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BIOGEOGRAPHICAL VARIATION ON CRANIOMANDIBULAR MORPHOLOGY IN PALLAS'S SQUIRREL *Callosciurus erythraeus* (Pallas, 1779) (Rodentia: Sciuridae) IN VIETNAM

Vu Thuy Duong[1], Nguyen Truong Son[1,2,*], Bui Tuan Hai[3], Ly Ngoc Tu[1,4],
Dang Huy Phuong[1], Tran Anh Tuan[1], Masaharu Motokawa[5],
Hideki Endo[6], Tatsuo Oshida[7,]**

[1]Institute of Ecology and Biological Resources, VAST, Vietnam
[2]Graduate University of Sciences and Technology, VAST, Vietnam
[3]Institute of Genome Research, VAST, Vietnam
[4]Center of Science and Technology, Ha Noi Metropolitan University, Vietnam
[5]The Kyoto University Museum, Kyoto University, Japan
[6]The University Museum, The University of Tokyo, Japan
[7]Laboratory of Wildlife Biology, Obihiro University of Agriculture
and Veterinary Medicine, Japan

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ABSTRACT

Different forest vegetations provide herbivorous small mammals with different resources, forcing adaptation since food habits depend on available resources. We expect differences in vegetation to be reflected in the size and shape of the skull and mandible as a result of potentially different feeding resources. Therefore, we analyzed the craniomandibular characteristics of Pallas's squirrel (*Callosciurus erythraeus*) in Vietnam. This species commonly occurs in different vegetations in Vietnam, making it a good model for examining morphological adaptation to vegetation type. We analyzed morphologically the skulls and mandibles of 156 specimens collected from 31 localities in Vietnam from 1960 to the present. Principal component analysis showed that females occurring in the tropical lowland evergreen rain forest were clearly separated from those in other vegetations.

Keywords: Indochina Peninsula, mandible, skull, vegetation.

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Corresponding author email*: truongsoniebr@gmail.com /*Co-corresponding author email:* oshidata@obihiro.ac.jp

INTRODUCTION

Herbivorous arboreal small mammals utilize food resources such as leaves, seeds and fruits occurring in their habitat. In rodents, food habit is adaptively reflected in the size and shape of the skull and mandible (e.g. Feldhamer et al., 2015). Within squirrels, morphological adaptations of skull and mandible for food habits are recognized. Morphological diversity of mandibles within the Callosciurinae (genera *Callosciurus*, *Dremomys*, *Exilisciurus*, *Funambulus*, *Lariscus*, *Menetes*, *Nannosciurus*, *Prosciurillus*, *Rhinosciurus*, *Sundasciurus* and *Tamiops*) are assumed to correspond to the diverse and continuously available food resources of tropical and subtropical forests in Southeast Asia (Casanova-Vilar & Van Dam, 2013). Based on comparative morphological analyses of skulls, Koyabu et al. (2009) showed that Pallas's squirrels *Callosciurus erythraeus* (Pallas, 1779) have a greater mechanical advantage in masseter and temporalis muscles for chewing and a correspondingly more robust zygomatic arch, compared to Asian red-cheeked squirrels *Dremomys rufigenis*. This is thought to be an adaptation for feeding on hard seeds. Within species, adaptations to different foods are recognized to vary among habitats. On Honshu Island of Japan, Tamura (2011; 2013) showed that regional populations of Japanese squirrels *Sciurus lis* mainly consume foods unique to the region, but hardly eat unique foods to other regions. Since small mammal species with wide distributions have adapted to different forest vegetations, there should be morphological differences in skulls and mandibles related to feeding habits in the different vegetations. Different tree species should result in different diets. In fact, Fan et al. (2010) suggested that in China, skull variation among populations of Chinese white-bellied rat *Niviventer confucianus* may primarily result from varying food habits. In the USA, Yu et al. (2017) found significant differences in toothrow length between urban and rural white-footed mice *Peromyscus leucopus*.

Vietnam, which occupies the eastern edge of the Indochina Peninsula, provides an opportunity to examine whether squirrel skull morphology varies with vegetation type. Vietnam runs north and south for over 1,000 km (Fig. 1). There are seven major vegetations in Vietnam: 1) montane laurel forest, 2) tropical lowland semi-deciduous and tropical moist deciduous forests, 3) savanna, 4) mangrove forest, 5) tropical evergreen seasonal forest, 6) tropical dry deciduous forest and 7) tropical lowland evergreen rain forest (FAO-Unesco, 1979, Table 1 & Fig. 1). In northern Vietnam, broad-leaved and conifer evergreen trees are dominant (Rundel, 1999; Sterling et al., 2006). In central Vietnam, the Annamite Mountain Range runs parallel to the coastline. It provides various vegetation types because of differences in elevation. Forest composition changes across latitude and across elevation. At elevations up to about 800 m, the main vegetation consists of evergreen broad-leaved trees; its canopy is dominated by tropical trees such as the dipterocarps (Sterling et al., 2006). Wet, sub-montane and montane forests are recognized at elevations of 1,000 m or more (Sterling et al., 2006). In southern Vietnam, there are evergreen and semi-evergreen forests in lowlands at elevations of 35–45 m where deciduous trees in the genus *Lagerstroemia* are dominant (Sterling et al., 2006).

C. erythraeus is widely distributed in southern China, Taiwan and the Indochina and Malay peninsulas (Koprowski et al., 2016). In the Indochina Peninsula, its distribution is restricted from the eastern edge of the peninsula and to the Irrawaddy River in Myanmar (e.g. Thorington et al., 2012). This squirrel is commonly found from northern to southern Vietnam. It is arboreal and seems very adaptable in its diets (e.g. Thorington et al., 2012). Therefore, *C. erythraeus* makes a good model to examine morphological adaptation to forest vegetation types. To test for morphological differences in different vegetation types, we morphologically examined the skull and mandible of *C.*

erythraeus specimens collected throughout Vietnam. Here, we discuss intraspecific adaptive variation in skull and mandible in different forest environments.

