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A DOCTORAL DISSERTATION

Molecular analysis of Korean *Apodemus* mitochondrial genome and possible historical migration routes of *A. chejuensis*

GRADUATE SCHOOL
JEJU NATIONAL UNIVERSITY

Department of Life Science

Dae-Ju Oh

August, 2012

한국산 붉은쥐속의 미토콘드리아 유전체 분석 및 제주등줄쥐의 역사적 이주경로 추정

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제주대학교 대학원

2012년 8월

Molecular analysis of Korean *Apodemus* mitochondrial genome and possible historical migration routes of *A. chejuensis*

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(Supervised by Professor Se-Jae Kim)

A dissertation submitted in partial fulfillment of the requirement for
the degree of Doctor of Science

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ABBREVIATION

A or Ala	alanine
AA	amino acid
ATPase	*ATPase subunit* gene
bp	base pairs
BRCA1	*breast cancer susceptibility gene 1*
C or Cys	cysteine
CO1-3	*cytochrome c oxidase subunit 1-3* gene
CR	control region
CSB	conserved sequence block
CYTB	*cytochorome b* gene
D or Asp	aspartic acid
DHU	dihydrouridine
D-loop	displacement loop
E or Glu	glutamic acid
EtBr	ethidium bromide
F or Phe	phenylalanine
G or Gly	glycine
GHR	*growth hormone receptor* gene
H or His	histidine
H-strand	heavy strand
I or ILe	isoleucine
IRBP	*interphotoreceptor retinoid-binding protein* gene
K or Lys	lysine
kbp	kilobase pairs
L or Leu	leucine
LCAT	*lecithin cholesterol acyl transferase* gene

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L-strand	light strand
M or Met	methionine
ML	maximum likelihood
mt	mitochondria(l)
Mya	million years ago
N or Asn	asparagine
ND1-6	*NADH dehydrogenase subunit 1-6* gene
O_L	light strand replication origin
P or Pro	proline
Q or Gln	glutamine
R or Arg	arginine
RAG1	*recombination activating gene 1*
rDNA	ribosomal DNA
rRNA	ribosomal RNA
S or Ser	serine
SNP	single nucleotide polymorphism
T or Thr	threonine
TAS	termination-association sequence
tRNA	transfer RNA
UV	ultraviolet
V or Val	valine
vWF	*von Willebrand factor* gene
W or Trp	tryptophan
Y or Tyr	tyrosine

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BACKGROUND

Rodentia is the largest order of mammals, encompassing 2,277 species (Musser and Carleton, 2005). Forty percent of mammal species are rodents, and they are found on all continents but Antarctica. Most rodents eat various plants or seeds, though some have more varied diets. Because they are fast growing mammals and vectors of fatal diseases such as the plague; humans have studied them for ecology, evolution, and genetics.

Since the mid-20th century, views on the size of the Rodentia have appreciated substantially from 1,591 species (Corbet and Hill, 1980) to 2,277 species (Musser and Carleton, 2005). Rodents include mice, rats, porcupines, beavers, squirrels, hamsters, and guinea pigs. Before the study by Graur *et al.* (1991), Rodentia was believed to be a monophyletic order of Mammalia. They questioned whether the guinea pig, *Cavia porcellus*, is a rodent. They analyzed amino acid sequences and suggested that the guinea pig diverged before the separation of the primates and artiodactyls from the myomorph rodents. In 1996, analysis of the complete guinea pig mitochondrial (mt) genome indicated that the species was not a rodent (D'Erchia *et al.,* 1996). Furthermore, hystricognaths including guinea pigs were treated as a separate mammalian order, and the Rodentia was conventionally viewed as polyphyletic (Graur *et al.,* 1992; Li *et al.,* 1992). However, many molecular studies strongly supported the Rodentia as a monophyletic order (Frye and Hedges, 1995; Cao *et al.,* 1997; Adkins *et al.,* 2001; Corneli, 2002; Waddell and Shelley, 2003), and Luckett and Hartenberger (1993) proposed rodent monophyly based on morphological and molecular data. Rodentia is currently believed to be a monophyletic order.

Rodentia consists of 5 suborders; Sciuromorpha, Castorimorpha,

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Myomorpha, Anomaluromorpha, and Hystricomorpha (Musser and Carleton, 2005). Sciuromorpha has 3 families (Aplodontiidae, Sciuridae, and Gliridae), Castorimorpha comprises 3 families (Castoridae, Geomyidae, and Heteromyidae), Myomorpha consists of 7 families (Dipodidae, Calomyscidae, Cricetidae, Muridae, Nesomyidae, Platacanthomyidae, and Spalacidae), Anomaluromorpha includes only 2 families (Anomaluridae and Pedetidae), and Hystricomorpha contains 18 families (Ctenodactylidae, Bathyergidae, Hystricidae, Petromuridae, Thryonomyidae, Heptaxodontidae, Abrocomidae, Capromyidae, Caviidae, Chinchillidae, Ctenomyidae, Dasyproctidae, Cuniculidae, Dinomyidae, Echimyidae, Erethizontidae, Myocastoridae, and Octodontidae) and an *incertae sedis* family (Diatomyidae). Among 5 suborders, Myomorpha is the largest, containing 1,137 species of mouse-like rodents, i.e., nearly a quarter of all mammal species. This suborder contains mice, rats, hamsters, lemmings, gerbils, and voles. Most myomorph species belong to the Muroidea superfamily, which is classified into 6 families, 310 genera, and 1,518 species (Musser and Carleton, 2005). Among the 6 families of the Muroidea, Muridae is the largest with 150 genera, with over 700 species (Musser and Carleton, 2005). In the Korean Peninsula and Jeju Island, 4 genera (*Apodemus*, *Micromys*, *Mus*, and *Rattus*) of Muridae are found (Yoon *et al.,* 2004). Muridae are relatively small mammals, generally around 10 cm long excluding the tail length. Some species are larger; the giant bushy-tailed cloud rat, *Crateromys schadenbergi*, is the largest at over 70 cm.

Although many researchers have tried to establish phylogeny and evolution of rodents (Nedbal *et al.,* 1996; Huchon *et al.,* 1999, 2000; Michaux *et al.,* 2001; Steppan *et al.,* 2004), the evolution of many small mammals including murids is unclear due to the incongruence between the molecular data and morphological information. Against traditional classification, many molecular taxonomists researched various nuclear and mt genes such as *growth hormone receptor* (*GHR*) gene, *breast cancer susceptibility* (*BRCA1*) gene,

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von Willebrand factor (*vWF*) gene, *lecithin cholesterol acyl transferase* (*LCAT*) gene, *interphotoreceptor retinoid-binding protein* (*IRBP*) gene, *recombination activating gene 1* (*RAG1*), *12S ribosomal RNA* (rRNA) gene, *cytochrome c oxidase subunits 1-3* (*CO1-3*) gene, and *cytochrome b* (*CYTB*) gene (Conroy and Cook, 2000; Robinson-Rechavi *et al.,* 2000; Suzuki *et al.,* 2000; Adkins *et al.,* 2001; Michaux *et al.,* 2001; Steppan *et al.,* 2005). These molecular studies broadened our knowledge of rodent phylogeny and evolutionary history. For instance, *CYTB* sequence analysis suggested that North American *Microtus* are derived from multiple invasions from Asia or, alternatively, as a single invasion followed by autochthonous speciation (Conroy and Cook, 2000), and combined analysis of nuclear and mt genes suggested that the murines originated in Southeast Asia and then rapidly expanded across the Old World (Steppan *et al.,* 2005).

With the rapid development of sequencing technology, phylogenetic and evolutionary studies using mt genome sequences have explosively increased. Since the first mt genome was sequenced in humans (Anderson *et al.,* 1981), mt genome sequences have been reported for various taxa, including fish (Miya *et al.,* 2003; Oh *et al.,* 2007b), mammals (Mouchaty *et al.,* 2001; Horner *et al.,* 2007), insects (Stewart *et al.,* 2003; Covacin *et al.,* 2006), reptiles (Dong and Kumazawa, 2005; Podnar *et al.,* 2009), birds (Valverde *et al.,* 1994; Harlid and Arnason, 1999), and amphibians (Zhang *et al.,* 2006; Oh *et al.,* 2007a), as well as other species (Milbury and Gaffney, 2005; Sinniger *et al.,* 2007). Remarkable studies were conducted using mass mt genome sequences for vertebrate phylogeny. Miya *et al.* (2003) sequenced 54 mt fish genomes and established higher teleostean phylogeny with 100 mt genome sequences. In amphibians, Zhang *et al.* (2006) sequenced 15 mt genomes of Asian salamanders and proposed the Asian hynobiid originated from North China. Arnason *et al.* (2008) analyzed 109 mt genome sequences including 11 newly sequenced mt genomes for placental mammalian phylogeny. Their analyses

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identified 4 basal monophyletic groups, Afroplacentalia, Xenarthra, Archontoglires, and Laurasiaplacentalia. They also estimated divergence time for basal placental divergence. As in various vertebrates, complete mt genome sequences are rapidly becoming available; nevertheless, only 33 mt genomes of rodent have been sequenced (37 mt genomes including below subspecies) until now.

The mt genome has several merits, such as its compact size (Cantatore and Saccone, 1987), lack of recombination (Clayton, 1982, 1992), maternal inheritance (Kondo *et al.,* 1990), fast evolutionary rate compared to nuclear sequences (Brown *et al.,* 1979), and multicopy status (Michaels *et al.,* 1982; Robin and Wong, 1988), for research in population genetics, phylogenetics, and evolution (e.g., Serizawa *et al.,* 2000; Liu *et al.,* 2004; Suzuki *et al.,* 2008). Comparisons of complete mt genome sequences are much more powerful for phylogenetic reconstruction than comparative analysis of single gene sequences (Ingman *et al.,* 2001; Parsons and Coble, 2001; Boore, Medina, and Rosenberg, 2004). In fact, phylogenetic analysis with enough sequences decreases stochastic uncertainty (Cao *et al.,* 1994). Accordingly, more mt genomes provide higher resolution for phylogenetic analysis.

The mt genomes are generally circular (Boore, 1999), although Cubozoa, Scyphozoa, and Hydrozoa have linear mt genomes (Bridge *et al.,* 1992). Animal mt genomes are usually around 15,000 - 20,000 base pairs (bp) in size and contain the same set of 37 genes, encoding 13 proteins, 2 rDNAs, 22 transfer RNAs (tRNA), and a control region (Boore, 1999). Commonly, mt gene contents are constant and gene arrangements are nearly identical in mammals. Various mammalian mt protein-coding genes end with an incomplete termination codon as TA or T, rather than a complete termination codon (TAA or TAG). Such incomplete termination codons can be modified by post-transcriptional polyadenylation to a complete termination codon (Ojala *et al.,* 1981). Among 13 protein-coding genes, *NADH dehydrogenase subunit*

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(*ND*) 6 is encoded by the light strand (L-strand); the others are encoded by the heavy strand (H-strand). *tRNA-Phe*, *tRNA-Val*, *tRNA-Leu*, *tRNA-Ile*, *tRNA-Met*, *tRNA-Trp*, *tRNA-Asp*, *tRNA-Lys*, *tRNA-Gly*, *tRNA-Arg*, *tRNA-His*, *tRNA-Ser*$^{(AGY)}$, and *tRNA-Thr* are encoded by the H-strand and the remainder are encoded by the L-strand (Wolstenholme, 1992). A major noncoding control region called the displacement loop (D-loop) is located between *tRNA-Pro* and *tRNA-Phe*. This sequence has several elements such as a termination-associated sequence (TAS) upstream of the 3′ end of the control region in mammals (Doda *et al.,* 1981; Mackay *et al.,* 1986) and conserved sequence blocks (CSBs) associated with mt DNA replication and transcription (Clayton, 1991; Shadel and Clayton, 1997). The L-strand replication origin (O_L) is between *tRNA-Asn* and *tRNA-Cys* and comprises approximately 30 nucleotides (Wolstenholme, 1992). The O_L sequence forms a stable stem–loop structure, and a conserved motif is located in the base of the stem of *tRNA-Cys*. This motif is found in various vertebrate mt genomes (Oh *et al.,* 2008; Oh *et al.,* 2010).

Although the mt genome structure of higher animals such as mammals is almost constant, some organisms, closer to the lower animals, have unique mt genome structures (Okimoto *et al.,* 1991; Le *et al.,* 2000; Helfenbein *et al.,* 2004). The mt gene arrangements are almost the same in major groups, especially the mammals (Boore, 1999). Nevertheless, several rearrangements have been found in nematodes (Okimoto *et al.,* 1991, 1992), arthropods (Boore *et al.,* 1995), bivalves (Hoffman *et al.,* 1992), pulmonate mollusks (Yamazaki *et al.,* 1997), echinoderms (Cantatore *et al.,* 1987; Jacobs *et al.,* 1988), and fruit flies (Clary and Wolstenholme, 1985). These mt gene rearrangements are considered rare evolutionary events and are used to reconstruct the phylogeny of various organisms (Singh, 2008).

Since the development of sequence analysis tools, many evolutionary studies using mt genes or genomes estimated divergence time between

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species. The molecular clock is used to estimate the time of speciation or radiation and significantly advanced the neutral theory of molecular evolution (Kimura, 1968). The divergence time estimation of rodents revealed their evolutionary histories (Jacobs and Downs, 1994; Adkins *et al.,* 2001; Douzery *et al.,* 2003; Liu *et al.,* 2004; Horner *et al.,* 2007; Arnason *et al.,* 2008; Robins *et al.,* 2008). The divergence time between Lagomorpha and Rodentia was estimated at 93 million years ago (Mya) and the deepest Rodentia divergence at around 88 Mya (Arnason *et al.,* 2008). Bayesian dating inferred from mt genomes indicate a rapid radiation within Glires around 60 Mya, and that within Rodentia occurred approximately 63 Mya (Horner *et al.,* 2007). Horner *et al.* (2007) also suggested that the divergence of the Muroidea + Dipodidae clade from the Sciuridae + Myoxidae clade occurred 53.4 Mya (protein) or 51.8 Mya (DNA). In addition, they estimated the divergence between *Mus* and *Rattus*, representative species of Muridae, occurred 15.1 (protein) or 15.9 (DNA) Mya, while the split between *Mus* and *Rattus* was approximately 13 – 19 Mya (Douzery *et al.,* 2003), 23 Mya (Adkins *et al.,* 2001), or 12 Mya (Jacobs and Downs, 1994). Molecular analyses of *Rattus* suggest that the deepest divergence within *Rattus* occurred 3.5 Mya (Robins *et al.,* 2008). For *Apodemus*, *A. peninsulae* diverged from the *A. speciosus* + *A. chevrieri* + *A. agrarius* clade about 8.39 Mya, and *A. agrarius* diverged from *A. chevrieri* about 2.68 Mya, during the first glacial period of the Quaternary (Liu *et al.,* 2004).

The whole species number is estimated from 10 to 100 million (Wilson, 1998). This wide range is due to difficulties in species definition. A species is one of the primary units of biological classification and a taxonomic rank. A biological species concept was used first by Jordan (1896) and later Mayr (1969). They defined a species as “group of interbreeding populations which are reproductively isolated from other groups”. Later, the biological species concept was redefined by Mayr (1982) as “a reproductive community of

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populations (reproductively isolated from others) that occupies a specific niche in nature." Baker and Bradley (2006) define genetic species as a group of genetically compatible interbreeding natural populations that is genetically isolated from other such groups. Since rapid development of DNA sequencing technology, many researchers have recognized and described species using DNA sequence data (Roca *et al.,* 2001; Baker *et al.,* 2002; Matocq 2002; Piaggio *et al.,* 2002), and the accumulation of DNA data solidify the adequacy of the genetic species concept.

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ABSTRACT

Chapter 1. Comparative analysis of the complete mitochondrial genome sequences of Korean *Apodemus*

The complete mitochondrial (mt) genomes of *Apodemus agrarius*, *A. chejuensis*, and *A. peninsulae* were determined to be 16,260, 16,261, and 16,266 base pairs (bp) long, respectively, and have been deposited in the GenBank database (Accession Nos. HM034866, HM034867, and HQ660074, respectively). Like other vertebrate mt genomes, the 3 mt genomes contain 13 protein-coding genes, 22 tRNAs, 2 rDNAs and a noncoding control region. The mt genomes of *A. agrarius* and *A. chejuensis* had protein-coding genes that use the most common initiation codon, ATG, and 2 unusual initiation codons: GTG and ATA. However, *A. peninsulae* had an additional unusual ATC codon for initiation in the *NADH dehydrogenase subunit* (*ND*) *2* gene. Overall, the nucleotide frequencies of all analyzed mt protein-coding genes were similar. Codon usage patterns based on mt protein-coding genes were similar in *A. agrarius* and *A. chejuensis*, while the mt protein-coding genes of *A. peninsulae* were slightly different. The *12S rRNA* gene sequences were 955, 955, and 956 bp long in *A. agrarius*, *A. chejuensis*, and *A. peninsulae*, respectively, and the *16S rRNA* gene sequences were 1,572, 1,573, and 1,571 bp long, respectively. *tRNA-Leu* and *tRNA-Ser* were identified two distinct forms, respectively. The Three tRNA clusters, IQM (isoleucine, glutamine, and methionine), WANCY (tryptophan, alanine, asparagine, cysteine, and tyrosine), and HSL (histidine, serine, and leucine), were conserved in *A. agrarius*, *A. chejuensis*, and *A. peninsulae*, as in the typical mt genomes of Rodentia.

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Generally, the mt genomes of mammals have 2 noncoding regions: O_L and CR, which is also called the displacement loop (D-loop). The CR sequences spanned 854, 857, and 866 bp in *A. agrarius*, *A. chejuensis*, and *A. peninsulae*, respectively, and was positioned between the *tRNA-Pro* and *tRNA-Phe* genes. The phylogenetic analysis of Rodentia using mt 13 protein-coding genes suggested that *Sciurus* and *Myoxus* was diverged earlier than other rodents, and *Rattus* consisted of two distinct clades. Korean *Apodemus* was closely related to *Mus* as sister group. Although phylogenetic relationships of *Apodemus* spp. have been studied by many researchers, some species remain controversial owing to wide distribution, subspecies problems, and fragmentary data. Thus, the mt genome of Korean *Apodemus* spp. will be useful information to clarify rodent, especially the *Apodemus*, phylogeny.

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Chapter 2. Possible historical migration routes of *Apodemus chejuensis*

Nineteen *CYTB* sequence haplotypes were defined in 24 *Apodemus agrarius* individuals, and 25 were defined in 49 *A. chejuensis* individuals. The most frequent haplotype group was Hap27, which was shared by 6 *A. chejuensis* individuals. The most frequent haplotype group in the *A. agrarius* was Hap15, which was shared by 3 individuals. Fu's *Fs* test showed that COR-II and CHE had significantly negative *Fs* values (-4.462 and -5.703, respectively), whereas the COR-I had a positive value (0.613). Mismatch distribution analyses suggested population expansion in COR-II and CHE and a stable COR-I population. Median-joining network data indicated that *A. chejuensis* is a clearly separate species containing 4 subgroups, but these subgroups did not correspond to local distribution patterns on Jeju Island. Interestingly, Hap42 of the CHE population was closely related to Hap9 of the COR-I. In addition, molecular clock calculations that estimate the time of divergence of *A. agrarius* and *A. chejuensis* suggest that those species diverged at approximately 0.3 million years ago (Mya). Based on these data, three historical migration routes were hypothesized. (1) The ancestral lineage of *A. agrarius* might migrate into the Korean Peninsula via North Korea; then, a group migrated to Jeju Island via the Yellow Sea basin when the sea level was lower. (2) The ancestral lineage of *A. chejuensis* might migrate to Jeju Island via the Yellow Sea basin, followed by a second migration into the western islet of the Korean Peninsula via the Yellow Sea basin when the sea level was lower. (3) The common ancestor of *A. agrarius* and *A. chejuensis* might have originated in eastern China, where it split into 2 lineages; one lineage moved to the western islet of the Korean Peninsula, and the other moved to Jeju Island. The estimation of divergence time suggested that *A.*

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agrarius and *A. chejuensis* diverged at approximately 0.3 Mya. Because *A. chejuensis* has been geographically and reproductively isolated from *A. agrarius* since the last glacial age, many researchers have proposed that populations diverged as species. This study supports the notion that *A. chejuensis* should be treated as a species; however, further study of North Korea and Chinese samples is needed to understand their biogeographic history fully.

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CHAPTER 1

Comparative analysis of the complete mitochondrial genome sequences of Korean *Apodemus*

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1.1. INTRODUCTION

Rodentia is the largest order of mammals, encompassing 2,277 species (Musser and Carleton, 2005). Among them, Muridae is the largest family with over 700 species (Musser and Carleton, 2005) and is often employed as a laboratory model for studies of human diseases. On the Korean Peninsula and Jeju Island, 4 genera (*Apodemus*, *Micromys*, *Mus*, and *Rattus*) of Muridae are found (Yoon *et al.,* 2004a).

The genus *Apodemus* contains at least 20 rodent species (Musser and Carleton, 2005), including several of the most common small rodent species and is widely distributed in the Palearctic region (the zoogeographical region consisting of Europe, Africa north of the Sahara, and most of Asia north of the Himalayas). *Apodemus* species are distributed in a variety of habitats, including woodlands, forests, and grasslands. Some species are often found in the same habitat, showing resource partitioning among syntopic species. This ecological feature could be associated with the biogeographic history of the genus and its speciation processes. The striped field mouse *Apodemus agrarius* and Korean Field mouse *A. peninsulae* are distributed throughout the Korean Peninsula and are the most common rodent species there, whereas the Jeju Striped Field mouse, *A. chejuensis*, is found only on Jeju Island (Won and Smith, 1999). Generally, *A. agrarius* inhabits rural flat lands, rivers, and agricultural farmlands, while the Jeju Striped Field mouse, *A. chejuensis*, is often found in bushy areas rich with small trees in mountainous areas. They are distributed from the coastal regions to the high-altitude regions of Mt. Halla.

The wide distribution, subspecies problems, and fragmentary data of *Apodemus* spp. were so complicated that even experts have been unable to

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comprehend its phylogenetic relationships (Suzuki *et al.,* 2008). Molecular and morphological analyses improved the taxonomic situation of *Apodemus* spp.; however, the difficult cases continue to complicate the relationships between closely related species (Musser and Carleton 2005). In particular, the taxonomic status of some species inhabiting the western Palearctic region including subgenus *Sylvaemus* are complicated owing to several new species in southern Europe and the Middle East (Musser and Carleton 2005). Their phylogenetic relationships are not established, and the species *A. sylvaticus* and *A. flavicollis* remain uncertain (Suzuki *et al.,* 2008). Previous phylogenetic results inferred from morphological and molecular data (Serizawa *et al.,* 2000; Filippucci *et al.,* 2002; Michaux *et al.,* 2002; Suzuki *et al.,* 2003; Liu *et al.,* 2004; Suzuki *et al.,* 2008), suggested that the genus *Apodemus* consists of 8 distinct lineages; nevertheless, previous data are insufficient to solve their phylogenetic complexity.

The low resolution of molecular phylogenies inferred from fragmentary data has prompted many researchers to analyze mitochondrial (mt) genome sequences. The mt are small organelles found in most eukaryotic cells and play an important role in metabolism (Brand, 1997), cell death *via* apoptosis (Kroemer *et al.,* 1998), various diseases (Graeber and Muller, 1998), and aging (Wei, 1998). The mt is essential for ATP production and has its own genome. In general, the vertebrate mt genome consists of 16–18 kilobase pairs (kbp) and contains 22 transfer RNAs (tRNAs) necessary for the translation of mt proteins, 2 ribosomal DNAs (rDNAs), 13 protein-coding genes related to oxidative phosphorylation, and a major noncoding region for replication and transcription initiation (Anderson *et al.,* 1981; Boore, 1999). Of the 13 protein-coding genes, 12 are encoded on the heavy strand (H-strand), and 1 gene, *NADH dehydrogenase subunit 6* (*ND*) gene, is encoded on the light strand (L-strand). Fourteen mt tRNAs are encoded on the H-strand and the rest are encoded on the L-strand (Wolstenholme, 1992). The mt

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protein-coding genes in most animals have incomplete termination codons such as TA or T. These abnormal termination codons can be modified to a complete termination codon by post-transcriptional polyadenylation (Ojala *et al.,* 1981). The mt genome has 2 noncoding regions: the major noncoding control region (CR) called the displacement loop (D-loop) and the L-strand replication origin (O_L), which mediates replication of the mt genome (Clayton, 1991; Shadel and Clayton, 1997).

