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HYBRIDIZATION AND POPULATION GENETICS OF TWO MACAQUE SPECIES IN SULAWESI, INDONESIA

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Abstract.—This study investigates hybridization and population genetics of two species of macaque monkey in Sulawesi, Indonesia, using molecular markers from mitochondrial, autosomal, and Y-chromosome DNA. Hybridization is the interbreeding of individuals from different parental taxa that are distinguishable by one or more heritable characteristics. Because hybridization can affect population structure of the parental taxa, it is an important consideration for conservation management. On the Indonesian island of Sulawesi an explosive diversification of macaques has occurred; seven of 19 species in the genus *Macaca* live on this island. The contact zone of the subjects of this study, *M. maura* and *M. tonkeana,* is located at the base of the southwestern peninsula of Sulawesi. Land conversion in Sulawesi is occurring at an alarming pace; currently two species of Sulawesi macaque, one of which is *M. maura,* are classified as endangered species. Results of this study indicate that hybridization among *M. maura* and *M. tonkeana* has led to different distributions of molecular variation in mitochondrial DNA and nuclear DNA in the contact zone; mitochondrial DNA shows a sharp transition from *M. maura* to *M. tonkeana* haplotypes, but nuclear DNA from the parental taxa is homogenized in a narrow hybrid zone. Similarly, within *M. maura* divergent mitochondrial DNA haplotypes are geographically structured but population subdivision in the nuclear genome is low or absent. In *M. tonkeana,* mitochondrial DNA haplotypes are geographically structured and a high level of nuclear DNA population subdivision is present in this species. These results are largely consistent with a macaque behavioral paradigm of female philopatry and obligate male dispersal, suggest that introgression between *M. maura* and *M. tonkeana* is restricted to the hybrid zone, and delineate one conservation management unit in *M. maura* and at least two in *M. tonkeana.*

Key words.—Hybrid zone, macaque monkeys, microsatellites, mitochondrial DNA, population structure, Southeast Asia.

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This study examines hybridization and population genetics in two species of Sulawesi macaque, the Moor macaque (*Macaca maura*) and the Tonkean macaque (*M. tonkeana*) using molecular markers in the mitochondrial and nuclear genomes. The goals are twofold: (1) to examine the genetic architecture of the *M. maura–M. tonkeana* hybrid zone; and (2) to identify population structure and conservation management units in these species.

Hybridization is the interbreeding of individuals from different parental taxa that are distinguishable by one or more heritable characteristics (Harrison 1990, 1993). Hybridization occurs when there are incomplete barriers to reproduction between parental taxa but gene flow among these taxa is too low or too recent to homogenize the hybrid system outside a zone of contact. Possible evolutionary consequences of hybridization are many. Parental species may diverge in spite of limited gene flow, they may amalgamate into a novel species of hybrid origin, they may produce a new species of hybrid origin while themselves remaining intact, and/or they may continue to hybridize without significant change in their respective genetic compositions (Arnold 1992). These diverse potential fates make hybrid zones interesting subjects for evolutionary study and important to conservation management policy.

Hybrid Zones

Much attention has been given to modeling the origin, persistence, and possible fate of hybrid zones in hopes of better understanding evolutionary processes (Darwin 1859; Endler 1977; Moore 1977; Barton and Hewitt 1985, 1989; Hewitt 1988; Harrison 1993). Mayr (1942) distinguishes hybrid zones that stem from primary contact, in which preexisting clines in character states become steeper in a continuously distributed taxon, and hybrid zones that result from secondary contact, in which formerly isolated taxa are reunited by the complete or partial removal of reproductive barriers. Evidence exists for some hybrid zones persisting over an extended period of time (White 1978; Hewitt 1989), posing the question of how hybrid zones are maintained. Theoretically, hybrid zones can be maintained by selection alone or by a balance between dispersal and selection. Environmental conditions could create a selection gradient that favors hybrid genotypes at the contact zone and parental genotypes outside of the contact zone (Moore 1977). Alternatively, hybrid genotypes might be maladaptive but persistent due to a balance between interbreeding of parental taxa in the hybrid zone and selection against hybrid individuals. Selection against hybrid genotypes might be due to an ecological gradient that favors each parental species outside of the hybrid zone but neither within it (Slatkin 1973; Endler 1977). Disruptive selection could also stem from nonenvironmental agents such as heterozygote disadvantage, epistasis, behavior, and/or morphology (Barton and Hewitt 1985). If the selective forces are not due to a stable environmental gradient, the location of a hybrid zone may move in geo-

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graphic space or change in width over time (Barton and Hewitt 1985). Hybrid zones can exist along a linear margin of contact between parental taxa or, when the distribution of parental taxa is patchy and/or intergraded, in a mosaic pattern (Harrison 1986).

Parental Taxa

A first step in studying hybrid zones is the diagnosis of parental taxa in and around the hybrid zone to identify what is hybridizing with what. The biological species concept of Dobzhansky (1937) and Mayr (1942) and the recognition species concept of Paterson (1985) do not categorize the parental taxa of a hybrid zone as distinct species due to the absence of complete barriers to reproduction. Other species concepts recognize that complete barriers to reproduction are sufficient but not necessary for a group of organisms to have an independent evolutionary history, be subject to a separate suite of selective constraints, and potentially merit species status. The cohesion species concept of Templeton (1989, 1994) considers genetic exchangeability and demographic exchangeability (associated with genetic drift and natural selection) in diagnosing species. This concept can be applied to asexual organisms and recognizes hybrid zones as places where genetic exchangeability is greater than demographic exchangeability. The phylogenetic species concept of Cracraft (1989) defines a species as a diagnostically distinct group within which there is a parental pattern of ancestry and descent. Phylogenetic concordance among multiple unlinked and nonepistatic markers (Avise and Ball 1990) may uncover polyphyly in species of hybrid origin but could be conservative because it relies on fixation of ancestral polymorphism before diagnosis is possible (Sites and Crandall 1997). In this study, we rely on an evolutionary species concept in which a species is an evolutionary lineage that persists through time between speciation events (Wiley 1978; de Quieroz 1998). Hybridization will not change the species statuses of two evolutionary species as long as gene flow between them is at a level low enough so as to not cause speciation by lineage amalgamation. The species criterion we use to diagnose an evolutionary species is fixed and heritable differences among multiple characters. These characters include a mitochondrial DNA (mtDNA) phylogeny that demonstrates monophyly of at least one of the parental taxa (Evans et al. 1999; this study), a fixed nucleotide difference in mtDNA (which is not a required characteristic of monophyly), fixed morphological differences (Fooden 1969; Albrecht 1978), and a fixed allele in an autosomal microsatellite.

The Macaca maura–M. tonkeana Hybrid Zone

The genus *Macaca* has the largest distribution of any nonhuman primate; species live in northwest Africa, much of tropical Asia, and the Indo-Malay region. On Sulawesi, an explosive diversification of macaques occurred; Sulawesi comprises a small fraction of the massive macaque range but is host to seven of the 19 species in the genus (Fooden 1980). Hybridization occurs among all parapatric species of Sulawesi macaque except the insular species *M. brunnescens* (Groves 1980; Ciani et al. 1989; Supriatna 1991; Watanabe and Matsumura 1991; Watanabe et al. 1991a,b; Supriatna et al. 1992; Bynum et al. 1997). Hybrid crosses and backcrosses between many combinations of captive macaque species produce fertile offspring in captivity (Bernstein and Gordon 1980).

Macaca maura and *M. tonkeana* live in southwestern and central Sulawesi, respectively, and are morphologically distinct outside of their contact zone at the base of the southwestern peninsula of Sulawesi (Fooden 1969; Albrecht 1978). *Macaca maura* has brown hair, oval ischial callosities, and a smaller stature than *M. tonkeana*, which has kidney shaped ischial callosities and is dark brown to black with white hair on the back of the hindlimbs and rump (Fooden 1969; Albrecht 1978). A phylogeny of mtDNA of macaques on Sulawesi and the Sunda shelf suggests that *M. maura* and *M. tonkeana* may be derived from separate dispersal events of *M. nemestrina* from Borneo to Sulawesi; this relationship is not well supported (Evans et al. 1999). Y-chromosome DNA (yDNA) in Sulawesi macaques is monophyletic with respect to other species of macaque, suggesting a single colonization or a selective sweep of this chromosome (Tosi et al. 2000).

Genetic Correlates of Macaque Behavior

Sexually dimorphic social behavior of cercopithecines has a profound effect on the distribution of genetic polymorphism in a species. Strict female sedentism (philopatry) causes sharp geographic clustering of maternally inherited mtDNA haplotypes in macaques (Melnick and Hoelzer 1992, 1996; Hoelzer et al. 1994). Female dispersal occurs via social group fission along matrilineal lines, with the smaller of the resulting groups generally being displaced to an adjacent home range (Melnick and Kidd 1983; Dittus 1988). Males leave their natal group before sexual maturity and may change social groups many times during their life. Changing social groups is not an easy task; it is associated with high variation in male reproductive success (Keane et al. 1997; de Ruiter et al. 1992) and even mortality (Dittus 1975). This behavior serves as a guard against inbreeding and homogenizes the distribution of genetic variation in the nuclear genome within a deme (Melnick et al. 1984).

In an ideal population in which mutations are neutral, the effective population size of uniparentally inherited, haploid genetic elements like mtDNA and yDNA is one-fourth that of biparentally inherited, diploid nuclear DNA. In macaques, female philopatry and differences in male reproductive success can increase the relative effective population size of mtDNA beyond neutral expectations (Hoelzer 1997; Hoelzer et al. 1998). Because a larger effective population size is associated with larger coalescence times among different haplotypes, polymorphisms in macaque mtDNA are potentially retained for prolonged periods. As a result, hierarchical relationships among mtDNA haplotypes should track evolutionary events in lineages of philopatric females, but may not reflect recent reticulating genealogical patterns in nuclear DNA that are influenced by male dispersal (Melnick and Hoelzer 1993).

