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Taxonomic revision of beautiful squirrels (*Callosciurus,* Rodentia: Sciuridae) from the *Callosciurus erythraeus/finlaysonii* complex and their distribution in eastern Indochina

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Abstract. This paper summarises all the currently available phylogeographic data of *Callosciurus* squirrels in continental Indochina. For the first time, all the available data on the genetic attribution of the squirrels of the *C. erythraeus/finlaysonii* complex of eastern Indochina (Vietnam) including novel ones from eastern Indochina are presented and the distribution pattern of mitochondrial lineages in Indochina as a whole is analysed. A comparative investigation of genetic (two mitochondrial, Cyt *b* and COI, and two nuclear genes, RAG1 and IRBP) and morphological variability (craniometric parameters and pelt colouration) made it possible to conclude that in eastern Indochina, the morphological variability of squirrels within *C. erythraeus/finlaysonii* complex does not correspond to the revealed phylogeographic pattern. Previously unknown genetic lineages of *C. finlaysonii*, which are widespread in central and southern Vietnam, were also discovered. Furthermore, we demonstrated that the morphus *flavimanus* is polyphyletic and should belong to *C. finlaysonii* instead of *C. erythraeus* as usually attributed. Results also revealed that populations inhabiting the southern part of eastern Indochina including *C. griseimanus* should be assigned to *C. finlaysonii*, not to *C. erythraeus*. These findings explain the inconsistency of the usage of the subspecies category within the *C. erythraeus/finlaysonii* complex. We discuss the utility of genetic methods to complement morphological data for species identification and delimitation of the *C. erythraeus*/*finlaysonii* complex.

Key words. biodiversity, phylogeography, rodents, subspecies, polymorphism, colouristic morpha

INTRODUCTION

Southeast Asia is a hotspot of mammalian species biodiversity (Ceballos & Ehrlich, 2006), including squirrels (Koprowski & Nandini, 2008; Koprowski et al., 2016). *Callosciurus* Gray, 1867, is a genus of squirrel widely distributed across Southeast Asia and contains 15 species (Corbet & Hill, 1992; Thorington & Hoffmann, 2005). The genus belongs to one of the major, morphologically diverse but monophyletic groups of Indo-Malayan arboreal squirrel lineages (clade III as defined by Mercer & Roth, 2003) that have traditionally been placed together in the tribe Callosciurini (Simpson, 1945; Moore, 1959) under the family Sciuridae. However, in-depth research using genetic methods on Sciuridae is still relatively scarce, excluding several recent works (Oshida et al., 2006, 2013, 2016; Hawkins et al., 2016a, b) and one new species description (Nguyen et al., 2018). A number of species in this family are represented by a series of colour morpha and subspecies, separated mainly based on pelage colouration (Moore & Tate, 1965; Corbet & Hill, 1992). Among them, two species, namely, Pallas's squirrel (*Callosciurus erythraeus* Pallas, 1779) and Finlayson's squirrel (*C. finlaysonii* Horsfield, 1823), are the most morphologically variable (Thorington & Hoffmann, 2005; Koprowski et al., 2016). Due to their close phylogenetic relationship and the fact that it often shows considerable colour variation, these species have been referred to by Timmins & Duckworth (2008) as the *C. erythraeus/finlaysonii* complex.

Callosciurus erythraeus occurs in Asia, ranging from Bhutan, Assam, Arunachal Pradesh, Manipur, and Meghalaya in northeastern India (Molur et al., 2005) to Myanmar, the Malay Peninsula, Thailand, eastern Cambodia, Laos, and Vietnam (Moore & Tate, 1965; Medway, 1969; Askins, 1977; Thorington & Hoffmann, 2005; Timmins & Duckworth, 2008, Lurz et al., 2013; Koprowski et al., 2016). The species is also distributed throughout southeastern China, including Hainan Island and Taiwan, where it occurs up to 3,000 m a.s.l. (Smith & Xie, 2008). It is absent from much of central Thailand and the surrounding lowlands, which are occupied by Finlayson's squirrel *C. finlaysonii* (Corbet & Hill, 1992; Koprowski et al., 2016). *Callosciurus finlaysonii* is distributed at Higher Burma, western Cambodia, the Mekong delta, and in a number of offshore islands in the Gulf of Siam. *Callosciurus erythraeus* is supposed to be sympatric with *C. finlaysonii* in isolated hill ranges in Laos (Timmins & Duckworth, 2008). No fossils are documented for either species.

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Debates on the subspecific classification of *Callosciurus* have been based on morphological characteristics, such as skull shapes and pelage patterns. Currently, they are divided into 16 and up to 26 geographically distributed subspecies for *C. finlaysonii* and *C. erythraeus* respectively (Corbet & Hill, 1992; Koprowski et al., 2016). Because of ambiguous descriptions in the literature, the distribution of certain subspecies are unclear. Of these, at least 18 were previously assigned to distinct species, for example, the belly banded squirrel *C. flavimanus* (Ellerman & Morrison-Scott, 1951; Moore & Tate, 1965). It was regarded as a subspecies of *C. erythraeus* (i.e., *C. e. flavimanus*) by Corbet & Hill (1992), who assigned all *C. flavimanus* subspecies to *C. erythraeus*. Similarly, four subspecies of *C. erythraeus* (namely, *zimmeensis*, *thai*, *pranis*, and *rubeculus*), which are distributed in western and southern peninsular Thailand (Moore & Tate, 1965; Askins, 1977; Thorington & Hoffmann, 2005), were combined by Corbet & Hill (1992) into a single subspecies, *C. e. erythraeus*.

To date, molecular phylogenetic analyses of *Callosciurus* species include studies of *C. erythraeus* in Sichuan Province, China (Guo et al., 2011), Taiwan (Oshida et al., 2006), and southern Vietnam (Oshida et al., 2013), in addition to a survey of molecular phylogenetic relationships among *C. finlaysonii* subspecies in Thailand (Boonkhaw et al., 2017) along with a *C. inornatus* survey in northern Vietnam (Oshida et al., 2011). The *Callosciurus* species is relatively diverse in mitochondrial DNA lineages, as 83 animals harboured 18 D-loop haplotypes in Hongya County, Sichuan, China (Guo et al., 2011), whereas 43 haplotypes of D-loop region were found among 71 animals in Taiwan (Oshida et al., 2006), and 8 haplotypes were found among 17 Japanese animals (Oshida et al., 2007). In Thailand, 12 subspecies/colour morpha of *C. finlaysonii* and *C. erythraeus* were investigated by Boonkhaw et al. (2017), who divided them into seven Cyt *b* and D-loop genetic groups (G1-G7) and up to 45 haplotypes, while more than 20 COI haplotypes have been documented in populations introduced in Europe (Mazzamuto et al., 2016). Along with a whole-length mitochondrial genome was recently obtained (Hu et al., 2014) as a reference, only two nuclear genes (c-myc and RAGl) have been sequenced from *C. erythraeus*, but the sequences were not published in open access (Steppan et al., 2004), and only a few RAG 1 sequences from Argentina (Gabrielli et al., 2014) are available.

The taxonomy and phylogeography of these squirrels are further complicated by the numerous instances of secondary human introductions. Recently, both *C. finlaysonii* and *C. erythraeus* have become popular pets worldwide, leading to wide introduction and invasion of these species into rural and forested areas in many countries such as Argentina, France, Belgium, Italy, Holland, Hong Kong, Singapore, and Japan (Oshida et al., 2007; Kuramoto et al., 2012; Beltolino & Lurz, 2013; Lurz et al., 2013; Gabrielli et al., 2014; Mazzamuto et al., 2016). However, correct species identification was difficult due to the high levels of variability and introgression between subspecies and species. Given the complicated history and taxonomic ambiguities surrounding this group, the goals of this study was to 1) summarise all currently available genetic data for *C. erythraeus/finlaysonii* group to compare geographical patterns of genetic lineages and morphological morpha; 2) assess the congruence of morphological and genetic variability and thus, delimit species boundaries and provide appropriate taxonomic assignments for various colour morpha and genetic lineages distributed in East Indochina and neighbor regions.

MATERIAL AND METHODS

Genetic samples. We examined *Callosciurus* specimens obtained during field surveys conducted in Vietnam during 2009–2018 by the Joint Russian-Vietnamese Tropical Research and Technological Centre. In total, 42 squirrels from 13 geographical localities were sampled to evaluate the species attribution of squirrel populations (see Supplementary Table S1, Appendix 1) and investigate phylogeographic patterns of these squirrels in eastern Indochina. DNA from 96% ethanol-preserved muscle tissue was extracted using a phenol-chloroform-proteinase K protocol (Kocher et al., 1989; Sambrook et al., 1989). The DNA was further purified by ethanol precipitation or a DNA Purification Kit (Fermentas, Thermo Fisher Scientific Inc., Pittsburgh, PA, USA). Four genes, which are relevant for the phylogenetic analysis within the Asiatic Sciuridae (Oshida et al., 2000, 2006; Mercer & Roth, 2003; Steppan et al., 2004; Chang et al., 2011; Li et al., 2008, 2013; Hawkins et al., 2016a, b) were targeted. Three of these genes were used in former analyses, including the complete cytochrome *b* (Cyt *b*) gene (1,140 bp), the 5′-proximal 658 bp portion of subunit I of the cytochrome oxidase gene (COI), usually used for genetic barcoding, and a long fragment (up to 2,038 bp) of the first subunit of the recombination activation factor gene (RAG1). We also sequenced a fragment (1,205 bp) of the first exon of the interphotoreceptor retinoid-binding protein (IRBP), which has never been used for *Callosciurus* phylogenetics before.

The *Cyt b* gene was amplified using the primers L14723 and H15915 (Irwin et al., 1991), while the COI gene was amplified with universal mammalian conservative primers BatL 5310 and R6036R (Kocher et al., 1989; Irwin et al., 1991). The following universal PCR protocol was used to amplify both mtDNA fragments: initial denaturation for 90 s at 95°C, denaturation for 30 s at 95°C, annealing for 60 s at 52°C, and elongation for 30 s at 72°C, followed by terminal elongation for 2 min at 72°C. The RAG1 gene was amplified using the previously published primers S70 and S71 and were used for both PCR and sequencing as described by Steppan et al. (2004). The IRBP gene was amplified using the IRBP125f, IRBP223, IRBP1435r, IRBP1125r, and IRBP1801r primers (Suzuki et al., 2000) according to the method of Stanhope et al. (1992). The double-stranded DNA products were directly sequenced in both directions using an ABI PRISM 3730xl Genetic Analyzer (Applied Biosystems, USA) and the BigDye® Terminator v3.1 Cycle Sequencing Kit, (Life Technologies Corporation, Carlsbad, CA,USA) in agreement with the manufacturer's protocol. All sequences were deposited in GenBank (MK256799–

MK256878). In addition to our original specimens from Vietnam, additional DNA sequences of *Callosciurus* species available in GenBank/NCBI/JNDB databases as of June 2018 were obtained (Supplementary, Table S1) together with one specimen of *Dremomys rufigenis*, used as the outgroup. In total, we combined most of the genetic data on *Callosciurus* available from Indochina and the neighbouring regions. Unfortunately, we were unable to use a few RAG1 gene sequences of *Callosciurus* that were used by Hawkins et al. (2016a), namely, KP126032 (*prevostii*), KP126014 (*orestes*), KP126013 (*phayrei*), KP126012 (*finlaysonii*), KP126011 (*notatus*) and KP126010 (*adamsi*), due to the nonhomology of the regions of the RAG1 gene.

Phylogenetic analyses. The final dataset includes 119 haplotypes for Cyt *b*, 76 for COI, 26 for RAG1 and 19 for IRBP genes (see Supplementary, Table S1). The sequences were aligned using BioEdit v. 7.1.11 (Hall, 1999) and ClustalW (incorporated into BioEdit and MEGA 6) software and were verified manually.Pairwise genetic distances (*d,* T3P) among groups of individuals were calculated based on Cyt *b* haplotypes using the GTR model and maximum likelihood algorithm (Tamura et al., 2004) as implemented in MEGA 6. As our objective was to determine the limits of the two these sister species and the analysis of geographical pattern of genetic variability within them, not complicated multi-taxa phylogeny, the main analyses were focused on the Cyt *b* gene (having the widest geography), and partly the COI gene. Nuclear genes were studied in the context of assessing the conformity of the evolution of the nuclear and mitochondrial genome, as well as to assess the possibility of hybridisation.

Bayesian phylogenetic trees were inferred using MrBayes v3.2. under default parameters (Huelsenbeck & Ronquist, 2001, Ronquist & Huelsenbeck, 2003). Two separate MCMC runs were initiated using four chains per run (default heating value) and the first 25% of samples were discarded as burn-in. The best-fit nucleotide substitution models were examined using Maximum Likelihood (lnL), the Bayesian Information Criterion (BIC) and the corrected Akaike Information Criterion (AICc) as implemented in MEGA 6. The general time-reversible with gamma distribution and invariable cites (GTR+G+I) substitution model was selected for all genes see. The gamma shape parameters were evaluated and calculated from a general dataset by MrBayes v3.2. and appeared as alpha =1.9801, pInv=0.5054 for Cyt *b*; as alpha =3.2481, pInv=0.6135 for COI; alpha=0.8747, pInv=0.7378 for RAG1 gene; and alpha=0.7919, pInv=0.6257 for IRBP. An average standard deviation of split frequencies (ASDSF) threshold of 0.0025 was used to assess stationarity among sampled trees and parameters. Consensus trees were built from last 75% portion of trees obtained (75×10^3, 45×10^3, 45×10^3 and 40×10^3 trees for Cyt *b*, COI, RAG1 and IRBP, respectively) during the MCMC procedure by MrBayes v.3.2. The robustness of the trees was assessed by posterior probabilities (pp). MCMC convergence was assessed by examining effective sample size (ESS) of parameters using Tracer v.1.7 (Rambaut et al., 2018). Trees were visualised and prepared by Interactive Tree Of Life (iTOL) 4.2.3 (Ciccarelli et al., 2006; Letunic & Bork, 2016) and by FigTree v1.4.3 software (Rambaut, 2012).

Divergence times were computed based on Cyt *b* gene sequences in MEGA 6 based on the RelTime method (Tamura et al., 2012), which does not require any pre-assumptions for lineage rate variations. We used the divergence time between *C. e. griseimanus* and *C. finlaysonii* evaluated by Oshida et al. (2013) based on transversional divergence rate (0.5%/ million year) at the third codon position of the mammalian cytochrome *b* gene (Irwin et al., 1991) and estimated as 0.7–1.2 Ma as a calibration point.