The mt genome has several merits for research in population genetics; phylogenetics; and evolution, such as its compact size; fast evolutionary rate; short coalescence time; and maternal inheritance (e.g., Serizawa *et al.,* 2000; Liu *et al.,* 2004; Suzuki *et al.,* 2008). Mammalian mt DNA has been used for phylogenetic and evolutionary studies since the development of DNA sequencing techniques. In the last decade, mt genome sequences have been reported for various taxa, including fish (Miya *et al.,* 2003; Oh *et al.,* 2007b), mammals (Mouchaty *et al.,* 2001; Horner *et al.,* 2007), insects (Stewart *et al.,* 2003; Covacin *et al.,* 2006), reptiles (Dong and Kumazawa, 2005; Podnar *et al.,* 2009), and amphibians (Zhang *et al.,* 2006; Oh *et al.,* 2007a), as well as other species (Milbury and Gaffney, 2005; Sinniger *et al.,* 2007). Although Rodentia contains the most mammal species and the mt genomes of the mouse and rat were sequenced first (Bibb *et al.,* 1981; Gadaleta *et al.,* 1989), and only a small proportion of mt genome sequences of Rodentia have been reported. The mt genome sequences of 33 species (excluding subspecies) in Rodentia have been determined (or 1.5% of the 2,277 species of Rodentia).

To provide the basal data set for *Apodemus* and all rodent phylogeny, the complete mt genome sequences of Korean *Apodemus*. were sequenced and their general features analyzed, including nucleotide composition, nucleotide frequency, codon usage, secondary cloverleaf tRNA structures, the O_L, and CR.

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1.2. MATERIALS AND METHODS

1.2.1. Sampling and DNA extraction

Apodemus agrarius and *A. peninsulae* were collected in traps in Cheongdo, Gyeongsangbuk-do; *A. chejuensis* was caught at Mt. Halla, Jeju, Korea. Genomic DNA was extracted from small pieces of tail or muscle using NucleoSpin® Tissue Kit (Macherey-Nagel, Germany). First, small pieces of tail or muscle was placed in a microcentrifuge tube with buffer T1 and proteinase K solution, then vortexed and incubated at 56°C until lysis was complete. The lysed samples were vortexed and buffer B3 was added. The tubes were vortexed and incubated at 70°C for 10 min. Ethanol lwas added and vortexed. For each sample, a NucleoSpin® Tissue Column was placed into a collection tube and the samples applied to the column. The assembly was centrifuged for 1 min at 11,000*g*. The flow-through was discarded, and the column was returned to the collection tube. To wash the silica membrane, buffer BW and buffer B5 were added in turn. The column-collection tube assembly was centrifuged for 1 min at 11,000*g* after each wash step. The silica membrane was dried by centrifugation. Last, the column was placed into a new 1.5 ml tube and prewarmed buffer BE was added, then incubated at room temperature for 1 min. The tube was centrifuged for 1 min at 11,000*g*, and the extracted DNA was stored at -20°C.

1.2.2. PCR, cloning, and sequencing

To amplify the complete mt genome, long PCR was performed with primers complementary to the aligned and complete nucleotide sequences of the mt genomes of several mouse species (Table 1.1). The long PCR reactions were carried out using Maxime™ PCR PreMix (iNtRON

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Biotechnology, Korea) according to the manufacturer's protocol. 50-100 ng of genomic DNA and 1 μl of each primer was added into Maxime™ PCR PreMix tubes. Reaction conditions included an initial 3 min denaturation at 95°C, followed by 35 cycles with denaturation at 95°C for 30 s, annealing for 30 s at 55°C and extension at 72°C for 2-5 min, and a final extension of 10 min at 72°C. Amplification products were confirmed by electrophoresis with 100 bp Plus DNA Ladder (Bioneer, Korea) as a size marker in 1% agarose gels, stained with ethidium bromide (EtBr), and visualized under ultraviolet (UV) light.

The amplified fragments were cloned using TOPO TA Cloning Kit (Invitrogen, USA). PCR products were ligated into the pCR2.1 TOPO vector according to the manufacturer's protocol. The ligation mixtures were mixed gently and incubated for 5 min at room temperature. The reaction mixtures were put on ice immediately and incubated for 2 min. Following ligation, 30 μl of competent cells were defrosted in ice and added to the reaction, which was heat shocked at 42°C for 30 s then put on ice for 2 min. SOC medium was added and the reaction mixtures were shaken at 37°C for 90 min. The reaction mixtures were spread on LB agar plates containing X-Gal, IPTG, and ampicillin. The plates were incubated at 37°C for 18 h. White colonies were picked into LB medium containing ampicillin and incubated at 37°C with shaking overnight.

Positive clones were verified by PCR with the original amplification primers and 1 μl of cultured cells as template. Reaction conditions included an initial 3 min denaturation at 95°C, followed by 25 cycles with denaturation at 95°C for 30 s, annealing for 30 s at 55°C, and extension at 72°C for 2-5 min, and a final extension of 10 min at 72°C. Amplification products were confirmed by electrophoresis with 100 bp Plus DNA Ladder (Bioneer, Korea) as size standard marker in 1% agarose gels, stained with EtBr, and visualized under UV light. Plasmid DNA was extracted from the positive clones.

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Plasmid DNA was extracted with the *AccuPrep*® Nano-Plus Plasmid Mini Extraction Kit (Bioneer, Korea). The cultured cells were centrifuged at 13,000 rpm for 1 min and the media was removed by pipetting. Resuspension buffer containing nanoparticles was added and the pellet was completely resuspended by pipetting. Cell lysis buffer was added and mixed by gently inverting the tube 3-4 times. Neutralization buffer was added and immediately mixed by gently inverting the tube 3-4 times. Cell debris was removed by centrifugation at 4°C and 13,000 rpm for 1 min and the cleared lysate was transferred to the DNA binding column. The columns were centrifuged at 13,000 rpm for 1 min and the flow-through was discarded. To wash the silica membrane, washing buffer was added to the column tube and centrifuged at 13,000 rpm for 1 min. Additional centrifugation was carried out at 13,000 rpm for 1 min to dry the silica membrane in the column. The DNA binding filter column was transferred to new 1.5 ml microcentrifuge tube and elution buffer was added and incubated at room temperature for 1 min. To recover the eluted plasmid DNA, the tube was centrifuged at 13,000 rpm for 1 min, and the DNA was transferred to a new 1.5 ml microcentrifuge tube.

Each cloned fragment was sequenced with TOPO vector inner primers (Invitrogen, USA) using an automatic DNA sequencer (ABI 3730xl; Applied Biosystems, USA) according to the manufacturer's protocol, and nested flanking sequencing primers were used to walk in both directions.

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Table 1.1. PCR primers used in this study

Name	Sequences (5’ → 3’)
Apomt-1F	TACCCTCACCTGAATTGGAGGC
Apomt-1R	GGGTTAATCGTATGACCGCG
Apomt-2F	CGCGGTCATACGATTAACCC
Apomt-2-1F*	GCAATGAAGTACGCACACACC
Apomt-2R	AGATAGAAACCGACCTGGATTGC
Apomt-3F	ACATCCCAATGGTGCAGAAG
Apomt-3-1F*	CCACTACCAATACCTCACCCTC
Apomt-3-2F*	TCATAGCGAGTATCCCACCAT
Apomt-3-3F*	ATTGGAGCATGAGGTGGACT
Apomt-3-2R*	CGTGGAAATGCTATGTCTGG
Apomt-3-1R*	GGCAGATGTGAAGTAAGCTCG
Apomt-3R	GGGGTTCGAWTCCTTCCTTTC
Apomt-4F	GAAAGGAAGGAATCGAACCCC
Apomt-4-1R*	GAATGAGTGAAGGCGGTTGT
Apomt-4R	GCATGRGTTTGGTGKGTCAT
Apnmt-5F	ATGACACACCAAACCCATGC
Apomt-5-1F*	GGATTTGAAGCAGCAGCATG
Apomt-5-1R*	CTGTTTGGCGTAAGCAGATTG
Apomt-5R	GGYTCCTAAGACCAAYGGAT
Apomt-6F	ATCCATTGGTCTTAGGAACC
Apomt-6-1F*	TGGACGATCAGACGCAAATAC
Apomt-6-2F*	CAACGCCTGAGCCCTAATAAT
Apomt-6-2R*	ATGAGCGGGTTTGTAGGTTG
Apomt-6-1R*	AGAAGCCCCCTCAGATTCAT
Apomt-6R	GCCTCCAATTCAGGTGAGGGTA

Asterisk indicates nested flanking primers.

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1.2.3. Sequence analysis of mt genomes of Korean *Apodemus*

The complete mt genome sequences of *Apodemus agrarius*, *A. chejuensis*, and *A. peninsulae* were compared with the mt genome sequences of other rodents in the GenBank database. The locations of the 13 protein-coding genes were determined by comparing nucleotide or amino acid sequences and identified 2 rDNAs and the CR. The 22 tRNA genes were identified using tRNAscan-SE (Lowe and Eddy, 1997) and ARWEN (Laslett and Canbäck, 2008).

The size of complete mt genome, gene lengths, and initiation and termination codons of the 13 protein-coding genes were compared. In addition, nucleotide composition, nucleotide frequency, and codon usage of the 13 protein-coding genes, O_L, and the putative tRNA cloverleaf structures of 3 Korean *Apodemus* mt genomes were compared.

1.2.4. Phylogenetic analysis

Phylogenetic relationships were analyzed by maximum likelihood (ML) methods. The mt 13 protein-coding genes of other Rodentia were available in GenBank database (Table 1.2) and aligned with those of Korean *Apodemus* using MEGA5 software (Tamura *et al.,* 2011). The best model of nucleotide evolution was determined using jmodeltest (Posada, 2008). The GTR+I+G model was determined based on the Akaike Information Criterion (Akaike, 1973). Tree reconstruction was conducted using MEGA5 software and bootstrap analysis were conducted with 1,000 replications. *Oryctolagus cuniculus* (AJ001588; Lagomorpha, Leporidae) was used as outgroup species.

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Table 1.2. List of Rodentia mitochondrial genomes

Order	Family	Species	Size	Accession Num.
Lagomorpha	Leporidae	*Oryctolagus cuniculus*	17,245	AJ001588
Rodentia	Anomaluridae	*Anomalurus sp.*	16,923	AM159537
	Caviidae	*Cavia porcellus*	16,801	AJ222767
	Cricetidae	*Cricetulus griseus*	16,284	DQ390542
	Cricetidae	*Eothenomys chinensis*	16,362	FJ483847
	Cricetidae	*Eothenomys regulus*	16,379	JN629046
	Cricetidae	*Mesocricetus auratus*	16,264	EU660218
	Cricetidae	*Microtus kikuchii*	16,312	AF348082
	Cricetidae	*Microtus levis*	16,283	DQ015676
	Cricetidae	*Proedromys sp.*	16,296	FJ463038
	Cricetidae	*Tscherskia triton*	16,488	EU031048
	Cricetidae	*Microtus fortis*	16,310	JF261174
	Dipodidae	*Jaculus jaculus*	16,546	AJ416890
	Gliridae	*Myoxus glis*	16,602	AJ001562
	Muridae	*Leggadina lakedownensis*	16,262	EU305668
	Muridae	*Mus musculus*	16,299	AY172335
	Muridae	*Mus terricolor*	16,310	EU352649
	Muridae	*Pseudomys chapmani*	16,249	EU305669
	Muridae	*Rattus exulans*	16,307	EU273710
	Muridae	*Rattus fuscipes*	16,301	GU570664
	Muridae	*Rattus leucopus*	16,297	GU570659
	Muridae	*Rattus norvegicus*	16,313	AY172581
	Muridae	*Rattus praetor*	16,293	EU273708
	Muridae	*Rattus rattus*	16,305	EU273707
	Muridae	*Rattus sordidus*	16,309	GU570665
	Muridae	*Rattus tanezumi*	16,306	EU273712
	Muridae	*Rattus tunneyi*	16,292	GU570662
	Muridae	*Rattus villosissimus*	16,303	GU570663
	Sciuridae	*Sciurus vulgaris*	16,507	AJ238588
	Spalacidae	*Spalax ehrenbergi*	16,408	AJ416891
	Thryonomyidae	*Thryonomys swinderianus*	16,626	AJ301644
	Muridae	*Apodemus agrarius*	16,260	This study
	Muridae	*Apodemus chejuensis*	16,261	This study
	Muridae	*Apodemus peninsulae*	16,266	This study

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1.3. RESULTS

1.3.1. Mitochondrial genomes of Korean *Apodemus*

The complete mt genomes of *Apodemus agrarius*, *A. chejuensis*, and *A. peninsulae* were determined to be 16,260, 16,261, and 16,266 bp long, respectively (Fig. 1.1 and Table 1.3-5), and have been deposited in the GenBank database (Accession Nos. HM034866, HM034867, and HQ660074, respectively). Like other vertebrate mt genomes, the *Apodemus* mt genomes contain 13 protein-coding genes, 22 tRNAs, 2 rDNAs, and a noncoding control region (Fig. 1.1).

1.3.2. Protein-coding genes

The mt genomes of *Apodemus agrarius* and *A. chejuensis* had protein-coding genes that use the most common initiation codon, ATG, and 2 unusual initiation codons: GTG and ATA (Table 1.3-5). *A. peninsulae* had an additional unusual ATC initiation codon in the *ND2* gene (Table 1.5).

Four termination codons were found in the *Apodemus agrarius*, *A. chejuensis*, and *A. peninsulae* mt protein-encoding genes: TAA, TAG, incomplete TA, and T (Table 1.3-5).

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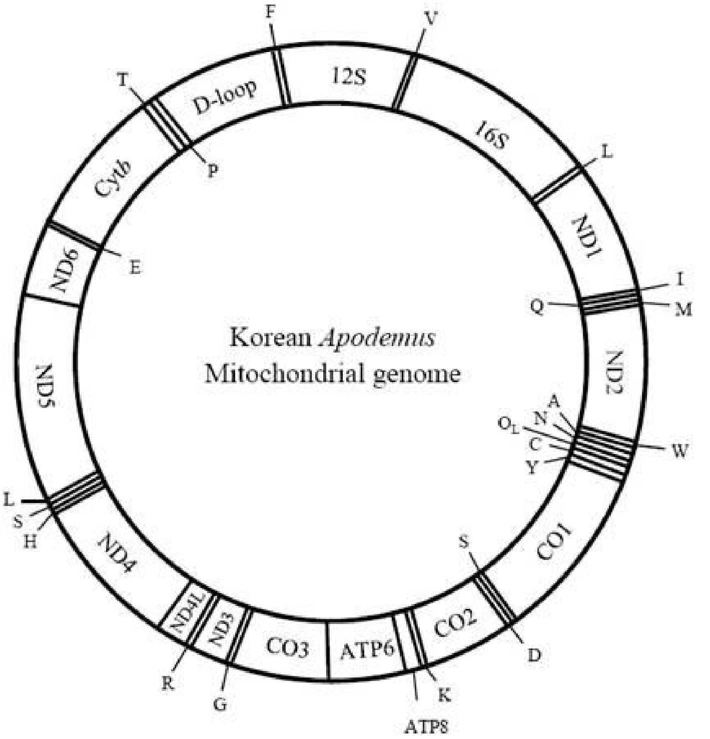

Figure 1.1. The mitochondrial genome structure of Korean *Apodemus*. The complete mt genome have 13 protein-coding genes, 22 tRNAs, 2 rDNAs, and control region. The mt gene order is identical to those of other mammalian mt genomes.

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Table 1.3. Location of feature in the mt genome of *A. agrarius*

Feature[a]	Position		Size (bp)	Codon	
	5’	3’		Initiaton	Termination
tRNA-Phe	1	67	67		
12S rRNA	68	1022	955		
tRNA-Val	1023	1091	69		
16S rRNA	1092	2663	1572		
tRNA-Leu$^{(UUR)}$	2664	2738	75		
ND1	2739	3695	957	GTG	T--
tRNA-Ile	3694	3762	69		
tRNA-Gln	3760	3834	75		
tRNA-Met	3835	3903	69		
ND2	3904	4941	1038	ATA	T--
tRNA-Trp	4940	5007	68		
tRNA-Ala	5009	5077	69		
tRNA-Asn	5079	5149	71		
O_L	5150	5180	31		
tRNA-Cys	5181	5248	68		
tRNA-Tyr	5249	5315	67		
CO1	5317	6861	1545	ATG	TAA
tRNA-Ser$^{(UCN)}$	6859	6927	69		
tRNA-Asp	6931	6999	69		
CO2	7000	7683	684	ATG	TAA
tRNA-Lys	7687	7750	64		
ATPase 8	7752	7955	204	ATG	TAA
ATPase 6	7913	8593	681	ATG	TAA
CO3	8593	9377	785	ATG	T--
tRNA-Gly	9377	9445	69		
ND3	9445	9792	348	ATA	TAA
tRNA-Arg	9794	9861	68		
ND4L	9864	10160	297	ATG	TAA
ND4	10154	11531	1378	ATG	T--
tRNA-His	11532	11599	68		
tRNA-Ser$^{(AGY)}$	11600	11658	59		
tRNA-Leu$^{(CUN)}$	11658	11729	72		
ND5	11729	13558	1830	ATA	TAA
ND6	13536	14054	519	ATG	TAA
tRNA-Glu	14055	14123	69		
CYTB	14127	15270	1144	ATG	T--
tRNA-Thr	15271	15339	69		
tRNA-Pro	15340	15406	67		
Control region	15407	16260	854		

[a] *ND1-6, NADH dehydrogenase subunit 1-6* gene; *CO1-3, cytochrome c oxidase subunit 1-3* gene; *ATPase 6* and *8*, *ATPase subunit 6* and *8* gene; *CYTB*, *cytochrome b* gene; O_L, L-strand replication origin; CR, control region.
Underlines indicate a gene encoded on the L-strand.

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Table 1.4. Location of feature in the mt genome of *A. chejuensis*

Feature^{a}	Position		Size (bp)	Codon	
	5’	3’		Initiaton	Termination
tRNA-Phe	1	67	67		
12S rRNA	68	1022	955		
tRNA-Val	1023	1091	69		
16S rRNA	1091	2663	1573		
tRNA-Leu$^{(UUR)}$	2664	2738	75		
ND1	2739	3695	957	GTG	T--
tRNA-Ile	3694	3762	69		
tRNA-Gln	3760	3830	71		
tRNA-Met	3835	3903	69		
ND2	3904	4941	1038	ATA	T--
tRNA-Trp	4940	5007	68		
tRNA-Ala	5009	5077	69		
tRNA-Asn	5079	5149	71		
O_L	5150	5180	31		
tRNA-Cys	5181	5248	68		
tRNA-Tyr	5249	5315	67		
CO1	5317	6861	1545	ATG	TAA
tRNA-Ser$^{(UCN)}$	6859	6927	69		
tRNA-Asp	6931	6998	68		
CO2	7000	7683	684	ATG	T--
tRNA-Lys	7687	7750	64		
ATPase 8	7752	7955	204	ATG	TAA
ATPase 6	7913	8593	681	ATG	TA-
CO3	8593	9377	785	ATG	T--
tRNA-Gly	9377	9444	68		
ND3	9445	9792	348	ATA	TAG
tRNA-Arg	9794	9861	68		
ND4L	9864	10160	297	ATG	TAA
ND4	10154	11531	1378	ATG	T--
tRNA-His	11532	11599	68		
tRNA-Ser$^{(AGY)}$	11600	11658	59		
tRNA-Leu$^{(CUN)}$	11658	11728	71		
ND5	11729	13558	1830	ATA	TAA
ND6	13536	14054	519	ATG	TAA
tRNA-Glu	14055	14123	69		
CYTB	14127	15270	1144	ATG	T--
tRNA-Thr	15271	15338	68		
tRNA-Pro	15339	15404	66		
Control region	15405	16261	857		

^{a}*ND1-6*, *NADH dehydrogenase subunit 1-6* gene; *CO1-3*, *cytochrome c oxidase subunit 1-3* gene; *ATPase 6* and *8*, *ATPase subunit 6* and *8* gene; *CYTB*, *cytochrome b* gene; O_L, L-strand replication origin; CR, control region.
Underlines indicate a gene encoded on the L-strand.

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Table 1.5. Location of feature in the mt genome of *A. peninsulae*

Feature[a]	Position		Size (bp)	Codon	
	5’	3’		Initiaton	Termination
tRNA-Phe	1	67	67		
12S rRNA	68	1023	956		
tRNA-Val	1024	1092	69		
16S rRNA	1093	2663	1571		
tRNA-Leu$^{(UUR)}$	2664	2738	75		
ND1	2739	3695	955	GTG	TAG
tRNA-Ile	3694	3762	69		
tRNA-Gln	3760	3830	71		
tRNA-Met	3834	3902	69		
ND2	3903	4940	1038	ATC	TAG
tRNA-Trp	4939	5006	68		
tRNA-Ala	5008	5076	69		
tRNA-Asn	5078	5148	71		
O_L	5149	5179	31		
tRNA-Cys	5180	5245	66		
tRNA-Tyr	5246	5312	67		
CO1	5314	6858	1545	ATG	TAA
tRNA-Ser$^{(UCN)}$	6856	6924	69		
tRNA-Asp	6928	6995	68		
CO2	6997	7680	684	ATG	TAG
tRNA-Lys	7684	7747	64		
ATPase 8	7749	7952	204	ATG	TAA
ATPase 6	7910	8590	681	ATG	TAA
CO3	8590	9374	785	ATG	TA-
tRNA-Gly	9374	9441	68		
ND3	9442	9789	348	ATA	TAA
tRNA-Arg	9791	9858	68		
ND4L	9861	10157	297	ATG	TAA
ND4	10151	11528	1378	ATG	T--
tRNA-His	11529	11595	67		
tRNA-Ser$^{(AGY)}$	11596	11654	59		
tRNA-Leu$^{(CUN)}$	11654	11724	71		
ND5	11725	13554	1830	ATA	TAA
ND6	13532	14050	519	ATG	TAA
tRNA-Glu	14051	14119	69		
CYTB	14123	15266	1144	ATG	T--
tRNA-Thr	15267	15333	67		
tRNA-Pro	15334	15400	67		
Control region	15401	16266	866		

[a] *ND1-6, NADH dehydrogenase subunit 1-6* gene; *CO1-3, cytochrome c oxidase subunit 1-3* gene; *ATPase 6* and *8, ATPase subunit 6* and *8* gene; *CYTB, cytochrome b* gene; O_L, L-strand replication origin; CR, control region.
Underlines indicate a gene encoded on the L-strand.

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Overall, the nucleotide frequencies of the analyzed mt protein-encoding genes were similar (Table 1.6). In Korean *Apodemus*, the nucleotide frequencies of *A. agrarius* and *A. chejuensis* were similar. However, those of *A. peninsulae* were different. The protein-coding genes of *A. peninsulae* had the greatest adenine and thymine content. In particular, *A. peninsulae* had the most thymine and adenine in the second and third position, respectively, in Korean *Apodemus*. Adenine frequency in the first position was relatively low but guanine in same position was much more frequent. In the second position, *A. peninsulae* had the most thymine. The third codon position in *A. peninsulae* was the most variable. Guanine frequency in the third position was lowest in *A. peninsulae*.

