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Original investigation

Colour polymorphism and genetic relationships among twelve subspecies of *Callosciurus finlaysonii* in Thailand

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ABSTRACT

Finlayson's squirrel (*Callosciurus finlaysonii*) is distributed in lowland forests in Southeast Asia. The pelage colour is conspicuously polymorphic, and 16 subspecies have been described based on pelage colour patterns. Among them, 12 subspecies are distributed in Thailand, of which 7 are on the mainland and 5 are on islands. In addition, the distribution range of another closely related species, Pallas's squirrel (*Callosciurus erythraeus*), overlaps the range of *C. finlaysonii* in western Thailand. In this study, phylogenetic analysis based on mitochondrial DNA suggested that *C. finlaysonii* and *C. erythraeus* did not form separate monophyletic groups. This *C. finlaysonii*/*C. erythraeus* complex in Thailand consisted of seven divergent groups, some of which may have arisen from isolation due to large rivers and seas: (1) *C. f. nox*/*cinnamomeus*, (2) *C. f. finlaysonii*/*folletti*/*trotteri*, (3) *C. f. menamicus*, (4) *C. erythraeus*, (5) *C. f. annellatus*, (6) *C. f. bocourti*/*boonsongi*/*floweri*, and (7) *C. f. frandseni*/*albivexilli*. Pelage colour did not consistently correspond to these genetic groups, suggesting that specific colours may have been acquired multiple times or the genes associated with colour may have variations and polymorphisms within subspecies. Several small populations in the lowlands and on small islands had lower genetic diversity. To conserve the local genetic diversity of *C. finlaysonii*, it may be necessary to enact legal restrictions on their trade and hunting.

Introduction

Southeast Asia is a hotspot of mammalian species richness and endemism (Ceballos and Ehrlich, 2006). The fauna of Southeast Asia arose from biogeographically diverse origins, and past sea level fluctuations facilitated further speciation (Meijaard, 2003; Sodhi et al., 2010). The family Sciuridae (squirrels) is one example of the high species richness of Southeast Asia (Koprowski and Nandini, 2008). However, accurate research using genetic methods on Sciuridae is lacking excluding recent several works (Oshida et al., 2006, 2013, 2016; Hawkins et al., 2016a,b), so that the establishment of Sciuridae diversity remains to be clarified.

Callosciurus is a genus of tree squirrels distributed widely in Southeast Asia, with 15 species (Corbet and Hill, 1992 Wilson and Reeder, 2005). Several of these species are divided into many subspecies, mainly based on pelage colour (Moore and Tate, 1965; Corbet and Hill, 1992). Finlayson's squirrel (*Callosciurus finlaysonii*), one of the most variable species in pelage colour, is divided into 16 subspecies distributed in the lowland forests of Myanmar, Thailand, Laos, Cambodia, and Vietnam (Fig. 1; Corbet and Hill, 1992 Wilson and Reeder, 2005). The main distribution range of this species is Thailand, and 12 of the 16 subspecies are distributed there, of which 7 are distributed on the mainland and 5 on the islands (Corbet and Hill, 1992). Pallas's squirrel (*Callosciurus erythraeus*), the most closely related species to *C. finlaysonii*, is distributed in Bhutan, India, Myanmar, Tibet, southern China, Taiwan, Laos, Cambodia, Vietnam, and Peninsular Malaysia (Fig. 1; Corbet and Hill, 1992 Wilson and Reeder, 2005). This species, which also varies in pelage colour, is divided into 25 subspecies (Wilson and Reeder, 2005). On the Malay Peninsula, *C. erythraeus* is known to inhabit only the high mountainous areas, and it inhabits hill forests in Laos (Medway, 1969; Timmins and Duckworth, 2008). Four subspecies (*C. erythraeus zimmeensis*, *C. e. thai*, *C. e. pranis*, and *C. e. rubeculus*) are distributed in western and southern peninsular Thailand