Morphological analyses. We examined *Callosciurus* museum specimens (skins and skulls) obtained during field surveys conducted from 1989 to 2018 in Vietnam along with other materials deposited in Zoological Museums of Moscow State University, Moscow, Russia (ZMMU) and Zoological Institute of Russian Academy of Sciences, Sankt-Petersburg, Russia (ZISP). In total, 65 intact skulls (including 25 genotyped individuals mentioned above) and 89 skins from 21 localities (Supplementary, Appendix 1) from southern China, Vietnam, and Laos were investigated to evaluate the level of correspondence between apparent phenotype and genetic attribution of squirrels from the natural populations in eastern Indochina. The age of animals was assessed using molar eruption and cranial seams. Only adult animals were used for analyses, without sex separation. Gender groups were not separately distinguished due to the insignificance of sexual dimorphism in cranial characters and skull structure compared with the scope of geographic variability (Lurz et al., 2013). Possible gender bias was compensated by equalization of male and female numbers in dataset. For comparison of the level of craniometrical variability within the *C. finlaysonii/erythraeus* group, we used 7 intact skulls of adult *C. inornatus*. Nineteen craniodental measurements were taken for each skull using digital callipers to the nearest 0.01 mm: greatest length of skull (ONL), palatal length (PL), interorbital breadth (IB), supraorbital breadth (SB), braincase breadth (BBC), braincase height (HBC), zygomatic breadth (ZB), diastema length (LD), length of the nasal bones (NL), palatal length (LBP), postpalatal length (PPL), upper molar row length (CLM), lower molar row length (CLm), breadth across the palatal bridge at the level of the first molar (BBP1), breadth across the palatal bridge at the level of the third molar (BBP3), length of incisive foramina (LIF), breadth of the mesopterygoid fossa (BMF), length of the auditory bulla (LB), and height of the auditory bulla (HB). Thirteen indices were additionally computed: auditory bulla length index (ILB=LB/ONL), general breadth index (GBI=BBC/ONL); zygomatic arch index (IZB=ONL/ ZB), interorbital index (IOB=ONL/IB), palatal index 1 (ILBP1=LBP/ONL), palatal index 2 (ILBP2=LBP/PL), molar index (IMOL=CLM/ONL), diastemal index (DI=LD/ CLM); general cranial index (GCI=PL/PPL), orbital processes index (OPI=SB/ZB), cranial height index (IBH=HBC/ONL), cranial index (CI=Sqrt(BBC×HBC)), and palatal area index (PI=(Sqrt(BBP1×BBP3)×LBP)/ONL).

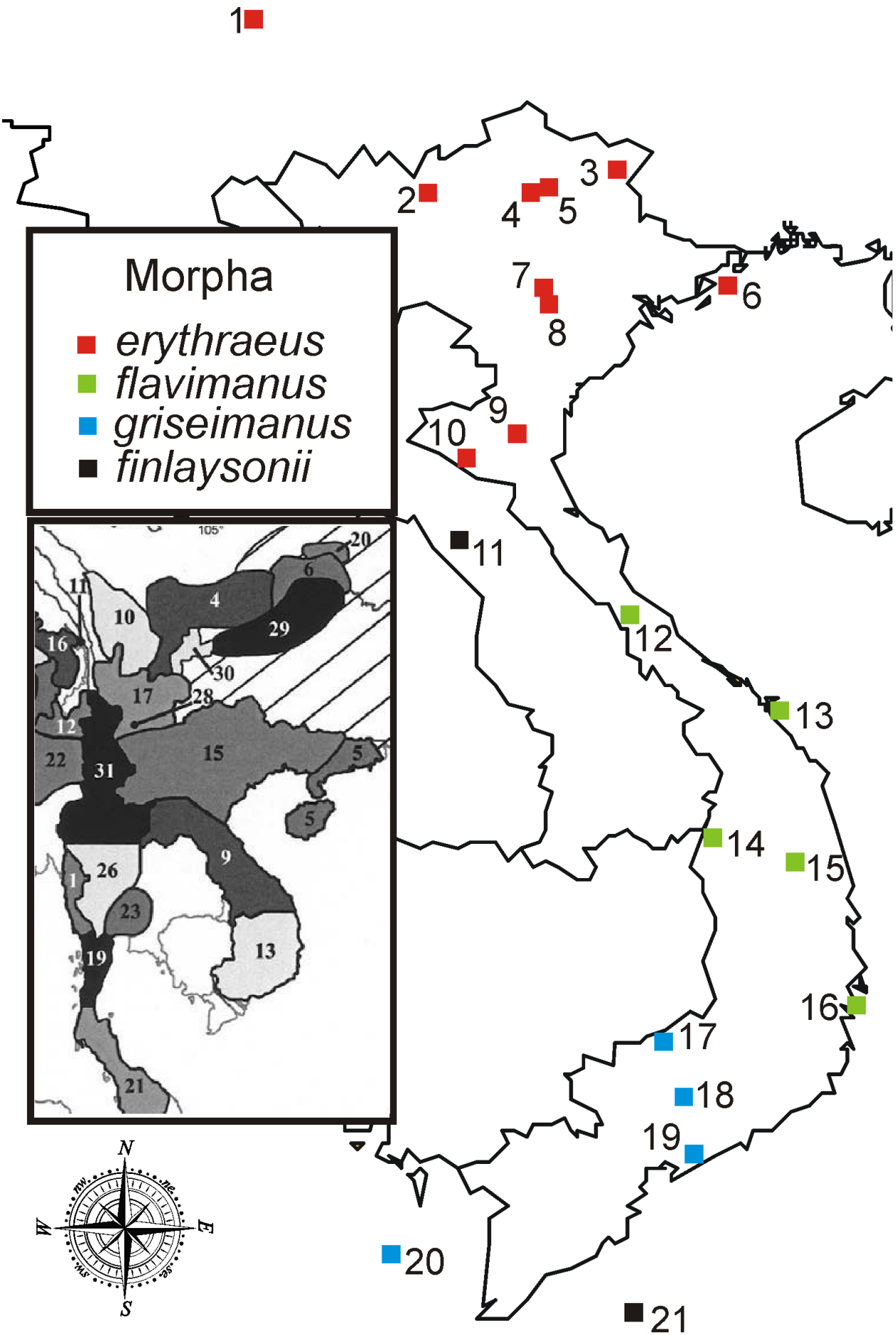

Fig. 1. Localities of morphologically investigated materials of *Callosciurus* in eastern Indochina. Site numbers correspond to those in Appendix 2 of Supplementary. Map of distribution of *Callosciurus* subspecies/colour morpha in SE Asia from Moore & Tate, 1965.

A principal components analysis (PCA) followed by canonical discriminant analysis (DFA) was performed using Statistica 10.0 (StatSoft Inc, 2011). The V-fold cross-validation method was used to determine the optimal number of principal components. The NIPALS algorithm was applied with the maximum number of iterations set as 50 and convergence criterion established as 0.0001. Minimum percentage of valid cases per variable was set as 80% with automatic removal of unqualified cases. The model components were extracted from a variance-covariance data matrix and were computed using direct metrical data without transformation. We used two alternative ways to group samples. First, based on external morphology (colour morpha), as well as on the basis of genetic data, for genotyped populations and individuals (mtDNA genetic lineages/species). These groups were generally consistent with each other, with the exception of a few individuals in populations in central and southern Vietnam.

Species attribution and samples grouping. We used various groupings for individuals based on morphological characters (according to Thorington et al., 2012 as the most comprehensive source), and inferred monophyletic genetic lineages. Under this conception, the genetic lineages found in the type locality of *C. finlaysonii* (Chang Island, Gulf of Siam) and related to it were considered as the true *C. finlaysonii*, whereas other genetic lineages belonged to *C. erythraeus*. In most cases, morphological and genetic species attribution coincided. In cases where morphotypes were not monophyletic, we performed a morphological analysis of the corresponding sample, referring it not to a species, but to the corresponding morphotype or colour morpha. Obvious discordance between morphological appearance and genetic relationship are discussed below.

RESULTS

General observation on morphological variability. Currently, in Vietnam, southern China, and eastern Indochina, several types of colouration of *Callosciurus erythraeus* are described, each of them regarded as an independent subspecies. Stroganova (1957) singled out *C. e. hendeei* Osgood, 1932 and *C. e. michianus,* Robinson & Wroughton, 1911, whereas Dao (1965) additionally recognised *C. e. erythraeus*, Pallas, 1779, *C. e. castaneoventris*, Gray, 1842, and *C. e. erythrogaster* Blyth, 1842, and further described *C. e. cucphuongis*, Dao, 1965, as a distinct taxon. Their appearance more or less corresponds to descriptions made in Corbet & Hill (1992) and Thorington et al. (2012). A few reliable records of *C. finlaysonii* in Vietnam are noted from Tho Chu, Con Dao (Kuznetsov, 2000, 2006) and Phu Quoc Islands (Lunde & Nguyen Truong Son, 2001; Abramov et al., 2007) and from Kon Tum province (Kuznetsov, 2006).

Our collection contained 84 skins from 20 localities in Vietnam, southern China and Laos. There were three main types of colouration or morphotypes, within which individual local variations are revealed (Fig. 1; Supplementary Appendix 2). These were as follows:

Morphotype N (Northern). Whole upper surface dark agouti grey, undersurface maroon or sometimes dark chocolate brown. Throat similar to the belly, without midventral wedge or stripe. Hands and feet similar to the back and even darker, darkening terminally to black. Tail from close to its base similar to the back, nearly uniform agouti, indistinctly annulated with black and pale buff, the tip black with a variable numbers of white and pale yellowish hairs.

Morphotype N variety N-R (Northern-reddish). Colour of body and limbs as in previous race, though the tip of tail has variable numbers of reddish hairs as opposed to pale or yellowish.

Morphotype N variety N-I (Northern-Insular, distributed in Bai Tu Long Archipelago). Similar to morphotype N but the general colour is considerably lighter with admixture of yellowish hairs. Olive agouti hue almost completely lacking, upper surface somewhat grizzled grey except for darker middorsal strip on the back. Tail similar to the body, annulated with black and pale, the tip black with variable numbers of white and pale hairs. Underside is typical for northern type.

Morphotype C (Central). General colour light agouti, almost or entirely without black grizzling, considerably lighter than northern races. Undersurface bright orange or rusty. Hands and feet rusty or yellow, much lighter than dorsum. Neck and throat similar to the dorsum for most specimens, some individuals may have a short wedge of agouti on the chest. Tail from close to its base coloured similar to the back, nearly uniform ochraceous, with inconspicuous blackish rings on the hairs, without blackish tip.

Morphotype C, variety C-I (Central-Insular, distributed in Cham Island, near Da Nang). Similar to Morphotype C but with lighter dorsum. Rostrum and cheeks rusty (similar with many *Dremomys* species). Underside also generally lighter, bright orange. Hands and feet rusty.

Morphotype S (Southern). Colour of dorsal body and limbs as in previous race but even lighter, though on average is more suffused with pale, so that the general tone is almost light greyish to olive. Underparts pale buff. Some individuals have rusty hue on hips and urogenital area. Hands and feet creamy white, just like throat. Tail from its base coloured similar to the back, with inconspicuous ochraceous zonal rings on the hairs, without dark tip.

Morphotype S, variety S-I (Southern Insular, distributed on Tho Chu Island, Gulf of Siam). Similar to Morphotype S but with perceptibly brighter buff or rusty hue on sides, which may distinguish younger individuals. Underside creamy white without reddish hue. Hands and feet similar to throat. Pelt longer and downy, milder than is common for mainland populations. Tail similar to the general type, but the tip of tail black with a number of white and pale hairs. It should be stressed here that the morpha is somewhat similar to the new species of *Callosciurus* from Hon Khoai Island, *C. honkhoaiensis* (Nguyen et al., 2018), but appreciably

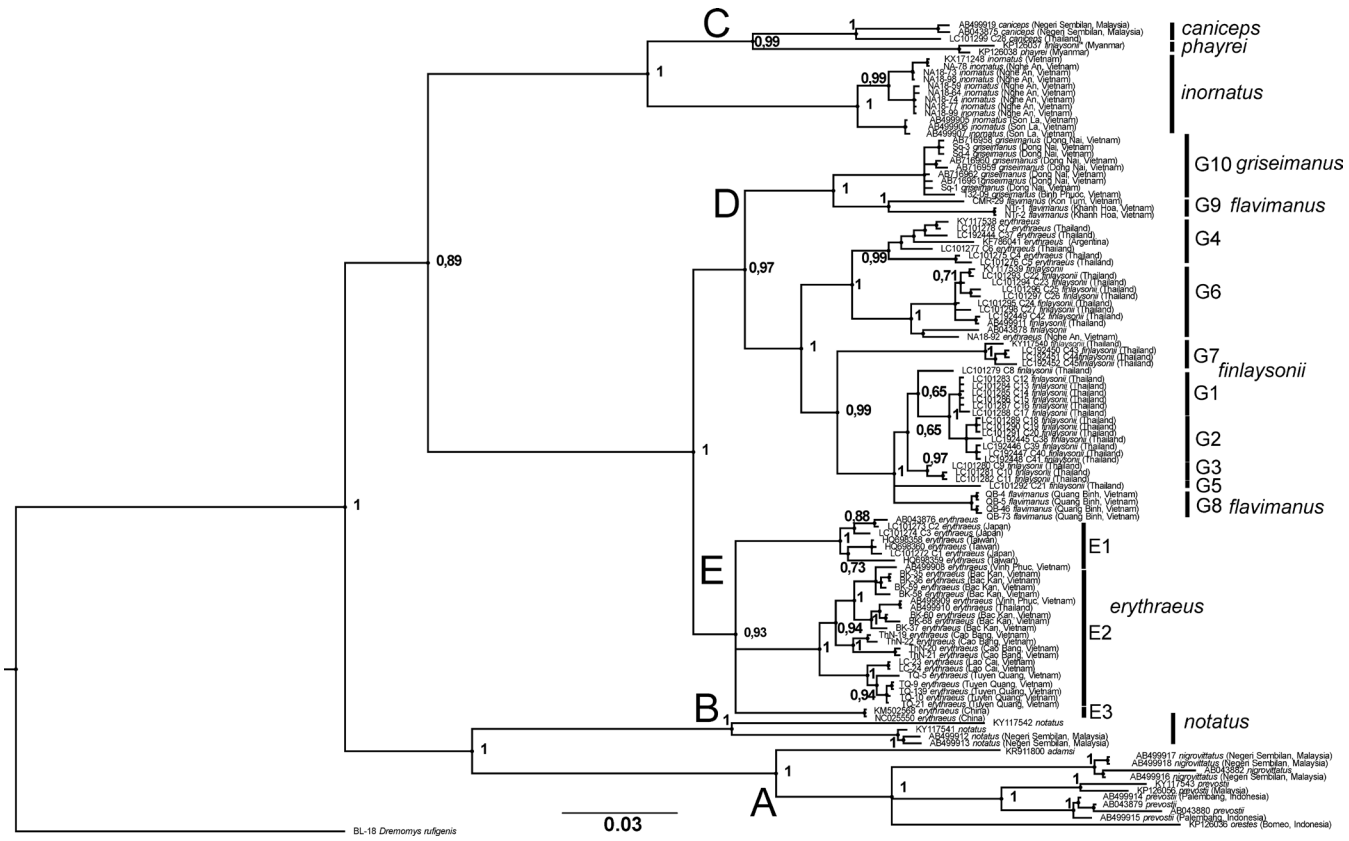

Fig. 2. The phylogenetic tree (Cyt *b*, Bayesian inherence) for *Callosciurus* genetic lineage radiation. The posterior probabilities are presented at the nodes. The sample labels and major phylogenetic lineage names are as indicated in Table 1 of Supplementary and in Fig. 4. Branches length scale is in the bottom.

larger. Unfortunately, we have no skulls or genetic samples for direct comparisons of these specimens.

Thus, by comparing the colour patterns and distributions of populations in this study, we concluded that the northern type matched the description of *C. e. hendeei* (Stroganova, 1957; Moore & Tate, 1965, Thorington et al., 2012), and the variety N-I corresponded to *C. e. cf. erythraeus* as singled out by Dao (1965). The central morphotype corresponded to *C. e. flavimanus* (Fig. S2), and the southern one to *C. e. griseimanus* as is currently accepted (Thorington et al., 2012; Oshida et al., 2013) (Fig. S1). We also examined two colouristic morpha from central Laos and Con Dao Island, which should be assigned to *C. finlaysonii menamicus* and *C. finlaysonii harnandi*, respectively (Fig. S2).