Codon usage based on mt protein-coding genes showed that the patterns of *A. agrarius* and *A. chejuensis* were similar, while those of *A. peninsulae* slightly differed (Table 1.7-9). With respect to the mt protein-coding genes, the most frequent codon was CUA for leucine (252 times and 254 times, respectively) in *A. agrarius* and *A. chejuensis* and AUU for isoleucine (277 times) in *A. peninsulae* whereas the most rare codons were ACG for threonine and CGG for arginine in *A. agrarius* (2 times, respectively) and UCG for serine and AAG for lysine in *A. chejuensis* (2 times, respectively) and CGG for arginine (0 time) in *A. peninsulae*. Of all the codon groups that encode a single amino acid, leucine was used most frequently (600 times/15.8%, 598 times/15.7%, and 590 times/15.5% in *A. agrarius*, *A. chejuensis*, and *A. peninsulae*, respectively). Conversely, the least used amino acid was the cysteine group [29 times/0.76% in *A. agrarius* and *A. chejuensis,* and 28 times/0.74% in *A. peninsulae*].

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Table 1.6. Nucleotide frequencies of 13 protein-coding genes

Position Num.	*A. agrarius*				*A. chejuensis*				*A. peninsulae*			
	T	C	A	G	T	C	A	G	T	C	A	G
1st	28.4	24.0	42.9	4.7	28.5	23.8	42.9	4.8	24.8	22.6	32.5	20.1
2nd	24.4	23.9	31.7	20.0	24.2	24.0	31.9	19.9	42.3	25.7	20.0	12.0
3rd	41.9	25.4	20.7	12.0	41.9	25.3	20.8	12.0	30.0	21.3	45.5	3.2
Total	31.5	24.5	31.8	12.2	31.5	24.4	31.9	12.2	32.3	23.2	32.7	11.8

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Table 1.7. Codon usage based on 13 protein-coding genes of *A. agrarius*

AA[a]	Codon	N[b]	AA	Codon	N	AA	Codon	N	AA	Codon	N
Phe	UUU	148	Ser	UCU	51	Tyr	UAU	74	Cys	UGU	9
	UUC	97		UCC	54		UAC	57		UGC	20
Leu	UUA	128		UCA	136	Stop	UAA	11	Trp	UGA	93
	UUG	9		UCG	3		UAG	2		UGG	13
	CUU	110	Pro	CCU	43	His	CAU	42	Arg	CGU	10
	CUC	80		CCC	30		CAC	54		CGC	7
	CUA	252		CCA	121	Gln	CAA	78		CGA	44
	CUG	21		CCG	5		CAG	5		CGG	2
Ile	AUU	220	Thr	ACU	80	Asn	AAU	81	Ser	AGU	20
	AUC	148		ACC	61		AAC	88		AGC	35
Met	AUA	197		ACA	159	Lys	AAA	94	Stop	AGA	0
	AUG	35		ACG	2		AAG	3		AGG	0
Val	GUU	50	Ala	GCU	69	Asp	GAU	31	Gly	GGU	43
	GUC	27		GCC	65		GAC	38		GGC	41
	GUA	84		GCA	93	Glu	GAA	78		GGA	101
	GUG	8		GCG	4		GAG	15		GGG	26

[a] Amino acid

[b] Frequency of codon

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Table 1.8. Codon usage based on 13 protein-coding genes of *A. chejuensis*

AA[a]	Codon	N[b]	AA	Codon	N	AA	Codon	N	AA	Codon	N
Phe	UUU	149	Ser	UCU	49	Tyr	UAU	80	Cys	UGU	9
	UUC	97		UCC	52		UAC	51		UGC	20
Leu	UUA	120		UCA	139	Stop	UAA	12	Trp	UGA	96
	UUG	13		UCG	2		UAG	1		UGG	8
	CUU	106	Pro	CCU	44	His	CAU	44	Arg	CGU	11
	CUC	82		CCC	29		CAC	52		CGC	6
	CUA	254		CCA	123	Gln	CAA	78		CGA	41
	CUG	23		CCG	4		CAG	5		CGG	6
Ile	AUU	225	Thr	ACU	83	Asn	AAU	78	Ser	AGU	20
	AUC	148		ACC	58		AAC	89		AGC	37
Met	AUA	199		ACA	156	Lys	AAA	97	Stop	AGA	0
	AUG	33		ACG	4		AAG	2		AGG	0
Val	GUU	46	Ala	GCU	66	Asp	GAU	32	Gly	GGU	42
	GUC	28		GCC	67		GAC	39		GGC	39
	GUA	86		GCA	91	Glu	GAA	73		GGA	104
	GUG	8		GCG	5		GAG	20		GGG	24

[a] Amino acid

[b] Frequency of codon

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Table 1.9. Codon usage based on 13 protein-coding genes of *A. peninsulae*

AA[a]	Codon	N[b]	AA	Codon	N	AA	Codon	N	AA	Codon	N
Phe	UUU	144	Ser	UCU	62	Tyr	UAU	76	Cys	UGU	10
	UUC	97		UCC	40		UAC	57		UGC	18
Leu	UUA	167		UCA	143	Stop	UAA	12	Trp	UGA	100
	UUG	11		UCG	1		UAG	1		UGG	4
	CUU	111	Pro	CCU	43	His	CAU	50	Arg	CGU	9
	CUC	57		CCC	25		CAC	50		CGC	12
	CUA	228		CCA	131	Gln	CAA	82		CGA	44
	CUG	16		CCG	2		CAG	1		CGG	0
Ile	AUU	277	Thr	ACU	78	Asn	AAU	68	Ser	AGU	17
	AUC	96		ACC	66		AAC	94		AGC	33
Met	AUA	206		ACA	161	Lys	AAA	95	Stop	AGA	0
	AUG	33		ACG	3		AAG	8		AGG	0
Val	GUU	45	Ala	GCU	66	Asp	GAU	39	Gly	GGU	42
	GUC	20		GCC	63		GAC	36		GGC	43
	GUA	86		GCA	90	Glu	GAA	81		GGA	111
	GUG	15		GCG	3		GAG	11		GGG	15

[a] Amino acid

[b] Frequency of codon

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1.3.3. rRNA and tRNA encoding genes

The *12S rRNA* gene was 955, 955, and 956 bp long in *Apodemus agrarius*, *A. chejuensis*, and *A. peninsulae*, respectively, and the *16S rRNA* gene was 1,572, 1,573, and 1,571 bp long, respectively. As in other vertebrates, including Rodentia, these genes were located between the *tRNA-Phe* and *tRNA-Leu*$^{(UUR)}$ genes and are separated by the *tRNA-Val* gene (Table 1.3-5).

The mt genome of Korean *Apodemus* contained 22 tRNA genes dispersed between rDNAs and protein-coding genes, as in other rodents (Fig. 1.2-4 and Table 1.3-5). I identified 2 forms of *tRNA-Leu* (UUR and CUN) and *tRNA-Ser* (UCN and AGY; Fig. 1.2-4 and Table 1.3-5). The 3 tRNA clusters, IQM (isoleucine, glutamine, and methionine), WANCY (tryptophan, alanine, asparagine, cysteine, and tyrosine), and HSL (histidine, serine, and leucine), were conserved in Korean *Apodemus*, as in the typical Rodentia mt genome. The putative structure of *tRNA-Ser*$^{(AGY)}$ was compared to the mt tRNAs of Rodentia. The abnormal structure of *tRNA-Ser*$^{(AGY)}$ was identified in the dihydrouridine (DHU) arm in the mt genome sequences of 3 Korean *Apodemus* (Fig. 1.5).

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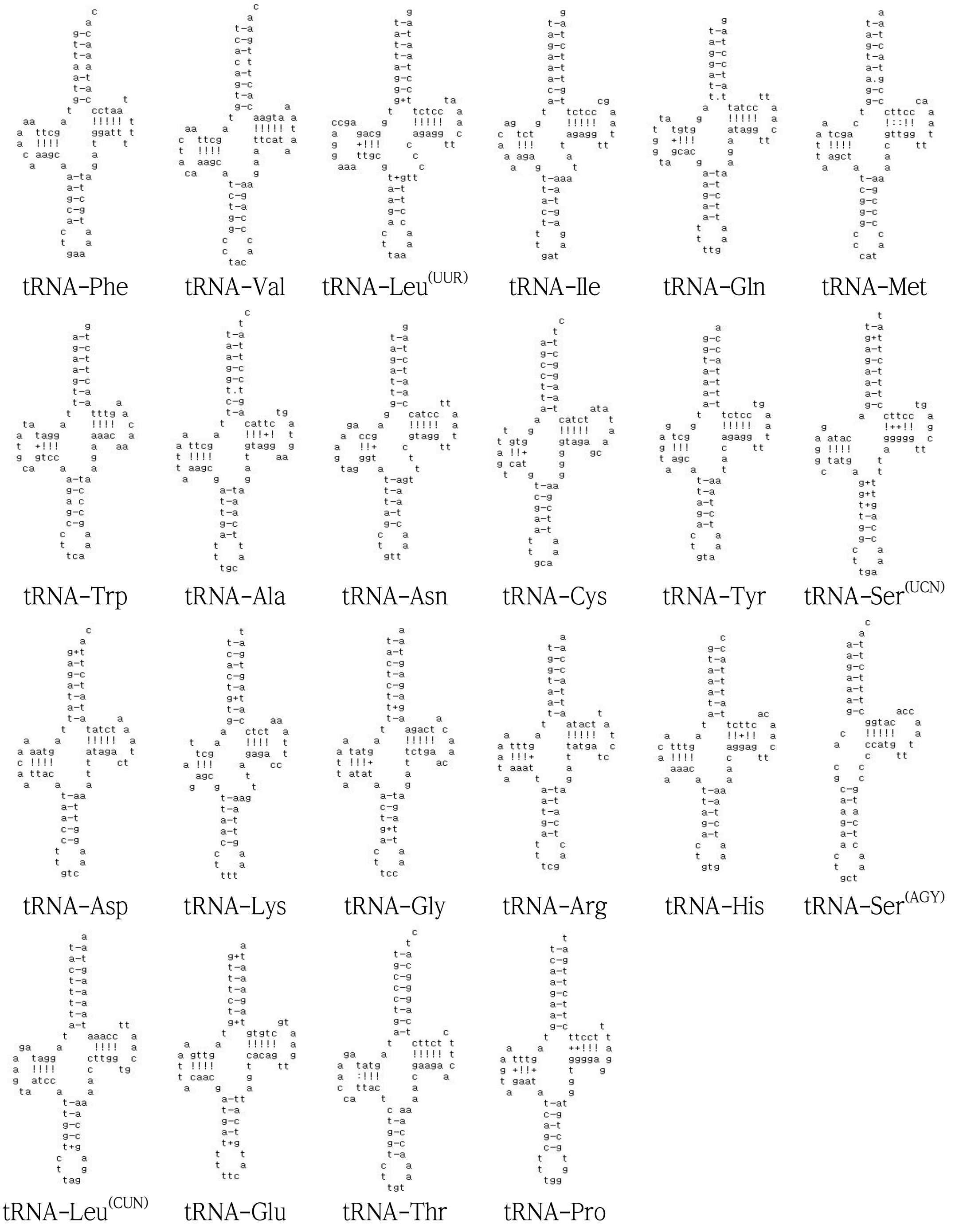

tRNA-Phe tRNA-Val tRNA-Leu$^{(UUR)}$ tRNA-Ile tRNA-Gln tRNA-Met

tRNA-Trp tRNA-Ala tRNA-Asn tRNA-Cys tRNA-Tyr tRNA-Ser$^{(UCN)}$

tRNA-Asp tRNA-Lys tRNA-Gly tRNA-Arg tRNA-His tRNA-Ser$^{(AGY)}$

tRNA-Leu$^{(CUN)}$ tRNA-Glu tRNA-Thr tRNA-Pro

Figure 1.2. The putative structures of the 22 tRNAs of *Apodemus agrarius*, inferred from nucleotide sequences of the tRNA genes. The tRNAs are labeled with the abbreviations of their corresponding amino acids.

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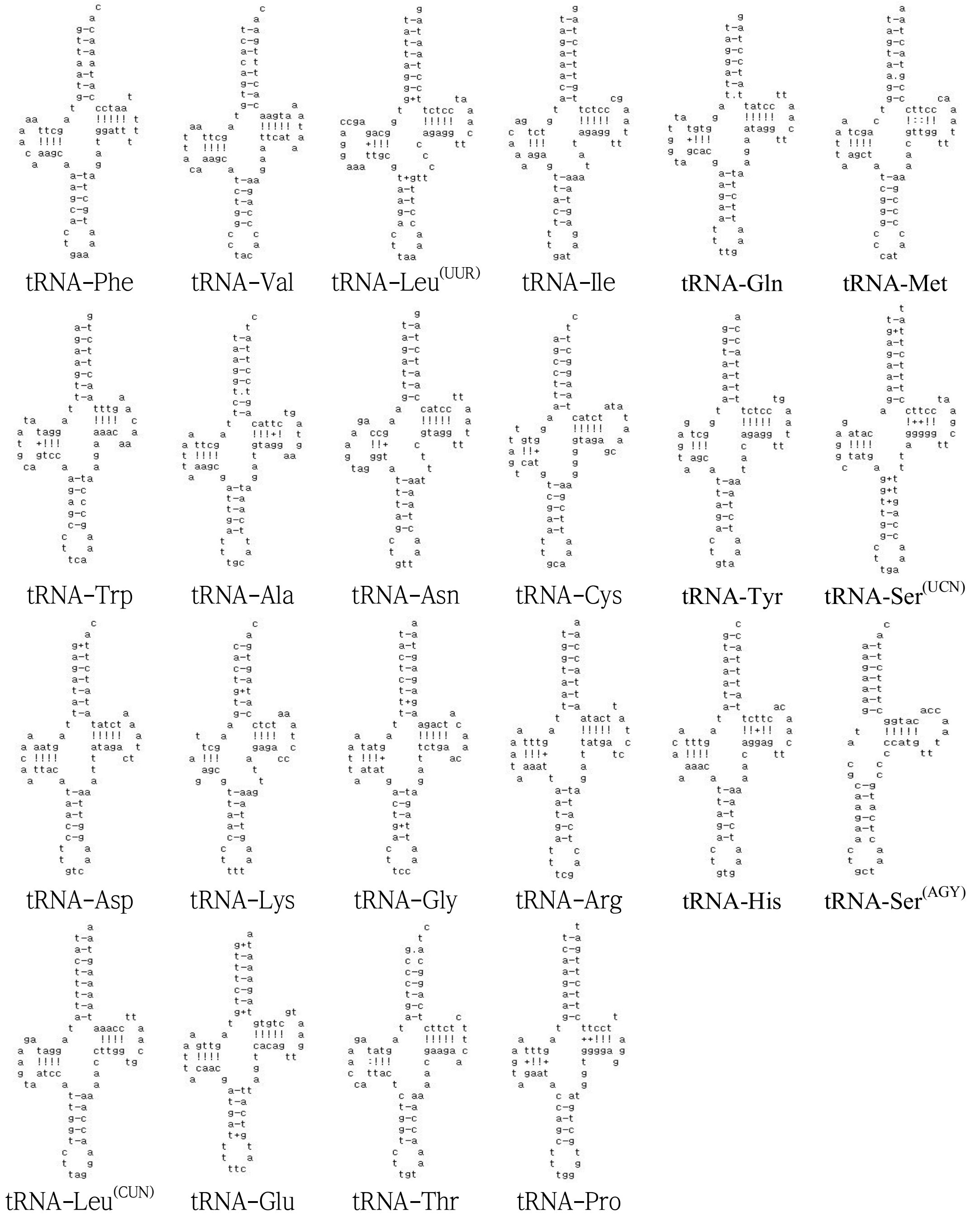
tRNA-Phe tRNA-Val tRNA-Leu$^{(UUR)}$ tRNA-Ile tRNA-Gln tRNA-Met

tRNA-Trp tRNA-Ala tRNA-Asn tRNA-Cys tRNA-Tyr tRNA-Ser$^{(UCN)}$

tRNA-Asp tRNA-Lys tRNA-Gly tRNA-Arg tRNA-His tRNA-Ser$^{(AGY)}$

tRNA-Leu$^{(CUN)}$ tRNA-Glu tRNA-Thr tRNA-Pro

Figure 1.3. The putative structures of the 22 tRNAs of *Apodemus chejuensis*, inferred from nucleotide sequences of the tRNA genes. The tRNAs are labeled with the abbreviations of their corresponding amino acids.

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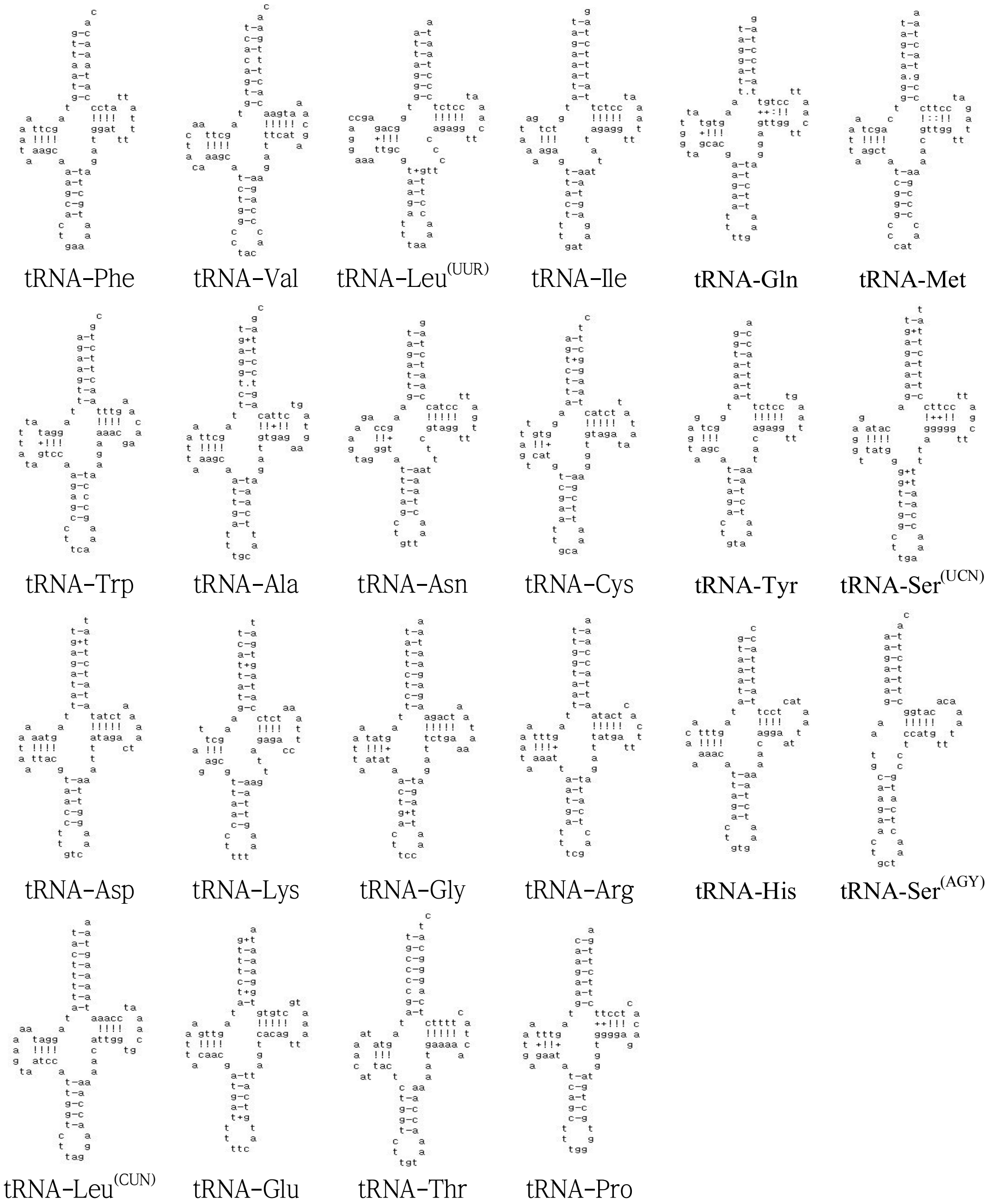

Figure 1.4. The putative structures of the 22 tRNAs of *Apodemus peninsulae*, inferred from nucleotide sequences of the tRNA genes. The tRNAs are labeled with the abbreviations of their corresponding amino acids.

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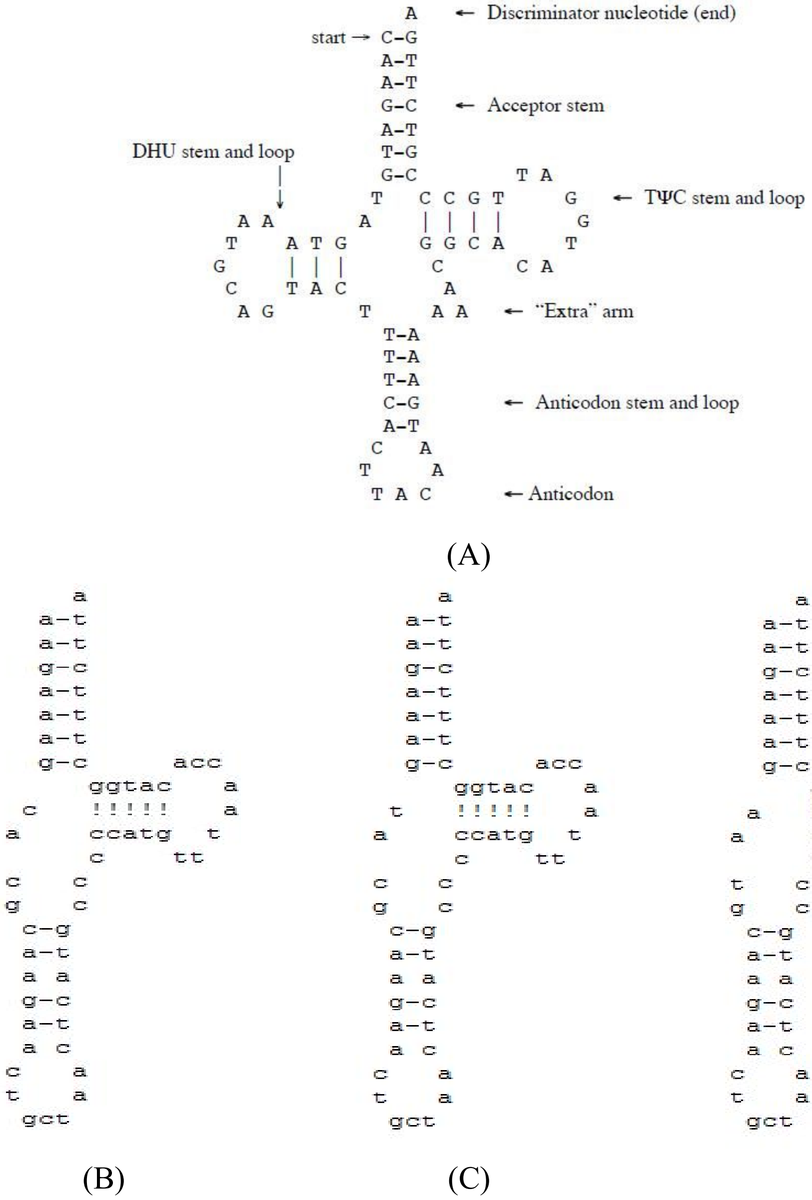

Figure 1.5. The putative structure of the tRNA-Ser in Korean *Apodemus*. The abnormal structure of *tRNA-Ser*$^{(AGY)}$ was identified in DHU arm. (A) shows secondary structure of general mt tRNAs (Wyman and Boore, 2003). General mt tRNAs have normal DHU arm with stem-loop structure. (B), (C), and (D) has abnormal structures with four nucleotides in DHU arm of mt *tRNA-Ser*$^{(AGY)}$ of *A. agrarius*, *A. chejuensis*, and *A. peninsulae*, respectively.