Table 1. Vegetation types of Vietnam defined by FAO–UNESCO (1979)

Vegetation	Dominant genera and/or families	Characteristics
Montane laurel forest	*Fokienia, Keteeleria, Pinus, Podocarpus*, Fagaceae, Juglandaceae, Lauraceae, Magnoliaceae	This forest is located in a mountainous area. The bioclimates are humid and characterized by a fairly cool season (lower than 15 ^{o}C).
Tropical lowland semideciduous rain forest and tropical moist deciduous forest	Anonaceae, Dipterocarpaceae, Euphorbiaceae, Leguminosae, Meliaceae, Papilionaceae, Sapindaceae, Rubiaceae	Lowland semideciduous rain forest consists of dense hemi-ombrophilous forests containing mainly evergreen species. Moist deciduous forest is represented by Leguminosae: teak occurs in Laos, but not in Vietnam.
Savanna	Gramineae	Savanna represents destroyed monsoon forest, consisting of grass vegetation with scattered trees.
Tropical evergreen seasonal forest	*Anisoptera, Dalbergia, Dipterocarpus, Mesua, Vatica*	This forest occurs in humid bioclimates with an average dry season of up to four or five months with an annual rainfall of over 2,000 mm, or a shorter dry season of one or two months with an annual rainfall of 1,500 mm to 2,000 mm.
Tropical dry deciduous forest	*Dipterocarpus, Shorea, Terminalia*	This forest is mainly confined to subhumid hot bioclimates with a dry season of five to sixmonths and an annual rainfall of 1,000 mm to 1,500 mm.
Tropical lowland evergreen rain forest	*Anisoptera, Dipterocarpus, Hopea, Parashorea*	High rainfall (usually, over 2,000 mm) and lack of a prolonged dry season
Mangrove forest	*Avicennia, Bruguiera, Ceriops, Heritiera, Lumnitzera, Rhizophora, Sonneratia*	This forest occurs only within the tidal range of estuaries and coasts.

MATERIALS AND METHODS

Squirrel specimens

Skull and mandible specimens of 156 *C. erythraeus* used in the present study are listed in Table 2. Based on eruption and wear of teeth (Hench et al., 1984; Viljoen, 1976), we identified all individuals as an adult. These specimens were collected from 31 localities in Vietnam (Fig. 1 & Table 2). We classified these specimens into six groups on the basis of vegetation types (FAO–UNESCO, 1979): montane laurel forest (MLf group; specimens from nos. 1–3, 10, 12, 13, 16, 21, 23, 24, 26 and 27), tropical lowland semi-deciduous and tropical moist deciduous forests (SDf & MDf group; specimens from nos. 4, 5, 11, 14, 15, 17, 22 and 25), savanna (S group; specimens from nos. 6, 7 and 18–20), tropical evergreen seasonal forest (ESf group; specimens from nos. 8 and 9), tropical dry deciduous forest (DDf group; specimens from nos. 28–30) and tropical lowland evergreen rain forest (ERf group; specimens from no. 31) (Fig. 1).

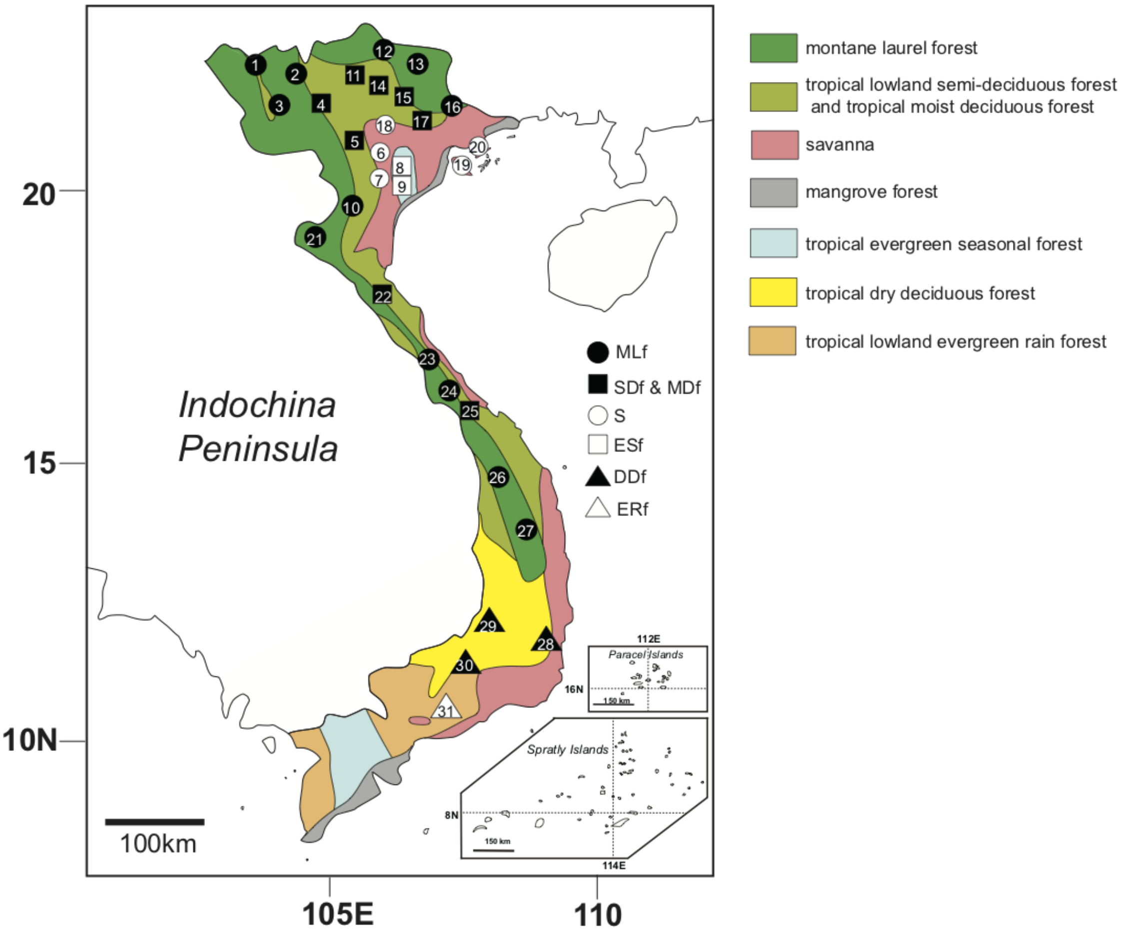

Figure 1. Outline of major vegetation types of Vietnam and collection localities of *Callosciurus erythraeus* used in the present study. We draw the outline of vegetation types based on information presented by FAO-UNESCO (1979) and Sterling et al. (2006). MLf, SDf & MDf, S, ESf, DDf and ERf indicate the vegetation groups defined in materials and methods

Thorington & Hoffmann (2005) describe 24 *C. erythraeus* subspecies. Also, many synonyms are described in Corbet & Hill (1992). Although we attempted to identify subspecies of specimens based on external characteristics (Moore & Tate, 1965), it was actually very difficult to preciously fall all specimens into subspecies. Therefore, we did not use subspecific classification. Specimens used in the present study are stored in the Biological Museum of the Vietnam National University of Science, Vietnam National University, Department of Zoological Museum, Institute of Ecology and Biological Resources (IEBR) and Department of Vertebrate Zoology, IEBR (Table 2).