It is curious to note that despite considerable stability in general colour pattern, the special varieties (see above) which were noticed over the whole natural area by Moore & Tate (1965) were most common for insular populations. To avoid confusion and to specifically refer to the morphological type of the animal, we hereafter use the term "morphotype *erythraeus*" for wild-type animals with agouti dorsum, dark feet and chestnut abdomen; "morphotype *griseimanus*" for animals that have a colour pattern of *C. griseimanus* (light dorsum, very light abdomen yellowish, very light, almost pale yellow in the feet, and forehands dorsal sides); "morphotype *flavimanus*" for animals with a light agouti colour on the back and distinctly ochreous, but not pale on the forehands and feet, as described for the corresponding taxon; "morphotype *finlaysonii*" for all other colour morphae with spots or stripes, as well as for any albinistic and melanistic morphae. The distribution of these morphotypes in eastern Indochina is presented in Fig. 1. It is clear that the pattern of morphotype distribution generally agrees with the map of *C. erythraeus* subspecies in eastern Indochina (Moore & Tate, 1965; Lurz et al., 2013), with the limits between the *erythraeus* and *flavimanus* morphotypes situated close to 18°N and between *flavimanus* and *griseimanus* at approximately 12°N.

Phylogenetic analyses. The final alignments included 1,140 bp and 119 specimens for Cyt *b*; 658 bp and 76 specimens for COI; 2,038 bp and 25 specimens for RAG1; and 1,205 bp and 18 specimens for IRBP. Because of the large number of independent lineages and the high level of sequence divergence, the, ME, ML and MP algorithms generally resulted in relatively weak bootstrap values for a number of clades and failed to return any consistent topology for the general data set. In contrast, Bayesian inference (BY) proved to be much more powerful with respect to topological resolution and resulted in highly supported topology for most nodes for mitochondrial genes and sufficiently robust structure for a number of nuclear clades. The tree topologies for Cyt *b* and COI were generally consistent and congruent for the main clades, which differed only in the bootstrap levels for certain branches (Figs. 2 and 3). The Cyt *b* tree was the most robust because it was the most widely representative both for sample number and for geographical range coverage (Fig. 4).

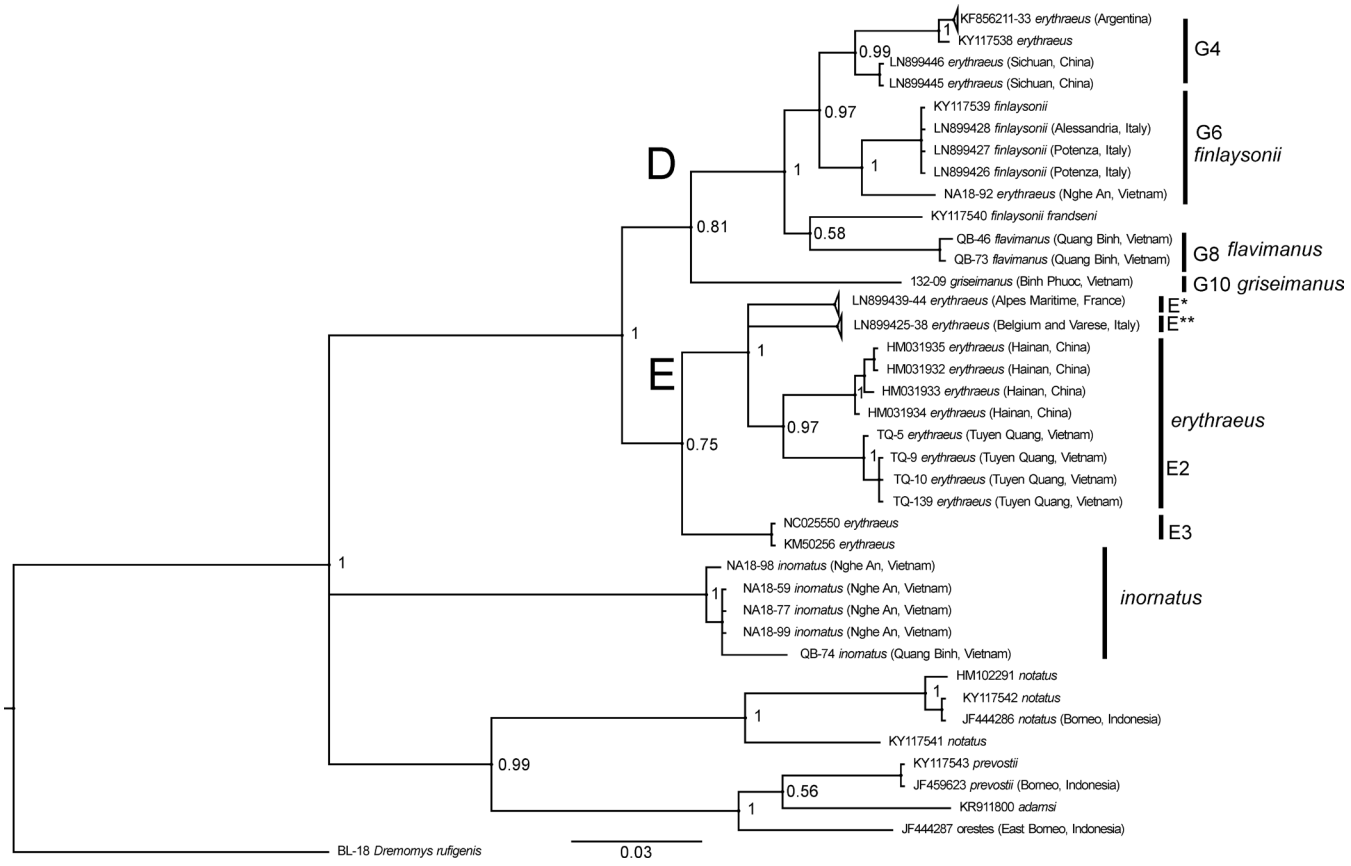

Fig. 3. The phylogenetic tree (COI, Bayesian inherence) for *Callosciurus* genetic lineage radiation. The posterior probabilities are presented at the nodes. The sample labels and major phylogenetic lineages names are as indicated in Table 1 of Supplementary and in Fig. 4. Branches length scale is in the bottom.

Footnote. E* and E** are special clades which can not be reliable attributed to any notable cyt *b* clades due to cyt *b* hapltypes were not available for these samples.

Special attention should be given to the distribution patterns of genetic lineages where three groups of clusters could be identified. The first group, formed by G4 and G6, was generally distributed in the northern part of the region. The second was formed by clusters G1−G3, G5, G7 and G8, scattered both in the south along the shores of the Gulf of Siam, with G3 and G8 distributed in the north and northeast. The means of such penetration are yet to be investigated. Finally, the third cluster consisted of G9 and a G10 group distributed at the extreme southeast of Indochina.

As revealed by Oshida et al., (2006), the Malayan and Sundaic species formed genetic lineages A and B; lineage C consisted of the species of the *inornatus/caniceps* group, whereas the population of *Callosciurus erythraeus* and *C. finlaysonii* constructed a deep dichotomy, which in turn could be divided into a number of geographically segregated and well-supported phylogenetic groups. Northern populations usually attributed to *C. erythraeus* constituted cluster E, composed of three phylogenetic lineages (E1−E3). In addition to the seven phylogenetic groups (G1−G7 of cluster D in Figs 2, 3) of *C. finlaysonii* discovered by Boonkhaw et al. (2017) in Thailand and another two discovered by Oshida et al. (2013) in southern Vietnam (G9 and G10), we found one more, formed by samples from Quang Binh Province, Vietnam, and attributed to the phenotypically usual *C. flavimanus* (Fig. S3). These samples formed a separate G8 cluster inside *finlaysonii*, sister to clusters G1, G2, G3, and G5, which are geographically distributed in eastern and northern Thailand. However, this branch was not sister to and was even fairly distantly related to clusters G9 and G10 as found earlier by Oshida et al. (2013). These clusters combined the representatives of *flavimanus* and *griseimanus* and included our samples from Nha Trang and Kon Tum Province, which were also phenotypically *flavimanus* specimens.

Thus, being undoubtedly related to *finlaysonii*, the light-coloured animals of southern Indochina usually attributed to *C. e. flavimanus* do not form a monophyletic group and thus cannot be considered as a natural taxon (ICZN, 1999).

In contrast, sample Na18-92, from Nghe An Province, provided another challenge. Phenotypically it had the ordinal *erythreus* morphotype, but fell into the cluster *finlaysonii* G6. To avoid confusion, hereinafter, we use the term "genetic lineage *finlaysonii*" to refer to a cluster labelled D in Figs. 2 and 3 that contained, among others, mitochondrial haplotypes of the G2 group derived from the type locality of this species (Sichang Island, Gulf of Siam) regardless of the morphological appearance of the animals bearing it. We follow here the nomenclature of Boonkhaw et al.

Table 1. Genetic distances between phylogenetic lineages of *Callosciurus* calculated based on the *Cyt b* gene sequence (1,140 bp, *d* T3P in the bottom left, SE in the top right).

		C.erythraeus			*C.finlaysonii*										*C.inornatus*	*C.phayrei*	*C.caniceps*	*C.notatus*	*C.adamsi*	*C.nigrovittatus*	*C.prevostii*	*C.orestes*
		E1	**E2**	**E3**	**G1**	**G2**	**G3**	**G4**	**G5**	**G6**	**G7**	**G8**	**G9**	**G10**								
C.erythraeus	E1		0.014	0.015	0.020	0.020	0.019	0.024	0.021	0.022	0.025	0.018	0.024	0.018	0.035	0.031	0.040	0.039	0.043	0.039	0.036	0.047
	E2	0.081		0.015	0.020	0.020	0.021	0.018	0.022	0.019	0.020	0.019	0.020	0.017	0.029	0.028	0.038	0.035	0.045	0.038	0.037	0.043
	E3	0.080	0.081		0.024	0.024	0.024	0.021	0.027	0.022	0.023	0.023	0.020	0.020	0.033	0.029	0.039	0.035	0.055	0.041	0.033	0.048
C.finlaysonii	G1	0.105	0.109	0.129		0.004	0.006	0.014	0.010	0.014	0.015	0.009	0.019	0.017	0.034	0.027	0.036	0.038	0.046	0.039	0.039	0.039
	G2	0.112	0.110	0.132	0.008		0.006	0.014	0.011	0.015	0.015	0.009	0.021	0.018	0.033	0.028	0.037	0.037	0.046	0.039	0.040	0.038
	G3	0.103	0.117	0.133	0.018	0.023		0.013	0.009	0.014	0.015	0.009	0.021	0.018	0.036	0.030	0.039	0.038	0.044	0.041	0.036	0.042
	G4	0.142	0.107	0.123	0.073	0.072	0.065		0.015	0.012	0.015	0.015	0.023	0.019	0.036	0.029	0.040	0.036	0.049	0.048	0.040	0.049
	G5	0.122	0.123	0.147	0.040	0.050	0.035	0.082		0.017	0.019	0.011	0.021	0.019	0.032	0.032	0.040	0.044	0.047	0.041	0.038	0.045
	G6	0.135	0.115	0.131	0.075	0.081	0.073	0.063	0.090		0.016	0.017	0.021	0.018	0.036	0.028	0.037	0.040	0.049	0.043	0.041	0.045
	G7	0.150	0.118	0.133	0.083	0.083	0.081	0.087	0.104	0.093		0.016	0.023	0.021	0.044	0.032	0.045	0.043	0.059	0.055	0.052	0.058
	G8	0.095	0.109	0.128	0.035	0.035	0.033	0.083	0.047	0.093	0.086		0.019	0.017	0.031	0.031	0.041	0.044	0.042	0.036	0.038	0.043
	G9	0.148	0.126	0.120	0.110	0.124	0.124	0.141	0.121	0.123	0.139	0.114		0.011	0.027	0.031	0.040	0.041	0.050	0.040	0.041	0.041
	G10	0.100	0.097	0.113	0.089	0.100	0.093	0.115	0.102	0.105	0.125	0.092	0.062		0.027	0.030	0.038	0.035	0.045	0.041	0.035	0.038
C.inornatus		0.221	0.183	0.200	0.204	0.203	0.211	0.218	0.194	0.218	0.270	0.191	0.165	0.165		0.028	0.027	0.042	0.046	0.041	0.056	0.048
C.phayrei		0.189	0.172	0.176	0.153	0.161	0.177	0.180	0.187	0.168	0.197	0.177	0.191	0.178	0.161		0.019	0.038	0.047	0.039	0.049	0.037
C.caniceps		0.256	0.243	0.239	0.219	0.224	0.242	0.252	0.244	0.236	0.277	0.248	0.250	0.238	0.167	0.110		0.043	0.048	0.042	0.051	0.039
C.notatus		0.250	0.227	0.231	0.234	0.233	0.241	0.233	0.266	0.253	0.274	0.263	0.260	0.232	0.266	0.240	0.273		0.035	0.039	0.035	0.037
C.adamsi		0.262	0.281	0.315	0.269	0.270	0.262	0.291	0.270	0.288	0.344	0.253	0.305	0.273	0.276	0.275	0.284	0.217		0.029	0.031	0.030
C.nigrovittatus		0.268	0.260	0.252	0.247	0.248	0.253	0.303	0.257	0.277	0.347	0.231	0.261	0.261	0.267	0.247	0.266	0.255	0.179		0.022	0.026
C.prevostii		0.240	0.248	0.220	0.244	0.253	0.234	0.261	0.237	0.261	0.323	0.240	0.271	0.226	0.342	0.291	0.311	0.244	0.194	0.141		0.024
C.orestes		0.277	0.257	0.289	0.229	0.225	0.250	0.298	0.262	0.271	0.348	0.245	0.255	0.227	0.286	0.222	0.233	0.236	0.166	0.152	0.140	

(2017) for these genetic lineages (G**) to avoid confusions. For the cluster labelled E in Figs. 2 and 3 that combined predominantly samples from eastern China and northern Vietnam, where *C. finlaysonii* has never been recorded and only *C. erythraeus* has been found, we apply the name "genetic lineage *erythraeus*", irrespective of their appearance.

According to our results, specimen KP126037, identified as a *C. finlaysonii* in GenBank, is erroneously attributed. Our phylogeny shows that this lineage, similar to KP126038, should instead be referred to as *C. phayrei*. Notably, the considerable length of this branch indicates an old diversification event that is relatively contemporaneous with the separation of such species as *C. adamsi, C. nigrovittatus, C. prevostii,* and *C. orestes*. However, it seems that the assumption of Moore & Tate (1965) about its proximity to *flavimanus* was incorrect as the species was undoubtedly included into *inornatus*/*caniceps* group. More genetic data and inclusion of additional museum collections are required to clarify the level of variability of this taxon.

Phylogenetic relationships among the three *Callosciurus* morpha in Vietnam (*erythraeus*, *flavimanus,* and *griseimanus*) were very similar with Oshida et al., (2013), showing a polytomic phylogenetic relationship. Based on the transversional divergence rate at the third codon position of the cytochrome b gene sequence (Oshida et al., 2013), the overall p-distances (T3P) were between 8.25–9.04%. Genetic distances (*d*, T3P) between the main phylogenetic lineages calculated from the Cyt *b* gene are shown in Table 1.

