



Tracing the phylogeographic history of Southeast Asian long-tailed macaques through mitogenomes of museum specimens



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ABSTRACT

The biogeographical history of Southeast Asia is complicated due to the continuous emergences and disappearances of land bridges throughout the Pleistocene. Here, we use long-tailed macaques (*Macaca fascicularis*), which are widely distributed throughout the mainland and islands of Southeast Asia, as a model for better understanding the biogeographical patterns of diversification in this geographically complex region. A reliable intraspecific phylogeny including individuals from localities on oceanic islands, continental islands, and the mainland is needed to trace relatedness along with the pattern and timing of colonization in this region. We used high-throughput sequencing techniques to sequence mitochondrial genomes (mitogenomes) from 95 Southeast Asian *M. fascicularis* specimens housed at natural history museums around the world. To achieve a comprehensive picture, we more than tripled the mitogenome sample size for *M. fascicularis* from previous studies, and for the first time included documented samples from the Philippines and several small Indonesian islands. Confirming the result from a previous, recent intraspecific phylogeny for *M. fascicularis*, the newly reconstructed phylogeny of 135 specimens divides the samples into two major clades: Clade A includes haplotypes from the mainland and some from northern Sumatra, while Clade B includes all insular haplotypes along with lineages from southern Sumatra. This study resolves a previous disparity by revealing a disjunction in the origin of Sumatran macaques, with separate lineages originating within the two major clades, suggesting that at least two major migrations to Sumatra occurred. However, our dated phylogeny reveals that the two major clades split ~1.88 Ma, which is earlier than in previously published phylogenies. Our new data reveal that most Philippine macaque lineages diverged from the Borneo stock within the last ~0.06–0.43 Ma. Finally, our study provides insight into successful sequencing of DNA across museums and shotgun sequencing of DNA specimens as a method to sequence the mitogenome.

1. Introduction

Southeast Asia is made up of a region of the Asian mainland along with thousands of islands varying in size (Fig. 1). Faunas differ fundamentally between the Sunda islands (Sundaland)—the biogeographical region encompassing the continental shelf that was exposed as a continuous landmass during Pleistocene glacial periods—and oceanic islands, those that have never been connected to the mainland (Wallace, 1863). These two major biogeographical regions are separated by what is called the Wallace Line (Fig. 1a). At the southern end, this line separates Bali and Lombok islands at the Strait of Lombok, which is only ~24 km wide. In the north, the separation occurs at the

129–370 km wide Makassar Strait between Borneo and Sulawesi (formerly Celebes) and extends east into the ~201 km wide and ~1500–2500 m deep strait in the Pacific Ocean between Mindanao and the Sanghir Islands (Bergman et al., 1996; George, 1981; Wallace, 1863). The islands to the east of the Wallace Line make up Wallacea. Huxley (1868) corroborated this division but drew the line directly north so that the Philippines, except for Palawan and its associated islands, lie to the east of the Wallace Line.

The colonization patterns and timing in this region are influenced by continuous geographical changes, especially throughout the Pleistocene (Heaney, 1986; Stepan et al., 2003; Jansa et al., 2006; Outlaw and Voelker, 2008; Delson, 1980; Fooden, 2006). Multiple

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glaciation periods allowed for the Sunda islands to be connected to the current mainland, creating land bridges on which organisms were able to migrate to the various islands. Within some primate groups, there is a unique split within or between species on the continental island of Sumatra. Specifically, a southernmost Sumatran orangutan population of the species *Pongo abelii* is in fact more closely related to the Bornean orangutan, *Pongo pygmaeus*, than it is to the northern populations of *P. abelii* (Nater et al., 2011, 2015). This divergence is also seen in gibbons, with the white-handed gibbon (*Hylobates lar*) occurring to the north and the mountain agile gibbon (*Hylobates agilis*) occurring to the South on Sumatra (Whittaker et al., 2007; Thinh et al., 2010). But there do not appear to be other studies that have identified splits like these in other taxa on Sumatra.

It is unlikely that any major land bridges formed between the Philippines and Sundaland, aside from a possible connection between Borneo and Palawan (Heaney, 1985). So humans are thought to have influenced the colonization of oceanic islands by bringing non-volant organisms to these islands in the very recent past (Heaney et al., 2016). However, if specific species were able to migrate to the Philippine islands without human aid, it is possible they would be able to easily colonize this oceanic region since several of the islands within the Philippines were likely connected via land bridges during glaciation periods (Heaney, 1985). In order to shed light on the patterns and timing of colonization throughout both Sunda and oceanic islands in Southeast Asia, it is necessary to study an organism that is widespread throughout the region. There appears to be a disjunction in faunal

occurrences on either side of Huxley's line, but *M. fascicularis* is an exception as one of the few species of non-volant mammals that occurs widely on the mainland, Sundaland, and on oceanic islands, making this species an excellent organism for studying biogeographical diversification throughout this entire region (Fig. 1).

