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Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group

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Abstract

The 12 presently recognized taxa forming the *Macaca silenus* group represent the most diverse lineage within the genus *Macaca*. The present study was set up to clarify the phylogenetic relationships of the extant members of the *M. silenus* group and to explain their geographical distribution patterns seen today. A combined approach involving the analysis of one paternal (TSPY) and two maternal (cyt b and 12S–16S rRNA) molecular markers enabled us to resolve the phylogenetic relationships within this lineage. Our Y chromosomal marker is not informative enough to allow detailed conclusion. Based on our mitochondrial data, however, *M. pagensis*, endemic to the three southern Mentawai islands (Sipora, North- and South Pagai), split off early (2.4–2.6 mya) and represents a sister clade to the macaques from the northern Mentawai island of Siberut and from those of the Southeast Asian mainland, which diverged in a radiation-like splitting event about 1.5–1.7 mya. By combining our new results with available data on behavioural as well as climate and sea level changes in Southeast Asia during the Plio- and Pleistocene, we have developed two scenarios for the evolutionary history of this primate group, which may help explain the current geographical distribution of its members.

Keywords: *M. silenus* group; Macaques; Phylogeny; Evolution; Biogeography; Cytochrome *b*; 12SrRNA; 16SrRNA; TSPY

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1. Introduction

According to fossil data, the genus *Macaca* arose about 7 mya in North Africa and subsequently spread throughout most of Asia during the past 5.5 million years (Delson, 1980, 1996; Delson and Andrews, 1975). Today, found in over 20 Asian countries and covering an area of more than 5 million km^2 (Fa, 1989), this genus of old world monkeys can be considered as the most successful of all the extant non-human primate radiations (Tosi et al., 2003). During its spread into Asia, the genus *Macaca* diversified into a number of distinct species groups which have been variously defined according to their geographical distribution, differences in male reproductive anatomy (Delson, 1980) and more recently, molecular genetic data (Hayasaka et al., 1996; Morales and Melnick, 1998; Tosi et al., 2003). Currently, five main species/phyletic groups are recognised as reflecting the major steps of radiation within the genus; these are the two monotypic groups *M. sylvanus* and *M. arctoides*, and the polytypic groups *M. fascicularis* and *M. sinica*, with four and five species, respectively, and the *Macaca silenus* group (Groves, 2001; Tosi et al., 2003; Sinha et al., 2005).

With 12 currently recognized taxa exhibiting a range of distinct morphological and behavioural differences (Abegg and Thierry, 2002b; Fooden, 1975), the *M. silenus* group is

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the most diverse lineage within the macaque genus. The group is also characterised by showing a wide distribution, its range extending from Southwest India (*M. silenus*) through mainland Southeast Asia (*M. leonina*), peninsular Malaysia, Sumatra and Borneo (*M. nemestrina*) to Sulawesi (seven taxa) in the East and the Mentawai archipelago (*M. pagensis* and *M. siberu*) off Sumatra's coast in the West (Fig. 1).

Although the general classification of the *M. silenus* group seems widely accepted (Evans et al., 2003; Fooden, 1980; Groves, 2001; Roos et al., 2003), the phylogenetic relationships among the various taxa and the biogeographic processes leading to their current distribution are not well understood. One of the main reasons for this is the extent and complexity of the geographical and environmental changes that repeatedly occurred during the recent past throughout their current distribution range. Notably, in both the Plio- and Pleistocene, a series of dramatic climatic changes profoundly influenced the geography and vegetation in the region, leading to shifts in the extension and distribution of different habitat types (Eudey, 1980; Morley and Flenley, 1987; Morley, 2000; Bird et al., 2005; also see Meijaard, 2003a; for an overview). In particular, periods of maximum glaciation reduced rainforest cover, resulting in the appearance of more open and deciduous vegetation types in many parts of Sundaland, (Bird et al., 2005; Kaars van der et al., 2001; Sun et al., 2000; Urushibara-Yoshino and Yoshino, 1997; Meijaard, 2003b). Moreover, due to the alternately falling and rising sea water levels during the several glacial and interglacial periods characterising the Plio- and Pleistocene periods (Molengraaff and Weber, 1920; Tjia, 1976; Jablonski and Whitfort, 1999; Meijaard, 2003a), connections and separations of landmasses were common, and repeated migration between habitats was possible (Verstappen, 1975; Tougard, 2001; Woodruff, 2003).