Conservation in Sulawesi

Sulawesi is an area of extreme biological diversity and, as a part of Wallacea, was recently prioritized as one of 25 world

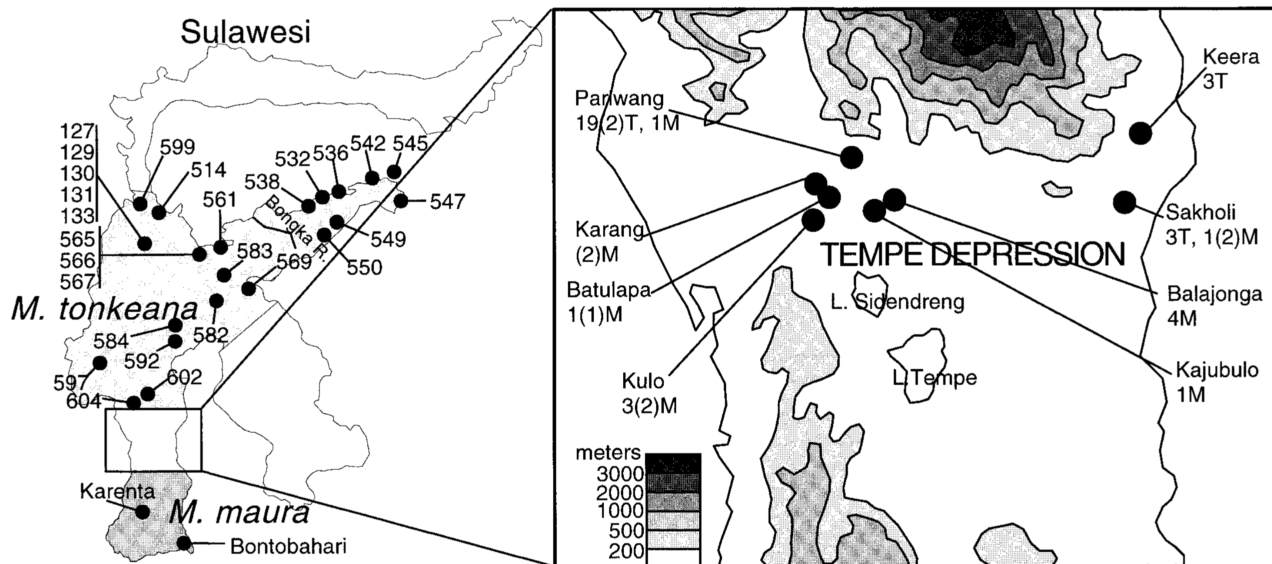

FIG. 1. Sample sites and mitochondrial DNA (mtDNA) in *Macaca tonkeana, M. maura,* and the hybrid zone. For *M. tonkeana,* the location of each sample is labeled with a sample identification number. For *M. maura,* 12 individuals at Bontobahari and 13 individuals at Karenta were sampled. Their identification numbers are listed in Figure 2 and the Appendix. The contact zone insert illustrates sample location and number of individuals with *M. maura* mtDNA (M) and *M. tonkeana* mtDNA (T) as discerned from analysis of mtDNA sequence; numbers in parenthesis are mtDNA haplotypes from additional male individuals from these locations as determined by Supriatna (1991).

hotspots for biological conservation (Myers et al. 2000). Patterns of endemicity of Sulawesi's fauna roughly overlap with distributions of macaque species in Sulawesi (Groves 1985; Musser 1987; Walton et al. 1997). Sulawesi is thus a critical, high-priority region for conservation of global biological diversity; Sulawesi macaque monkeys are valuable indicator species for conservation management on this island.

Habitat disturbance and fragmentation is a principal cause of recent declines in population estimates for *M. maura* and *M. tonkeana* and may affect population structure and hybridization of these species. In 1983 the census number was 56,000 for *M. maura* and 385,000 for *M. tonkeana* (MacKinnon 1983); by 1994 census estimates for *M. maura* were under 10,000 individuals and estimates for *M. tonkeana* were about 100,000 individuals (Bynum et al. 1999). *Macaca maura* is recognized as an endangered species, as is *M. nigra,* another species of Sulawesi macaque (International Union for Conservation of Nature 1994).

MATERIALS AND METHODS

Genetic Samples

Tissue samples used in this study were obtained from 88 wild and pet animals that were captured throughout central and southwestern Sulawesi and the contact zone between *M. maura* and *M. tonkeana* (Fig. 1, Appendix). Samples from all wild-caught individuals and three pet individuals were collected in 1988 and 1989 (Supriatna 1991; Supriatna et al. 1992); samples from other pet animals were collected in 1996 (Evans et al. 1999). Pet owners were interviewed about the origin of the animal, method of capture, and the age of the animal. Because many pet macaques were encountered in Sulawesi, we were able to select genetic samples from pets that were caught either by the owner or a member of the owner's family and of known provenance. Twenty-five wild *M. maura* samples were obtained from two trapping locations, one in Bontobahari and one in Karenta (Fig. 1). Thirty-three wild and three pet individuals from the central (Pariwang, Batulapa, Kulo, Balajonga, and Kajubulo) and the eastern (Keera and Sakholi) contact zones were sampled (Fig. 1). Five wild *M. tonkeana* samples were obtained in Lore Lindu National Park; additional samples were collected from 22 pets that were caught throughout the range of *M. tonkeana* (Fig. 1).

Pet and wild-caught animals were anesthetized with a dose of ketamine hydrochloride that varied according to the estimated weight of the individual. Blood (1–3 ml) was drawn from the femoral vein using a 21-gauge needle and a 3-cc syringe. Blood was either stored in liquid nitrogen or preserved by mixing it with an equal volume of a buffer containing 100 mM EDTA, 100 mM Tris pH 8, and 1% SDS and then storing the blood/buffer mixture at room temperature until it could be frozen (three days to two months). Total genomic DNA was extracted from blood using the Qiagen DNA extraction kit (Valencia, CA) according to the manufacturer's protocol.

Mitochondrial DNA

To examine the distribution of mtDNA haplotypes in the contact zone between *M. maura* and *M. tonkeana* and within the ranges of each parental species, a 415-bp portion of the mitochondrial genome spanning the 3′ end of the 12S rDNA was sequenced in all individuals using primers 284f-EX (5′

GGA TTA GAT ACC CCA CTA TGC TTG 3′) and Up630-R (5′ TGC TTG GGG CTA GTV TTG GCT CAA GG 3′) (Tosi et al. 2002). This region was amplified using the polymerase chain reaction (PCR) with 35 cycles of the following temperature profile: denature at 94°C for 1 min, primer annealing at 55°C for 1 min, and extension at 72°C for 1 min; these cycles were followed by a final extension at 72°C for 7 min. Primers were removed from PCR amplifications with the Qiagen Purification Kit and cycle sequenced in both directions with the FS-DNA sequencing kit (Perkin Elmer-Applied Biosystems Inc., Foster City, CA). Unincorporated flourescently labeled nucleotides were removed from cycle sequence reactions with CentriSep Spin Columns (Princeton Separations, Princeton, NJ); the reactions were then electrophoresed on an ABI 377 PRISM automated DNA sequencer (Perkin Elmer-Applied Biosystems Inc.). Sequences were compiled with the AutoAssembler program (Perkin Elmer-Applied Biosystems Inc.,), and aligned with sequences from the outgroup taxa *M. fascicularis* from Sepilok, Malaysia, and *M. sinica* sample code 716 (Tosi et al. 2000) with the Sequence Navigator program (Perkin Elmer-Applied Biosystems, Inc.). These sequences have been deposited in Genbank (accession nos. AF383991–AF384021).

To evaluate evolutionary relationships among mtDNA, unique haplotypes were analyzed under the parsimony criterion. Heuristic searches for the most parsimonious trees were conducted using 100 replications of random addition of taxa and the tree bisection-reconnection algorithm of branch swapping with a test version of PAUP* (D. Swofford). Strict and 50% majority-rule consensus trees were constructed from the set of equally parsimonious trees that were recovered from the search. Branch support was estimated with 2000 replications of nonparametric bootstrap analysis, each with a single replication of random addition of taxa. Additionally, Bremmer support indices were calculated with the Autodecay Program (ver. 4.0; Bremmer 1994; Eriksson 1999). Because mtDNA haplotypes of *M. maura* are monophyletic with respect to haplotypes of *M. tonkeana,* haplotypes of contact zone individuals were diagnosed as being derived either from *M. maura* or from *M. tonkeana* females based on the clade to which their haplotype clustered. Additionally, to evaluate average genetic distances among haplotypes in each species, uncorrected *p*-distances between haplotypes were calculated with PAUP*.

One concern in analyzing phylogenetic relationships from nucleotide sequences that code for RNA molecules is that some character changes are not independent because of complementary base-pair changes needed to maintain internal stem structures in the RNA molecule. To examine the impact of complementary and potentially nonindependent character changes in the 12S mtDNA dataset, pairwise comparisons were conducted to identify the positions of pairs of polymorphic characters that have complementary nucleotides in all individuals. Because these characters are potentially nonindependent, parsimony analysis was carried out on the dataset after excluding characters at one of the positions of each complementary pair, and the resulting tree topology was compared to that recovered from all of the data. This approach relies on the assumption that the secondary structure of the RNA molecule is conserved across the taxa being studied.

To evaluate subdivision of different mtDNA sequence haplotypes, the Arlequin program (ver. 2.0; Schneider et al. 2000) was used to compute F_{ST} for all pairs of populations based on haplotype frequencies and based on a distance matrix of the pairwise number of differences among haplotypes in each population. A *P*-value of each genetic distance was obtained with 3000 permutations of the haplotypes among populations; the *P*-value is the proportion of the permutations that lead to an F_{ST} estimate greater than or equal to the observed value. To control for Type I error in each population, the sequential Bonferroni correction was applied for a posteriori significance testing ($\alpha = 0.05$, $k = 15$ tests; Rice 1989).

Autosomal Microsatellites

Nine unlinked autosomal microsatellite loci, each polymorphic in *M. maura* and *M. tonkeana,* were identified from a screen with human microsatellite primers. Amplifications were carried out with 30 cycles of the following temperature profile: denature at 94°C for 30 sec, annealing at 48–52°C for 30 sec, and extension at 72°C for 30 sec; these cycles were followed by a 7-min extension at 72°C. Alleles amplified with flourescently labeled primers (Research Genetics, Inc., Huntsville, AL) for loci listed in the Appendix were run on an ABI 377 automated sequencer and analyzed using the ABI GeneScan analysis software (ver. 2.0.2; Perkin Elmer). Alleles were scored based on size as determined by comparing the migration of the amplified product to that of a flourescently labeled size standard (Tamra 500, Perkin Elmer). At the D12S1075 locus, an artifactual PCR product of length 265 bp was present in some individuals; this band was not included in the analyses.

Y-Chromosome Microsatellite

Woolley-Barker (1999) reports a human Y-chromosome microsatellite locus, DY391, that is polymorphic in male baboons; this locus is also polymorphic in *M. maura* and *M. tonkeana.* Males' genotypes were assessed at this locus using the same PCR parameters as for autosomal microsatellites; amplification was not achieved in all individuals, even at a range of PCR conditions.