Table 2. Craniomandibular measurements of six *Callosciurus erythraeus* groups in Vietnam (mm). SDs mean standard deviation. MLf, SDf & MDf, S, ESf, DDf and ERf indicate the vegetation groups defined in materials and methods

Variables	MLf				SDf & MDf				S				Esf				DDf				ERf			
	Female		Male		Female		Male		Female		Male		Female		Male		Female		Male		Female		Male	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
ML	54.64 (0.86)	52.90–56.17	54.47 (1.26)	52.37–58.25	54.82 (1.19)	52.63–57.33	54.24 (1.00)	52.36–55.89	55.50 (1.02)	52.50–56.83	55.00 (1.20)	53.02–58.07	54.04 (1.54)	53.02–55.81	53.58 (1.34)	51.74–54.95	53.77 (0.09)	53.70–53.83	54.15 (0.31)	53.93–54.37	51.51 (0.48)	51.08–52.33	53.70 (1.50)	51.04–55.80
LR	16.00 (0.63)	14.55–17.65	16.12 (0.75)	14.57–17.97	16.49 (0.70)	15.17–18.12	16.02 (0.64)	15.21–17.15	16.49 (0.76)	14.85–17.94	16.26 (1.00)	14.86–18.15	15.68 (0.77)	14.80–16.22	15.53 (0.66)	14.92–16.58	16.33 (0.25)	16.15–16.50	15.76 (1.02)	15.04–16.48	14.77 (0.53)	14.19–15.62	15.97 (0.83)	14.33–16.77
MWN	8.56 (0.52)	7.43–9.41	8.66 (0.47)	7.57–9.70	8.76 (0.48)	7.55–9.48	8.36 (0.59)	7.14–9.10	8.75 (0.52)	7.75–9.90	8.73 (0.56)	8.09–9.86	7.85 (0.27)	7.61–8.15	8.16 (0.28)	7.68–8.42	8.61 (0.69)	8.12–9.10	8.28 (0.23)	8.11–8.44	7.62 (0.33)	7.15–8.00	8.19 (0.53)	7.15–8.90
LBC	19.35 (0.86)	17.21–20.91	19.53 (0.88)	18.05–21.38	19.94 (1.07)	18.57–22.09	19.18 (1.00)	17.26–21.14	19.29 (0.63)	18.08–20.45	19.62 (0.88)	17.64–21.11	19.42 (0.95)	18.33–20.04	18.62 (0.88)	17.14–19.46	19.49 (0.11)	19.41–19.56	19.50 (0.56)	19.10–19.89	18.16 (0.58)	17.17–18.67	19.37 (0.78)	17.96–20.32
ZB	32.45 (0.71)	31.41–33.88	32.37 (1.00)	29.44–34.69	32.62 (1.00)	31.15–34.68	31.80 (0.83)	30.30–33.28	32.65 (1.11)	31.22–34.80	32.78 (1.14)	30.98–35.08	32.36 (1.03)	31.69–33.55	31.73 (0.80)	30.88–32.82	31.56 (0.88)	30.94–32.18	33.11 (0.24)	32.94–33.28	30.90 (0.95)	29.97–32.44	31.72 (0.88)	29.74–32.71
GNB	23.92 (0.43)	23.02–24.54	24.44 (0.73)	22.93–25.86	24.15 (0.97)	23.01–26.80	24.43 (0.55)	23.68–25.83	24.38 (0.82)	23.19–25.74	24.59 (0.76)	23.23–25.98	24.36 (0.74)	23.53–24.95	24.08 (0.76)	23.07–25.16	23.11 (0.01)	23.10–23.12	25.00 (0.11)	24.92–25.08	24.12 (0.77)	22.98–25.04	23.92 (0.74)	23.30–25.38
CL	49.60 (0.87)	47.41–51.15	49.24 (1.31)	46.53–53.10	49.62 (1.41)	47.20–52.73	48.83 (0.98)	47.19–50.52	50.21 (1.25)	47.95–52.32	49.79 (1.22)	47.63–52.45	49.52 (1.73)	48.36–51.51	48.42 (0.87)	47.64–49.84	49.12 (0.35)	48.87–49.36	49.51 (0.01)	49.50–49.52	47.07 (0.94)	45.82–48.05	48.64 (0.98)	47.63–50.73
MWR	7.77 (0.37)	6.73–8.67	7.78 (0.52)	6.85–9.06	7.99 (0.47)	6.84–9.13	7.36 (0.47)	6.60–8.09	7.94 (0.48)	7.01–8.53	7.67 (0.38)	7.09–8.56	7.07 (0.59)	6.56–7.72	7.44 (0.20)	7.24–7.75	7.67 (0.12)	7.58–7.75	7.38 (0.18)	7.25–7.51	6.47 (0.41)	6.14–7.14	7.29 (0.52)	6.46–7.81
LIF	3.87 (0.17)	3.54–4.19	3.79 (0.31)	3.22–4.41	3.88 (0.40)	3.30–4.96	3.88 (0.30)	3.40–4.68	3.98 (0.23)	3.58–4.39	3.88 (0.39)	3.23–4.64	3.93 (0.04)	3.90–3.98	3.63 (0.22)	3.41–3.91	3.77 (0.08)	3.71–3.83	4.11 (0.13)	4.01–4.20	3.49 (0.04)	3.42–3.53	3.96 (0.26)	3.66–4.28
LBP	16.33 (0.63)	14.84–17.78	16.58 (0.58)	15.35–17.55	16.65 (0.66)	15.54–17.70	16.31 (0.62)	15.26–17.73	17.00 (0.59)	15.93–18.15	16.86 (0.64)	15.56–17.88	16.41 (0.02)	16.40–16.43	16.17 (0.54)	15.64–16.93	15.22 (0.91)	14.58–15.86	15.23 (0.23)	15.07–15.39	16.30 (0.81)	15.22–17.46	15.82 (0.53)	15.34–16.93
DIM	26.13 (0.77)	25.05–27.89	25.79 (0.84)	24.41–28.10	26.05 (0.76)	24.60–27.49	25.71 (0.69)	24.73–26.96	26.62 (0.79)	25.14–28.10	26.08 (0.86)	24.81–27.98	26.06 (0.41)	25.65–26.47	25.10 (0.62)	24.24–25.93	27.03 (2.16)	25.50–28.56	25.29 (0.32)	25.06–25.51	24.85 (0.83)	23.76–25.85	25.46 (0.56)	24.68–26.41
MPL	29.26 (0.82)	27.68–30.41	29.28 (0.92)	27.83–31.70	29.59 (0.99)	28.35–31.80	29.07 (0.53)	28.05–29.93	29.90 (0.59)	28.72–31.12	29.60 (0.89)	28.19–31.40	29.31 (0.06)	29.24–29.35	28.64 (0.52)	27.96–29.33	28.39 (0.09)	28.32–28.45	28.93 (0.06)	28.89–28.97	28.06 (0.33)	27.80–28.62	28.77 (0.55)	28.17–29.70