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1.3.4. Control region

Generally, the mt genomes of mammals have 2 noncoding regions: O_L and CR, which is also called the D-loop. The O_L of Korean *Apodemus* was 31 bp long and was located between *tRNA-Asn* and *tRNA-Cys* (Table 1.3-5), consistent with other mammals. The stem‐loop region, conserved motif (5′-TAAGG-3′), and the L-strand replication initiation site (GGC) are presented in Fig. 1.6.

The CR of *A. agrarius*, *A. chejuensis*, and *A. peninsulae* spanned 854 bp, 857 bp, and 866 bp, respectively, and was positioned between the *tRNA-Pro* and *tRNA-Phe* genes (Table 1.3-5). The CR contains several conserved sequences (Fig. 1.7): the termination-associated sequence (TAS) and conserved sequence blocks (CSBs). These elements show some sequence variation but are generally conserved among Rodentia.

1.3.5. Phylogenetic relationships

Generally, the ML tree shows that phylogenetic relationships are highly supported by sequences of 13 protein-coding genes of Rodentia mt (Fig. 1.8). Muridae was grouped with Cricetidae as sister taxon. *Rattus* was divided into distinct two clades, and Korean *Apodemus* and *Mus* derived from common ancestors. The branch support value of *Anomalurus+Cavia+Thryonomys* was lower than 50%. *Microtus levis* and *Proedromys* sp. was grouped with very low support value (10%). The monophyly of Muroidea (Muridae, Cricetidae, and Spalacidae) was well supported with 100% bootstrap value.

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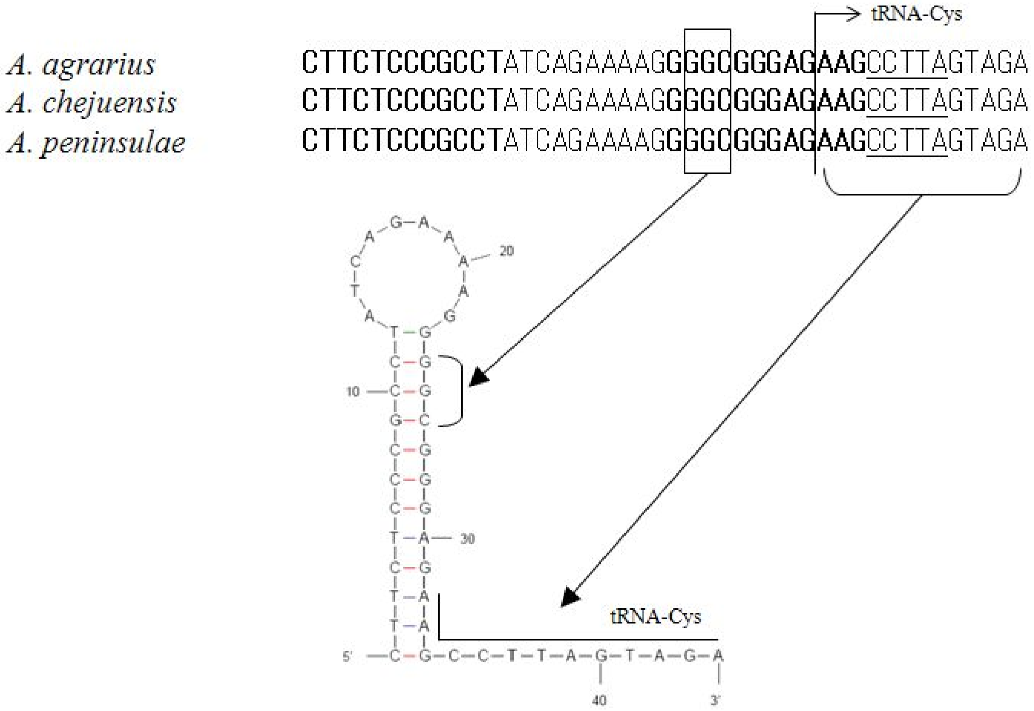

Figure 1.6. Common features of L-strand replication origin of Korean *Apodemus*. The O_L sequences of Korean *Apodemus* mt DNA was identical. The O_L has the potential to form a stable stem-loop structure. The initiation site "GGC' for L-strand replication is located on stem region. Bold and underlines indicate stem region and vertebrate conserved motif, respectively.

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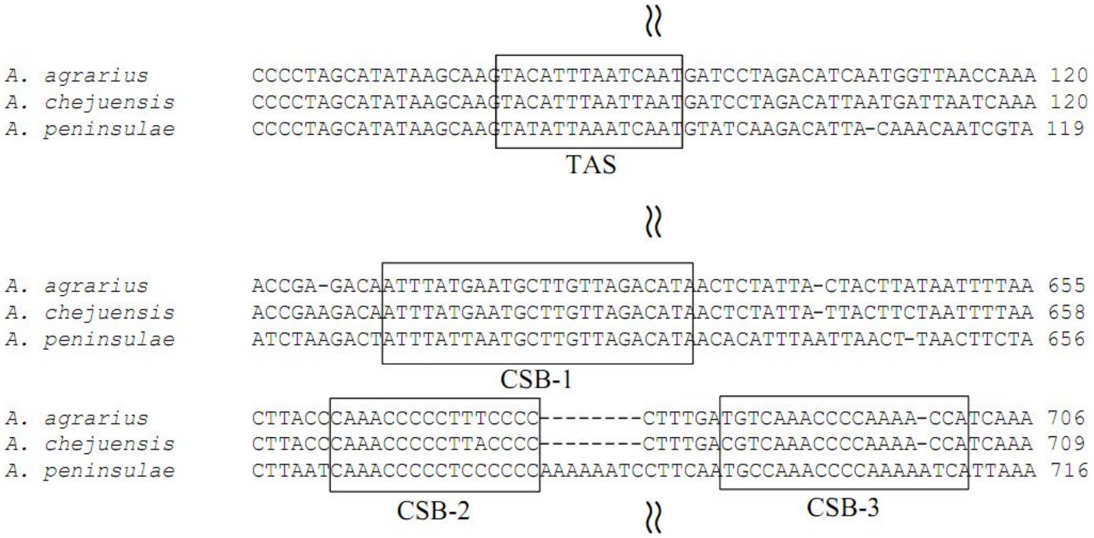

```
A. agrarius       CCCCTAGCATATAAGCAAGTACATTTAATCAATGATCCTAGACATCAATGGTTAACCAAA 120
A. chejuensis     CCCCTAGCATATAAGCAAGTACATTTAATTAATGATCCTAGACATTAATGATTAATCAAA 120
A. peninsulae     CCCCTAGCATATAAGCAAGTATATTAAATCAATGTATCAAGACATTA-CAAACAATCGTA 119

A. agrarius       ACCGA-GACAATTTATGAATGCTTGTTAGACATAACTCTATTA-CTACTTATAATTTTAA 655
A. chejuensis     ACCGAAGACAATTTATGAATGCTTGTTAGACATAACTCTATTA-TTACTTCTAATTTTAA 658
A. peninsulae     ATCTAAGACTATTTATTAATGCTTGTTAGACATAACACATTTAATTAACT-TAACTTCTA 656

A. agrarius       CTTACCCAAACCCCCTTTCCCC--------CTTTGATGTCAAACCCCAAAA-CCATCAAA 706
A. chejuensis     CTTACCCAAACCCCCTTACCCC--------CTTTGACGTCAAACCCCAAAA-CCATCAAA 709
A. peninsulae     CTTAATCAAACCCCCTCCCCCCAAAAAATCCTTCAATGCCAAACCCCAAAAATCATTAAA 716
```

Figure 1.7. Conserved sequences of the mitochondrial control region of Korean *Apodemus*. TAS and CSB-1, CSB-2, and CSB-3, which occur near the 3′ and 5' terminus, respectively. Sequences of TAS and CSB-1-3 were slightly different among control region of Korean *Apodemus*. Omitted sequence regions were marked as double waved lines.

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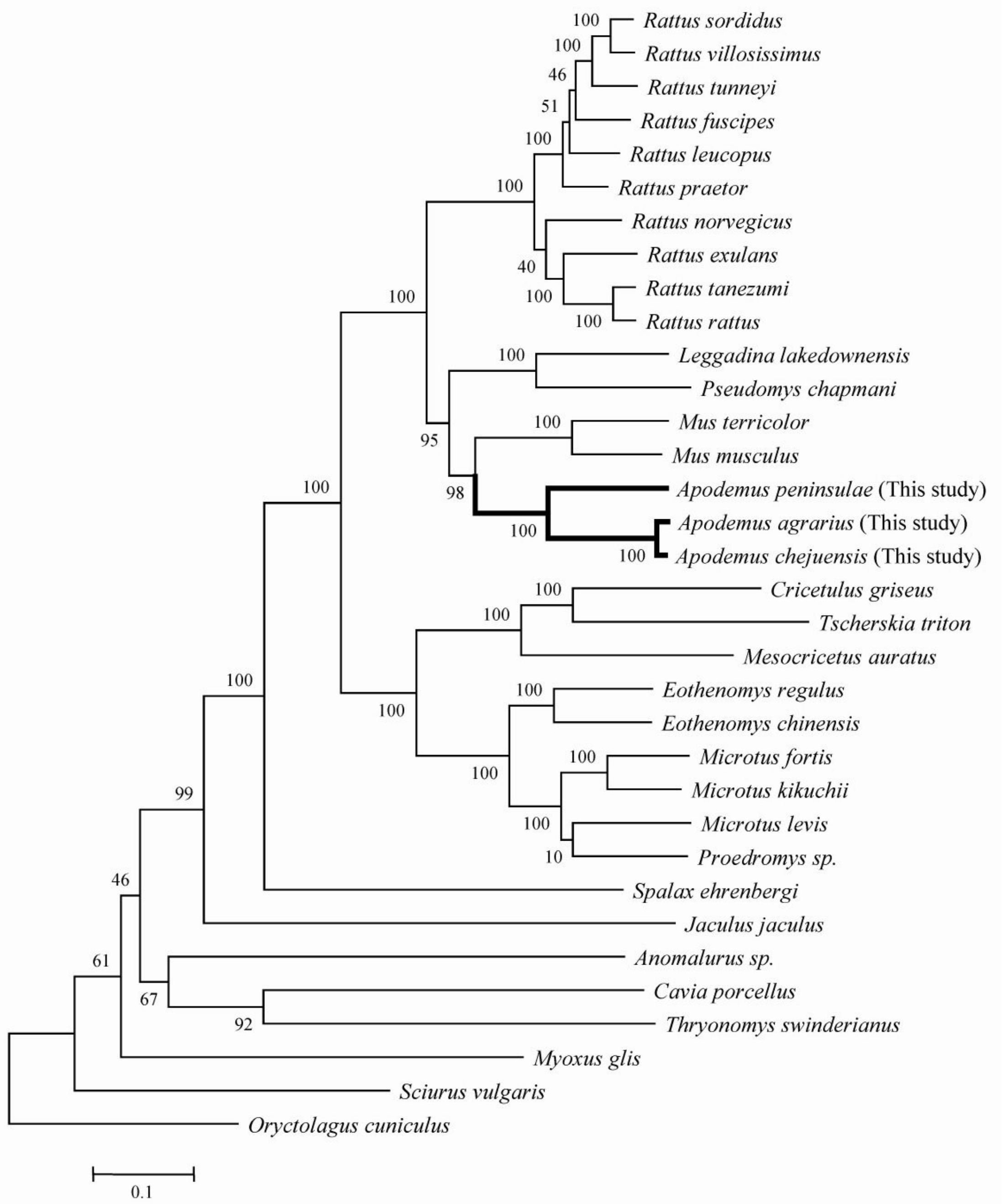

Figure 1.8. Phylogenetic tree of Korean *Apodemus*. The ML tree (lnL = −168970.343) was reconstructed using GTR+I+G model. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) are shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site.

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1.4. DISCUSSION

1.4.1. Comparative analysis of mitochondrial genome sequences

Korean *Apodemus* contain relatively small mt genomes in the order Rodentia, according to the GenBank database (Table 1.2). The higher animals exhibit significantly less variation in mt genome size and tend to have smaller mt genomes than lower animals (Rand, 1993). Rand (1993) thought these patterns are due to differential metabolic rates and reduced mutation pressures. This theory would suggest that Korean *Apodemus* spp. might have evolved late in the evolutionary history of Rodentia.

General features of mt genome of the Korean *Apodemus* are similar to those of other Rodentia. The gene rearrangements of mt genomes were reported in various vertebrates such as marsupials (Pääbo *et al.,* 1991), birds (Bensch and Härlid. 2000), reptiles (Yan *et al.,* 2008), fishes (Mabuchi *et al.,* 2004), and amphibians (Mueller and Boore, 2005). However, gene rearrangements have not been identified in mt genomes of Rodentia, including *Apodemus* spp. This indicates that mt genomes of Rodentia are very stable and highly conserved.

The mt protein-coding genes of Korean *Apodemus* used various initiation and termination codons. The mt protein-coding genes of *A. agrarius* and *A. chejuensis* used 3 types of initiation codons (ATG, ATA, and GTG) and those of *A. peninsulae* used 4 types of initiation codons (ATG, ATA, ATC and GTG). ATG is the most common initiation codon, but various vertebrate mt genes use non-canonical starts (Mouchaty *et al.,* 2001; Mabuchi *et al.,* 2004; Mueller and Boore, 2005; Horner *et al.,* 2007). These alternative

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initiation codons are translated as methionine or formylmethionine (Touriol *et al.,* 2003). Five types of initiation codons (ATG, GTG, ATC, ATA, and ATT) have been identified in the Rodentia. ATT is not used in Korean *Apodemus*.

The mt protein-coding genes of *A. agrarius*, *A. chejuensis*, and *A. peninsulae* used 2 (TAA and T), 4 (TAA, TAG, TA, and T), and 3 (TAA, TAG, and T) types of termination codons, respectively. Korean *Apodemus* mt genes also used incomplete termination codons such as TA and T, as occurs in other vertebrates (Oh *et al.,* 2007a; 2007b; Yan *et al.,* 2008; Oh *et al.,* 2010). These incomplete termination codons are completed via post-transcriptional polyadenylation (Ojala *et al.,* 1981).

Overall, the nucleotide frequencies of the analyzed mt protein-coding genes were slightly different in Korean *Apodemus*. Especially, guanine frequency at the first codon position in *A. peninsulae* mt was remarkably higher than in *A. agrarius* and *A. chejuensis*, while guanine frequency at the third codon position of *A. peninsulae* mt was much lower. The relatively low frequencies of guanine at the first codon position of *A. agrarius* and *A. chejuensis* have not been reported in Muridae. For instance, guanine at the first codon position of *Rattus norvegicus* mt genes were relatively more frequent at 19% (Gadaleta *et al.,* 1989). In the protein coding genes, the proportion of guanine at the third codon position is relatively low, as previously reported (Reyes *et al.,* 1998; Inoue *et al.,* 2000; Bayona-Bafaluy *et al.,* 2003). The variation in base composition at the 3 codon positions is related to gene expressivity (Gutiérrez *et al.,* 1996). Accordingly, the differential nucleotide preference for codon position may affect mt gene expression across Korean *Apodemus*.

The codon usage pattern was similar to those of other rodents (Lin *et al.,* 2002; Horner *et al.,* 2007; Partridge *et al.,* 2007). Codon usage also might be related to translation of mt genes. Jia and Higgs (2008) discovered very little evidence for translational accuracy selection in mt genes. They suggested that the selection for translational efficiency might lead to codon preferences.

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Moreover, Knight *et al.* (2001) suggested low codon frequencies can be related to codon reassignment, and highly expressed genes have a strong preference for a subset of codons, while low-expression genes have a more uniform pattern of codon usage (Ikemura, 1981; Gouy and Gautier, 1982). Therefore, some frequently used codons such as CUA (*tRNA-Leu*), AUC (*tRNA-Ile*), AUA (*tRNA-Met*), etc., of Korean *Apodemus* mt may be associated with highly expressed genes while infrequently used codons like UCG (*tRNA-Ser*), ACG (*tRNA-Thr*), CGG (*tRNA-Arg*), etc., might be related to rarely expressed genes.

The mt genomes of Korean *Apodemus* contain 22 tRNA genes interspersed between rRNAs and protein-coding genes. The general features of the mt tRNA genes were identical to those found in other rodents (Lin *et al.,* 2002; Horner *et al.,* 2007; Partridge *et al.,* 2007). The tRNA genes ranged from 59 to 75 nucleotides.

The *tRNA-Ser*$^{(AGY)}$ found in the mt genomes of Korean *Apodemus* had no discernible DHU stem, similar to other rodents (Gadaleta *et al.,* 1989; Horner *et al.,* 2007; Partridge *et al.,* 2007). The *tRNA-Ser*$^{(AGY)}$ lacking the DHU stem works in the mt translation system but has low translational activity in an *in vitro* translation system of bovine mitochondria (Hanada *et al.,* 2001). Accordingly, *tRNA-Ser*$^{(AGY)}$ of Korean *Apodemus* also might work with some molecular disadvantages on ribosomes in the mt translation system.

The O_L sequence has the potential to form a stable stem - loop structure, and a conserved motif (5′-TAAGG-3′) is located in the base of the stem within *tRNA-Cys*. This motif has been reported to exhibit some sequence variation in vertebrates such as *Lialis* (5′-ACCGG-3′), *Varanus* (5′-CCCTG-3′), *Bipes* (5′-GCCAG-3′) (Macey *et al.,* 1997), *Halichoeres* (5′-GCCGG-3′ Oh *et al.,* 2008), and *Hynobius* (5′-TCCGG-3′ Oh *et al.,* 2007a). The pentanucleotide motif is conserved among vertebrates (Noack *et al.,* 1996). This sequence may play an important role in *in vitro* replication of

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the L-strand (Hixson *et al.,* 1986). The O_L of Korean *Apodemus* mt contained an A-rich region in the loop. Other rodents are not A-rich or have only a single A in the loop in *Jaculus jaculus* (AJ416890) and *Mus musculus* (AY172335). These dissimilarities may result in slight differences in the structural recognition efficiency of mt DNA primase (Wong and Clayton, 1985; Hixson *et al.,* 1986). In addition, the stem region of O_L has the initiation site (GGC) for L-strand replication (Brennicke and Clayton, 1981), which was identical in all Korean *Apodemus*.

Within the CR, several conserved features were found such as TAS and CSB-1-3. The TAS element was identified upstream from the 3′ end of the control region in mammals (Doda *et al.,* 1981; Mackay *et al.,* 1986). This is associated with the termination of D-loop strand synthesis (Broughton *et al.,* 2001). The TAS elements slightly differed between *A. agrarius*, *A. chejuensis*, and *A. peninsulae*. The CSB sequences were identical and/or slightly different. The CSB sequences are associated with mt DNA replication and transcription (Clayton, 1991; Shadel and Clayton, 1997). Accordingly, replication and/or transcription efficiency might differ between Korean *Apodemus* spp.

1.4.2. Phylogenetic relationships of Korean *Apodemus*

The ML analysis placed *Sciurus* and *Myoxus* at the base of the phylogenetic tree of rodents showing similar to the phylogenetic tree of major rodent clades inferred from six nuclear genes (Blanga-Kanfi *et al.,* 2009). The result showed that major rodent clades comprised a squirrel-related clade, a mouse-related clade, and Ctenohystrica suggested that the basal position of a squirrel-related clade might be the most suitable for rodent evolutional scenario (Blanga-Kanfi *et al.,* 2009).

Rattus consisted of two distinct clades with 100% bootstrap support value,

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which phylogeny corresponded to previous study (Robins *et al.,* 2008; Robins *et al.,* 2010). Robins *et al.* (2008) suggested that the divergence between *Rattus* and *Mus* was occurred at about 12 Mya, and the deepest divergence within *Rattus* at 3.5 Mya, however subsequent research using 16 mt genomes of *Rattus* proposed the most recent common ancestor of *Rattus* diverged at about 2.7 Mya (Robins *et al.,* 2010). The phylogenetic relationships among *Rattus* spp. is very complex so that ML analysis using mt genome sequences of *Rattus* could not fully resolved their relationships.

The phylogeny of two native Australian rodents, *Leggadina lakedownensis* and *Pseudomys chapmani* showed that these two species related to *Mus* as a sister group (Nilsson *et al.,* 2010). However, the phylogenetic analysis including *Apodemus* showed that *Mus* was the closest related to *Apodemus* (Fig. 1.8). The closed relationships between *Mus* and *Apodemus* was reported in previous researches (Suzuki *et al.,* 2000; Steppan *et al.,* 2005), however, those studies contained just a few species of Muridae.

To date, the mt genome sequences of Rodentia were reported only 33 species (37 mt genomes including below subspecies). Accordingly, the phylogenetic analysis of Rodentia using mt genome sequences could not clarify the their relationships. However, the sequence data of single gene have accumulated via continued efforts to explain the phylogenetic relationships of rodents using nuclear and mt gene sequences. Especially, DNA barcoding project contributed to accumulate DNA sequences of mt gene such as *CO1* and *CYTB*. Accordingly, mt *CO1* and/or *CYTB* gene sequences might be very useful for rodent phylogeny and species identification (Robins *et al.,* 2010).

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Chapter 2

Possible historical migration routes of *Apodemus chejuensis*

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2.1 INTRODUCTION

The genus *Apodemus* contains at least 20 species (Musser and Carleton, 2005), including several of the most common small rodent species, and is widely distributed in the Palearctic region.

The striped field mouse *A. agrarius* is distributed throughout nearly the entire Korean Peninsula and is the most common rodent species in Korea; another striped field mouse, *A. chejuensis*, is found only on Jeju Island off the southern coast of the Korean Peninsula (Won and Smith, 1999; Yoon *et al.,* 2004a). Generally, *A. agrarius* inhabits rural flat lands, rivers, and agricultural farmlands. They breed 3 - 4 times a year and have 2 - 8 offspring per litter (Yoon *et al.,* 1997). They eat seeds of rice, fruits, and grasses (Kang, 1971). *A. agrarius* are known to be a vector of the fatal epidemic hemorrhagic fever and tsutsugamushi disease (Lee and Lee, 1976; Lee *et al.,* 1991). The Jeju Striped Field mouse, *A. chejuensis*, is often found near bush and mountainous area populated by shrubbery. They are distributed from the coastal region to the high-altitude region of Mt. Halla. They breed 3 - 4 times per year and usually have 4 - 5 offspring per litter. Similar to *A. agrarius*, they eat rice, fruits, and grass plants.

Although Jones and Johnson (1965) originally classified *A. chejuensis* as one (*A. agrarius chejuensis*) of the 4 subspecies of *A. agrarius*, subsequent molecular studies suggested that *A. chejuensis* is a distinct species (Han *et al.,* 1996; Koh *et al.,* 2000). The ability of offspring to hang to the mother's papilla, known as tenacious nipple attachment, is observed only in *A. chejuensis* (Oh and Mori, 1998b); the results of crossbreeding experiments led to the conclusion that *A. chejuensis* are separate biological species (Oh and Mori, 1998a). However, researchers are still performing molecular genetic

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studies of *A. agrarius* and *A. chejuensis* (Koh *et al.,* 2000; Yoon *et al.,* 2004b), and the taxonomic status of *A. chejuensis* still remains a matter of debate (Musser and Carleton, 2005).

