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## Lost in synonymy: Integrative species delimitation reveals two unrecognized species of Southern Asian tree squirrels (Rodentia: Sciuridae: Callosciurinae)

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## Abstract

We present a comprehensive integrative taxonomic review of *Callosciurus caniceps* and *Tamiops mcclellandii* as they are currently defined. This review combines published molecular evidence, craniodental morphometrics, pelage and bacular variation, evaluations of potential hybrid zones using museum specimens and citizen science photographs, and, for *C. caniceps*, bioacoustic evidence. Our findings lead to the recognition of two species that had been lost in synonymy and highlight future perspectives on species delimitation in Sciuridae. By comparing phenotypic differentiation across climatic and vegetation transitions and contextualizing our results with the evolutionary history of our study systems, we provide insights into distribution, ecogeographical patterns, and speciation drivers in Southeast Asian vertebrates.

## Keywords

Baculum, bioacoustics, biodiversity, citizen science, Mammalia, morphometrics, Southeast Asia, speciation, taxonomy

## Introduction

In our recent effort (Hinckley et al. 2023a) to reconstruct the evolutionary history of the gray-bellied squirrel (*Callosciurus caniceps* Gray, 1842), Himalayan striped squirrel (*Tamiops mcclellandii* Horsfield, 1840), and redcheeked squirrel species complex (*Dremomys rufigenis* Blanford, 1878 and *Dremomys ornatus* Thomas, 1914, referred to as *D. rufigenis* sensu lato), we focused on evaluating patterns of genetic divergence across the biogeographic transition zone between Indochina and Sundaland, surrounding the Isthmus of Kra (IoK; fig. 1 of Hinckley et al. 2023a). We used Bayesian Inference/Maximum Likelihood mitochondrial genome phylogenies,

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nuclear loci (eleven introns) haplowebs and conspecificity matrices, and uncorrected pairwise distances of the cytochrome b gene (cyt b) to conduct divergence dating and population structure inference. A consistent finding across all three study taxa was that current species limits may not accurately reflect their evolutionary histories.

Callosciurus caniceps is an omnivorous, mostly arboreal species, that lives in a wide range of habitats including primary and secondary forests, gardens, and plantations in Thailand, peninsular Myanmar, peninsular Malaysia and adjacent islands (Fig. 1). It is typically found in the understory at elevations from sea level up to 1500 m above sea level (a.s.l.), although it is more common at lower elevations. This species exhibits a high degree of geographically structured pelage variation and moderate craniodental differentiation across its distribution range (Moore and Tate 1965; Hayashida et al. 2007; Thorington et al. 2012). Regional pelage variation has historically led to the description of sixteen nominal species, which are currently considered junior synonyms of C. caniceps (Moore and Tate 1965; Corbet and Hill 1992; Koprowski et al. 2016): Sciurus chrysonotis Blyth, 1847, S. bimaculatus Temminck, 1853, S. concolor Blyth, 1856, S. epomophorus Bonhote, 1901, S. lancavensis Miller, 1903, S. adangensis Miller, 1903, S. sullivanus Miller, 1903, S. domelicus Miller, 1903, S. bentincanus Miller, 1903, S. matthaeus Miller, 1903, S. lucas Miller, 1903, S. casensis Miller, 1903, S. altinsularis Miller, 1903, S. helgei Gyldenstolpe, 1917, Callosciurus erubescens Cabrera, 1917, C. moheius Thomas & Robinson, 1921. Trouessart (1899) treated Sciurus chrysonotis and S. concolor as synonyms of S. caniceps, and considered S. concolor a variety. Bonhote (1901) described Sciurus epomophorus and recognized the specific status of S. caniceps and S. concolor, although he also treated the latter as a senior synonym of S. inornatus. Species boundaries in C. caniceps have remained largely stable since Robinson and Kloss (1918) synonymized all sixteen nominal species. Apart from three forms (crumpi, thaiwanensis, and shanicus) initially included in C. caniceps by Ellerman and Morrison-Scott (1951) but later reassigned to C. erythraeus by Corbet and Hill (1992), posterior taxonomic revisions have centered on the subspecific classification-or its omission-of certain forms within C. caniceps and have not altered this species concept (Ellerman and Morrison-Scott 1951; Moore and Tate 1965; Corbet and Hill 1992; Thorington and Hoffmann 2005; Koprowski et al. 2016). Seventeen subspecific names have been described within the species boundaries of C. caniceps (Corbet and Hill 1992), but only eight subspecies are currently accepted: C. c. caniceps, C. c. bimaculatus and C. c. concolor on the mainland, and C. c. adangensis, C. c. altinsularis, C. c. casensis, C. c. domelicus, and C. c. fallax on several small islands off the coast of peninsular Thailand (Thorington et al. 2012; Koprowski et al. 2016; Fig. 1).

The past two decades have provided insights into the molecular systematics of *C. caniceps*. A recent phylogenetic analysis based on cyt *b* that included a single *C. caniceps* population demonstrated that this species is most closely related to *C. phayrei* (Oshida et al. 2021). A later





**Figure 1.** Map of tropical East Asia indicating the localities of museum specimens examined in this study for *Callosciurus caniceps*. Different subspecies are labeled with different symbols, while different colors illustrate the potential distribution of the two major genetic lineages described by Hinckley et al. (2023a), inferred from pelage variation. Darker background shades correspond to higher elevations.

study based on mitochondrial and nuclear loci evidence across this species distribution supported the existence of two separately evolving lineages, potentially across the IoK, or the Kangar-Pattani Line (KPL) vegetation transition (Hinckley et al. 2023a). The northern lineage corresponds to the nominal subspecies and C. c. bimaculatus and the southern lineage corresponds to C. c. concolor (Fig. 1). These lineages diverged approximately 2.5 million years ago (mya), during the Pliocene-Pleistocene transition, as estimated by mitogenome divergence dating, which likely predates species divergence. The levels of differentiation among these lineages indicated by cyt b pairwise distances (4-5%) suggest that they could represent distinct species. These data clearly warrant further study according to the Genetic Species Concept (Bradley and Baker 2001; Hinckley et al. 2023a).

The taxon *Tamiops mcclellandii* is largely insectivorous and strictly arboreal, inhabiting the trunks and main branches of tall trees of forests and plantations (Bonhote, 1903; Moore and Tate 1965). It is found from eastern Nepal through Assam and Mizoram (India), northern and central Myanmar, Tibet and the Chinese province of Yunnan, northwestern Laos, northern Vietnam, Cambodia, and south through Thailand to peninsular Malaysia (Thorington et al. 2012; Fig. 2). It occupies a wide elevational range in hills and montane forests over 3200 m a.s.l. in some parts of its range (northwest) and reaching sea level in other regions (Moore and Tate 1965; Chakraborty 1975; Thorington et al. 2012). This species exhibits regional pelage and craniodental differentiation

(Moore and Tate 1965; Li et al. 2005; Thorington et al. 2012). Regional pelage variation led to the description of five nominal species, which are currently considered junior synonyms of T. mcclellandii (Moore and Tate 1965; Corbet and Hill 1992; Koprowski et al. 2016): Sciurus pembertoni Blyth, 1843, S. barbei Blyth, 1847, Tamias leucotis Temminck, 1853, S. novemlineatus Miller, 1903, T. inconstans Thomas, 1920. Trouessart (1899) synonymized all these species (along with heterospecific rodolphii and swinhoei) with T. mcclellandii, and considered barbei and swinhoei as distinct varieties. Bonhote (1900) and Robinson and Kloss (1918) followed Trouessart's (1899) species concept, but treated barbei, manipurensis, leucotis, novemlineatus, and/or kongensis as subspecies. They also reassigned maritimus, monticolus, swinhoei, formosanus, hainanus, riudoni, and/ or sauteri to T. mcclellandii. These forms were later allocated to Tamiops swinhoei (Ellerman and Morrison-Scott 1951) and Tamiops maritimus and T. rodolphii (Moore and Tate 1965). Currently, six subspecies are recognized: mcclellandii, barbei, collinus, inconstans, kongensis, and leucotis (Moore and Tate 1965; Corbet and Hill 1992; Thorington et al. 2012; Koprowski et al. 2016; Fig. 2). Both Moore and Tate (1965), and Li et al. (2005; regionally in China), identified the greatest pelage and craniodental differentiation, respectively, between the nominal subspecies and other subspecific forms.

Recent phylogenetic analyses (Hinckley et al. 2023a) revealed that *T. mcclellandii* is paraphyletic. Nominotyp-





Figure 2. Map of tropical East Asia indicating the localities of museum specimens examined in this study for *Tamiops mcclellandii*. Different subspecies are labeled with different symbols, while different colors illustrate the potential distribution of the two major genetic lineages described by Hinckley et al. (2023a), inferred from pelage variation. Darker background shades correspond to higher elevations.

ical populations from the eastern Himalayas and Arakan range (west of the Ayeyarwady/Irrawaddy River) are sister to a clade including Tamiops maritimus and Tamiops swinhoei. This clade in turn is sister to Sundaic and Indochinese populations to the east of the Himalayas and Arakan ranges, and Ayeyarwady/Irrawaddy River (T. m. barbei, T. m. collinus, T. m. inconstans, T. m. kongensis, and T. m. leucotis; Fig. 2). These "western" and "eastern" lineages display significant differentiation, with cyt b pairwise distances ranging from 9.7% to 12.5%, and an ancient divergence of approximately 10 mya (estimated via mitogenome divergence dating, which likely predates species divergence; Hinckley et al. 2023a). Nuclear loci species delimitation (CoMa) supported these two major lineages (Hinckley et al. 2023a). Therefore, molecular evidence suggests the necessity of reassessing species limits with additional lines of evidence.

Hinckley et al. (2023a) also evaluated a third taxon, *D. rufigenis* sensu lato, revealing additional complexities in this genus. The intricate evolutionary history of *D. rufigenis* sensu lato, coupled with unpublished findings, underscores the imperative of incorporating further taxa to reassess the taxonomy of this species complex, hence this taxon was excluded from the present research.

Here, we present a comprehensive integrative taxonomic review of *C. caniceps* and *T. mcclellandii* based on the molecular evidence of Hinckley et al. (2023a), along with new morphological data from museum specimens, verified records from both museum collections and citizen science across their distribution, and bioacoustic evidence (for *C. caniceps*). This review leads to the recognition of two species that had been lost in synonymy. By evaluating phenotypic differentiation across climatic and vegetation transitions and integrating our results with the evolutionary history of our study taxa, we gain insights into the distribution and ecogeographical patterns and speciation drivers in Southeast Asian vertebrates.

