Zoological Studies **56:** 6 (2017)
doi:10.6620/ZS.2017.56-06

Zoological Studies

The Phylogeography of Red Spiny Rats *Maxomys surifer* (Rodentia, Muridae) in Indochina with Comments on Taxonomy and Description of New Subspecies

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(Received 8 December 2016; Accepted 26 February 2017; Published 19 April 2017; Communicated by Jian-Nan Liu)

Alexander Evgenievich Balakirev, Alexei Vladimirovich Abramov, and Viatcheslav Vladimirovich Rozhnov (2017) The phylogeographic pattern of *Maxomys surifer* across most of its geographic range was investigated based on existing sequencing from GenBank and new original data from Vietnam to evaluate its natural subdivision and taxonomic structure in Indochina and neighboring regions. Seven major phylogenetic clusters/groups are apparent on the cytochrome *b* (Cyt *b*) and cytochrome c oxydase subunit 1 gene (COI) trees, corresponding to geographical subpopulations of the species. Among them, distinct position of most divergent, clade Msur7 is also supported by analyses of nuclear (IRBP) gene. The taxonomic implication of these findings is tested by comparison of morphological features of this Northern (labeled by Msur7) and Southern Vietnamese populations widely distributed over the Indochina labeled by Msur3 mtDNA genetic marker. Direct comparisons of skulls measurements and multivariate analyses performed for these southern and northern populations showed that latter specimens are distinctive in being significantly larger in a number of cranial characters, with diagnostically smaller teeth relative to *M. surifer* from southern Vietnam, bearing also some traits in its external appearance, like relative tail length and coloration pattern. The pattern of genetic and cranial variation in *M. surifer* revealed in the present study suggests the existence of distinct genetic lineages and suspected longitudinal isolation, corresponding to morphologically distinctive forms. It is evident that at least some of these lineages merit subspecific status. We provide a taxonomical description elevating the northern Vietnamese populations to a new subspecies *M. s. tonkinensis* subsp. nov. We discuss the taxonomic implications, tentative range, and appropriate synonyms for all main genetic lineages over the range of *M. surifer* in the Sundaic region.

Key words: Mammals, Rodents, Southeast Asia, Taxonomy, Biodiversity.

BACKGROUND

Spiny rats of the genus *Maxomys* Sody, 1936 are widely distributed in evergreen and semi-evergreen forests of Southeast Asia (Corbet and Hill 1992; Nowak 1999). These rats are considered as the most abundant, morphologically and ecologically variable, and geographically widely distributed group of rats in Southeast Asia (Musser and Carleton 1993, 2005). In accordance with the currently accepted taxonomic understanding (Musser et al. 1979; Musser and Newcomb 1983; Musser and Holden 1991; Corbet and Hill 1992; Musser and Carleton 1993, 2005; Pavlinov 2005),

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the genus comprises 17 recent species. A new species was recently described from Borneo (Achmadi et al. 2012), and two more undescribed species are supposed to inhabit Sulawesi (Achmadi et al. 2013). The overwhelming majority of *Maxomys* species have rather narrow insular distributions, except for the red spiny rat *Maxomys surifer* (Miller, 1900). *M. surifer* is the only species of *Maxomys* whose natural range encompasses almost the entire continental Indochinese and Sundaic faunal regions, which may reflect its long evolutionary history and considerable ecological plasticity. The early presence of *Maxomys surifer* in the Indomalayan region is supported by late Pliocene to middle Pleistocene fossils, where *Maxomys* and related forms were discovered (Chaimanee 1998; van der Meulen and Musser 1999).

The taxonomic composition and phylogenetic structure of *M. surifer* is far from being finally established. Previous studies (Musser and Newcomb 1983; Musser et al. 1979) demonstrated at least two groups of populations, descended from Sunda Islands and from peninsular Malaya, that differ considerably in morphological differences. The same was noticed by Kloss (1919) for Indochinese and Malayan specimens. Corbet and Hill (1992) detected a geographic pattern in pelage coloration. In spite of abundant materials, actual complexity of entire genus *Maxomys* composition and fragmentariness of data prevent from taxonomical assessment of these forms. It still also ambiguous whether distribution of morphological and molecular traits concordant with one another. Musser and Carleton (2005) recognize this group as a species complex in need of detailed taxonomical revision.

Phylogenetic analyses of mtDNA cytochrome *b* (cyt *b*) and D-loop sequences by Gorog et al. (2004) identified six distinct lineages in what is now defined as *M. surifer* associated with 1) Java, 2) Sumatra, 3) Borneo, 4) the Malay Peninsula, 5) southern Vietnam, and 6) central Vietnam. Six mitochondrial DNA lineages, but of lower divergence level (both cyt *b* and COI gene associated) were also discovered for the species in Thailand by Latinne et al. (2013). Some of them proved to correspond to Malayan and South Vietnamese ones delimited by Gorog et al. (2004). A considerable amount of genetic data is currently available for this species complex, including new genetic data from Vietnam. We combine these data to assess the phylogeographic patterns across most of the geographic range of *M. surifer* and provide taxonomic changes resulting from genetic subdivisions.

MATERIALS AND METHODS

Field works were conducted by the Joint Russian-Vietnamese Tropical Research and Technological Centre in Southern and Central Vietnam from 2009-2015 in full agreement with current Vietnam regulations in field of Nature Protection and Biodiversity Conservation. We followed guidelines of the American Society of Mammalogists during the collection and handling of the animals used in this work (Gannon et al. 2011).

DNA extraction, PCR amplification, and sequencing

In total, 33 original specimens from 7 localities in Vietnam were collected in the present study and sampled for genetic analysis (Appendix 1, Fig. 1). Small fragments of liver and muscle tissue, fingertips, or earlaps were stored in 96% alcohol and used for DNA extraction. Total genomic DNA was extracted using a routine phenol/chloroform/proteinase K protocol (Kocher et al. 1989; Sambrook et al. 1989). The DNA was further purified either by double ethanol precipitation or by using a DNA Purification Kit (Thermo Scientific).

Targeted genes included a complete or substantial portion of the Cytochrome *b* gene (cyt *b*, 950-1140 bp), a portion of the first exon of Interphotoreceptor Retinoid Binding Protein gene (IRBP; up to 1600 bp) and 5'-proximal 680 bp portion of subunit I of the Cytochrome C Oxidase subunit 1 gene (COI), which is generally used for species diagnoses and for DNA-barcoding in Metazoa (Hebert et al. 2003). The cyt *b* was amplified using the primers H15915R, (Kocher et al. 1989; Irwin et al. 1991), CytbRglu and CytbRCb9H (Robins et al. 2007). The COI gene was amplified using the primers BatL5310 and R6036R (Robins et al. 2007) and universal conservative primers LCO1490 and HCO2198 (Hebert et al. 2003). The following PCR protocol was used to amplify both mtDNA fragments: initial denaturation for 1 min 30 sec at 95°C, followed by 40 cycles of denaturation for 30 sec at 95°C, annealing for 1 min at 52°C, and elongation for 30 sec at 72°C, followed by terminal elongation for 2 min at 72°C. The PCR reaction was performed in a 30-50 ml volume that contained 2.5-3 μml 10 x

standard PCR buffer (Thermo Scientific), 50 mM of each dNTP, 2 mM $MgCl_2$, 10-12 pmol of each primer, 1 unit of Taq DNA polymerase (Fermentas) and 0.5 μml (20-50 ng) of total DNA template per tube. The reaction was performed using a Tercik (DNK-Tehnologia) thermocycler. The IRBP gene (1000-1600 bp in length) was amplified using the IRBP125f, IRBP1435r, IRBP1125r and IRBP1801r primers, according to the protocol of Stanhope et al. (1992). PCR products were purified using a DNA Purification Kit (Thermo Scientific).

The resulting double-stranded DNA products were directly sequenced in both directions using the Applied Biosystems 3130 Genetic Analyzer and the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit with the same primers as have been used for routine PCR. We also brought into study all the samples of *M. surifer* from a number localities used by Achmadi et al. (2013), Pages et al. (2010), Latinne et al. (2013) and some others obtained by C.M. Francis and A.G. Servent (deposited in GenBank and BOLD databases, unpublished) taken from a number of sites in Vietnam, Thailand, Laos, Malay Peninsula, Borneo, Sumatra and Java. Sequenced specimens cover almost completely the geographic range of the species. As outgroups, we used some sequences from several other *Maxomys* spp. and *Leopoldamys sabanus* (see Appendix 1). All sequence data have been submitted to the GenBank databases (www.ncbi.nlm.nih.gov/Genbank) under accession numbers KU057301-KU057344.