Populations

Macaca maura individuals were divided into a population from Bontobahari (BON, $n = 12$) and a population from Karenta (KAR, $n = 13$). In *M. tonkeana,* the Bongka River has been proposed as a significant biogeographical barrier (Froehlich et al. 1996). *Macaca tonkeana* individuals were thus divided into a population west of the Bongka River (WEST, $n = 19$) and east of the Bongka River (EAST, $n = 8$). Individuals in the contact zone were divided into two populations based on the type of mtDNA in each individual. Eleven individuals from the contact zone that had *M. maura* mtDNA were included in the MHYB population. Twenty-five contact zone individuals with *M. tonkeana* mtDNA were included a second contact zone population THYB; this population includes four individuals with mtDNA haplotypes that

are of unresolved relationship relative to other *M. maura* and *M. tonkeana* haplotypes.

Linkage Disequilibrium

All autosomal loci in this study are located on different human chromosomes except two that are 90 map units apart on human chromosome 12 and thus unlinked in humans (Research Genetics, Inc.). Chromosomal location of homologous microsatellite loci tend to be conserved in closely related taxa such as macaques and humans (Moore et al. 1991; Stallings et al. 1991; Blanquer-Maumont and Crouau-Roy 1995); it is therefore unlikely that these loci are linked in macaques. As a further evaluation of linkage among these microsatellite loci in macaques, we tested for genotypic disequilibrium, which is a deviation from independent assortment of genotypes at different loci, for each pair of loci in each population. A Markov chain method was used to estimate the exact *P*-value of the null hypothesis that genotypes at one locus are independent from genotypes at another locus within a population (Genepop, ver. 3.1b; 10,000 dememorizations, 1000 batches, and 10,000 iterations per batch; Raymond and Rousset 1995). A global test of genotypic linkage disequilibrium was also performed for each pair of loci across all populations (Genepop). The sequential Bonferroni correction was applied for a posteriori significance testing of linkage disequilibrium in pairwise tests among loci within each population and in pairwise tests across all populations ($\alpha = 0.05$, $k = 8$ tests; Rice 1989).

Hardy-Weinberg Equilibrium

Many analyses of population structure assume that the geographic partitioning of molecular variation arises from an interaction of the processes of genetic drift, migration, and mutation and not from selective pressures on alleles. Population structure can be underestimated if alleles in different populations are under stabilizing selection or it can be overestimated if selection causes alternative alleles to be fixed in different populations. Hardy-Weinberg equilibrium (HWE) is an idealized genetic condition characterized by the random union of alleles at a neutral locus in the formation of zygotes in an infinitely large population. Testing for HWE can offer insight into selection, outbreeding, inbreeding, null alleles (which result in homozygote excess due to unamplified and undetected alleles), and the Wahlund effect (homozygote excess due to pooling of genetically subdivided populations).

Because X^2-tests of HWE can be inaccurate for allelic data with small sample sizes and rare alleles (Weir 1996), a Markov chain method was used to obtain an unbiased estimate of the exact Hardy-Weinberg probability of autosomal microsatellite alleles in each population (Guo and Thompson 1992; Genepop 10,000 dememorizations, 1000 batches, and 10,000 iterations per batch). In this method, the *P*-value is equal to the sum of the probability of the observed genotypes sampled in a population and probabilities of other genotype assemblages with the same allelic counts that are of equal or lower probabilities (Raymond and Rousset 1995). To control for Type I error in each population, the sequential Bonferroni correction was applied for a posteriori significance testing ($\alpha = 0.05$, $k = 9$ tests; Rice 1989). F_{IS} is an index of the component of population subdivision attributed to inbreeding. When mating is random, F_{IS} is equal to zero; as inbreeding increases, F_{IS} approaches one. F_{IS} was estimated for each population with the algorithms of Weir and Cockerham (1984; Genepop).

Population Subdivision

For autosomal data, population structure among populations and among species was quantified using an unbiased estimator of R_{ST} (Slatkin 1995; Goodman 1997) and F_{ST} (Weir and Cockerham 1984). R_{ST} evaluates population structure based on variation in allele size within versus among populations, whereas F_{ST} relies on allele frequencies (Wright 1965; Slatkin 1995). Because R_{ST} relies on a stepwise mutation model of microsatellite evolution to estimate population structure, this statistic is expected to be more responsive to ancient population subdivision in which sufficient time has elapsed for mutations to arise in the microsatellite alleles. In contrast, F_{ST} is expected to be sensitive to recent population dynamics that might influence the distribution of microsatellite allele frequencies to a greater extent than the distribution of allele sizes. To avoid a biased estimate of R_{ST} caused by different variances in allele size at each locus, data from each locus was transformed such that all loci have the same mean allele size and standard deviation before computing the multilocus R_{ST} (RstCalc ver. 2.2; Slatkin 1995; Goodman 1997). An exact *P*-value of the null hypothesis that each R_{ST} and F_{ST} estimate is not significantly different from zero was obtained with 1000 permutation tests of the standardized data (RstCalc ver. 2.2; Arlequin ver. 2.0). The sequential Bonferroni correction was applied for a posteriori significance testing ($\alpha = 0.05$, $k = 15$ tests, Rice 1989). The effective number of migrants per generation (N_em) between populations was derived from R_{ST} estimates according to the relationship $R_{ST} = 1/(4N_em + 1)$; this relationship assumes selective neutrality of the microsatellite loci and equilibrium between genetic drift and migration.

Likelihood Calculation for Individual Genotypes

To evaluate the degree to which individual autosomal genotypes in the hybrid zone correspond to allele frequencies of each parental species, we calculated the negative log likelihood that each multilocus genotype came from the parental species using a shared allele approach (Paetkau et al. 1995; Waser and Strobeck 1998). In this approach, the likelihood of a multilocus genotype is equal to the product of the likelihoods of the genotype at each locus after subtracting the focus genotype from each population. Likelihoods of each genotype were calculated from allele frequencies in *M. maura* (BON and KAR populations) and in *M. tonkeana* (WEST and EAST populations) using Arlequin (ver. 2.0; Schneider et al. 2000). This calculation assumes that all loci are independent and that populations are in HWE (see above).

RESULTS

Mitochondrial DNA

Five unique mitochondrial DNA sequences were recovered from *M. maura,* 19 from *M. tonkeana,* and five from the

contact zone (Table 1). When compared to the *M. sinica* and *M. fascicularis* outgroups, 350 characters were constant, 24 variable characters were parsimony uninformative, and 41 characters were parsimony informative. Parsimony analysis of unique sequences produced 256 trees each of 83 steps. Strict and majority rule consensus trees constructed from the set of most parsimonious trees differed in the resolution of three branches (Fig. 2). MtDNA haplotypes from the range of *M. maura* are monophyletic with respect to those of *M. tonkeana.* MtDNA haplotypes from the contact zone clustered either with *M. maura,* with *M. tonkeana,* or in an unresolved basal position in the tree (Fig. 2). The *M. maura* clade could be distinguished from *M. tonkeana* haplotypes by a fixed character change in position 340 (Table 1). In addition to being more diverse, the mtDNA haplotypes of *M. tonkeana* are considerably more divergent; the average uncorrected *p*-distance among *M. tonkeana* haplotypes is 1.9% relative to 0.8% among *M. maura* haplotypes (Table 2).

Pairwise comparisons revealed 13 pairs of potentially nonindependent polymorphic nucleotide positions (e.g., position 20 is complementary to position 59 or 99 in all individuals and was counted as one potentially nonindependent pair; Table 1). All of these pairs, except complementary nucleotide positions 324 and 363, involved polymorphisms between the outgroup taxa and the ingroup taxa; this suggests that potentially nonindependent base-pair changes are uncommon among the ingroup's polymorphic nucleotides in this region of mtDNA. This can be explained by a bias toward polymorphism in regions that correspond to loops in the RNA hairpins rather than stems. After excluding one character position from each of these pairs and repeating parsimony analysis, parsimony analysis recovered 256 trees of 72 steps each. The topology of the consensus trees were identical to those recovered from the complete dataset.

The mtDNA haplotypes of wild-caught *M. maura* are completely partitioned according to locality. Haplotypes from Bontobohari, Karenta, and the hybrid zone are each divergent and monophyletic by location (Fig. 2). In *M. tonkeana,* with the exception of the haplotype of individual PM514, all haplotypes in the WEST population cluster in a single clade with most of the THYB haplotypes (Fig. 2). Within this WEST *M. tonkeana* clade, most of the haplotypes from the southern part of this population near the hybrid zone are monophyletic with haplotypes from the hybrid zone (THYB). The five wild individuals from Lore Lindu National park contained five distinct mtDNA haplotypes, some of which are more closely related to pet individuals that were not sampled from this park. Eight individuals from east of the Bongka River in the EAST population have six individual haplotypes in two clades. F_{ST} estimates calculated from mtDNA haplotype frequencies and genetic distances are significant and high. The highest F_{ST}-value is that among *M. maura* populations that have geographically clustered lineages of mtDNA (Table 3).

At least three major lineages of mtDNA exist in the contact zone. Two of these lineages cluster within a lineage from each of the parental species, and a third occupies an unresolved basal position in the mtDNA phylogeny. The reciprocal monophyly of the mtDNA from each parental species allowed us to identify the parental species from which the mtDNA in most contact-zone individuals is derived. There is some uncertainty in assigning the four basal haplotypes (WM031, PF012, PM020, and PF021) from the contact zone; these haplotypes are assigned to the THYB population although they might have a paraphyletic relationship to other *M. tonkeana* haplotypes. In general, mtDNA haplotypes show a sharp transition in the contact zone; individuals from the southern contact zone (Karang, Batulapa, Kulo, Kajubulo, Balajonga) had *M. maura* mtDNA and individuals from the northern contact zone (Pariwang, Keera) had *M. tonkeana* mtDNA. In the eastern contact zone, individuals sampled in Sakholi include one female and two males with *M. tonkeana* mtDNA and one male with *M. maura* mtDNA. One male from Pariwang (of 22 surveyed in this study and Supriatna 1991) had *M. maura* mtDNA. The contact zone between mtDNA haplotypes occurs slightly farther south in the east than in the west (Fig. 1).

Autosomal Microsatellites

In the nine autosomal microsatellite loci assessed, 108 alleles were found (Appendix). About half of these alleles (53) showed a clinal distribution in which the allele was found in only one of the parental species or in the contact zone and one parental species. Five alleles were present only in *M. maura,* 17 were only in *M. tonkeana,* three were in *M. maura* and the contact zone, and 28 were in *M. tonkeana* and the contact zone. Four alleles were found exclusively in the hybrid zone. Fifty-one alleles were in both parental taxa; of these, 15 showed a clinal decrease in frequency from one parental taxon through the hybrid zone to the other parental taxon.