## **Materials and Methods**

#### Molecular and morphological data

Molecular (Hinckley et al. 2023a) and morphological samples were analyzed for both species included in this study (Table S1). All recognized subspecies were included in the analyses in order to have a robust representation of the morphological variation of each species (Table S1). We measured 86, and 218 specimens of *Callosciurus caniceps* and *Tamiops mcclellandii*, respectively. These specimens are housed in the following natural history repositories: **AMNH**, **FMNH**, **MCZ**, **USNM**, and **NHMUK** (Table S1). Skins were examined visually, and a geographically balanced subset were photographed for further evaluation. Specimens were identified to subspecies based on their pelage characteristics according to Moore and Tate (1965). Fusion of presphenoid-basisphenoid and basisphenoid-basioccipital sutures and dental eruption and wear patterns were examined to estimate age of specimens. Only adults were included in the craniodental morphometric analyses and baculum and pelage descriptions. We combined data from males and females in the morphometric analyses after running a statistical test to evaluate sex-biased patterns (see "Morphometric Statistical Analyses" and File S1). Craniodental measurements were taken with high precision electronic digital calipers to the nearest 0.01 mm.

Twenty-six craniodental measurements were collected by M. Hawkins for C. caniceps. These were collected as defined in Hayashida et al. (2007) except in two additional measurements: length of nasal bone (NL; defined as the most anterior tip of the nasal bone to the posterior suture with the frontal bone), and length of postorbital processes (LPOP; defined as the distance from the highest point of the orbit in parallel to the orientation of the skull to the most distal point of the postorbital process). After conducting an exploratory Principal Component Analysis on 40 specimens with 26 variables (Table S1), we identified a subset of eleven variables with the highest variance contribution: profile length (PL), short lateral facial length (SL), maximum width of the nasal bone (MWN), least breadth between the orbits (LBO), median palatal length (MPL), dental length (DL), length of molar row (LMR1), greatest palatal breadth (GPB), length from basion to staphylion (LBS), length from basion to the sagittal and rostral point of temporal bone (LBSR), and LPOP. These variables were then measured for an additional 44 specimens in C. caniceps.

Twenty-six measurements were collected by A. Hinckley for T. mcclellandii, as defined in Hinckley et al. (2020) for the cranium variables [occipitonasal length (ONL), zygomatic breadth (ZB), interorbital breadth (IB), length of nasals (LN), anterior nasal breadth (ANB), length of rostrum (LR), height of rostrum (HR), mastoid breadth (MB), height of braincase (HBC), length of orbit (LO), length of diastema (LD), length of bony palate (LBP), breadth of bony palate at fourth premolar (BBP), length of auditory bulla (LB), crown length of maxillary cheek teeth (CLPMM), median palatal length (MPL) and least breadth of caudal point of zygomatic process of frontal bone (LBC)] and Hayashida et al. (2007) for the mandible variables and braincase height [length from the condyle (LC), length of molar row (LMR2), thickness of mandible at middle point of M1 (TM), height of the mandible at M1 (HM), aboral height of the vertical ramus (AHR), oral height of vertical ramus (OHR), height from Akrokranion to Basion (HAB)]. We examined, measured and/or photographed all of the recognized subspecies types (Thorington et al. 2012), except for C. c. bimaculatus, C. c. fallax, T. m. barbei, for which topotypes were included (Table S1). Selected external measurements (in millimeters) including total length (TL), length of tail (T), length of hind foot including claws (HF), length of ear from notch (Ear), and weight in grams (W) were collected from specimen tags or field catalogs. When not provided, the length of head and body (HB) was calculated by subtracting the length of tail from total length. Only

hindfoot measurements (including nail) from American collections were included (Table S1).

We followed the terminology of Moore and Tate (1965) for describing pelage variation and of Thomas (1915) for defining baculum features. All available bacula at USNM were scanned, representing five in *Callosciurus* and twelve in Tamiops. Seven bacula were extracted and "cleaned", eight were retained inside the study skin phallus, and two were stored in situ in fluid specimens. The latter penises were removed from the specimens near the base of the phallus and stored in microcentrifuge tubes before being scanned. Bacula were scanned on a GE Phoenix v|tome|x M 240/180kV Dual Tube micro-computed tomography (µCT) scanner at the USNM. Scans were performed with the following settings: 90 kVp, 155 uA, without Al filter, exposure time of 500 msec, and voxel size of 8-10.5 µm in C. caniceps, and 7.6-9.7 µm in T. mcclellandii. Image stacks were visualized and segmented using 3D Slicer v5.6.0 (Fedorov et al. 2012). Hard tissues were separated from the background using the "threshold" function within the "Segment Editor" module and visualized with the "Volume rendering" module.

#### Morphometric Statistical Analyses

We log-transformed each measurement prior to computing the principal component analysis (PCA) so that the data was analyzed on the basis of correlations instead of covariances. PCA was implemented in R (R Core Team 2013), with results extracted and visualized with the following functions of the 'factoextra' package (Kassambara and Mundt 2017): 'fviz pca ind' for plotting PCA results; 'fviz pca biplot', for biplots of individuals and variables, "get eigenvalue" for extracting eigenvalues, variance percentage and cumulative variance percentage and 'get\_pca\_var' for outputting each variable's contribution to variance. To overcome issues arising from the damaged state of many skulls we followed two approaches to increase the number of samples, geographic coverage and types in our analyses. After running a preliminary PCA with all measurements, a second PCA was run with a higher number of samples but with just eleven measurements in C. caniceps, and without mandible variables, LO and jugal bone height in T. mcclellandii. Only measurements missing in many samples and/or that had a low variance contribution were removed, leaving a total of eleven measurements for C. caniceps, and seventeen for T. mcclellandii (Table S3). Bivariate plots of craniodental and standard external measurements were computed to include badly damaged but informative specimens thereby improving sample size and geographic sampling. Several selected external measurement outliers were removed after the initial exploratory bivariate plots. These outliers were frequently restricted to the same specimens (e.g., USNM 535166, 356726, 297003, which had both HB and HF outliers) and were excluded after skin reexamination and re-measuring.

We followed the standardized and statistically robust framework proposed by Chan and Grismer (2021) to provide statistical validation for potential diagnostic distinctions among putative species and to mitigate the influence of body size on such comparisons. This approach enabled comparisons across putative species of varying sizes by incorporating the allometric growth model as articulated by Thorpe (1975) to adjust for ontogenetic variations in body size. This framework assesses sex dimorphism, identifies outlier measurements, and evaluates univariate normality and homogeneity of variance prior to size correction and subsequent application of t-tests/ANOVAs (Chan and Grismer 2021; File S1). These analyses complement descriptive univariate statistics, which are essential for species delineation and comparative purposes, particularly as size-corrected variables may not be applicable in field conditions.

#### Citizen science records

Museum specimen-based evidence was complemented with citizen science data from iNaturalist, Observation, and India Biodiversity records with associated images. Morphological results indicated that separately evolving metapopulation lineages within C. caniceps and T. mcclellandii were diagnosable based on pelage features. This approach allowed us to gain insights into the finescale distribution and phenological pelage variation of putative species. Verified records with pictures were retrieved from GBIF. In addition, unverified iNaturalist records, with less than three identifications, were also examined across the putative contact area among both C. caniceps lineages in May 2024 (Table S2). Several counties generally associated with protected areas, touristic sites or cities (e.g., Kaeng Krachan NP, Khao Yai NP, Fraser Hill, Chiang Dao, Phuket, Hat Yai, Bangkok, Kuala Lumpur, etc.) had many records and were far away from the contact zone. In these counties a single record was generally kept for the sake of simplicity. We were able to confidently verify a total of 189 citizen science records from unique localities for C. caniceps and 39 for T. mcclellandii. We generated species occurrence maps in RStudio v. 2023.09 with these citizen science records and verified museum specimen records, following the multispecies species occurrence map tutorial at https://github. com/wtesto/SpeciesOccurrenceMapping.

#### Mating call recording and analysis

A total of 84 mating call events emitted by males were recorded by N. Tamura for the putative/recognized species *C. caniceps, C. concolor*, and *C. inornatus*, in the course of several published studies (Tamura et al. 2018, 2021) and ongoing research on *Callosciurus* bioacoustics and systematics (Table S4). Tamura followed the methods outlined in these studies. Each species was recorded in a single locality with a sound recorder in a 16-bit WAV format using the internal microphone of a Sony PCM- D1, positioned at a height of about 1.5 m. Recording localities were: Ulu Gombak, Selangor, Malaysia (3.324769, 101.752711; C. concolor); Sublangka Wildlife Sanctuary, Lopburi, Thailand (15.567933, 101.358142; C. caniceps); Dong Phaya Yen WRS, Nakhon Ratchasima, Thailand (14.316667, 101.918611; C. caniceps); Xishuangbanna, Yunnan, China (22.027075, 100.874761; C. inornatus). Five variables were measured: (1) number of pulses per call, (2) total duration (s), (3) pulse interval (s), (4) dominant frequency (= maximum energy; Hz), and (5) frequency modulation (Hz).

Principal Component Analysis and univariate plots were run as described for the craniodental morphometrics methodology. Discriminant analysis (DA) and standard univariate statistics were run following Tamura et al. (2018). Mating call sonograms of Callosciurus spp. are shown in the File S1, while DA and standard univariate statistics results are shown in Table S4.

## Results

#### Craniodental and external selected measurement morphometric analyses

Morphometric evidence was consistent with the molecular evidence of Hinckley et al. (2023a), showing that the two major lineages within C. caniceps and T. mcclellandii were morphologically distinct with minimal morphospace overlap in PCA and bivariate plots (Figs 3, 4, S1, S2).

In C. caniceps, the craniodental PCA discriminated the northern and southern lineages based on size, with a small degree of overlap (Fig. 3). PC1 and PC2 accounted for c. 57 and 29% of the variance, respectively (File S1 [Table S5]). On PC1, all variables had positive loadings indicating that most variation was size-related. PC2 was highly correlated with LPOP. The southern lineage showed a

C. c. adangensis  $\wedge$ C. c. fallax C. c. helvus  $\bigcirc$ 

smaller size than the northern lineage, with the exclusion of two dwarf specimens from Koh Tao island (referred to as form *helvus*), and relatively larger postorbital processes (Fig. 3; File S1 [Table S5]). The morphospace of the northern and southern lineages only overlapped in the PCA due to a very old adult of the smaller southern species (USNM 488172; Fig. 3). Similarly, an LBO/LPOP bivariate plot largely distinguished both lineages, with only very young "north" specimens from Mergui, Ranong, and Phanggan (USNM 355609, 355756, 356718) slightly overlapping with "south" populations (Fig. S1B). Potentially admixed individuals with an intermediate pelage coloration (USNM 256872, 355078) clustered within the southern lineage morphospace, but close to the north cluster (Fig. 3). To sum up, the Sundaic lineage showed a smaller size, relatively larger postorbital processes and a smaller ear (Fig. S1). Koh Tao pygmy specimens lacked external data and could not be included n external variable comparisons. Statistical analyses on the craniodental dataset supported a lack of sexual dimorphism in C. caniceps. Significant differences in PL, DL, and MPL were found between the northern and southern lineages. The parametric t-test supported the difference in PL, while the non-parametric Wilcoxon test supported the differences in DL and MPL (File S1 [Table S6]).

