



A new species of squirrel (Sciuridae: *Callosciurus*) from an isolated island off the Indochina Peninsula in southern Vietnam

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We describe a new species of squirrel (Sciuridae, *Callosciurus*) from Hon Khoai Island, located off the coast of southern Vietnam (centered at ca. 8°26'08"N, 104°49'58"E) and discuss its phylogenetic position in the genus *Callosciurus*. Compared to other *Callosciurus* occurring on the Indochina Peninsula, the new species (*Callosciurus honkhoaiensis*) is strikingly small, especially head and body length, body mass, and hind foot length. Unlike other species of *Callosciurus*, the hairs at the tip of the tail are white with a black base, and the venter and feet are whitish cream. The new species at present is known only from the type locality, Hon Khoai Island. Phylogenetically, the new species is closely related to *C. caniceps*, suggesting that it evolved from *C. caniceps* or an ancestor in common with *C. caniceps*, possibly during the Pliocene. Genetic distances between the 2 species calculated from comparison of mitochondrial cytochrome *b* sequences are 10.1–10.3%. During both glaciations and interglaciations of the Pleistocene, the new species may have been isolated from other *Callosciurus* populations by rivers and sea, respectively.

Key words: island endemic species, geographic isolation, Sciuridae, Southeast Asia, Sunda Shelf

During the Pleistocene, glacial and interglacial periods repeatedly alternated (e.g., Williams et al. 1993; Cox and Moore 2005). In Southeast Asia, maximum lowering of sea level during Pleistocene glaciations was about 200 m, enough to have exposed the Sunda Shelf (Hutchison 1989). This lower sea level would have provided land linkages from mainland Southeast Asia (the Indochina and Malay Peninsulas) to the islands of the Sunda Shelf (Borneo, Sumatra, and Java), thereby forming a large continental mass known as Sundaland (Tjia 1980; Williams et al. 1993; MacKinnon et al. 1996; Hanebuth et al. 2000). After the last glacial period, Sundaland disappeared and the present-day geological structures were formed (MacKinnon et al. 1996).

During the Pleistocene, many mammal species were biogeographically affected by the geological changes in Sundaland

(Abegg and Thierry 2002; Meijaard 2003; Harrison et al. 2006; Nater et al. 2017). During glacial periods, geographic barriers such as large rivers separated populations of mammal species on Sundaland (MacKinnon et al. 1996). After the last glacial period, rising sea levels separated islands from the Asian continent, thereby forming additional geographic barriers for mammals. At present, there are many small islands off the coast of the southern Indochina Peninsula in the northern Gulf of Thailand, on which numerous mammal species are to be found (Kuznetsov 2000). These islands are thought to have been a part of Sundaland and were isolated from the mainland as water levels rose following glaciations (Tjia 1980; MacKinnon et al. 1996). The Gulf of Thailand is relatively shallow: average and maximum depths are only about 45 m and 80 m, respectively (Bridges 1990; Rundel 1999; Tran

et al. 2012). Therefore, mammals on islands in this body of water have not long been geographically isolated from those on the mainland. Seventeen species of mammals on Phu Quoc Island also are found on the mainland (Abramov et al. 2007). On the other hand, a new shrew species (*Crocidura phuquocensis*) has been described from Phu Quoc Island (Abramov et al. 2008) and the psychedelic rock gecko (*Cnemaspis psychedelica*) was described as a new species endemic to Hon Khoai and Hon Tuong Islands (Grismer et al. 2010; Ngo et al. 2016), suggesting that the islands located south of the Indochina Peninsula (Fig. 1) may have a more unique fauna and complicated geological history than previously thought. One of these islands, Hon Khoai (Fig. 1) is located 18 km from the southern tip of the Ca Mau Peninsula and is part of the Hon Khoai archipelago (Hon Lon, Hon Nho, Hon Tuong, Hon Sao, and Hon Doi Hon Islands—Ministry of Culture, Sport and Tourism, Vietnam [2017]). Hon Khoai is only 8.0 km² in area and has a dense tree cover of primary tropical forest.

One species of squirrel, *Callosciurus* Gray, 1867, is found on this small island. The genus *Callosciurus* occurs widely in South and Southeast Asia and is presently hypothesized to contain 14 species (Thorington et al. 2012): *C. adamsi* Kloss, 1921, *C. baluensis* Bonhote, 1901, *C. caniceps* Gray, 1842, *C. erythraeus* Pallas, 1779, *C. finlaysonii* Horsfield, 1823, *C. inornatus* Gray, 1867, *C. melanogasteri* Thomas, 1895, *C. nigrovittatus* Horsfield, 1823, *C. notatus* Boddaert, 1785, *C. orestes* Thomas, 1895, *C. phayrei* Blyth, 1856, *C. prevostii* Desmarest, 1822, *C. pygerythrus* I. Geoffroy Saint Hilaire, 1833, and *C. quinquestriatus* Anderson, 1871. Each species shows extensive geographic variation and several named subspecies (Corbet and Hill 1992; Thorington and Hoffmann 2005); as a consequence, the taxonomy of the genus *Callosciurus* remains poorly understood.

The genus *Callosciurus* could be a useful model for testing biogeographic and phylogeographic hypotheses due to its apparent sensitivity to geographic changes. In Southeast Asia, rivers could potentially constitute barriers that induce speciation in *Callosciurus* species (Oshida et al. 2001, 2011, 2013, 2016), thus adding support to the riverine barrier hypothesis (e.g., Salo et al. 1986; MacKinnon et al. 1996; Meijaard and Groves 2006; Arora et al. 2010). In Taiwan, mountain ranges likely acted as a geographic barrier dividing populations of *C. erythraeus*, producing genetically distinct phylogroups (Oshida et al. 2006). Insofar as testing for the effects of geographic isolation, *Callosciurus* could, therefore, constitute an informative model system. In the present study, we tested the hypothesis that the Hon Khoai Island squirrel is a geographic variant of a *Callosciurus* species already occurring on the Indochina Peninsula against its alternative, that the Hon Khoai Island *Callosciurus* is instead endemic to Hon Khoai Island and should be treated as a new species.

We examined external and cranial morphological characters of the Hon Khoai squirrel and analyzed its phylogenetic relationships with other *Callosciurus* species by using mitochondrial (mt) DNA cytochrome *b* (*Cytb*) sequences. Here, we assess the taxonomic status of the *Callosciurus* from Hon Khoai Island resulting from our test of the above hypothesis and discuss the influence of geographic isolation between the Indochina Peninsula and adjacent small islands.

MATERIALS AND METHODS

Study region.—Hon Khoai Island is located off the southern end of the eastern Indochina Peninsula (8°25'00"–8°27'15"N 104°49'10"–104°50'45"E; Fig. 1). Annual averages for temperature and humidity are $26.7 \pm 0.84^\circ\text{C}$ and $83.9 \pm 3.4\%$, respectively (Grismer et al. 2010; Tran et al. 2012; Ngo et al. 2016).

