Comparative phylogenetics offer new insights into the biogeographic history of *Macaca fascicularis* and the origin of the Mauritian macaques

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Running head: mtDNA and YDNA phylogenies of *M. fascicularis*

ABSTRACT

We employ a comparative phylogenetic analysis to gain insight into the recent evolutionary history of *Macaca fascicularis*, the long-tailed macaque. Mitochondrial and Y-chromosomal topologies both show that, in general, the deepest intraspecific bifurcations separate Indochinese and Sundaic forms of this species. Sumatran populations, however, are an exception: they carry one Y-chromosomal lineage that clusters with continental populations, and another that clusters with insular stocks. This discovery provides insight into two events in the history of *M. fascicularis*. First, the presence of the 'continental' Y-lineage on Sumatra is one of the strongest lines of evidence to date for recent (Late Pleistocene) gene flow between Indochinese and Sundaic populations. Second, since Sumatra is the only region known to carry 'continental' YDNA and 'insular' mtDNA, it is considered the most likely source of the Mauritian macaques – an important biomedical research stock that appears to carry this mtDNA/YDNA combination exclusively.

INTRODUCTION

The primate genus *Macaca* displays an extreme level of sex-biased dispersal (Pusey & Packer 1987; Melnick & Hoelzer 1993), resulting in mitochondrial and Y-chromosomal topologies that record different aspects of population history. The sedentary nature of female macaques leads to geographically structured mitochondrial haplotypes and a phylogenetic tree that is likely to maintain an ancient record of population-level cladogenic events. In contrast, male dispersal often erases these cladogenic patterns from Y-chromosomal trees and replaces them with more recent patterns of nuclear exchange. Differences in mtDNA and YDNA topologies can therefore frequently help researchers parse gene flow from cladogenesis in the phylogeographic history of macaque species. The long-tailed macaque, *Macaca fascicularis*, has been a prime candidate for such study given its expansive distribution through most of Southeast Asia (Fig. 1).

Earlier studies of *M. fascicularis* have revealed two cases of mtDNA/YDNA conflict. In the first case, these molecular markers yield different dates for the divergence of continental (Indochinese) and insular (Sundaic) populations (Tosi *et al*. 2003). The mtDNA date of 1.2 (+/-0.2) million years ago (MYA) indicates that *M. fascicularis* was present on both the Asian mainland and Sunda Shelf by the latter part of the early Pleistocene. By comparison, the YDNA date of 0.4 (+/-0.1) MYA argues that mainland and island populations were able to exchange nuclear alleles several hundred thousand years later – presumably during a glacial period when the emergent Sunda Shelf was adjoined to Indochina (Fooden 1995). The second case of mtDNA/YDNA conflict involves a difference in divergence patterns. Recent studies (Hayasaka *et al*. 1996; Tosi

et al. 2002) have revealed that mitochondrial lineages of *M. fascicularis* are monophyletic with respect to other macaque species, but Y-chromosomal lineages are paraphyletic with respect to *M. mulatta*. Arguments based on relative lineage sorting periods indicate that the YDNA pattern is almost certainly the result of nuclear gene flow from *M. mulatta* into (north Indochinese) *M. fascicularis* (Tosi *et al*. 2002).

Unfortunately, these earlier studies failed to survey one area very likely to carry populations with distinct mitochondrial and Y-chromosomal signals: Sumatra. We may expect to find 'insular' mtDNA on Sumatra, based on the bifurcation of mainland and island stocks depicted in recent studies (Tosi *et al*. 2002, 2003). Yet, we may also expect to find 'continental' YDNA on Sumatra, considering the high probability of nuclear exchange with peninsular Malaysia during Pleistocene glacial periods (Fooden 1995; van den Bergh *et al*. 2001; Tougard 2001). Indeed, Sumatran and peninsular Malaysian long-tailed macaques are separated by one of the narrowest and shallowest waterways on the Sunda Shelf (Voris 2000) and almost certainly experienced lengthy periods of contact in the Pleistocene. The addition of Sumatran representatives to earlier datasets will help evolutionary biologists test for conflicting maternal and paternal signals often indicative of such nuclear exchange.