In T. mcclellandii, the craniodental PCA discriminated between northern and southern lineages based on shape, with only a small degree of overlap (Fig. 4). PC1 and PC2 accounted for c. 53% and 12.5% of the variance, respectively (File S1 [Table S7]). Positive loadings in all variables in PC1 suggest it is also correlated with size. Southern and northern lineages were discriminated along the PC2 axis, which had high loading values for rostrum height, braincase height, and interorbital breadth (Fig. 4; File S1 [Table S7]). Southern lineage specimens have a deeper rostrum and broader interorbital constriction, but a more flattened braincase than

C. c. altinsularis C. c. bimaculatus C. c. bimaculatus-concolor C. c. caniceps C. c. casensis C. c. concolor C. c. domelicus

Figure 3. Morphometric variation in Callosciurus caniceps. First and second principal components from an analysis of 11 craniodental variables. Samples are colored according to the two main lineages from Indochina (in blue) and Sundaland (in orange), and the Koh Tao dwarf population (in pink). Different subspecies are labeled with different symbol-color combinations.





**Figure 4.** Morphometric variation in *Tamiops mcclellandii*. A First and second principal components from an analysis of 17 craniodental variables. **B** Second and third principal components of the same analysis. Samples are colored according to the two major lineages: Sundaland and Indochina (in blue and green), and Himalayas and Arakan Range (in orange). The former of which is further subdivided in two lineages shown here for the sake of comparison: NE Indochina (in green) and remaining Indochina and Sundaland (in blue). Different subspecies are labeled with different symbols.

north lineage specimens. In T. mcclellandii, the southern lineage populations from western and central Indochina showed a longer tail than northern lineage and the remaining southern lineage populations (Fig. S2A). Thus, parapatric populations of the south and north lineages show a distinct head and body-tail ratio. Northern and southern lineages can also be discriminated based on their height of rostrum/height of braincase ratio, although there is some overlap, particularly between the northern lineage and T. m inconstans (Fig. S2B). Statistical analyses on the craniodental dataset supported a lack of sexual dimorphism in T. mcclellandii. Significant differences in ZB, BR, HR, HBC, BBP, LB, HAB, CBL, IB, LD, LBP, and LN were found between the northern and southern lineages. The parametric t-test supported the difference in ZB, BR, HR, HBC, BBP, LB, and HAB, while the non-parametric Wilcoxon test supported the differences in CBL, IB, LD, LBP, and LN (File S1 [Table S8]).

#### Pelage and bacular variation

Pelage is a key trait in subspecific taxonomy and appears to reflect evolutionary history in *C. caniceps*, and

T. mcclellandii, since major lineages within each taxon are diagnosable based on this trait (see taxonomic section for a description of pelage variation in each of these lineages). Conversely, pelage was largely inconsistent based on molecular evidence within the south T. mcclellandii lineage. A careful examination of a large series at NHMUK suggests that the red suffusion in the dorsal pelage displayed by Indochinese T. m. barbei is affected by sex and phenology. Specimens of T. m. leucotis and T. m. barbei collected at the same localities (Perak, Semangko Pass, Ginting Bidai) and time of the year suggest that females usually exhibit a more reddish suffusion than males. Similarly, a comparison of specimens or iNaturalist pictures from same locations but different times of the year showed that specimens had a more reddish coloration during the wet season. The differentiation between T. m. kongensis and T. m. collinus seems to be the result of ecophenotypic variation, since the former represents a wetter area form, and the latter, a drier area form. These subspecies lack cohesive ranges since some individuals that resemble *collinus* are in the range of *kongensis* (drier central Thailand).

Bacular variation reflects evolutionary history in *C. caniceps*, and *T. mcclellandii*, since major lineages within each of these taxa are diagnosable based on several features (see taxonomic section for a description of baculum variation in each of these lineages).

#### Mating call variation

Both, the PCA and DA discriminated the northern and southern genetic lineages of C. caniceps and its close relative C. inornatus with just some minor overlap (Fig. 5A; Table S4). Most overlap between C. caniceps lineages in the PCA was due to a single "outlier" call from the southern population (Fig. 5A). PC1 and PC2 accounted for 72% and 19.5% of the variance, respectively (Fig. 5A). PC1 was highly correlated with frequency modulation and PC2 was mainly correlated with number of pulses and pulse interval (File S1). Southern lineage mating calls are characterized by a higher number of pulses and frequency modulation (Fig. 5B, 5D; File S1, Part B) but a lower pulse interval than northern lineage calls (Fig. 5C; File S1, Part B). The DA results are consistent with the PCA findings, identifying the number of pulses and pulse interval as the variables with the highest discriminatory power between the C. caniceps lineages. These variables accounted for most of the variance in function 1, which effectively

distinguished the putative species (Table S4). The correct classification rate was high at 86.9%. Notably, *C. inorna-tus* exhibited a more distinct mating call with geographically closer northern lineage populations than with the more distant southern lineage (Fig. 5A; Table S1).

#### **Taxonomic revision**

Based on our findings, which unite molecular phylogenetic (Hinckley et al. 2023a), morphological evidence described below and in previous studies (Pocock 1923; Moore and Tate 1965; Hayashida et al. 2006), and bioacoustic data (in *C. caniceps* sensu lato), we conclude that the populations of *Callosciurus caniceps* sensu lato inhabiting Sundaland, and *Tamiops mcclellandii* sensu lato populations to the east of the Himalayas and Arakan range, should be recognized as distinct species. We revalidate the specific status of *Callosciurus concolor* (Blyth, 1855) and *Tamiops barbei* (Blyth, 1847), as these names represent the earliest descriptions of these separately evolving lineages. Additionally, we provide emended diagnoses and detailed species comparisons for both taxa and their sister species.



**Figure 5.** Variation in mating calls of *Callosciurus* species. A Principal Component Analysis highlighting mating call variation. **B** Univariate plot showing the number of pulses per call. **C** Univariate plot of pulse intervals, in seconds. **D** Univariate plot of frequency modulation, in Hz. Different taxa are represented by distinct symbols.

#### Callosciurus caniceps (Gray, 1842)

#### Common name. Northern gray-bellied squirrel

- Sciurus caniceps Gray, 1842, Annals and Magazine of Natural History (Series 1) 10: 263.
- Sciurus chrysonotus Blyth, 1847, Journal of the Asiatic Society of Bengal 16: 873.
- *Sciurus bimaculatus* Temminck, 1853, Esquisses zoologiques sur la côte de Guiné, Mammifères: 251.
- *Sciurus epomophorus* Bonhote, 1901, Annals and Magazine of Natural History (Series 7) 7: 272.
- Sciurus davisoni Bonhote, 1901, Annals and Magazine of Natural History (Series 7) 7: 273.
- Sciurus sullivanus Miller, 1903a, Smithsonian Miscellaneous Collections 45: 17.
- Sciurus domelicus Miller, 1903a, Smithsonian Miscellaneous Collections 45: 18.
- Sciurus bentincanus Miller, 1903a, Smithsonian Miscellaneous Collections 45: 19.
- Sciurus matthaeus Miller, 1903a, Smithsonian Miscellaneous Collections 45: 19.
- Sciurus casensis Miller, 1903a, Smithsonian Miscellaneous Collections 45: 19.
- Sciurus lucas Miller, 1903a, Smithsonian Miscellaneous Collections 45: 20.
- Sciurus altinsularis Miller, 1903a, Smithsonian Miscellaneous Collections 45: 21.
- Sciurus epomophorus milleri Robinson & Wroughton, 1911, Journal of the Federated Malay States Museum 4: 233.
- Sciurus concolor fallax Robinson & Kloss, 1914, Annals and Magazine of Natural History (Series 8) 13: 225.
- Sciurus concolor samuiensis Robinson & Kloss, 1914, Annals and Magazine of Natural History (Series 8) 13: 226.
- *Sciurus epomophorus inexpectatus* Kloss, 1916, Journal of the Natural History Society of Siam 2: 178.
- Sciurus helgei Gyldenstolpe, 1917, Kungliga Svenska Vetenskapsakademiens Handlingar 57: 34.
- Callosciurus epomophorus nakanus Thomas & Robinson, 1921, Annals and Magazine of Natural History (Series 9) 7: 120.
- Callosciurus epomophorus mapravis Thomas & Robinson, 1921, Annals and Magazine of Natural History (Series 9) 7: 120.
- Callosciurus epomophorus panjius Thomas & Robinson, 1921, Annals and Magazine of Natural History (Series 9) 7: 119.
- Sciurus caniceps helvus Shamel, 1930, Journal of Mammalogy 11: 72.

**Holotype.** Not specified in species description. Robinson and Kloss (1918) substitute the erroneous Bhutan type locality by North Tenasserim, and mention the "type" is at the "British Museum" (NHMUK) but do not specify its catalog number. Moore and Tate (1965) and NHMUK staff suggest the following lectotype: NHMUK 41.1817, field number 213a, an adult male prepared as a mounted skin with a damaged tail & cleaned damaged skull (Fig. 6A).

**Type locality.** N Tenasserim, Burma [= Tanintharyi province, Myanmar]. Emended diagnosis. A relatively large-sized Callosciurus (average HB = 228.6 mm, PL = 52.6 mm; Table S6) distinguishable from all other relatives by a sharply marked black tail tip along with two alternative pelage combinations corresponding to its subspecies. In the northern part of its distribution, it displays a bright ochraceous/rufus orange on the flanks and dorsum during the dry season and agouti gray in the wet season. The bright orange fades into agouti gray as it approaches the venter, crown, and proximal one-tenth of the tail. The ears are agouti gray, generally with white hairs along the rim, occasionally resembling a tuft (C. c. caniceps; Moore and Tate 1965). In the southern part of its distribution, "the upper parts of the head, neck, all the back and the tail as far as the tip bear a ... pelage regularly ringed with ashy and black ..." (Temminck 1853), with a rusty reddish suffusion in the side of the neck, and frequently, in the flanks and upper part of the legs; venter coloration is whitish gray, with a red suffusion in the groin area in adult specimens (C. c. bimaculatus and C. c. helvus). Its baculum consists of a shaft and blade; shaft lacks a dorso-lateral expansion at its proximal end; blade base has a reduced lateral expansion at its posterior half, giving it a straight appearance from a lateral view, and a relatively triangular shaped appearance from a dorsal view (Fig. 7); mating call characterized by an average of 8.1 pulses, mean pulse interval of 0.195 seconds, and average frequency modulation of 493 Hz.

**Comparisons.** A detailed comparison with its closest relative, *C. concolor*, has been included in the following account. *Callosciurus caniceps* can be distinguished from all parapatric/sympatric squirrels, including *C. concolor*, by the combination of gray ventral pelage, lack of a black band in the flank, presence of an abruptly marked black tail tip, and during the dry season, bright ochraceous/rufus orange in flanks and dorsum or rusty reddish suffusion on the side of the neck and groin.