Sequence editing and phylogenetic analyses

All the sequences in the dataset were aligned using BIOEDIT 3.0 (Hall 1999) and CLUSTAL W (incorporated into BIOEDIT and MEGA 5.05) software and were verified manually. Basic sequence parameter calculations (*i.e.*, variable sites, parsimony-informative sites, base composition biases, nucleotide frequencies and nucleotide substitution tables), codon evolution model testing, and inter- and intra-population divergence (d, Tamura 3 parameter, T3P genetic divergence algorithm (Tamura et al. 2012)) evaluations were performed using MEGA 5.05 software (Tamura et al. 2011). Maximum parsimony (MP), maximum likelihood (ML), minimum evolution (ME), and neighbor-joining (NJ) were applied to phylogenetic reconstructions using MEGA 5.05 software. The best-fitting models of gene evolution out of 24 possible codon evolution models were determined using the Maximum Likelihood value (lnL), the Bayesian Information Criterion (BIC) and the corrected Akaike Information Criterion (AICc) as implemented in MEGA 5.05. The TN93+G+I substitution model was applied for the cyt *b* and COI genes, and the GTR+G substitution model was used for the IRBP gene (Nei and Kumar 2000). The calculated gamma shape parameters were 1.76, 1.53 and 1.11 for the cyt *b*, COI and IRBP genes respectively. The robustness of the tree was assessed using a bootstrap procedure with 1000 replications. All trees were constructed and visualized directly with MEGA 5.05 or with TREEVIEW 1.6.6 software (Page 1996). Divergence time approximation was performed by Maximum Likelihood method on the T3P model (Tamura 1992).

Morphological analysis

The morphological study was performed based on 138 skulls from 10 localities across Vietnam, including the genetically investigated vouchers (Appendix 2, Fig. 1). We used only adults for the analysis in order to minimize age variation. Age assessed by teeth wearing and cranial seams conditions. Specimens kept in the collections of the Zoological Museum of the Moscow State University (ZMMU, Moscow, Russia), the Zoological Institute of the Russian Academy of Sciences (ZIN, Saint Petersburg, Russia), and the Institute of Ecology and Biological Resources of the Vietnamese Academy of Science and Technology (IEBR, Hanoi, Vietnam).

The skulls originated from ten localities in Vietnam: The northern most populations were represented by three localities: Ba Vi Nature Reserve, Ha Tay province (*n* = 24), Nghe An Province (*n* = 9) and Vu Quang Natural Park, Ha Tinh Province (*n* = 15) whereas seven more, namely Cat Tien Nature Park, Dong Nai Province (*n* = 11), Gia Lai Province (*n* = 18), Kon Tum Province (*n* = 6), Lo Go Xa Mat Nature Reserve, Tay Ninh Province (*n* = 6), Ma Da Forest, Dong Nai Province (*n* = 20), Phu Quoc Island, Kien Giang Province (*n* = 26) and Xuyen Moc, Ba Ria - Vung Tau Province (*n* = 3) are originated from southern regions. These localities cover the main part of species range in eastern Indochina (Appendix 2).

Only intact skulls of adult specimens were measured irrespectively to the sex. Twenty measurements were taken on each skull using digital calipers to the nearest 0.1 mm, cranial measurements followed Musser and Newcomb

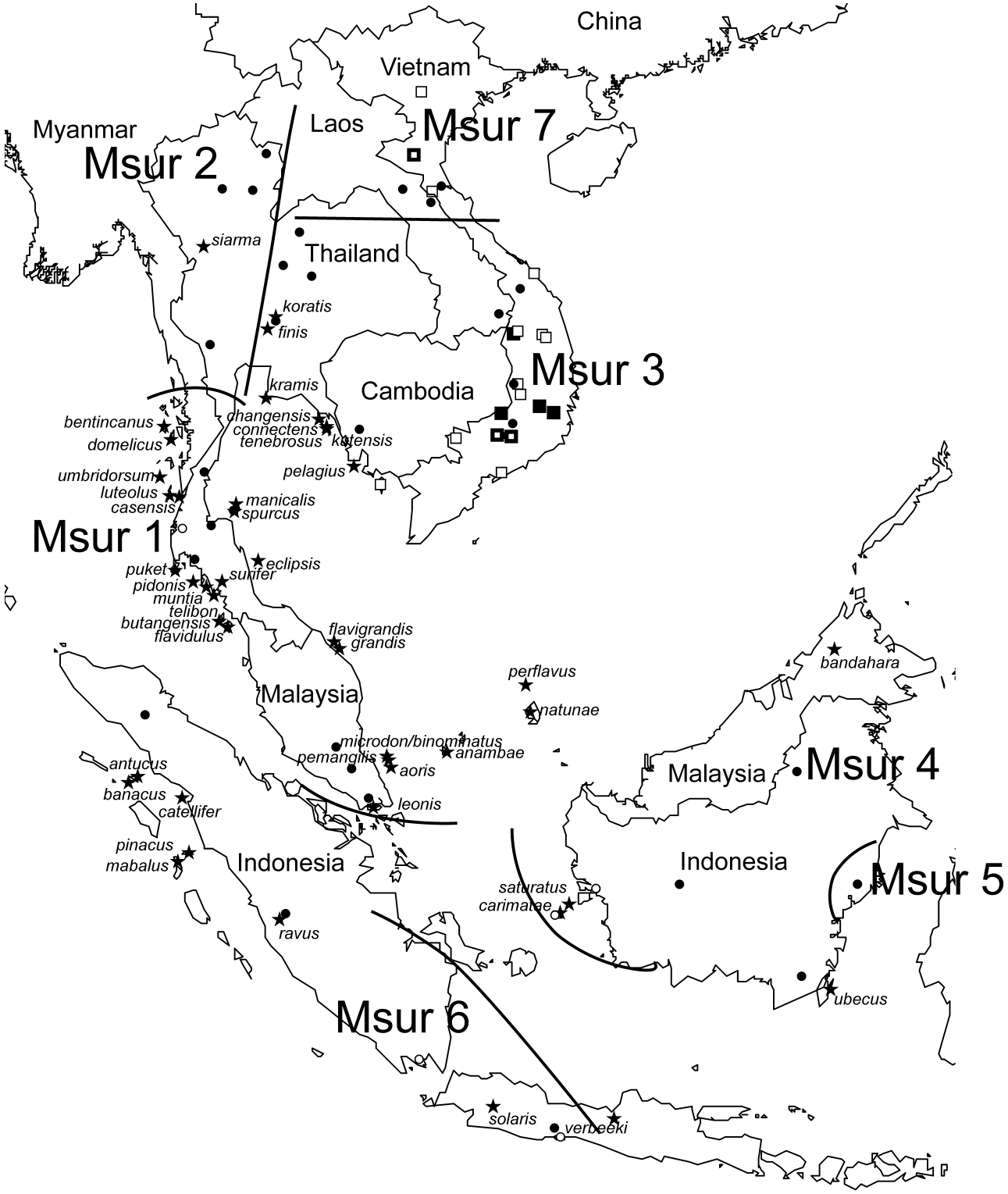

Fig. 1. Localities of investigated specimens and geographic distribution of the mtDNA lineages of *Maxomys surifer* in Indochina and Sunda region. See the precise samples locations in Appendices 1 and 2. The following symbols indicate the locality source of specimens: filled squares, specimens collected for this study; open squares, specimens used in morphological analyses (thick-lined if genotyped, thin-lined when not); filled circles, specimens drawn from GenBank; open circles, Gorog et al. (2004) sampling sites for D-loop. Stars with names indicate the type localities for subspecies or synonyms of *M. surifer*.

(1983) and Musser et al. (2006); occipitonasal length, or the greatest length of the skull (ONL), zygomatic breadth (ZB), interorbital breadth (IB), 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), palatal length (LBP) (palatal bridge), breadth across palate at first molars (BBP), postpalatal length (PPL), breadth of mesopterygoid fossa (BMF), length of bulla (LB), crown length of maxillary molar row (CLM1-3), crown breadth of M1 (BM1), crown length of mandibular row (CLm1-3), crown breadth of m1 (Bm1). This set of characters is mutually applied for investigation of cranil variation within Muridae. The principal components analysis (PCA) and the canonical discriminant analysis (CDA) have been used to evaluate a degree of cranial differentiation between geographical populations labeled by different genetic lineages. A one-way analysis of variance (ANOVA) was performed to test the differences among groups on all cranial variables. The Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA) software has been used for all analytical procedures.

RESULTS

In total, datasets obtained comprise more then two hundred cyt *b* sequences with 78 unique haplotypes and 142 individuals with as many as 142 haplotypes for COI gene and 32 unique sequences for IRBP gene genes (See Appendix 1). No insertions, deletions or premature stop codons or any others signs of NUMT (pseudogenes) occurrence were observed for mtDNA.