Mitochondrial and Y-chromosomal phylogenies of *M. fascicularis* are also of interest to biomedical researchers. Their non-recombining lines of descent make them excellent references for identifying the provenance of colony animals. Moreover, the discovery of historical episodes of gene flow, inferred from comparative phylogenetic analysis, may provide useful insight into the basic evolutionary history of research animals. For example, the discovery that *M. mulatta* alleles are introgressing into

northern *M. fascicularis* stocks (Tosi *et al*. 2002, 2003) may be correlated with the higher levels of aggression exhibited by Indochinese *M. fascicularis* relative to their insular conspecifics (Brent & Veira 2002).

Knowledge of provenance background is particularly important for studies using Mauritian *M. fascicularis*. The population on the Indian Ocean island of Mauritius was founded only 400 to 500 years ago, and the genetic homogeneity of the ~30,000 descendants (Sussman & Tattersall 1986) suggests this stock holds great promise as a primate model for immunological studies (Leuchte *et al*. 2004; Krebs *et al*. 2005). Though it behooves us to know as much as possible about the biological and evolutionary history of the Mauritian animals, the provenance of their Asian parental population remains unclear (Kondo *et al*. 1993). Intraspecific phylogenies provide one means of tracking the parental stock.

The present study was therefore performed with two goals. First, we fill a gap in the phylogeographic history of *M. fascicularis* by adding Sumatran representatives to earlier mtDNA and YDNA phylogenies. Second, we use these expanded maternal and paternal topologies as frameworks for identifying the Asian provenance of the Mauritian founders. This work broadens our knowledge of *M. fascicularis* history in areas relevant to both evolutionary biologists and biomedical researchers.

MATERIALS & METHODS

Samples

Mitochondrial and Y-chromosomal data were gathered from 40 male cercopithecine monkeys, including 29 *M. fascicularis* sampled across the species range (Table 1). The DNA sequences of 14 *M. fascicularis* (ten from Mauritius, four from Sumatra) were newly surveyed; the sequences of all other animals were drawn from the datasets of Tosi *et al*. (2002, 2003). The Mauritian individuals were trapped at multiple sites across the island. The Sumatran samples were collected from colony animals descended from populations in Palembang and Lampung. Whole blood (10 mL) was collected from the 14 newly surveyed animals using VACUTAINERs w/ sodium heparin. Total genomic DNA was isolated using the DNeasy Tissue Kit (Qiagen, Cat. No. 69504).

Mitochondrial DNA

A 1.5 kb fragment of mtDNA spanning the 3' end of the 12S ribosomal gene (550 bp), tRNA-val (70 bp), and the 5' end of the 16S ribosomal gene (930 bp) was amplified and sequenced. Previous studies of *M. fascicularis* (Tosi *et al*. 2002, 2003) surveyed this region and provide a valuable comparative framework for the sequences collected here. We employed a long-amplification technique (Raaum *et al*. 2005) to reduce the chance of targeting nuclear insertions of mtDNA. We used primers 8191F (5' CACTCATTCACACCAACCACTCAACTTTCC 3') and 2730R (5' CACGTAGGACTTTAATCGTTGAACAAACGAACC 3') to amplify a ~11 kb segment

from ATP6 to 16S and then sequenced the 12S/tRNA-val/16S region with a battery of internal primers designed by Tosi *et al*. (2002).

Y-chromosomal loci

SRY and TSPY, two loci located in the non-recombining portion of the Y-chromosome, and totaling 3.1 kb, were amplified and sequenced using primers and protocols described by Tosi *et al*. (2000). These two loci have been extensively examined in cercopithecine monkeys, and GenBank data again provide a comparative framework for the sequences gathered here. SRY (Sex-determining Region, Y-chromosome) is a single-copy gene that acts as a genetic switch initiating the development of the testes (Knower *et al*. 2003). TSPY (Testis-Specific Protein, Y-chromosome) is a multigene family believed to have a function in spermatogonial proliferation (Vogel & Schmidtke 1998). Data already collected on this gene family suggest that it is maintained by a mechanism of concerted evolution in cercopithecine monkeys (Tosi *et al*. 2000, 2005).

Sequencing and Contig Assembly

Amplified products were cleaned with exonuclease I and shrimp alkaline phosphatase (Hanke & Wink 1994) and cycle-sequenced using BigDye chemistry (Applied Biosystems, Foster City, CA). Cycle-sequence products were cleaned via ethanol precipitation, and subsequently analyzed using an ABI 3730 automated DNA sequencer. Complementary strands were sequenced as a proofreading check of the data. The sequence reads from each amplicon were processed with the software FACTURA

(ABI, Perkin-Elmer) and assembled into a single contig using the program AUTOASSEMBLER (ABI, Perkin-Elmer). Alignment of the contigs was made by eye and through the use of SEQUENCE NAVIGATOR (ABI, Perkin-Elmer).