**Distribution, habitat, and natural history.** Distributed across mainland Thailand west to the Mekong and up to ca. 19°N latitude, covering the northern two thirds of peninsular Thailand, and southern Myanmar (Figs 1, S3; south of the Salween River; Moore and Tate 1965). Pelage and craniodental variation suggest its southern distribution limits are in Trang, Surat Thani, and Nakhon Si Thammarat provinces (Fig. S3). However, these provinces were not included in the genetic sampling of Hinckley et al. (2023a), which only included specimens north of 7.99 and south of 7.15 latitude. For a more detailed description of this species' southern distribution extent, see the account and discussion for *C. concolor*.

Generalist species found in dry deciduous forest and dry evergreen forest, bamboo forest, secondary forest, parks, gardens, and coconut plantations (Moore and Tate 1965; Kobayashi et al. 2020). In northern Thailand it is only common in bamboo-forests at rather high altitudes (Gyldenstolpe 1914). In Sakaerat Biosphere Reserve in northeastern Thailand, *C. caniceps* frequently used the ground (34.7%; Kobayashi et al. 2018), which contrasts



**Figure 6.** Dorsal and ventral views of the skins of (**A**) *Callosciurus caniceps* (NHMUK 41.1817, lectotype); live images of (**B**) *C. caniceps caniceps* taken by Natthaphat Chotjuckdikul (Te') in Bangkok, Thailand; (**C**) *C. caniceps bimaculatus* taken by Pattaraporn Vangtal in Railay Bay Beach, Krabi, Thailand; and (**D**) *C. concolor* taken by Cheong Weng Chun in Fraser's Hill, Pahang, Malaysia.



Figure 7. Baculum comparison between *Callosciurus caniceps* and *C. concolor*. A Lateral view of *C. caniceps* (USNM296998). B Dorsal view of *C. caniceps* (USNM296998). C Lateral view of *C. concolor* (USNM283481). D Dorsal view of *C. concolor* (USNM283481).

with little ground use by its sister species' (ca. 2%; Abdullah et al. 2001; Tamura 1995). In support of this observation, there are 29 records of *C. caniceps* on the ground from iNaturalist, compared to just two for *C. concolor*. Further research is required to determine if these behavioral differences are consistent across both species' ranges. *Callosciurus caniceps* is frequently found in sympatry with *C. finlaysoni*, with which it minimizes competition through diet preferences and/or vertical zonation segregation (Kobayashi et al. 2018).

This species has been observed feeding on fruits of *Terminalia catappa* and *Tamarindus indica*, and flowers of *Triplaris americana* in Bangkok parks, and on ten species of plants including *Ficus* fruits, *Sterculia pexa* and *Acasia* seeds, or *Mucuna macrocarpa* nectar in Sakaerat Biosphere Reserve, and *Musa acuminata* in Kanchanaburi (Marod et al. 2010; Sommung and Hawkesgood 2016; Kobayashi et al. 2018, 2019, 2020). Fruits and seeds accounted for 71.4% of observed food items in a human-disturbed area of Sakaerat, while bark was the most common food item (ca. 33%) in adjacent undisturbed forests, suggesting a flexible diet (Kobayashi et al. 2018, 2020).

Reproductive information is scarce. A female collected on 11 March 1900 in the Mergui archipelago had two embryos (W.L. Abbott field notes, USNM Mammal Division Archives). No other reproductive information was easily obtained.

**Conservation.** Recorded in several protected areas, including Doi Pha Hom Pok, Khao Yai, Kaeng Krachan, Erawan, Nam Tok Tham Sadet, Sirinat, Mu Ko Lanta, Khao Luang, and Hat Chao Mai National Parks, Sakaerat Biosphere Reserve, and Chiang Dao Wildlife Sanctuary (iNaturalist; Table S1). Despite these records, the frequency of detection of *C. caniceps* was lower in areas with human activity compared to adjacent forests even when human activity and fragmentation impacts were minimal (Kobayashi et al. 2020). This species (sensu lato) is currently considered of least concern. However little is known about its population density, and one study found it to be far less common than a congeneric species, *Callosciurus finlaysonii* (Kobayashi et al. 2020).

**Comments.** The subspecies *C. c. bimaculatus* and *C. c. caniceps* represent two distinct but recently diverged mitochondrial clades, exhibiting limited nuclear differentiation (Hinckley et al. 2023a). Interestingly, both subspecies seem to be present in Koh Tao island. A single Koh Tao "*caniceps*" could be included in the craniodental PCA and this was clustered with the mainland populations while the two specimens resembling "*bimaculatus*" (USNM

253434, 253438), actually representing the form "helvus", showed a distinct morphospace due to their dwarf nature. Unfortunately, the only Koh Tao individuals sequenced in Hinckley et al. (2023a) belonged to the "caniceps" form. Thus, given its distinct morphospace (Fig. 3) and pending molecular evidence, we here consider the pygmy Koh Tao population a valid subspecies: C. caniceps helvus. This subspecies was wrongly synonymized with nominotypical C. caniceps in Moore and Tate (1965) given that the holotype pelage resembles that of C. c. bimaculatus. Previously recognized island subspecies are here synonymized since these generally resemble the closest mainland populations but with slight variations such as a pale tail underside (casensis, and fallax) or a darker (domelicus, fallax) or paler (altinsularis) dorsum.

#### Callosciurus concolor (Blyth, 1855)

#### Common name. Southern gray-bellied squirrel

- Sciurus concolor Blyth, 1855, Journal of the Asiatic Society of Bengal 24: 474.
- Sciurus adangensis Miller, 1903a, Smithsonian Miscellaneous Collections 45: 17.
- Sciurus lancavensis Miller, 1903a, Smithsonian Miscellaneous Collections 45: 16.
- Sciurus concolor terutavensis Thomas & Wroughton, 1909, Annals and Magazine of Natural History (Series 8) 4: 535.
- Callosciurus erubescens Cabrera, 1917, Boletín de la Real Sociedad Española de Historia Natural 17: 518.
- Callosciurus concolor telibius Thomas & Robinson, 1921, Annals and Magazine of Natural History (Series 9) 7: 121.
- *Callosciurus moheius* Thomas & Robinson, 1921, Annals and Magazine of Natural History Annals and Magazine of Natural History (Series 9) 7: 122.
- Callosciurus moheius mohillius Thomas & Robinson, 1921, Annals and Magazine of Natural History (Series 9) 7: 122.

**Holotype.** ZSI9328. Skin and skull, collected or donated by G. Moxon in 1847. This specimen was not cited in the "Annotated Catalogue of the Type Specimens of the Indian Museum" (Khajuria et al. 1977), but the skin is still housed in the National Zoological Collection of the Zoological Survey of India (Uttam Saikia pers. comm.). Other catalog numbers linked to this specimen are: Zoological Survey of India barcode number: ZSI 0000004087; Indian Museum of Kolkata catalog number: "w".

**Type locality.** From the vicinity of Malacca" [Melaka, Malaysia].

**Emended diagnosis.** A medium-sized *Callosciurus* (average HB = 218.3 mm, PL = 49.1 mm) that can be distinguished from all other relatives by the combination of the following morphological characters: "reddish suffusion of color occurring on the mid dorsum [that usually extends to the proximal section of the tail] but not on the sides of the neck and body...; absence of a sharply marked off, quite black tip of the tail... [except in north-

ern edge populations; see following sections], and a cool silvery gray color of the venter" (Moore and Tate 1965), that lacks a reddish suffusion in the groin area; cranium with relatively long postorbital processes (LPOP: 3.8–5.8 mm), particularly proportionally to its least interorbital length (LBO: 16.3–18.8 mm); baculum consists of a shaft and blade, shaft has a dorso-lateral (right) expansion at its proximal end, blade base has a large lateral expansion at its posterior half, giving it a sinuous appearance from a lateral view, and a relatively rounded/oval shaped appearance from a dorsal view (Fig. 7); mating call characterized by an average of 17.9 pulses, mean pulse interval of 0.098 seconds, and an average frequency modulation of 1476 Hz.

Comparisons. Callosciurus concolor can be distinguished from its closest relative, C. caniceps, by its smaller size (average HB: 220 vs 235 mm; with the exception of the C. caniceps Koh Tao Island dwarf population, which is even smaller than C. concolor and excluded from this comparison). Additionally, this species exhibits relatively longer postorbital processes and a distinct distribution of ornamented pelage coloration. During the dry season, its dorsum has a reddish suffusion in the midline that generally extends to the most proximal side of the tail, while C. caniceps has a brighter, ochraceous/rufus orange in flanks and dorsum (C. c. caniceps) or a rusty reddish suffusion in the side of the neck and groin, and frequently, in the flanks and upper part of the legs (C. c. bimaculatus; Fig. 6). In the wet season, this reddish suffusion disappears or becomes less conspicuous in both species, but C. caniceps generally still retains a yellow/orange-brown hue. This hue can at least be noted in the side of the neck and groin in C. c. bimaculatus and in a few small patches throughout the dorsum in C. c. caniceps, which greatly contrast with the darker gray ash coloration in the latter. The venter of Callosciurus concolor is silvery gray distinct from the whitish gray (C. c. bimaculatus) or agouti gray (C. c. caniceps). Another diagnostic feature is the absence of a sharply marked off, black tail tip throughout most of C. concolor populations, whereas C. caniceps typically exhibits such feature. Notably, C. concolor populations in Langkawi, Adang, Terutao (1/8 specimens), and Songkhla have a black tail tip that is generally shorter and/or less intensely black than that of C. caniceps, resulting in a less pronounced contrast. However, in Trang, Surat Thani, and Nakhon Si Thammarat, the black tail tip of C. concolor is highly contrasted as in C. caniceps. Examined specimens from the latter two provinces, and all the rain-shade area until Singora have a washed dorsum coloration and possibly lack an ornamented dorsum midline during the breeding season. Thus, the absence of reddish suffusion in the groin area of C. concolor, compared to its presence in C. caniceps bimaculatus, along with the presence or absence of red suffusion on the side of the neck, appear to be the best diagnostic features for distinguishing these species in the contact areas of Surat Thani, Trang, and Nakhon Si Thammarat, and perhaps also in Satun, Phatthalung and Songkhla. However, juvenile and subadult specimens lack this reddish hue, sug-

gesting this feature is diagnostic primarily in adults. The skull of C. concolor is smaller (PL: 46-51.5 vs 49.7-56.2 mm) with a shorter rostrum (SL: 18.0-21.2 vs 20.4-24.4 mm) and interorbital breadth (LBO: 16.3-18.8 vs 18.3-21.7 mm; Fig. S1A), but relatively larger postorbital processes (average LPOP: 4.7 vs 4.8 mm; Fig. S1B) than C. caniceps. As mentioned, the allopatric dwarf population on Koh Tao island has a smaller size than C. concolor and was excluded from these comparisons, but it shows a distinct shape and its morphospace does not overlap with C. concolor, due to the combination of relatively larger postorbital processes and relatively shorter interorbital breadth of C. concolor with regard to the Koh Tao population (Figs 3, S1A, B). Allometric size-controlled statistical analyses only supported significant differences in PL, DL, and MPL between C. concolor and C. caniceps (File S1). Paradoxically, these measurements are the largest, perhaps suggesting an allometric size effect in the data, and that these sister species differ mainly in size, with little shape differentiation.