LBS	20.57 (0.48)	19.60–21.34	20.37 (0.71)	19.17–21.89	20.47 (0.81)	18.79–21.77	19.99 (0.53)	19.23–21.28	20.71 (0.78)	19.70–22.41	20.39 (0.71)	19.39–21.56	21.11 (1.45)	20.02–22.75	20.29 (0.34)	19.90–20.69	20.84 (0.31)	20.62–21.06	21.07 (0.31)	20.85–21.29	18.85 (1.08)	17.76–20.39	20.39 (0.57)	19.70–21.59
LAB	10.16 (0.44)	9.27–10.96	10.17 (0.43)	9.13–10.92	10.21 (0.54)	9.12–11.14	10.52 (0.33)	9.86–11.13	10.60 (0.38)	9.63–11.34	10.49 (0.51)	9.47–11.21	10.85 (0.47)	10.33–11.23	10.40 (0.21)	10.19–10.64	10.71 (0.24)	10.54–10.88	10.28 (0.54)	9.90–10.66	9.96 (0.32)	9.45–10.26	10.13 (0.34)	9.35–10.37
GLMR1	10.52 (0.34)	9.82–11.05	10.45 (0.32)	9.84–11.10	10.69 (0.53)	9.60–11.40	10.59 (0.45)	10.04–11.34	10.87 (0.42)	10.27–11.62	10.75 (0.51)	10.02–11.64	10.61 (0.09)	10.53–10.70	10.41 (0.42)	9.87–11.00	10.61 (0.14)	10.51–10.71	10.76 (0.10)	10.69–10.83	10.55 (0.46)	9.96–11.05	10.39 (0.27)	9.98–10.65
LBRZ	40.22 (0.69)	38.74–41.53	40.09 (1.06)	37.98–42.50	39.93 (1.22)	37.49–42.50	39.98 (0.78)	38.13–41.28	40.65 (0.97)	38.50–41.66	40.25 (0.96)	38.61–41.60	40.74 (0.77)	40.09–41.59	39.30 (1.04)	38.06–40.15	40.20 (0.01)	40.19–40.21	39.81 (0.37)	39.54–40.07	38.28 (1.12)	36.67–39.39	39.30 (0.67)	38.41–40.19
LBRO	39.81 (0.87)	38.31–42.3	39.51 (1.55)	32.09–42.60	39.94 (1.01)	37.93–41.78	39.57 (0.65)	38.55–41.13	40.44 (0.84)	39.05–42.47	40.07 (0.58)	39.24–40.91	40.58 (0.99)	39.89–41.72	39.30 (1.06)	38.19–40.68	39.27 (0.73)	38.75–39.78	40.09 (0.08)	40.03–40.15	37.56 (0.86)	36.36–38.45	39.38 (0.61)	38.47–40.13
LBSR	18.31 (0.81)	16.60–19.56	18.29 (0.92)	16.73–20.38	18.63 (0.68)	17.30–19.79	18.74 (0.93)	17.39–20.12	18.83 (1.02)	16.88–19.95	18.30 (1.07)	16.92–20.90	18.02 (0.54)	17.39–18.37	17.61 (0.48)	17.15–18.36	18.41 (0.76)	17.87–18.95	18.18 (1.09)	17.41–18.95	17.15 (1.03)	16.16–18.86	17.48 (0.99)	16.46–19.10
HBPNB	12.56 (0.43)	11.52–13.71	12.43 (0.47)	11.67–13.88	12.60 (0.34)	12.08–13.31	12.43 (0.37)	11.61–13.01	12.92 (0.71)	11.67–14.82	12.64 (0.62)	11.31–13.98	12.71 (0.09)	12.62–12.79	12.32 (0.19)	12.00–12.50	12.22 (0.77)	11.67–12.76	12.60 (0.99)	11.90–13.30	11.54 (0.69)	10.81–12.48	12.36 (0.40)	11.85–12.96
BCH	17.47 (0.50)	16.41–18.58	17.53 (0.54)	16.46–19.03	17.78 (0.58)	16.96–19.33	17.68 (0.38)	16.61–18.14	17.66 (0.67)	16.33–18.40	17.36 (0.57)	16.04–18.24	16.61 (0.39)	16.29–17.05	17.12 (0.67)	16.58–18.04	17.20 (0.16)	17.09–17.31	18.05 (0.36)	17.79–18.30	16.73 (0.68)	16.10–17.68	17.06 (0.45)	16.45–17.66
HAB	14.50 (0.38)	13.48–15.21	14.69 (0.45)	13.57–15.91	14.60 (0.51)	13.85–15.75	14.40 (0.33)	13.89–15.00	14.75 (0.35)	13.91–15.29	14.79 (0.50)	14.14–16.15	14.27 (0.52)	13.76–14.8	14.52 (0.46)	13.98–15.25	14.09 (0.07)	14.04–14.14	14.71 (0.28)	14.51–14.91	14.27 (0.32)	13.89–14.75	14.22 (0.26)	13.78–14.66
AHR	17.65 (0.59)	16.61–19.22	17.43 (0.66)	15.75–18.79	17.52 (0.63)	16.13–18.74	17.63 (0.45)	16.74–18.36	18.25 (0.61)	17.22–19.61	17.98 (0.81)	16.63–19.45	18.41 (0.56)	17.84–18.96	17.64 (0.71)	16.63–18.43	17.52 (0.03)	17.50–17.54	18.33 (0.55)	17.94–18.72	16.73 (0.50)	16.18–17.30	17.88 (0.64)	16.81–18.69
OHR	16.88 (0.58)	16.04–18.19	16.69 (0.72)	15.16–18.02	16.83 (0.77)	15.21–18.10	16.95 (0.50)	16.37–17.97	17.23 (0.71)	15.55–18.37	17.28 (0.69)	16.28–18.55	17.67 (0.92)	16.87–18.67	16.90 (0.41)	16.26–17.27	17.53 (0.13)	17.44–17.62	16.78 (0.08)	16.72–16.83	16.01 (0.40)	15.57–16.53	16.92 (0.69)	16.07–17.86
LC	34.55 (0.81)	32.49–35.86	34.19 (0.93)	31.65–35.90	34.87 (0.87)	33.18–36.67	33.98 (0.99)	32.23–35.38	35.13 (0.87)	33.96–37.51	34.99 (0.79)	33.94–36.59	35.15 (1.03)	34.15–36.21	33.70 (0.52)	33.00–34.44	33.04 (0.62)	32.60–33.47	33.33 (0.60)	32.90–33.75	32.93 (0.89)	32.18–34.43	33.92 (0.69)	32.72–34.70
GLMR2	10.61 (0.43)	9.83–11.58	10.42 (0.41)	9.75–11.44	10.65 (0.43)	9.94–11.53	10.51 (0.73)	8.25–11.62	10.80 (0.46)	10.08–11.64	10.63 (0.56)	10.04–11.70	10.47 (0.22)	10.22–10.62	10.37 (0.50)	9.55–10.80	10.16 (0.71)	9.65–10.66	10.61 (0.41)	10.32–10.90	10.29 (0.24)	10.01–10.57	10.25 (0.22)	9.77–10.43
TM	4.43 (0.24)	3.97–5.02	4.38 (0.26)	3.71–4.85	4.41 (0.26)	3.78–4.84	4.31 (0.20)	3.87–4.60	4.51 (0.23)	4.02–4.97	4.40 (0.26)	3.92–4.94	4.25 (0.31)	3.89–4.48	4.16 (0.12)	4.03–4.28	4.00 (0.13)	3.90–4.09	4.36 (0.26)	4.17–4.54	4.16 (0.29)	3.72–4.45	4.20 (0.22)	3.88–4.48
HM	8.49 (0.39)	7.74–9.66	8.53 (0.37)	8.09–9.79	8.65 (0.43)	8.02–9.60	8.39 (0.34)	7.74–8.80	8.75 (0.52)	7.67–9.64	8.63 (0.49)	7.72–9.49	8.45 (0.18)	8.24–8.58	8.24 (0.29)	7.78–8.53	8.06 (0.81)	7.48–8.63	8.47 (0.17)	8.35–8.59	8.43 (0.19)	8.31–8.76	8.47 (0.13)	8.31–8.72

