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Molecular phylogeny and evolution of prosimians based on complete sequences of mitochondrial DNAs

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ABSTRACT

Prosimians (tarsiers and strepsirrhini) represent the basal lineages in primates and have a close bearing on the origin of primates. Although major lineages among anthropoidea (humans, apes and monkeys) are well represented by complete mitochondrial DNA (mtDNA) sequence data, only one complete mtDNA sequence from a representative of each of the infraorders in prosimians has been described until quite recently, and therefore we newly determined complete mtDNA sequences from 5 lemurs, 4 lorises, one tarsier and one platyrrhini. These sequences were provided to phylogenetic analyses in combination with the sequences from the 15 primates species reported to the database.

The position of tarsiers among primates could not be resolved by the maximum likelihood (ML) and neighbor-joining (NJ) analyses with several data sets. As to the position of tarsiers, any of the three alternative topologies (monophyly of haplorhini, monophyly of prosimians, and tarsiers being basal in primates) was not rejected at the significance level of 5%, neither at the nucleotide nor at the amino acid level. In addition, the significant variations of C and T compositions were observed across primates species. Furthermore, we used AGY data sets for phylogenetic analyses in order to remove the effect of different C/T composition bias across species. The analyses of AGY data sets provided a medium support for the monophyly of haplorhini, which might have been screened by the variation in base composition of mtDNA across species.

To estimates the speciation dates within primates, we analyzed the amino acid sequences of mt-proteins with a Bayesian method of Thorne and Kishino. Divergence dates were estimated as follows for the crown groups: about 35.4 million years ago (mya) for lorisiformes, 55.3 mya for lemuriformes, 64.5 mya for strepsirrhini, 70.1 mya for haplorhini and 76.0 mya for primates. Furthermore, we reexamined the biogeographic scenarios which have been proposed for the origin of strepsirrhini (lemuriformes and lorisiformes) and for the dispersal of the lemuriformes and lorisiformes.

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1. Introduction

Primate evolution draws special attention because of its direct relevance to the human origin, and there are several phylogenetic problems concerning prosimians.

The first question is whether tarsiers have a close relationship with anthropoidea (Schmitz et al., 2001; Poux and Douzery, 2004; Gibson et al., 2005) or with strepsirrhini (Eizirik et al., 2001; Murphy et al., 2001; Jow et al., 2002; Schmitz et al., 2002; Hudelot et al., 2003), although the position of tarsier depends on the molecular and morphological data sets. Some data even suggested tarsiers to be a basal group of primates (Arnason et al., 2002). Recent studies of nuclear DNA seem to have established a consensus with respect to the phylogenetic position of tarsiers (Schmitz et al., 2001; Poux and Douzery, 2004). The presence/absence patterns of the short interspersed elements (SINE) are regarded to be informative molecular cladistic markers, and Schmitz et al. (2002) found three Alu insertions at orthologous loci suggesting the monophyly of haplorhini (anthropoidea and tarsiiformes). However, analyses using mtDNA gave contradictory results (Eizirik et al., 2001; Murphy et al., 2001; Jow et al., 2002; Schmitz et al., 2002; Hudelot et al. 2003).

Abbreviations: ML, maximum likelihood; NJ, neighbor-joining; mya, million years ago; SINE, short interspersed element; PCR, Polymerase chain reaction; CS, codon substitution; BP, bootstrap probability; RELL, resampling of estimated log-likelihoods; K/T, Cretaceous/Tertiary; MCMC, Markov chain Monte Carlo; KH test, Kishino–Hasegawa test; SH test, Shimodaira–Hasegawa test; WSH test, weighted Shimodaira–Hasegawa test; AU, approximately unbiased.

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Therefore, we examined carefully problematic characteristics of the mt genes and their effects on phylogenetic resolution of primates (for example, differences of base compositions, 3rd codon position attributes, and heterogeneities of substitution rates).

The base composition bias of mtDNA from several mammal species has been reported (Perna and Kocher, 1995; Springer and Douzery, 1996; Schmitz et al., 2002; Philips and Penny, 2003; Gibson et al., 2005). Schmitz et al. (2002) compared 26 mammalian mt genomes. They focused on the mt genome of the *Tarsius bancanus* and compared its base composition with those of other primates. They suggested that the overall nucleotide composition changed dramatically; decrease of T and A composition and increase of C composition on the lineage leading to higher primates at both silent and nonsilent sites, and these changes of nucleotide composition have caused change of amino acid composition. Philips and Penny (2003) mentioned the incongruence in the deep divergences of the mammalian tree obtained from mt genomes was caused by the difference of T and C frequencies among different species. Gibson et al. (2005) carried out a comprehensive analysis of base composition in 69 mammalian mt genomes. They examined whether the variation in base composition across genes and species affects the phylogenetic analysis. If there are large variations in base composition across species, then conventional models may be unable to compensate for these variations (Foster and Hickey, 1999) and may prevent the recovery of the true evolutionary history. If variation in nucleotide composition occurred at the synonymous positions, the codon usage will become different across species. If nonsynonymous positions are affected by compositional bias, then the encoded proteins will change their amino acid composition (Singer and Hickey, 2000).