Baculum morphology provides additional distinguishing characteristics between *C. concolor* and *C. caniceps*: Presence vs absence of a dorso-lateral (right) expansion at shaft proximal end in *C. caniceps*; presence vs absence of a large lateral expansion at blade base posterior half in *C. caniceps*, giving a sinuous (*C. concolor*) vs straight (*C. caniceps*) appearance from a lateral view, and a relatively rounded/oval (*C. concolor*) vs triangular (*C. caniceps*) shaped appearance from a dorsal view (Fig. 7).

Finally, *C. concolor* can be easily distinguished from its closest genetic relative, *C. caniceps*, by its generally distinct mating call (Fig. 5A; Table S4, correct discrimination rate = 87%). This is characterized by an average of 17.9 pulses, mean pulse interval of 0.098 seconds, and average frequency modulation of 1476 Hz vs an average of 8.1 pulses, mean pulse interval of 0.195 seconds, and average frequency modulation of 493 Hz in *C. caniceps* (Fig. 5B–D).

It can be easily distinguished from sympatric congeneric *C. notatus* and *C. nigrovittatus* by its lack of lateral stripes, and from *C. erythraeus* by its silvery gray venter, grayish head and limbs which contrast with the remaining dorsum, and darker tail tip vs reddish brown, reddish or agouti venter, homogeneously olive brown colored dorsum, including head, limbs and tail. It can be distinguished from sympatric *Sundasciurus robinsoni*, *S. tahan*, and *S. tenuis* by its larger size, grayish head and limbs, bushier dark-tipped tailed, and thinner and less contrasted pale eye ring, and from *S. hippurus* by its silvery gray venter coloration with just some black or dark gray/brown in the tail tip vs rusty red venter with entirely black tail in *S. hippurus*.

**Distribution, habitat, and natural history.** Distributed across the Thai-Malay peninsula extending from Melaka to Trang province in the west coast and from central Pahang to Surat Thani in the east coast (Figs 1, S3). Habitat generalist recorded in lowland and hill primary and secondary dipterocarp forests recorded up to ca. 1135 m a.s.l., plantations, and urban/suburban areas (Moore and

Tate 1965; Tamura and Yong 1993; Abdullah et al. 2001; Saiful and Nordin 2004). In Ulu Gombak (Malaysia), C. concolor preferred bushy areas with a larger number of small trees, in contrast with C. notatus that showed preference for the opposite (Tamura and Yong 1993). In this reserve, the four species of squirrels use different levels of the habitat: L. insignis uses the ground, C. concolor lower levels, C. notatus middle levels, and C. nigrovittatus the highest levels of trees (Tamura 1995). In the same site, it was shown to feed on 13 species of plants-on fruits (45%), leaves (21%), bark (17%), and flowers (10%)with "others" comprising the rest of its diet. These consisted mainly of the fruits of Artocarpus elasticus, Piper adancum and Ficus spp., and leaves of Bambusa vulgaris (Abdullah et al. 2001). Other studies in Malaysia based on stomach content examination instead of feeding observations showed that all specimens contained fruit and vegetable matter, and six contained insect remains (n = 9;Harrison 1954, 1961). In Ulu Gombak, the average size of home ranges of males was 2.65 and 3.73 ha, and that of females was 0.79 and 1.54 ha, and females ranges overlap, contrasting with the lack of overlap in other Callosciurus spp. (Tamura 1993; Saiful et al. 2001). Mating bouts were observed from March to July in this site (Tamura 1993). In Selangor, this species has been recorded in sympatry with C. nigrovittatus, C. notatus, C. erythraeus, Sundasciurus tenuis, Sundasciurus hippurus, Lariscus insignis, Rhinosciurus laticaudatus (R. Traub field notes; USNM Mammal Division archives).

Conservation. Recorded in Labis and Ulu Gombak Forest Reserves, Hala Bala Wildlife Sanctuary, Perlis, Gunong Stong and Selangor State Parks, Tasik Bera Ramsar Site, and Taman Negara National Park (Jayaraj et al. 2013; Ling et al. 2018; William-Dee et al. 2019; Munian et al. 2020; Fauzi et al. 2021; iNaturalist; USNM specimens). It was the most abundant *Callosciurus* species in a logged hill forest (8.1 individuals/ha) but the least abundant one in a primary hill forest, perhaps suggesting a preference for secondary forests (Tamura and Yong 1993; Saiful et al. 2001; Saiful and Nordin 2004). Similarly, it was not recorded in the primary forest of Krau Game Reserve but it was frequently seen in rubber plantations around the reserve (Mackinnon 1978). This species is destructive in plantations of Artocarpus integrifolia and Cocos nucifera in various states of Malaysia (Moore and Tate 1965).

**Comments.** Northwestern edge populations from the islands of Langkawi (named form *lancavensis*), Telibun [Ko Libong] (named form *telibius*), Adang (named form *adangensis*) and Mohea, Nakhon Si Thammarat (named forms *mehoeius/mohillius*), have a pelage that is somewhat intermediate between *C. concolor* and *C. caniceps bimaculatus*, but more similar to the former (This study; Moore and Tate 1965). These have a more sharply marked-off, black tip of the tail than other *C. concolor* populations (*bimaculatus*); generally lack the red suffusion in the neck side (*concolor*), except a single specimen in Lankawi, Ko Terutao and Ko Libong which had some faint yellow *C. c. bimaculatus*; lack a reddish suffusion in

flanks and groin (concolor), and generally have a venter gray coloration that seems intermediate between concolor and bimaculatus (This study; Moore and Tate 1965). Specimens from Langkawi, Adang and Terutao islands were included in the craniodental PCA and are however clearly within the morphospace of C. concolor. Ko Libong museum specimens could not be examined but citizen science pictures suggest these are C. concolor, and/or potential hybrids (Table S3). Remarkably, museum specimens (USNM 83235) and pictures taken 3 km away, in the mainland (Prahmon, Yan Ta Khao District, Hat Chao Mai NP and Mot Tanoi Beach) show a C. caniceps skull and/or pelage. The mouth of the Trang and/ or Palian River might represent the northwestern limit for this species at the west coast since a specimen from "Trang" (USNM 86780), which must have been collected in a locality east of this river (according to W.L. Abbott's field notes all localities sampled during the timeframe in which the specimen was collected were east of this river) and Kao Soi Dao (7.35, 99.86; USNM 258917-8), which is southeast of Trang River, showed C. concolor craniodental morphospace and/or pelage. Potential hybrid specimens are recorded at this river headwaters, in Lay Song Hong (7.83, 99.45; USNM 83495-7), while C. c. bimaculatus with a faintly ornamented pelage side are recorded in Khao Chong (USNM 258916; 7.54, 99.79), at the foothills of the Nakhon Si Thammarat Range (NSTR). This suggests that the Trang and/or Palian Rivers and NSTR might have constituted physical barriers to gene flow to some extent. Similarly, on the east coast, C. caniceps seems to have its southern limit around Surat Thani city and Ban Ta Yai (8.38, 99.87), potentially at the confluence of two major rivers: Ta Pi and Phum Duang. Tha Lo, which is SW of the city, has potential hybrids (Fig. S4). The species C. caniceps seems to be distributed north of these rivers and west of NSTR (e.g., Ban Kok Klap, 8.88, 99.28; Robinson and Kloss 1915), while C. concolor seems to be found to the east of this range (Ban Ta Yai, Nakhon Si Thammarat; Figs 1, S3). Furthermore, specimens (USNM 355078, 355079, 35580, 535161; Fig. S4) collected in this mountain range or at its foothills (Doi Kaeo, Nam Tok Tha Phae, and Ban Tha Phae, at Lan Saka and Chawang districts) have a hybrid pelage (red infusion in mid-line but also in the sides, particularly on the neck, and groin area, or C. concolor venter with C. caniceps dorsum coloration). However, specimens from Ban Nam Tok, Ban Na and Thafa, unknown localities also at Chawang district (USNM 535159, 535163-8), have C. caniceps pelage. Just at 30 km from the potential hybrid population of Nam Tok Tha Phae, and at the east side of NSTR, there is Ban Ta Yai (8.38, 99.87) which has C. concolor pelage. Craniodental data is quite consistent with pelage since localities from Nakhon Si Thammarat and Trang are intermingled with those of N and S groups in the PCA of Hayashida et al. (2007). However, localities from Prachuap Khiri Khan, Chumphon, Krabi and some from Mergui archipelago were also in between the morphospace of C. caniceps and C. concolor, but this study and/or Hinckley et al. (2023a) craniodental, pelage and/or molecular evidence show these populations represent *C. caniceps* (Hayashida et al. 2006). The addition of the diagnostic postorbital process length variable might have contributed to a better resolution in this study. Similarly, Hayashida et al. (2007) considered specimens with completed molar eruption as adults while this study was more conservative, considering specimens with deciduous or partially erupted premolars as subadults. According to molecular data, the southern limit of *C. caniceps* is between 6.5–8°N, specimens sequenced further south in Hinckley et al. (2023a) are from Phuket at east coast and Ko Tao at west coast, but sampling at Trang and Nakhon Si Thammarat provinces is lacking.

#### Tamiops mcclellandii (Horsfield, 1839)

Common name. Himalayan striped squirrel

- Sciurus mcclellandi Horsfield, 1839, Proceedings of the Zoological Society of London 1839: 152.
- Sciurus pembertoni Blyth, 1842, Journal of the Asiatic Society of Bengal 11: 887.
- Sciurus macclellandi manipurensis Bonhote, 1900, Annals and Magazine of Natural History (Series 7) 5: 51.

**Holotype.** Holotype not specified in description. Two examined specimens are labeled as cotypes: NHMUK 79.11.21.372, skin and skull, an adult male, also marked as "lectotype", and NHMUK 79.11.21.373, skin and skull, a young adult marked as "lectoparatype".

Type locality. "Assam" [= Assam, India].