Phylogeographic Analysis

The TSPY and SRY datasets were combined prior to analysis because both loci are located on the non-recombining portion of the Y-chromosome and are effectively a single linkage group. Moreover, topologies generated from TSPY and SRY independently (not shown) do not yield any conflicting clades. By contrast, the concatenated Y-chromosomal dataset was not combined with the mitochondrial dataset because, in macaques, these two genetic systems differ in mode of inheritance (paternal vs. maternal), dispersal rate (emigrating males vs. philopatric females), and effective population size (fewer sires than dams). These differences have been shown to result in distinct evolutionary topologies and divergence dates in earlier surveys of macaque phylogeny (Tosi *et al*. 2002, 2003).

The 12S/tRNA-val/16S and TSPY/SRY datasets were analyzed with Modeltest 3.04 (Posada & Crandall 1998) to determine the substitution model that best fit the data according to a hierarchical likelihood ratio test. The TrN+I+G and HKY+G models were selected for the mitochondrial and Y-chromosomal datasets, respectively. Each dataset was then subjected to maximum likelihood analysis in PAUP 4.0b10 (Swofford 2002) using the appropriate model, empirical base frequencies, and a heuristic search algorithm. Clade support was measured by 100 bootstrap replicates.

RESULTS

Sumatran Lineages

Mitochondrial (Fig. 2A) and Y-chromosomal (Fig. 2B) topologies reveal slightly different patterns with respect to the position of Sumatran *M. fascicularis*. Analyses of the 12S/tRNA-val/16S dataset indicate that the deepest mitochondrial split within *M. fascicularis* is a bifurcation of continental vs. insular lineages (Fig 2A), and that Sumatran animals clearly belong to the insular clade. However, the Y-chromosomal pattern (Fig. 2B) is more complex. *M. fascicularis* from north of the Khlong Marui Fault (Fig. 1) carry an *M. mulatta* Y-chromosomal lineage, as a result of hybridization between Indochinese populations of the two species (Tosi *et al*. 2002, 2003). *M. fascicularis* populations south of the fault retain true long-tail Y-chromosomes and subdivide into a pattern reminiscent of the continental vs. insular bifurcation, but with one exception: *Sumatran lineages cluster in both clades*.

Though high bootstrap values ally Sumatran mitochondrial lineages exclusively with insular stocks (Fig. 2A), lower bootstrap values call into question the assignment of Sumatran Y-chromosomal lineages to both insular and continental clades (Fig. 2B). Indeed, inspection of the TSPY/SRY dataset reveals that both clades are supported by only a single point mutation, and tree comparison tests indicate that topologies constrained for Sumatran monophyly are statistically equivalent to the unconstrained tree presented here (Fig. 2B). Yet, two lines of reasoning bolster support for the unconstrained Y-chromosomal pattern. First, mutations at the sites defining the Y-chromosomal clades are evolutionarily rare and therefore carry great weight. A review of

all Old World Monkey TSPY and SRY sequences on GenBank, including 12 genera and 45 species, reveals that the TSPY site defining the "insular + Sumatra" clade (site #2175) exhibits a mutation in only two other species, while the SRY site defining the "continental + Sumatra" clade (site #214) is conserved among all other monkeys. Second, the Y-chromosomal pattern makes sense geographically. The two clades discussed here represent groupings of animals from *neighboring* regions, rather than a mixture of animals from random areas as would be expected if the Y-chromosomal sites described above were mutational 'hotspots' producing homoplasious changes. Thus, the "insular + Sumatra" and "continental + Sumatra" clades (Fig. 2B) represent a robust working hypothesis of *M. fascicularis* Y-chromosomal relationships south of the Khlong Marui Fault.

Mauritian Lineages

All ten Mauritian macaques carry identical 12S/tRNA-val/16S and TSPY/SRY sequences, providing further support for the idea that these animals originate from a small founding population (Kondo *et al*. 1993; Lawler *et al*. 1995; Leuchte *et al*. 2004; Krebs *et al*. 2005). Inspection of their TSPY and SRY sequences reveals two indels shared in common with *M. fascicularis* populations south of the Khlong Marui Fault (Tosi *et al*. 2002, 2003). Interestingly, the Mauritian macaques cluster with insular stocks in the mitochondrial tree (Fig. 2A), but with continental stocks in the Y-chromosomal tree (Fig. 2B). A similar mtDNA vs. YDNA conflict is witnessed in (some) animals from Sumatra. Based on these evolutionary patterns, the Mauritian macaques appear to be derived either solely from Sumatran stocks, or from a mixture of continental males and insular females.

