26.10.4.184.
Vietnam, Ha Tinh Province, Cam Xuyen District, Ke Go Nature Reserve (18°06’30′N, 106°01’01′E): ZIN 103040.
Thailand, Loei Province: CERoPath R5237.
Laos, Xieng Kuang: BMNH 26.10.4.185, holotype of *H. pasquieri* (young specimen, not included in PCA).

Hapalomys longicaudatus (n=8).
Malaysia, Cameron Highlands, Kelantan: BMNH 63.1159, BMNH 63.1160, BMNH 63.1161, BMNH 63.1162, BMNH 63.1163.
Myanmar, Tavoy: BMNH 90.10.1.1.
Myanmar, Bankachon: BMNH 14.2.8.147.
Thailand, Quaa Noi (14°30′N, 98°50′E): BMNH 14.5.3.1.