Emended diagnosis. A small-sized Tamiops (average HB = 116.5 mm, W = 56.7 g, GLS = 32.7 mm; Table S8;Moore and Tate 1965; Liu et al. 2022) that can be distinguished from all other relatives by the combination of the following characters: relatively weakly striped summer pelage, with outer dark stripes paler than inner dark stripe; narrow (maximum width: 3-5 mm) outer pair of light stripes which are connected to a distinct pale facial stripe; outer light stripes are paler than inner light stripes and have a different width; no traces of rust/orange suffusion in venter (except very rarely in the chest), crown, or nape; absence of a yellow/orange hue in ear tufts; venter hairs have a great extent of gray at their base, which is not entirely covered by the tip lighter coloration, giving the venter an overall dull yellow-buff mixed with gray/ brown coloration; golden/yellow tipped tail hairs; relatively large baculum with shaft and blade, shaft lacks a small concavity where the blade is attached, blade lacks ridges, blade attachment orientation is tangent to shaft orientation (Figs 8A, D and 9A, B).

**Comparisons.** It can be externally distinguished from its allopatric relatives *Tamiops maritimus* and *T. mishanica*, as well as the allopatric/elevational parapatric *T. swinhoei*, based on its smaller size and outer pair of light stripes which are connected to a light facial stripe in *T. mcclellandii*, but just extend to the shoulder in the



**Figure 8.** Dorsal and ventral views of the skins of (**A**) *Tamiops mcclellandii* (NHMUK 79.11.21.372, lectotype), (**B**) *T. barbei barbei* (NHMUK 1914.7.8.36, topotype), and (**C**) *T. barbei inconstans* (NHMUK 12.7.25.31, holotype); live images of (**D**) *T. mcclellandii* taken by Lee Alloway in Kumarkata, Assam, India, and (**E**) *T. barbei* taken by Andaman Kaosung in Kaeng Krachan District, Thailand.

other species (except in T. swinhoei in which it can be rarely connected with a faint line). Its pelage is also generally harsher, thinner, and shorter vs softer, denser and longer in T. swinhoei (although these features are affected by latitude, elevation and seasonality), and it lacks a yellow/orange hue in its ear tufts and reddish suffusion in crown while these features are frequently present in T. swinhoei. Its facial stripe is distinctive vs diffuse in T. minshanica, and its venter is buff or gray colored, lacking any red hue vs rust colored in T. minshanica (Liu et al. 2022). It can be differentiated from allopatric Tamiops rodolphii based on the following external features: outer light lines are thinner but more distinctive, contrasted and lighter than inner light lines which are less conspicuous vs outer and inner light lines are of equal width and similar brightness, distinctiveness, and contrast with the dorsum in T. rodolphii; outer dark line coloration is homogeneous along the anterior-posterior axis vs outer dark lines grade posterior-anteriorly from black/dark brown to brown/reddish-brown in T. rodolphii; absence of a thin pale brown line across the black mid-dorsal line vs presence of a thin pale brown line across the black mid-dorsal line in *T. rodolphii* (except in SE Thailand populations); generally duller, venter coloration which goes from buff to yellow (without any trace of red, except in the chest of three Mishmi Hill female specimens) vs generally brighter, orange-yellow to salmon-ochraceous in T. rodolphii. A

comparison with *Tamiops barbei* has been included in the following account, after this species has been formally revalidated.

Distribution, habitat and natural history. Distributed across the Eastern Himalayas including Nepal, Sikkim (NE India), Bhutan, Assam and Arunachal Pradesh (NE India), Kachin (Myanmar), and Yingjiang County, north of the Daying River (SW China; Figs 2, S5). It extends southward across the Arakan Range including the Garo, Khasi, Lushai, Mishmi, Naga and Chin Hills (Table S1; iNaturalist; Li et al. 2005; Thapa et al. 2016). Its distribution is possibly limited to the southeast by the Irrawaddy River basin and to the east by the Taping/ Daying, Shweli/Longjiang, or Nu Jiang/Salween Rivers since the allopatric T. barbei has been recorded at Maymyo (Mandalay) and Zhenkang (Yunnan), to the west of these rivers (Table S1; iNaturalist; Li et al. 2005). It has been recorded from ca. 170 to 2743 m a.s.l. in tropical and subtropical forest. This species seems to be replaced, perhaps outcompeted, at higher elevations by Tamiops swinhoei in northern Myanmar (Table S1; Ronald Kaulback field notes, NHMUK specimen tags; Moore and Tate 1965). Tamiops mcclellandii rarely comes to the ground, often observed "high up in tall trees, moving in short rushes and then staying motionless, sometimes head downward, often some min-

utes at a time...never seen one in low bushes" (Lord Cranbrook letter, described in Moore and Tate 1965). Similarly, in Arunachal Pradesh, T. mcclellandii was not recorded on the ground and was shown to mainly forage on bark along tree trunks below 10 m, particularly on bark of the species Kydia calycina, Pterospermum acerifolium, and Amoora wallichii (Datta and Goyal 2008). In northern Myanmar, it was collected at 12 meters up in dead pine tree in dense pine tree and rhododendron forest at 2743 m a.s.l., but also in a yam field surrounded by "light" (possibly secondary) forest at 914 m a.s.l. (Ronald Kaulback field notes, NHMUK specimen tags). Recorded in pairs or small groups often sharing the same tree with Dremomys lokriah (Moore and Tate 1965), and feeding on the bark of Dipterocarpus macrocarpus (iNaturalist). Mating recorded in April in Bhutan (https://www.inaturalist.org/observations/210973847).

**Conservation.** Recorded in Neora Valley, Royal Manas, Namdapha, Jigme Singye Wangchuck, Phrumsengla, and Nat Ma Taung National Parks, Buxa and Pakke Tiger Reserves, Eaglenest and Pangolakha Wild-life Sanctuaries, and Cherrapunji-Mawsynram Reserve Forest (Table S1; iNaturalist; Datta and Goyal 2008). Also recorded very close to Khangchendzonga and Phawngpui National Parks (Table S1). This species was recorded in logged forest, but it was significantly less abundant than in nearby unlogged primary forest (Datta and Goyal 2008).

**Comments.** Cyt *b* pairwise uncorrected genetic distances between populations from Sikkim and the Arakan Range are relatively high (ca. 5–6%) but there is little nuclear differentiation (Hinckley et al. 2023a).

#### Tamiops barbei (Blyth, 1847)

Common name. Southeast Asian striped squirrel

- Sciurus barbei Blyth, 1847, Journal of the Asiatic Society of Bengal 16: 875.
- *Tamias* [sic] *leucotis* Temminck, 1853, Esquisses zoologiques sur la côte de Guiné, Mammifères: 252.
- Sciurus mcclellandi kongensis Bonhote, 1901, Proceedings of the Zoological Society of London 1901: 55.
- Sciurus novemlineatus Miller, 1903b, Proceedings of the Biological Society of Washington 16: 147.
- *Tamiops inconstans* Thomas, 1920, Annals and Magazine of Natural History (Series 9) 5: 306.
- *Tamiops mcclellandi collinus* Moore, 1958, American Museum Novitates 1879: 1.

**Holotype.** Two syntypes are housed in the National Zoological Collection of the Zoological Survey of India: ZSI9482 and ZSI9483. These represent two unsexed study skins and skulls collected by J. Barbe and have been previously cited by their former Indian Museum catalog numbers: c2 and d2. The third syntype described by Blyth could not be found in this collection (Khajuria et al. 1977). These specimens could not be examined in this study but a topotype was examined (NHMUK 1914.7.8.36).

**Type locality.** Zami River, Ye Province, 100 miles south of Moulmein, Tenasserim, Burma [= c. 161 km south of Mawlamyine, Mon, Myanmar; ca. 16.21°N, 97.74°E].

Emended diagnosis. A small-sized Tamiops [average HB = 107-114 mm (*T. b. inconstans/T. b. barbei*), W = 47 g, GLS = 32 mm; Moore and Tate 1965; Liu et al. 2022] that can be distinguished from all other relatives by the combination of the following features: Outer light stripes are paler than inner light stripes and have a different width; rust/orange suffusion in venter but not in crown or nape; absence of yellow/orange hue in ear tufts; venter hairs have a very small extent of basal gray that is entirely covered by the colored hair tips, giving the venter a homogeneous and bright coloration; white/buff tipped tail hairs (Fig. 8B, C, E). It can also be discriminated based on one of the following combinations of characters, which correspond to its two subspecies. Tamiops barbei barbei: Strongly striped, with outer dark stripes as dark as inner dark stripe; wide outer pair of light stripes (maximum width: 6–9 mm), which are connected to a distinct light facial stripe; relatively small-sized baculum with shaft and blade, shaft has a small concavity where the blade is attached, blade is inserted in this concavity, blade attachment orientation is perpendicular to shaft orientation (Fig. 9C, D). Tamiops barbei inconstans: Faintly striped, with outer dark stripes less dark than inner dark stripe.

Comparisons. In general terms, T. barbei is distinguished from its parapatric relative T. mcclellandii by its more colorful venter and paler tipped tail hairs, and at the turnover area between these species (west and central Indochina), by its strongly striped appearance and longer tail (Figs 8, S2A). Since the dorsal pelage of T. barbei barbei and T. b. inconstans is quite different, and the latter is here considered a candidate species (see comments section), each of these subspecies will be compared separately with T. mcclellandii. Parapatric T. b. barbei and T. mcclellandii can be externally distinguished based on the following pelage features: outer dark stripes as black as inner dark stripe vs paler than inner dark stripe in T. mcclellandii during spring-summer; great vs little contrast between inner light and outer dark stripe pairs in T. mcclellandii; outer pair of light stripes wide (maximum width: 6-9 mm) vs narrow (maximum width: 3-5 mm) in T. mcclellandii; venter gray hair bases are short and entirely covered by the colored hair tips vs venter gray hair bases are long and not entirely covered by colored hair tips in T. mcclellandii, giving T. b. barbei a homogeneous bright yellow/orange ventral coloration vs yellow-buff mixed with gray/brown in T. mcclellandii; white/buff vs golden/yellow tipped tail hairs in T. mcclellandii.

Allopatric *T. b. inconstans* and *T. mcclellandii* can be externally distinguished based on less pelage features: venter gray hair bases are short and entirely covered by

the colored hair tips vs venter gray hair bases are long and not entirely covered by colored hair tips in *T. mcclellandii*, giving *T. b. inconstans* a homogeneous bright orange ventral coloration vs yellow-buff mixed with gray/brown in *T. mcclellandii*; buff/pale yellow vs golden/yellow tipped tail hairs in *T. mcclellandii*.

It can also be distinguished from *T. mcclellandii* by its longer (106–163 mm) vs shorter (75–113 mm) tail in their distribution contact area (west and central Indochina; Fig. S2A). Similarly, cranium morphospace is also more distinct between parapatric *T. b. barbei* and *T. mcclellandii*, than between allopatric *T. b. inconstans* and *T. mcclellandii* (Figs 4, S2B). More specifically, *T. barbei* has a deeper rostrum and broader interorbital constriction, but a more flattened braincase than *T. mcclellandii* (Figs 4, S2B).