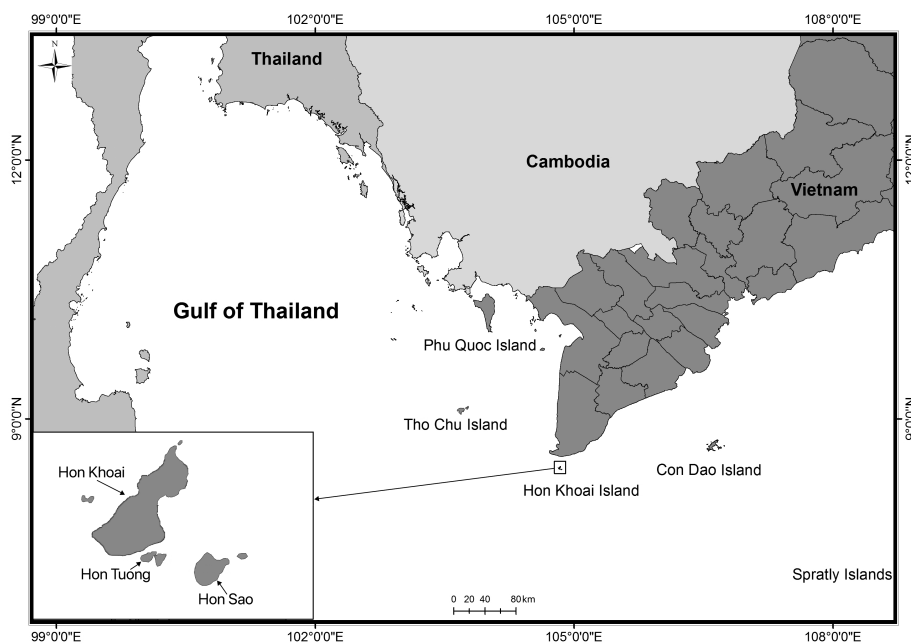


Fig. 1.—Locality of Hon Khoai Island, Vietnam.

The island's peak elevation is 318 m above sea level. Hon Khoai is a rocky island covered with tropical primary forests mainly consisting of *Ficus* spp. (Rosales: Moraceae), *Garicinia* spp. (Malpighiales: Clusiaceae), *Knema saxatilis* (Magnoliales: Myristicaceae), *Lagerstroemia caryculata* (Myrtales: Lythraceae), *Sandoricum koetjape* (Sapindales: Meliaceae), *Semecarpus cochinchinensis* (Sapindales: Anacardiaceae), *Syzygium* spp. (Myrtales: Myrtaceae), *Terminalia calaman-sanai* (Myrtales: Combretaceae), and *Wrightia pubescens* (Gentianales: Apocynaceae) (Nguyen 2017).

Collecting.—In January 2017, we used cage traps (15 cm × 15 cm × 25 cm) to collect 3 *Callosciurus* specimens from Hon Khoai Island: 2 females (specimen numbers HK-2017.44 and HK-2017.48) and 1 male (HK-2017.31), following methods approved in the Animal Care and Use Guidelines of the American Society of Mammalogists (Sikes et al. 2016). Specimens are deposited at the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Hanoi, Vietnam.

External characters and cranial measurements.—We recorded pelage characters of the squirrels in detail and measured head and body length (HB), tail length (T), hind foot length (HF), and ear length (E) in millimeters, and body mass (BW) in grams. Following Endo et al. (2004a, 2004b), Musser et al. (2006), and Hayashida et al. (2007), 30 skull dimensions were measured with a digital caliper (Mitsutoyo, NTD12-15PMX, Kawasaki, Japan) to an accuracy of 0.01 mm. Cranial measurements included: maximum (greatest) length of skull (ML), condylobasal length (CL), distance from anterior incisor to posterior last molar (DIM), median palatal breadth (MPL), maximum width across both nasal bones (MWN), maximum width of rostrum (MWR), least breadth between the orbits (LBO), least breadth of caudal point of zygomatic process of frontal bone (LBC), greatest neurocranium breadth (GNB), greatest occipital breadth (GOB), zygomatic breadth (ZB), length of rostrum (LR), greatest length of molar tooth row (GLMR1), length of bony palate (LBP), longest length of incisive foramina (LIF), greatest palatal breadth (GPB), length from basion to the most rostral point of zygomatic arch (LBRZ), length from basion to the most rostral point of orbit (LBRO), length from basion to the sagittal and rostral point of temporal bone (LBSR), length from basion to staphylion (LBS), length of auditory bulla (LAB), height from bony palate to the end of nasal bone (HBPNB), braincase height (BCH), and height from akrokranium to basion (HAB). Mandible measurements included: greatest length from the condyle (LC), greatest length of molar tooth row (GLMR2), thickness of mandible at middle point of M1 (TM), height of the mandible at M1 (HM), aboral height of the vertical ramus (AHR), and oral height of the vertical ramus (OHR) (Fig. 2).

DNA extraction, amplification, and sequencing.—Total genomic DNA was extracted from 99% ethanol-preserved muscle tissue using DNeasy Blood & Tissue Kit (QIAGEN K.K., Tokyo, Japan). The complete mitochondrial *Cytb* gene sequence (1,140 bases) was amplified with PCR using primer set L14724 5′-GATATGAAAACCATCGTTG-3′ and

H15910 5′-GATTTTTGGTTTACAAGACCGAG-3′ (Kocher et al. 1989 and Oshida et al. 2000, respectively). The 50 µl reaction mixture contained approximately 100 ng of genomic DNA, 0.25 µM of each primer, 200 µM dNTPs, 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 mM MgCl₂, and 2.5 units of *rTaq* DNA polymerase (Takara, Tokyo, Japan). Amplification was carried out for 35 cycles. PCR cycle protocol was: 94°C for 1 min, 55°C for 1 min, and 72°C for 2 min. A final extension reaction after 35 cycles was carried out at 72°C for 10 min. PCR products were purified with PCR Clean Up-M (Viogene, Taipei, Taiwan) and directly sequenced by the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit V3.1 (Applied Biosystems, Carlsbad, California) and automated DNA sequencer (ABI PRISM 377-96 Sequencer, the ABI PRISM 3100 Genetic Analyzer, Applied Biosystems). For sequencing, we used the same primers used for PCR. Purification of PCR products and sequencing were carried out by Mission Biotech Co. Ltd. (Taipei, Taiwan).

Molecular phylogenetic analyses.—Sequences were aligned with the software program DNASIS (Hitachi, Tokyo, Japan). We found 2 haplotypes among the 3 specimens: DNA Data Bank of Japan (DDBJ) accession number LC306835 (HK-2017.31 and HK-2017.44) and DDBJ accession number LC306836 (HK-2017.48). To resolve the phylogenetic position of the Hon Khoai *Callosciurus*, we compared the resulting sequences to available GenBank sequence data for *C. caniceps* (AB499918-19), *C. erythraeus* (AB499908-9), *C. finlaysonii* (AB499910-11), *C. inornatus* (AB499905-7), *C. nigrovittatus* (AB499916-17), *C. notatus* (AB499912-13), and *C. prevostii* (AB499914-15) generated by Oshida et al. (2011). We calculated *p*-distances among all squirrel sequences. To root phylogenetic trees, we used sequence data from the 3-striped ground squirrel, *Lariscus insignis* (AB499904—Oshida et al. 2011). This is the most appropriate outgroup for resolving phylogenetic relationships among *Callosciurus* species given its hypothesized sister relationship to *Callosciurus* (Mercer and Roth 2003).