Phylogenetic analyses

To examine the phylogenetic structure across the entire range *M. surifer*, we combined our genetic data from Vietnamese specimens to those of previous studies (Gorog et al. 2004; Achmadi et al. 2012, 2013; Latinne et al. 2013). Phylogenetic trees constructed based on cyt *b* and COI sequences presented generally the same topology with the only exclusion of Sumatra-Javanese branch in COI tree in lack of sampling (Figs. 2-3). Six major phylogenetic clusters/groups can be seen on the COI tree. One more, additional seventh branch also appears at geographically more representative cyt *b* tree. Most part of basal branches does not demonstrate reliable level of support due to higher level of genetic diversity and indicates ancient radiation of the group. While the *M. surifer* relationships are not supported at the deeper nodes of the tree, distinct geographically localized phylogroups are apparent and named Msur 1-7 (Figs. 1-3). The geographic distribution of these phylogenetic clades presented in figure 1.

Phylogroup Msur1 includes samples from continental Malaysia and peninsular Thailand, cluster Msur2 includes the populations of western and northern Thailand and cluster Msur3 combines the populations from major part of Indochina (central and eastern Thailand, Cambodia, southern Laos and southern Vietnam). The lineage Msur4 is distributed over the most of Borneo, where one more distinct lineage Msur5 appears from a single locality on extreme east of the island. As it can be seen on the cyt *b* tree, an additional small subclade appeared in Borneo together with two another corresponding to Msur4 and Msur5 in COI tree. Another large clade Msur6 is evidently monophyletic but may be additionally subdivided into two subclades from Java and Sumatra islands respectively. An extremely poor sampling (only a few samples from two localities) hamper to outline its geographical distribution in considerable details.

Finally, Msur7 is found in northern and central Vietnam and central Laos. This is the most divergent clade among *M. surifer* phylogroups. Its level of divergence is significantly higher than that demonstrated for other lineages. The genetic divergence for cyt *b* (d, T3P) of northern Vietnamese *M. surifer* from another six clades reaches to 0.09-0.11, whereas, for example, the distance of Malayan-Javanese populations from that of Borneo do not exceed 0.06-0.08 (and about 0.08 for corresponding populations of *M. whiteheadi* (Achmadi et al. 2013).

The distinct position of Msur7 lineage is also supported by analyses of nuclear genes. The IRBP gene tree is shown on figure 4. In spite of scarcity of samples, the branch corresponding to Msur 7 in mitochondrial trees appeared as an independent one. This branch is reliably depicted by high support values whereas all the other samples do not demonstrates significant reciprocal monophyly.

Morphological analysis

A summary of the descriptive statistics of cranial variables for southern and northern groups is given in table 1. Multivariate analysis of cranial characters was done for populations of northern

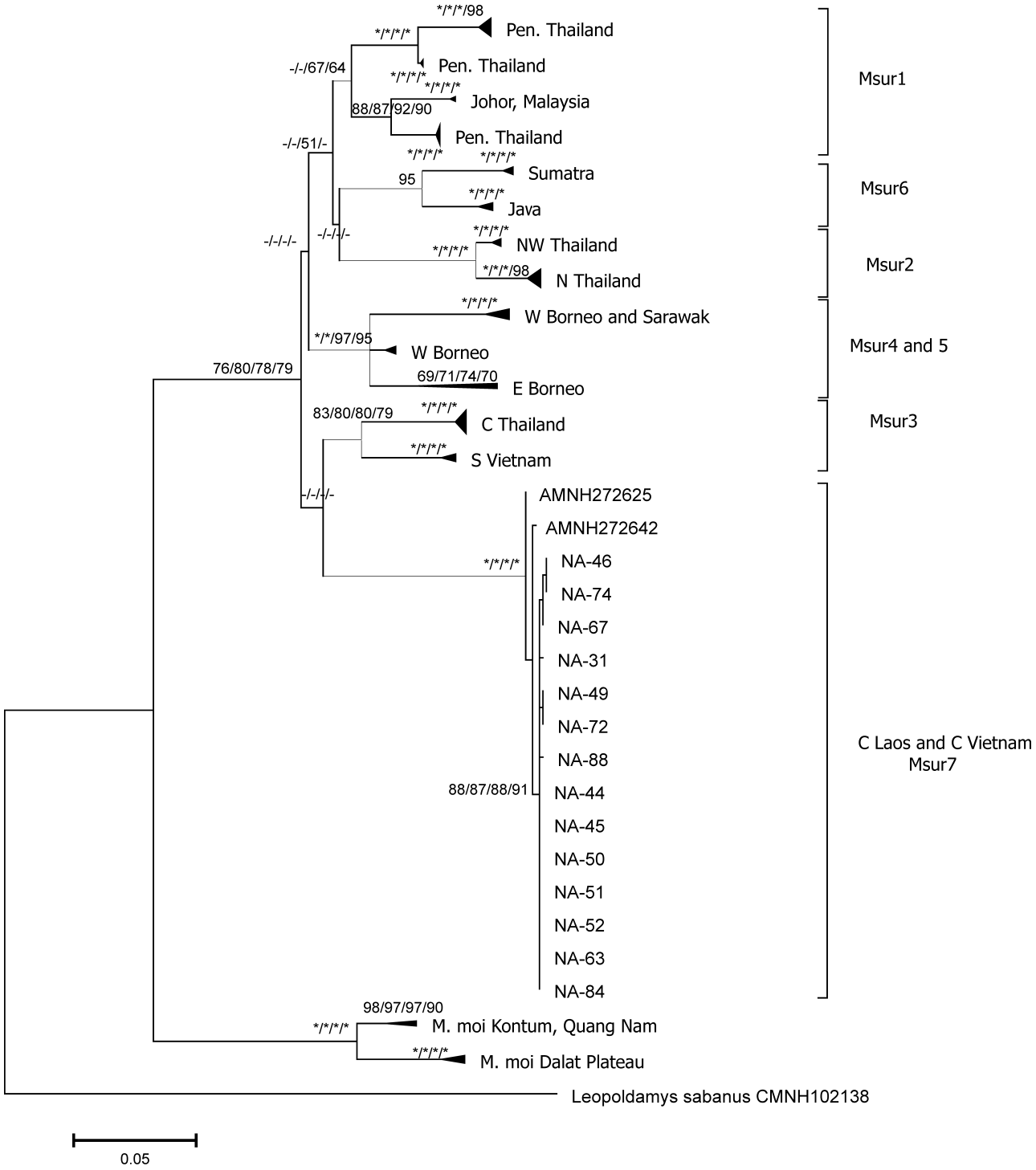

Fig. 2. The phylogenetic tree (cyt *b*, ML, 950 bp long) tree for the *Maxomys surifer* genetic lineages radiation. The bootstrap values (for different tree-constructing methods, NJ/ML/ME/MP, /*/ if 99-100, /-/ when below 50) are indicated above the nodes. The names for major phylogenetic lineages as indicated in figure 1.

and central Vietnam representing the genetic clade Msur7 and for other ones from southern Vietnam belonging to distinct clade Msur3. Results of the PCA for mean values of ten geographic samples are shown in figure 5 and table 2. It can be seen the northern and southern populations diverge mainly along the first principal component PC1, reflecting considerable differences in overall cranial size. Direct comparisons of skulls from southern and northern lineages showed that northern specimens are distinctive in being significantly differ in many (six out of twenty) of cranial characters including appreciably larger general size of skull, with diagnostically smaller teeth relative to *M. surifer* from southern Vietnam. Thus, the specimens from northern populations show the largest average meanings of skull measurements, whereas those from southern and central Vietnam are appeared as the smallest one.