Measurements of craniomandibular characteristics

The 27 craniomandibular characteristics are defined and shown in Fig. 2. These characters are frequently used for taxonomic comparison between squirrel species (Hayashida et al., 2007; Nguyen et al., 2018). We measured to the nearest 0.01 mm using a digital caliper. Raw measurements and standardized measurements were log-transformed before use in analyses of size and shape, respectively.

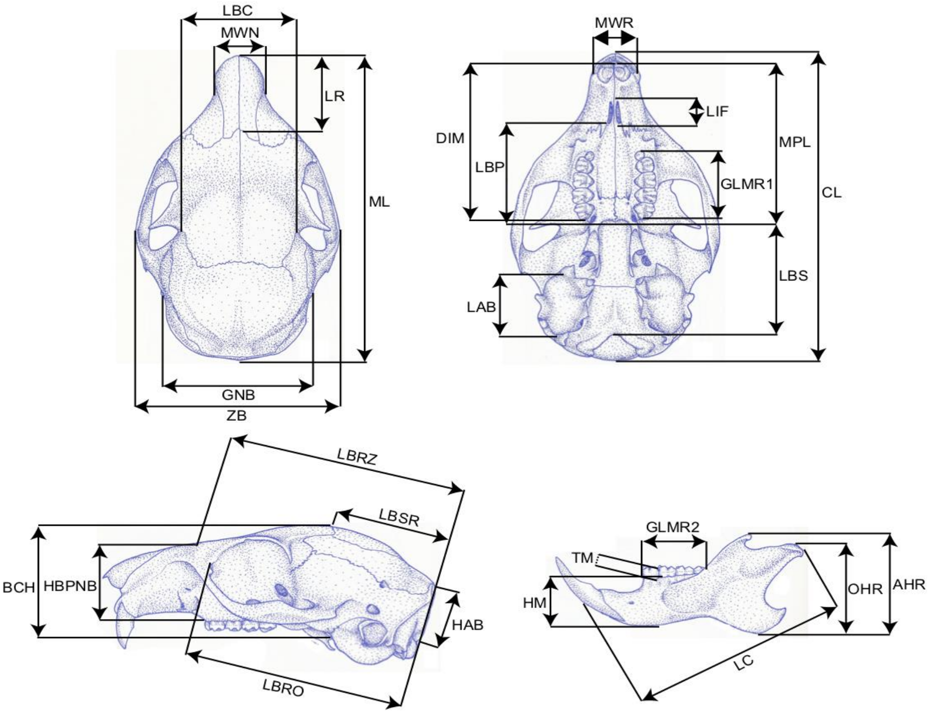

Figure 2. Craniomandibular measurements used in the present study follow Nguyen et al. (2018). Images were adapted from Abe (2000). AHR = aboral height of the vertical ramus; BCH = braincase height; CL = condylobasal length; DIM = distance from anterior incisor to posterior last molar; GLMR1 = greatest length of upper molar tooth row; GLMR2 = greatest length of lower molar tooth row; GNB = greatest neurocranium breadth; HAB = height from akrokranion to basion; HBPNB = height from bony palate to the end of nasal bone; HM = height of the mandible at M1; LAB = length of auditory bulla; LBC = least breadth of caudal point of zygomatic process of frontal bone; LBP = length of bony palate; LBRO = length from basion to the most rostral point of orbit; LBRZ = length from basion to the most rostral point of zygomatic arch; LBS = length from basion to staphylion; LBSR = length from basion to the sagittal and rostral point of temporal bone; LC = greatest length from condyle; LIF = longest length of incisive foramina; LR = length of rostrum; ML = maximum length of skull; MPL = median palatal length; MWN = maximum width across both nasal bones; MWR = maximum width of rostrum; OHR = oral height of vertical ramus; TM = thickness of mandible at middle point of M1; and ZB = zygomatic breadth

Supplementary Material

Supplementary Data (SD) 1: Specimens of *Callosciurus erythraeus* used in the present study. Indel, F and M mean missing data, female and male, respectively. Locality numbers and vegetation groups correspond to those in Figure 1. VNU

(Biological Museum of the Vietnam National University of Science, Vietnam National University); DZM (Department of Zoological Museum, IEBR); and DVZ (Department of Vertebrate Zoology, IEBR).

Statistical analyses

Female biased sexual dimorphism is reported in *Callosciurus* squirrels (Nandini, 2011). Therefore, for each population, we analyzed measurements of males and females separately. We examined notable differences in the craniomandibular measurements between sexes and among populations by a multivariate analysis of variance (MANOVA) with a Wilk's lamda with associated Rao's *F* and a Pillai trace with approximate *F*. If the MANOVA shows the significant overall difference between groups, the analysis proceeds to pairwise comparisons between groups. Alpha levels less than 5% were considered indicative of statistically significant differences.

For each sex, we clarified variation in size and shape among populations with the principal component analysis (PCA). We compared plots of the first principal component (PC1) and second principal component (PC2). All statistical analyses were performed by the software PAST (Hammer et al., 2001).

RESULTS AND DISCUSSION

Maximum, minimum and mean values with standard deviations of 27 craniomandibular measurements in 73 females and 83 males are presented in Table 2. In both the raw and standardized data sets, the MANOVA showed that females were significantly different among groups: in raw data, Wilk's lambda and Pillai trace were 0.0129 and 2.699, respectively ($P < 0.05$) and in standardized data, those were 0.0175 and 2.722, respectively ($P < 0.05$).