We used MODELTEST 3.06 (Posada and Crandall 1998) to select the model of molecular evolution based on the Akaike Information Criterion (AIC) for the maximum likelihood (ML) analyses. The resulting model obtained was the general time reversible (GTR) model of substitution (Rodríguez et al. 1990; Yang et al. 1994), taking into account the proportion of invariable sites (0.5380), with a gamma distribution for variable sites (1.6406) (GTR + I + Γ). Base frequencies were estimated as A = 0.2759, C = 0.3297, G = 0.1166, and T = 0.2778. The rate matrix was estimated as A–C = 1.4476, A–G = 21.0174, A–T = 3.4345, C–G = 0.5485, C–T = 38.9655, and G–T = 1.0000. Using the genetic distances correlated by this model, we also carried out a neighbor-joining (NJ) analysis (Saitou and Nei 1987). In addition, we carried out an unweighted maximum parsimony (MP) analysis. Both ML and MP trees were constructed using the heuristic search option with tree-bisection-reconnection (TBR). To assess nodal supports, bootstrapping (Felsenstein 1985) was conducted with 1,000 replications in ML analysis and 5,000 replications in

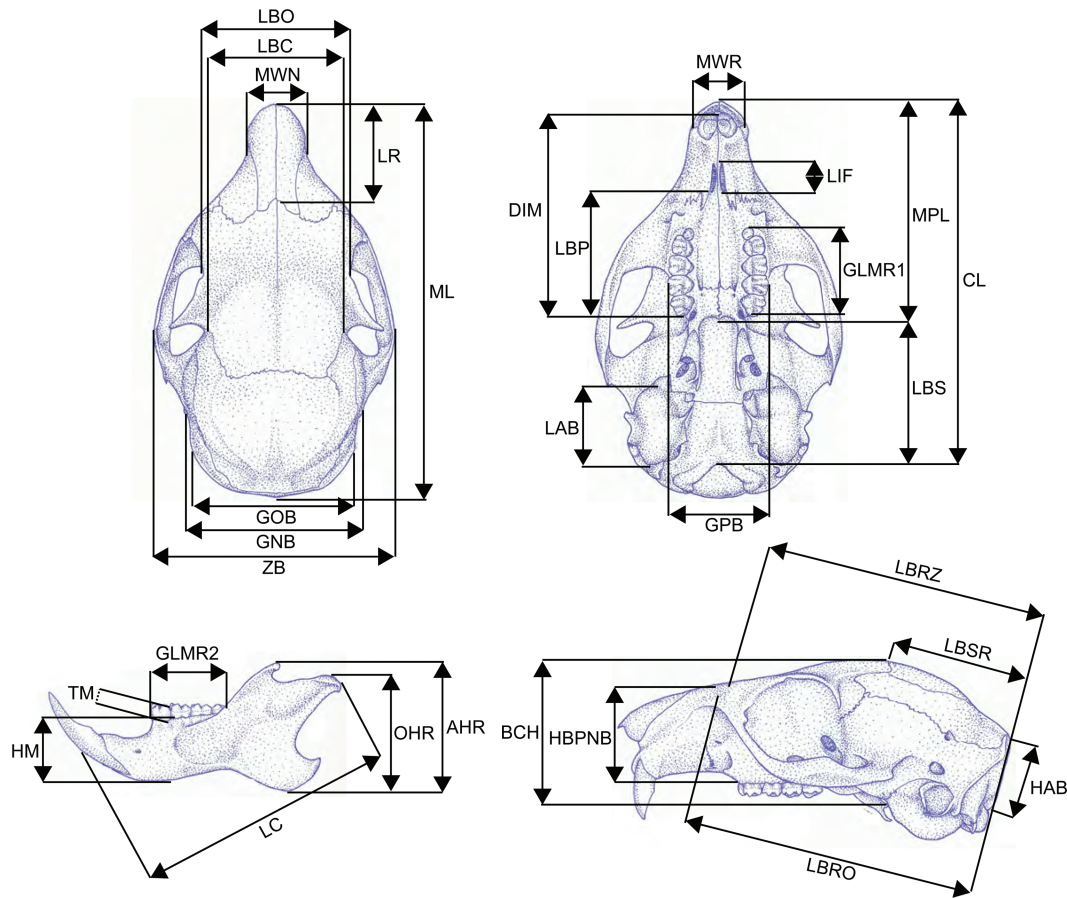


Fig. 2.—Cranial and mandibular measurements used in the present study. See text for additional information. Figures were adapted from [Abe \(2000\)](#). AHR = aboral height of the vertical ramus; BCH = braincase height; CL = condylobasal length; DIM = distance from anterior incisor to posterior last molar; GLMR1 = greatest length of molar tooth row; GLMR2 = greatest length of molar tooth row; GNB = greatest neurocranium breadth; GOB = greatest occipital breadth; GPB = greatest palatal breadth; HAB = height from akrokranium to basion; HBPNB = height from bony palate to the end of nasal bone; HM = height of the mandible at M1; LAB = length of auditory bulla; LBC = least breadth of caudal point of zygomatic process of frontal bone; LBO = least breadth between the orbits; LBP = length of bony palate; LBRO = length from basion to the most rostral point of orbit; LBRZ = length from basion to the most rostral point of zygomatic arch; LBS = length from basion to staphylion; LBSR = length from basion to the sagittal and rostral point of temporal bone; LC = greatest length from the condyle; LIF = longest length of incisive foramina; LR = length of rostrum; ML = maximum (greatest) length of skull; MPL = median palatal breadth; MWN = maximum width across both nasal bones; MWR = maximum width of rostrum; OHR = oral height of the vertical ramus; TM = thickness of mandible at middle point of M1; ZB = zygomatic breadth.

MP and NJ analyses. The ML analysis and the MP and NJ analyses were undertaken using RAxML v8.2.X ([Stamatakis 2014](#)) in the CIPRES Science Gateway ([Miller et al. 2015](#)) and PAUP* 4.0b10 ([Swofford 2001](#)), respectively. Bayesian inference (BI) reconstruction was carried out using MrBayes 3.0b4 ([Huelsenbeck and Ronquist 2001](#)). Bayesian analysis was also conducted using the GTR substitution model selected by MODELTEST for our dataset. This analysis was carried out using 2 runs of 1 million iterations, using 4 Markov chain Monte Carlo (MCMC) chains sampling every 1,000 generations and a burn-in of 10%. A 50% majority rule consensus tree was generated based on the remaining trees. Posterior probabilities were used to assess nodal support of the BI tree.

Divergence times among *Callosciurus* species were estimated using BEAST v. 1.8.3 ([Drummond et al. 2016](#)). Divergence time among the squirrel genera *Callosciurus*, *Dremomys*, and *Sundasciurus* was estimated to be ca. 11.0 ± 1.2 million

years ago (mya) by [Mercer and Roth \(2003\)](#). To set a temporal calibration point, we, therefore, included sequences of *Dremomys pernyi* (HQ698361—[Chang et al. 2011](#)), *D. rufigenis* (EF539341, [Li et al. 2008](#)), and *Sundasciurus mindanensis* (AB444722) in this analysis. We applied a normal distribution as the prior model for calibration and a relaxed molecular clock to allow for uncertainty in the evolutionary rate.

RESULTS

We captured 3 *Callosciurus* individuals on Hon Khoai Island: all materials were used in the present study. We describe the characteristics of these squirrels in detail below.