Molecular evolutionary and phylogenetic studies have been conducted by several researchers focused on Korean *Apodemus*. Koh and Yoo (1992) analyzed mitochondrial (mt) DNA polymorphisms of *A. agrarius* and *A. chejuensis* by using 8 restriction enzymes. Thirty-one fragments were recognized and 15 clones were identified in 15 specimens of *A. a. coreae* and 6 specimens of *A. a. chejuensis*. Thus, *A. agrarius* were grouped into 4 major subgroups, but the taxonomic status of the subgroup remained unclear. Koh and Yoo (1992) suggested that the *A. chejuensis* specimens are indicative of a distinct species. In 1996, Han *et al.* also conducted restriction fragment analysis by using 11 restriction enzymes with nuclear ribosomal RNA spacers and mt DNA and suggested that geographic conditions may preserve various mtDNA haplotypes. Since the 2000s, molecular studies of DNA sequences have been used to establish the biogeographic, phylogenetic, and evolutionary status of Korean *Apodemus*. The analysis of mt *cytochrome b* (*CYTB*) sequences of *A. agrarius* and *A. chejuensis*. from the Korean Peninsula, southern coastal islets, and Jeju Island showed significant genetic structuring by geographical area and suggested that the hypothesized oldest haplotypes were obtained by the Jeju population and *A. agrarius* might be derived from *A. chejuensis* (Yoon *et al.,* 2004b).

Suzuki *et al.* (2008) suggested that the European lineage is a likely descendant of the Asian lineage and some genetic elements from Asia contributed to the mt DNA found in Europe. Phylogenetic analyses of mt and nuclear gene sequences indicated that *A. agrarius* and *A. chevrieri* are the most closely related sister species (Suzuki *et al.,* 2003; Liu *et al.,* 2004). Moreover, *A. agrarius* diverged from *A. chevrieri* about 2.68 million years ago (Mya), during the first glacial age of the Quaternary (Liu *et al.,* 2004). The

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most reasonable theory of the origin of Asian *Apodemus* was suggested by Xia (1984). He proposed that Asian *Apodemus* occurred in the Hengduan Mountain region. This region contains extreme topographic and climatic complexity (Zang, 2002) that led to species differentiation during the glacial period of the Quaternary (Liu *et al.,* 2004). If the ancestor of *A. agrarius* inhabitants in the Korean Peninsula originated from the Hengduan Mountains, they may have moved into the peninsula or the North Korea via the Yellow Sea basin during the glacial age (Fig. 2.1).

The mt *CYTB* gene is commonly located between 2 transfer RNA (tRNA) genes, *tRNA-Glu* and *tRNA-Thr*, in the mammalian mt genome. This gene is generally used in as a phylogenetic marker in vertebrate population genetics and phylogenetic inferences (Iwasa *et al.,* 2000; Koh *et al.,* 2001; Hodgkinson *et al.,* 2003; Yoon *et al.,* 2004b). The *CYTB* gene contains both conserved and variable codon positions and its molecular phylogenetic utility has been demonstrated in vertebrates (Irwin *et al.,* 1991; Graybeal, 1993; Zardoya and Doadrio, 1999). Therefore, this gene is suitable for investigations of animal phylogenetic status (Meyer, 1994; Lovejoy and de Araújo, 2000).

In 2009, Dubey *et al.* suggested that the *CYTB* pseudogene can lead to phylogenetic misinterpretations in Muridae. The existence of a nuclear copy of the *CYTB* pseudogene had been not widely recognized. The nuclear sequences can cause major problems in systematic analyses due to different selection pressures and rate of nucleotide substitutions. Therefore, such sequence analysis can lead to inaccurate interpretations (Zhang and Hewitt, 1996, 2003; Triant and DeWoody, 2007).

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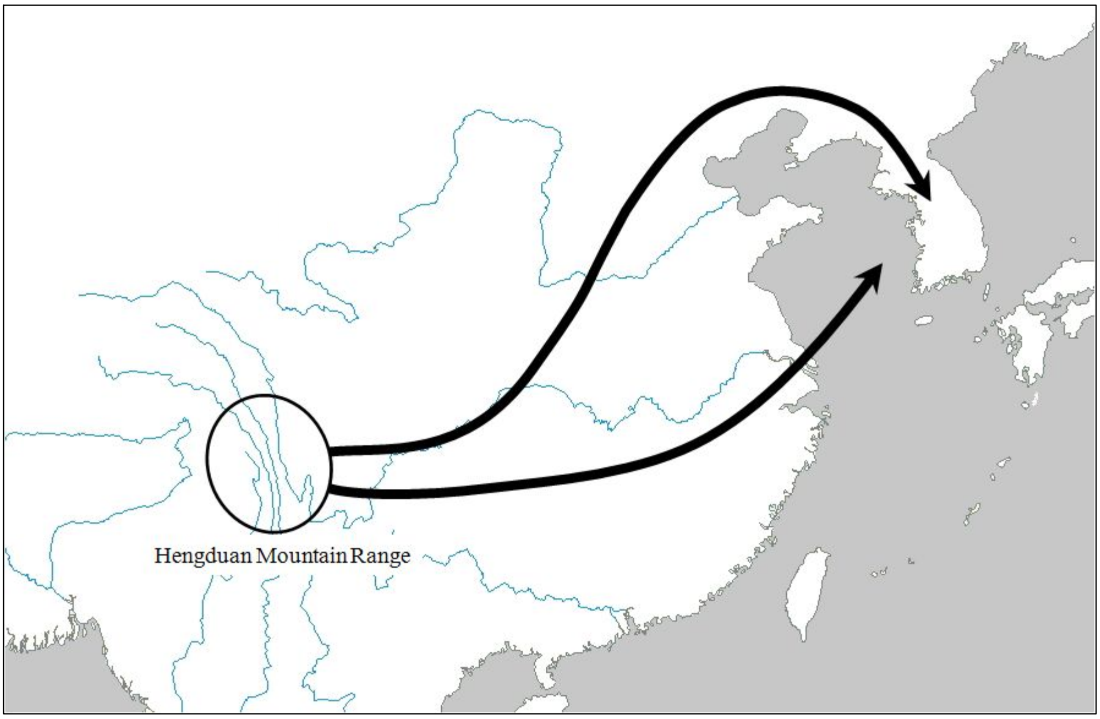

Figure 2.1. Origination and expansion of ancestral lineage of *A. agrarius* into the Korean Peninsula. An open circle is Hengduan Mountain Range considered as origination of Asian *Apodemus* (Xia, 1984). Arrows refer to possible migration routes of ancestor lineages of *A. agrarius*. The gray region represents the sea.

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Despite the various data regarding the distribution, morphology, and molecular genetics of *A. agrarius* (Han *et al.,* 1996; Serizawa *et al.,* 2000; Liu *et al.,* 2004; Yoon *et al.,* 2004b; Suzuki *et al.,* 2008) and *A. chejuensis* (Han *et al.,* 1996; Koh *et al.,* 2000; Yoon *et al.,* 2004b), their historic migration routes into the Korean Peninsula and Jeju Island, respectively, are unclear. The biogeographic history of *A. chejuensis* has not been established. The most reasonable theory regarding *A. chejuensis*, based on recent genetic data, is that *A. agrarius* have descended from a population on Jeju Island (Yoon *et al.,* 2004b). Jeju Island is considered to have been a “refugium” during the last glacial age, so that the maternal lineages that occur on Jeju Island could have originated there or elsewhere.

Jeju Island is located southwest of the Korean Peninsula and consists mainly of basaltic and pyroclastic flows (Yoon *et al.,* 1995). The island formed via volcanic eruption about 2 Mya (Yoon, 1997). Yoon (1997) summarized the formation history of Jeju Island. After the formation of the first Jeju volcanic edifice (about 2 Mya), the volcanic edifice subsided, and marine transgression occurred about 1.8 Mya. The main volcanic edifice was formed about 0.89-0.47 Mya. At this time, marine regression occurred, and the older Jeju Island area became land. Subsequent volcanic activity led to the formation of various major topographic features of Jeju Island. About 0.07 Mya, the summit of Mt. Halla was formed, and the central part of the main volcanic edifice was uplifted by rising magma. During this time, marine transgression occurred again and the Jeju volcanic edifice became Jeju Island.

Sea level changes affect biogeographic distributions (Mercer and Roth, 2003; Won and Renner, 2006). During the glacial epoch, global sea levels fluctuated repeatedly (Voris, 2000; Zhong *et al.,* 2004), and researchers have suggested that some species migrated from the Korean Peninsula to Jeju Island or vice versa during the glacial epoch (Shim and Park, 1998). Therefore, integrated analysis of the distribution of terrestrial animals and

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geological changes is important to understanding the biogeographic history.

This chapter has been attempted to explain the population history of *A. agrarius* and *A. chejuensis* and migration of *A. chejuensis* on the basis of the mt *CYTB* gene sequences of *A. agrarius* and *A. chejuensis* from the Korean Peninsula and Jeju Island.

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2.2. MATERIALS AND METHODS

2.2.1. Sampling and DNA extraction

Forty-nine *Apodemus chejuensis* individuals and 24 *A. agrarius* individuals were collected in the wild at various sites on Jeju Island and the Korean Peninsula, respectively (Table 2.1 and Fig. 2.2). Among all tissue samples of *A. agrarius*, 13 samples (samples Agr11 – 23) from various locations were obtained from the Conservation Genome Resource Bank for Korean Wildlife.

Genomic DNA was extracted from small pieces of tail or muscle using a NucleoSpin Tissue Kit (Macherey-Nagel, Germany). First, small pieces of tail or muscle was placed in a microcentrifuge tube with buffer T1 and proteinase K solution and then vortexed. The tubes were incubated at 56°C until complete lysis was obtained. The lysed samples were vortexed, and buffer B3 was added. The tubes were vortexed and incubated at 70°C for 10 min. Ethanol was added and the samples were vortexed vigorously. For each sample, a NucleoSpin® Tissue Column was placed into a collection tube, and the samples applied to the column. The assembly was centrifuged for 1 min at 11,000*g*. The flow-through was discarded and the column returned to the collection tube. To wash the silica membrane, buffer BW and buffer B5 were added in turn. The column-collection tube assembly was centrifuged for 1 min at 11,000*g* after each buffer addition. The silica membrane was dried by centrifugation. Finally, the column was placed into a new 1.5 ml tube; prewarmed buffer BE was added, and then incubated at room temperature for 1 min. The tube was centrifuged for 1 min at 11,000*g*, and the extracted DNA was stored at -20°C.

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2.2.2. PCR and sequencing

A 1.2 kbp fragment of the *CYTB* gene was amplified from the mt DNA by PCR using primers L14115 and H15288 (Martin *et al.,* 2000). PCR was carried out in 50 μl reaction mixtures containing 5 μl of 10× *Pfu*-X buffer (Solgent, Korea), 2 μl of dNTP mix (2.5 mM of each dNTP), 1 μl of each primer (10 μM), 0.5 μl of *Pfu*-X DNA polymerase (2.5 U/μl), 50-100 ng of genomic DNA, and sterile distilled water. Amplified products were examined by electrophoresis on 1% agarose gels, stained with EtBr, visualized under UV light, and purified using an AccuPrep PCR purification kit (Bioneer, Korea). The PCR products were directly sequenced using a BigDye Terminator Sequencing Kit (Applied Biosystems) on an ABI 3730xl automatic DNA sequencer with the newly designed inner primers ApoCYTB-F (5′-CAAATCTCCTCTCAGCCATCC-3′) and ApoCYTB-R (5′-CTGTTGGGTTGTTTGAGCCTG-3′).

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Table 2.1. Specimens and collection sources

Species	Specimen Num.	Collection site	Accession Num.	Haplotype Num.
A. agrarius	Agr1	Boreumdo, Incheon-si	HM034868	Hap1
	Agr2	Cheongdo, Gyeongsangbuk-do	HM034869	Hap2
	Agr3	Cheongdo, Gyeongsangbuk-do	HM034870	Hap3
	Agr4	Cheongdo, Gyeongsangbuk-do	HM034871	Hap2
	Agr5	Cheongdo, Gyeongsangbuk-do	HM034872	Hap4
	Agr6	Yangsan, Gyeongsangnam-do	HM034873	Hap5
	Agr7	Yangsan, Gyeongsangnam-do	HM034874	Hap6
	Agr8	Yangsan, Gyeongsangnam-do	HM034875	Hap5
	Agr9	Yangsan, Gyeongsangnam-do	HM034876	Hap7
	Agr10	Yangsan, Gyeongsangnam-do	HM034877	Hap8
	Agr11	Kanghwa, Incheon-si	HM034878	Hap9
	Agr12	Kanghwa, Incheon-si	HM034879	Hap10
	Agr13	Samcheok, Kangwondo	HM034880	Hap11
	Agr14	Macheon, Gyeongsangnam-do	HM034881	Hap12
	Agr15	Macheon, Gyeongsangnam-do	HM034882	Hap12
	Agr16	Seokmodo, Incheon-si	HM034883	Hap13
	Agr17	Seokmodo, Incheon-si	HM034884	Hap14
	Agr18	Seokmodo, Incheon-si	HM034885	Hap15
	Agr19	Seokmodo, Incheon-si	HM034886	Hap15
	Agr20	Seokmodo, Incheon-si	HM034887	Hap15
	Agr21	Hwacheon, Gangwon-do	HM034888	Hap16
	Agr22	Hwacheon, Gangwon-do	HM034889	Hap17
	Agr23	Hwacheon, Gangwon-do	HM034890	Hap18
	Agr24	Naju, Jeonranam-do	HM034891	Hap19
A. chejuensis	Che1	Hallim, Jeju-do	HM034892	Hap20
	Che2	Seongsan, Jeju-do	HM034893	Hap21
	Che3	Seongsan, Jeju-do	HM034894	Hap22
	Che4	Seongsan, Jeju-do	HM034895	Hap23
	Che5	Seongsan, Jeju-do	HM034896	Hap24
	Che6	Hallim, Jeju-do	HM034897	Hap25
	Che7	Jocheon, Jeju-do	HM034898	Hap26
	Che8	Andeok, Jeju-do	HM034899	Hap27
	Che9	Ara, Jeju-do	HM034900	Hap25
	Che10	Yonggang, Jeju-do	HM034901	Hap28
	Che11	Yonggang, Jeju-do	HM034902	Hap29
	Che12	Yonggang, Jeju-do	HM034903	Hap28
	Che13	Gujwa, Jeju-do	HM034904	Hap30
	Che14	Sanghyo, Jeju-do	HM034905	Hap31
	Che15	Sanghyo, Jeju-do	HM034906	Hap32
	Che16	Pyoseon, Jeju-do	HM034907	Hap33
	Che17	Pyoseon, Jeju-do	HM034908	Hap34
	Che18	Pyoseon, Jeju-do	HM034909	Hap27

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Che19	Pyoseon, Jeju-do	HM034910	Hap27
Che20	Pyoseon, Jeju-do	HM034911	Hap33
Che21	Ara, Jeju-do	HM034912	Hap35
Che22	Ara, Jeju-do	HM034913	Hap36
Che23	Ara, Jeju-do	HM034914	Hap37
Che24	Ara, Jeju-do	HM034915	Hap22
Che25	Ara, Jeju-do	HM034916	Hap32
Che26	Ara, Jeju-do	HM034917	Hap35
Che27	Ara, Jeju-do	HM034918	Hap36
Che28	Yeongpyeong, Jeju-do	HM034919	Hap23
Che29	Yeongpyeong, Jeju-do	HM034920	Hap38
Che30	Ara, Jeju-do	HM034921	Hap39
Che31	Ara, Jeju-do	HM034922	Hap35
Che32	Ara, Jeju-do	HM034923	Hap37
Che33	Hallim, Jeju-do	HM034924	Hap20
Che34	Hallim, Jeju-do	HM034925	Hap28
Che35	Sanghyo, Jeju-do	HM034926	Hap31
Che36	Sanghyo, Jeju-do	HM034927	Hap27
Che37	Sanghyo, Jeju-do	HM034928	Hap40
Che38	Seongsan, Jeju-do	HM034929	Hap39
Che39	Pyoseon, Jeju-do	HM034930	Hap27
Che40	Pyoseon, Jeju-do	HM034931	Hap41
Che41	Pyoseon, Jeju-do	HM034932	Hap33
Che42	Pyoseon, Jeju-do	HM034933	Hap27
Che43	Pyoseon, Jeju-do	HM034934	Hap33
Che44	Pyoseon, Jeju-do	HM034935	Hap42
Che45	Pyoseon, Jeju-do	HM034936	Hap20
Che46	Pyoseon, Jeju-do	HM034937	Hap43
Che47	Pyoseon, Jeju-do	HM034938	Hap33
Che48	Seogwipo, Jeju-do	HM034939	Hap44
Che49	Seogwipo, Jeju-do	HM034940	Hap20

(Continued)

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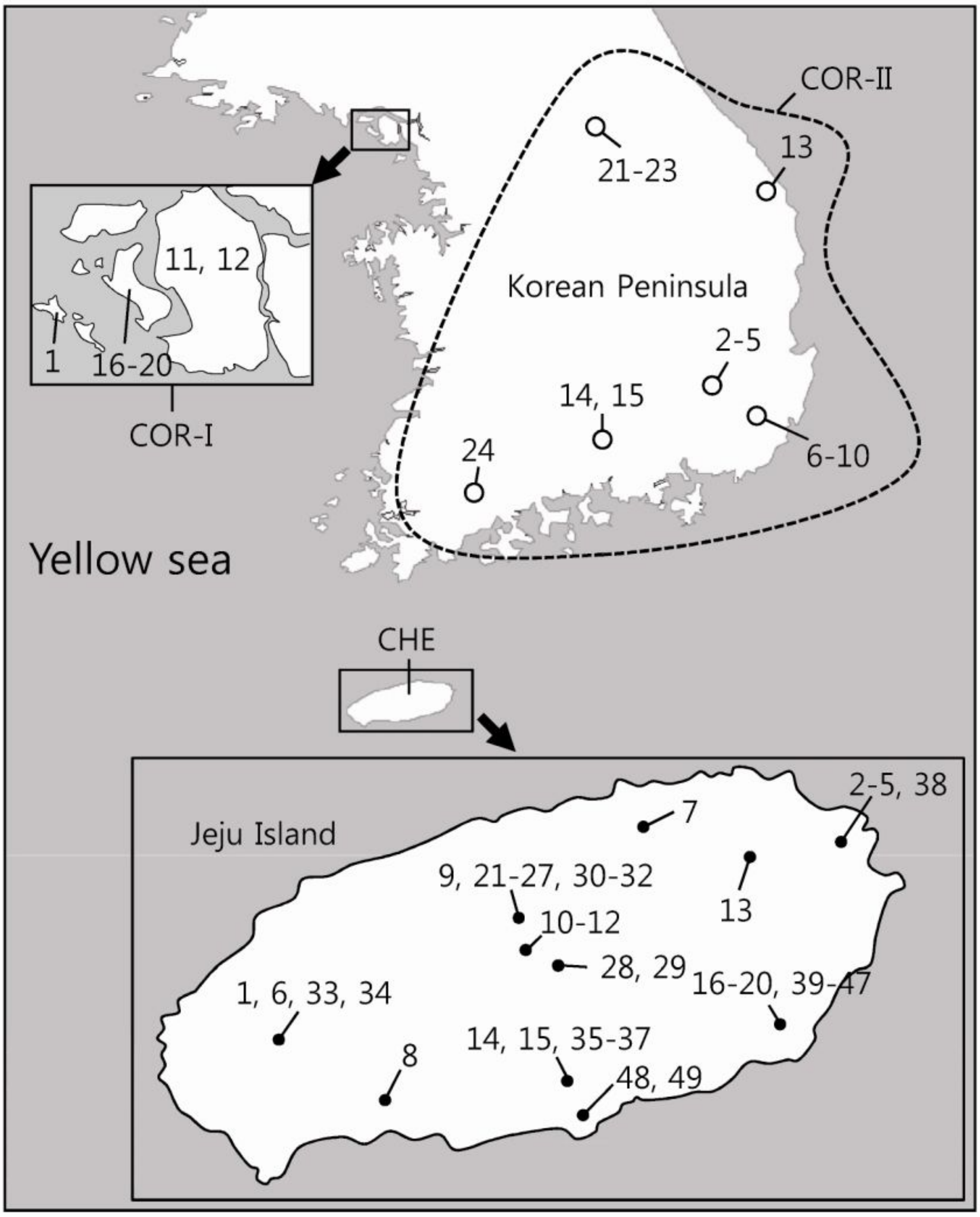

Figure 2.2. Collection sites of *A. agrarius* and *A. chejuensis*. Each specimen is indicated by a number on the map. Small open and closed circles indicate *A. agrarius* and *A. chejuensis* collection sites, respectively. Each local population of *A. agrarius* is indicated by an dotted line and a square. COR, Korean Peninsula; CHE, Jeju Island. Open squares indicate COR-I (western islet of the Korean Peninsula) collection sites. Details are shown in the magnified area. The gray region represents the sea.

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2.2.3. Sequence analysis

The sequence analysis was conducted using 73 new *CYTB* sequences from *A. agrarius* and *A. chejuensis* (Table 2.1). Collection sites were classified for biogeographic analysis as follows: COR-I and COR-II, the western islets and inland of the Korean Peninsula, respectively; and CHE, Jeju Island (Fig. 2.2). All complete *CYTB* sequences were aligned using the ClustalX program (Thompson *et al.,* 1997) and detected single nucleotide polymorphism (SNP) sites. For *CYTB* haplotype analysis, MEGA5 software (Tamura *et al.,* 2011) and DNAsp 5.0 software (Librado and Rozas, 2009) were used to estimate the Kimura two-parameter genetic distances (Kimura, 1980), the number of haplotypes and polymorphic sites, the average number of nucleotide differences, and the level of haplotype and nucleotide diversity. Fu's *Fs* test was used to assess evidence of population expansion (Fu, 1997) by using Arlequin 3.5 software (Excoffier and Lischer, 2010). A mismatch distribution analysis using DNAsp 5.0 software was conducted to estimate population dynamics (Librado and Rozas, 2009).

To construct a phylogenetic median-joining network, Network 4.5.1.6 software (http://www.fluxus-engineering.com) was used with haplotype data.

2.2.4. Divergence time estimation

The divergence time between the *A. agrarius* and *A. chejuensis* was calculated according to the method of Liu *et al.* (2004). The maximum likelihood distances were calculated using the TN93+G model (Tamura and Nei, 1993), which was selected as the best model for nucleotide evolution, based on the Akaike Information Criterion (AIC; Akaike, 1973) using jModeltest software (Posada, 2008). To calibrate the divergence time, 2.68 Mya was employed as the divergence time between *A. agrarius* and *A. chevrieri* (Liu *et al.,* 2004). Because excessive rate heterogeneity affects the

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molecular clock, the heterogeneity of evolutionary change along the different lineages was estimated. Using χ^2 tests (Felsenstein, 1988), I compared the likelihood trees created with and without an enforced molecular clock. Rate constancy among lineages was assumed for the tree with the enforced molecular clock.

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2.3. RESULTS

2.3.1. Haplotype and demographic analysis

Nineteen *CYTB* sequence haplotypes were defined in 24 *A. agrarius* individuals, and 25 were defined in 49 *A. chejuensis* individuals (Table 2.1). The most frequent haplotype group was Hap27, which was shared by 6 *A. chejuensis* individuals. The most frequent haplotype group in the *A. agrarius* population was Hap15, which was shared by 3 individuals.

The variable sites of *CYTB* sequence haplotypes were estimated. In 1,140 sites of *CYTB* sequence, 105 sites were variable and 43 sites were singleton variable sites (Fig. 2.3). In *A. agrarius*, variable and singleton variable sequences were found in 56 sites and 33 sites, respectively, while 53 variable sites and 20 singleton variable sites were found in *A. chejuensis*. Among variable sites, 6 were completely different between the *A. agrarius* and *A. chejuensis*.

The genetic distances of *CYTB* haplotypes showed that Hap9 is closest to Hap42, while Hap7 is farthest from Hap36 (Table 2.2). Each haplotype of the COR-I population, excluding Hap10 (Agr12), were relatively closer to each other of COR-I than to haplotypes of the COR-II population. In *A. chejuensis*, all haplotypes were closer to each other than to haplotypes of *A. agrarius*.