The distances between groups G and E (0.095–0.150) were higher than the estimates of Oshida et al. (2007) that were obtained from a smaller sample size. Those authors evaluated the divergence time between *C. erythraeus cf. hendeei* (E2) and *C. e. griseimanus* (G10) as 1.6–1.8 million years ago (Ma) and between *C. erythraeus cf. hendeei* (E2) and *C. finlaysonii* (G6) as 1.9–2.1 Ma. Applying these estimates and taking into consideration the basal radiation of the Malayan and Sundaic group interval from 11.4 to 10.5 Ma, which marks the lowest pre-Pleistocene sea stand of the Cenozoic (de Graciansky et al., 1998; Haq et al., 1987) and coincides with the explosive diversification among tree squirrel genera in Indochina and the Sunda Shelf islands and the divergence of *Callosciurus* and *Dremomys*, we estimated the time of formation of the main phylogenetic lineages within *C. erythraeus* (E1–E3) as 1.21–1.43 Ma. The separation of the South Indochinese lineages G9–G10 (*griseimanus* in the interpretation of Oshida et al., 2013) from the rest of the *finlaysonii* lineages was approximately 1.60–1.89 Ma. Divergences among the eight *finlaysonii* lineages (G1–G8) were between 0.41 and 1.21 Ma.

The tree estimated based on the COI gene (Fig. 3) was less illustrative, since most of the currently known nucleotide sequences came from populations introduced in Europe and South America. At the same time, a significant number of individuals resulted in only a few unique haplotypes. However, the *finlaysonii/erythraeus* dichotomy was still recovered, corresponding to clusters D and E in the Cyt

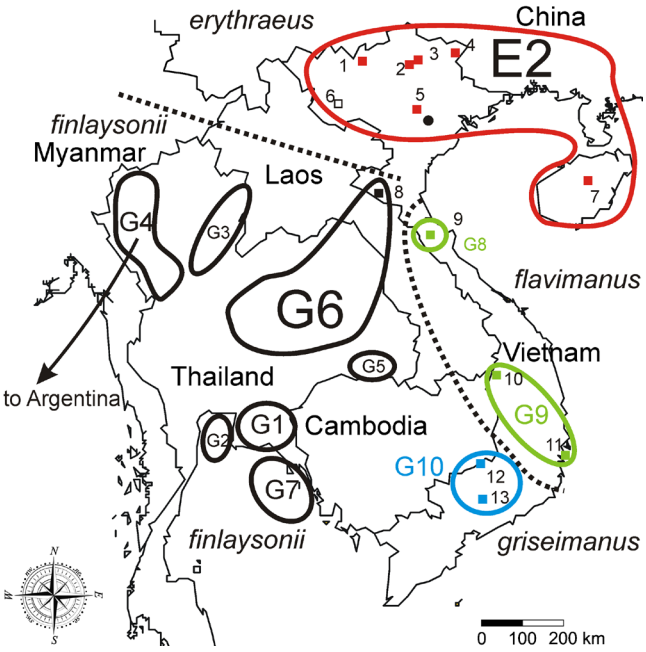

Fig. 4. Localities of genetically sampled materials and geographic distribution of the mtDNA lineages of *Callosciurus* in Indochina. Site numbers and direct locations are as indicated in Table 1 and Appendix 1 of Supplementary.

Footnote. About samples attributions see in Discussion section.

b tree. In each of these clusters, 4 to 7 internal groups were apparent. Unambiguous matching of these lineages to the Cyt *b* phylogeny was difficult due to the scarcity of overlapping samples, except for Argentinean ones, which obviously represented the G4 lineage. It should be noted that in Argentina, all introduced squirrels were morphologically identified as *C. e. thai* (Aprile & Chicco, 1999); however, the subspecies could also correspond to *C. e. atrodorsalis* (Cassini & Guichón, 2009). Variation in pelage colour has been described from the original site of introduction, in Luján, where individuals had the typical olive-brown agouti dorsal pelage with a black stripe on the back and reddish ventral colouration. However, squirrels with yellow-creamy underparts and no black stripe on their backs were also found (Cassini & Guichón, 2009). Gabrielli et al. (2014) showed high variability in pelage colour, including squirrels with a reddish ventral pelage and a black stripe on the back, others with yellow-creamy underparts and no black stripe on their backs, and intermediate variations such as reddish belly with yellow-creamy or orange chest, groin and/or genital area, and with or without a black stripe on the back. Regardless of such variability, the animals demonstrated a higher level of genetic homogeneity. Only one haplotype of COI was found in Argentina, which was phylogenetically closer to sequences of native *C. finlaysonii* from Thailand (G4 group) and particularly to the two haplotypes sampled in Japan that had been morphologically identified as *C. erythraeus* (Oshida et al., 2007). The same was true for Cyt *b* haplotypes derived from the same animals. The only haplotype found in Cañada de Gómez was closely related to *C. finlaysonii* (G4 group).

The RAG1 gene phylogeny was the most unresolved, with the *erythraeus/finlaysonii* groups forming a polytomy,

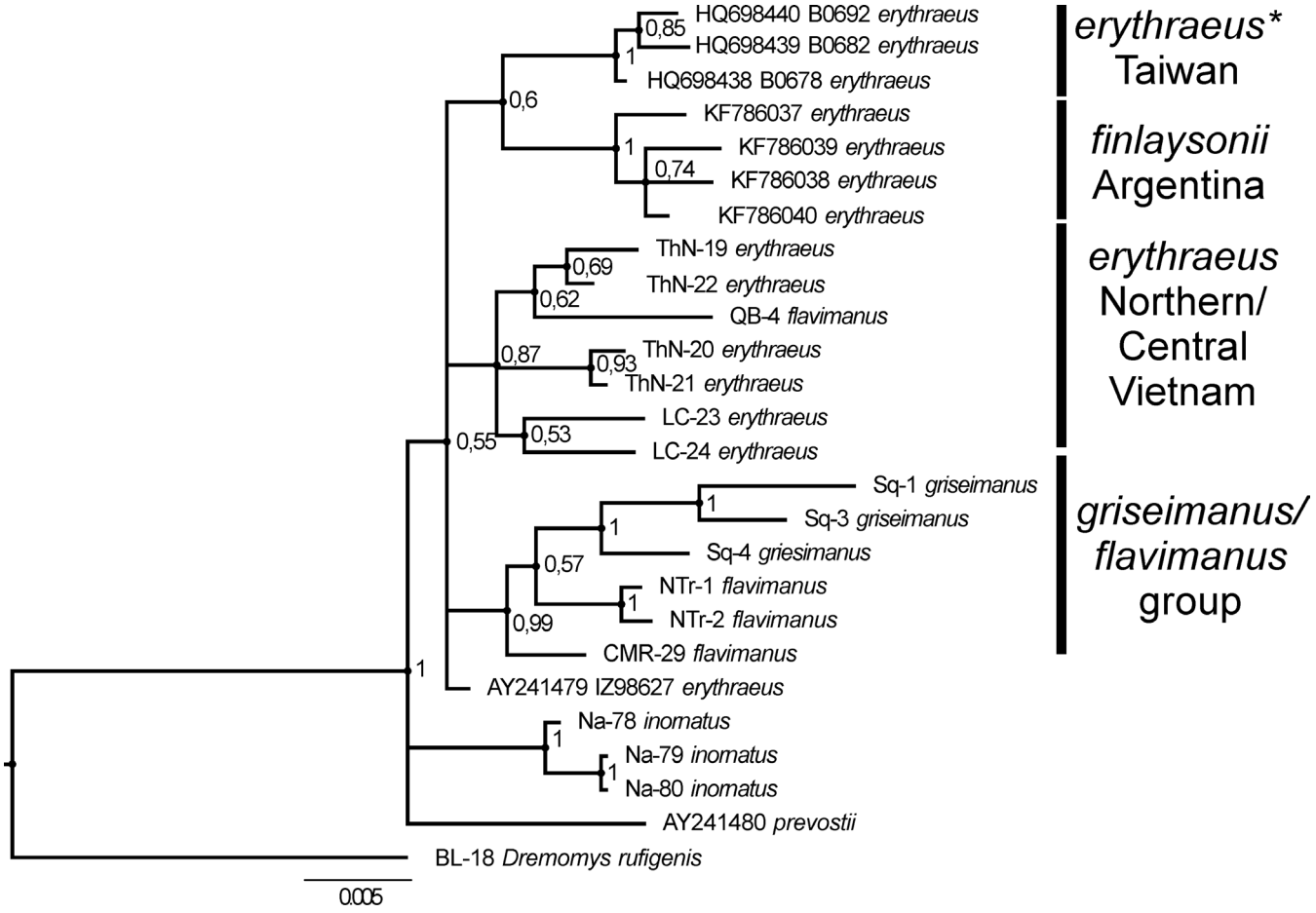

Fig. 5. The phylogenetic tree (RAG1, Bayesian inherence) for *Callosciurus* genetic lineage radiation. The posterior probabilities are presented at the nodes. The morphotype labels are in branch tips Branches length scale is in the bottom.

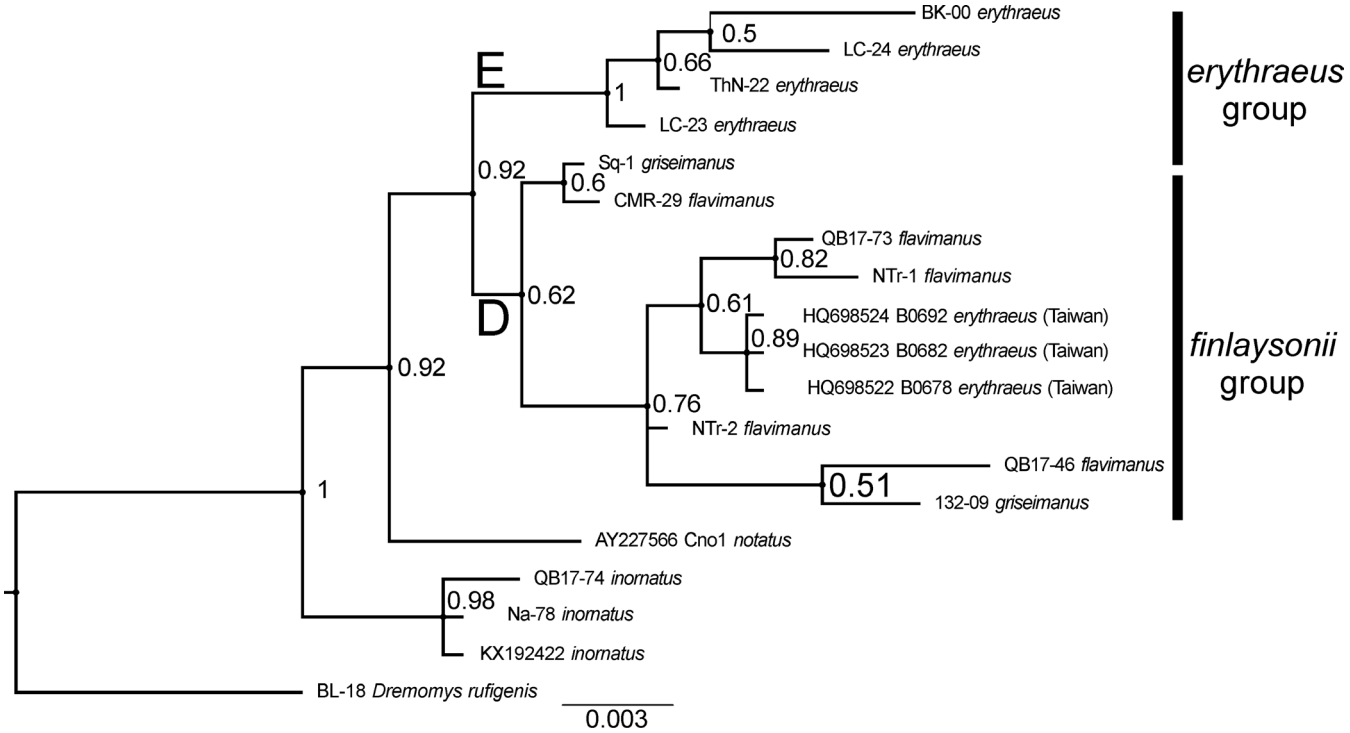

Fig. 6. The phylogenetic tree (IRBP, Bayesian inherence) for *Callosciurus* genetic lineage radiation. The posterior probabilities are presented at the nodes. The morphotype labels are in branch tips. Branches length scale is in the bottom.

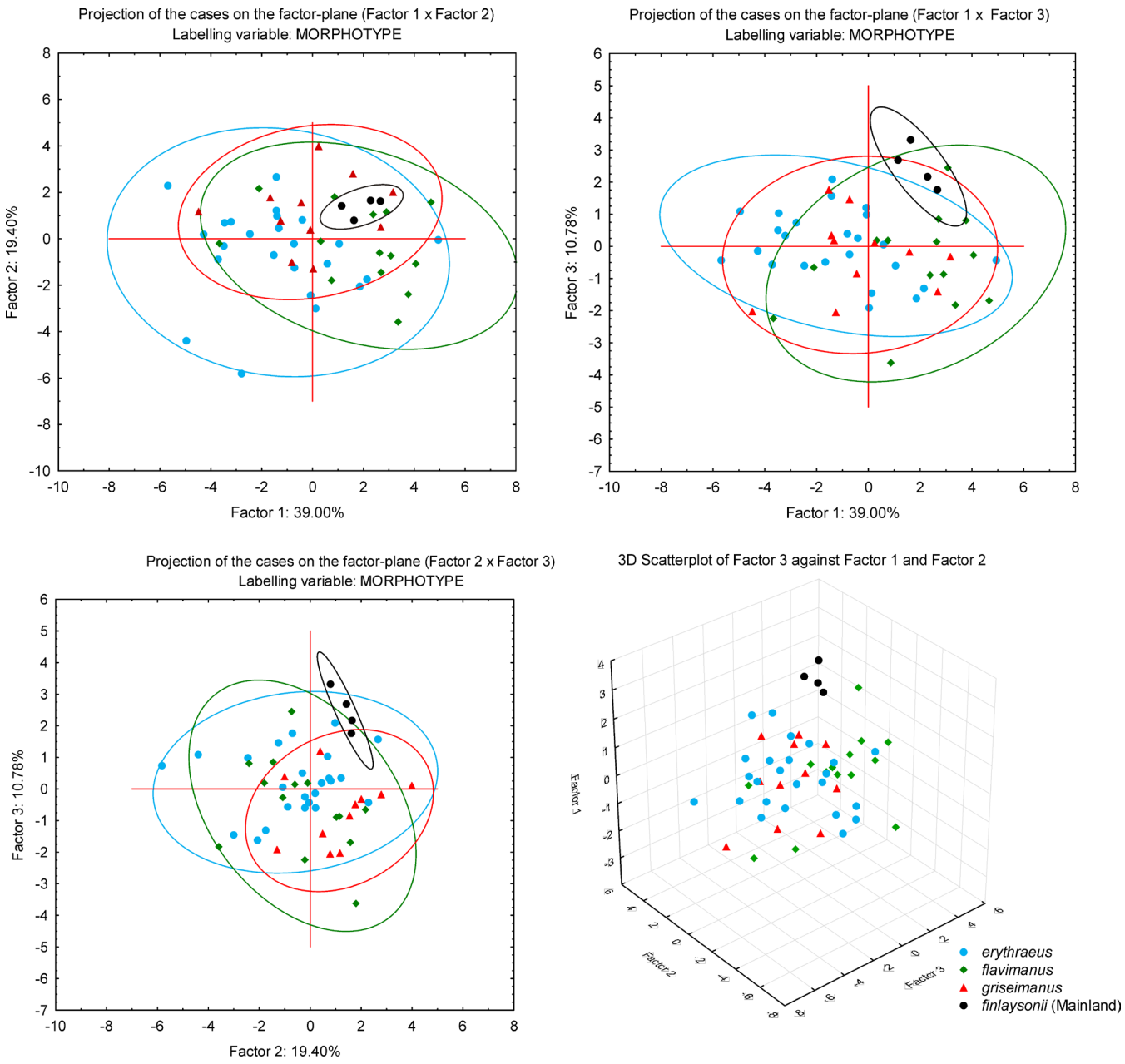

Fig. 7. Projection of the cases on the factor-plane in PCA factorial space. Only continental *C. erythraeus/finlaysonii* phenotypic morphae (*erythraeus*, *flavimanus*, *griseimanus*, *finlaysonii*) are included. Ellipses correspond to 95% reliability intervals.

presumably due to insufficient phylogenetic information (Fig. 5). However, even though the basal branching were polytomous, samples from Taiwan and Argentina, northern and central Vietnam, the *griseimanus/flavimanus* group, and one *erythraeus* sample of unknown geographical origin were distinguished as four independent clusters.