Pelage characteristics.—Photographs of one of the Hon Khoai squirrels (IEBR-M-6439; field number HK-2017.44) are shown in [Fig. 3](#). Dorsal pelage is agouti, with predominant hue bright orange-brown, agouti bands consisting of black color at

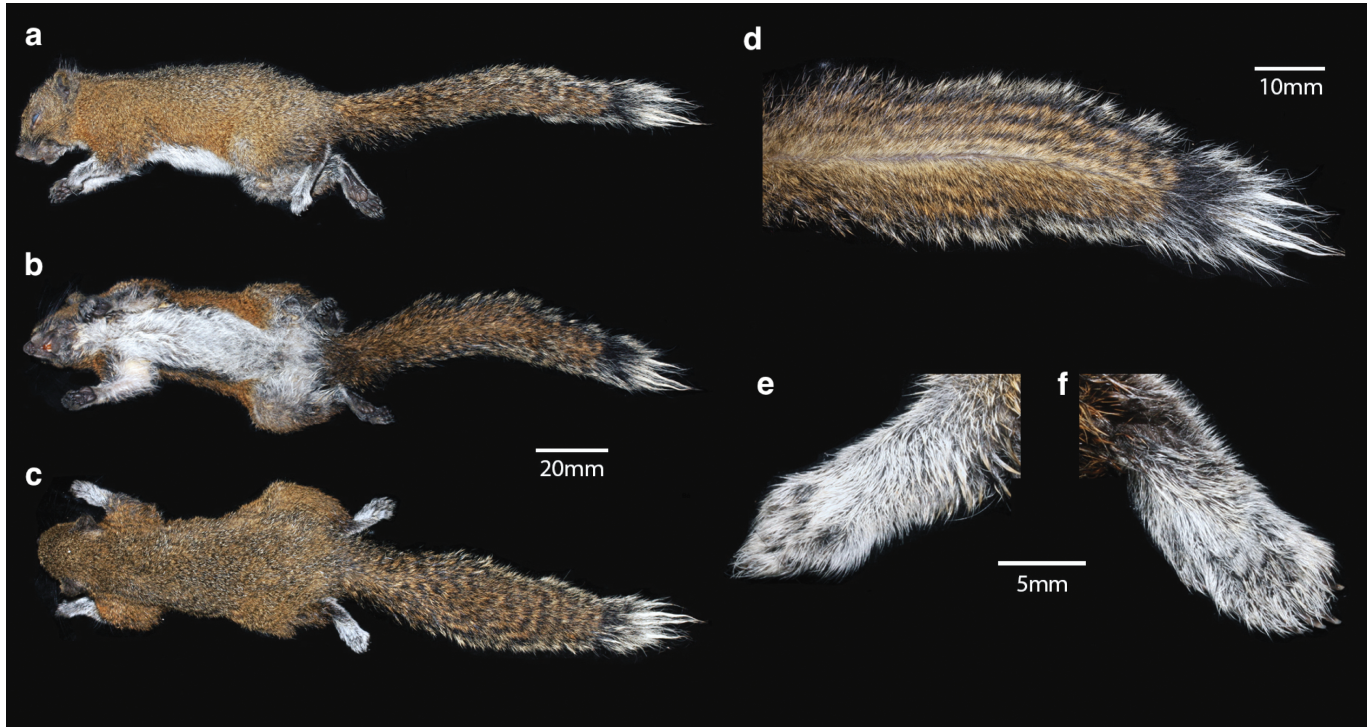


Fig. 3.—A *Callosciurus* from Hon Khoai Island, Vietnam: a) lateral pelage, b) ventral pelage, c) dorsal pelage, d) ventral tail fur, e) forelimb, and f) hind limb; the specimen shown (IEBR-M-6439; field number HK-2017.44) is designated as the holotype of a new species in the present study.

base with another band of bright orange-brown color distally (Fig. 3), but muzzle is slightly pale orange buff. Ears are dark gray. Feet are whitish cream. Ventral hairs are mostly whitish cream. Fur on the sides of the body is mostly agouti consisting of black color at base with another band of bright orange-brown color distally, with a sharp demarcation between dorsal and ventral fur. Tail is entirely agouti: bands are black color at base, with another band of bright orange-brown color, and white color distally, but tip hairs near the terminus of the tail (50–55 mm) are unique: the distal portion of each hair is white with a black base.

External measurements.—External measurements of the squirrel are shown in Table 1, which includes available measurement information of all *Callosciurus* species, combining data from Moore and Tate (1965), Medway (1978), Payne et al. (1985), Lekagul and McNeely (1988), Corbet and Hill (1992), Lunde and Son (2001), Francis (2008), Hoffmann and Smith (2008), and Thorington et al. (2012). Of the *Callosciurus* species occurring in the Indochina Peninsula, the sample from Hon Khoai had the smallest HB (165.0–175.0 mm), HF (37–38 mm), and BW (150.0–156.0 g).

Skull measurements.—Cranium and mandible are shown in Fig. 4. We considered the 3 specimens as adult on the basis of their fully fused basioccipital and basisphenoid. Overall shapes are similar to those of other *Callosciurus* species (e.g., Moore and Tate 1965; Lunde and Son 2001), but sizes of both cranium and mandible are smaller than other *Callosciurus* species (Table 2). Our sample number ($n = 3$) was too small for multivariate analyses: measurements for greatest length of skull and length of maxillary tooth row are included in Table 1. Maxillary

tooth row length (8.8–8.9 mm) was within the range of variation of other *Callosciurus* species occurring in the Indochina Peninsula, but greatest length of skull (45 mm) was smaller than all *Callosciurus* species except *C. caniceps*.

Phylogenetic analysis.—Complete *Cytb* sequences (1,140 bp) were deposited in DDBJ under accession numbers LC306835 and LC306836. The ML search produced a single tree (Fig. 5). Branching patterns of the NJ, MP, and BI trees were similar to those of the ML tree (data not shown). Under all models, 3 major lineages were obtained: 1) *C. caniceps*, *C. erythraeus*, *C. finlaysonii*, *C. inornatus*, and *C. sp.* from Hon Khoai; 2) *C. notatus*; and 3) *C. nigrovittatus* and *C. prevostii*. Except for the additional *C. sp.* from Hon Khoai, phylogenetic relationships were essentially similar to those previously elucidated by Oshida et al. (2011).

The lineage including *Callosciurus* species occurring in the Indochina Peninsula and on Hon Khoai Island (Fig. 5) had high support values (83% in the ML tree, 83% in the MP tree, 96% in the NJ tree, and 1.0 in the BI tree). Within this lineage, there were 2 sublineages: 1 consisting of *C. erythraeus* and *C. finlaysonii*, the other with *C. caniceps*, *C. inornatus*, and *C. sp.* from Hon Khoai Island. These sublineages had 100% support values in the ML, MP, and NJ trees and 1.0 in the BI tree (Fig. 5). The Hon Khoai squirrels were most closely related to *C. caniceps*, with high support values in the MP tree (84%), NJ tree (91%), and BI tree (1.0), but not in the ML tree (60%). The *p*-distances between the Hon Khoai *Callosciurus* and other congeners are shown in Table 3. *Cytb* sequence divergences (*p*-distances) between the Hon Khoai *Callosciurus* and other *Callosciurus* species from the Indochina Peninsula are 10.1–14.8%. The

Table 1.—External and cranial measurements of all *Callosciurus* species. Our original data are in bold.