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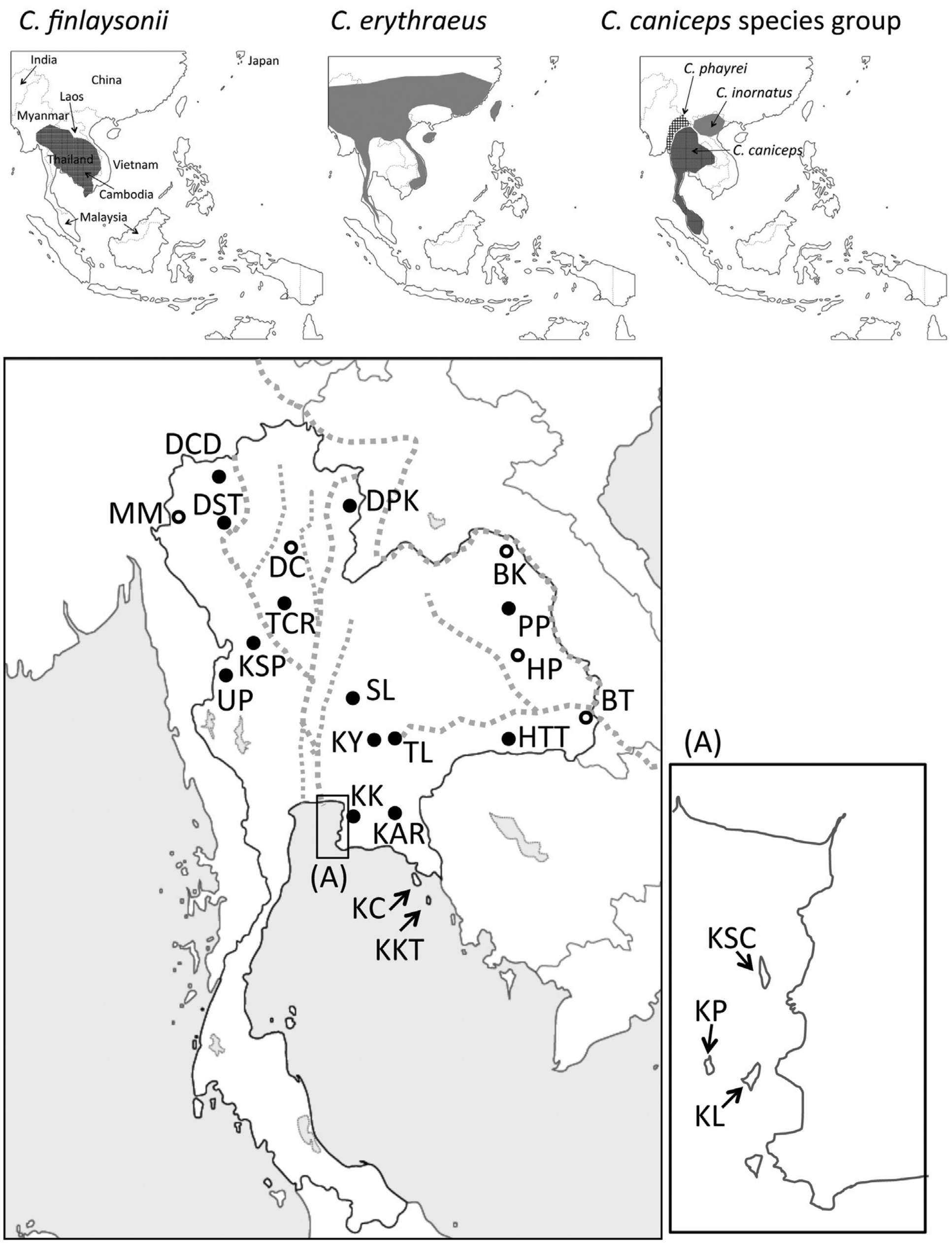

Fig. 1. Distribution maps of *C. finlaysonii*, *C. erythraeus*, and *C. caniceps* species groups (*C. caniceps* from Thailand to Peninsular Malaysia, *C. inornatus* from Laos to northern Vietnam, and *C. phayrei* in Myanmar), and the trapping sites in Thailand. Abbreviations are follows: KAR: Khao Ang Runai Wildlife Sanctuary; KK: Khao Kheow Wildlife Conservation Station; HTT: Huai Thap Than – Huai Samran Wildlife Sanctuary; SL: Sublungka Wildlife Sanctuary; KY: Khao Yai National Park; TL: Thap Lan National Park; BT:Buntharik; HP: Huai Phueng; PP: Phu Phan National Park; BK: Bung Khla; DPK: Doi Phu Kha National Park; DC: Den Chai; TCR: Tham Chao Ram Wildlife Sanctuary; UP: Um Phang Wildlife Sanctuary; KSP: Khao Sanam Preang Wildlife Sanctuary; DST: Doi Suthep-Pui National Park; DCD: Doi Chiang Dao National Park; MM: Maerao Maese Wildlife Sanctuary; KSC: The Aquatic Resources Research Institute, Chulalongkorn University, Koh Sichang; KP: Koh Phai; KL: Koh Lan; KC: Koh Chang; KKT: Koh Kut. The area labeled (A) is magnified outside the margin.

(Moore and Tate, 1965; Lekagul and McNeely, 1977; Wilson and Reeder, 2005), but these four subspecies and most other subspecies were combined as the single subspecies *C. erythraeus erythraeus* by Corbet and Hill (1992). A third *Callosciurus* species, *Callosciurus caniceps*, inhabits Thailand. This species, which is distributed from eastern Myanmar to Peninsular Malaysia, is closely related to *Callosciurus phayrei* in Myanmar and *Callosciurus inornatus* from Laos to northern Vietnam (Fig. 1; Corbet and Hill, 1992 Wilson and Reeder, 2005).

We are faced with the confusion of phylogenetic relationships among species and subspecies of these *Callosciurus* species, which is claimed by the molecular phylogenetic studies seeking the origins and genetic diversities of the introduced populations of *C. finlaysonii* and *C. erythraeus* to Japan (Oshida et al., 2007; Kuramoto et al., 2012), Argentina (Gabrielli et al., 2014), and Europe (Mazzamuto et al., 2016). Both *C. finlaysonii* and *C. erythraeus* are popular pets that are established worldwide, including in Belgium, France, Italy, The Netherlands, Hong Kong, Singapore, Japan, and Argentina (Bertolino and Lurz, 2013). The negative impacts of introduced squirrels on native animals and agricultural or forestry products are well known (Palmer et al., 2007; Bertolino, 2009; Bertolino and Lurz, 2013). Therefore, molecular analyses are necessary to identify these