Macaca species belong to one of the most widely distributed primate genera, occurring on two continents and multiple islands. Fossil evidence indicates that this highly successful genus originated in Africa around 7 million years ago (Ma) (Delson, 1980), after which macaques expanded into Asia approximately 5.5 Ma (Alba et al., 2014; Delson, 2000). Twenty-two species subdivided into seven species groups are currently recognized based on distribution, morphology, behavior and genetics (Li et al., 2009; Tosi et al., 2003). Based mostly on morphological data, three of these groups are monospecific: *M. sylvanus*, which is the only extant macaque in northern Africa and southern Europe, *M. fascicularis*, and *M. arctoides*. The remaining four groups are poly-specific, with six species in the Sulawesi group, five in the *M. silenus* group, three in the *M. mulatta* group, and five in the *M. sinica* group (Zinner et al., 2013a). However, classification into species groups has changed over time in tandem with extensive debate. Originally, *M. mulatta*, *M. cyclopis*, *M. fuscata*, and *M. fascicularis* were all included in the *M. fascicularis* species group (Fooden, 1976). Groves (2001) and Zinner et al. (2013a) then combined *M. mulatta*, *M. cyclopis*, and *M. fuscata* in a *M. mulatta* species group. Groves (2001) also added *M. arctoides* to the *M. fascicularis* species group, but Zinner et al. (2013a) subsequently classified *M. arctoides* and *M. fascicularis* as two separate

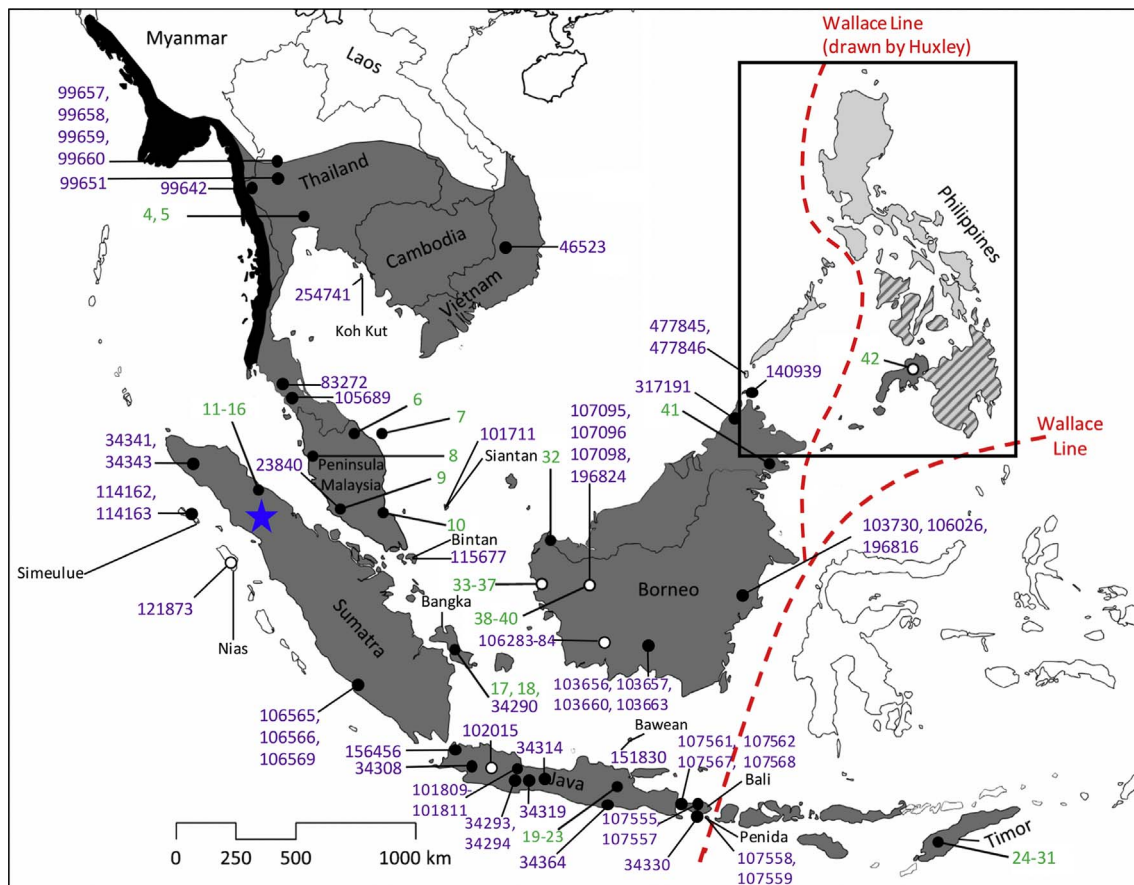


Fig. 1. Maps of Southeast Asia. (a) A map of Southeast Asia derived from Liedigk et al. (2015) marked with specimens from the current study and Liedigk et al.'s (2015) study. The black, dark grey and light grey regions respectively indicate the ranges of *M. f. aureus*, *M. f. fascicularis* and *M. f. philippinensis*. The region colored in light and dark grey lines is the putative area of intergradation of *M. f. fascicularis* and *M. f. philippinensis* based on studies by Fooden (1995, 2006). White circles represent approximate location whereas black circles represent exact location. ID numbers of *M. fascicularis* museum specimens in green correspond to samples sequenced in Liedigk et al. (2015) and those in purple are the newly sequenced samples in this study. Lake Toba is marked with a blue star. (b) A map of the Philippines (Philippines region in rectangular box from (a) magnified), derived from Heaney (1986), marked with specimens from the current study. The circles and colored ID numbers of *M. fascicularis* specimens are labeled according to the description in map (a). All ID numbers correspond to those in Fig. 2 and Supplementary Data 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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