Principle component analysis using raw data readily distinguished females of the ERf group from females of all other groups along the 1st axis (Fig. 3). For males, there was no clear separation of any group (data not shown). The 1st three principle components accounted for 53.24% (PC1 33.53%, PC2 11.50% and PC3 8.22%) of the total variation in females (Table 3). Characters mainly contributing to PC1 were MWN and MWR. Characters mainly contributing to PC2 and PC3 were MWR and LIF and TM, respectively. For standardized data, there was no clear separation of any group in both sexes (data not shown).

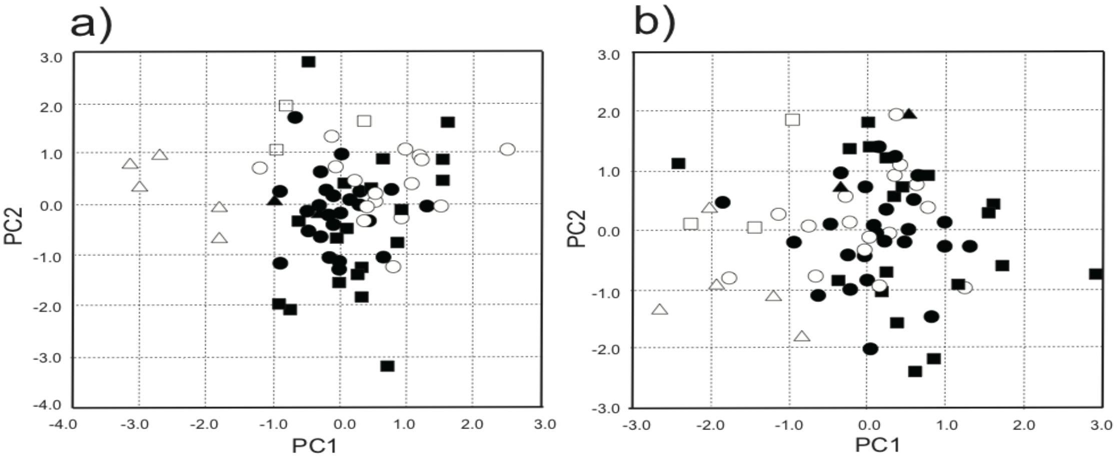

Figure 3. Bivariate plots of the first two principle components from an analysis of 27 log-transformed craniomandibular measurements from females of six groups of *Callosciurus erythraeus* in Vietnam: a) raw data and b) standardized data. Symbols correspond to those in Figure 1

Table 3. Variables with high character factor loadings for principal components analysis

Variable	Raw data			Standardized data		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
MWN	0.394	-0.277	-0.236	0.493	0.174	-0.038
MWR	0.436	-0.489	-0.199	0.687	0.080	0.133
LIF	0.295	0.537	0.016	-0.169	0.529	0.707
TM	0.119	-0.216	0.777	0.009	-0.652	0.457
Eigenvalue	0.003	0.001	0.001	0.001	0.001	0.001
% variance	33.52	11.50	8.22	18.72	13.31	9.58

Note: The log-transformed raw data and standardized data of females of six *Callosciurus erythraeus* groups in Vietnam. Higher factor loadings (> |0.350|) are shown in bold.

DISCUSSION

Principle component analysis using raw data showed that females of the ERf group were clearly separated from the other groups (Fig. 3). This may be an example of adaptation by mammals to forest environments. This group is the only one inhabiting tropical lowland evergreen rain forest (Fig. 1). Therefore, our hypothesis that the morphology of *C. erythraeus* varies with vegetation may be supported. We did not, however, find clear separation among male groups. One possible explanation could be differences in the home range. Females defend their home ranges from other females, but ranges of males overlap females and other males (Tamura et al., 1989). Male home ranges are more than twice as wide as female home ranges (Tamura et al., 1989). In addition, females tend to stay near their natal area, but almost all males disperse (Tamura et al., 1989). Because their movements are more restricted, females may be more adapted to regional vegetation.

In PCA using raw data, MWN, MWR and LIF contributed to separate females of the ERf group from females of the other groups, but we did not find such separation in PCA using standardized data. This means that females of the ERf group could differ from females of the other groups in the size of MWN, MWR and LIF, but not in the shape of any variables.

The nasal region (MWN and MWR) of females of the ERf group is smaller than that of the other five female groups. Food availability in the tropical lowland evergreen rain forest may be more stable compared to other vegetations. Stable and continuous sources of foods may make olfaction less necessary than areas such as the montane laurel forest and/or the tropical lowland semi-deciduous rain forest where food resources varies seasonally (Fig. 1). Olfaction is important for arboreal squirrels to find seasonal food resources in the forests. The northern flying squirrel *Glaucomys sabrinus* finds truffles by the olfaction (Pyare & Longland, 2001). The western grey squirrel *Sciurus griseus* and the eastern fox squirrel *Sciurus niger* find nuts they buried with memory and olfaction (Koprowski, 1994; Carraway & Verts, 1994).

Based on geometric morphometrics of 228 species of sigmodontine rodents, Maestri et al. (2018) suggested that larger incisive foramina is associated with highly seasonal and less vegetated areas. In the Asian midday jird *Meriones meridianus*, intraspecific variation of LIF is related to geography (Yazdi et al., 2011). Females in the ERf group had the smallest LIF of all groups and inhabit the most stable vegetation: tropical lowland evergreen rain forest. Compared to the habitat of the ERf group, those of the other five groups would be more highly seasonal. Although it is difficult to explain the functional meanings of incisive foramina, our results do not contradict the findings of Maestri (2018).

In the present study, we did not consider the evolutionary history of this species. *C.*

erythraeus is most closely related to Finlayson's squirrel *Callosciurus finlaysonii* (Hoesfield, 1823) (Oshida et al., 2001; 2011). Oshida et al. (2013) suggested that *C. erythraeus griseimanus* occurring in southern Vietnam might be more closely related to *C. finlaysonii* than other *C. erythraeus* subspecies. Recently Balakirev & Rozhnov (2019) proposed the new taxonomic status of *C. erythraeus*, suggesting that the *C. erythraeus* population in southern Vietnam may actually be regarded as a form of *C. finlaysonii*. Although this new taxonomic status is not received yet in general, our results may support the taxonomic and evolutionary status of the *C. erythraeus*/*finlaysonii* complex.