At locus D22S345, all *M. maura* individuals were fixed for an allele that was 126 bp in size (including the amplified flanking sequences and the microsatellite repeat). This allele was not present in *M. tonkeana.* To evaluate whether this allele was an example of a protomicrosatellite that had not expanded, the allele was sequenced. In *M. maura* this allele has a repeat sequence of $(GT)_3GCC(GT)_{11}$ and in *M. tonkeana* the sequence is $(GT)_3GCC(GT)_{(11+n)}$, where n is an integer greater than zero. To check whether fixation at this locus was a primitive or derived condition in *M. maura,* the genotypes of each species of Sulawesi macaque and the non-Sulawesi ancestor taxa *M. fascicularis* and *M. nemestrina nemestrina* and *M. nemestrina pagensis* were assessed at this locus. The *M. nemestrina pagensis* individual was homozygous for allele length 131 bp; the two other non-Sulawesi macaques were homozygous for allele size 126 bp. All other Sulawesi species were heterozygous or homozygous for alleles larger than 126 bp (data not shown).

Genotypic Disequilibrium and Hardy-Weinberg Equilibrium

No pair of loci showed evidence of genotypic linkage disequilibrium in pairwise comparisons between loci within each population or in the global test across all populations ($\alpha = 0.05$, $k = 8$ independent tests). All populations have no significant deviation from Hardy-Weinberg expectations at any of the nine loci ($\alpha = 0.05$, $k = 9$ tests) except the THYB population, which has significant deviation from expectations at the D22S345 locus due to an excess of homozygotes ($P = 0.0031$, $F_{IS} = 0.265$). The average F_{IS} across all loci for MHYB is -0.018 and for THYB is 0.027.

TABLE 1. Positions of variable nucleotides in 415-bp region of mitochondrial DNA. Dashes represent gaps in sequences; a plus sign after a sample code denotes a sequence recorded in multiple individuals. Character 340 has a fixed difference between the *Macaca maura* and *M. tonkeana* clades.

Taxon	Position
	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 4 4
	2 3 4 4 4 5 5 7 9 9 9 0 1 2 2 2 3 3 3 3 5 6 6 6 9 9 9 0 0 1 1 1 2 2 2 2 3 3 4 5 6 8 8 8 9 9 0 1 2 3 3 3 3 3 4 4 5 5 5 6 6 7 9 0 1
	2 0 9 0 4 5 2 9 3 1 4 9 0 2 3 4 7 2 4 5 7 3 4 7 1 2 3 2 4 4 6 7 4 5 7 8 0 4 8 5 7 0 4 7 4 6 5 6 4 2 3 4 6 8 0 8 0 5 7 3 5 0 3 8 5
M. fascicularis	C G C C C C T C C A G C T G T G G A T A C A C - T T T C C C T T C T A A G T C T T C C T C C C T A G G A T T C A G A T T T A C G T
M. sinica	C A C C C C T T C G G T C G - A A G A G T A C A T C T T T C C T C C G G G C T T T C C T C C C T A G G A C T T A G A T T T A C G T
M. tonkeana	
PM514	C A C C T C T T C G A T T A T A G A A A C A G - C A T C C T T T T C G A A C C T T C C T C T C C A G G A C T T A G A T T T G T A T
PM538	C A C C T C T T C G A T T A C A G A A A C A G - C A T T C T T C C C G A A C C T T T C T C T C C A G G A C T T A G C T T T G T A C
PM545	C A C C T C T T C G A T T A C A G A A A C A G - C A T T C T T C C C G A A C C T T T C T C T C C A G G A C T T A G A T T T G T A C
PM542	C A C C T C T T C G A T T A T A G A A A C A G - C A T T C T T C C C G G A C C T T T C T C T C C A G G A C T T A G A T T T G T A C
PM547+	T A C C T C T T C G A T T A T A G A A A C A G - C A T C C T T T C C G A A C C T C C C T C T C C G A G G C T T A A A C C T G T A T
PM536	C A C C T C T T C G A T T A T A G A A A C A G - C A T C C T T T C C G A A C C T C C C T C T C C G A G G C T T A A A C C T G T A T
PM549	C A C C T C T T C G A T T A T A G A A A C A G - C A T C C T T T C C G A A C C T C C C T C T C C G A G G C T T A A A C C T G T A C
WM129	C A C C T C T T C G A T T A T G G A A A C A G G C A T C C T T T C C A A A C C T T C C T C T C C G A G G C T T A A A T C T τ3T A C
WF131	C A C C T C T T G G A T T A T G G A A A C A G G C A T C C T T T C C A A A C C T T C C T G T C C G A G G C T T A A A T C T G T A C
WM127	C A A C T C T T C G A T T A T G G A A A C A G G C A T C C T T T C C A A A C C T T C C T C T C C G A G A C T T A A A T C T G T A C
WM126	C A C C T C T T G G A T T A T G G A A A C G G G C A T C C T T T C C A A A C C C T C C T C T C C G A G G C T T A A A T C T G T A C
WM133	C A C C T C T T C G A T T A T G G A A A C G G G C A T C C T T T C C A A A C C C T C C T C T C C G A G G C T T A A A T C T G T A C
PM561	C A C C T C T T C G A T T A T G G A A A C G G G C A T C C T T T C C A A A C C T T C C T C T C C G A G G C T T A A A T C T G T A T
PF599+	C A C C T C T T C G A T T A T G G A A A C G G G C A T C C T T T C C A A A C C T T C C T C T C C G A G G C T T A A A T C T G T A C
PM583	C A C C T C T T C G A T T A T G G A A A C A G - C A T C C T T T C C A A A C C T T C C T C T C C G A G G C T T A A G T C C G T A C
PM604+	C A C C T C T T C G A T T A T G G A A A C A G G C A T C C T T T C C A A A C C T T C C T C T C C G A G G C T T A A G T C C G T A C
PM582	C A A C T C T T C G A T T A T G G A A A C A G G C A T C C T T T C C A A A C C T T C C T C T C C G A G G C T T A A G T C C G T A C
PM602	C A C C T C T T G G A T T A T G G A A A C A G G C A T C C T T T C C A A A C C T T C C T C T G C G A G G C T T A A G T C C G T A C
PF597	C A C C T C T T C G A T T A T G G A A A C A G G C A T C C T T T C C A A A C C T T C C T C T C C G A A G C T T A A G T C C G T A C
THYB	
WF080+	C A C C T C T T C G A T T A T G G A A A C A G G C A C C C T T T C C A A A C C T T C C T C T G C G A G G C T T A A G T C C G T A C
WM100+	C A C C T C T T C G A T T A T G G A A A C A G G C A C C C T T T C C A A A C C T T C C T C T C C G A G G C T T A A G T C C G T A C
PM020+	C A C T T C T T C G A T T A T A G A A A C A G - C A T C C T T T C C G A A C C T T C C T C T C C A G G A C T T A G A T T T G T A T
MHYB	
WM034	C A C T T C T T C G A T T A T G G A A A C A G - C A T C C T T T C C G A A C C T T C T T C T C C A G G A C T C A G A T T T G T A C
WF050+	C A C T T C T T C G A T T A T G G A A A C A G - C A T C C T T T C C G A A C C T T C T T C T C C A G G A C T C A G A C T T G T A C
M. maura	
WF013+	C A C T T G C T C G A T T A T G G A A A C A G - C A T C C T T T C C G A A C C T T C C T C T C C A G G A C C C A G A T T T G T A C
WM016	C A C T T G T T C G A T T A T G G A A A C A G - C A T C C T T T C C G A A C C T T C C T C T C C A G G A C C C A G A T T T G T A C
WM020	C A C T T G T T C G A T T A T G G A A A C A G - C A T C C T T T C C G A A C C T C C T C T C C A G G A C T C A G A T T T G T A C
WM003+	C A C T T C T T C G A T T A T G G A A A C A G - C A T C C T T T C C A A A C C T T C C T C T C C A G G A C T C G G A T T T G T A C
WM008+	C A C T T C T T C G A T T A T G G A A A C A G - C A T C C T T T C C A A A C C T T C C C C T C C A G G A C T C G G A T T T G T A C

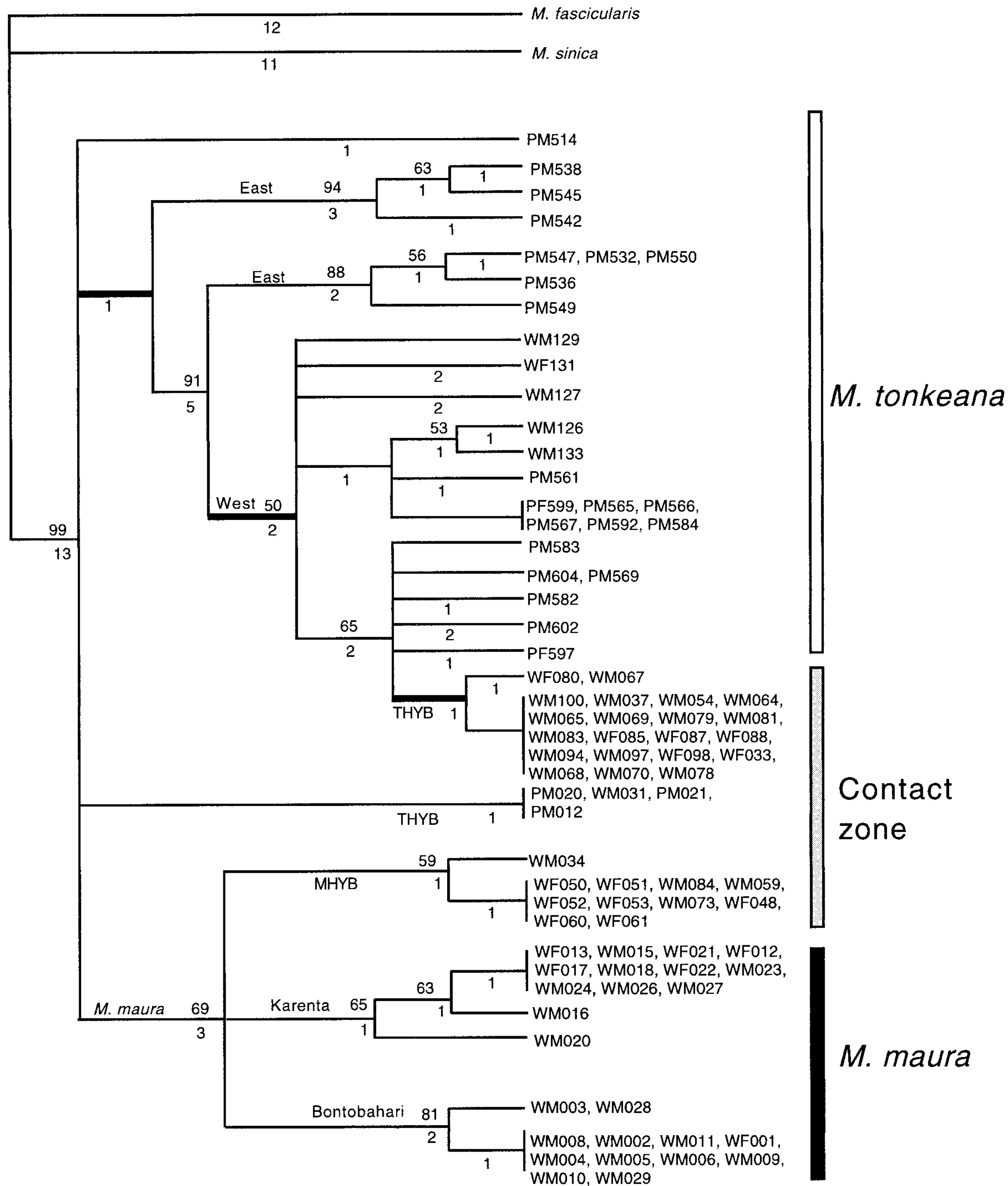

FIG. 2. A 50% majority rule consensus tree of 256 most parsimonious topologies of relationships among mitochondrial DNA sequences from *Macaca maura, M. tonkeana,* and contact-zone individuals. Numbers above branches are bootstrap values; below branches are Bremmer decay values. The strict consensus tree has the same topology as this tree except that branches in bold are collapsed in the strict tree.