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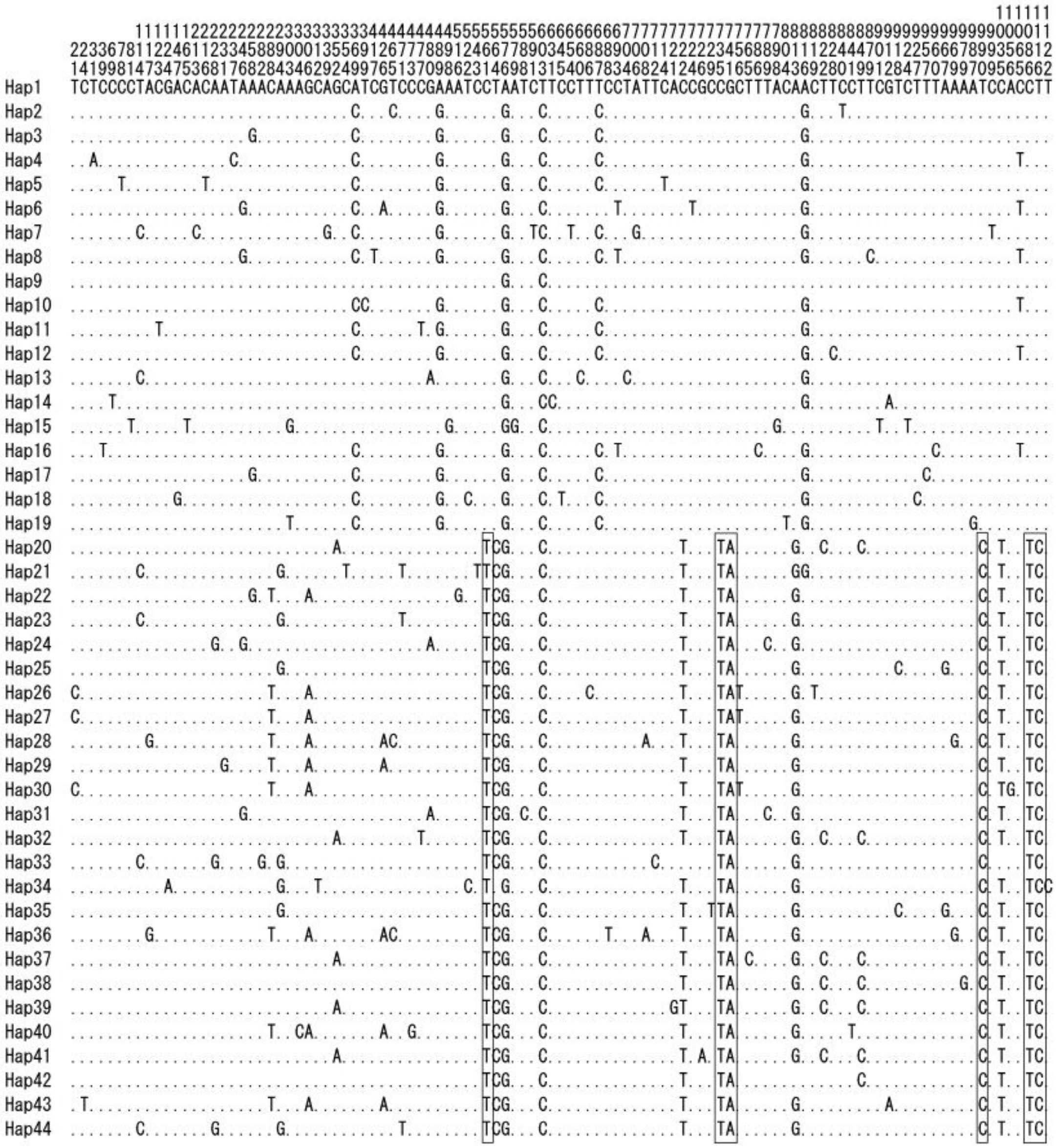

Figure 2.3. The variable sites in the *CYTB* haplotype sequences of *A. agrarius* and *A. chejuensis*. Nucleotides are numbered from the 5′ end of the *CYTB* sequences. Boxes present identical SNPs of *A. chejuensis*. Dots indicates matching with sequence of Hap1. Hap1-19, *A. agrarius*; Hap20-44, *A. chejuensis*.

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Table 2.2. Genetic distance matrix among haplotype sequences

	Hap1	Hap2	Hap3	Hap4	Hap5	Hap6	Hap7	Hap8	Hap9	Hap10	Hap11	Hap12	Hap13	Hap14	Hap15	Hap16	Hap17	Hap18	Hap19	Hap20	Hap21	Hap22
Hap1																						
Hap2	0.082																					
Hap3	0.071	0.029																				
Hap4	0.092	0.050	0.039																			
Hap5	0.093	0.050	0.040	0.060																		
Hap6	0.105	0.083	0.072	0.071	0.094																	
Hap7	0.139	0.093	0.082	0.104	0.105	0.141																
Hap8	0.116	0.072	0.061	0.060	0.083	0.050	0.128															
Hap9	0.019	0.060	0.050	0.070	0.071	0.082	0.115	0.093														
Hap10	0.082	0.040	0.029	0.029	0.050	0.061	0.093	0.050	0.060													
Hap11	0.082	0.040	0.029	0.050	0.050	0.083	0.093	0.072	0.060	0.040												
Hap12	0.082	0.040	0.029	0.029	0.050	0.061	0.093	0.050	0.060	0.019	0.040											
Hap13	0.072	0.093	0.082	0.104	0.105	0.116	0.127	0.128	0.050	0.093	0.093	0.093										
Hap14	0.061	0.082	0.071	0.092	0.093	0.105	0.139	0.116	0.040	0.082	0.082	0.082	0.072									
Hap15	0.106	0.153	0.141	0.165	0.166	0.180	0.220	0.193	0.083	0.153	0.153	0.153	0.142	0.130								
Hap16	0.116	0.072	0.061	0.060	0.083	0.072	0.128	0.061	0.093	0.050	0.072	0.050	0.128	0.116	0.193							
Hap17	0.082	0.040	0.010	0.050	0.050	0.083	0.093	0.072	0.060	0.040	0.040	0.040	0.093	0.082	0.153	0.072						
Hap18	0.105	0.061	0.050	0.071	0.072	0.106	0.116	0.094	0.082	0.061	0.061	0.061	0.116	0.105	0.180	0.094	0.061					
Hap19	0.092	0.050	0.039	0.060	0.060	0.093	0.104	0.082	0.070	0.050	0.050	0.050	0.104	0.092	0.152	0.082	0.050	0.071				
Hap20	0.168	0.222	0.208	0.234	0.237	0.252	0.298	0.268	0.142	0.222	0.222	0.222	0.210	0.196	0.255	0.268	0.222	0.252	0.234			
Hap21	0.210	0.237	0.222	0.249	0.252	0.268	0.281	0.285	0.182	0.237	0.237	0.237	0.196	0.210	0.305	0.285	0.237	0.268	0.249	0.094		
Hap22	0.182	0.237	0.193	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.208	0.268	0.249	0.072	0.106	
Hap23	0.168	0.222	0.208	0.234	0.237	0.252	0.265	0.268	0.142	0.222	0.222	0.222	0.182	0.196	0.255	0.268	0.222	0.252	0.234	0.061	0.029	0.072
Hap24	0.182	0.237	0.222	0.249	0.252	0.237	0.315	0.252	0.155	0.237	0.237	0.237	0.196	0.210	0.272	0.285	0.237	0.268	0.249	0.072	0.106	0.083
Hap25	0.168	0.222	0.208	0.234	0.237	0.252	0.298	0.268	0.142	0.222	0.222	0.222	0.210	0.196	0.255	0.268	0.222	0.252	0.234	0.061	0.072	0.072
Hap26	0.210	0.268	0.252	0.281	0.285	0.302	0.352	0.319	0.182	0.268	0.268	0.268	0.255	0.240	0.305	0.319	0.268	0.302	0.281	0.094	0.130	0.061
Hap27	0.182	0.237	0.222	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.237	0.268	0.249	0.072	0.106	0.040
Hap28	0.222	0.249	0.265	0.295	0.298	0.281	0.366	0.333	0.193	0.281	0.281	0.281	0.268	0.252	0.319	0.333	0.281	0.315	0.295	0.105	0.141	0.071
Hap29	0.182	0.237	0.222	0.249	0.252	0.237	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.237	0.268	0.249	0.072	0.106	0.040
Hap30	0.196	0.252	0.237	0.265	0.268	0.285	0.333	0.302	0.168	0.252	0.252	0.252	0.240	0.225	0.288	0.302	0.252	0.285	0.265	0.083	0.118	0.050
Hap31	0.182	0.237	0.222	0.249	0.252	0.237	0.315	0.252	0.155	0.237	0.237	0.237	0.196	0.210	0.272	0.285	0.237	0.268	0.249	0.072	0.106	0.083
Hap32	0.182	0.237	0.222	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.208	0.237	0.225	0.210	0.272	0.285	0.237	0.268	0.249	0.010	0.106	0.083
Hap33	0.168	0.222	0.208	0.234	0.237	0.252	0.265	0.268	0.142	0.222	0.222	0.222	0.182	0.196	0.255	0.268	0.222	0.252	0.234	0.106	0.094	0.118
Hap34	0.182	0.237	0.222	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.237	0.237	0.249	0.094	0.106	0.106
Hap35	0.182	0.237	0.222	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.237	0.268	0.249	0.072	0.083	0.083
Hap36	0.237	0.265	0.281	0.311	0.315	0.298	0.386	0.352	0.208	0.298	0.298	0.298	0.285	0.268	0.337	0.352	0.298	0.333	0.311	0.116	0.153	0.082
Hap37	0.182	0.237	0.222	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.237	0.268	0.249	0.010	0.106	0.083
Hap38	0.168	0.222	0.208	0.234	0.237	0.252	0.298	0.268	0.142	0.222	0.222	0.222	0.210	0.196	0.255	0.268	0.222	0.252	0.234	0.019	0.094	0.072
Hap39	0.182	0.237	0.222	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.237	0.268	0.249	0.010	0.106	0.083
Hap40	0.205	0.262	0.247	0.275	0.278	0.262	0.343	0.311	0.178	0.262	0.262	0.262	0.249	0.234	0.298	0.311	0.262	0.295	0.275	0.092	0.127	0.060
Hap41	0.182	0.237	0.222	0.249	0.252	0.268	0.315	0.285	0.155	0.237	0.237	0.237	0.225	0.210	0.272	0.285	0.237	0.268	0.249	0.010	0.106	0.083
Hap42	0.130	0.180	0.166	0.191	0.193	0.208	0.249	0.222	0.106	0.180	0.180	0.180	0.168	0.155	0.210	0.222	0.180	0.208	0.191	0.029	0.083	0.061
Hap43	0.196	0.252	0.237	0.265	0.268	0.252	0.333	0.302	0.168	0.252	0.252	0.252	0.240	0.196	0.288	0.302	0.252	0.285	0.265	0.083	0.118	0.050
Hap44	0.182	0.237	0.222	0.249	0.252	0.268	0.281	0.285	0.155	0.237	0.237	0.237	0.196	0.210	0.272	0.285	0.237	0.268	0.249	0.072	0.040	0.083

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Hap23	Hap24	Hap25	Hap26	Hap27	Hap28	Hap29	Hap30	Hap31	Hap32	Hap33	Hap34	Hap35	Hap36	Hap37	Hap38	Hap39	Hap40	Hap41	Hap42	Hap43	Hap44
0.072																					
0.040	0.072																				
0.094	0.106	0.094																			
0.072	0.083	0.072	0.019																		
0.105	0.116	0.105	0.093	0.071																	
0.072	0.083	0.072	0.061	0.040	0.050																
0.083	0.094	0.083	0.029	0.010	0.082	0.050															
0.072	0.019	0.072	0.106	0.083	0.116	0.083	0.094														
0.072	0.083	0.072	0.106	0.083	0.116	0.083	0.094	0.083													
0.061	0.094	0.083	0.142	0.118	0.153	0.118	0.130	0.118	0.118												
0.072	0.106	0.072	0.130	0.106	0.141	0.106	0.118	0.106	0.106	0.118											
0.050	0.083	0.010	0.106	0.083	0.116	0.083	0.094	0.083	0.083	0.094	0.083										
0.116	0.128	0.116	0.105	0.082	0.010	0.060	0.093	0.128	0.128	0.166	0.153	0.128									
0.072	0.083	0.072	0.106	0.083	0.116	0.083	0.094	0.083	0.019	0.118	0.106	0.083	0.128								
0.061	0.072	0.061	0.094	0.072	0.105	0.072	0.083	0.072	0.029	0.106	0.094	0.072	0.116	0.029							
0.072	0.083	0.072	0.106	0.083	0.116	0.083	0.094	0.083	0.019	0.118	0.106	0.083	0.128	0.019	0.029						
0.092	0.104	0.092	0.081	0.060	0.070	0.039	0.070	0.104	0.104	0.139	0.127	0.104	0.081	0.104	0.092	0.104					
0.072	0.083	0.072	0.106	0.083	0.116	0.083	0.094	0.083	0.019	0.118	0.106	0.083	0.128	0.019	0.029	0.019	0.104				
0.050	0.061	0.050	0.083	0.061	0.093	0.061	0.072	0.061	0.040	0.094	0.083	0.061	0.105	0.040	0.029	0.040	0.081	0.040			
0.083	0.094	0.083	0.072	0.050	0.060	0.029	0.061	0.094	0.094	0.130	0.118	0.094	0.071	0.094	0.083	0.094	0.049	0.094	0.072		
0.010	0.061	0.050	0.106	0.083	0.116	0.083	0.094	0.083	0.083	0.050	0.083	0.061	0.128	0.083	0.072	0.083	0.104	0.083	0.061	0.094	

(Continued)

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The overall haplotype and nucleotide diversity values of *A. agrarius* were 0.978 and 0.007, respectively, while those of *A. chejuensis* were 0.962 and 0.007, respectively (Table 2.3). The haplotype diversity of the COR-I was the lowest of all biogeographic populations. The COR-II was the most diverse. Although this analyses included more CHE than COR individuals, the COR exhibited greater genetic diversity (Table 2.3).

Fu's *Fs* test showed that the COR-II and CHE had significantly negative *Fs* values (-4.462 and -5.703, respectively), whereas the COR-I had a positive value (0.613). Mismatch distribution analyses suggested population expansion in the COR-II and CHE but stable COR-I, respectively (Fig. 2.4).

Median-joining network data indicated that *A. chejuensis* is a clearly separate species (Fig. 2.5) containing 4 subgroups, but these subgroups did not correspond to local distribution patterns on Jeju Island. The Hap42 (Che44) haplotype was located in the closest linear descendant position of the common ancestor of *A. chejuensis*. In *A. agrarius*, all COR-II individuals shared a single maternal lineage, and most COR-I individuals were close to the ancestral position of the *A. agrarius*. In particular, Hap9 (Agr 11) was located in the ancestral lineage position of the *A. agrarius* (Fig. 2.5).

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Table 2.3. Population analysis of *A. agrarius* and *A. chejuensis*

Subspecies	Population	S	N	υ	k	h (SD)	π (SD)	*Fs*
	COR-I	8	6	23	8.321	0.893 (0.111)	0.007 (0.001)	0.613
A. agrarius	COR-II	16	13	37	6.067	0.975 (0.029)	0.005 (0.000)	-4.462^{*}
	All	24	19	56	8.413	0.978 (0.019)	0.007 (0.001)	-6.207^{*}
A. chejuensis	CHE	49	25	53	7.776	0.962 (0.012)	0.007 (0.000)	-5.703^{*}

S, sample size; N, number of haplotypes; υ, variable sites; k, average nucleotide difference; *h*, haplotype diversity; π, nucleotide diversity; SD, standard deviation; *Fs*, Fu's *Fs*.
Asterisks mean a significant difference between populations ($P<0.01$).

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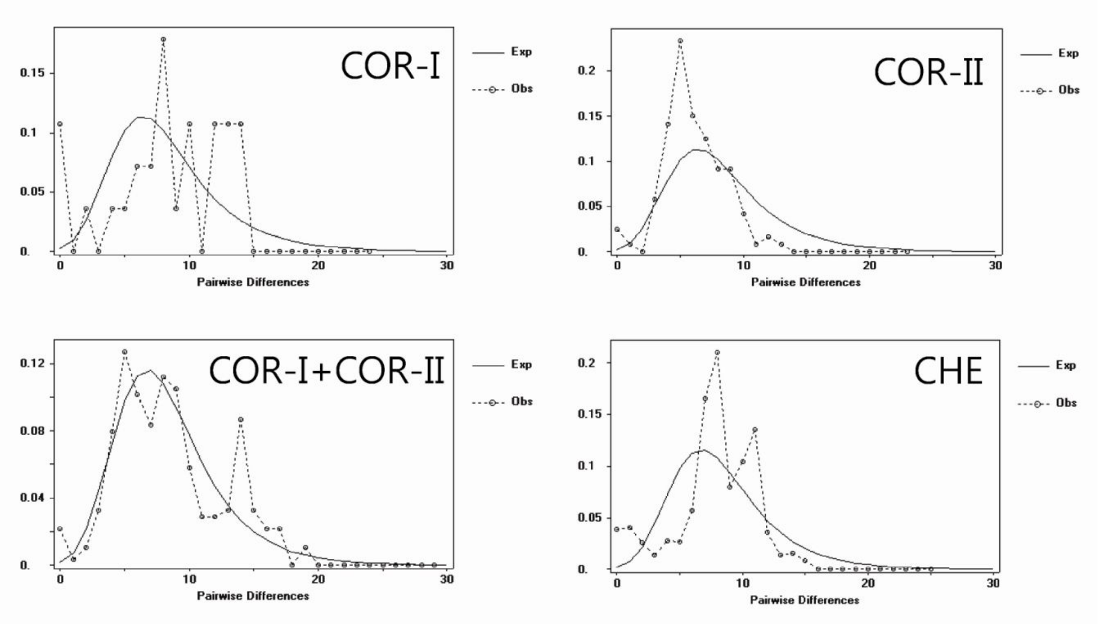

Figure 2.4. Mismatch distribution analysis in the *CYTB* gene sequences in *Apodemus* populations. The location of the COR-I, COR-II, and CHE is presented in Fig. 2.2. The dotted line with open circle is the observed distribution, the solid line is the expected in an expanding population.

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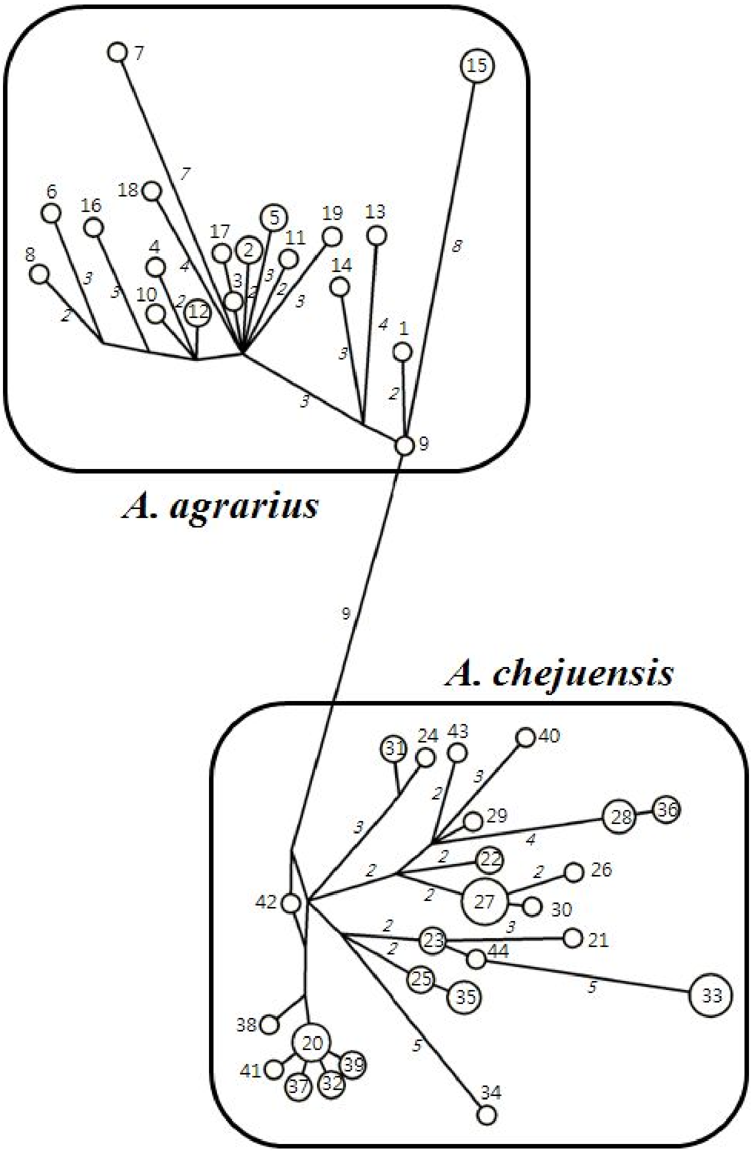

Figure 2.5. Median network tree inferred from *CYTB* haplotypes. Each circle indicates a haplotype (represented as a number), and the size of each circle is proportional to the number of individuals with that haplotype. Mutational steps between haplotypes are represented by a line. More than one mutational step is represented by italic numbers.

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2.3.2. Divergence time

The maximum likelihood tree assuming a constant rate for the lineage (lnL = –2451.999) presented the same topology as the tree without an enforced molecular clock (lnL = –2451.966). The likelihood ratio test failed to reject the hypothesis of rate constancy between these 2 models (χ^2 = 0.033, df = 7, $P > 0.05$). Thus, rate heterogeneity among lineages did not appear to affect the molecular clock calibration. The TN93+G distance between *Apodemus agrarius* and *A. chevrieri* was about 0.079, which corresponds to an evolution rate of 0.015 per million years, a result similar to that of Liu *et al.* (2004). Thus, I suggest that the split between *A. agrarius* and *A. chejuensis* occurred at approximately 0.3 Mya, in the late Pleistocene.

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2.4. DISCUSSION

2.4.1. Haplotype analysis of *Apodemus agrarius* and *A. chejuensis*

The *CYTB* haplotype sequence alignment showed that the sequences of *Apodemus chejuensis* are distinct from those of *A. agrarius*. Among the sequence differences, 6 nucleotides could be used as a SNP marker to discriminate between *CYTB* haplotype sequences of *A. agrarius* and *A. chejuensis*. Distinguishing between *A. agrarius* and *A. chejuensis* in the wild is difficult because of their extremely similar morphology. Molecular markers inferred from sequence differences are often used in molecular systematics (van Embden *et al.,* 1993; Chu *et al.,* 2001; Gupta *et al.,* 2001). Consequently, those SNP sites can be used as a marker for species or subspecies identification from wild samples.

The genetic distances among haplotype sequences suggest that the CHE population is genetically close to the COR-I population. The geographical distance between the COR-I region and Jeju Island is farther than the distance from the southern region of the Korean peninsula to Jeju Island. Smaller genetic distances indicate a close genetic relationship (Machado *et al.,* 2000). Accordingly, this result suggests that the common ancestor of the CHE population is derived from the ancestor of the COR-I population.

Haplotype diversity was very high and nucleotide diversity was very low in *A. agrarius* and *A. chejuensis*, suggesting that the populations of two species expanded rapidly after a period of low effective population size (Grant and Bowen, 1998). Although the analyses included more *A. chejuensis* than *A. agrarius* individuals, the *A. agrarius* exhibited greater genetic diversity.

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Assuming that *A. agrarius* and *A. chejuensis* have a common ancestor and diverged recently, this finding suggests that *A. chejuensis* diverged from an *A. agrarius* ancestor. In addition, network analysis showed that *A. agrarius* migrated inland and dispersed from the COR-I population, and that *A. chejuensis* diverged from an ancestral lineage of the COR-I population and migrated to Jeju Island; these populations dispersed rapidly to the Korean peninsula and Jeju Island, respectively. *Fs* estimation and mismatch distribution analysis support this hypothesis.