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Specimens of *Callosciurus erythraeus* used in the present study. Indel, F and M mean missing data, female and male, respectively. Locality numbers and vegetation groups correspond to those in Fig. 1

No.	Collection locality	Vegetation group	Identitiy number	Sex	Total length (mm)	Weight (g)	Collection date	Recource
1	Lai Chau	MLf	109	F	-	-	-	DZM
2	Lao Cai	MLf	128	F	-	-	-	DZM
2	Lao Cai	MLf	580	M	-	-	-	DZM
2	Lao Cai	MLf	Mn2107	M	-	-	Aug. -, 1962	VNU
3	Son La	MLf	190_2	M	-	-	-	DZM
3	Son La	MLf	54	F	-	-	-	DZM
3	Son La	MLf	200	M	428	400	Jan. 7, 2008	DVZ
3	Son La	MLf	176	M	474	305	Jan. 5, 2008	DVZ
3	Son La	MLf	852	F	-	-	-	DZM
3	Son La	MLf	858	F	-	-	-	DZM
4	Yen Bai	SDf & MDf	Mn0021	F	-	-	Oct. 11, 1961	VNU
4	Yen Bai	SDf & MDf	827	M	-	-	-	DZM
4	Yen Bai	SDf & MDf	2120	M	-	-	Jul. 19, 1965	VNU
4	Yen Bai	SDf & MDf	Mn0088	M	450	345	Jul. 13, 1965	VNU
4	Yen Bai	SDf & MDf	Mn2132	M	-	-	Jul. 14, 1965	VNU
4	Yen Bai	SDf & MDf	2111	M	-	-	Jul. 18, 1965	VNU
5	Phu Tho	SDf & MDf	2112 rs 73	M	-	-	Jun. 17, 1961	VNU
6	Ha Noi	S	HS2017.01	M	495	290	Jan. -, 2017	DVZ
6	Ha Noi	S	HS2017.11.01	F	446	295	Nov. 1, 2017	DVZ
6	Ha Noi	S	HS2018.01.07	F	495	300	Jan. 7, 2018	DVZ
6	Ha Noi	S	Mn0028	F	-	-	Aug. 4, 1962	VNU
7	Hoa Binh	S	1299	F	-	-	-	DZM
7	Hoa Binh	S	Mn0912	F	505	-	May 20, 1960	VNU
7	Hoa Binh	S	2134	M	-	-	Sep. 29, 1960	VNU

7	Hoa Binh	S	Mn2101	M	-	-	May 20, 1960	VNU
7	Hoa Binh	S	RS6 2088	M	-	-	Sep. 29, 1960	VNU
8	Ha Nam	ESf	NTS2019.13	M	420	274	Jan. 5, 2019	DVZ
9	Ninh Binh	ESf	2128	M	-	-	Apr. 19, 1963	VNU
9	Ninh Binh	ESf	2114 (2014)	M	-	-	Apr. 15, 1963	VNU
9	Ninh Binh	ESf	NTS2019.09.10	M	435	270	Sep. 10, 2019	DVZ
9	Ninh Binh	ESf	NTS2019.09.11	M	440	280	Sep. 11, 2019	DVZ
9	Ninh Binh	ESf	179	F	443	240	Jan. 5, 2008	DVZ
9	Ninh Binh	ESf	190	F	469	250	Jan. 6, 2008	DVZ
9	Ninh Binh	ESf	2091	F	-	-	Apr. 5, 1963	DVZ
10	Thanh Hoa	MLf	616	M	-		-	DZM
10	Thanh Hoa	MLf	661	M	-	-	-	DZM
10	Thanh Hoa	MLf	698	M	-	-	-	DZM
10	Thanh Hoa	MLf	677	F	-	-	-	DZM
10	Thanh Hoa	MLf	667	F	-	-	-	DZM
11	Ha Giang	SDf & MDf	4	F	-	-	-	DZM
11	Ha Giang	SDf & MDf	10	F	-	-	-	DZM
11	Ha Giang	SDf & MDf	30	F	-	-	-	DZM
11	Ha Giang	SDf & MDf	1	F	-	-	-	DZM
12	Cao Bang	MLf	13	F	-	-	-	DZM
12	Cao Bang	MLf	17	F			-	DZM
12	Cao Bang	MLf	28	F	-	-	-	DZM
12	Cao Bang	MLf	166	M	448	410	Dec. 23, 2006	DVZ
12	Cao Bang	MLf	1	M	-	-	-	DZM
12	Cao Bang	MLf	2	M	-	-	-	DZM
12	Cao Bang	MLf	22	M	-	-	-	DZM

12	Cao Bang	MLf	25	M	-	-	-	DZM
12	Cao Bang	MLf	29	M	-	-	-	DZM
13	Bac Kan	MLf	2035	F	-	350	Jul. 26, 1967	VNU
13	Bac Kan	MLf	Mn2036	F	-	-	May 29, 1969	VNU
13	Bac Kan	MLf	2037	M	458	361	Jun. 16, 1968	VNU
13	Bac Kan	MLf	2039	M	473	350	Oct. 5, 1968	VNU
13	Bac Kan	MLf	2043	M	-	-	Sep. 6, 1969	VNU
13	Bac Kan	MLf	2124	M	-	-	Mar. -, 1961	VNU
13	Bac Kan	MLf	2129	M	-	-	Dec. 3, 1961	VNU
14	Tuyen Quang	SDf & MDf	55	M	-	-	-	DZM
14	Tuyen Quang	SDf & MDf	Mn2126	M	-	-	Apr. 15, 1962	VNU
14	Tuyen Quang	SDf & MDf	37	F	-	-	-	DZM
14	Tuyen Quang	SDf & MDf	50	F	-	-	-	DZM
15	Thai Nguyen	SDf & MDf	2016	F	-	-	-	VNU
16	Lang Son	MLf	2102	F	-	-	-	VNU
16	Lang Son	MLf	Mn0027	F	-	-	Jan. 6, 1962	VNU
16	Lang Son	MLf	Mn2093	F	-	-	Jun. 28, 1962	VNU
16	Lang Son	MLf	Mn2103	F	-	-	Jun. 30, 1961	VNU
16	Lang Son	MLf	Mn2125	F	-	-	Jul. -, 1962	VNU
16	Lang Son	MLf	2094	M	-	-	Jun. 30, 1962	VNU
16	Lang Son	MLf	2097	M	-	-	Jun. 30, 1962	VNU
16	Lang Son	MLf	2100	M	-	-	May 20, 1964	VNU
16	Lang Son	MLf	2108	M	-	-	May 26, 1964	VNU
16	Lang Son	MLf	2122	M	-	-	May 19, 1964	VNU
16	Lang Son	MLf	JP 829	M	-	-	-	DVZ
16	Lang Son	MLf	Mn2018	M	-	-	Oct. 7, 1961	VNU