Population Subdivision

R_{ST} is not significantly greater than zero among the *M. maura* populations BON and KAR ($P = 0.03$) or among contact zone populations MHYB and THYB ($P = 0.072$), and F_{ST} among these populations is also low (Table 4). In contrast, population subdivision among the *M. tonkeana* populations WEST and EAST is significant and large. Pairwise comparisons indicate that the EAST population is highly subdivided from all populations including the parapatric WEST population; intraspecific population subdivision within *M. tonkeana* is almost as high as interspecific subdivision between the *M. tonkeana* WEST population and the *M. maura* BON or KAR populations (Table 4).

The MHYB population is about the same genetic distance

TABLE 2. Pairwise uncorrected *p*-distances between the 415 bp of mtDNA sequences from *Macaca maura, M. tonkeana,* hybrids, and outgroups. A plus sign after the sample code denotes a sequence recorded in multiple individuals (Fig. 2).

	M. fascicularis	*M. sinica*	WM003+	WM008+	WF013+	WM016	WM020	WM034	WF050+	WF080+	WM100+	PM020+	PM547+	PM549	PF599+	PM604+
M. fascicularis	—															
M. sinica	0.0540	—														
WM003+	0.0586	0.0707	—													
WM008+	0.0611	0.0732	0.0024	—												
WF013+	0.0660	0.0732	0.0122	0.0146	—											
WM016	0.0635	0.0707	0.0097	0.0122	0.0024	—										
WM020	0.0611	0.0683	0.0073	0.0097	0.0049	0.0024	—									
WM034	0.0611	0.0683	0.0073	0.0097	0.0097	0.0073	0.0049	—								
WF050+	0.0635	0.0708	0.0097	0.0122	0.0122	0.0097	0.0073	0.0024	—							
WF080+	0.0783	0.0877	0.0292	0.0317	0.0365	0.0341	0.0317	0.0317	0.0341	—						
WM100+	0.0758	0.0853	0.0268	0.0292	0.0341	0.0316	0.0292	0.0292	0.0316	0.0024	—					
PM020+	0.0610	0.0585	0.0122	0.0146	0.0146	0.0122	0.0097	0.0097	0.0122	0.0317	0.0293	—				
PM547+	0.0782	0.0756	0.0341	0.0365	0.0365	0.0341	0.0316	0.0316	0.0292	0.0244	0.0219	0.0219	—			
PM549	0.0783	0.0756	0.0292	0.0316	0.0316	0.0292	0.0268	0.0268	0.0243	0.0195	0.0171	0.0219	0.0049	—		
PF599+	0.0709	0.0804	0.0219	0.0244	0.0292	0.0268	0.0244	0.0244	0.0268	0.0121	0.0097	0.0244	0.0171	0.0122	—	
PM604+	0.0734	0.0828	0.0244	0.0268	0.0316	0.0292	0.0268	0.0268	0.0292	0.0049	0.0024	0.0268	0.0195	0.0146	0.0073	—
WM126	0.0758	0.0853	0.0268	0.0292	0.0341	0.0317	0.0292	0.0292	0.0317	0.0170	0.0146	0.0293	0.0219	0.0171	0.0049	0.0121
WM133	0.0734	0.0828	0.0244	0.0268	0.0316	0.0292	0.0268	0.0268	0.0292	0.0146	0.0121	0.0268	0.0195	0.0146	0.0024	0.0097
WM129	0.0684	0.0779	0.0195	0.0219	0.0268	0.0243	0.0219	0.0219	0.0243	0.0097	0.0073	0.0219	0.0146	0.0097	0.0024	0.0049
WF131	0.0733	0.0828	0.0244	0.0268	0.0317	0.0292	0.0268	0.0268	0.0292	0.0146	0.0121	0.0269	0.0195	0.0147	0.0073	0.0097
WM127	0.0684	0.0779	0.0195	0.0219	0.0267	0.0243	0.0219	0.0219	0.0243	0.0146	0.0121	0.0219	0.0195	0.0146	0.0073	0.0097
PM514	0.0610	0.0585	0.0170	0.0195	0.0195	0.0170	0.0146	0.0146	0.0170	0.0317	0.0293	0.0049	0.0219	0.0219	0.0244	0.0268
PM561	0.0685	0.0779	0.0244	0.0268	0.0316	0.0292	0.0268	0.0268	0.0292	0.0146	0.0121	0.0220	0.0146	0.0146	0.0024	0.0097
PM602	0.0783	0.0877	0.0293	0.0317	0.0366	0.0341	0.0317	0.0317	0.0341	0.0049	0.0073	0.0317	0.0244	0.0195	0.0121	0.0049
PF597	0.0758	0.0853	0.0268	0.0292	0.0341	0.0316	0.0292	0.0292	0.0316	0.0073	0.0049	0.0293	0.0219	0.0171	0.0097	0.0024
PM583	0.0734	0.0805	0.0243	0.0268	0.0316	0.0292	0.0268	0.0268	0.0292	0.0049	0.0024	0.0268	0.0195	0.0146	0.0073	0.0000
PM536	0.0758	0.0732	0.0316	0.0341	0.0341	0.0316	0.0292	0.0292	0.0268	0.0219	0.0195	0.0195	0.0024	0.0024	0.0146	0.0171
PM582	0.0758	0.0853	0.0268	0.0292	0.0341	0.0316	0.0292	0.0292	0.0316	0.073	0.0049	0.0293	0.0219	0.0171	0.0097	0.0024
PM538	0.0734	0.0635	0.0243	0.0268	0.0268	0.0243	0.0219	0.0219	0.0243	0.0366	0.0341	0.0170	0.0341	0.0292	0.0317	0.0317
PM542	0.0709	0.0585	0.0219	0.0243	0.0243	0.0219	0.0195	0.0195	0.0219	0.0366	0.0341	0.0146	0.0316	0.0268	0.0293	0.0317
PM545	0.0709	0.0609	0.0219	0.0243	0.0243	0.0219	0.0195	0.0195	0.0219	0.0366	0.0341	0.0146	0.0316	0.0268	0.0293	0.0317

	WM126	WM133	WM129	WF131	WM127	PM514	PM561	PM602	PF597	PM583	PM536	PM582	PM538	PM542	PM545
WM126	—														
WM133	0.0024	—													
WM129	0.0073	0.0049	—												
WF131	0.0073	0.0097	0.0049	—											
WM127	0.0121	0.0097	0.0049	0.0097	—										
PM514	0.0293	0.0268	0.0219	0.0269	0.0219	—									
PM561	0.0073	0.0049	0.0049	0.0097	0.0097	0.0220	—								
PM602	0.0121	0.0146	0.0097	0.0097	0.0146	0.0317	0.0146	—							
PF597	0.0146	0.0121	0.0073	0.0121	0.0121	0.0293	0.0121	0.0073	—						
PM583	0.0122	0.0097	0.0049	0.0098	0.0097	0.0268	0.0097	0.0049	0.0024	—					
PM536	0.0195	0.0171	0.0122	0.0171	0.0170	0.0195	0.0122	0.0220	0.0195	0.0170	—				
PM582	0.0146	0.0121	0.0073	0.0121	0.0073	0.0293	0.0121	0.0073	0.0049	0.0024	0.0195	—			
PM538	0.0366	0.0341	0.0292	0.0341	0.0292	0.0170	0.0341	0.0366	0.0341	0.0316	0.0316	0.0341	—		
PM542	0.0341	0.0317	0.0268	0.0317	0.0268	0.0146	0.0317	0.0366	0.0341	0.0316	0.0292	0.0341	0.0073	—	
PM545	0.0341	0.0317	0.0268	0.0317	0.0268	0.0146	0.0317	0.0366	0.0341	0.0316	0.0292	0.0341	0.0024	0.0049	—

TABLE 3. F_{ST} among populations of *Macaca maura* (BON and KAR), *M. tonkeana* (WEST and EAST), and the contact zone (MHYB and THYB) calculated from mitochondrial DNA haplotype frequencies above diagonal and from a matrix of pairwise nucleotide differences below diagonal. All values are significant at $\alpha = 0.05$ with Bonferroni correction.

	BON	KAR	MHYB	THYB	WEST	EAST
BON	—	0.70	0.76	0.63	0.36	0.44
KAR	0.93	—	0.76	0.64	0.37	0.45
MHYB	0.95	0.93	—	0.67	0.41	0.50
THYB	0.78	0.81	0.79	—	0.36	0.42
WEST	0.79	0.82	0.80	0.28	—	0.10
EAST	0.75	0.75	0.69	0.55	0.50	—

from the BON and KAR populations of *M. maura* as it is from the WEST population of *M. tonkeana.* In contrast, the THYB population has a low level of population subdivision from the WEST population but is moderately differentiated from *M. maura* populations.

All pairwise comparisons of population subdivision between *M. maura, M. tonkeana,* and the hybrid zone were significant ($\alpha = 0.05$, $k = 3$ tests); R_{ST}- and F_{ST}-values among *M. maura* and *M. tonkeana* are 0.29 and 0.11, respectively; between *M. maura* and the hybrid zone are 0.16 and 0.06; and between *M. tonkeana* and the hybrid zone are 0.08 and 0.05.

Likelihood of Individual Genotypes

A plot of the relative likelihoods that an individual autosomal genotype originates from each parental population clusters parental individuals from each species (Fig. 3). Genotypes from the MHYB and THYB contact-zone populations generally appear of intermediate genotype, that is, more *M. maura*–like than pure *M. tonkeana* samples but more *M. tonkeana*–like than pure *M. maura* samples. Four samples from MHYB individuals appear intermediately *M. maura* and *M. tonkeana*; four are more *M. maura*–like and three are more *M. tonkeana*–like. In THYB at least two individuals are more *M. maura*–like and seven are more *M. tonkeana*–like.