DISCUSSION

The phylogeographic history of Sumatran *M. fascicularis*

Mitochondrially, Sumatran *M. fascicularis* cluster within a clade of insular populations (Fig. 2A). Y-chromosomally, too, some Sumatran animals cluster with insular stocks, but others cluster with continental populations, particularly those of peninsular Malaysia (Fig. 2B).

Why are both insular and continental Y-chromosomal lineages found on Sumatra? The coexistence of divergent genetic variants can generally be explained by either ancestral polymorphism or secondary contact. However, a hypothesis of ancestral polymorphism is inconsistent with the broader phylogeographic picture gleaned here. The mitochondrial bifurcation of continental and insular stocks at ~ 1.2 MYA (Fig. 2A) (Tosi *et al*. 2003) indicates that long-tailed macaque populations were already present on both the Asian mainland and the Sunda Shelf long before the divergence of the two extant Y-chromosomal types at ~ 0.4 MYA (Fig. 2B) (Tosi *et al*. 2003). Therefore, if the continental and insular Y-lineages truly stem from a Sumatran common ancestor, they must have replaced pre-existing Y-lineages as they spread across peninsular Malaysia and the Sunda Shelf, respectively (Fig. 2B). A scenario in which these two lineages could so readily replace others across large portions of Southeast Asia, does not easily agree with their retention on the smaller landmass of Sumatra.

Secondary contact is a far better explanation for the coexistence of Y-chromosomal lineages in this case. Like other animals (van den Bergh *et al*. 2001; Tougard 2001), *M. fascicularis* populations almost certainly experienced a ripple effect in

which some continental stocks were pushed onto the Sunda Shelf during Pleistocene glacial periods (Fooden 1995). Under these conditions, Sumatra is likely to have received an immediate wave of immigrating male macaques considering that the waterway separating it from peninsular Malaysia is one of the first to dissipate with lowering sea levels (Voris 2000; Bird *et al*. 2005). Though there were at least six such glacial periods in the Late Pleistocene when an emergent land bridge would have allowed for the continental Y-lineage to enter into Sumatran *M. fascicularis* (Voris 2000), we postulate that this haplotype is a recent genetic immigrant (i.e. Last Glacial Maximum) based on the fact that it presently coexists with the 'insular' Y-haplotype. By comparison, a deep window of time since the last episode of Y-chromosomal exchange would predict one lineage to have reached fixation on Sumatra. It is possible that the phylogeographic pattern revealed here (Fig. 2B) depicts a continental Y-lineage *in the process* of replacing the native insular form.

The source population of Mauritian *M. fascicularis*

Though previous protein analyses (Kondo *et al*. 1993) could not conclusively determine the geographic origin of the Mauritian parental population, they did identify stocks on Java, Sumatra, and peninsular Malaysia as the most likely candidates. The present study sheds light on this issue. The 12S/tRNA-val/16S tree (Fig. 2A) allies Mauritian mitochondrial lineages with those from the Sunda Shelf islands, and the TSPY/SRY tree (Fig. 2B) clusters Mauritian Y-chromosomal lineages with those from the Asian mainland. Sumatran animals represent the only southeast Asian population to mirror this mtDNA vs. YDNA pattern, leading to the working hypothesis that Mauritian

M. fascicularis are derived from Sumatran stocks. A Sumatran origin also draws support from historical records. During the 1500s, the Portuguese held control of trade through the Malacca Straits, the waterway separating Sumatra and peninsular Malaysia. From 1521-1524, they maintained a fortress at Pasai, northern Sumatra (Subrahmanyam 1993), and may have taken pet macaques from the surrounding area. The Portuguese also 'discovered' Mauritius between 1505 and 1507 and used it as a regular stopover to and from the East Indies. They are known to have introduced pigs and goats to Mauritius, and likely released macaques there as well.