Canonical discriminant analyses drawing on

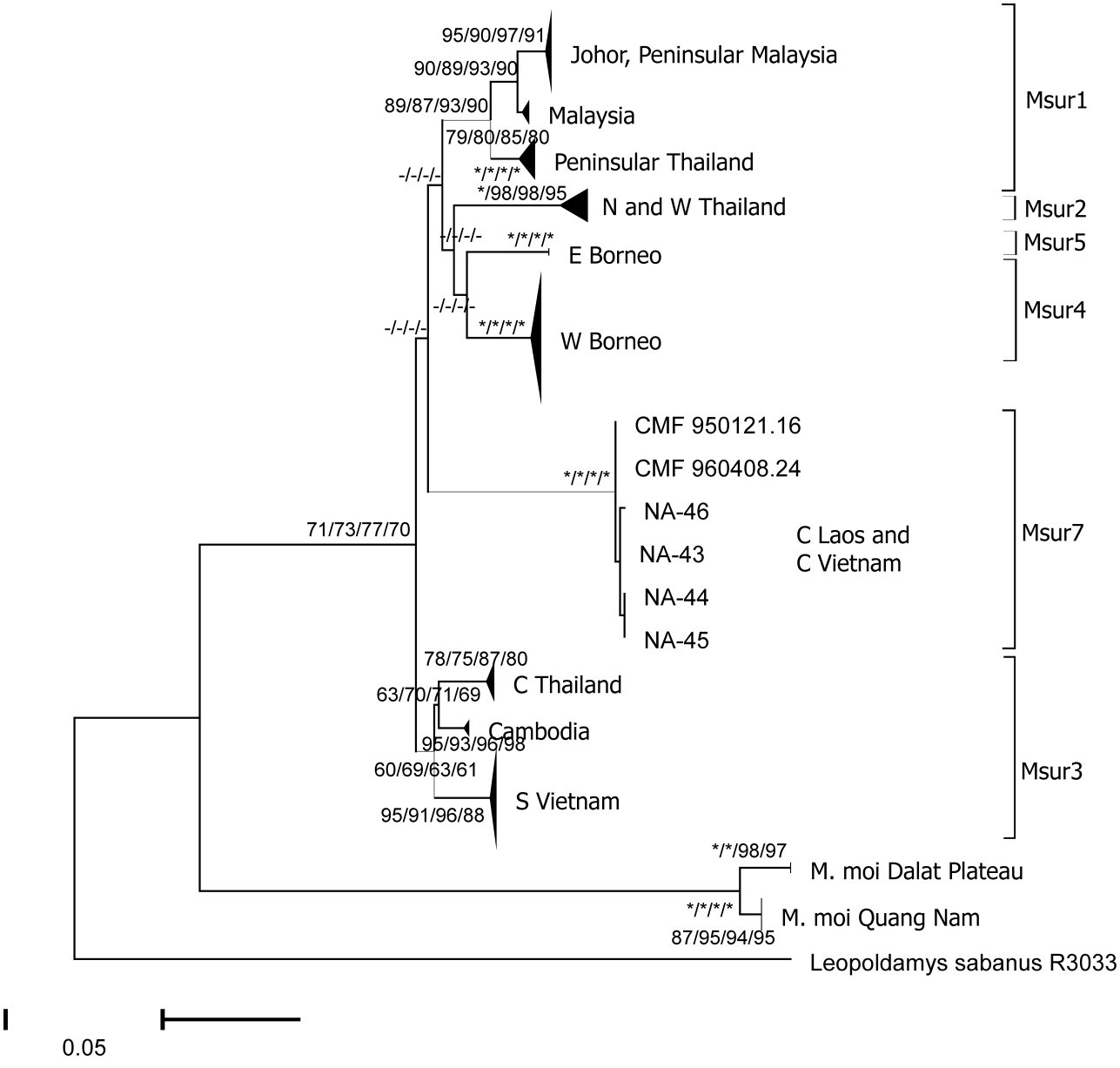

Fig. 3. The phylogenetic tree (COI, ML, 630 bp long) tree for the *Maxomys surifer* genetic lineages radiation. The bootstrap values (for different tree-constructing methods, NJ/ML/ME/MP, /*/ if 99-100, /-/ when below 50) are indicated above the nodes. The names for major phylogenetic lineages as indicated in figure 1.

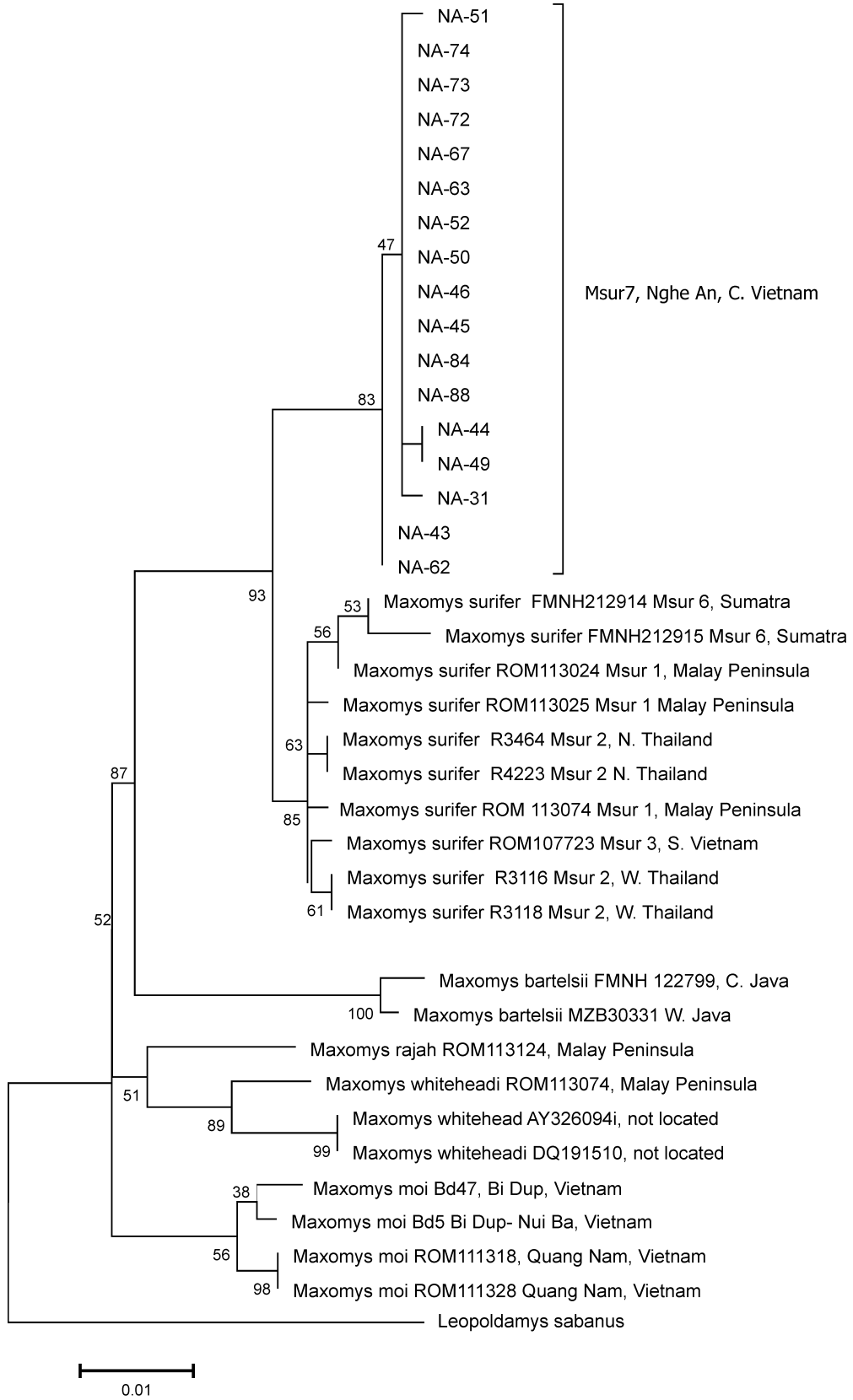

Fig. 4. The phylogenetic tree (IRBP, ML, 1080 bp long) tree for the *Maxomys surifer* genetic lineages radiation. The bootstrap values are indicated above the nodes. The names for major phylogenetic lineages as indicated in figure 1.