Finally, *T. b. barbei* can also be differentiated from *T. mcclellandii* through the following baculum characteristics: Presence vs absence of a small concavity where the blade is attached to shaft in *T. mcclellandii*; blade attachment orientation is perpendicular vs tangent to shaft orientation in *T. mcclellandii*; shorter (4.70–5.09 mm) vs longer (6.15–6.65 mm) shaft in *T. mcclellandii* (Fig. 9).

It is currently thought to have an allopatric distribution with its relatives *Tamiops maritimus*, *T. mishanica* and *T. swinhoei* (although *T. barbei inconstans* might have a sympatric/parapatric elevational distribution with T. swinhoei/maritimus in Yunnan and northern Vietnam) from which it can be externally distinguished based on its outer pair of light stripes, which are connected to the light facial stripe in T. barbei barbei (except in some T. barbei inconstans specimens), but just extend to the shoulder in the other species (except in T. swinhoei in which it is rarely connected with a faint line). Its pelage is also harsher, thinner, and shorter vs softer, denser and longer in T. swinhoei, and it lacks a yellow/orange hue in its ear tufts and reddish suffusion in crown while these features are frequently present in T. swinhoei. Its facial stripe is distinctive vs diffuse in T. minshanica, and its crown is characterized by a dull brown gray vs bright reddish-brown coloration in T. mishanica. It can be differentiated from parapatric T. rodolphii based on the following external features: outer light lines are thinner but more distinctive, contrasted and lighter than inner light lines, which are less conspicuous vs outer and inner light lines are of equal width and similar brightness, distinctiveness, and contrast with the dorsum in T. rodolphii; outer dark lines' coloration is homogeneous along the anterior-posterior axis vs outer dark lines generally grade posterior-anteriorly from black/dark brown to brown/reddish-brown in T. rodolphii; absence of a thin pale brown line across the black mid-dorsal line vs presence of a thin



**Figure 9.** Baculum comparison between *Tamiops barbei* and *T. mcclellandii*. A Lateral (left) view of *T. mcclellandii* (USNM564453); **B** ventrolateral view of *T. mcclellandii* (USNM564453); **C** lateral (left) view of *T. barbei* (USNM297043); **D** ventrolateral view of *T. barbei* (USNM297043).

pale brown line across the black mid-dorsal line in *T. ro-dolphii* (except in SE Thailand populations).

Finally, the glandes penis and bacula among *T. min-shanica*, *T. swinhoei*, *T. maritimus*, *T. barbei barbei*, and *T. barbei inconstans* differ distinctly from each other (Pocock 1923; Liu et al. 2022).

**Distribution, habitat and natural history.** Distributed from the Irrawaddy River to the West to the Northwest provinces of Vietnam to the East (A. E. Balakirev pers. comm.), southern Yunnan (China) ca. 23.5° N to the North, and to Selangor (Malaysia) to the South (Figs 2, S5). In Thailand, the Chao Phraya River Basin might constitute a barrier for this species and its eastern limit, since this species is replaced by *T. rodolphii* to the east of the Chao Phraya/Pa Sak River (Chon Buri and Chaiyaphum provinces). The only exceptions are several iNaturalist records from Khao Yai National Park, which is just to the East of this river, most of which seem to represent *Tamiops barbei*. Recorded from sea level to 2130 m a.s.l. (Table S1).

Recorded feeding on cherry blossom flowers/nectar, *Mudhuca floribunda, Ficus hirta, Musa acuminata*, and *Castanopsis acuminatissima* (iNaturalist; Rueangket et al. 2019).

**Conservation.** Recorded in Khao Sok, Khao Yai, Ko Tarutao, Thai Muang, Kaeng Krachan, Khoa Luang, Phu Suan Sai, Phu Kradueng, Thale Ban, Khao Pu-Khao Ya, Mae Ping, Si Satchanalai and Doi Luang, Doi Inthanon National Parks, Lentang Forest Reserve, Fraser's Hill and Krau Wildlife Reserves, Chiang Dao, Phu Luang, and Huai Kha Khaeng Wildlife Sanctuaries (iNaturalist; Table S1).

Comments. The subspecies Tamiops barbei inconstans might merit species-level recognition. It is well differentiated from T. barbei barbei populations based on mitochondrial DNA, having divergerged ca. 3.54 million years ago with cyt b pairwise uncorrected genetic distances ca. 5% (Hinckley et al. 2023a). Ecologically, it is adapted to subtropical forests instead of monsoon forests/rainforests. Morphologically, it exhibits a highly distinct dorsal pelage, a shorter tail than Indochinese T. b. barbei populations, and a somewhat overlapping but distinct craniodental morphospace. Its baculum also differs from that of nominotypical T. barbei populations (Pocock 1923; Liu et al. 2022). Unfortunately, Hinckley et al. (2023a) were limited by the sampling of only a single T. b. inconstans population and the absence of nuclear data. Future research should expand geographic and genetic sampling to more thoroughly assess whether this subspecies warrants full species recognition.

In *T. barbei barbei*, morphological sampling in Kra sensu lato complemented and supported the limited molecular evidence in this area of Hinckley et al. (2023a), suggesting a phenotype transition/contact zone between Trang and Hat Sanuk (circa 7.5–12°N). Molecular evidence showed specimen FMNH82879 from Tenasserim Town (west coast, 12°N) had south and north haplotypes for different markers. Additionally, FMNH82879 and other specimens from this latitude and all the way south to Trang (west coast, 7.5°N) also showed an intermediate morphology among north and south groups in the PCA or measurement biplots. However, specimens from Chong Bueng (14.6°N) show most external measurements in the range of the north group (and *T. m. kongensis* pelage) while specimens from Nakhon Sri Thammarat and Surat Thani (east coast, circa 8–10°N) cluster with the south group.

## Discussion

The recognition of two additional species of Asian tree squirrels (Callosciurinae) illuminates the amount of taxonomic work remaining in many understudied genera in this subfamily. Taxonomic instability seems not only rampant in Tamiops (Chang et al. 2011; Liu et al. 2022) and Callosciurus (Boonkhaw et al. 2017; Nguyen et al. 2018; Balakirev and Rozhnov 2019; Tamura et al. 2021), but also in other genera such as Dremomys (Oshida et al. 2017; Balakirev et al. 2022; Hinckley et al. 2023a), Prosciurillus, Hyosciurus (Hawkins et al. 2016a), and Sundasciurus (Hawkins et al. 2016b; Hinckley et al. 2020). Furthermore, species and subspecies diversity of the remaining genera has been poorly represented in both molecular and morphology-based systematic studies, so it also seems unlikely that species limits are well understood in these taxa.

# Future perspectives on species delimitation in Sciuridae

This research supports an integrative future for Sciuridae species delimitation (Padial et al. 2010). Recognizing the specific status of T. barbei would have been relatively straightforward with a single line of evidence, such as mitochondrial DNA, due to the detected ancient divergence and paraphyly. However, the specific status of C. concolor might have been overlooked through the lens of mitochondrial DNA, due to its relatively shallow differentiation (cyt b p-distances: 4-5%). Ultimately, it was the integration of nuclear DNA, pelage, craniodental and baculum variation, bioacoustics, ecology, and distribution evidence, which supported this species level recognition hypothesis. Thus, it is likely that many other recent speciation events among allopatric sister species have gone overlooked and will be identified in the future through similar integrative approaches.

The examination of museum specimens and citizen science pictures supported the clear distinction between these two species pairs and their homogeneity across vast areas of Southeast Asia, indicating that they are independent evolutionary lineages. Despite possible limited introgression in a small contact zone between *C. caniceps–C. concolor* (Fig. 4), they do not seem to represent

a single reproductively continuous lineage connected by broad zones of genetic introgression (Hillis 2019; Hinckley et al. 2023a). Thus, citizen science photographs can complement museum specimens by providing additional distribution data for externally diagnosable, separately evolving lineages. These photographs offer complementary insights not only geographically but also temporally, thereby enhancing the understanding of current putative species distributions in conjunction with historical specimen records.

Squirrel species and subspecies were historically described based on pelage characters, but this and additional ongoing research suggests that many of such species have been lost in synonymy during the last decades. The data presented here, along with other integrative taxonomic revisions (Nguyen et al. 2018; Balakirev et al. 2022; Liu et al. 2022), suggests pelage differentiation can be indicative of species boundaries in Callosciurinae tree squirrels. This is in contrast with other studies; Voipio and Hissa 1970; Koprowski 1994; Balakirev and Rozhnov 2019). The integration of molecular evidence into squirrel systematics has significantly enhanced the identification and recognition of diagnostic pelage traits. Interestingly, Tamura et al. (2017) also identified these pelage characters through experimental color vision tests. More specifically, their research revealed that brilliant orange, white and/or black, the pelage colors that were of greater significance in defining and identifying valid species in our study taxa, may represent effective clues for species and/or subspecies recognition in Callosciurus.

The use of baculum variation for species delimitation in squirrels is not novel. Pocock (1923) and Thomas (1915) bacular morphology studies were foundational for Sciuridae supraspecific systematics. Similarly, bacula have been highly valuable diagnostic features at the species level in Tamiops, Neotamias, and other taxa that are similar in cranial and external characters such as Sciurus and Tamiasciurus (Mossman et al. 1932; Layne 1952; Patterson and Thaeler 1982; Liu et al. 2022). Despite Thomas (1915) suggesting that bacula in squirrels are a superior taxonomic character compared to skull and dentition, they have generally been discarded by historic collectors and are thus poorly represented in scientific collections. As an example, only five of 408 C. caniceps-C. concolor specimens housed at USNM had associated bacula, three of which were initially unavailable, and found inside dry study skins. In this context of scarcity, µCT scanning can represent a promising avenue to unlocking additional potential of natural history collections through the scanning of these "hidden" and generally overlooked bacula. Simultaneously, this shortfall supports once again the necessity of additional specimen collection.

Ecological and behavioral divergences, and the resulting morphological differentiation, seem to be consequences rather than initial drivers of speciation, yet they may further contribute to the isolation process (Dufresnes and Hernandez 2023). In fact, "local differences in acoustic characteristics are one of the mechanisms that promote reproductive isolation of geographically distant populations of *Callosciurus*" (Tamura et al. 2021). In this study, we

show an interesting pattern of mating call differentiation among allopatric/parapatric relatives C. caniceps, C. concolor, and C. inornatus. Similarly, as shown in this system and in Sundasciurus (Hinckley et al. 2020), local adaptation to different ecological niches, particularly through varying degrees of scansoriality, can also contribute to speciation. In this context, synergies between systematists and behavioral ecologists could greatly enhance species delimitation in this genus and beyond. One promising approach would be to establish an essential reference mating call collection for all recognized Callosciurinae species through active field campaigns. Subsequently, the use of passive acoustic recorders could aid in detecting geographic variation in mating calls, defining species distribution limits, and monitoring environmental changes. Finally, cooperation between field ecologists carrying out camera trap, pollination and seed dispersal studies, and citizen scientists could also greatly benefit squirrel taxonomists by improving knowledge on ecological niche divergence among putative species.