Though Sumatra is the most probable origin of the Mauritian macaques, we cannot fully discount Java and peninsular Malaysia. It is possible that the Mauritian founders were a mixed stock including females from Java (hence their insular mitochondrial lineage, Fig. 2A) and males from Malaysia (hence their continental Y-chromosomal lineage, Fig. 2B). However, we consider this scenario less likely because it requires multiple acquisitions of animals and, perhaps, multiple transfers to Mauritius. It is also possible that some Javanese animals indeed carry the combination of continental YDNA and insular mtDNA indicative of a relationship with the Mauritian macaques, but the limited survey of Java included here (n=1) has failed to detect this genotype. In theory, the continental Y-lineage could easily have spread into Javanese populations during a Pleistocene glacial period, considering that emergent land bridges would connect this island with peninsular Malaysia and Sumatra during any drop in sea level below ~ 40 m (Voris 2000; Bird *et al*. 2005). Thus, a Javan origin of the Mauritian macaques remains a viable alternative hypothesis that cannot be discounted without first expanding the Y-chromosomal survey of the Greater Sunda Islands.

Future Research

The mitochondrial and Y-chromosomal relationships discussed here provide valuable insight into *M. fascicularis* phylogeography. However, increased sampling is essential to bring the history of this species into greater focus. More intensive surveys are needed through peninsular Malaysia and Sumatra, in particular. These crossroads of the *M. fascicularis* range have the highest likelihood of experiencing the ebb and flow of continental and insular genetic fronts associated with Pleistocene glacial periods. The present study has already revealed the existence of the continental Y-lineage in Sumatra; it is possible that future studies will discover the insular Y-lineage in Malaysia. It is also possible, despite the slow geographic expansion of matrilines, that continental and insular mtDNA types have diffused to a limited extent between these two landmasses.

Finally, biomedical researchers can use the phylogeographic patterns revealed here to track the origin and basic evolutionary history of their long-tailed macaque colonies. Researchers using Mauritian macaques should be particularly cognizant of the history of these animals. Though these monkeys have a high degree of genetic homogeneity, their combination of insular mtDNA and continental YDNA suggests that their (presumed) Sumatran ancestors received influxes of alleles from Malaysian *M. fascicularis*. Consequently, if Mauritian long-tailed macaques exhibit a biomedically valuable trait, researchers should be prepared to search for its genetic and evolutionary underpinnings among both Sumatran and Malaysian populations.

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Table 1. Genetic Samples List

#	Taxon	Origin	Designation	GENBANK #s (SRY, TSPY, mtDNA)
1	Macaca cyclopis	Taiwan	2682	AF284296, AF284245, AF424945
2	M. cyclopis	Taiwan	#1	AF425289, AF425274, AF424944
3	M. f. fascicularis	Vietnam	290.WB	AF284304, AF284253, AF424958
4	M. f. fascicularis	Vietnam	SV#4	AF425284, AF425269, AF424961
5	M. f. fascicularis	Cambodia	Camb.#3	AF425286, AF425271, AF424955
6	M. f. fascicularis	Cambodia	Camb.#4	AF425287, AF425272, AF424956
7	M. f. fascicularis	Tum Chompol, Thailand	791.Tum.Chompol	AF425288, AF425273, AF424954
8	M. f. fascicularis	Songkhla, Thailand	668.Songkhla	AF425295, AF425280, AF424962
9	M. f. fascicularis	Johor, Malaysia	Johor.DJ.95	AF425292, AF425277, AF424965
10	M. f. fascicularis	Selangor, Malaysia	UKM.003	AF425293, AF425278, AF424963
11	M. f. fascicularis	Selangor, Malaysia	UKM.004	AF425294, AF425279, AF424964
12	M. f. fascicularis	West Malaysia	DM2687	AF284297, AF284246, ----------
13	M. f. fascicularis	Sarawak, Malaysia	Sarawak	AF284299, AF284248, AF424967
14	M. f. fascicularis	Sepilok, Malaysia	Sepilok	AF284300, AF284249, AF424968
15	M. f. fascicularis	Kalimantan, Indonesia	Borneo.PM666	AF284302, AF284251, AF424966