16	Lang Son	MLf	Mn2109	M	-	-	Jun. 30, 1968	VNU
17	Bac Giang	SDf & MDf	1131	F	-	-	-	DZM
17	Bac Giang	SDf & MDf	1132	F	-	-	-	DZM
17	Bac Giang	SDf & MDf	206	F	474	344	Dec. 27, 2008	DVZ
17	Bac Giang	SDf & MDf	210	F	454	268	Dec. 27, 2008	DVZ
17	Bac Giang	SDf & MDf	1129	F	-	-	-	DZM
17	Bac Giang	SDf & MDf	1130	M	-	-	-	DZM
17	Bac Giang	SDf & MDf	211	M	489	430	Dec. 27, 2008	DVZ
18	Vinh Phuc	S	1403	F	-	-	-	DZM
18	Vinh Phuc	S	TD10102017	F	487	330	Oct. 10, 2017	DVZ
18	Vinh Phuc	S	1400	M	-	-	-	DZM
18	Vinh Phuc	S	Mn0026	M	-	-	Apr. 4, 1962	VNU
18	Vinh Phuc	S	TD04	M	-	-	-	DVZ
19	Quang Ninh	S	2	F	-	-	-	DZM
19	Quang Ninh	S	12	F	-	-	-	DZM
19	Quang Ninh	S	14	F	-	-	-	DZM
19	Quang Ninh	S	1108	F	-	-	-	DZM
19	Quang Ninh	S	1112	F	-	-	-	DZM
19	Quang Ninh	S	1126	F	-	-	-	DZM
19	Quang Ninh	S	1130	F	-	-	-	DZM
19	Quang Ninh	S	1159	F	-	-	-	DZM
19	Quang Ninh	S	Mn2089	F	-	-	Dec. -, 1961	VNU
19	Quang Ninh	S	37	M	-	-	-	DZM
19	Quang Ninh	S	34	M	-	-	Dec. -, 1961	DZM
19	Quang Ninh	S	1102	M	-	-	Dec. -, 1961	DZM
19	Quang Ninh	S	1120	M	-	-	Dec. -, 1961	DZM

19	Quang Ninh	S	1	M	-	-	Dec. -, 1961	DZM
19	Quang Ninh	S	2095	M	-	-	Dec. -, 1961	VNU
19	Quang Ninh	S	Mn2092	M	-	-	Apr. 7, 1961	VNU
20	Hai Phong	S	2237	M	-	-	-	DZM
20	Hai Phong	S	2250	M	-	-	-	DZM
21	Nghe An	MLf	t11	F	-	-	-	VNU
21	Nghe An	MLf	Mn2017rs24	F	-	-	Sep. 16, 1960	VNU
21	Nghe An	MLf	2098	F	-	-	Jun. 22, 1961	VNU
21	Nghe An	MLf	2090	F	-	-	Aug. 18, 1960	VNU
21	Nghe An	MLf	t91	F	-	-	-	VNU
21	Nghe An	MLf	Pm,2017,09	M	443	310	Sep. -, 2017	DVZ
21	Nghe An	MLf	t26	M	-	-	-	VNU
21	Nghe An	MLf	t12	M	-	-	-	VNU
22	Ha Tinh	SDf & MDf	272187	F	-	-	-	DZM
22	Ha Tinh	SDf & MDf	64	F	-	-	-	DZM
22	Ha Tinh	SDf & MDf	406	F	-	-	-	DZM
22	Ha Tinh	SDf & MDf	82	F	-	-	-	DZM
22	Ha Tinh	SDf & MDf	84	F	-	-	-	DZM
22	Ha Tinh	SDf & MDf	69	F	-	-	-	DZM
22	Ha Tinh	SDf & MDf	89	F	-	-	-	DZM
22	Ha Tinh	SDf & MDf	90	M	428	220	Dec. 24, 2004	DVZ
22	Ha Tinh	SDf & MDf	77	M	-	-	-	DZM
23	Quang Binh	MLf	53 (609)	M	-	-	-	DZM
23	Quang Binh	MLf	605	M	-	-	-	DZM
24	Quang Tri	MLf	162	F	400	247	Dec. 23, 2006	DVZ
24	Quang Tri	MLf	167	F	474	295	Dec. 23, 2006	DVZ

25	Thua Thien-Hue	SDf & MDf	95	M	497	335	Dec. 25, 2004	DVZ
25	Thua Thien-Hue	SDf & MDf	101	M	484	325	Dec. 26, 2004	DVZ
25	Thua Thien-Hue	SDf & MDf	97	M	448	300	Dec. 25, 2004	DVZ
26	Kon Tum	MLf	2048	F	433	312	Jan. 22, 1980	VNU
26	Kon Tum	MLf	1801	M	-	-	-	DZM
26	Kon Tum	MLf	1802	F	-	-	-	DZM
26	Kon Tum	MLf	245	M	-	-	-	DZM
26	Kon Tum	MLf	268	F	-	-	-	DZM
26	Kon Tum	MLf	2046	M	455	-	May 21, 1980	VNU
26	Kon Tum	MLf	2033	M	466	-	Mar. 22, 1974	VNU
27	Gia Lai	MLf	KKK85	M	-	-	-	DVZ
28	Khanh Hoa	DDf	HB04	M	-	-	Nov. 10, 2011	DVZ
28	Khanh Hoa	DDf	HB07	M	-	-	Nov. 10, 2011	DVZ
29	Dak Nong	DDf	Nnu2017.17	F	489	200	Oct. 2017	DVZ
30	Lam Dong	DDf	251	F	-	-	-	DZM
31	Dong Nai	ERf	IEBR10	F	-	-	Dec. 2003	DVZ
31	Dong Nai	ERf	IEBR19	F	-	-	Dec. 2003	DVZ
31	Dong Nai	ERf	IEBR17	F	-	-	Dec. 2003	DVZ
31	Dong Nai	ERf	IEBR18	F	-	-	Dec. 2003	DVZ
31	Dong Nai	ERf	PL30	F	-	-	Jan. 1, 2008	DVZ
31	Dong Nai	ERf	CAl1cattien	M	-	-	-	DVZ
31	Dong Nai	ERf	CAl3cattien	M	-	-	-	DVZ
31	Dong Nai	ERf	CAl4cattien	M	-	-	-	DVZ
31	Dong Nai	ERf	CAl5cattien	M	-	-	-	DVZ
31	Dong Nai	ERf	PL31	M	-	-	Jan. 1, 2008	DVZ
31	Dong Nai	ERf	187	M	455	270	Jan. 6, 2008	DVZ

31	Dong Nai	ERf	120	M	478	280	Nov. 15, 2005	DVZ
31	Dong Nai	ERf	186	M	418	240	Jan. 6, 2008	DVZ

Notes: VNU (Biological Museum of the Vietnam National University of Science, Vietnam National University); DZM (Department of Zoological Museum, Institute of Ecology and Biological Resources); and DVZ (Department of Vertebrate Zoology, Institute of Ecology and Biological Resources).