### Sundaic-Indochinese transition in small non-volant mammals

Two major mammal species distribution transitions have been described in the boundary between Sundaland and Indochina: the IoK and the Kanggar Pattani Line (Woodruff and Turner 2009). However, in this research, it is the northern extent of the Nakhon Si Thammarat Range (NSTR), including areas like Kao Nawng [Khao Nong], and Khao Tha Phet and the area to the west that marks the northern limit of C. concolor and Sundaic T. barbei barbei phenotypes. Similarly, many other Sundaic genera (Sundasciurus, Lariscus, Rhinosciurus, Echinosorex) and species (Callosciurus notatus, Ratufa affinis, Rhinosciurus laticaudatus, Sundasciurus hippurus, S. robinsoni, S. tenuis, Maxomys rajah, M. whiteheadi, Tupaia glis, and Echinosorex gymnurus) reach their northern distribution limit in this area (Robinson and Kloss 1915; Sargis et al. 2013; Pimsai et al. 2014; iNaturalist; USNM collection). A few kilometers west of NSTR, near Ban Kok Klap [Ban Na], lies what is thought to be the southern (east coast) limit of Indochinese genera such as Menetes (Robinson and Kloss 1915).

Remarkably, on the western side of the NSTR, the transition seems to be further south, in Trang, for both *C. caniceps–C. concolor*, and many other taxa (e.g., *R. affinis*: Lay Hong Son, 7.84, 99.48; *Maxomys whiteheadi* and *M. rajah*: Trang; *Sundasciurus hippurus*: Trang-Krabi border; *Tupaia belangeri* vs *Tupaia glis*: Ko Lanta, 7.58, 99.07 vs Trang, Khao Sai Dao, 7.35, 99.85; Sargis et al. 2013; Pimsai et al. 2014; Juman et al. 2022; iNaturalist; USNM collection).

However, other non-commensal taxa break this pattern, with their northern or southern distribution limits at different latitudes. These include *Callosciurus nigrovittatus*, *Pithecheir parvus*, *Niviventer cremoriventer*, *Sundamys annandalei*, *Sundamys muelleri*, and *Hylomys maxi* (Pimsai et al. 2014, Hinckley et al. 2023b). Finally, few small mammal surveys have been undertaken in provinces just south of these putative transitions, such as Satun and Phattalung, potentially oversimplifying spatial patterns, as suggested for plants (Parnell 2013). It is also worth noting that our inferences regarding the precise transition of C. caniceps-C. concolor have been made based on morphological evidence. While this line of evidence seems to have reflected evolutionary history in this system, it should still be interpreted with caution. The combination of additional field sampling, and population genomic approaches such as UCEs, GBS or RADseq, will allow the exploration of potential hybridization, introgression or speciation zones in this transition area. Niche modeling in combination with genetic and morphometric studies of historic and modern populations will be pivotal to predict and track potential climate change driven shifts in the distribution of mammals in this enigmatic biogeographic transition.

This research underscores the important role of topography in the diversification of tropical east Asia's fauna (Sheldon et al. 2015; Rowsey et al. 2018; He et al. 2019; Camacho-Sánchez and Leonard 2020; Klabacka et al. 2020; Shaney et al. 2020; Balakirev et al. 2021; Chomdej et al. 2021; Esselstyn et al. 2021; Hinckley et al. 2021, 2023a; Arifin et al. 2022; Bannikova et al. 2022, 2023b). Topography might have maintained genetic differentiation following allopatric speciation in rainforest refugia in these study systems (Sheldon et al. 2015; Hinckley et al. 2023a). One potential explanation is that physical barriers, such as the Trang/Palian and Ta Pi/Phum Duang Rivers for C. caniceps-C. concolor, and the Irrawaddy/ Daying Rivers for T. mcclellandii-T. barbei, isolated populations of these lineages during periods of rainforest expansion and potential connectivity. Alternatively, or in combination, these river basins and/or mountain ranges, such as NSTR, might have served as habitat barriers, particularly during periods of rainforest contraction and the expansion of grasslands, savannas and mountain forests (Suraprasit et al. 2023). These results mirror the findings of Moore and Tate (1965) who suggested that rivers delimit the distribution of Tamiops barbei-T. rodolphii and Callosciurus pygerythrus-C. phayrei-C. caniceps-C. inornatus. Finally, in the Khlong Marui Fault region, including Krabi, Surat Thani and Nakhon Si Thammarat, the peninsula may have periodically halved in area, potentially leading to local extinctions (Woodruff and Turner 2009). Ultimately, the combination of physical (rivers and mountains) and past and current habitat barriers (grassland, savannah, montane forest), habitat divergence across barriers (rain shadow effect with the west side of southern Peninsular Thailand being wetter than east) and latitude (KPL vegetation transition), or the interplay of these different factors, might have shaped this transition area (Hinckley et al. 2023a). To sum up, the Sundaic-Indochinese transition represents a relatively diffuse zone, not a precise and abrupt break at a specific latitude (Parnell 2013). However, taxon-specific transitions do not seem to be homogeneously distributed across this filter zone. In mammals, taxa turnovers seem to be mostly restricted to three zones: Kangar-Pattani Line (5°N-6.5°N),

Trang-Nakhon Si Thammarat-Surat Thani region (ca.  $7^{\circ}N-9^{\circ}N$ ), and the area where the Thai-Malay Peninsula meets the mainland ( $13^{\circ}N-16^{\circ}N$ ; Catullo et al. 2008; Woodruff and Turner 2009; Hughes et al. 2011; Hinckley et al. 2023a; this study).

#### **Ecogeographical patterns**

Our study taxa, C. caniceps-C. concolor and T. barbei barbei, followed a Bergmannian size pattern in the PCA, with higher latitude Indochinese populations/species exhibiting a larger size than Sundaic ones (Bergmann 1847). Interestingly, this contrasts with the few studies from tropical regions, which do not support Bergmann's rule (Hinckley et al. 2022). For instance, a negative effect of latitude/temperature on body size has been described in the common treeshrew (Tupaia glis) in the Malay Peninsula and northern treeshrew (Tupaia belangeri) in Indochina, indicating the inverse of Bergmann's rule (Sargis et al. 2018; Juman et al. 2022). The only population that did not follow Bergmann's rule in C. caniceps was (partially) that of Koh Tao, a small (21 km2) and isolated island located 70 km east of the mainland. Ecological release and resource limitation hypotheses predict that body-size changes will be intensified in smaller and more isolated islands such as Koh Tao (Heaney 1978; Benítez-López et al. 2020). The Island Rule predicts that small-bodied mammals tend to be larger on islands than on the mainland, while larger mammals follow the opposite pattern (Lomolino et al. 2005; Benítez-López et al. 2020). Heaney (1978) showed with Callosciurus prevosti that medium-sized mammals can behave as either "small" or "large" mammals, depending upon the circumstances. This third possibility appears to be the one exhibited by Callosciurus caniceps, which reacted in Koh Tao like a larger mammal. The lack of dwarfism in other larger and/ or wetter west coast island populations (Mergui Archipelago, Phuket, Langkawi) or larger and less isolated east coast islands (Ko Samui and Ko Pha Ngan) might suggest resource limitation-driven dwarfism.

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## **Supplementary Material 1**

#### Figures S1-S5

Authors: Hinckley A, Maldonado JE, Tamura N, Leonard JA, Hawkins MTR (2024) Data type: .zip

- Explanation notes: Figure S1 Callosciurus caniceps and C. concolor bivariate plots of craniodental and selected external measurements. Figure S2 Tamiops mcclellandii and T. barbei bivariate plots of craniodental and selected external measurements. Figure S3 Distribution map and potential hybrid zone between Callosciurus caniceps and C. concolor, derived from museum specimens and verified citizen science records. Figure S4 Comparison of Callosciurus caniceps, C. concolor, and potential hybrid specimens from the contact zone in southern Peninsular Thailand. Specimens are displayed in the following order from top to bottom: USNM355628 (C. concolor, Nathawi, Songkhla), USNM555161 (potential hybrid, Lan Saka, Nakhon Si Thammarat), USNM355080 (potential hybrid, Ban Tah Pae, Chawang, Nakhon Si Thammarat), USNM355078 (potential hybrid, Doi Kaeo, Chawang, Nakhon Si Thammarat), USNM256872 (potential hybrid, Tha Lo, Bandon [Surat Thani]), USNM256871 (C. caniceps bimaculatus, Tha Lo, Bandon [Surat Thani]). Figure S5 Distribution map of Tamiops barbei and T. mcclellandii, derived from museum specimens and verified citizen science records.
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Link: https://doi.org/10.3897/vz.74.e133467.suppl1

## **Supplementary Material 2**

#### Tables S1-S4

Authors: Hinckley A, Maldonado JE, Tamura N, Leonard JA, Hawkins MTR (2024)

Data type: .zip

- Explanation notes: Table S1 Specimens included in this study and associated information. Table S2 Citizen science records. Table S3 Craniodental and selected external measurements. Table S4 Mating call data for *Callosciurus caniceps*.
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Link: https://doi.org/10.3897/vz.74.e133467.suppl2

## **Supplementary Material 3**

#### File S1

Authors: Hinckley A, Maldonado JE, Tamura N, Leonard JA, Hawkins MTR (2024) Data type: .docx

- Explanation notes: File S1 Part A (Morphometrics): Table S5A, B PCA results for *Callosciurus caniceps* and *Callosciurus caniceps* and *Callosciurus concolor*; Table S6A Craniodental and selected external measurements (mm), weight (g) of adult *Callosciurus caniceps* and *Callosciurus concolor*. The dwarf *Callosciurus caniceps* population of Koh Tao island and potential hybrids are shown separately for the sake of comparison. Mean, standard deviation (±), ranges and sample size (n) are specified for each measurement; Table S6B Univariate normality assumption check; Table S6C Homogeneity of variance check; Table S6D Welch Two Sample t-test; Table S6E Wilcoxon rank sum exact test; Table S7A PCA results for *Tamiops barbei* and *T. mcclellandii*; Table S7B Variable contribution to variance; Table S8A Craniodental and selected external measurements (mm), weight (g) of adult *Tamiops mcclellandii* and *Tamiops barbei*. Mean, standard deviation (±), ranges and sample size (n) are specified for each measurement; Table S8B *Tamiops*: Sex dimorphism analysis; Table S8C Univariate normality assumption check; Table S8E Welch Two Sample t-test; Table S8D Homogeneity of variance check; Table S8E Welch Two Sample t-test; Table S8D Homogeneity of variance check; Table S8E Welch Two Sample t-test; Table S8D Homogeneity of variance check; Table S8E Welch Two Sample t-test; Table S8D Homogeneity of variance check; Table S8E Welch Two Sample t-test; Table S8F Wilcoxon rank sum exact test. Part B (Bioacoustics): A Mating call sonograms of Callosciurus spp; B Mating call PCA results; variable contribution to variance.
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