Table 1. Cont'd

#	Taxon	Origin	Designation	GENBANK #s (SRY, TSPY, mtDNA)
16	M. f. fascicularis	Java, Indonesia	Java.34	AF284303, AF284252, AF424969
17	M. f. fascicularis	Mauritius	10-236	DQ832590, DQ832604, DQ832618
18	M. f. fascicularis	Mauritius	3321	DQ832591, DQ832605, DQ832619
19	M. f. fascicularis	Mauritius	4124	DQ832592, DQ832606, DQ832620
20	M. f. fascicularis	Mauritius	6499	DQ832593, DQ832607, DQ832621
21	M. f. fascicularis	Mauritius	6621	DQ832594, DQ832608, DQ832622
22	M. f. fascicularis	Mauritius	7600	DQ832595, DQ832609, DQ832623
23	M. f. fascicularis	Mauritius	8944	DQ832596, DQ832610, DQ832624
24	M. f. fascicularis	Mauritius	9456	DQ832597, DQ832611, DQ832625
25	M. f. fascicularis	Mauritius	R209	DQ832598, DQ832612, DQ832626
26	M. f. fascicularis	Mauritius	X-957	DQ832599, DQ832613, DQ832627
27	M. f. fascicularis	S. Sumatra, Indonesia	A1828	DQ832600, DQ832614, DQ832628
28	M. f. fascicularis	S. Sumatra, Indonesia	A8097	DQ832601, DQ832615, DQ832629
29	M. f. fascicularis	S. Sumatra, Indonesia	A9652	DQ832602, DQ832616, DQ832630
30	M. f. fascicularis	S. Sumatra, Indonesia	A12133	DQ832603, DQ832617, DQ832631

Table 1. Cont'd

#	Taxon	Origin	Designation	GENBANK #s (SRY, TSPY, mtDNA)
31	M. f. philippinensis	Sibuyan Is., Philippines	Philippines	AF284298, AF284247, AF424970
32	M. fuscata	Japan	13751	AF425290, AF425275, AF424946
33	M. fuscata	Japan	22086	AF284306, AF284255, AF424948
34	M. mulatta	Burma	Burma.23269	AF284309, AF284258, AF424949
35	M. mulatta	S.E. China	China.20156	AF284310, AF284259, AF424950
36	M. mulatta	N. India	India.92B.560	AF284311, AF284260, AF424952
37	M. mulatta	N. India	16805	AF425291, AF425276, AF424951
38	M. sylvanus	N.W. Africa	1076	AF425296, AF425281, AF424973
39	Papio hamadryas	E. Africa	73-347	AF284328, AF284277, AF424974
40	Theropithecus gelada	E. Africa	891096	AF284329, AF284278, AF424975

Figure Legends

Figure 1. Present range of *Macaca fascicularis*. White circles indicate the origins of samples for which precise location is known. Black circles indicate the approximate origins of samples for which provenance data is known only to the level of country or general geographic region.

Figure 2. Likelihood trees generated from the mitochondrial and Y-chromosomal datasets. Bootstrap values of 50 and above (100 replicates, 'fast' stepwise-addition) are included throughout the trees. Asterisks highlight the positions of Sumatran and Mauritian lineages. Since all ten Mauritian animals carry identical 12S/tRNA-val/16S and TSPY/SRY sequences, only one sample (10-236) was used in each of the above analyses. Note also that one W. Malaysian sample (DM2687) was exhausted during the TSPY/SRY survey and therefore does not appear in the mtDNA tree. Divergence dates are from Tosi *et al*. (2003).