It is also unclear whether the hybrid origin of the Taiwanese population was supported. The use of an alternative nuclear marker, i.e., the IRBP gene provided slightly more clarity, with the basal split between the *erythraeus* and the *finlaysonii/griseimanus/flavimanus* group recovered with relatively high support (pp=0.92; Fig. 6).

Unexpectedly, the basal group was represented by *C. inornatus* samples, not Sundaic *C. notatus* (AY227566), if it was properly attributed. Although branch support for most terminal branches was low (pp=0.51–0.82), main clusters corresponding to Cyt *b* clusters D and E were recovered. All *flavimanus* and *griseimanus* samples fell into the cluster D, formed by individuals labelled by G8, G9, and G10 mitochondrial phylogenetic lineages of *finlaysonii*, whereas all samples from northern Vietnam formed an alternative cluster of the *erythraeus* group. The most surprising results were the samples from Taiwan, which are considered morphotypically *erythraeus* and bearing Cyt *b* haplotypes of the E1 group, but falling into the same cluster as *finlaysonii*.

Craniometrical analyses. Means, ranges, and standard deviations of the craniodental measurements and indices for three groups that were identified by the genetic analyses (*erythraeus, flavimanus,* and *griseimanus*) are given in Supplementary Table S2. As revealed by a t-test, specimens of the *erythraeus*, *finlaysonii*, *flavimanus,* and *griseimanus*

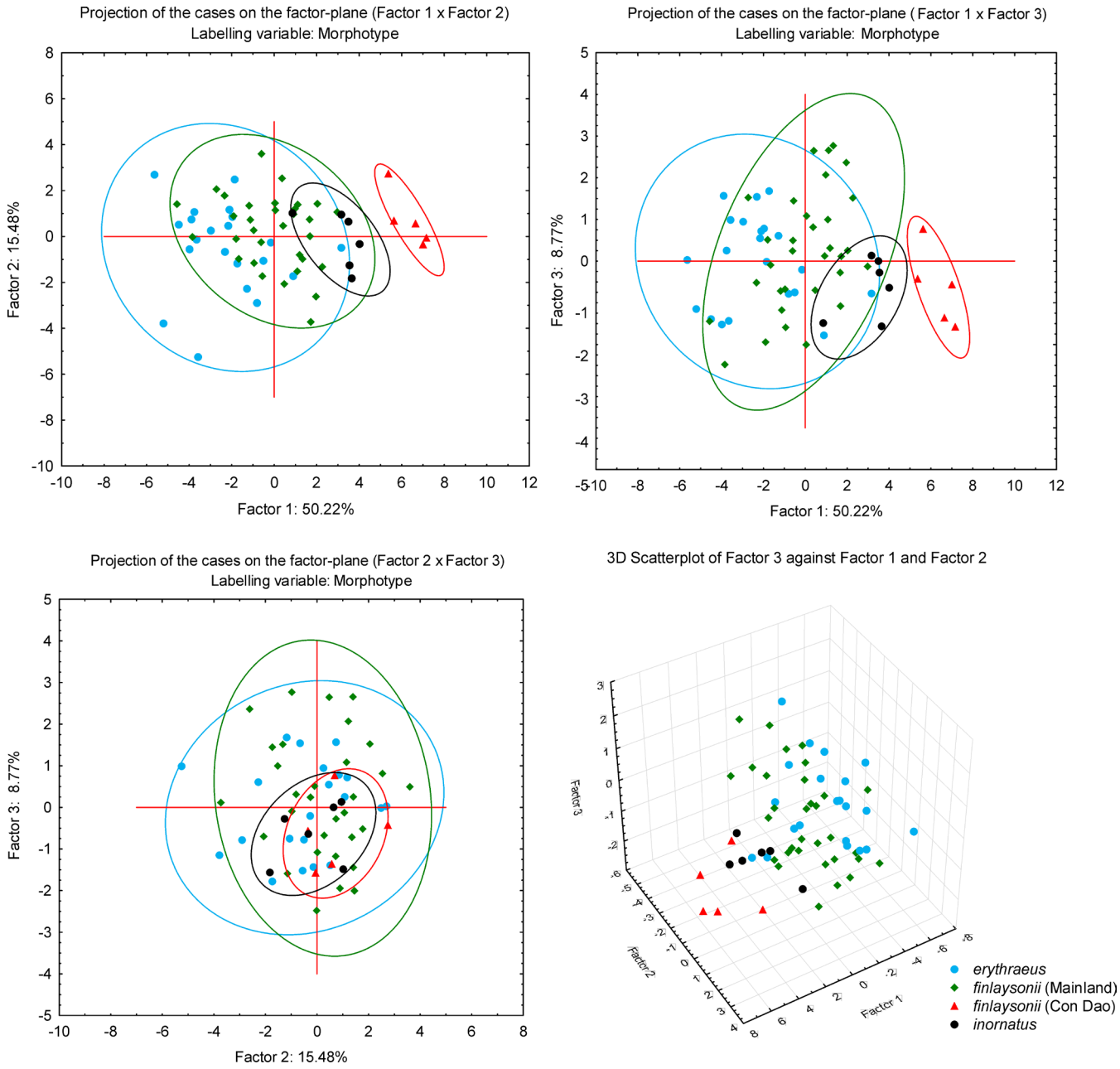

Fig. 8. Projection of the cases on the factor-plane in PCA factorial space. *C. inornatus* and *C. finlaysonii* from Con Dao island are included. Phenotypic morphae *flavimanus* and *griseimanus* are treated as *finlaysonii* and compared with phenotypic *erythraeus*. Ellipses correspond to 95% reliability intervals.

groups demonstrated significant variability within groups and significantly differed ($p<0.05$) from each other in 18 cranial characters, between one pair of groups at least. Overall, the northern populations were generally the largest in size and had significantly larger ZB, LD, LBP, BBP1, BBP3, LB and PL and significantly higher ILBP1, ILBP2, GCI, and PI, whereas the southern ones had significantly larger LD, LBP, BBP1, and SB and significantly higher in ILBP1, ILBP2, and GCI compared with central ones. We did not detect significant differences between any morphologically or genetically defined groups for six skull characters (BBC, IB, LIF, PPL, NL and HB) and five indices (IZB, IOB, OPI, IBH, GBI), which were excluded from the principal component analyses. By analysis optimisation, we also excluded three more characters, namely, PL, ILBP2, and GCI, from the final dataset to obtain the highest factor loadings and groups separation. The final analysis was performed with 18 characters and indices that demonstrated reliable differences between groups with two alternative grouping variables: in the first iteration, all morphotypes (*erythraeus, flavimanus, griseimanus,* and *finlaysonii*) were tested independently from each other, and in the second iteration, some of these groups were united together and compared with *C. inornatus*. Factor loadings and cumulative variance for the principal components in the PCA analysis are shown in Supplementary Table S3. Projections of the cases on the factor-plane in PCA factorial space for individual colouristic morpha are presented in Fig. 7.

All colouristic morpha demonstrated almost complete overlapping in factorial space despite significant differences between the subgroups shown by the t-tests. This could be

due firstly to the large range of skull size character variability (Supplementary Table S2) recorded for all groups and was also demonstrated for a number of populations (Chakraborty, 1985; Corbet & Hill, 1992; Li et al., 2006; Koyabu et al., 2009). The only group that showed slight separation was from a single Laotian population of *C. finlaysonii* (black circles; Fig. 7). This indicates low variability among populations. This observation impelled us to do a second round of analyses with alternative specimens' attributes, where all southern continental populations of *finlaysonii* sensu stricto, *flavimanus* and *griseimanus* were pooled together under the name *finlaysonii* and compared with *erythraeus* sensu stricto and *C. inornatus* (Fig. 8).

The latter assortment resulted in better segregation (Supplementary Table S3) although the extent of overlap remained significant. Two notable observations are *C. finlaysonii* specimens from Con Dao Island, which were obviously segregated from the other specimens along the first axis, forming an independent cluster. Due to the animal's smaller size, it tends to be closer to *C. inornatus*, though, as demonstrated by paired t-test, they significantly differed in almost all craniodental characters investigated here. Bearing in mind recent new species findings in offshore islands of southern Indochina (Nguyen et al., 2018), special attention should be given to the Con Dao squirrel population. Nevertheless, samples of northern *erythraeus* populations still cannot be confidently separated morphologically from southern continental *flavimanus, griseimanus,* and *finlaysonii* populations according to the skull characters analysed, which underscores the high level of morphological variability within the *C. erythraeus/finlaysonii* group.

A canonical analysis was applied using the same variables as applied for PCA to reduce the high dispersion of intragroup characters and shrink the samples around groups centroids, which resulted in better separations in 3D-root space (Fig. 9). The canonical analysis revealed statistically significant group centroid separation, indicating that the groups may be separated by applied statistical approaches. The final model provides a high resolution with respect to group identification (Wilks's lambda F (6.359) = 5.27, $p < 0.001$). It is notable also that all but one specimen was correctly assigned. This sole incorrect specimen was exactly Na18-92 (ZMMU S-200613) individual from Nghe An province, Vietnam (Fig. 9) misassigned to *erythraeus* morphotype group rather than to any *finlaysonii* associated groups where it should be placed based on its genetic attribution (G6 mitochondrion lineage). This specimen may well be hybrid origin of any generation, unfortunately, we cannot test it directly. Special surveys are desirable to perform in Nghe An province specially aimed to *C. erythraeus*/*C. finlaysonii* possible hybridisation at contact zone.

Thus, analysis indicates that in spite of higher levels of individual variability and, in many cases, similar patterns of variability within populations of these closely related *Callosciurus* species, they can be reliable segregated by discriminant analyses. However, this segregation reflects the morphological originality of local populations rather than

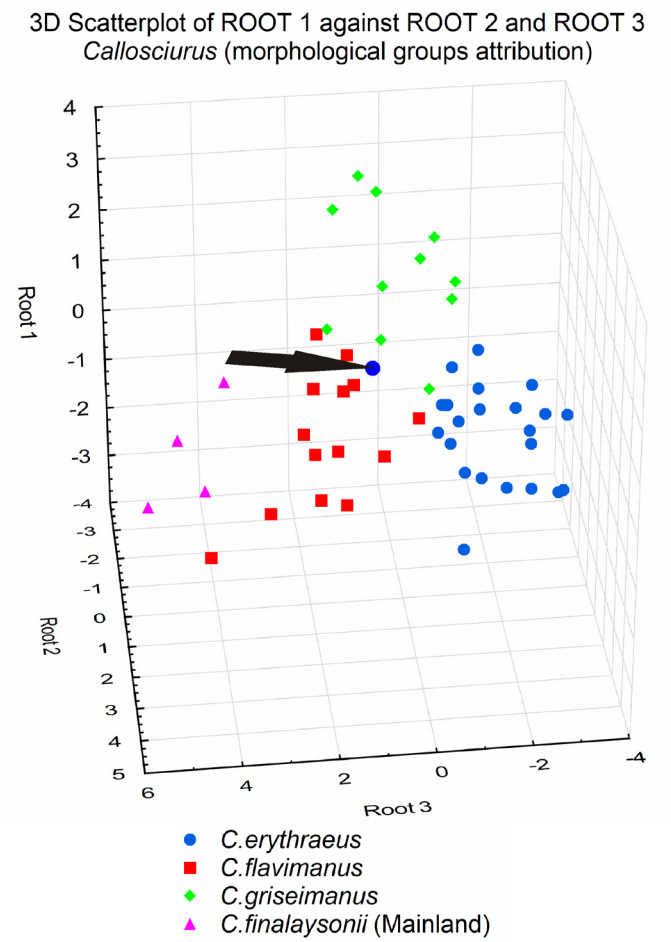

Fig. 9. Projection of the cases in DFA factorial space. Only continental *C. erythraeus/finlaysonii* phenotypic morpha (*erythraeus*, *flavimanus*, *griseimanus*, *finlaysonii*) included. Specimen Na18-92 labeled by arrow.

species peculiarities as a whole, since, as we can see from the example of *flavimanus*, morphotypes may not correspond to any monophyletic genetic lineages.

DISCUSSION

Variability. The *Callosciurus finlaysonii/erythraeus* group as currently understood, shows a complex phylogeographic pattern as elucidated by genetic and morphological data. Both for its native area in general (at least in the investigated part of it) and in eastern Indochina in particular, it is not possible to unambiguously match well-distinguished phenotypic morphae and genetic lineages distributed in the respective populations. Even the mitochondrial phylogeny, which is currently the most representative in terms of geographic sampling and robust in terms of statistical support, does not unambiguously correspond to the distribution pattern of historically described subspecies both for *C. finlaysonii* and *C. erythraeus*. For the phylogeny based on nuclear genes, the data currently available are still deficient and give ambiguous results due to slower evolving nuclear genome. As we demonstrate here, the IRBP gene may be a promising genetic marker to provide clarification for relationships and taxa limits within the genus *Callosciurus*. However, this will require more data from the entire natural range

of *Callosciurus*, especially among the westernmost and northernmost populations.

The variability of cranial characteristics and size of the skull may even exceed the variability in pelage colouration. Even though published material on cranial measurements is based on individual and geographically limited studies, these measurements show large variations and are not appropriate to determine a systematic size gradient across the specific and subspecific ranges (Lurz et al., 2013). Thus, the general range of variation of greatest skull length (ONL) for *C. erythraeus* may exceed 20% (48—57 mm. and a number of cranial characters vary considerably (Chakraborty, 1985; Corbet & Hill, 1992; Li et al., 2006; Koyabu et al., 2009).

Our data demonstrate that taxonomical boundaries cannot be drawn solely on the basis of morphology, either of pelt colouration or craniometrical characteristics, since both species show the highest level of polymorphism in most or a large part of the natural range. A black and tan colour morph was known within *Callosciurus* long ago (Gray, 1867), which is usually caused by a specific mutation of the agouti locus. The genetic basis of melanistic phenotypes has been investigated for several species of arboreal squirrels (McRobie et al., 2009, 2014). Melanistic morpha in squirrels are associated with the melanocortin-1 receptor (MC1R) gene, but in cases where colour variations are as prominent as seen within *Callosciurus*, several other genes besides MC1R may be involved in colouration polymorphism (McRobie et al., 2014). This topic for natural populations of *Callosciurus* is still far for being sufficiently explored.

Taxonomical implications. On the basis currently available data, some important conclusions can be made regarding the relationships and taxonomic composition of *Callosciurus*. First of all, *C. inornatus* forms a fairly dense homogeneous cluster sister to *C. caniceps*. Oshida et al. (2001, 2011) stressed that *C. caniceps* and *C. inornatus* were divided by the Mekong River in the northern Indochina. As was first demonstrated by Boonkhaw et al. (2017) in Thailand, the *C. caniceps* species group (*C. c. caniceps, C. c. concolor, C. phayrei,* and *C. inornatus*) is clearly distinct from *C. erythraeus* and *C. finlaysonii*. However, from our data, intragroup genetic distances (*d*, T3P = 0.0132±0.0034) and branch length in the *C. inornatus* Cyt *b* cluster are significantly shorter than in clusters of the *C. erythraeus* and *C. finlaysonii* groups (Tajima relative test value, F=5.86). This may indicate that the colonisation of the territories currently inhabited by these species did not occur simultaneously. We may assume more recent *C. inornatus* expansion to eastern Indochina, by which time the region was probably already inhabited by congeneric populations.