Y-Chromosome Microsatellite

At Y-chromosome microsatellite Y391, amplified *M. maura* alleles range from 268 bp to 280 bp; *M. tonkeana* alleles have a bimodal distribution of sizes 254–270 bp and 286–292 bp (Fig. 4). *Macaca maura* and *M. tonkeana* share alleles

TABLE 4. R_{ST} (below diagonal) and F_{ST} (above diagonal) of pairwise comparisons among populations of *Macaca maura* (BON and KAR), *M. tonkeana* (WEST and EAST), and the contact zone (MHYB and THYB). All values are significant at $\alpha = 0.05$ ($k = 15$ independent tests) except where indicated (*).

	BON	KAR	MHYB	THYB	WEST	EAST
BON	—	0.06	0.04	0.06	0.10	0.12
KAR	0.06*	—	0.06	0.10	0.14	0.15
MHYB	0.11	0.13	—	0.02	0.04	0.05
THYB	0.20	0.20	0.03*	—	0.06	0.08
WEST	0.32	0.29	0.12	0.08	—	0.04
EAST	0.47	0.47	0.27	0.28	0.25	—

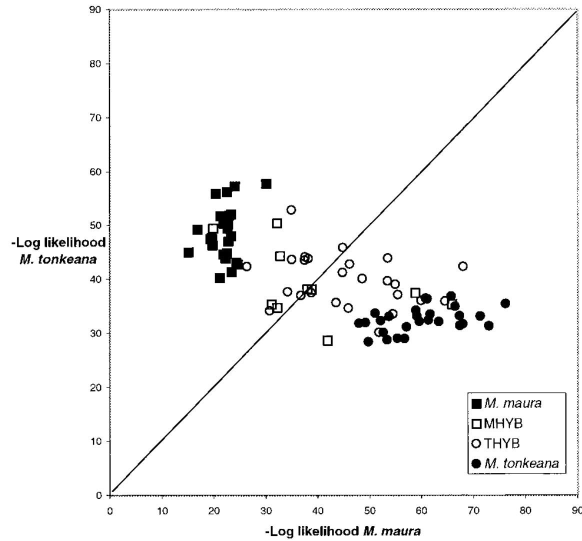

FIG. 3. Plot of the negative log likelihood that individual parental taxa (*Macaca maura* and *M. tonkeana*) and hybrid taxa with *M. maura* or *M. tonkeana* mitochondrial DNA (MHYB and THYB) originated from *M. tonkeana* versus *M. maura* based on autosomal microsatellite allele frequencies. Points that fall on the diagonal are equally likely to be members of *M. maura* or *M. tonkeana.*

of size 268 bp and 270 bp. Y-chromosome alleles of three MHYB males were all of size 262 bp, a common allele size in the *M. tonkeana* WEST population (50% frequency) that is absent in *M. maura.* This allele was also prevalent in the THYB population (54%); other THYB males carry alleles

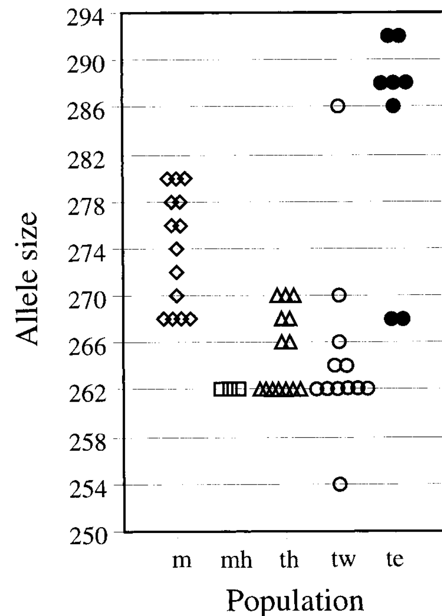

FIG. 4. Y-chromosome microsatellite allele size in *Macaca maura* (m), *M. maura* hybrids (mh), *M. tonkeana* hybrids (th), *M. tonkeana* WEST population (tw), and *M. tonkeana* EAST population (te).

270 bp and 268 bp in size that were found in both *M. maura* and *M. tonkeana* populations and alleles of 266 bp that were recorded in *M. tonkeana* WEST but not *M. maura.* The WEST and EAST population of *M. tonkeana* show subdivision in Y-chromosome allele size and frequency; 92% of alleles in the WEST population were less than 272 bp and 75% of alleles in the EAST population were larger than 284 bp.

Discussion

Genetic Structure of the Macaca maura–M. tonkeana Contact Zone

Fooden (1969) proposed a model of macaque speciation in which each species evolved in allopatry while the seven parts of Sulawesi were isolated by oceanic inundations during times of high sea level and/or lower tectonic position of different parts of the island. Recent geological reconstructions suggest that the southwestern peninsula was separated from the rest of Sulawesi for a significant period of time during the last 5 million years (Hall 1998), in part corroborating Fooden's (1969) vicariance scenario and supporting the notion that this hybrid zone is an example of secondary contact (Supriatna 1991).

The distribution of mtDNA haplotypes on the northern extent of the low-lying Tempe Depression suggests that *M. maura* females colonized this region since the last oceanic retreat. *Macaca maura* females may be better adapted to the lowland conditions of this region, more likely to disperse, or able to exclude *M. tonkeana* females. The sharp boundary between species-specific mtDNA haplotypes agrees with genetic expectations for strict philopatry of macaques and their hybrids. This study finds two examples of migration of males with *M. maura* mtDNA north into *M. tonkeana* territory but no evidence that males with *M. tonkeana* mtDNA migrated south into *M. maura* territory. However, because males do not transmit mtDNA to the next generation, male-mediated mtDNA admixture is genetically ephemeral.

In contrast to the distribution of mtDNA haplotypes in the contact zone, gene flow of autosomal DNA (aDNA) has occurred for multiple generations within the hybrid zone and has homogenized the distribution of aDNA microsatellite alleles. R_{ST} is not significantly greater than zero among the contact zone populations MHYB and THYB and N_em between these populations is higher than any other pairwise comparison in this study (7.23). Fixation of a single allele in *M. maura* at locus D22S345 permits an assessment of the minimum number of hybrids sampled in the hybrid zone. Of 36 individuals sampled at the contact zone, 15 carry the *M. maura*–specific 126-bp allele in heterozygosity with a *M. tonkeana* allele, six of 12 homozygotes for this allele have *M. tonkeana* mtDNA, and five individuals with *M. maura* mtDNA are homozygous for *M. tonkeana* alleles at locus D22S345. In addition, individual WM059 carries *M. maura* mitochondria and is homozygous for the *M. maura* allele at the D22S345 locus, but carries a Y-chromosome allele size recorded in *M. tonkeana* but not *M. maura.* This suggests that, at minimum, 27–28 of 36 individuals ($> 75\%$) sampled in the contact zone are first- or second-generation hybrids and that hybridization has been occurring for multiple generations.

An examination of pairwise autosomal population subdivision between the hybrid zone and the parental taxa indicates that the WEST population of *M. tonkeana* exchanges more immigrants with MHYB than the BON or KAR populations of *M. maura* exchange with THYB (Table 4). Also, the level of autosomal subdivision between MHYB and the *M. tonkeana* WEST population is similar to that between MHYB and *M. maura* populations (BON or KAR). However, R_{ST} among THYB and *M. maura* populations (BON and KAR) is twice as large as that among THYB and the *M. tonkeana* WEST population. This suggests that more autosomal genes flow into the contact zone from the WEST population of *M. tonkeana* than from the BON or KAR populations of *M. maura.* Moreover, Y-chromosome microsatellite alleles in the hybrid zone also suggest *M. tonkeana* males migrate into the hybrid zone more frequently than *M. maura* males because most males in the hybrid zone carry alleles found exclusively in *M. tonkeana* (Fig. 4). Thus biased gene flow into the hybrid zone, most likely mediated by *M. tonkeana* males, results in hybrids that retain *M. maura* mtDNA while harboring *M. tonkeana* nuclear alleles. Directional gene flow may be caused by reduced migration of male *M. maura* into the contact zone due to habitat fragmentation or low population numbers. Behavioral differences also could promote disassortative mating in a hybrid zone; this has been proposed in another cercopithecine hybrid zone between anubis and hamadryas baboons in Ethiopia (Woolley-Barker 1999). Supriatna (1991) reported a more aggressive disposition of *M. tonkeana* males compared to *M. maura* males and more promiscuous behavior of *M. maura* females compared to *M. tonkeana* females. If these behavioral differences lead to biased hybrid pairing, more hybrid progeny would be born from *M. maura* females than *M. tonkeana* females. Backcrossing of hybrid female progeny with aggressive *M. tonkeana* males would increase the proportion of *M. tonkeana* nuclear genes in hybrids without affecting the geographic distribution of *M. maura* mtDNA. These results from the autosomal genome, which suggest that gene flow of aDNA has a southern bias from *M. tonkeana* to *M. maura,* differ from data from the mitochondrial genome, which show no evidence of southerly migration of *M. tonkeana* males, and data that reveal the presence of homozygotes for *M. maura* aDNA with *M. tonkeana* mtDNA. These discrepancies are exceptions to a general pattern in which *M. tonkeana* contributes a larger proportion of genes to the contact zone and suggest that gene flow into the contact zone is not completely unidirectional.

Origin and Persistence of the Macaca maura–M. tonkeana Hybrid Zone

Outside of the contact zone, *M. maura* and *M. tonkeana* are morphologically and molecularly differentiated. Fixed morphological differences are present; the D22S245 locus is fixed for a single allele in *M. maura,* at 54% frequency in the hybrid zone, and absent in *M. tonkeana.* MtDNA haplotypes of *M. maura* are monophyletic relative to *M. tonkeana*; at autosomal loci, significant subdivision is present between parental populations and the hybrid zone and many alleles exhibit sharp clines in frequency that correspond with the hybrid zone. However, within the hybrid zone there is

low (F_{ST}) or nonsignificant (R_{ST}) population subdivision between hybrids from the north and the south of the hybrid zone, which have mtDNA haplotypes from *M. tonkeana* and *M. maura,* respectively. Taken together, these results suggest that gene flow between parental species is not occurring at a significant level despite high levels of admixture in the hybrid zone. Three possible explanations are: (1) hybridization is so recent that significant introgression has not yet occurred between *M. maura* and *M. tonkeana,* that is, genes have not yet had time to diffuse beyond the hybrid zone; (2) hybrid genotypes are beneficial to ecological conditions unique to the hybrid zone; or (3) hybrid genotypes are maladaptive but persistent as a result of a balance between dispersal of parental taxa into the contact zone and selection against hybrid progeny.