Figure 1

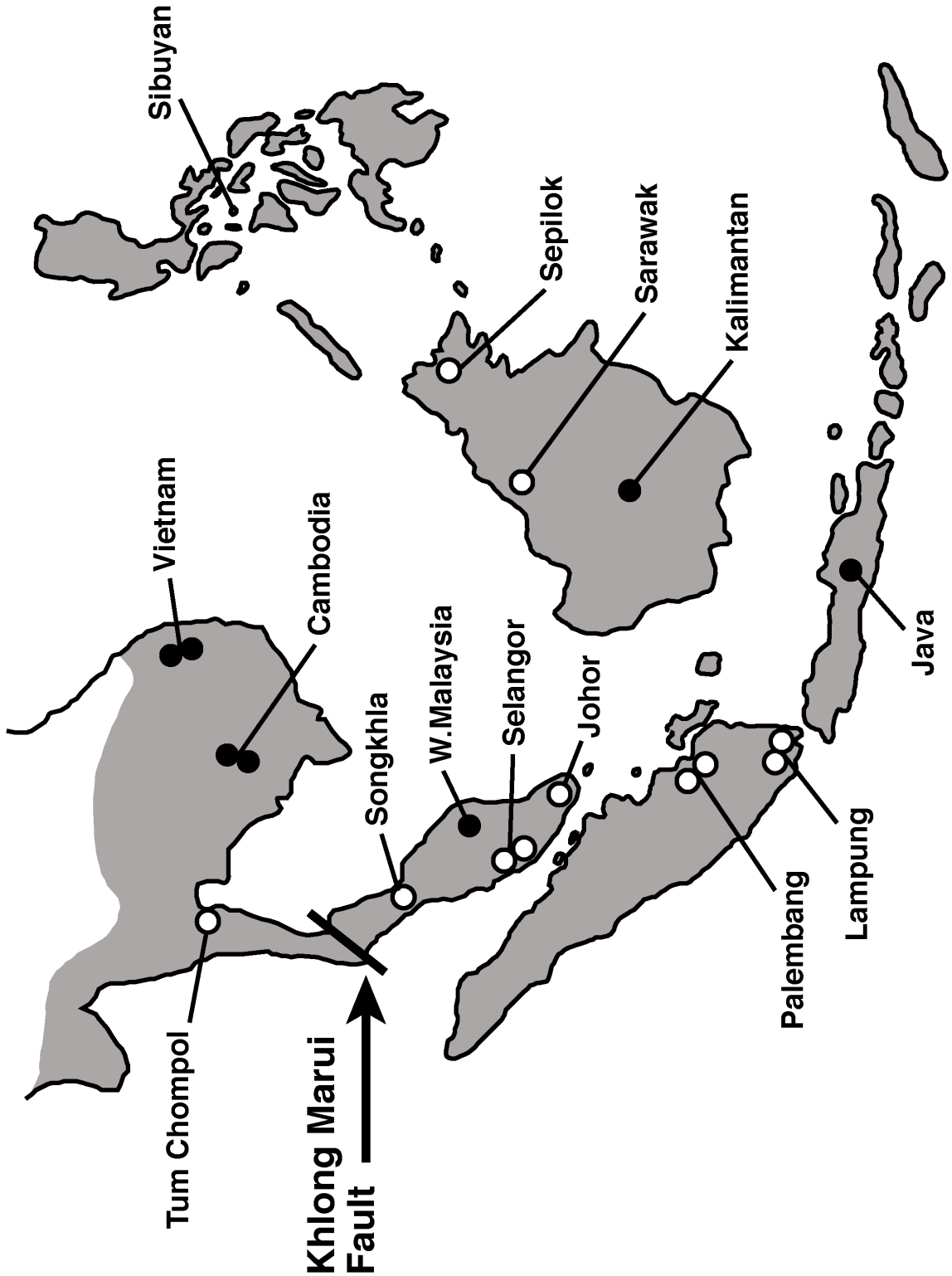
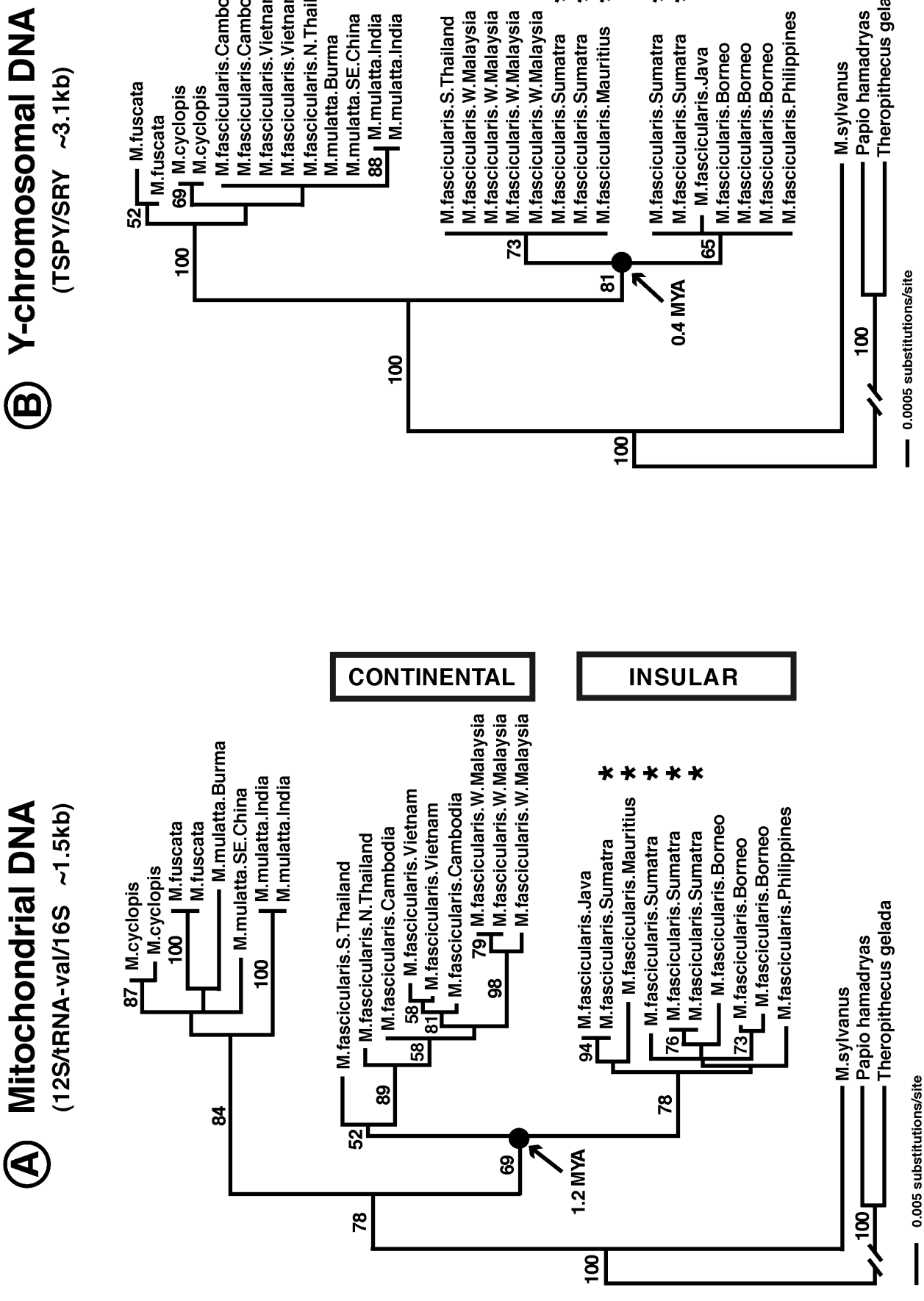