Clear genetic segregation is also evident within the *Callosciurus erythraeus/finlaysonii* group accompanied by high polymorphism of morphological characters and colour patterns for both species. This is further complicated by incongruence between genetic and morphological variability due to possible hybridisation. This discordance indicates that intraspecific taxonomy that is solely based on pelt colouration is inadequate and does not provide a sound basis for taxa attribution. The phenotypic morpha of *flavimanus* and *griseimanus* are undoubtedly genetically related to *C. finlaysonii*, not to *C. erythraeus*, as was generally accepted for a long time. However, as we demonstrated, *flavimanus* is not a monophyletic group; instead, it is represented by at least two non-sister lineages clustered together with other genetic lineages of *C. finlaysonii* sensu stricto, most of them distributed in Thailand. From this perspective, the names of *flavimanus* and *griseimanus* may be regarded as junior synonyms of *C. finlaysonii*, and not *C. erythraeus* (ICZN, 1999) as previously suggested (Ellerman & Morrison-Scott, 1951; Moore & Tate, 1965). The distribution of these taxa in eastern Indochina in general terms corresponds to the map of subspecies distribution presented by Moore & Tate (1965) and reproduced by Lurz et al. (2013) with the limits between *C. e. hendeei* and *C. finlaysonii* morphus *flavimanus* situated close to 18°N. However, it was also demonstrated that at least fourteen subspecies/colouristic morpha of *C. finlaysonii* distributed in Thailand can be divided into at least eight genetic groups (G1–G8), with no agreement with their morphological attributions. Moreover, the G4 group may be treated as *C. erythraeus* proper based on its agouti pelage colouration. Phylogenetic analyses demonstrated 4 distinct mtDNA phylogroups (northern, western, southern, and eastern) of the phenotypical *C. erythraeus* that inhabit Taiwan.

Geographical variation of *C. erythraeus* in Taiwan on the basis of pelage patterns was reported by Horikawa (1932). Based on the ventral pelage patterns, he classified *C. erythraeus* into 3 subspecies (*thaiwanensis, roberti,* and *centralis)*, which together were treated under the same name, *C. flavimanus thaiwanensis* by Moore & Tate (1965) and were adopted under *C. e. erythraeus* by Jones et al. (1971) and Corbet & Hill (1992). A similar situation was found by Oshida et al. (2006) in Taiwan, however, haplotype variation was not always associated with the pelage variation. Thus, the taxonomic status and origin of the Taiwanese population (and Japanese ones, which most likely descended from it) needs special consideration. It tends to be related to *finlaysonii*, not the *erythraeus* group, as inferred by nuclear markers. It may be that *C. finlaysonii* (including *flavimanus* or *griseimanus* morpha from southern Indochina) was introduced to the island in early historical times. In this case, the *finlaysonii/erythraeus* polymorphism of nuclear genes is expected in the Taiwanese population.

On the appropriateness of subspecies for this species complex. Despite limitations and misuse of the subspecies concept, particularly in the early 20th century, several leading evolutionary biologists (Mayr, 1982; Crusz, 1986; Avise, 1989; Mallet, 1995; Moritz, 2002) and conservation biologists (Haig et al., 2006) are in favour of subspecies as taxonomical units. Subspecies represent a lower valid unit of biological organisation, which is also relevant in biodiversity conservation (Ryder, 1986; Avise, 1989; Haig et al., 2006). However, a number of taxonomic and conservation problems associated with mammalian subspecies have been reviewed (Stanford, 2001; Gippoliti & Amori, 2007) in recent decades.

O'Brien & 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. However, as seen, in our case, the second and third conditions are not explicitly satisfied, i.e. morphotypes are not monophyletic. There is no concordance between phenotypic characters and phylogeography, and preliminary results suggest that gene flow may be present between some morphae and that some of them even have a hybrid origin. Therefore, we consider it inappropriate to apply the category of subspecies within the complex *C. erythraeus/finlaysonii.* In this situation, it seems that all the *finlaysonii/erythraeus* subspecies (including *griseimanus*) previously described from east and south Indochina should be regarded as invalid. In consideration of their appropriateness, the names used now for the subspecies should not be further applied for taxonomy but only to refer to colour morphae. The question of the appropriateness of nomena for taxa allocated for western and northern populations (in easternmost India and Myanmar especially and Chinese ones) requires additional clarification and wider investigations.

Phylogeography and recent mammalian fauna formation in Indochina. From a phylogeographic point of view, the current distribution pattern of genetic lineages suggests that east Indochina was populated by *Callosciurus* (*C. finlaysonii*, and later by *C. inornatus*) populations in the Pleistocene from the south and west, not from the north (Yunnan and Guanxi) where related genetic lineages extend south no further than 18°N. This is also true for some rodents such as species of *Leopoldamys* (Balakirev et al., 2013) and *Dremomys* (unpublished data). It has been suggested that major rivers may have shaped allopatric patterns of squirrel species and subspecies distribution (Oshida et al., 2001, 2011). For example, the observed distribution of *C. erythraeus* in Myanmar may be explained by barriers such as the Irrawaddy River, where *C. e. sladeni* was reported to oppose *C. flavimanus gordoni* and *C. f. shanicus* (Moore & Tate, 1965 p. 121). The Mekong River as a geographical barrier for speciation within *Callosciurus* has been specifically stressed because *C. caniceps* and *C. inornatus* were divided by this river in northern Indochina (Oshida et al., 2011). The same is true for a number of subspecies of *C. pygerythrus* (Geoffroy Saint-Hilaire, 1831) divided by the Irrawady, Brahmaputra, and Chindwin Rivers (Moore & Tate, 1965). A phylogeographic study by Oshida et al. (2006) suggested that arboreal animals such as squirrels may also show phylogeographic differentiation by mountain ranges (in Taiwan) because their dispersal is restricted to forest environments. However, as discussed above, haplotype variation was not always associated with pelage variation, indicating that intraspecific taxonomy built based on pelt colouration pattern for this species is not appropriate. Based on the most recent and wide-ranging phylogeographic data, this presumption about evident geographic barriers is only true for the *caniceps* group and not for the *C. finlaysonii/erythraeus* group, where the high levels of colour polymorphism hampers specific taxonomic attribution.

There are many small islands off the coast of southern Indochina in the Gulf of Siam, on which a number of endemic mammal and specific morpha may be found (Abramov et al., 2008; Nguyen et al., 2018). These islands were part of the mainland and have been isolated as water levels rose following deglaciations (Tjia, 1980; MacKinnon et al., 1996). The fact that significant portions of the *C. finlaysonii* populations inhabiting central and eastern Indochina acquired distinct colour pattern (several dozen patterns of colour morpha) instead of the original (most probably agouti) colouration may have originated from the fragmentation of the natural area into a number of small isolated populations during the Late Pleistocene glacial processes (climate oscillations) in the Sunda region, both into islands and at the mainland. Continuous forested cover in Indochina existed during a considerable period of the Plio- and Pleistocene (Meijaard & Groves, 2006), but substantial forest contraction is supposed to have occurred during the last glacial periods, as evidenced in Peninsular Malaysia and Palawan (Wurster et al., 2010). Gathorne-Hardy et al. (2002) and Cranbrook (2000) stressed that most areas in this region were covered with savannah vegetation during long periods of the Quaternary, whereas Raes et al. (2014) demonstrated that Dipterocarp rainforests persisted in Sundaland during glacial maxima. Thus, considerable oscillations of vegetation coverage actually happened repeatedly in the region during Pleistocene. Finally, one cannot exclude the possibility of the influence of the areal fragmentation over historical time when small patches of forests are currently interrupted by the huge deforested areas by human activity during the last two millennia, as is the case in central Thailand, Korat Plateau, and Cambodia. These events are thought to have contributed to autogenetic processes (genetic drift and founder effect), resulting in considerable morphological changes. This assumption is confirmed by the fact that most of the colouristic morphae are actually distributed in the territories subjected to multiple transgression of forests coverage and some adjacent territories (coastal zone). In addition, we can see the same processes in recent insular populations on the islands of the South China Sea and the Gulf of Siam (Kuznetsov, 2000; our observation), which are almost universally inhabited by squirrels, demonstrating special, unique pelt colouration patterns. On the other hand, the northern continental and highlands populations apparently did not undergo a similar process to the same extent and in many cases retained the original agouti type of colouration. In the zones of secondary contact of populations that were subjected and not subjected to insularisation (for example in the mountainous regions of Thailand), it is possible that both the formation of genetic polymorphism in hybrid populations and the occurrence of secondary polymorphism of colouration patterns and restoration of the wild-type colouration occurred.

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SUPPLEMENTARY MATERIAL

Table S1. List of specimens used for phylogenetic analyses: species and samples name (as it presented in Figures), phenotypic morpha, geographic location and GenBank accession numbers.

Samples	Genetic Species/ Lineage	Phenotypic Morpha	Locality	Genes			
				mtDNA		nDNA	
				Cyt b	COI	RAG1	IRBP
Original Materials							
ThN-19	E2 erythraeus	erythraeus	4	MK256799		MK256872	
ThN-20	E2 erythraeus	erythraeus	4	MK256800		MK256873	
ThN-21	E2 erythraeus	erythraeus	4	MK256801		MK256874	
ThN-22	E2 erythraeus	erythraeus	4	MK256802		MK256875	MK256852
CMR-29	G9 finlaysonii	flavimanus	10	MK256803		MK256868	MK256858
Sq-1	G10 finlaysonii	griseimanus	13	MK256804		MK256863	MK256856
Sq-3	G10 finlaysonii	griseimanus	13	MK256805		MK256864	
Sq-4	G10 finlaysonii	griseimanus	13	MK256806		MK256865	
LC-23	E2 erythraeus	erythraeus	1	MK256808		MK256876	MK256854
LC-24	E2 erythraeus	erythraeus	1	MK256809		MK256877	MK256855
NTr-1	G9 finlaysonii	flavimanus	11	MK256810		MK256866	MK256859
NTr-2	G9 finlaysonii	flavimanus	11	MK256811		MK256867	MK256860
QB-4	G8 finlaysonii	flavimanus	9	MK256812		MK256878	
QB-5	G8 finlaysonii	flavimanus	9	MK256813			
QB-46	G8 finlaysonii	flavimanus	9	MK256814	MK256847		MK256850
QB-73	G8 finlaysonii	flavimanus	9	MK256815	MK256848		MK256851
BK-00	E2 erythraeus	erythraeus	3				MK256853
BK-35	E2 erythraeus	erythraeus	3	MK256816			
BK-36	E2 erythraeus	erythraeus	3	MK256817			
BK-37	E2 erythraeus	erythraeus	3	MK256818			
BK-58	E2 erythraeus	erythraeus	3	MK256819			
BK-59	E2 erythraeus	erythraeus	3	MK256820			
BK-60	E2 erythraeus	erythraeus	3	MK256821			
BK-68	E2 erythraeus	erythraeus	3	MK256822			
132-09	G10 finlaysonii	griseimanus	12	MK256807	MK256846		MK256857
Na18-92	G6 finlaysonii	erythraeus	8	MK256829	MK256839		
TQ-5	E2 erythraeus	erythraeus	2	MK256832	MK256842		
TQ-9	E2 erythraeus	erythraeus	2	MK256833	MK256843		
TQ-10	E2 erythraeus	erythraeus	2	MK256834	MK256844		
TQ-21	E2 erythraeus	erythraeus	2	MK256835			
TQ-139	E2 erythraeus	erythraeus	2	MK256836	MK256845		
Na-78	inornatus	inornatus	8	MK256823		MK256869	MK256861
Na-79	inornatus	inornatus	8	KX171248		MK256870	
Na-80	inornatus	inornatus	8			MK256871	
Na18-59	inornatus	inornatus	8	MK256824	MK256837		
Na18-64	inornatus	inornatus	8	MK256825			
Na18-73	inornatus	inornatus	8	MK256826			
Na18-74	inornatus	inornatus	8	MK256827			
Na18-77	inornatus	inornatus	8	MK256828	MK256838		
Na18-98	inornatus	inornatus	8	MK256830	MK256840		
Na18-99	inornatus	inornatus	8	MK256831	MK256841		
QB-74	inornatus	inornatus	9		MK256849		MK256862
Involved Materials							
CG11	G4 finlaysonii	erythraeus	Ar		KF856212	KF786037	
CU23	G4 finlaysonii	erythraeus	Ar		KF856213		
CU24	G4 finlaysonii	erythraeus	Ar		KF856214		
CU27	G4 finlaysonii	erythraeus	Ar		KF856229	KF786038	
CU29	G4 finlaysonii	erythraeus	Ar		KF856230		
CU30	G4 finlaysonii	erythraeus	Ar		KF856215	KF786039	

Samples	Genetic Species/ Lineage	Phenotypic Morpha	Locality	Genes			
				mtDNA		nDNA	
				Cyt b	COI	RAG1	IRBP
EMiB	G4 finlaysonii	erythraeus	Ar		KF856233	KF786040	
IZ 98627		erythraeus				AY241479	
B0678	E1 erythraeus	erythraeus	Tw	HQ698358		HQ698438	HQ698522
B0682	E1 erythraeus	erythraeus	Tw	HQ698359		HQ698439	HQ698523
B0692	E1 erythraeus	erythraeus	Tw	HQ698360		HQ698440	HQ698524
NC025550		erythraeus		NC025550	NC025550		
KM502568		erythraeus			KM502568		
EMiA	G4 finlaysonii	erythraeus	Ar		KF856232		
EMiC	G4 finlaysonii	erythraeus	Ar		KF856231		
CG13	G4 finlaysonii	erythraeus	Ar		KF856228		
CG18	G4 finlaysonii	erythraeus	Ar	KF786041	KF856227		
CG19	G4 finlaysonii	erythraeus	Ar		KF856226		
CG20	G4 finlaysonii	erythraeus	Ar		KF856225		
EMi4	G4 finlaysonii	erythraeus	Ar		KF856211		
EMi37	G4 finlaysonii	erythraeus	Ar		KF856224		
EMi38	G4 finlaysonii	erythraeus	Ar		KF856223		
EMi71	G4 finlaysonii	erythraeus	Ar		KF856222		
EMi63	G4 finlaysonii	erythraeus	Ar		KF856221		
EMi55	G4 finlaysonii	erythraeus	Ar		KF856220		
EMiD	G4 finlaysonii	erythraeus	Ar		KF856219		
EMi39	G4 finlaysonii	erythraeus	Ar		KF856218		
EMi34	G4 finlaysonii	erythraeus	Ar		KF856217		
EMi32	G4 finlaysonii	erythraeus	Ar		KF856216		
KY117539	G6 finlaysonii	finlaysonii	Th	KY117539			
KY117540	finlaysonii	finlaysonii	Th	KY117540			
KY117538	G4 finlaysonii	erythraeus	Th	KY117540			
LN899446	G4 finlaysonii	erythraeus	Ch		LN899446		
LN899445	G4 finlaysonii	erythraeus	Ch		LN899445		
LN899444	E*	erythraeus	Fr		LN899444		
LN899443	E*	erythraeus	Fr		LN899443		
LN899442	E*	erythraeus	Fr		LN899442		
LN899441	E*	erythraeus	Fr		LN899441		
LN899440	E*	erythraeus	Fr		LN899440		
LN899439	E*	erythraeus	Fr		LN899439		
LN899438	E**	erythraeus	Bg		LN899438		
LN899437	E**	erythraeus	Bg		LN899437		
LN899436	E**	erythraeus	Bg		LN899436		
LN899435	E**	erythraeus	Bg		LN899435		
LN899434	E**	erythraeus	Bg		LN899434		
LN899433	E**	erythraeus	Bg		LN899433		
LN899432	E**	erythraeus	It		LN899432		
LN899431	E**	erythraeus	It		LN899431		
LN899430	E**	erythraeus	It		LN899430		
LN899429	E**	erythraeus	It		LN899429		
LN899428	G6 finlaysonii	finlaysonii	It		LN899428		
LN899427	G6 finlaysonii	finlaysonii	It		LN899427		
LN899426	G6 finlaysonii	finlaysonii	It		LN899426		
LN899425	E**	erythraeus	It		LN899425		
HM031935	E2 erythraeus	erythraeus	Hn		HM031935		
HM031934	E2 erythraeus	erythraeus	Hn		HM031934		
HM031933	E2 erythraeus	erythraeus	Hn		HM031933		
HM031932	E2 erythraeus	erythraeus	Hn		HM031932		
AB716958	G10 griseimanus	griseimanus	14	AB716958			
AB716960	G10 griseimanus	griseimanus	14	AB716960			
AB716961	G10 griseimanus	griseimanus	14	AB716961			