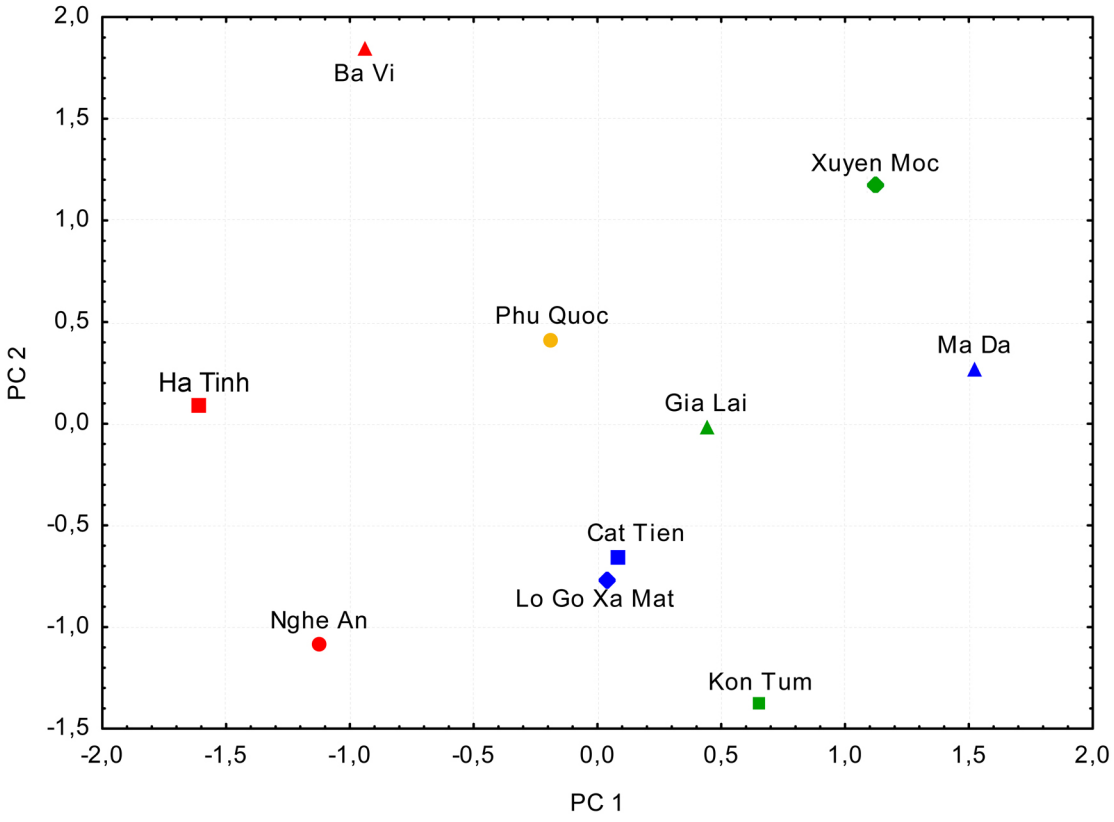

Fig. 5. Ungrouped morphometric separation (principal components analysis) of ten *Maxomys surifer* samples, drawing from means of craniodental measurements. Northern populations marked as red, southern - by green, yellow and blue colors.

Table 1. Descriptive statistics (mean, range, standard deviation) for skull measurements (in mm) for Vietnamese *Maxomys surifer*

Characters	Northern form (*n* = 48)				Southern form (*n* = 90)				ANOVA	
	Mean	Min	Max	Std.Dev.	Mean	Min	Max	Std.Dev.	F	*p*
ONL	45.83	41.43	49.09	1.58	44.77	40.84	49.43	1.65	1.08	0.778
ZB	20.23	18.23	21.49	0.77	20.00	18.09	22.74	0.95	1.52	0.118
IB	7.33	6.79	7.90	0.26	7.03	6.24	8.17	0.41	2.34	0.002
LR	16.10	14.44	17.38	0.68	15.70	13.90	17.55	0.77	1.29	0.347
BR	8.10	7.42	9.32	0.38	8.01	7.05	9.84	0.52	1.82	0.026
BBC	17.10	16.46	17.99	0.38	16.73	15.68	17.76	0.47	1.56	0.098
HBC	12.46	11.75	13.44	0.36	11.86	10.98	12.90	0.38	1.12	0.685
BZP	4.10	3.43	4.58	0.28	4.25	3.67	4.89	0.24	1.35	0.222
LD	12.79	11.78	13.91	0.49	12.48	10.70	13.93	0.63	1.70	0.047
LIF	6.95	6.00	7.89	0.40	6.25	5.31	7.31	0.42	1.13	0.650
BIF	3.61	2.95	4.12	0.28	3.62	2.96	4.34	0.31	1.22	0.457
LBP	8.86	7.98	9.68	0.43	9.01	8.18	10.20	0.47	1.20	0.505
BBP	4.68	3.72	5.13	0.27	4.37	3.56	5.07	0.32	1.37	0.241
PPL	16.82	14.70	18.24	0.74	15.91	14.30	18.03	0.80	1.16	0.590
BMF	3.30	2.71	4.02	0.33	3.12	2.62	3.83	0.24	1.83	0.015
LB	5.00	4.47	5.53	0.24	5.01	4.44	5.52	0.18	1.87	0.012
CLM1-3	6.56	6.11	7.01	0.23	6.61	6.15	7.10	0.21	1.14	0.592
BM1	2.00	1.82	2.20	0.10	2.10	1.78	2.36	0.10	1.00	1.000
CLm1-3	6.20	5.74	6.70	0.23	6.37	5.90	6.81	0.20	1.27	0.330
Bm1	1.69	1.42	1.90	0.10	1.72	1.53	1.88	0.08	1.86	0.012

the same variables provide another means to trace these and other morphometric distinctions (Fig. 6, Table 1). We used genetically typed specimens (Msur7 and Msur3 haplotypes lineages) for a priori sample set subdivision by DFA. Based on the analyses all specimens were separated between two clearly distinct groups: a geographically more wide, comprising the specimens from southern and central Vietnam, and another one consisting of the populations from the northern part of the range (Ha Tinh and Nghe An provinces and Ba Vi area). The discrimination between northern and southern groups has been most evident based upon exactly the first canonical axis CAN 1. It should be noticed that all samples of southern group show different variation pattern and trend to dispose along second canonical axis CAN 2, whereas the samples of northern group located along the first axis. This difference is also demonstrative to support specificity of these two population groups.

For practical usage it would be reasonable to indicate any visual traits of cranium may be useful to separate these southern and northern populations and phylogroups. The skulls of representatives of different continental Indochinese populations are shown in figures 7-9 including the holotype of *M. surifer*. It looks like a little surprising, but except for size which appreciably larger (see also Table 1), we can not find any specific features characteristic for these geographical populations.

Due to its size which evidently (on an average 10%) larger for northern populations in comparison with southern ones, some of another skull characters which usually correlated with general size (relatively short upper and lower tooth rows and length of incisive foramina) are also tend to be greater. Apparently this is the reason of specific position of these samples at PCA along PC 1 axis. But as it can be seen (Figs. 7-9), cranial shape and proportions are apparent to be very stable. These findings approve us that at this case we deal with subspecies rather then full species category. Just like that is the case for cranial characters, its eternal morphology is also very similar both for body proportions and pelt coloration (Figs. 10, A and B). So, the only perceptible trait which should be noted is longer tail and the pattern of tail coloration. The progressive discoloration is much

Table 2. Factor loadings and explained variance for the principal components PC1 and PC2 in the PCA (Fig. 5); standardized canonical coefficients and explained variance for the canonical axes CAN1 and CAN2 in the DFA (Fig. 6)

Characters	PC 1	PC 2	CAN 1	CAN 2
ONL	-0.933	0.067	-0.671	1.012
ZB	-0.674	-0.499	0.178	0.903
IB	-0.918	0.091	-0.216	0.217
LR	-0.878	-0.084	-0.283	0.027
BR	-0.532	-0.175	0.198	-0.623
BBC	-0.366	-0.422	0.624	-1.007
HBC	-0.809	0.093	-0.794	-0.144
BZP	0.125	-0.835	0.489	-0.017
LD	-0.861	0.276	0.255	0.629
LIF	-0.774	0.174	-0.501	-0.345
BIF	-0.456	-0.459	0.315	0.219
LBP	0.433	-0.358	0.598	-0.743
BBP	-0.841	-0.238	-0.240	-0.077
PPL	-0.945	0.175	-0.137	-0.878
BMF	-0.559	-0.379	0.175	-0.090
LB	-0.216	-0.783	-0.095	0.090
CLM1-3	-0.006	-0.771	-0.402	0.013
BM1	0.594	-0.626	0.410	0.078
CLm1-3	0.107	-0.940	0.420	0.346
Bm1	-0.047	-0.814	0.080	-0.107
Explained variance	40.4%	25.0%	46.0%	24.8%

Footnotes: Cranial measurements named as indicated in Materials and Methods.