Sibuyan
Sepilok
Sarawak
Kalimantan
Vietnam
Cambodia
Songkhla
W.Malaysia
Selangor
Johor
Java
Tum Chompol
Khlong Marui
Fault
Palembang
Lampung

Figure 2


Ⓐ Mitochondrial DNA
(12S/tRNA-val/16S ~1.5kb)
M.cyclopis
M.cyclopis
M.fuscata
M.fuscata
M.mulatta.Burma
M.mulatta.SE.China
M.mulatta.India
M.mulatta.India
M.fascicularis.S.Thailand
M.fascicularis.N.Thailand
M.fascicularis.Cambodia
M.fascicularis.Vietnam
M.fascicularis.Vietnam
M.fascicularis.Cambodia
M.fascicularis.W.Malaysia
M.fascicularis.W.Malaysia
M.fascicularis.W.Malaysia
M.fascicularis.Java
M.fascicularis.Sumatra
M.fascicularis.Mauritius
M.fascicularis.Sumatra
M.fascicularis.Sumatra
M.fascicularis.Sumatra
M.fascicularis.Borneo
M.fascicularis.Borneo
M.fascicularis.Borneo
M.fascicularis.Philippines
CONTINENTAL
INSULAR
1.2 MYA
M.sylvanus
Papio hamadryas
Theropithecus gelada
0.005 substitutions/site
Ⓑ Y-chromosomal DNA
(TSPY/SRY ~3.1kb)
M.fuscata
M.fuscata
M.cyclopis
M.cyclopis
M.fascicularis.Cambodia
M.fascicularis.Cambodia
M.fascicularis.Vietnam
M.fascicularis.Vietnam
M.fascicularis.N.Thailand
M.mulatta.Burma
M.mulatta.SE.China
M.mulatta.India
M.mulatta.India
M.fascicularis.S.Thailand
M.fascicularis.W.Malaysia
M.fascicularis.W.Malaysia
M.fascicularis.W.Malaysia
M.fascicularis.W.Malaysia
M.fascicularis.Sumatra
M.fascicularis.Sumatra
M.fascicularis.Mauritius
M.fascicularis.Sumatra
M.fascicularis.Sumatra
M.fascicularis.Java
M.fascicularis.Borneo
M.fascicularis.Borneo
M.fascicularis.Borneo
M.fascicularis.Philippines
CONTINENTAL
INSULAR
0.4 MYA
M.sylvanus
Papio hamadryas
Theropithecus gelada
0.0005 substitutions/site