Samples	Genetic Species/ Lineage	Phenotypic Morpha	Locality	Genes			
				mtDNA		nDNA	
				Cyt b	COI	RAG1	IRBP
AB716962	G10 griseimanus	griseimanus	14	AB716962			
AB043876	E1 erythraeus	erythraeus		AB043876			
AB499908	E2 erythraeus	erythraeus	5	AB499908			
AB499909	E2 erythraeus	erythraeus	5	AB499909			
AB499910	E2 erythraeus	erythraeus	Th	AB499910			
KM502568	E3 erythraeus	erythraeus	Ch	KM502568			
C1	E1 erythraeus	erythraeus	Jp	LC101272			
C2	E1 erythraeus	erythraeus	Jp	LC101273			
C3	E1 erythraeus	erythraeus	Jp	LC101274			
C4	G4 finlaysonii	erythraeus	Th	LC101275			
C5	G4 finlaysonii	erythraeus	Th	LC101276			
C6	G4 finlaysonii	finlaysonii	Th	LC101277			
C7	G4 finlaysonii	erythraeus	Th	LC101278			
C8	G1 finlaysonii	finlaysonii	Th	LC101279			
C9	G3 finlaysonii	finlaysonii	Th	LC101280			
C10	G3 finlaysonii	finlaysonii	Th	LC101281			
C11	G3 finlaysonii	finlaysonii	Th	LC101282			
C12	G1 finlaysonii	finlaysonii	Th	LC101283			
C13	G1 finlaysonii	finlaysonii	Th	LC101284			
C14	G1 finlaysonii	finlaysonii	Th	LC101285			
C15	G1 finlaysonii	finlaysonii	Th	LC101286			
C16	G1 finlaysonii	finlaysonii	Th	LC101287			
C17	G1 finlaysonii	finlaysonii	Th	LC101288			
C18	G2 finlaysonii	finlaysonii	Th	LC101289			
C19	G2 finlaysonii	finlaysonii	Th	LC101290			
C20	G2 finlaysonii	finlaysonii	Th	LC101291			
C21	G5 finlaysonii	finlaysonii	Th	LC101292			
C22	G6 finlaysonii	finlaysonii	Th	LC101293			
C23	G6 finlaysonii	finlaysonii	Th	LC101294			
C24	G6 finlaysonii	finlaysonii	Th	LC101295			
C25	G6 finlaysonii	finlaysonii	Th	LC101296			
C26	G6 finlaysonii	finlaysonii	Th	LC101297			
C27	G6 finlaysonii	finlaysonii	Th	LC101298			
C37	G4 finlaysonii	erythraeus	Th	LC192444			
C38	G2 finlaysonii	finlaysonii	Th	LC192445			
C39	G2 finlaysonii	finlaysonii	Th	LC192446			
C40	G2 finlaysonii	finlaysonii	Th	LC192447			
C41	G2 finlaysonii	finlaysonii	Th	LC192448			
C42	G6 finlaysonii	finlaysonii	Th	LC192449			
C43	G7 finlaysonii	finlaysonii	Th	LC192450			
C44	G7 finlaysonii	finlaysonii	Th	LC192451			
C45	G7 finlaysonii	finlaysonii	Th	LC192452			
AB043878	G6 finlaysonii	finlaysonii		AB043878			
AB499911	G6 finlaysonii	finlaysonii	Th	AB499911			
KX192422	inornatus	inornatus					KX192422
AB499905	inornatus	inornatus	6	AB499905			
AB499906	inornatus	inornatus	6	AB499906			
AB499907	inornatus	inornatus	6	AB499907			
AB499918	caniceps		Ml	AB499918			
AB499919	caniceps		Ml	AB499919			
AB043875	caniceps		Ml	AB043875			
C28	caniceps		Th	LC101299			
AY227566	notatus						AY227566
KY117542	notatus			KY117542	KY117542		
KY117541	notatus			KY117541	KY117541		

Samples	Genetic Species/ Lineage	Phenotypic Morpha	Locality	Genes			
				mtDNA		nDNA	
				Cyt b	COI	RAG1	IRBP
HM102291	notatus				HM102291		
JF444286	notatus		Br		JF444286		
AB499912	notatus		Ml	AB499912			
AB499913	notatus		Ml	AB499913			
AB499917	nigrovittatus		Ml	AB499917			
AB043882	nigrovittatus		Ml	AB043882			
AB499916	nigrovittatus		Ml	AB499916			
AY241480	prevostii					AY241480	
KY117543	prevostii			KY117543	KY117543		
JF459623	prevostii				JF459623		
AB499914	prevostii		In	AB499914			
AB499915	prevostii		In	AB499915			
AB043879	prevostii			AB043879			
AB043880	prevostii			AB043880			
KP126056	prevostii		Ml	KP126056			
KP126037	phayrei		Mr	KP126037			
KP126038	phayrei		Mr	KP126038			
KR911800	adamsi		Br	KR911800	KR911800		
JF444287	orestes		Br		JF444287		
KP126036	orestes			KP126036			
BL-18	*D. rufigenis*		Vn	KX171237	KX171261	KX171268	KX171253

Footnotes: Phenotypic morpha *finlaysonii* applied for any colour morpha except for wild type dark-feet agouti-dorsum colouration which attributed to phenotypic morpha *erythraeus*; *griseimanus* and *flavimanus* phenotypes applied for animals whose exterior are in agreement with corresponding taxa description; locality number as indicated in Appendix 1 of the Supplementary and Fig. 1, Ar=Argentina, Fr=France, It=Italy, Bg=Belgium, Ch=Mainland China, Hn=Hainan, Tw=Taiwan, Jp=Japan, Ml=Malaysia (peninsular), Br=Borneo, In=Indonesia, Vn=Vietnam, Mr=Myanmar, Th=Thailand, see the GenBank reference information for precise location.

Table S2. Descriptive statistics (mean, range, standard deviation) for skull measurements (mm) and cranial indices of adult *Callosciurus* specimens originating from Eastern Indochina. Filed by gray characters were used for principal components analyses (PCA).

	C. erythraeus					*C. flavimanus*					*C. griseimanus*					*C. finlaysonii*					*C. inornatus*				
	N	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**
ONL	24	54.32	50.50	57.86	1.686	14	53.12	50.95	57.29	1.981	11	53.76	52.02	55.92	1.322	9	49.79	46.00	53.80	3.334	6	49.76	48.91	50.56	0.646
BBC	24	24.40	22.10	25.60	0.925	14	24.20	22.93	26.63	0.979	11	24.03	23.10	25.39	0.707	9	22.41	21.41	23.52	0.701	7	23.25	22.82	23.92	0.448
HBC	24	17.11	15.81	18.52	0.576	14	16.83	16.19	17.30	0.381	11	16.78	16.10	17.62	0.548	9	15.77	15.10	16.88	0.596	7	16.56	16.26	17.30	0.360
ZB	24	32.10	29.31	34.29	1.236	14	31.27	29.83	33.63	1.154	11	32.03	30.88	34.53	1.018	9	29.49	27.23	31.89	1.920	7	29.97	29.38	30.59	0.439
IB	24	19.50	16.79	21.79	1.138	14	19.44	17.73	21.19	0.986	11	19.91	18.56	21.62	0.807	9	17.59	16.17	18.56	0.842	6	16.76	15.73	17.66	0.662
LD	24	12.94	11.65	14.36	0.697	14	12.33	11.35	13.94	0.689	11	13.02	12.20	13.96	0.544	9	11.67	10.51	12.92	0.983	7	12.08	11.52	13.01	0.517
LIF	24	3.60	3.03	4.34	0.343	14	3.55	2.92	4.36	0.403	11	3.69	3.29	4.55	0.378	9	3.25	2.69	3.98	0.468	7	3.31	3.00	4.13	0.381
LBP	24	16.66	14.99	17.84	0.770	14	15.62	14.70	17.55	0.795	11	16.22	15.29	16.63	0.364	9	15.01	14.13	16.12	0.744	7	14.77	14.24	15.33	0.333
BBP1	24	6.79	6.25	7.42	0.349	14	6.36	5.92	7.10	0.300	11	6.72	5.84	7.51	0.464	9	6.30	5.61	6.85	0.389	7	6.36	6.12	6.70	0.199
BBP3	24	6.90	6.24	7.45	0.352	14	6.54	6.15	7.00	0.269	11	6.71	5.57	7.27	0.566	9	6.23	5.56	6.82	0.404	7	6.41	6.11	6.87	0.233
PPL	24	20.53	18.62	22.54	0.862	14	20.74	19.75	22.38	0.816	11	20.28	16.08	22.08	1.595	9	19.19	17.28	21.12	1.422	6	19.33	18.78	20.18	0.474
BMF	24	4.77	4.24	5.22	0.276	14	4.59	4.10	5.17	0.298	11	4.62	3.85	5.00	0.357	9	4.20	3.84	4.53	0.216	7	4.18	3.90	4.55	0.231
LB	24	10.10	8.86	11.05	0.595	14	9.63	8.84	10.62	0.514	11	9.72	9.15	10.15	0.335	9	9.63	8.37	10.98	1.008	7	8.95	8.41	9.38	0.347
HB	23	9.10	7.83	10.00	0.497	14	9.04	8.09	10.24	0.596	11	9.11	8.46	10.01	0.498	9	9.03	7.56	10.63	1.294	7	8.68	8.12	9.30	0.482
CLM	24	10.58	9.89	11.63	0.422	14	10.31	9.70	10.90	0.366	11	10.12	9.70	10.69	0.302	9	9.54	8.75	10.34	0.587	7	9.81	9.52	10.12	0.218
CLm	24	10.21	9.47	11.29	0.420	14	9.99	9.43	10.60	0.372	11	9.87	9.37	10.32	0.298	9	9.46	8.78	10.09	0.485	7	9.81	9.38	10.15	0.297
PL	19	26.86	24.50	29.46	1.182	14	25.98	24.67	28.46	1.120	11	26.52	25.43	27.40	0.613	0					0				
SB	24	28.34	23.91	30.97	1.573	14	27.46	25.60	29.50	1.355	11	28.63	27.75	31.00	0.889	9	25.45	24.10	26.20	0.759	6	25.24	24.50	26.57	0.736
NL	24	16.95	15.21	18.18	0.750	13	16.44	14.82	19.38	1.166	11	16.94	15.78	18.13	0.845	9	15.85	13.05	17.70	1.734	7	15.83	15.46	16.47	0.356
ILB	24	0.19	0.17	0.20	0.007	14	0.18	0.16	0.20	0.011	11	0.18	0.17	0.19	0.006	9	0.19	0.18	0.20	0.008	6	0.18	0.17	0.19	0.006
IZB	24	1.69	1.59	1.78	0.054	14	1.70	1.61	1.75	0.041	11	1.68	1.62	1.74	0.035	9	1.69	1.63	1.74	0.032	6	1.67	1.63	1.72	0.036
IOB	24	2.79	2.53	3.01	0.123	14	2.74	2.59	2.91	0.091	11	2.70	2.57	3.00	0.122	9	2.83	2.53	2.96	0.129	6	2.97	2.77	3.15	0.122
ILBP1	24	0.31	0.29	0.33	0.010	14	0.29	0.28	0.31	0.009	11	0.30	0.29	0.31	0.008	9	0.30	0.28	0.32	0.012	6	0.29	0.29	0.30	0.003
ILBP2	19	0.62	0.58	0.64	0.018	14	0.60	0.58	0.62	0.012	11	0.61	0.60	0.63	0.011	0					0				

	C. erythraeus					*C. flavimanus*					*C. griseimanus*					*C. finlaysonii*					*C. inornatus*				
	N	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**	**N**	**Mean**	**Min**	**Max**	**SD**
IMOL	24	0.19	0.18	0.21	0.008	14	0.19	0.18	0.21	0.009	11	0.19	0.18	0.20	0.006	9	0.19	0.18	0.20	0.004	6	0.20	0.19	0.20	0.005
GCI	19	1.30	1.19	1.39	0.052	14	1.25	1.19	1.31	0.032	11	1.31	1.24	1.61	0.100	0					0				
OPI	24	0.88	0.82	0.94	0.028	14	0.88	0.83	0.91	0.024	11	0.89	0.88	0.92	0.013	9	0.86	0.82	0.90	0.035	6	0.85	0.81	0.88	0.023
IBH	24	0.32	0.30	0.35	0.011	14	0.32	0.30	0.33	0.009	11	0.31	0.30	0.34	0.012	9	0.32	0.30	0.33	0.012	6	0.33	0.33	0.34	0.006
CI	24	20.43	18.69	21.77	0.631	14	20.17	19.27	20.87	0.490	11	20.08	19.29	21.15	0.527	9	18.80	17.98	19.93	0.628	7	19.62	19.28	19.93	0.261
PI	24	2.10	1.93	2.41	0.124	14	1.90	1.76	2.16	0.105	11	2.03	1.79	2.18	0.137	9	1.89	1.75	2.07	0.088	6	1.89	1.85	2.01	0.062
GBI	24	0.45	0.42	0.48	0.015	14	0.46	0.44	0.52	0.024	11	0.45	0.42	0.46	0.013	9	0.45	0.42	0.48	0.020	6	0.47	0.45	0.47	0.007
DI	24	1.23	1.04	1.40	0.082	14	1.20	1.04	1.30	0.078	11	1.29	1.17	1.41	0.066	9	1.22	1.14	1.29	0.049	7	1.23	1.15	1.34	0.064

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

Table S3. Factor loadings and cumulative variance for the principal components in the PCA analysis. See explanation at text for groups segregation applied.