Species	Head and body length (mm)		Tail length (mm)		Hind foot length without nail (mm) ^a		Body mass (g)		Greatest skull length (mm) ^a	Maxillary tooth row (mm) ^a	
	Range ^a	Mean (n) ^b		Range ^a	Mean (n) ^b		Range ^a	Mean(n) ^b			
		Female/male			Female/male			Female/male			
North of the Isthmus Kra											
<i>C. caniceps</i>	180–240	222.3 (11)/215.5 (11)	184–242	219.4 (9)/242.5 (15)	45–50	165–315	312.9 (15)/316.4 (10)	44–57	8.2–10.5		
<i>C. erythraeus</i>	200–260	217.4 (142)/227.9 (15)	201–267	216.6 (10)/205.3 (15)	41–55	270–350	375.1 (343)/359.2 (371)	48–57	8.2–10.2		
<i>C. finlaysonii</i>	188–240	191.8 (13)/190.1 (14)	160–254	172.8 (13)/173.4 (14)	46–49		278.0 (2) ^c	45–57	8.0–10.2		
<i>C. sp.</i>	165–175	175.0 (1)/170.0 (2)	175–190	180.0 (1)/182.5 (2)	37–38	150–156	152.0 (1)/153.0 (2)	45	8.8–8.9		
<i>C. inornatus</i>	187–230	203.0 (8)/191.0 (10)	191–224	204.8 (6)/210.8 (4)	43–51	188–258	229.6 (13)/226.9 (15)	52	9.6–9.7		
<i>C. phyrei</i>	190–250	237.1 (7)/231.5 (4)	160–270	249.0 (6)/246.8 (4)	50–54		377.4 (6)/375.6 (2)	46–54	7.7–10.3		
<i>C. pygerythrus</i>	170–230	189.2 (17)/187.5 (22)	110–210	175.1 (16)/168.5 (22)	41–48	230–300	252.0 (1) ^c	45–50	7.9–9.0		
<i>C. quinquestriatus</i>	200–240	226.5 (n = 2)/–	180–210	202.0 (1)/–	44–55	258–315		50–52	9.7–10.1		
South of the Isthmus Kra											
<i>C. adamsi</i>	150–183	170.3(4)/157.0 (1)	152–167	148.7(3)/158.0 (1)	33–40	115–154	150.0 (1)/–				
<i>C. batuensis</i>	210–255	244.0 (1)/242.5 (2)	215–260	251.0 (1)/247.5 (2)	48–55		370.5 (2) ^c				
<i>C. melanogaster</i>	195–230	212.0 (5)/209.3 (9)		180.6 (5)/179.6 (28)	43–51		292.3 (3) ^c				
<i>C. nigrovittatus</i>	170–240	186.9 (12)/184.3 (11)	145–230	165.5 (2)/159.2 (5)	40–50		239.4 (7)/202.8 (7)	45–52	8.4		
<i>C. notatus</i>	150–225	237.8 (25)/233.6 (26)	160–210	170.0 (25)/186.5 (26)	38–47	150–280	227.9 (18)/233.9 (17)	47–50	8.4–9.8		
<i>C. orestes</i>	130–170	154.0 (5)/148.0 (4)	128–170	139.8 (5)/157.5 (4)	32–40		278.0 (1) ^c				
<i>C. prevostii</i>	200–270	237.7 (45)/238.9 (43)	202–273	233.3 (44)/233.0 (42)	45–61	250–500	361.9 (27)/357.3 (17)	52–60	10.4–11.2		

^aExcept for our original data, we combined data reported by Moore and Tate (1965), Medway (1978), Payne et al. (1985), Lekagul and McNeely (1988), Corbet and Hill (1992), Lunde and Son (2001), Francis (2008), and Hoffmann and Smith (2008).

^bData reported by Thorington et al. (2012).

^cSex not stated data.

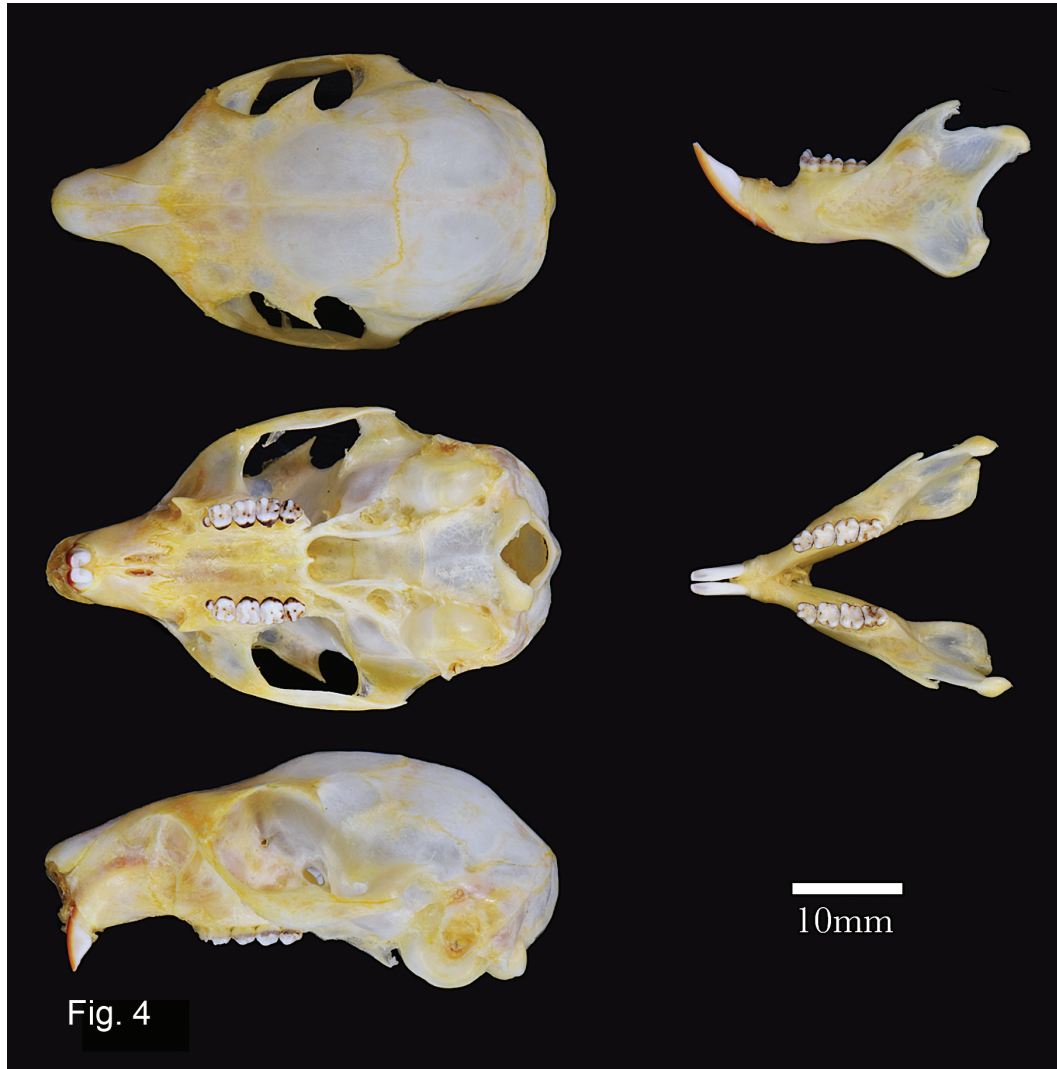


Fig. 4

Fig. 4.—Cranium and mandible of *Callosciurus* from Hon Khoai Island; the specimen shown (IEBR-M-6439; field number HK-2017.44) is designated as the holotype of a new species in the present study.

p-distances between Hon Khoai squirrels and *C. caniceps* were 10.1–10.3%. Chronological analysis estimated that Hon Khoai squirrels diverged from *C. caniceps* approximately 3.6 mya (95% confidence interval [CI] = 2.7–4.6 mya).