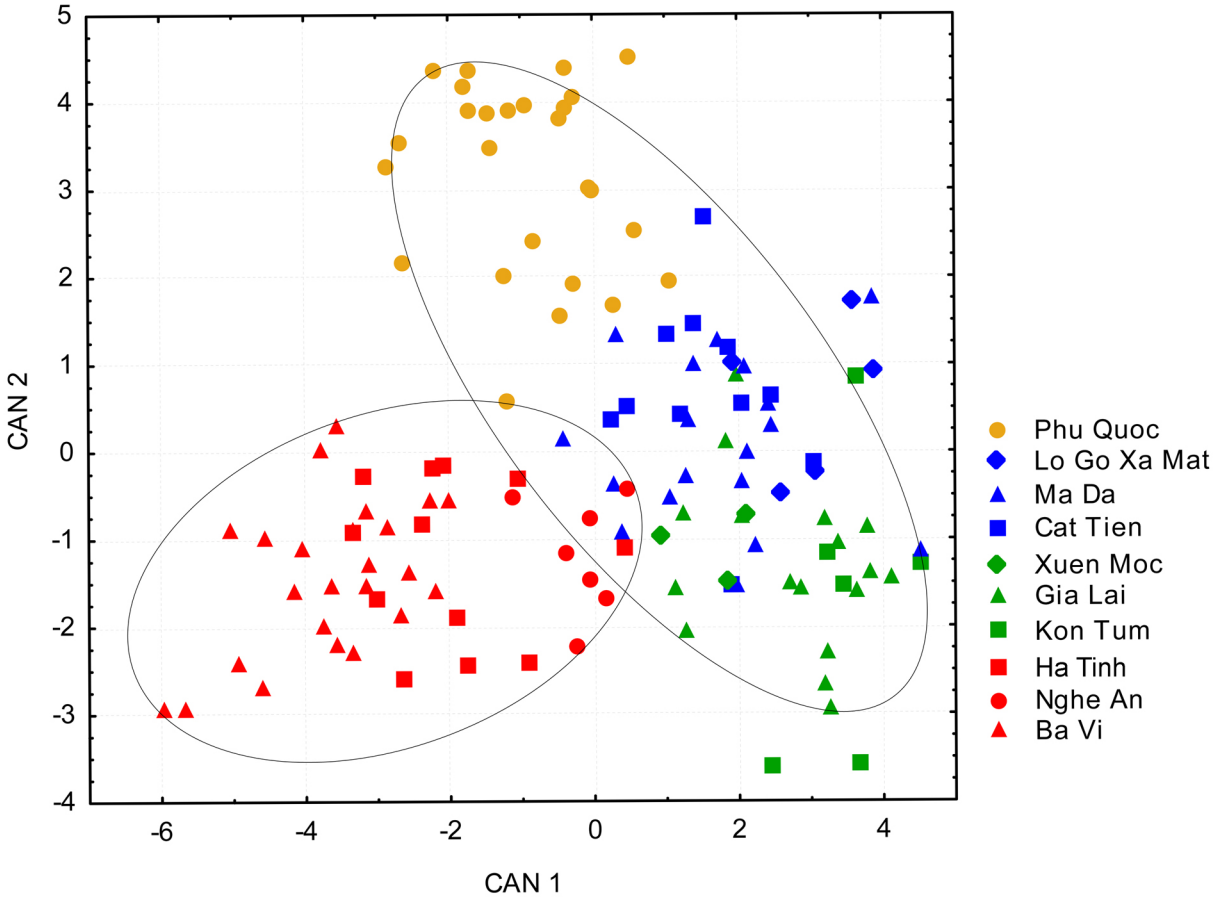

Fig. 6. Grouped morphometric separation (canonical discriminant analysis) drawn from all specimens of *Maxomys surifer* from ten Vietnamese localities. Northern populations marked as red, southern - by green, yellow and blue colors.

Fig. 7. The holotype of *Maxomys surifer* Miller, 1899; USNM 86746, Trong, Peninsular Thailand. Dorsal, ventral and lateral views of skull. Scale bar = 1 cm.

more evident than at representatives of southern populations and holotypes. Discolorations starts much earlier and much more apparent, it begins approximately from the middle of tail and terminal one third usually became completely white.

DISCUSSION

Musser and Carleton (2005) recognize this group as a species complex in need of detailed taxonomical revision. Recent phylogenetic study

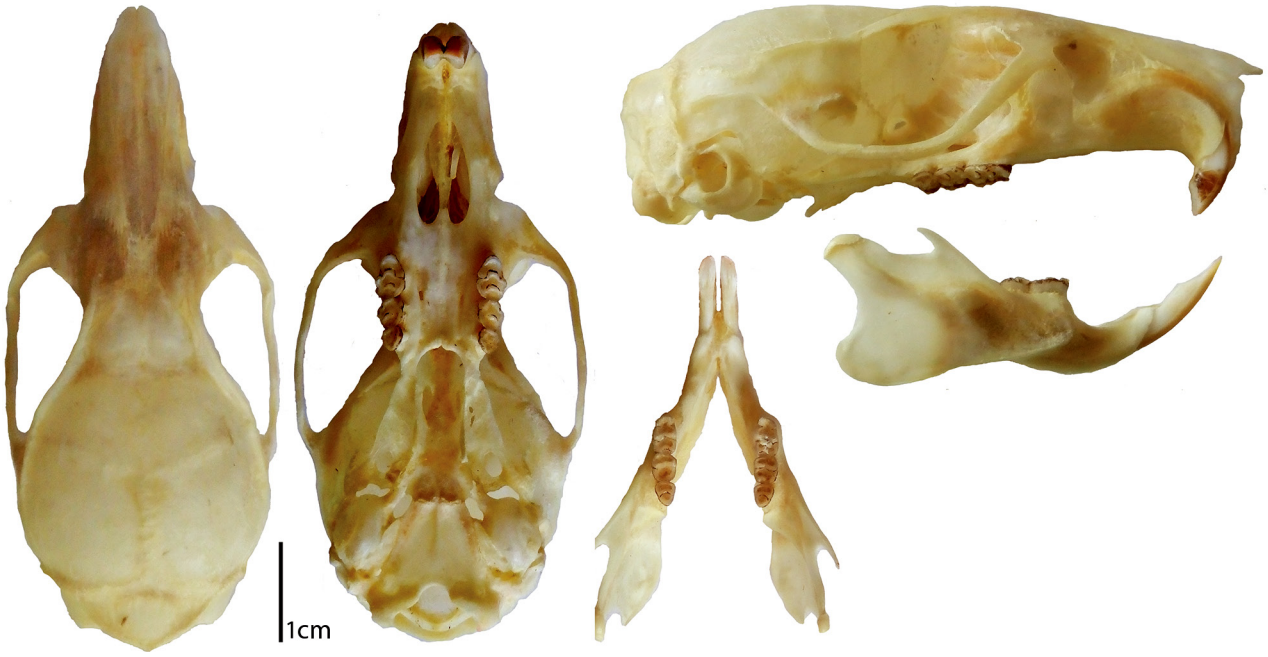

Fig. 8. The paratype of *Maxomys surifer tonkinensis* subsp. nov. ZMMU S-194722, genetic voucher Na-72; (male, collected 10.03.2014). Dorsal, ventral and lateral views of skull. Scale bar = 1 cm.

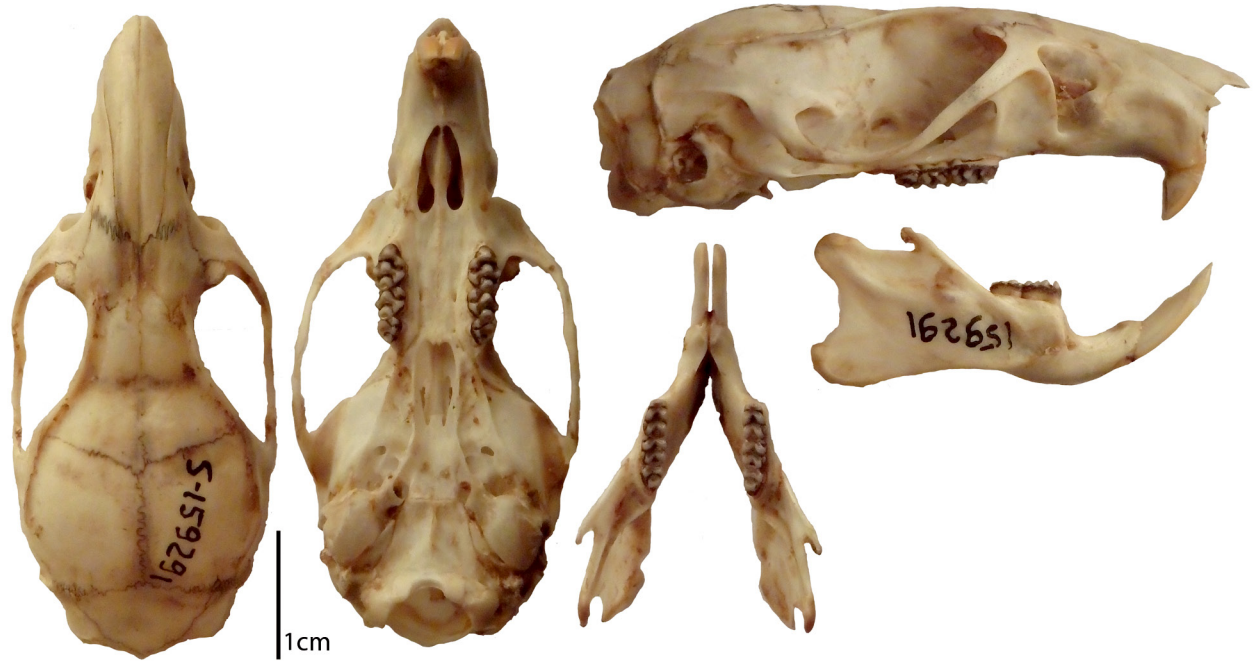

Fig. 9. *Maxomys surifer finis* ZMMU S-159291, (female, collected 25.10.89), Vietnam, Dong Nai Province, Ma Da forest. Dorsal, ventral and lateral views of skull. Scale bar = 1 cm.