It is therefore reasonable to assume that climatic and geological factors have played an important role in influencing the biogeographic patterns leading to the current distribution of the *M. silenus* group members (and other terrestrial animals) in Southeast Asia (Ferguson, 1993; Abegg and Thierry, 2002b; Evans et al., 2003). Nevertheless, the details remain unclear of how such factors operated to affect the process of macaque radiation through Southeast Asia. Existing hypotheses that have attempted to explain the occurrence of the different *M. silenus* group members in different habitats and regions (Abegg and Thierry, 2002b; Fooden, 1980) are based on incomplete data and cannot be considered to be comprehensive.

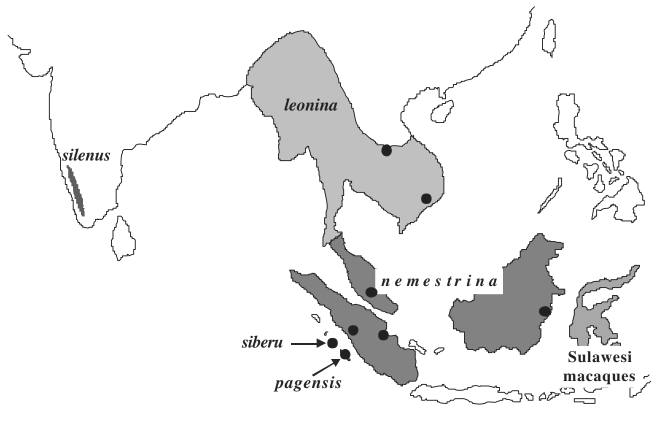

Fig. 1. Distribution of the members of the *M. silenus* group. Origin of samples are indicated by black dots (see also Table 1).

Thus, further clarification of this issue requires not only knowledge about former palaeogeographical and -climatic conditions in Southeast Asia but also (and in particular) more complete information on the phylogenetic relationships within the species group and the splitting times among its members. In contrast to the numerous studies on the radiation of the macaque genus as a whole (Deinard and Smith, 2001; Delson, 1980; Hayasaka et al., 1996; Morales and Melnick, 1998; Tosi et al., 2003), information about the phylogenetic relationships within the *M. silenus* group is scarce, and data that do exist are incomplete and at times contradictory (Evans et al., 2003; Roos et al., 2003; Tosi et al., 2003). For example, available molecular data indicate that the *M. silenus* group originated in the Sunda region and that the Sulawesi macaques and *M. silenus* probably stem from *M. nemestrina* like ancestors (Evans et al., 2003), contradicting the hypothesized ancestral position of these species based on morphological and behavioural data (Abegg and Thierry, 2002a,b). Moreover, it has recently been shown that Mentawai macaques are mitochondrially paraphyletic, with the northernmost form from Siberut being more closely related to *M. nemestrina* from Sumatra than they are to the form present on the three southern islands of the archipelago (Roos et al., 2003). This unexpected finding remains to be explained, but may indicate two independent colonisations of the Mentawai islands, as suggested by Roos et al. (2003).

However, all available hypotheses, whether based on genetic, morphological, or behavioural data are to some extent contradictory and consequently no consensus exists concerning the radiation of the *M. silenus* group. Our aim in the present study was to attempt an explanation of the evolutionary history of the *M. silenus* group and the biogeographic patterns leading to its current distribution by comparing information about past geological and climatic conditions with phylogenetic relationships and splitting times as revealed from molecular data. A comprehensive dataset is provided, in which sequences from one Y chromosomal locus and two mitochondrial loci have been generated for all species and major populations present in the group.

2. Materials and methods

2.1. Sample collection

Faecal material from macaques was collected in zoos, from pet monkeys, or during field surveys. In order to obtain a broad geographic and taxonomic sampling of the