On the basis of both morphological and molecular evidence presented above, we describe the squirrels from Hon Khoai Island, Vietnam, as a new species, with the name mentioned below:

Callosciurus honkhoaiensis, sp. nov.
 Hon Khoai squirrel
 (Figs. 3 and 4)

Holotype.—Museum of the IEBR, Hanoi, Vietnam: number IEBR-M-6439; field number HK-2017.44; adult female; skin, skull, and skeleton. Tissue samples are deposited in IEBR. Holotype collected by Son Truong Nguyen and Phuong Huy Dang on 6 January 2017.

Type locality.—Vietnam: Hon Khoai Island in Rach Gia Bay, Ca Mau province.

Paratypes.—Skin, skull, and skeleton of 1 male (IEBR-M-6426; field number HK-2017.31) and 1 female

(IEBR-M-6443; field number HK-2017.48), collected on 7 January 2017, also are deposited in the Museum of the IEBR.

Etymology.—The specific epithet *honzhoaiensis* refers to Hon Khoai Island, Ca Mau province, where the holotype was collected. We recommend “Hon Khoai squirrel” as an English common name.

Nomenclatural statement.—A Life Science Identifier (LSID) was obtained for the new species (*C. honkhoaiensis*): urn:lsid:zoobank.org:pub:5E76A4B0-E680-42A7-A140-0FC286C786D9.

Diagnosis.—*Callosciurus honkhoaiensis* is distinguished as the smallest among *Callosciurus* species from the Indochina Peninsula; head and body and body mass are smallest; tail medium; hind foot medium; ear medium; greatest length of skull almost smallest. Pelage color of the dorsum is agouti consisting of bright orange-brown and black; sides are agouti consisting of bright orange-brown and black; venter is whitish cream; feet are whitish cream; tail is agouti consisting of bright orange-brown, black, and white (the hairs at the tip of the tail are white with a black

Table 2.—Skull measurements of 3 specimens of *Callosciurus* sp. nov. from Hon Khoai Island, Vietnam. AHR = aboral height of the vertical ramus; BCH = braincase height; CL = condylobasal length; DIM = distance from anterior incisor to posterior last molar; GLMR1 = greatest length of molar tooth row; GLMR2 = greatest length of molar tooth row; GNB = greatest neurocranium breadth; GOB = greatest occipital breadth; GPB = greatest palatal breadth; HAB = height from akrokranium to basion; HBPNB = height from bony palate to the end of nasal bone; HM = height of the mandible at M1; LAB = length of auditory bulla; LBC = least breadth of caudal point of zygomatic process of frontal bone; LBO = least breadth between the orbits; LBP = length of bony palate; LBRO = length from basion to the most rostral point of orbit; LBRZ = length from basion to the most rostral point of zygomatic arch; LBS = length from basion to staphylion; LBSR = length from basion to the sagittal and rostral point of temporal bone; LC = greatest length from the condyle; LIF = longest length of incisive foramina; LR = length of rostrum; ML = maximum (greatest) length of skull; MPL = median palatal breadth; MWN = maximum width across both nasal bones; MWR = maximum width of rostrum; OHR = oral height of the vertical ramus; TM = thickness of mandible at middle point of M1; ZB = zygomatic breadth.

Variable	Range of measurements (mm)
ML	44.65–45.40
CL	40.04–41.00
DIM	20.50–21.30
MPL	23.17–23.90
MWN	9.76–10.92
LBO	15.40–15.56
LBC	16.61–17.30
GNB	21.00–22.20
GOB	19.39–20.05
ZB	26.42–27.00
LR	11.66–11.95
GLMR1	8.84–8.90
MWR	5.55–5.97
LIF	2.45–2.63
LBP	11.93–12.08
LBS	16.33–16.80
LAB	8.31–8.80
GPB	11.10–11.21
LBRO	28.98–29.63
HBPNB	10.10–11.29
LBRZ	32.92–33.60
LBSR	15.74–16.36
BCH	15.77–16.60
HAB	12.19–12.33
AHR	15.25–16.06
OHR	14.67–15.15
LC	28.99–29.29
GLMR2	8.34–8.59
HM	7.84–8.01
TM	2.43–2.85

base); ears are dark gray. The color patterns of tail hairs and whitish cream hairs on the feet constitute important diagnostic characteristics.

Distribution.—*Callosciurus honkhoaiensis* is presently known only from Hon Khoai Island located off the coast of the Indochina Peninsula in southern Vietnam (Fig. 1).

Measurements.—External measurements of the holotype: head and body length, 175.0 mm; tail length, 180.0 mm;

hindfoot without nail, 38.0 mm; hindfoot with nail, 39.0 mm; ear, 19.5 mm; body mass, 152.0 g. Cranial measurements (in mm) of the holotype are: ML 45.30, CL 41.00, DIM 21.20, MPL 23.70, MWN 10.70, MWR 5.78, LBO 15.56, LBC 16.61, GNB 21.56, GOB 19.80, ZB 26.80, LR 11.95, GLMR1 8.84, LBP 11.93, LIF 2.45, GPB 11.10, LBRZ 33.60, LBRO 29.54, LBSR 15.75, LBS 16.55, LAB 8.53, HBPNB 10.23, BCH 16.03, and HAB 12.19. Mandible measurements (in mm) of the holotype: LC 29.29, GLMR2 8.50, TM 2.85, HM 8.01, AHR 16.06, and OHR 15.15.

Comparisons.—Among species of *Callosciurus* from the Indochina Peninsula, *C. honkhoaiensis* is remarkably small, particularly insofar as concerns head and body length and body mass (Table 1). In cranial measurements, with the caveat that it is based on 3 individuals, the greatest length of skull is smallest among the *Callosciurus* species occurring in the Indochina Peninsula (Table 1), being similar to the smallest record of 3 other species of the genus. Species such as *C. finlaysonii* have a broad range of variable pelage patterns (Lekagul and McNeely 1988), making it difficult to distinguish *C. honkhoaiensis* using only pelage characters. However, *C. honkhoaiensis* is distinguishable from *C. caniceps* in pelage patterns. At present, 8 *C. caniceps* subspecies are recognized (Moore and Tate 1965; Thorington et al. 2012): *C. c. adangensis* (Miller, 1903), *C. c. altinsularis* (Miller, 1903), *C. c. bimaculatus* (Temminck, 1853), *C. c. caniceps* (Gray, 1842), *C. c. casensis* (Miller, 1903), *C. c. concolor* (Blyth, 1855), *C. c. domesticus* (Miller, 1903), and *C. c. fallax* (Robinson and Kloss, 1914). In addition, Thorington and Hoffmann (2005) showed 25 synonyms that were not allocated to subspecies. Of those, 23 synonyms have yet to be allocated to any subspecies: *bentincanus* (Miller, 1903), *chrysonotus* (Blyth, 1847), *fluminalis* (Robinson and Wroughton, 1911), *hastilis* Thomas, 1923, *helgei* (Gyldenstolpe, 1917), *helvus* (Shamel, 1930), *inexpectatus* (Kloss, 1916), *lancavensis* (Miller, 1903), *lucas* (Miller, 1903), *mapravis* Thomas and Robinson, 1921, *mathaeus* (Miller, 1903), *moheius* Thomas and Robinson, 1921, *mohillius* Thomas and Robinson, 1921, *nakanus* Thomas and Robinson, 1921, *panjioli* Thomas and Robinson, 1921, *panjius* Thomas and Robinson, 1921, *pipidonis* Thomas and Robinson, 1921, *samuiensis* (Robinson and Kloss, 1914), *sullivanus* (Miller, 1903), *tabaudius* Thomas, 1922, *tacopiis* Thomas and Robinson, 1921, *telibius* Thomas and Robinson, 1921, and *terutavensis* (Thomas and Wroughton, 1909). We compared the pelage characters of *C. honkhoaiensis* with those of every subspecies and synonyms described previously, but did not find any similar to *C. honkhoaiensis* (Table 4). The *Cytb* sequence divergences (*p*-distances) between *C. honkhoaiensis* and other *Callosciurus* species occurring in the Indochina Peninsula are 10.1–14.8%, and those between *C. honkhoaiensis* and *C. caniceps* were 10.1–10.3% (Table 3).