Macaca maura and *M. tonkeana* hybrids are found in the northern extent of the Tempe Depression; this region may have been submerged by oceanic intrusion as recently as 2000 years ago (Whitten et al. 1987). Given a macaque generation time of roughly five years (Dittus 1975; Lindburg and Harvey 1996), 400 generations have transpired since the last oceanic retreat from the *M. maura–M. tonkeana* hybrid zone. Even with modest rates of migration, an island model of gene flow would predict convergence to a common equilibrium set of allele frequencies in both populations, ignoring genetic drift, over this period of time (Hartl and Clark 1997). Thus, there is not strong geological evidence that this hybrid zone is young enough in terms of macaque generations for neutral alleles to have not had time to spread out of the narrow zone of contact. In fact, hybridization among *M. maura* and *M. tonkeana* may be a reoccurring circumstance depending on sea level and tectonics of Sulawesi's southwestern peninsula.

Other explanations for how clines in molecular polymorphism and morphology might persist for many generations invoke selection as a limit to gene flow. It is difficult to tease apart the impact of environmental selection from other evolutionary factors in a hybrid zone. The Tempe Depression corresponds with an ecological transition from the dry, low-elevation forest of the southwestern peninsula to the moister, mid- to high-elevation forest of central Sulawesi (Supriatna 1991; Supriatna et al. 1992). However, if conditions limited to this ecotone favor hybrid genotypes (the bounded hybrid superiority model), beneficial hybrid heterozygous genotypes should be more common than random expectations. A test for HWE suggests the opposite; homozygous genotypes are actually significantly more common than random expectations at one locus in the THYB population and that levels of heterozygosity in other loci do not deviate significantly from expectations in MHYB or THYB.

A balance between dispersal and selection against hybrids also could shape hybridization. Selection against hybrids could be due to ecological factors and/or other behavioral, morphological, and genetic incompatibilities between hybrids and the parental taxa. Heterosis (hybrid vigor) has been reported in size for other macaque hybrids (Smith and Scott 1989) but in the *M. maura–M. tonkeana* hybrid zone, hybrid animals often have webbed fingers (Supriatna 1991), suggesting hybrids may have lower fitness. Thus, it seems possible that introgression in this hybrid zone is constrained by selection against hybrid individuals.

What are the implications of hybridization for *M. maura* and *M. tonkeana*? In general, N_em greater than one is sufficient for two populations to retain most heterozygosity and not differentiate through inbreeding and drift (Slatkin 1987). Pairwise N_em estimates between *M. maura* and *M. tonkeana* are low; R_{ST}-based estimates of N_em between populations range from 0.28 to 0.61, and between-species N_em is 0.61. Additionally, *M. tonkeana* and especially *M. maura* have small population census sizes and differences in reproductive success of females and males further decreases the effective population sizes of these species relative to their small census sizes (Hoelzer 1997). Low effective population sizes of each species means genetic drift may play a significant role in the accumulation of fixed differences between them. In consideration of these issues and the severe fragmentation of the habitat in the Tempe Depression that undoubtedly hinders migration between the two species, the current level of effective gene flow between *M. maura* and *M. tonkeana* does not appear sufficient to homogenize their respective genomes in the future.

Population Structure within Macaca maura

In *M. maura,* geographic structuring in mtDNA is high. In terms of shared clades of mtDNA, F_{ST} between Bontobohari and Karenta is equal to one because each locality is fixed for a monophyletic mtDNA clade. F_{ST} based on mtDNA haplotype frequencies and genetic distances are also high (Table 3). The sharp geographic clustering of mtDNA haplotypes in *M. maura* is consistent with the social system of female philopatry observed in macaque societies (Dittus 1988; Melnick and Hoelzer 1992), but could also stem from extended geographic isolation of these populations. Supriatna (1991) reports a larger body size of *M. maura* from Bontobohari than from Karenta that could be a consequence of environmental factors, such as differences in food quality and/or genetic factors related to population structure. However, in the nuclear genome low or zero population subdivision underlies the monophyletic clades of the mtDNA of *M. maura* in Karenta and Bontobohari (Table 4). R_{ST} between these populations is not significantly different from zero and F_{ST} is low, suggesting these regions are portions of an undifferentiated population that is homogenized by male migration. Thus, if the monophyletic clades of mtDNA haplotypes in Bontobohari and Karenta each evolved in situ, females have not sucessfully dispersed between these relatively nearby regions for a long time, enough time for distinct mutations to accumulate in mtDNA from each region. The disparity between levels of population subdivision in mtDNA ($F_{ST} \approx 1$) and nuclear DNA (R_{ST} and $F_{ST} \approx 0$) of *M. maura* populations approaches its theoretical maximum and is a striking empirical example of how differences in male and female behavior can differentially affect molecular evolution, genetic drift, and gene flow of different genetic elements depending on their mode of inheritance.

The fixed allele at the D22S345 locus in *M. maura* contains microsatellite tandem repeats and is thus presumably subject to the same mechanisms that produce allele length variants at microsatellite loci. Genotypic data from other macaque species at the D22S245 locus suggest that the 126-bp allele

was present in the ancestors of the Sulawesi macaques. Size expansion may be a derived condition found in some species of macaque on Sulawesi and on the Mentawai Islands. Monomorphism at this locus could also be the result of a recent bottleneck in *M. maura* (which presumably did not affect mtDNA).

Population Structure within Macaca tonkeana

More mtDNA haplotype lineages were recorded in *M. tonkeana* than in *M. maura,* as expected from a species with a larger effective population size. MtDNA in the EAST population is paraphyletic with respect to other haplotypes in *M. tonkeana* (Evans et al. 1999; this study). In *M. tonkeana* population subdivision among mtDNA haplotypes is higher than that among nuclear DNA, although the contrast is to a lesser extent than in *M. maura.* Like *M. maura,* the disparity in levels of population structure of mtDNA and nuclear DNA is congruent with the expected genetic consequence of female philopatry and obligate male migration. The different magnitudes of difference in population subdivision among mtDNA and nuclear DNA in these species could be an artifact of sampling and/or a consequence of variation in the degree to which the sexes of each species adhere to this social paradigm.

Buttikofer (1917) tentatively recognized two species in central Sulawesi, *M. tonkeana* and *M. tonsus.* Fooden (1969) and Albrecht (1978) find no morphological evidence for separate species status of *M. tonsus,* although these studies rely on a patchy sampling of *M. tonkeana* that is predominately from northwestern-central Sulawesi and a feral population on Malenge Island in the Togian archipelago. The macaques on Malenge Island are probably descended from very few introduced individuals and may not adequately represent morphological variation in the rest of central Sulawesi. Froehlich and colleagues (Froehlich and Supriatna 1996; Froehlich et al. 1996) propose an eighth species of Sulawesi macaque based on dermatoglyphic (fingerprint) data that correspond with the EAST population in this study (east of the Bongka River). This study does not identify monophyletic relationships among mtDNA haplotypes or fixed molecular markers in nuclear DNA that would support separate species status for this population. However, autosomal and Y-chromosome microsatellites indicate that *M. tonkeana* is highly subdivided. The R_{ST} estimate among *M. tonkeana* populations is of similar magnitude to those among *M. tonkeana* and *M. maura* populations, and alleles at a Y-chromosome microsatellite differ in size and frequency among *M. tonkeana* populations. These results must be interpreted with caution, however, because this approximation of population subdivision could be exaggerated by the small sample size of the EAST population.

Conservation Management of Macaca maura and M. tonkeana

Macaca maura and *M. tonkeana* are characterized by a suite of species-specific morphological and behavioral characters (Fooden 1969; Albrecht 1978; Supriatna 1991). MtDNA of these species is monophyletic with respect to each other, although mtDNA of *M. tonkeana* is paraphyletic with respect to northern species of Sulawesi macaque (Evans et al. 1999). Additionally, fixed differences between these species are present in mtDNA and in alleles at microsatellite locus D22S345. Although extensive hybridization and introgression is occurring between *M. maura* and *M. tonkeana* within a zone of contact, introgression has not occurred beyond the narrow boundary (~ 30 km) of this zone. Hybridization, therefore, does not pose a threat to the species autonomy of *M. maura* or *M. tonkeana* in the foreseeable future. These taxa are distinct and should be considered as separate conservation units for management (Moritz 1994, 1995; Goldstein et al. 2000). Within *M. maura,* little or no population subdivision is present in the nuclear genome despite highly structured mtDNA. This species should be managed as a single conservation unit to insure that historical routes of male migration between populations remain open. In *M. tonkeana,* significant population structure is present in the nuclear genome, although fixed differences have not been identified in the WEST and EAST populations. To preserve historical patterns of gene flow within this species, each population (WEST and EAST) should be managed separately, although measures should be taken in conservation planning to preserve the low level of gene flow between these management units.

Conclusions

MtDNA haplotypes of *M. maura* and *M. tonkeana* have a sharp border at the contact zone between the species ranges. Some *M. maura* haplotypes have dispersed north across this border by male migration, but these haplotypes are genetically ephemeral.

Autosomal DNA of individuals in the contact zone are not subdivided. Autosomal gene flow into the hybrid zone is higher from *M. tonkeana* than from *M. maura,* but is significant in both directions. Y-chromosome DNA in the hybrid zone is predominately from *M. tonkeana.*

The contact zone between *M. maura* and *M. tonkeana* is probably maintained by a balance between dispersal of males from each species into neighboring philopatric groups and selection against resulting hybrid progeny. However, selection is not so severe as to prevent second- and third-generation backcrossing.

Macaca maura and *M. tonkeana* clearly represent two distinct species because they have reciprocally monophyletic mtDNA, diagnosibly distinct morphology, and fixed mtDNA, and microsatellite differences. Within these species, only one management unit is present in *M. maura*; at least two management units are present in *M. tonkeana.*

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Appendix

Mitochondrial DNA and microsatellite alleles at nine autosomal loci of *Macaca maura, M. tonkeana,* and contact-zone individuals. MtDNA is listed as m (*M. maura*), t (*M. tonkeana*), t* (unresolved). Number of alleles are indicated in parentheses, loci are tetrameric and dimeric (d), and na indicates Y-chromosome loci for which amplification was not successful. Individual codes indicate whether the animal was sampled from the wild (W) or as a pet (P), the sex of the animal (M or F), and an identification number.