(Achmadi et al. 2013) revealed several species within *Maxomys* with geographically structured genetic diversity that require closer taxonomic investigations, such as *M. whiteheadi* from the Sunda Shelf and populations of *M. surifer*.

Phylogeographic pattern in *M. surifer* is consistent with that we found within *Leopoldamys* spp. in Indochina and Sunda region (Balakirev et al. 2013). Similar observations have been made for some other Sunda Shelf taxa (Esselstyn et al. 2010; Wilting et al. 2012). Likewise that in *Leopoldamys* spp. *M. surifer* consists of a number of distinct genetic clades represented by geographical populations from southern and northern Vietnam, Borneo, Java, Sumatra, Thailand, and the Malay Peninsula. As it was recently demonstrated (Achmadi et al. 2013) typical interspecies uncorrected genetic distances for cyt *b* gene in the genus are at the limits of 0.11-0.15 with the least values between most closely related geographically vicariate species such as *M. tajuddinii-M. hylomyoides* is 0.08, *M. whiteheadi-M. hylomyoides* is 0.09, and *M. rajah-M. pagensis* even only 0.06. The discovered level of genetic divergence (d, T3P) of northern Vietnamese *M. surifer* from another six clades reaches to 0.096-0.115. This level is also consistent with previous findings for *Leopoldamys* species (d, T3P 0.080 to 0.125, Balakirev et al. 2013) in spite of the facts what here we deal with assumed intraspecific divergence.

In spite of the fact what it is difficult to calculate reliably timings for major branch segregation points it may be appreciated based on estimation of molecular mtDNA evolution of Muridae calibrated for genus *Mus*. This value evaluated as equal about 10% per Myr (She et al. 1990), so the evolution time between populations of Java, Sumatra and Borneo is 0.61-0.93 Myr, and between the Sunda Islands and mainland is 0.96-1.19 Myr. These timings is well exceed the limits of glacial events of Pleistocene accompanied by corresponding sea level fluctuations in Sunda Shelf (Heaney 1991) and comparable with average survival time for mammalian species over the past 20 Myr has been 2.33 Myr (Vrba 2000; Vrba and DeGusta 2004). So, there are all reasons to believe that actual phylogenetic structure discovered in *M. surifer* originated by a longitudinal evolution of geographical populations instead of resulted from invasions by recent range increment followed by segregation. This phylogenetic structure, thereby,

Fig. 10. (A) The holotype of *Maxomys surifer* Miller, 1899; USNM 86746, Trong, Peninsular Thailand. Skin, dorsal, ventral and lateral views. (B) The holotype of *Maxomys surifer tonkinensis* subsp. nov. ZMMU S-194718, genetic voucher Na-52; (male, collected 08.03.2014). Dorsal, ventral and lateral views of body and lateral view.

has to reflect the taxonomical diversity, namely the set of subspecies to be described within the species.

The pattern of genetic and cranial variation in *M. surifer* revealed in the present study suggests the existence of distinct genetic lineages, suspected longitudinal isolation and corresponding morphologically distinctive forms. It is evident also, that all of these lineages obviously merit to be treating as ESUs, Evolutionary Significant Units, (Moritz 1994, 2002; Waples 1995). Hence, there are reasons to recognize these northern populations as vicariate subspecies based on its genetic and morphological distinctness. Nevertheless, up to the moment, there are no any drastic morphological characters to be described nor any traces of specific isolation ever recorded for genetic lineages of *M. surifer* over its range. This fact, together with our commitment to polytypic species conception (Mayr 1970; Mallet 1995, Zachos 2016) tend us to restrict taxonomical inflation based on genetic diversity discovered and depict the special geographic populations of widely distributed species as subspecies instead of new species. At least up to the moment then complex of evidences in favor of its isolation other then geographical one will be obtained.

Subspecies represent a lower unit of biological organization and also are relevant in biodiversity conservation (Ryder 1986; Avise 1989; Zink 2004; Haig et al. 2006). The taxonomic and conservation problems associated with subspecies have been extensively reviewed for mammals (Stanford 2001; Gippoliti and Amori 2007), birds (Mayr 1982; Cracraft 1983; Zink 2004; James 2010), insects (Braby et al. 2012), and plants (Hamilton and Reichard 1992; McDade 1995). Despite limitations and misuse of the subspecies concept, particularly in the early 20th century, several evolutionary biologists (Mayr 1982; Crusz 1986; Avise 1989; Mallet 1995; Moritz 2002; Descimon and Mallet 2009) and conservation biologists (Haig et al. 2006) hold the positions in favor of subspecies as taxonomical units. The crucial point here is the polytypic biological species, which are generally accepted now, cannot logically constitute the lowest level taxonomic “unit of evolution” because these species composed of a variable number of evolutionary units each possessing their own geographic, phenotypic and genetic integrity (Cracraft 1983). An application of subspecies category to phylogenetic groups may also facilitate to bring to one point the phylogenetic species conception (de Queiroz and Gauthier 1994) and biological one. This approach also provides a natural interaction between concepts of taxonomy and biodiversity (Pavlinov 2001). O’Brien and Mayr (1991) suggested the following criteria be used for recognition of subspecies: (1) allopatry with a unique geographical range (or habitat); (2) phylogenetically concordant phenotypic characters; (3) genetically divergent as a result of an absence of gene flow; and (4) a unique natural history relative to other subdivisions of the species. Under this set of four properties, they predicted that most subspecies will be monophyletic and have the potential to become new species over evolutionary time. For our case, we have all four conditions, including unique habitat (limestone formations of Laos and Central Vietnam) where unique Msur7-populations occur, may evaluate different way as its relatives Msur3-bearing ones during its natural history. This advocate the intention to raise the taxonomical rank for even some of genetic lineages reveled over the natural range of this species to subspecies. In spite of the fact that here we presented the most distributed dataset ever discussed for the species, the morphological materials available and original samples analyzed allow us to present the formal description only for one subspecies; we think it natural to examine the questions as more wide as possible to outline the limits for another suspected ones over specific range and delimit valid nomens for it will ever been described.

Taxonomical implication

Maxomys surifer (Miller, 1900) was described from Trang, Peninsular Thailand. Up to the present time at least 46 synonyms, many of which represent putative island endemics are listed for this taxon (Musser and Carleton 2005), most of them are potentially appropriate to be used as valid subspecies names. These are, *changensis* (Kloss, 1916), *connectens* (Kloss, 1916), *finis* (Kloss, 1916), *koratis* (Kloss, 1919), *kramis* (Kloss, 1919), *kutensis* (Kloss, 1916), *pelagius* (Kloss, 1916), *siarma* (Kloss, 1919) and *tenebrosus* (Kloss, 1916) in Indochina and neighbor islands along north-eastern shore of Gulf of Siam; *aoris* (Robinson, 1912), *bentincanus* (Miller, 1903), *butangensis* (Miller, 1900), *casensis* (Miller, 1903), *domelicus* (Miller, 1903), *eclipsis* (Kloss, 1916), *flavidulus* (Miller, 1900), *flavigrandis* (Kloss, 1911), *grandis* (Kloss, 1911), *leonis* (Robinson and Kloss, 1911), *luteolus* (Miller, 1903), *manicalis* (Robinson and Kloss, 1914), *microdon* (Kloss,

1908), *binominatus* (Kloss, 1915), *muntia* (Chasen, 1940), *pemangilis* (Robinson, 1912), *pidonis* (Chasen, 1940), *puket* (Chasen, 1940), *spurcus* (Robinson and Kloss, 1914), *surifer* (Miller, 1900), *telibon* (Chasen, 1940) and *umbridorsum* (Miller, 1903) described from Malay Peninsula, Singapore, Mergui Archipelago islands and islets in Straits of Malacca or those scattered along with a eastern shore of Malay Peninsula*; anambae* (Miller, 1900), *natunae* (Chasen, 1940) and *perflavus* (Lyon, 1911) distributed on South China Sea islands; *antucus* (Lyon, 1916), *banacus* (Lyon, 1916) *catellifer* (Miller, 1903)*, mabalus* (Lyon, 1916)*, ravus* (Robinson and Kloss, 1916), *solaris* (Sody, 1934) and *pinacus* (Lyon, 1916) have its type localities on Java, Sumatra, Nias and Mentawai islands, as well as *bandahara* (Robinson, 1921), *carimatae* (Miller, 1906), *saturatus* (Lyon, 1911) and *ubecus* (Lyon, 1911) originate from Borneo or a number of smaller islands in the Karimata Strait. The type localities for all these nomens are shown on the figure 1 together with genetic lineages geographical distributions.