2.4.2. Possible migration histories of *Apodemus chejuensis*

It is estimated that Jeju Island was formed by volcanic activity about 2 Mya, and is younger than the Korean Peninsula (Yoon, 1997). The previous reports have been postulated that *A. chejuensis* migrated through the southern region of the Korean Peninsula because Jeju Island is located closer to the southern Korean peninsula than eastern China or Japan, and is the youngest in terms of geographic history, scientists suggested that the Southern Sea acted as a bridge between the Korean Peninsula and Jeju Island (Han *et al.,* 1996; Koh *et al.,* 2000; Yoon *et al.,* 2004b).

However, the results of this study showed that the closer relationship between the population (CHE) of *A. chejuensis* and COR-I of *A. agrarius* than that between both populations (COR-I and -II) of *A. agrarius*. Although Jeju Island is much closer to the southern area of the Korean peninsula than it is to the western islets, indicating that these were inconsistent with previous opinions on the migration routes of *A. chejuensis*.

Based on the results of the present study, new hypotheses can be postulated (Fig. 2.6). At first, the ancestors of *A. agrarius* probably immigrated from northeastern China through the northern part of the Korean Peninsula and reached around the COR-I region, then they arrived on Jeju

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Island through the Yellow Sea shelf about 0.3 Mya (Fig. 2.6A). Although Jeju Island is remarkably closer to the southern peninsula than to COR-I, the genetic distance between the CHE and COR-I is higher; it is also supposed that the geographical conditions of southern parts of the Korean Peninsula was unsuitable for migration or habitation of their ancestors.

At second, the ancestor of *A. chejuensis* might have come from the eastern coastal regions of China via the Yellow Sea basin during glacial period when the sea level was enough low to pass by walking. Part of the CHE, an ancestral lineage of *A. chejuensis*, moved across the Yellow Sea basin from Jeju Island to the western islets of the Korean Peninsula about 0.3 Mya (Fig. 2.6B).

Finally, since *A. agrarius* might migrate from eastern China to the Yellow Sea basin when the sea level was lower (Fig. 2.6D), the species diverged into 2 lines about 0.3 Mya. As the sea level dropped further (Fig. 2.6D), one of these lines could reach the western islet of the Korean peninsula, and the other might reach Jeju Island (Fig. 2.6C). The ancestor of the COR-II scattered rapidly throughout the Korean Peninsula. Differing from the previous reports proposed the southern parts of the Korean Peninsula as a bridge for migration of *A. chejuensis* between the Korean Peninsula and Jeju Island, in all hypotheses of this study, the Yellow Sea basin may have acted as a migration route of *A. chejuensis*. Because the Yellow Sea has an average depth of 55 m (maximum, 100 m) (Yang *et al.,* 2003), small animals were able to cross the Yellow Sea when the sea level was low (Park *et al.,* 2004). Han *et al.* (1996) suggested that *A. agrarius* and *A. chejuensis* diverged 1.2 Mya, whereas Koh *et al.* (2000) estimated that these species diverged about 7000–500,000 years ago, although both referred to the last ice age as a critical period. Therefore, the ancestral lineage of *A. chejuensis* possibly migrated to Jeju Island through the Yellow Sea basin and dispersed quickly after colonizing the island; this lineage eventually became the distinct

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subspecies *A. chejuensis*.

There has been considerable controversy about the taxonomic status of *A. agrarius* and *A. chejuensis*. The population found on Jeju Island was classified as a subspecies of *A. agrarius* by Jones and Johnson in 1965. However, subsequent molecular studies suggested that *A. chejuensis* is a species distinct from *A. agrarius* (Han *et al.,* 1996; Koh *et al.,* 2000). Crossbreeding experiments conducted by Oh and Mori (1998a) led them to conclude that the 2 populations are separate biologic species. The results of this study support the suggestion that *A. chejuensis* is a separate species (Han *et al.,* 1996; Oh and Mori, 1998a; Koh *et al.,* 2000).

The results of this study suggest that *A. agrarius* and *A. chejuensis* are clearly distinct populations, and that *A. chejuensis* migrated to Jeju Island through the Yellow Sea basin after divergence from the common ancestral lineage of *A. agrarius*. Assessment of additional mouse samples from North Korea and China may help to understand the evolutionary and biogeographic history of these 2 species

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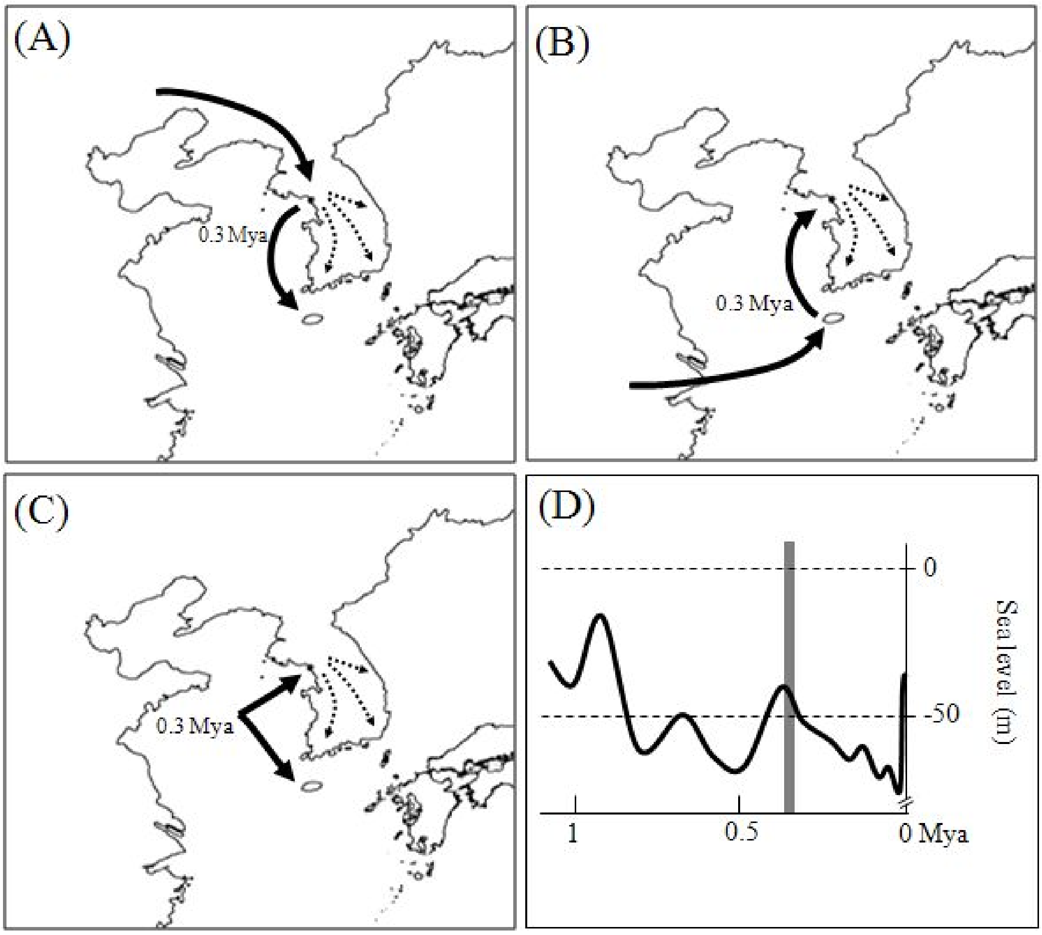

Figure 2.6. Hypothetic migration routes of *A. agrarius* and *A. chejuensis* in Korea. (A) The ancestral lineage of *A. agrarius* might migrate into the Korean Peninsula via North Korea and then could migrate to Jeju Island via the Yellow Sea basin when the sea level was low. (B) The ancestral lineage of *A. chejuensis* might migrate to Jeju Island via the Yellow Sea basin and then could migrate to the western islet of the Korean Peninsula via the Yellow Sea basin when the sea level was low. (C) The common ancestor of *A. agrarius* and *A. chejuensis* might had originated in eastern China, where it split into 2 lineages; one lineage could moved to the western islet of the Korean Peninsula, and the other could moved to Jeju Island. Arrows with dotted lines indicate dispersion of *A. agrarius*. (D) Modified eustatic sea level history (Zhong *et al.,* 2004): Gray bar indicates divergence time (0.3 Mya) of *A. agrarius* and *A. chejuensis*.

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국문 초록

제 1장. 한국산 붉은쥐속의 미토콘드리아 유전체 비교 분석

붉은쥐속(*Apodemus*)을 포함하는 쥐목(Rodentia)의 계통학적 분석을 위한 기초정보를 제공하기 위해 한국산 붉은쥐속인 등줄쥐(*Apodemus agrarius*)와 제주등줄쥐(*Apodemus chejuensis*) 그리고 흰넓적다리붉은쥐(*Apodemus peninsulae*)의 미토콘드리아 유전체의 전체 염기서열을 분석하였다. 분석된 미토콘드리아 유전체 서열은 등줄쥐, 제주등줄쥐, 그리고 흰넓적다리붉은쥐에서 각각 16,260, 16,261, 그리고 16,266 bp로 확인되었다. 다른 척추동물들과 마찬가지로 한국산 붉은쥐속 3종의 미토콘드리아 유전체에는 13 개의 단백질 유전자, 22 개의 tRNAs 유전자, 2 개의 rDNAs, 그리고 비암호화 영역인 조절부위(Control region)를 포함하고 있었다. 등줄쥐와 제주등줄쥐의 미토콘드리아 유전체에서는 단백질 암호화 유전자에서 ATG 코돈이 개시코돈으로 가장 많이 사용되었고, GTG와 ATA 개시코돈도 확인되었다. 한편, 흰넓적다리붉은쥐에서는 추가로 ATC 개시코돈도 ND2 유전자에서 사용되고 있음을 확인할 수 있었다. 13개 단백질 암호화 유전자에서의 뉴클레오티드의 출현 빈도는 한국산 붉은쥐속 3종 모두 비슷하게 나타났다. 코돈내 뉴클레오티드 출현 양상은 등줄쥐와 제주등줄쥐가 매우 유사하였고, 흰넓적다리붉은쥐는 다소 차이를 보였다. 12S rDNA는 등줄쥐와 제주등줄쥐가 955 bp로 동일하였고, 흰넓적다리붉은쥐는 956 bp로 확인되었다. 반면에 16S rDNA에서는 등줄쥐와 제주등줄쥐, 그리고 흰넓적다리붉은쥐가 각각 1,572, 1,573, 그리고 1,571 bp이었다. tRNA 유전자들 중에서는 tRNA-Leu(UUR과 CUN)과 tRNA-Ser(UCN과 AGY)이 두 형태로 존재함을 확인하였고, 전형적인 설치류에서처럼 3종 모두에서 3 종류 tRNA cluster(IQM, WANCY, HSL)들이 모두 보존되어 있었다. 일반적으로 포유류의 미토콘드리아 게놈은 2개의 비암호화 영역을 포함하고 있다. 그 중 하나는 light strand의 복제기점(O_L)이며 나머지는 D-loop으로도 불리는 조절부위(CR)이다. 특히 조절부위는 tRNA-Pro와 tRNA-Phe 유전자의 중간에 위치하고 있었으며, 이들의 크기는

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각각 등줄쥐에서 854 bp, 제주등줄쥐에서 857 bp, 그리고 흰넓적다리붉은쥐에서 866 bp이었다. 미토콘드리아 13 개 단백질 암호화 유전자들을 이용한 쥐목의 계통학적 분석에서 청설모(*Sciurus vulgaris*)와 큰동면쥐(*Myoxus glis*)의 분기가 쥐목 중에서도 가장 초기에 분화된 종임을 보여주고 있으며, 집쥐속(*Rattus*)은 두 개의 그룹으로 명확히 구분되고, 한국산 붉은쥐속은 분석된 종들 중에서 생쥐속(*Mus*)과 가장 근연종으로 확인되었다. 현재까지 붉은쥐속 종들간의 계통학적인 유연관계에 대한 여러 연구보고들이 있지만, 아직까지도 일부 종에 대해서는 분포범위가 매우 광범위하고, 아종으로써의 취급 문제 및 단편적인 정보들로 인하여 논쟁거리로 남아있다. 따라서 본 연구에서 얻은 미토콘드리아 게놈 정보는 향후 쥐목 및 붉은쥐속의 종들간의 계통학적 관계를 밝히는데 기초자료로 활용될 것으로 기대된다.

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제 2장. 제주등줄쥐의 역사적 이주 경로 추정

등줄쥐(*Apodemus agrarius*)와 제주등줄쥐(*Apodemus chejuensis*) 집단에서 미토콘드리아 *CYTB* 유전자의 haplotype의 상관관계를 분석함으로서 두 종의 진화적 상관관계와 분포적 특성을 추정하였다. 등줄쥐에서 19 개, 제주등줄쥐에서는 24 개의 *CYTB* haplotype들이 확인되었다. 가장 빈도가 높은 haplotype는 Hap27로 제주등줄쥐 6 개체에서 관찰되었고, 등줄쥐 집단에서는 Hap15가 가장 많은 3 개체에서 관찰되었다. 등줄쥐와 제주등줄쥐 집단의 확장 상태를 확인하기 위해 mismatch distribution 분석과 Fu's *Fs* 분석을 수행하였고, 그 결과는 COR-II와 CHE 집단이 확장되었음을 보여주었다. 반면, COR-I 집단은 확장이 멈춘 집단임을 추정할 수 있었다. 또한, median-joining network 분석에서 제주등줄쥐는 등줄쥐와 확연히 구분되는 종임을 알 수 있었고, 제주등줄쥐는 다시 4 개의 subgroup으로 구분되었으나, subgroup 간의 지역적 연관성을 나타내지는 않았다. 흥미로운 점들 중 하나는 제주등줄쥐 Hap42가 등줄쥐 Hap9와 가장 가까운 거리지수를 보인다는 점이다. 이에, 등줄쥐와 제주등줄쥐 두 종의 분기연대를 추정하기 위한 분자시계를 계산한 결과, 이 두 종은 약 30만 년 전에 분화된 것으로 추정되었다. 이상의 분석 결과들을 바탕으로 제주등줄쥐와 등줄쥐의 이주 경로에 대한 3 가지 가설을 제시할 수 있었다. 첫째는 등줄쥐의 조상계보가 중국 북동부 지역을 거쳐 북한 지역을 통해 한반도로 유입되었고, 빙하기를 거치면서 해수면이 현재보다 낮아짐으로 인해 황해지역이 육지가 되었을 때 등줄쥐 집단 중 일부가 황해를 거쳐 제주도로 유입되었을 가능성이다. 둘째는 중국 동부에 서식하던 제주등줄쥐의 조상계보가 황해를 건너 제주도로 유입되면서, 그 중 일부가 COR-I 지역까지 도달했을 가능성이 있다는 점이다. 마지막 가설은 중국 동부 지역에 서식하던 등줄쥐 집단 중 일부가 동쪽으로 서식범위를 넓히는 과정에서 집단 중 일부는 COR-I 지역으로, 다른 일부는 제주도로 거의 동시에 유입되었을 가능성도 배제할 수 없다는 점이다. 그리고 세 가설 모두에서 등줄쥐와 제주등줄쥐의 분기 시점이 약 30만 년 전이라고 추정된다. 현재 등줄쥐와 제주등줄쥐는 지리적으로 서로 완벽히 분리되어 있을 뿐만 아니라, 생식적으로도 두 종은 완전

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히 격리되었음을 감안하면 제주등줄쥐와 등줄쥐는 완전히 별개의 종으로 취급해야 할 것이다. 본 연구 결과는 제주등줄쥐가 종으로써의 지위를 가져야 한다는 점을 지지한다. 그러나 등줄쥐와 제주등줄쥐의 정확한 유입 경로를 확정하기위해서는 북한 및 중국 지역의 등줄쥐 개체들을 이용한 추가적인 연구가 필요하다.

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APPENDICES

Appendix 1. The sequence of mitochondrial genome of *Apodemus agrarius*

```
LOCUS       HM034866               16260 bp    DNA     circular ROD 30-DEC-2011
DEFINITION  Apodemus agrarius mitochondrion, complete genome.
ACCESSION   HM034866
VERSION     HM034866.1  GI:296100340
KEYWORDS    .
SOURCE      mitochondrion Apodemus agrarius (Eurasian field mouse)
  ORGANISM  Apodemus agrarius
            Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi;
            Mammalia; Eutheria; Euarchontoglires; Glires; Rodentia;
            Sciurognathi; Muroidea; Muridae; Murinae; Apodemus.
REFERENCE   1  (bases 1 to 16260)
  AUTHORS   Oh,D.-J., Jung,Y.-H., Kim,T.-W., Chang,M.-H., Oh,H.-S., Han,S.-H.
            and Kim,S.-J.
  TITLE     Biogeography and speciation of Korean striped field mice Apodemus
            agrarius and A. chejuensis inferred from mitochondrial DNA
  JOURNAL   Unpublished
REFERENCE   2  (bases 1 to 16260)
  AUTHORS   Oh,D.-J., Jung,Y.-H., Kim,T.-W., Chang,M.-H., Oh,H.-S., Han,S.-H.
            and Kim,S.-J.
  TITLE     Direct Submission
  JOURNAL   Submitted (25-MAR-2010) Department of Biology, Jeju National
            University, 66 Jejudaehakno, Jeju 690-756, Republic of Korea
FEATURES             Location/Qualifiers
     source          1..16260
                     /organism="Apodemus agrarius"
                     /organelle="mitochondrion"
                     /mol_type="genomic DNA"
                     /specimen_voucher="JBRI-Mam-001"
                     /db_xref="taxon:39030"
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     rRNA            68..1022
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     tRNA            1023..1091
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                     /product="tRNA-Leu"
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     gene            2739..3693
                     /gene="ND1"
     CDS             2739..3693
                     /gene="ND1"
                     /note="TAA stop codon is completed by the addition of 3' A
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                     /protein_id=″ADG95699.1″
                     /db_xref=″GI:296100341″
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                     VLQPFADAMKLFIKEPMRPLTTSISLFIIAPTLSLTLALSLWIPLPMPHPLINLNLGL
                     LFILATSSLSVYSILWSGWASNSKYSLFGALRAVAQTISYEVTMAIILLSVLLMSGSF
                     SLQMLIYTQEHMWLILPAWPMAMMWYISTLAETNRAPFDLTEGESELVSGFNVEYAAG
                     PFALFFMAEYTNIILMNALTSIVFLGPIHMINYPELYSINFMTETLLLSTTFLWIRAS
                     YPRFRYDQLMHLLWKNFLPLTLALCTWHISLPIFMASVPPYI″
     tRNA            3694..3762
                     /product=″tRNA-Ile″
     tRNA            complement(3760..3834)
                     /product=″tRNA-Gln″
     tRNA            3835..3903
                     /product=″tRNA-Met″
     gene            3904..4939
                     /gene=″ND2″
     CDS             3904..4939
                     /gene=″ND2″
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                     SMKLGLAPFHFWLPEVTQGIPLHMGLILLTWQKIAPLSILFQFYQLLNPTIIMILAIS
                     SILIGAWGGLNQTQMRKIMAYSSIAHMGWMLAILPYNPTMTLLNLLIYIILTVPMFLM
                     LMLNASTTINSISLLWNKAPTTLVLIPLILLSLGGLPPLTGFLPKWAIITELLKNNCL
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                     LILPLSPQLII″
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                     /note=″L-strand replication origin″
     tRNA            complement(5181..5248)
                     /product=″tRNA-Cys″
     tRNA            complement(5249..5315)
                     /product=″tRNA-Tyr″
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                     /gene=″CO1″
     CDS             5317..6861
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                GALLGDDQIYNVIVTAHAFVMIFFMVMPMMIGGFGNWLVPLMIGAPDMAFPRMNNMSF
                WLLPPSFLLLLASSMVEAGAGTGWTVYPPLAGNLAHAGASVDLTIFSLHLAGVSSILG
                AINFITTIINMKPPAMTQYQTPLFVWSVLITAVLLLLSLPALAAGITMLLTDRNLNTT
                FFDPAGGGDPILYQHLFWFFGHPEVYILILPGFGIISHVVTYYSGKKEPFGYMGMVWA
                MMSIGFLGFIVWAHHMFTVGLDVDTRAYFTSATMIIAIPTGVKVFSWLATLHGGNIKW
                SPAMLWALGFIFLFTVGGLTGIVLSNSSLDIVLHDTYYVVAHFHYVLSMGAVFAIMAG
                FVHWFPLFTGYTLDDMWAKTHFAIMFVGVNMTFFPQHFLGLSGMPRRYSDYPDAYTTW
                NTVSSMGSFISLTAVLLMIFMIWEAFASKREVLTVSYSSTNLEWLHGCPPPYHTFEEP
                SYVKVK"
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                /note="codons recognized: UCN"
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gene            7000..7683
                /gene="CO2"
CDS             7000..7683
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                /translation="MAYPFQLGLQDATSPIMEELMNFHDHTLMIVFLISTLVLYIISL
                MLTTELTHTSTMDAQEVETVWTILPAVILILIALPSLRILYMMDEINNPVLTVKTMGH
                QWYWSYEYTDYEDLCFDSYMIPTTDLKPGDLRLLEVDNRVVLPMGLPIRMLISSEDVL
                HSWAVPSLWLKTDAIPGRLNQATVTSNRPGLFYGQCSEICGSNHSFMPIVLEMVPLKH
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                     FQHWLIKLIIKQMMLIHTPKGRTWTLMIVSLIMFIGSTNLLGLLPHTFTPTTQLSMNL
                     SMAIPLWAGAVLLGFRHKLKSSLAHFLPQGTPISLIPMLIIIETISLFIQPMALAVRL
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                     SLYLHDNT"
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                     LGLLANTLTMYQWWWDIIREGTYQGHHTPIVQKGLRYGMILFIVSEVFFFAGFFWAFY
                     HSSLVPTHDLGGCWPPTGITPLNPLEVPLLNTSVLLASGVSITWAHHSLMEGKRNHMN
                     QALLITILLGLYFTMLQASEYFETPFSISDGIYGSTFFMATGFHGLHVIIGTTFLVVC
                     LLRQLKFHFTSKHHFGFEAAAWYWHFVDVVWLFLYVSIYWWGS"
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     gene            9445..9791
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     CDS             9445..9791
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                     /db_xref="GI:296100348"
                     /translation="MNLMIIMFINTILSLILISVAFWLPQMNLYTEKANPYECGFDPS
                     SSARLPFSMKFFLVAITFLLFDLEIALLLPLPWAIQTTNTNVMVTSALILVTILSLGL
                     TYEWTQKGLEWTE"
     tRNA            9794..9861
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     gene            9864..10160
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     CDS             9864..10160
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                     /translation="MSSAFINLTLAFMLSLLGTLTFRSHLMSTLLCLEGMMLSLFIMT
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15661 tctatatatc taccatcctc cgtgaaacca acaacccgcc cacctatgcc cctcttctcg
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Appendix 2. The sequence of mitochondrial genome of *Apodemus chejuensis*