	Independent Group Analyses			**United Group Analyses**		
	Factor 1	**Factor 2**	**Factor 3**	**Factor 1**	**Factor 2**	**Factor 3**
ONL	–0.918132	0.122020	0.138870	–0.908862	0.139197	0.18923
HBC	–0.757520	–0.213632	–0.060965	–0.754413	–0.265314	0.230095
ZB	–0.897759	0.027957	0.108441	–0.901397	0.069118	0.171969
LD	–0.869346	0.391098	–0.031991	–0.856885	0.413475	–0.040478
LBP	–0.865905	–0.024377	–0.177501	–0.850985	–0.0382	–0.345552
BBP1	–0.813831	0.088950	–0.213993	–0.809466	0.105167	–0.250489
BBP3	–0.732981	0.062413	–0.100827	–0.734098	0.091199	–0.049917
BMF	–0.696103	0.097410	0.036187	–0.687451	0.110197	0.081218
LB	–0.692777	0.206214	0.617255	–0.491374	0.37647	0.400907
CLM	–0.748261	–0.602198	0.173162	–0.77195	–0.558756	0.161869
CLm	–0.651637	–0.571992	0.147009	–0.672129	–0.529101	0.139233
SB	–0.843598	0.035859	–0.007402	–0.844497	0.058985	0.037068
ILB	–0.064730	0.181938	0.762909	–0.006811	0.178977	0.160823
ILBP1	–0.205236	–0.209471	–0.513197	–0.191769	–0.251586	–0.862281
IMOL	0.139850	–0.938641	0.055568	0.071227	–0.934442	–0.008731
CI	–0.818937	–0.219092	–0.007794	–0.816678	–0.252932	0.237584
PI	–0.784576	–0.040947	–0.379344	–0.778285	–0.041682	–0.540871
DI	–0.313183	0.899096	–0.170229	–0.257263	0.90704	–0.173126
Explained variance	50.22%	15.48%	8.77%	39.00%	19.40%	10.78%
Quality of representation		74.47%			79.18%	

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

Appendix 1. Genetically investigated samples of *Callosciurus* from Vietnam.

LC- *** Vietnam, Ha Giang Province, Quan Ba, 4 km SE from Tam Son, 23°02.423N 105°01.615E. ZMMU S-195578, ZMMU S-195579.
TQ-*** Vietnam, Tuyen Quang Province, Na Hang district, Khong May, Nang Kha. 22°23.001 N 105°20.294 E. ZMMU S-200620, ZMMU S-200621, ZMMU S-200622, ZMMU S-200625, ZMMU S-200642.
BK-*** Vietnam, Bak Kan Province, Dong Phuc district, Ba Be Nature Reserve. 22.18.838 N; 105.43.244 E. ZMMU S-198982, ZMMU S-198983, ZMMU S-198984, ZMMU S-198986.
ThN-*** Vietnam, Cao Bang Province, Ha Lang district, Thanh Nhat, 22°40N, 106°41.757E. S-191966, S-191967, S-191968, S-191969.
Vietnam, Vinh Phuc Province, Tam Dao Nature Reserve, Tam Dao near 21°50.0N 105°66.6E (see Oshida et al., 2013).
Vietnam, Son La Province, Thuan Chau, Co Ma and Phu Yen, Hon localities (see Oshida et al., 2013). Only *C. inornatus* samples.
China, Hainan Island, Qiongzhong. (see Lu et al., 2012).
NA18-*** Vietnam, Nghe An Province, Tuong Duong district, 8 km N from Xoong Con, 19°15.129N 104° 19.025 E. ZMMU S-200600, ZMMU S-200602, ZMMU S-200604, ZMMU S-200605, ZMMU S-200608, ZMMU S-200613, ZMMU S-200617, ZMMU S-200618.
QB-*** Vietnam, Quang Binh Province, Le Thuy district, Sa Khia, 17°04.095 N; 106°527E. ZMMU S-196846, ZMMU S-196847, ZMMU S-198985, ZMMU S-198987, ZMMU S-198988, ZMMU S-198994.
CMR-*** Vietnam, Kon Tum Province, Chu Mom Ray Nature Reserve. 14°30.013N 107°43.208E. ZMMU S-195563.
NTr-*** Vietnam, Khanh Hoa Province, Nha Trang City, Tre Island. 12°11.85N 109°17.45E. ZMMU S-196844, ZMMU S-196845.
132-09 Vietnam, Binh Phuoc Province, Bu Gia Map Nature Reserve. 12°19.41N 107°20.638E. ZMMU S-186540.
Sq-*** Vietnam, Dong Nai Province, Nam Cat Tien Nature Reserve. 11°41.66N 107°41.66E. ZMMU S-195565, ZMMU S-195566, ZMMU S-195567, ZMMU S-195568.

Appendix 2. List of *Callosciurus* specimens (skins and skulls) examined.

China, Yunnan, Man Hun. Kuzyakin A., 1957. ZMMU S-161905, ZMMU S-136281, ZMMU S-136282. (*C. e. gordani* Anderson). 2 skins, 3 skulls.
Lao Cai Province, Sapa, Phan Si Pan Mountain, Kuznetsov G.V., 1996. (*C. e. hendeei*). ZMMU S-179697, ZMMU S-179698. 2 skins.
Cao Bang Province, Ha Lang district, Thanh Nhat 22°40N, 106°41.757E Balakirev A.E., 2013 (*C. e. hendeei*) ZMMU S-179697, S-191966, S-191967, S-191968, S-191969. 5 skins, 5 skulls.
Tuyen Quang Provonce, Na Hang district, Khong May, Nang Kha, 22°23.001 N 105°20.294 E, Balakirev A. E., 2018. (*C. e. hendeei*), ZMMU S-200620, ZMMU S-200621, ZMMU S-200622, ZMMU S-200625, ZMMU S-200642. 4 skins, 4 skulls.
Bac Kan Province. Phong Huan, 10 km S from Bang Lung, near 22º08.333N, 105º66.66E. Rozhnov V.V., 1989. (*C. e. hendeei*) ZMMU S-148500, ZMMU S-148502, ZMMU S-148503, ZMMU S-148504, ZMMU S-148505, ZMMU S-148506, ZMMU S-148507, ZMMU S-148496, ZMMU S-148497, ZMMU S-148498. 10 skins, 6 skulls.
Quang Ninh Province, Dang Ho Island, Bai Tu Long Archipelago, Kuznetsov G.V., 1987, (*C. e. hendeei*) ZMMU S-144631. 1 skin.
Phu Tho Province, "Ha Son Binh, Rong village", 90 km, SW from Hanoi, Kuznetsov G.V., 1978, (*C. e. erythraeus*) ZMMU S-115217, ZMMU S-115218. 2 skins.
Phu Tho Province, Ba Vi Nature Reserve, about 40 km W from Hanoi. Kuznetsov G. V., (*C. e. hendeei*) ZMMU S-115166, ZMMU S-115167, ZMMU S-115168. 3 skulls.
Nghe An Province, Quy Chau district, Ke Can village. 19°31.184N 105°10.282E, Balakirev A.E. 2011 (*C. e. hendeei*) ZMMU S-195561, ZMMU S-195562. 3 skins, 2 skulls + 7 skins and 7 skulls of *C. inornatus*.
Nghe An Province, Tuong Duong district, 8 km N from Xoong Con, 19°15.129N 104°19.025 E, Balakirev A.E. 2018. ZMMU S-200613, (*C. e. hendeei*), 1 skin, 1 skull.
Laos, Khammoune Province, Ban Doy Village, 18 km N from Thakhek, Abramov A.V., Tikhonov A.N. 2008. ZIN98322, ZIN98323, ZIN98324, ZIN98322. (*C. finlaysonii menamicus*), 4 skins, 4 skulls.
Quang Binh Province, Le Thuy district, Sa Khia, 17°04.095 N; 106°527E. Balakirev A.E. 2016-2017 ZMMU S-196846, ZMMU S-196847, ZMMU S-198985, ZMMU S-198987, ZMMU S-198988, ZMMU S-198994 (*C. flavimanus*), 5 skins, 5 skulls.
Da Nang, Cham Island, about 15 km SE from Da Nang. Kuznetsov G.V., 1987. ZMMU S-144683, ZMMU S-144695. (*C. flavimanus*) 2 skins.
Kon Tum Province, Chu Mom Ray Nature Reserve. 14°30.013N 107°43.208E, Balakirev A.E. 2014. ZMMU S-195563 ZMMU S-195564. (*C. flavimanus*) 2 skins, 2 skulls.

Gia Lai Province, K'Bang district, so called "Buon Luoi", Ba and Con Rivers interfluve, about 50 km N from An Khe, 14° 21′N, 108°36′E. Kuznetsov G.V., 1978-1989, Rozhnov V.V. 1990. ZMMU S-115169, ZMMU S-115170, ZMMU S-123536, ZMMU S-132772, ZMMU S-134700, ZMMU S-134701, ZMMU S-134702, ZMMU S-144530, ZMMU S-144531, ZMMU S-144532, ZMMU S-144533, ZMMU S-146240, ZMMU S-151280, ZMMU S-151281, ZMMU S-155396, ZMMU S-155397, ZMMU S-155398, ZMMU S-155399, ZMMU S-155400, ZMMU S-155401, (*C. flavimanus*) 18 skins, 10 skulls.

Khanh Hoa Province, Nha Trang City, Tre Island. 12°11.85N 109°17.45E Balakirev A.E. 2014. ZMMU S-196844, ZMMU S-196845, (*C. flavimanus*) 2 skins, 2 skulls.

Binh Phuoc Province, Bu Gia Map Nature Reserve. 12°11′39″N 107°12′23″E. Schinov A., 2009, ZMMU S-186540. 1 skin.

Dong Nai Province, Nam Cat Tien Nature Reserve. 11°25′N 107°25′E, Kuznetsov G.V., 2004-2006, Balakirev A.E., 2007-2011. ZMMU S-178884, ZMMU S-178885, ZMMU S-180626, ZMMU S-180627, ZMMU S-184194, ZMMU S-191629, ZMMU S-191631, ZMMU S-195565, ZMMU S-195566, ZMMU S-195567, ZMMU S-195568, ZMMU S-195569. (*C. griseimanus*) 7 skins, 8 skulls.

Ba Ria-Vung Tau Province, Binh Chau Nature Reserve, Xuyen Moc. Kuznetsov G.V., 2005, Suntsov V.V., 1991. ZMMU S-153172, ZMMU S-178888. (*C. griseimanus*) 2 skins, 1 skull.

Kien Giang Province, Tho Chu Island, Gulf of Thailand, about 100 km SW from Phu Quoc. Kuznetsov G.V., 1987. ZMMU S-144689, ZMMU S-144694, ZMMU S-144697. (*C. griseimanus*) 3 skins.

Ba Ria-Vung Tau Province, Con Son Island, 08°70.00N 06°58.33E. Abramov A.V. 2010. ZIN99790, ZIN99791 ZIN99792, ZIN95793, ZIN99828 (*C. finlaysonii harnandi*). 5 skins, 5 skulls.

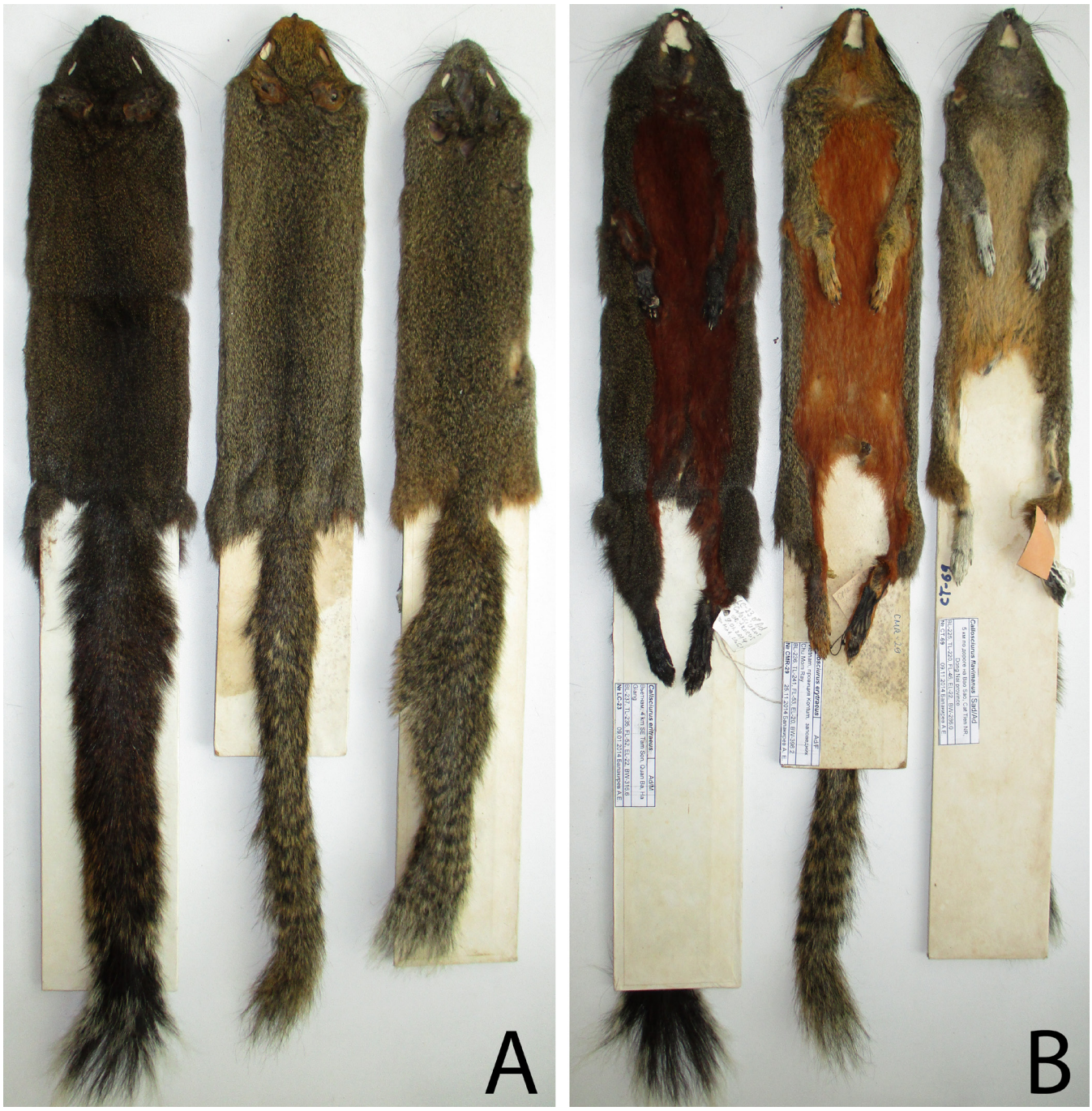

Fig. S1. Colour morpha usually attributed to *C. erythraeus* distributed in eastern Indochina. Flat skins, dorsal (A) and ventral views (B). Left, C. erythraeus, LC-23, ZMMU S-195578, Ad, male, Quan Ba, Ha Giang, Vietnam; Central, C. cf. flavimanus, CMR-29, ZMMU S-195563, Ad, female, Chu Mom Ray Nature Reserve, Kon Tum, Vietnam; Right, C. cf. griseimanus, CT-69, ZMMU S-195569, young adult, male, Nam Cat Tien Nature Reserve, Dong Nai, Vietnam.

Fig. S2. Colour morpha usually attributed to *C. finlaysonii* distributed in eastern Indochina. Stuffed skins, dorsal (A) and ventral views (B). Left, C. f. germanii, 212-2010, ZIN99790, Ad, female, Con Son Island (Condao=Condor), Ba Ria-Vung Tau, Vietnam; Right, C. f. menamicus, 219-2008, ZIN98325, Ad, male, Ban Doy, Khammouane, Laos.

Fig. S3. *Callosciurus finlaysonii* morpha "flavimanus", genetic voucher QB-5 (genetic lineage G8); ZMMU S-196847, Ad, female. Cam Ly, Ngan Thuy, 14 km to the west from Kien Giang, Quang Binh Province, Vietnam. Photo © Alexander E. Balakirev, taken 28 February 2016.

Fig. S4. Genetically confirmed *C. finlaysonii* that bears the morphotype of C. e. hendeei; genetic voucher NA18-92 (genetic lineage G6); ZMMU S-200613, Ad, female. Xoong Con, Thuong Duong, Nghe An Province, Vietnam.