DISCUSSION

Phylogenetic position of *Callosciurus honkhoaiensis*.—Based on morphological characters, *Callosciurus* are separated

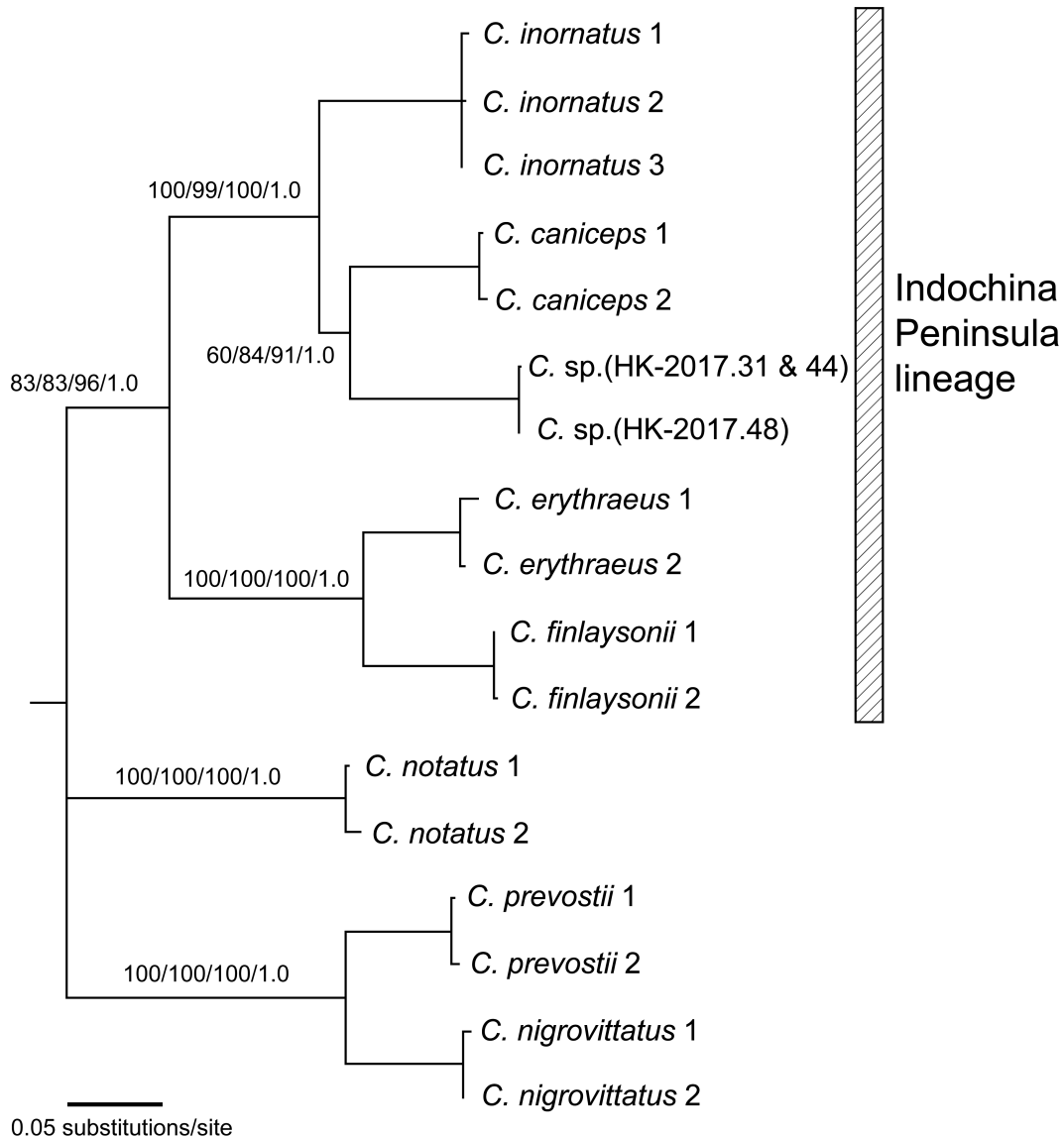


Fig. 5.—Maximum likelihood (ML) phylogeny of *Callosciurus* constructed using mitochondrial cytochrome *b* sequences, under the GTR + I + Γ model of evolution. From left, numbers above branches represent bootstrap values from: 1,000 replicates of ML, 5,000 replicates each of unweighted maximum parsimony and neighbor-joining analyses, and posterior probability supports in Bayesian analysis.

Table 3.—The *p*-distances (%) of *Cytb* sequences (1,140 bp) among *Callosciurus* species.

	<i>C. caniceps</i>	<i>C. erythraeus</i>	<i>C. finlaysonii</i>	<i>C. inornatus</i>	<i>C. nigrovittatus</i>	<i>C. notatus</i>	<i>C. prevostii</i>	<i>C. sp. nov.</i>
<i>C. caniceps</i>		15.44–15.79	14.74–14.83	10.53–10.79	16.58–16.93	16.14–16.67	17.02–17.49	10.10–10.30
<i>C. erythraeus</i>			8.51–9.04	13.51–13.77	16.14	15.18–15.44	15.97–16.32	14.40–14.60
<i>C. finlaysonii</i>				14.56–14.83	16.93	16.32–16.58	16.58–16.93	14.70–14.80
<i>C. inornatus</i>					16.05–16.14	15.79–16.23	16.84–17.19	11.10–11.30
<i>C. nigrovittatus</i>						15.35–15.61	8.68–8.95	17.00–17.30
<i>C. notatus</i>							15.00–15.79	15.20–15.40
<i>C. prevostii</i>								17.60–18.30
<i>C. sp. nov.</i>								

into 2 geographic units: a Mainland unit and a Sundaland unit, which are distributed north and south of the Isthmus of Kra, respectively (Moore and Tate 1965; Corbet and Hill 1992). These biogeographic units also are supported by molecular data (Oshida et al. 2001). In the present study, we identified 3 major

phylogenetic lineages. Species occurring in the Indochina Peninsula clustered together with high support values. The Sundaland species *Callosciurus nigrovittatus* and *C. prevostii* clustered together with high support values, although *C. notatus* was not included in a singular Sundaland unit. However,

Table 4.—Comparison of pelage characters between *Callosciurus honkhoaiensis* and previously described forms of *C. caniceps*.