```
LOCUS       HM034867               16261 bp    DNA     circular ROD 30-DEC-2011
DEFINITION  Apodemus chejuensis mitochondrion, complete genome.
ACCESSION   HM034867
VERSION     HM034867.1  GI:296100354
KEYWORDS    .
SOURCE      mitochondrion Apodemus chejuensis (Jeju striped field mouse)
  ORGANISM  Apodemus chejuensis
            Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi;
            Mammalia; Eutheria; Euarchontoglires; Glires; Rodentia;
            Sciurognathi; Muroidea; Muridae; Murinae; Apodemus.
REFERENCE   1  (bases 1 to 16261)
  AUTHORS   Oh,D.-J., Jung,Y.-H., Kim,T.-W., Chang,M.-H., Han,S.-H., Oh,H.-S.
            and Kim,S.-J.
  TITLE     Biogeography and speciation of Korean striped field mice Apodemus
            agrarius and A. chejuensis inferred from mitochondrial DNA
  JOURNAL   Unpublished
REFERENCE   2  (bases 1 to 16261)
  AUTHORS   Oh,D.-J., Jung,Y.-H., Kim,T.-W., Chang,M.-H., Han,S.-H., Oh,H.-S.
            and Kim,S.-J.
  TITLE     Direct Submission
  JOURNAL   Submitted (25-MAR-2010) Department of Biology, Jeju National
            University, 66 Jejudaehakno, Jeju 690-756, Republic of Korea
FEATURES             Location/Qualifiers
     source          1..16261
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                     /organelle="mitochondrion"
                     /mol_type="genomic DNA"
                     /specimen_voucher="JBRI-Mam-002"
                     /db_xref="taxon:754351"
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     rRNA            68..1022
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     tRNA            1023..1091
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     rRNA            1091..2663
                     /product="16S ribosomal RNA"
     tRNA            2664..2738
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     gene            2739..3693
                     /gene="ND1"
     CDS             2739..3693
                     /gene="ND1"
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                     /codon_start=1
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                     /transl_table=2
                     /product="NADH dehydrogenase subunit 1"
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                SLQMLIYTQEHMWLILPAWPMAMMWYISTLAETNRAPFDLTEGESELVSGFNVEYAAG
                PFALFFMAEYTNIILMNALTSIVFLGPIHMINYPELYSINFMTETLLLSTTFLWIRAS
                YPRFRYDQLMHLLWKNFLPLTLALCTWHISLPIFMASIPPYI″
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                /product=″tRNA-Ile″
tRNA            complement(3760..3830)
                /product=″tRNA-Gln″
tRNA            3835..3903
                /product=″tRNA-Met″
gene            3904..4939
                /gene=″ND2″
CDS             3904..4939
                /gene=″ND2″
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                SILIGAWGGLNQTQMRKIVAYSSIAHMGWMLAILPYNPTMTLLNLLIYIILTVPMFLM
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              AINFITTIINMKPPAMTQYQTPLFVWSVLITAVLLLLSLPVLAAGITMLLTDRNLNTT
              FFDPAGGGDPILYQHLFWFFGHPEVYILILPGFGIISHVVTYYSGKKEPFGYMGMVWA
              MMSIGFLGFIVWAHHMFTVGLDVDTRAYFTSATMIIAIPTGVKVFSWLATLHGGNIKW
              SPAMLWALGFIFLFTVGGLTGIVLSNSSLDIVLHDTYYVVAHFHYVLSMGAVFAIMAG
              FVHWFPLFTGYTLDDMWAKTHFAIMFVGVNMTFFPQHFLGLSGMPRRYSDYPDAYTTW
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CDS           7000..7683
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gene          7913..8593
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                SMAIPLWAGAVLLGFRHKLKSSLAHFLPQGTPISLIPMLIIIETISLFIQPMALAVRL
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                HSSLVPTHDLGGCWPPTGITPLNPLEVPLLNTSVLLASGVSITWAHHSLMEGKRNHMN
                QALLITILLGLYFTMLQASEYFETPFSISDGIYGSTFFMATGFHGLHVIIGTTFLVVC
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gene            9445..9792
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gene            9864..10160
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CDS             9864..10160
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gene            10154..11531
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CDS             10154..11531
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                LIALIFIQNSMGTLNFTMLSLTTNPLNPLWSNNILWLACMMAFMIKMPLYGVHLWLPK
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                LRQTDLKSLIAYSSVSHMALVIASIMIQTPWSFMGATMLMIAHGLTSSLLFCLANSNY
                ERIHSRTMIMARGLQMIFPLMATCWLVASLANLALPPSINLMGELFITMSLFSWSNFS
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                FSSWYMHSDPHINRFIKYLLLFLITMLILTSANNLFQLFIGWEGVGIMSFLLIGWWFG
                RADANTAALQAILYNRIGDIGFILAMTWFCLNMNSWELQQILLTNNNNLIPLLGLLIA
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                LCLGALTTLFTAICALTQNDIKKIVAFSTSSQLGLMMVTLGINQPYLAFLHICTHAFF
                KAMLFMCSGSIIHSLNDEQDIRKMGNMMKTMPFTSSCLTIGSLALTGMPFLTGFYSKD
                LIIEAINTCNTNAWALLITLIATSMTAIYSMRIIYFVVMTKPRFPPLISINENNPDLT
                NPIKRLAFGSILAGFFITYNIPPTNIQVLTMPWYLKTTALLISILGFLLALELNNLTL
                NLSMSKKNSYSSFSTSLGYFPSIIHRIIPNKTLNLSFKTSLNLLDLYWLEKSIPKSTS
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gene            complement(13536..14054)
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CDS             complement(13536..14054)
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     gene            14127..15270
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13141 cccaccaact aacatccaag ttctcactat accatgatac ttaaaaacta cagccctgct
13201 aatctctatc ctaggctttc tactagccct agaactaaat aacctcacat taaacctttc
13261 cataagtaaa aaaaactcgt attcatcatt ttccacatca ctaggctact tcccatcaat
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13381 tctagatctg tattgactag agaaatcaat cccaaaatct acttcaacta tacactctta
13441 tatatcaaaa ctactaacta accaaaaagg attagtaaaa ctatatttta tatcattttt
13501 actttctatt ctactaacca ctaccctctt tatcattaat ctcgagtgat ttcaataata
13561 ataaaaattc cagcaaacaa agaccatcca gcaactacta ttattcaagt agcacaacta
13621 tacatcgcgg caaccccaat accaccctct aatattacac caacatcatc aatctcatac
13681 atcaatcaat cacctagact atcaaaatca actacctcct ccccattata ataatcaaga
13741 aaatacacaa aaaacatttc cattaaaacc cctgcaatta aaaaaccaaa aacaaaccaa
13801 ttagaccctc aagtctcagg atactcctca gtagctatag ctgtcgtata cccaaacact
13861 actattattc ctcccaaata aattaaaaac accattagac ctaaaaagga tccaccaaac
13921 cctaaaacta ttagacaacc cacaaaccca ctcataatta aaccaaaccc cccataaata
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13981 ggagaaggct ttaaagctaa cccaagacaa ccagtcaaaa ataataaact taaaacaaaa
14041 atatagttag tcattatttc tacacagcat tcaactgtga ctaatgacat gaaaaatcat
14101 cgttgtaatt caactacaga aacctaatga caaacatccg aaaaactcac ccccctattta
14161 aaatcattaa ccactctttc atcgacctcc ctgccccatc taacatctca tcctgatgaa
14221 actttggctc cctcctaggt ctatgcctcg taattcaaat tcttacaggc ttattcctag
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14581 ccatcccata tatcggcact accctggtag aatgaatttg aggaggattc tcagtagata
14641 aagccacttt aacacgtttc ttcgcattcc attttattct cccatttatc atcgcagccc
14701 tggtaatcgt ccatctccta tttctccacg aaacaggctc aaacaaccca acaggtctaa
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14881 acccagataa ttacacacca gcaaatccac ttaatacacc accacatatc aaaccagagt
14941 gatacttcct atttgcatat gcaatcctac gctccattcc aaacaaacta ggaggagtcc
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15121 ttctcgtcct tacctgaatc ggcggacaac cagttgaata tccattcgta atcatcggcc
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15241 tcgaaaataa tatactaaaa tgaaacctat gccctgatag tatagaacca ttactctggt
15301 cttgtaaacc aaaaacgaag aacttctctt ctcaggcatc aagaagaagg aatcctcccc
15361 accatcagca cccaaagctg gtattctact taaactactt cttgagtaca taaaattaca
15421 tagtacattc atacatatat gtatatagta cattaaatta tttacccccta gcatataagc
15481 aagtacattt aattaatgat cctagacatt aatgattaat caaatatatc tcttctccca
15541 catgaatatt caggacttac attttaatta atgatcttaa gacatatctg cgttatctta
15601 catacaccat tcagtcataa actcttctct tccatatgac tatccctctc cacatttggt
15661 ctatatatct accatcctcc gtgaaaccaa caacccgccc acctatgccc ctcttctcgc
15721 tccgggccca taaaacttgg gggtagctaa cctgaaactt tatcagacat ctggttccta
15781 cttcagggcc atcaaatgcg ttatcgccca tacgttcccc ttaaataaga catctcgatg
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15901 atttttagga tgctgtgact caccatagcc gtcaaggcat gaaggtcagc ccaccatgaa
15961 gctggactta cagtgaagga tcatttatcc acataaaaca accaccgaag acaatttatg
16021 aatgcttgtt agacataact ctattattac ttctaatttt aacttaccca aacccccctta
16081 ccccctttga cgtcaaaccc caaaaccatc aaagacttaa cttaaattcc ataagtttta
16141 ttctattcta gtagttcaca aaattaaact tatattacag tattgggcaa aattttataa
16201 aaaattaatt ttgaattatc aaaaactcac cttattcaaa tttcctaata aatttatata
16261 a
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Appendix 3. The sequence of mitochondrial genome of *Apodemus peninsulae*

```
LOCUS       HQ660074               16266 bp    DNA     circular ROD 30-DEC-2011
DEFINITION  Apodemus peninsulae mitochondrion, complete genome.
ACCESSION   HQ660074
VERSION     HQ660074.1  GI:316993300
KEYWORDS    .
SOURCE      mitochondrion Apodemus peninsulae (Korean field mouse)
  ORGANISM  Apodemus peninsulae
            Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi;
            Mammalia; Eutheria; Euarchontoglires; Glires; Rodentia;
            Sciurognathi; Muroidea; Muridae; Murinae; Apodemus.
REFERENCE   1  (bases 1 to 16266)
  AUTHORS   Oh,D.J., Kim,T.W., Chang,M.H., Han,S.H., Oh,H.S. and Kim,S.J.
  TITLE     The mitochondrial genome of Apodemus peninsulae (Rodentia, Muridae)
  JOURNAL   Mitochondrial DNA 22 (4), 99-101 (2011)
   PUBMED   22040077
REFERENCE   2  (bases 1 to 16266)
  AUTHORS   Oh,D.-J., Jung,Y.-H., Kim,T.-W., Han,S.-H., Chang,M.-H., Oh,H.-S.
            and Kim,S.J.
  TITLE     Direct Submission
  JOURNAL   Submitted (29-NOV-2010) Department of Biology, Jeju National
            University, 66 Jejudaehakno, Jeju 690-756, Republic of Korea
FEATURES             Location/Qualifiers
     source          1..16266
                     /organism="Apodemus peninsulae"
                     /organelle="mitochondrion"
                     /mol_type="genomic DNA"
                     /db_xref="taxon:105297"
     tRNA            1..67
                     /product="tRNA-Phe"
     rRNA            68..1023
                     /product="12S ribosomal RNA"
     tRNA            1024..1092
                     /product="tRNA-Val"
     rRNA            1093..2663
                     /product="16S ribosomal RNA"
     tRNA            2664..2738
                     /product="tRNA-Leu"
                     /note="codons recognized: UUR"
     gene            2739..3693
                     /gene="ND1"
     CDS             2739..3693
                     /gene="ND1"
                     /note="TAA stop codon is completed by the addition of 3' A
                     residues to the mRNA"
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                     /transl_table=2
                     /product="NADH dehydrogenase subunit 1"
                     /protein_id="ADU78207.1"
                     /db_xref="GI:316993301"
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                LFILATSSLSVYSILWSGWASNSKYSLFGALRAVAQTISYEVTMAIILLSVLLMSGSF
                SLQTLIYTQEHMWLIVPTWPMAMMWYISTLAETNRAPFDLTEGESELVSGFNVEYAAG
                PFVLFFMAEYMNIILMNALTSIIFLGPMHKIYYPEFYSINFMTETLILSTTFLWIRAS
                YPRFRYDQLMHLLWKNFLPLTLAFCMWHISLPIFMASIPPYM″
tRNA            3694..3762
                /product=″tRNA-Ile″
tRNA            complement(3760..3830)
                /product=″tRNA-Gln″
tRNA            3834..3902
                /product=″tRNA-Met″
gene            3903..4938
                /gene=″ND2″
CDS             3903..4938
                /gene=″ND2″
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                /transl_table=2
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                /protein_id=″ADU78208.1″
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                SMKLGLAPFHFWLPEVTQGIQLHTGLILLTWQKIAPLSMLIQNYYLLDHTIIMIFSIL
                SIFIGAWGGLNQTQMRKIMAYSSIAHMGWMLAILPFNPTMTLLNLMIYIILTIPMFLV
                HMFNSSTTMNSISLMWNKTPTTLIMIPLILLSLGGLPPLTGFLPKWAIITELLKNNCL
                IMTTMMAMMALLNLFFYMRLIYSTTLTMFPTNNNSKMLTHHTNHKYNIILPSLTIIST
                LMLPLSPQLII″
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tRNA            complement(5008..5076)
                /product=″tRNA-Ala″
tRNA            complement(5078..5148)
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                /direction=LEFT
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                AINFITTIINMKPPAMTQYQTPLFVWSVLITAVLLLLSLPVLAAGITMLLTDRNLNTT
                FFDPAGGGDPILYQHLFWFFGHPEVYILILPGFGIISHVVTYYSGKKEPFGYMGMVWA
                MMSIGFLGFIVWAHHMFTVGLDVDTRAYFTSATMIIAIPTGVKVFSWLATLHGGNIKW
                SPAMLWALGFIFLFTVGGLTGIVLSNSPLDIVLHDTYYVVAHFHYVLSMGAVFAIMAG
                FVHWFPLFTGYTLDDMWAKTHFAIMFVGVNMTFFPQHFLGLSGMPRRYSDYPDAYTTW
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                SYVKVK"
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                /note="codons recognized: UCN"
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                /product="tRNA-Asp"
gene            6997..7680
                /gene="CO2"
CDS             6997..7680
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                /transl_table=2
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                /protein_id="ADU78210.1"
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                HSWAVPSLGLKTDAIPGRLNQATVTSNRPGLFYGQCSEICGSNHSFMPIVLEMVPLKH
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gene            7749..7952
                /gene="ATP8"
CDS             7749..7952
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                /transl_table=2
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                /protein_id="ADU78211.1"
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                /translation="MNENLFASFITPSVMGLPIVVTIIMFPSILFPSSERLINNRLHS
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                HSSLVPTHDLGGCWPPTGITPLNPLEVPLLNTSVLLASGVSITWAHHSLMEGKRNHMN
                QALLITILLGLYFTILQASEYFETPFSISDGIYGSTFFMATGFHGLHVIIGTSFLIVC
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gene            9442..9789
                /gene=″ND3″
CDS             9442..9789
                /gene=″ND3″
                /codon_start=1
                /transl_table=2
                /product=″NADH dehydrogenase subunit 3″
                /protein_id=″ADU78214.1″
                /db_xref=″GI:316993308″
                /translation=″MNLAIILLINTTLSLILISVAFLLPYMNLYSEKTNPYECGFDPS
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                TYEWTQKGLEWTE″
tRNA            9791..9858
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gene            9861..10157
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CDS             9861..10157
                /gene=″ND4L″
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                /transl_table=2
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                /db_xref=″GI:316993309″
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gene            10151..11528
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CDS             10151..11528
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                     QILLVMTFSATELIMFYILFEATLIPTLIIITRWGNQTERLNAGIYFLFYTLIGSIPL
                     LIALIFMQTSMGTLNFSMLSLMPSPLDSLWSNNILWLACMMAFMIKMPLYGVHLWLPK
                     AHVEAPIAGSMILAAILLKLGSYGMMRIAIMLDPLTKFMAYPFILLSLWGMIMTSSIC
                     LRQTDLKSLIAYSSVSHMALVIASIMIQTPWSFMGATMLMIAHGLTSSLLFCLANSNY
                     ERIHSRTMIMARGLQMIFPLMATWWLVASLTNLALPPSINLIGELFITMSLFSWSNFS
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                     PKFITGLTM"
tRNA                 11529..11595
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                     /product="tRNA-Ser"
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gene                 11725..13554
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                     /db_xref="GI:316993311"
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                     FSSWYMHSDPHINRFIKYLLLFLITMLILTSANNLFQLFIGWEGVGIMSFLLIGWWFG
                     RSDANTAALQAILYNRIGDIGFILAMTWFCLNMNSWELQQILLTENNNLIPLLGLLIA
                     ATGKSAQFGLHPWLPSAMEGPTPVSALLHSSTMVVAGIFLLVRFHPLTSNNPKILTMM
                     LCLGGLTTLFTAICALTQNDIKKIVAFSTSSQLGLMMVTLGINQPYLAFLHICTHAFF
                     KAMLFMCSGSIIHSLNDEQDIRKMGNMMKTMPFTSSCLTIGSLALTGMPFLTGFYSKD
                     LIIEAMNTCNTNAWALMITLIATSMTAIYSMRIIYFVTMTKPRFPPMILINENDPNLM
                     NPIKRLALGSIMAGFFISYNIPPTNIQILTMPWYLKTTALFISILGFLMALELNNLTL
                     KLSMNKKNLYSSFSTSLGYFPSIIHRIIPNKTLNLSLKTSLNLLDLYWLENSIPKPIS
                     TMHSYASKLLTNQKGLVKLYFLSFFLSILLTVILYIINLEWSQ"
gene                 complement(13532..14050)
                     /gene="ND6"
CDS                  complement(13532..14050)
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                     /transl_table=2
                     /product="NADH dehydrogenase subunit 6"
                     /protein_id="ADU78218.1"
                     /db_xref="GI:316993312"
                     /translation="MTNYIFVLRLLFLTGCLGLALKPSPIYGGFGLIMSGFVGCLMVL
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                     GFGGSFLGLMVFLIYLGGMMVVFGYTTAMATEEYPETWGSNWFVFGSLIIGVLMELFF
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                     AGIFIIIEITRD"
     tRNA            complement(14051..14119)
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     gene            14123..15266
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                     VEWIWGGFSVDKATLTRFFAFHFILPFIIAALAVVHLLFLHETGSNNPTGLNSDADKI
                     PFHPYYTIKDILGIFILVGFLMTLVLFSPDLLGDPDNYMPANPLNTPPHIKPEWYFLF
                     AYAILRSIPNKLGGVLALILSILILALLPFLHTSKQRSLMFRPITQTLYWILVANLLT
                     LTWIGGQPVEHPFVIIGQLASISYFSIILILMPLSGIIEDKILKWNL"
     tRNA            15267..15333
                     /product="tRNA-Thr"
     tRNA            complement(15334..15400)
                     /product="tRNA-Pro"
     D-loop          15401..16266
ORIGIN
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       61 ataaacacaa aggtttggtc ctagccttat aattagttgg aggtaagatt acacatgcaa
      121 atgtccataa accagtgtaa aatcccttaa atatttttac aaaatttaag gagagggtat
      181 caagcacata aaatagctta agacaccttg cctagccaca cccccacggg actcagcagt
      241 gataaatatt aagcaatgaa cgaaagtttg actaagctat gcctcttagg gttggtaaat
      301 ttcgtgccag ccaccgcggt catacgatta acccgaacta attactctcg gcgtaaaacg
      361 tgttcactat aaacttacta atagaattaa aattcaactt atatgtaaaa attcattgtt
      421 agaacttaaa ctcaataacg aaagtaattc taataacatt attttacacg atagctaaga
      481 tccaaactgg gattagatac cccactatgc ttagccctaa accttaataa ttagataaca
      541 aaattatttg ccagagaact actagctata gcttaaaact caatggactt ggcggtactt
      601 tatatccatc tagaggagcc tgttctataa tcgataaacc ccgctttacc tcaccatctc
      661 ttgctaattc agcctatata ccgccatctt cagcaaaccc taaaaaggaa taatagtaag
      721 cacaagaaca aacataaaaa cgttaggtca aggtgtagcc aatgagatgg gaagaaatgg
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      841 ggatttagta gtaaattaag aatagagagc ttaattgaat agagcaatga agtacgcaca
      901 caccgcccgt caccctcctc aaactaaata aatttatata tataaataat ttctaaattg
      961 atatttacta gaggagataa gtcgtaacaa ggtaagcata ctggaaagtg tgcttggaat
     1021 aatcacagtg tagcttaact acaaagcatc tggcctacac ccagaagatt tcatagcaaa
     1081 tgaacacttt gaactaatac tagcccttat attttattaa ttaaattatt ttattatata
     1141 aattaaatca tttaacttat taaaagtatt ggagaaagaa attataagac aggagcaata
     1201 gagtaagtac cgtaagggaa agatgaaaga acaattaaaa gtacaaaaaa gcaaagatta
     1261 taccttgtac cttttgcata atgaattaac tagaaaaaat ttgactaaaa gaatttaagc
     1321 caaatacccc gaaaccaaac gagctaccta agaacaattt tatgaatcaa cccgtctatg
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16261 tactaa
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감사의 글

박사학위를 받기까지 저를 도와주시고, 응원해주신 많은 분들에게 감사를 드립니다. 우선 살아계셨다면 가장 크게 기뻐하셨을 아버님, 늘 저를 믿어주시고 응원해주신 어머님께 감사드리며, 하나뿐인 동생 종철이에게도 고맙다는 말을 전하고 싶습니다. 그리고, 잦은 야근에도 불구하고 항상 걱정해주고 격려해 준 아내와 많이 놀아주지 못해 항상 미안한 우리 딸들 유진, 유현에게 고맙고 미안한 마음을 전합니다. 또한, 일을 핑계로 집안일에 소홀한 저를 대신해 제 아내와 두 딸을 많이 보살펴주신 장인 장모님께도 감사의 말씀을 전하며, 공부하느라 바쁜 와중에도 누나의 일이라면 항상 적극적으로 도와주는 처남 웅이에게도 고맙다는 말을 전합니다.

석사과정에서부터 부족한 저를 이끌어주시고 박사학위를 받을 수 있도록 항상 저를 응원해주시고 지도해주신 김세재 교수님과 연구를 진행하는데 큰 도움을 주신 오홍식 교수님께 무한한 감사를 드립니다. 뿐만 아니라, 지난 수년간 저에게 많은 것을 가르쳐주시고, 이 자리까지 올 수 있도록 음양으로 적극 지원해주신 정용환 소장님과 평소 일에 치여 지내면서도 어려움이 있을 때마다 항상 도움을 주시는 박수영 부장님, 연구방향 및 결과 분석에 많은 도움을 주신 선배 한상현 박사님께 진심으로 감사를 드립니다.

현재 몸담고 있는 생물종다양성연구소에서 같이 근무하고 있는 바이오기술개발부의 고미희 박사님, 원종이형, 영민이에게도 감사의 마음을 전하고 싶습니다. 그리고, 항상 성실한 자세로 맡은 업무에 최선을 다하는 모습이 믿음직한 전형식 형님께도 감사의 말을 전하며, 곤충연구에 연구소 업무에 정신없이 지내는 경식이, 지금은 퇴사했지만 그 동안 많은 고생을 함께 했던 지영이와 정아, 그리고 현재 연구소에서 각 분야 업무에 충실히 매진하고 있는 동료 연구원들에게도 고맙다는 말을 전합니다.

학부시절부터 시간이 날 때면 서로의 넋두리를 들어주고 서로에 대한 조언을 아끼지 않았던 후배 강성일 박사, 석사과정에 있을 때부터 같이 실험실 생활을 해왔던 박사과정 혜선이와 현재 열심히 연구에 매진하고 있는 정환이, 승우, 선

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아에게도 감사의 말을 전함과 동시에 앞으로 좋은 연구 성과를 기대합니다. 그리고, 자주 모이지는 못 하지만 오랜 친구들 성하, 효진, 길홍, 종석, 정석, 후영, 세미, 희선, 은정이에게도 그 동안 힘이 돼주어 고맙다는 말을 전하고 싶습니다.

마지막으로 지면을 통해 일일이 언급을 하지 못했지만 그 동안 저를 아끼고 사랑해주신 분들께 다시 한 번 진심으로 감사를 드립니다.

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