Individual	Locality	Mt-DNA	D14S306 (10)		D12S391 (20)		D13S317 (11)		D12S1075 (8)		D17S1290 (11)		D1S550 (6)		D4S243 (21)		D7S503 (9d)		D22S345 (12d)		DY391 (14d)
M. maura																					
WF001	BON	m	172	184	309	341	241	273	275	279	232	240	154	158	191	199	136	138	126	126	
WM002	BON	m	180	184	321	341	241	241	279	279	240	244	154	158	191	215	136	138	126	126	na
WM003	BON	m	176	180	301	325	257	257	275	283	244	248	158	158	183	195	138	138	126	126	278
WM004	BON	m	172	180	317	321	245	249	279	279	244	244	154	154	171	203	136	138	126	126	na
WM008	BON	m	176	176	309	321	249	257	275	283	244	244	154	158	199	215	136	138	126	126	280
WM010	BON	m	176	180	325	333	241	257	279	279	236	240	150	154	195	203	136	136	126	126	268
WM011	BON	m	176	180	309	341	241	241	275	279	244	252	158	158	179	203	136	138	126	126	280
WM005	BON	m	184	188	325	333	245	245	275	279	236	248	158	158	199	203	136	138	126	126	268
WM006	BON	m	172	172	321	341	253	253	275	279	232	232	154	158	195	195	138	138	126	126	278
WM009	BON	m	172	176	325	341	245	245	275	283	256	264	154	154	195	211	134	134	126	126	na
WM028	BON	m	176	176	321	341	249	253	267	275	236	240	158	158	203	211	136	136	126	126	na
WM029	BON	m	176	180	309	333	253	257	271	279	236	248	158	158	199	215	136	138	126	126	268
WM026	KAR	m	176	176	301	325	261	265	271	279	236	240	150	154	195	255	138	138	126	126	280
WM027	KAR	m	172	184	313	325	241	261	267	279	236	240	154	158	183	207	136	136	126	126	268
WF012	KAR	m	176	176	317	325	257	261	263	271	232	244	150	162	195	199	136	136	126	126	
WF013	KAR	m	176	176	313	325	241	253	271	279	232	240	154	158	195	203	136	138	126	126	
WM015	KAR	m	176	176	317	337	229	253	267	275	240	244	154	162	195	199	136	138	126	126	276
WM016	KAR	m	172	176	301	349	245	261	271	271	232	248	158	158	195	195	136	138	126	126	274
WF017	KAR	m	176	176	317	325	253	253	271	271	232	244	154	154	203	203	136	136	126	126	
WM018	KAR	m	176	176	301	337	229	249	275	275	236	252	158	158	191	203	136	138	126	126	na
WM020	KAR	m	176	176	321	325	237	257	267	271	232	232	154	162	191	203	138	138	126	126	270
WF021	KAR	m	176	176	325	337	249	253	267	267	240	240	150	158	195	207	134	138	126	126	
WF022	KAR	m	172	176	313	337	249	261	275	287	236	236	150	162	195	203	138	138	126	126	
WM023	KAR	m	172	176	313	337	229	241	275	271	240	240	154	162	195	203	134	138	126	126	276
WM024	KAR	m	176	176	313	317	249	253	267	279	236	240	154	158	195	195	136	138	126	126	272
Contact zone																					
WF033	SAK	t	172	180	273	321	237	253	279	283	236	240	154	158	223	263	138	138	126	126	
WM034	SAK	m	160	176	301	313	241	241	275	283	236	260	150	154	199	203	136	136	126	130	na
WM031	SAK	t*	176	184	313	333	245	257	271	275	240	248	158	158	199	227	136	138	126	126	na
WM037	SAK	t	172	176	305	313	241	245	267	283	240	252	158	162	203	203	136	136	126	140	262
WF048	BAT	m	172	176	317	321	253	253	279	283	244	248	154	158	195	219	136	138	126	126	
WM059	KULO	m	176	176	321	333	237	241	283	283	236	244	150	150	203	203	138	140	126	126	262
WF060	KULO	m	176	180	321	325	245	245	279	283	236	244	154	158	195	195	138	138	126	126	
WF061	KULO	m	168	176	273	333	241	249	263	279	232	236	154	154	195	203	134	138	126	126	
WF050	BALA	m	172	180	305	329	241	245	267	283	236	256	154	158	183	219	138	140	136	140	
WF051	BALA	m	172	184	313	317	241	253	279	267	236	240	158	158	203	227	136	138	126	140	
WF052	BALA	m	176	176	317	329	249	253	275	283	240	244	158	158	203	227	138	138	130	140	
WF053	BALA	m	172	176	301	317	241	245	275	283	236	248	154	158	199	219	136	138	126	136	
WM073	KAJ	m	172	176	297	321	233	241	279	283	232	248	154	154	223	259	140	142	130	140	262
PF012	KEERA	t*	176	184	277	313	245	249	275	283	236	236	150	158	203	231	136	136	126	130	
PM020	KEERA	t*	172	176	293	325	237	241	267	279	228	236	158	166	179	179	138	142	126	126	na
PF021	KEERA	t*	180	192	301	333	245	245	263	279	248	252	158	162	195	207	136	140	140	140	
WM065	PARI	t	164	176	277	329	241	245	275	283	248	248	158	158	219	219	138	140	126	140	262
WM067	PARI	t	172	172	301	309	237	241	279	283	240	244	154	158	199	199	136	138	126	140	270

APPENDIX. Continued.

Individual	Locality	Mt-DNA	D14S306 (10)		D12S391 (20)		D13S317 (11)		D12S1075 (8)		D17S1290 (11)		D1S550 (6)		D4S243 (21)		D7S503 (9d)		D22S345 (12d)		DY391 (14d)
WM054	PARI	t	176	184	305	321	245	245	263	283	236	252	154	154	183	183	138	138	126	126	na
WM064	PARI	t	164	164	321	321	241	245	275	283	228	236	158	158	191	199	138	140	126	126	262
WM068	PARI	t	172	176	305	309	241	245	267	283	240	256	158	162	199	235	136	140	126	140	262
WF080	PARI	t	172	180	273	321	237	253	279	283	236	240	158	162	223	263	136	138	126	126	
WM081	PARI	t	172	176	273	301	237	249	279	279	248	236	158	162	247	263	136	138	126	126	262
WM097	PARI	t	172	172	277	277	237	249	275	283	240	252	158	158	203	203	136	138	126	126	268
WF098	PARI	t	164	180	277	317	237	245	283	283	228	252	154	158	223	231	136	140	126	140	
WM083	PARI	t	164	176	309	317	241	253	283	283	236	240	158	162	191	199	140	140	130	142	262
WM084	PARI	m	180	184	309	313	245	249	271	275	236	248	154	162	195	207	138	138	130	140	262
WF085	PARI	t	164	180	309	317	245	253	267	279	240	240	158	158	195	199	140	140	126	130	
WM094	PARI	t	176	184	273	297	241	245	275	279	236	248	158	162	199	203	138	138	126	132	268
WM069	PARI	t	164	164	273	297	237	237	283	283	228	248	158	158	199	199	136	140	126	142	266
WM070	PARI	t	168	176	305	325	237	249	275	283	236	252	158	158	227	247	138	140	126	142	262
WM078	PARI	t	172	176	305	317	241	253	283	295	236	244	154	162	199	203	136	138	132	138	270
WM079	PARI	t	172	176	313	317	237	249	283	279	228	244	154	158	199	223	138	140	140	140	266
WF087	PARI	t	184	184	297	309	237	249	283	283	248	248	158	158	199	199	138	140	132	146	
WF088	PARI	t	176	176	305	317	245	249	263	263	228	236	158	158	179	223	136	140	126	140	
WM100	PARI	t	176	176	301	309	237	237	263	283	252	260	154	162	199	199	138	140	126	140	270
M. tonkeana																					
WM126	WEST	t	164	168	285	329	237	241	267	279	232	260	162	162	231	235	136	138	132	148	262
WM127	WEST	t	176	176	285	313	237	241	267	279	240	244	158	158	215	231	132	138	130	148	262
WM129	WEST	t	172	184	297	333	233	237	267	275	248	260	162	166	227	243	132	138	130	130	262
WF131	WEST	t	172	184	297	317	233	237	275	279	248	256	162	166	231	231	136	136	130	130	
PM514	WEST	t	172	172	285	305	241	253	275	283	236	248	154	154	223	231	140	146	130	130	264
PF599	WEST	t	160	160	293	309	241	241	263	267	240	244	158	158	231	231	136	138	140	140	
WM133	WEST	t	164	168	329	329	237	241	267	279	232	260	162	162	179	231	138	138	132	148	262
PM561	WEST	t	172	172	265	293	237	249	275	275	244	248	158	162	235	239	134	138	132	136	262
PM565	WEST	t	164	184	277	289	229	245	271	283	240	244	146	154	203	227	138	138	130	144	262
PM566	WEST	t	164	180	277	289	229	245	279	283	240	240	150	154	219	227	136	142	128	144	254
PM567	WEST	t	164	172	277	301	245	257	279	283	244	248	150	154	199	207	138	138	136	136	262
PM569	WEST	t	156	176	277	321	241	245	279	279	240	256	154	158	207	255	138	140	142	148	286
PM582	WEST	t	156	160	289	289	253	261	267	279	244	248	154	154	215	235	136	136	146	148	262
PM583	WEST	t	160	184	301	305	241	245	267	279	244	244	154	162	179	179	136	142	132	148	262
PM584	WEST	t	184	188	309	333	237	253	263	267	240	268	150	158	191	235	134	140	138	142	270
PF597	WEST	t	176	188	317	325	249	253	267	271	244	248	162	166	227	235	138	138	132	138	
PM604	WEST	t	176	176	277	345	241	245	283	283	244	248	154	154	243	263	134	136	130	140	266
PM602	WEST	t	176	180	277	309	245	245	263	275	244	252	154	158	199	239	140	142	128	132	266
PM592	WEST	t	156	180	301	301	229	241	275	279	232	240	154	154	247	247	136	138	132	138	262
PM532	EAST	t	176	176	285	289	241	253	275	283	240	244	150	150	203	235	136	142	140	140	288
PM536	EAST	t	172	176	317	325	245	249	275	279	244	244	158	158	171	179	142	146	140	144	268
PM538	EAST	t	176	176	321	325	245	253	279	279	252	260	158	158	223	231	142	146	136	142	292
PM542	EAST	t	176	176	273	321	241	245	287	287	240	240	150	154	211	223	140	142	148	150	292
PM545	EAST	t	184	184	289	309	249	253	275	279	244	248	150	158	215	227	136	142	138	142	288
PM547	EAST	t	176	184	305	317	253	257	275	275	236	256	150	150	219	223	140	140	142	144	288
PF549	EAST	t	168	180	313	349	241	253	279	283	240	244	154	154	215	243	138	144	142	142	268
PM550	EAST	t	188	188	277	333	245	249	283	283	232	240	154	154	211	227	142	148	142	142	286