<i>C. caniceps</i> forms	Pelage characters of <i>C. caniceps</i> forms distinct from <i>C. honkhoaiensis</i>	References
Subspecies ^a		
<i>adangensis</i>	Dull gray venter	Miller (1903)
<i>altinsularis</i>	Smoke-gray dorsum	Miller (1903)
<i>bimaculatus</i>	Black tail tip	Temminck (1853)
<i>caniceps</i>	Black tail tip	Gray (1842)
<i>casensis</i>	Pale gray on the underside of the tail	Miller (1903)
<i>concolor</i>	Reddish suffusion in the midline of the back	Blyth (1856)
<i>domelicus</i>	Dull cinnamon-rufous and grizzled gray venter	Miller (1903)
<i>fallax</i>	Grizzled black and buff dorsum	Robinson and Kloss (1914)
Synonyms ^b		
<i>bentincanus</i>	Chest and belly with a distinct reddish wash	Miller (1903)
<i>chrysonotus</i>	Pale grizzled ashy venter	Blyth (1847)
<i>fluminalis</i>	Olive gray dorsum; black tail tip	Robinson and Wroughton 1911
<i>hastilis</i>	Nearly uniform finely grizzled grayish olive	Thomas (1923)
<i>helgei</i>	Slaty gray venter	Gyldenstolpe (1916)
<i>helvus</i>	Grayish throat and belly	Shamel (1930)
<i>inexpectatus</i>	Paler pelage	Kloss (1916)
<i>lancavensis</i>	Dull gray venter	Miller (1903)
<i>lucas</i>	Ferruginous sides of neck and of body	Miller (1903)
<i>mapravis</i>	Whole lateral side is ferruginous; white ears	Thomas and Robinson (1921)
<i>matthaeus</i>	Reddish area on sides and neck	Miller (1903)
<i>moheius</i>	Deep buffy dorsum; grayish white venter; black tail tip	Thomas and Robinson (1921)
<i>mohillius</i>	Yellowish coloration; black tail tip	Thomas and Robinson (1921)
<i>nakanus</i>	Ferruginous whole lateral side	Thomas and Robinson (1921)
<i>panjioli</i>	Black tail tip	Thomas and Robinson (1921)
<i>panjius</i>	Black tail tip	Thomas and Robinson (1921)
<i>pipidonis</i>	Venter is rufous duller anteriorly with ochraceous on the groin-patches	Thomas and Robinson (1921)
<i>samuiensis</i>	Grizzled silvery-gray venter	Robinson and Kloss (1914)
<i>sullivanus</i>	Dull smoke-gray venter with an indistinct darker wash along median line	Miller (1903)
<i>tabaudius</i>	Dark gray dorsum with intense median line on chest	Thomas (1922)
<i>tacopius</i>	Ochraceous venter	Thomas and Robinson (1921)
<i>telibius</i>	Black tail tip	Thomas and Robinson (1921)
<i>terutavensis</i>	Midrib of the tail below and the bases of the hairs of each side to a length of 5–6 mm colored ochraceous buff	Thomas and Wroughton (1909)

^a Subspecies are as recognized by Thorington et al. (2012).

^b These names are not allocated with certainly to existing subspecies (Thorington and Hoffmann 2005).

we stress that we did not use all *Callosciurus* species from Sundaland in the present molecular analyses, but used instead all species occurring on the mainland near Hon Khoai Island; broader taxonomic sampling could lead to changes in the phylogenetic relationships obtained.

Callosciurus caniceps, *C. inornatus*, and *C. honkhoaiensis* are clustered together (Fig. 5), with *C. honkhoaiensis* most closely related to *C. caniceps*, the latter of which is distributed in Thailand, peninsular Myanmar, and peninsular Malaysia and adjacent islands (Lekagul and McNeely 1988; Corbet and Hill 1992; Thorington et al. 2012). There are 8 *C. caniceps* subspecies: *adangensis*, *altinsularis*, *bimaculatus*, *caniceps*, *casensis*, *concolor*, *domelicus*, and *fallax*. Five of these (*adangensis*, *altinsularis*, *casensis*, *domelicus*, and *fallax*) are endemic to small islands off the coast of the Malay Peninsula (Thorington et al. 2012).

Based on the estimated divergence time (3.6 mya [95% CI = 2.7–4.6 mya]) between the most recent common ancestor of *C. honkhoaiensis* and *C. caniceps*, we propose here a possible scenario to explain the evolutionary history of *C. honkhoaiensis*. Contrary to our expectations, this estimated divergence time was during the Pliocene rather than the Pleistocene. The

Indochina Peninsula was connected via the Malay Peninsula to Borneo throughout the Miocene, and this connection persisted for several million years until the beginning of the Pliocene (Hall 1998, 2009). Therefore, during the early Pliocene (Zanclean), the ancestral stock of both species might have had a wider distribution in Sundaland, and subsequently diverged into different species. During the early Pliocene, similar divergence events in shrews (Eulypotyphla: Soricidae—Dubey et al. 2008; Esselstyn et al. 2009; Yuan et al. 2013) and murine rodents (Ruedas and Kirsch 1997; Gorog et al. 2004) also have been recognized in the Sundaland. Unfortunately, it is difficult to explain what factors may have affected their divergence. However, sediment cores from a 12-myr record in Lake Baikal indicate that global climatic condition deteriorated suddenly in the early and middle Pliocene (Kashiwaya et al. 2001). The increasingly unstable climates in the Pliocene might have brought about divergence of small-sized mammals. In the present study, the estimated divergence time (3.6 mya) between the most recent common ancestor of *C. honkhoaiensis* and *C. caniceps* lies at the junction of the Zanclean and Piacenzian. Therefore, climatological factors may have contributed to their divergence. Subsequently, during the Pleistocene, the distribution of both

descendant species likely would have been reduced and fragmented because of appearance of the Gulf of Thailand. At that time, mainland *C. caniceps* populations could have become isolated from island *C. honkhoaiensis*. This geological process also may have resulted in the development of the island subspecies of *C. caniceps* (*adangensis*, *altinsularis*, *casensis*, *dome-licus*, and *fallax*), according to the precepts of the vicariance speciation model (Futuyma 1998) or the model of peripheral isolate formation of Frey (1993). In addition, *C. honkhoaiensis* likely evolved into a more distinct species *in situ* on the island. Moreover, during the Pleistocene, *C. honkhoaiensis* may have been geographically isolated from other *C. caniceps* populations by ancient river systems through Sundaland (MacKinnon et al. 1996); although the Hon Khoai population was not completely isolated by the large rivers, these would have impaired or slowed dispersal among populations. Therefore, during both glaciations and interglaciations of the Pleistocene, *C. honkhoaiensis* may have been isolated from other *Callosciurus* populations by both rivers and sea. Because of these factors, it is possible that this species may eventually be found to inhabit other islands in the southern part of Vietnam. Additional faunal studies will be required to adequately resolve the exact distribution of *C. honkhoaiensis*.

At present, we have no robust estimate of the population size of *C. honkhoaiensis*. Because Hon Khoai Island is very small (8.0 km²), both the number of squirrels and the magnitude of available resources likely are limited. Preservation of remaining forests on the island is therefore critical for conservation of *C. honkhoaiensis*.

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