From the nomens listed above, *surifer* (Miller, 1900) serve as oldest for populations of Malayan Peninsula labeled as Msur1 phylogenetic lineage. Its morphological peculiarities were stressed earlier by Musser et al. (1979) and Musser & Newcomb (1983). Nomen *siarma* (Kloss, 1919), have to be apparently used for lineage Msur2 as a single one described from the area where this genetic lineage proved to be distributed. For the Msur3 lineage which shown to be distributed over a huge area of southern Indochina only two competing synonyms originating from mainland available. Namely *finis* (Kloss, 1916), and *koratis* (Kloss, 1919), its type localities (Nachon Ratchasima Province, central Thailand) does not leave any doubt about its genetic attribution. From the last pair, the former has to be chosen based on priority rule. All another nomens are susceptible because originate from small islands in Gulf of Siam, the population which still never been genetically sampled yet.

The situation with Sundaic lineages is more complicated. Nomen *bandahara* (Robinson, 1921) may be considered as available name for Borneo population labeled by phylogenetic lineage Msur4. However, as it was recorded by Gorog et al. (2004) based on mDNA D-loop analysis the population inhabits Island Karimata belong to the same genetic lineage as a number of populations of western and central Borneo, whereas another one descended from eastern Borneo fall into different cluster we name here as Msur5. We cannot investigate here the different genes at the same tree, but there is a reason to conclude that both most part of mainland Borneo and islands of Karimata Strait actually inhabits by genetically closely related populations belonging to Msur4 lineage. The nomen *carimatae* (Miller, 1906), used to describe new taxon from exactly Karimata Island underlie the *bandahara* (Robinson, 1921) and have to be used as senior synonym.

Maxomys surifer ubecus, described from Subuku Island lies near of south-eastern Borneo, may be the only possible pretender for subspecies representing Msur5 genetic lineage in case of sufficient morphological originality will be demonstrated between populations of western-central and eastern Borneo. At the other case special, new nomen should be used for Msur5 clade. That is also possible that the actual number of divergent lineages in Borneo underestimated and exceeds the two which discussed here. Special study based on much more extensive geographical sampling material has to be performed to investigate this topic in considerable details. Seemingly, there are every reasons to suppose that the populations of Java and Sumatra, representing Msur6 clade have to be attributed to distinct one or even (more probable) two different subspecies. At this case, *M. s. ravus* looks like as the most appropriate for Sumatran subclade, whereas *verbeeki* is the oldest from a pair of Javanese names.

Meanwhile, that is apparent that the populations inhabits northern Indochina and bearing Msur7 haplotypes are merit to be arisen to distinct subspecies. We failed to find any appropriate nomens ever proposed for these populations of the species and pretend to be used as valid names. Therefore, in agreement with ICZN (1999) this form is described here as new subspecies *M. surifer tonkinensis* subsp. nov.

***Maxomys surifer tonkinensis* Balakirev subsp. nov.**

urn:lsid:zoobank.org:act:7E8A1428-2943-4A06-9FC5-263DD4DCC7F5

Holotype: ZMMU S-194718, adult male, skull, skin, body in ethanol, field number Na-52, genetic voucher Na-52, collected 8 March 2014 by Alexander E. Balakirev.

Type locality: Vietnam, Nghe An Province, Quy Chau District, vicinity of Ban Ke Can Village, 19°31.184'N; 105°10.282'E, altitude 95 m a.s.l.

Paratypes: ZMMU S-194710 (male, body at

ethanol, collected 6.03.2014), ZMMU S-194711 (female, skull and skin, collected 7.03.2014), ZMMU S-194712 (male, skull and skin, collected 7.03.2014), ZMMU S-194713 (male, skull and skin, collected 7.03.2014), ZMMU S-194714 (male, skull, collected 7.03.2014), ZMMU S-194715 (male, body at ethanol, collected 8.03.2014), ZMMU S-194716 (male, body at ethanol, collected 8.03.2014), ZMMU S-194717 (male, skull, collected 8.03.2014), ZMMU S-194719 (male, skull, collected 9.03.2014, trapped near Ban Dom1 Village), ZMMU S-194720 (male, skull, collected 9.03.2014, trapped near Ban Dom1 Village), ZMMU S-194721 (female, body at ethanol, collected 9.03.2014), ZMMU S-194722 (male, skull, collected 10.03.2014), ZMMU S-194723 (male, skull, collected 10.03.2014), ZMMU S-194724 (female, skull, collected 10.03.2014), ZMMU S-194725 (male, skull, collected 11.03.2014), ZMMU S-194726 (female, body at ethanol, collected 12.03.2014).

All collected by Alexander E. Balakirev and Tran Quang Tien from the same locality as the holotype or in closest vicinity.

Etymology: The new subspecies is named after Tonkin, the former name of northern part of Eastern Indochina, with the Latin suffix *-ensis* (belonging to).

Diagnosis: Medium-sized rat, larger on average in its external and cranial measurements than the nominotypical *M. surifer* with a longer tail (106-115% of body length for most individuals).

Description and comparisons: Head and body length 170-222 mm, tail 193-227 mm, ear 24-29 mm, weight 127-210 g. figure 10 B.

New subspecies differs from the *M. s. finis* which distributed over southern Indochina in the larger skull sizes and in the relatively short upper and lower toothrows. The most evident morphological features at skull construction are also be noticed the size and shape of incisive foramina. In contrast with *M. s. finis*, which usually has shorter, reniform openings with clearly pointed cranial edge of notch, *M. s. tonkinensis* has more elongated foramina with more or less rounded cranial and caudal edges of notch figures 7-9, its somewhat reassemble in shape to the foramina characteristic to representatives of genus *Leopoldamys* but much wider at caudal side. The most remarkable external feature is the pattern of tail coloration, namely the character of tail tip discoloration. This progressive discoloration, characteristic for all *M. surifer* starts appreciably earlier than it usually happens with representatives of southern populations, discolorations starts approximately from the middle of tail and terminal one third usually became completely white, whereas for *M. s. finis* discolorations launched from approximately terminal third with only very tip about 1/5 of tail length being completely discolored.

Distribution: Northern Vietnam from Ha Tinh Province in its extreme south to Ba Vi (Hanoi area) in the north; central Laos (Khammouane and Bolikhamxai provinces). It may be probably found in southernmost Yunnan, China (Wang 2003) and northern Laos, but its presence there has to be approved by investigation of museum specimens or new field records.

Acknowledgment: This work and the one new subspecies name have been registered with Zoo Bank under urn:lsid:zoobank.org:pub:017C3A9D-9B40-4C8C-A621-7BF5883DD1D7. This study was realized with the support of the Joint Russian-Vietnamese Tropical Research and Technological Centre, Hanoi, Vietnam. We thank Dr. Victor V. Suntsov (A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia), Dr. Sergey V. Kruskop (Zoological Museum of Moscow State University, Moscow, Russia), Dr. Charles M. Francis (Canadian Wildlife Service, Environment Canada, Ottawa, Canada), Dr. Vu Dinh Thong (Zoological Museum of Institute of Ecology and Biological Resources, Vietnamese Academy of Science and Technology) who allow us to access for samples and museum collections and datasets, Dr. Nguyen Dang Hoi, Dr. Bui Xuan Phuong, Mr. Tran Quang Tien and Ms. Pham Mai Phuong (all from the Joint Russian-Vietnamese Tropical Research and Technological Centre, Hanoi, Vietnam), who made considerable efforts in preparing for a number of expeditions and who supplied us with a significant number of specimens. We also want to express our warmest gratitude to Dr. Kristofer M. Helgen, Mr. Craig Ludwig and Mr. Renee Regan (all from the Smithsonian Institution; National Museum of Natural History, Division of Mammals, Washington, USA) for their kind assistance in the investigation and photography of holotype specimen. Finally, we thank the administrations of Ba Vi, Nam Cat Tien, Bi Dup-Nui Ba, Bu Gia Map, Lo Go Xa Mat, Dong Nai, Phu Quoc and Binh Chau National Parks and Nature Reserves for their aid in the management of our studies. This study was supported in part by the Research Program “Living nature: modern state and problems of development” of the Presidium of the Russian Academy of Sciences, by

the Zoological Institute' Program No.0125-2016-004, the Russian Foundation for Basic Research (grant 16-04-00085) and the Russian Science Foundation (grant 17-14-01160).

List of abbreviation (not explained in text)

DNA - deoxyribonucleic acid
ICZN - International Code of Zoological Nomenclature
PCR - polymerase chain reaction

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Appendix 1. List of specimens used for the genetic study: species name, geographic location, collection ID, GenBank accession No. (download)

Appendix 2. List of *Maxomys surifer* and *M. moi* specimens used for morphological analysis. (download)