So, we analyzed these aspects by comparing the base composition of 26 primates mt genomes with 3 outgroup species on each category of gene separately (protein, rRNA, and tRNA) and examined its effect on the performance of the phylogenetic methods. Furthermore, we measured the effect of change in base composition on the codon usage and amino acid composition.

The second question is on the origin and dispersal history of the primate suborder strepsirrhini. Madagascar lemuriformes and Afro-Asian lorisiformes have been enigmatic groups concerning the phylogenetic relationships among lemuriforms (Jung et al., 1992; Crovella et al., 1993; Yoder, 1994; Del Pero et al., 1995; Yoder et al., 2000; Yang and Yoder, 2003; Pastorini et al., 2000, 2001a,b, 2002, 2003), lorisiformes (Yoder et al., 2001; Masters et al., 2005), and their biogeography (Yoder et al., 1996).

Although the phylogenetic relationships of living primate species are relatively well established, the divergence times among them are still controversial. Furthermore, the divergence date of lemuriformes–lorisiformes and the adaptive radiation among lemurs endemic to Madagascar are still problematic due to the lack of terrestrial fossils for the direct common ancestors in the Tertiary of Madagascar. This controversy has been yielded partly because different authors have used different types of molecular data with different statistical methods and different calibration points.

In this study, we present the first systematic analyses using new abundant mt genome data derived from 11 prosimians representing each of the major groups of lemuriformes, representatives of three families out of five, and lorisiformes, the Asian lorisidae (south Asia, south-east Asia) and the African lorisidae and galagidae as regional representatives, and tarsiiformes. The purposes of this study are (i) to clarify problematic relationships among prosimians based on mtDNA data and (ii) to investigate the advantage of mtDNA data in studying the phylogenetics of primates. In addition, we estimate and discuss the divergence dates among primate species. To estimate the speciation dates within primates, particularly with strepsirrhini, we used the new complete mt genome data from 11 primates together with those from 15 primates and 26 non-primate mammals available in public databases. We used amino acid sequences encoded in mtDNA in estimating the divergence times including the distantly related species.

2. Materials and methods

2.1. Primate samples

Blood samples from *Eulemur fulvus fulvus*, *Eulemur fulvus mayottensis* and *Eulemur macaco macaco*, were from captive individuals in the Research Institute of Evolutionary Biology. A liver sample from *Daubentonia madagascariensis* was provided by the Ueno Zoological Gardens. DNA samples from *Varecia variegate variegate*, *Loris tardigradus* and *Perodicticus potto* were provided by the Chiba Zoological Park and the Research Institute of Evolutionary Biology. Liver samples from *Tarsius syrichta* and *Otolemur crassicaudatus*, and DNA samples from *Saimiri sciureus* and *Galago senegarensis* were provided by University of Tokyo.

2.2. DNA extraction and PCR amplification

The method used for DNA extraction depended on the sample type. Concerning the blood and tissue samples, total DNA was isolated from the buffy coat of the blood and homogenates of organ tissues using the proteinase K digestion followed by phenol, chloroform, and isoamyl alcohol (Sambrook et al., 1989).

Polymerase chain reaction (PCR) was performed in ABI 9600 and 9700 Thermal Cyclers. To avoid an inadvertent PCR amplification of possible mt pseudogenes within the nuclear genome, we amplified initially four long-range fragments approximately 4 to 6 kb in length that overlap by about 1000 bp.

We used the PCR kit (Takara Ex Taq, Takara Bio, Inc.) to amplify fragments of the mtDNA genomes of each species. Primers were designed for amplifying fragments based on conserved sequences in the complete mtDNA of *Lemur catta* and *Nycticebus coucang* in the public databases. Perfectly matching primers were then constructed for each species based on the DNA sequence of their fragment sequences.

All template sequences are the consensus of at least two different double-stranded PCR amplification reactions for which both strands in their entirety were sequenced directly using BigDye v1.1 (Applied Biosystems, Inc.). The sequencing reactions were carried out with the BigDye Terminator Cycle Sequencing Ready Reaction Kits (Applied Biosystems, Inc.).

The sequencing products were analyzed with an ABI PRISM 377 DNA Sequence Analysis System and the ABI-3700 capillary sequencing apparatus (Applied Biosystems, Inc.). All complete mt genome sequences have been deposited in DDBJ/EMBL/GenBank under the accession numbers in Table 1.

2.3. Alignment

In addition to the 15 published primates sequences containing *Propithecus verreauxi coquereli* data determined from feces sample by us (Matsui et al., 2007), complete mtDNA sequences of 40 non-primate mammalian species were retrieved from DDBJ/EMBL/GenBank (Table 1).

Concerning the 11 primate complete mtDNA sequences determined in this study, mtDNA-encoded genes (13 protein-coding loci, two rRNAs, and 22 tRNAs) were aligned against the homologous region of the human mtDNA sequence (Anderson et al., 1981).

Alignments for the 13 protein-coding sequences were performed using default settings in ClustalX (Thompson et al., 1997) and were adjusted manually with reference to codon boundaries of the aligned amino acid sequences. Special attention was paid to the structural conformation in aligning the rRNA and tRNA genes. Alignments for the

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