COMPARATIVE GENETICS OF *APODEMUS AGRARIUS* (RODENTIA: MAMMALIA) FROM INSULAR AND CONTINENTAL EURASIAN POPULATIONS: CYTOCHROME *B* SEQUENCE ANALYSES

Koh, Hung Sun[1,*], Shaner, Pei Jen[2], Csorba, Gábor[3], Wang, Yuchi[4]
Jang, Kyung Hee[1] and Lee, Jong Hyek[1]

[1] *Department of Biology, Chungbuk National University, Cheongju 361-763, Korea*
[2] *Department of Life Science, National Taiwan Normal University, Taipei 10617, Taiwan*
[3] *Department of Zoology, Hungarian Natural History Museum*
H-1083 Budapest, Baross u. 13, Hungary
[4] *School of Life Science, Shandong University, Jinan 250100, China*
* Corresponding author: e-mails: syskoss@chungbuk.ac.kr

To reexamine genetic divergence of *Apodemus agrarius* in insular Taiwan and the Korean Jeju from other populations in continental Eurasia, we obtained 91 cytochrome *b* complete sequences of *A. agrarius* across Eurasia, and these sequences were compared to eight corresponding sequences of *A. agrarius*, obtained from GenBank. We first found that the two insular populations are two clades, and that each of them is divergent from continental Eurasian populations, clustered into another clade. Each of the two insular clades appeared to be isolated in spite of land connection to nearby continent during the last glacial period, and we considered the two insular forms as *A. a. insulaemus* and *A. a. chejuensis* and one continental Eurasian form as *A. a. agrarius*, although further analyses are needed to confirm our present findings. Additionally, the Taiwan clade seemed to be composed of two subclades (western and eastern), separated by Taiwan's central mountain range.

Key words: DNA systematics, cytochrome *b* gene, biogeography, Taiwan *Apodemus agrarius insulaemus*, Jeju *A. a. chejuensis.*

INTRODUCTION

Corbet (1978) arranged 24 nominal subspecies of the striped field mouse (*Apodemus agrarius* Pallas, 1771) into three subspecies (*A. a. agrarius* from Europe and western Asia; *A. a. ningpoensis* from eastern Asia except southwestern China; and *A. a. chevrieri* from southwestern China). However, Jones and Johnson (1965) classified *A. agrarius* from mainland Korea as *A. a. coreae* and that from Jeju as *A. a. chejuensis*, and Wang (1985) classified the subspecies *chevrieri* as a distinct species, whereas Zhang *et al.* (1997) recognized five subspecies from China and Taiwan (*A. a. agrarius* from Xinjiang, *A. a. ningpoensis* from south of Changjiang basin, *A. a. pallidior* from basins of Changjiang and Huanghe, *A. a. mantchuricus* from Hebei and northeastern China, and *A. a. insulaemus* from Taiwan). Furthermore, Musser and Carleton (2005) noted that *A. agrarius*, distributed from Germany to Korea, is composed of 25 subspecies, indicating that subspecies classification of *A. agrarius* is still controversial.

The phylogenetic relationships among species in the genus *Apodemus* were inferred from nuclear *IRBP, RAG1, I7*, and vWF and mitochondrial cytochrome *b* genes (Suzuki *et al*. 2008), cytochrome *b* gene (Suzuki *et al*. 2003, Belliniva 2004, Sakka *et al*. 2010), and control region (Liu *et al*. 2004). Moreover, mitochondrial DNA (mtDNA) is a highly sensitive genetic marker, which is suitable for studies of closely related taxa and for the examination of population structures within a species (Sunnucks 2000). Lack of genetic divergence between *A. agrarius* from mainland Korea and northeastern China was reported from mtDNA cytochrome *b* (1054 bp) and control region (860 bp) sequence analyses (Koh *et al*. 2011).

All geographically isolated populations have only limited or no gene exchange with other populations of their species (Mayr & Ashlock 1991), and island populations are also of interest for their differentiation as well as their species diversity (Berry 1986). Based on nine cytochrome *b* complete sequences (1140 bp) of Eurasian *A. agrarius,* one Taiwan haplotype was not distinctly divergent from eight haplotypes in continental Eurasia (Suzuki *et al*. 2008), but from cytochrome *b* partial sequences (402 bp; site nos 1–402) of *A. agrarius* in Eurasia three subgroups (I, Taiwan; II, Guizhou in central China; and III, Germany, Chelyabinsk, and Primorye) were recognized (Suzuki *et al*. 2003), and on the basis of partial (from 319 bp of site nos 76–394 to 1081 bp) and complete sequences of the cytochrome *b* gene from Asian *A. agrarius*, five major groups (Taiwan, China, mainland Korea, far-eastern Russia, and central Asia) were found (Sakka *et al*. 2010), indicating that the previous results on genetic distinctness of *A. agrarius* from insular Taiwan based on cytochrome *b* partial or/and complete sequences are not concordant with one another and that the former studies are based on less than ten haplotypes with cytochrome *b* complete sequences from Eurasia.

Genetic distinctness of insular Jeju *A. agrarius* from mainland Korean population was also reported from partial sequences (282 bp) of mtDNA control region (Koh *et al*. 2000), although most of the specimens from Wan Island, which is connected to mainland Korea by a bridge, clustered with Jeju specimens. Among mtDNA sites cytochrome *b* gene is more conservative than the control region in their evolutionary rates (Lopez *et al*. 1997). Thus, it becomes necessary to reexamine genetic divergences of insular Taiwan and Jeju populations from other *A. agrarius* from continental Eurasia, by utilizing cytochrome *b* complete sequences of more numerous specimens from insular Taiwan and Jeju and continental Eurasian populations.

MATERIAL AND METHODS

We collected 91 specimens of *A. agrarius* from 29 locations in Eurasia, as given in Table 1, and the 29 collection sites are shown in Figure 1. Small pieces of muscle were collected and preserved in a deep freezer.

Total cellular DNA was extracted using a genomic DNA extraction kit (Intron Co., Daejeon, Korea). The cytochrome *b* gene was PCR-amplified using primers L14724 and H15915, designed by Irwin *et al*. (1991). The PCR thermal cycle employed was as follows: 94 °C for 5 min; 94 °C for 1 min, 59 °C for 1 min, 72 °C for 1 min (32 cycles); and 72 °C for 5 min. To remove primers and unincorporated nucleotides, the amplified products were purified using a DNA PrepMate kit with a silica-based matrix (Intron Co., Korea). For sequencing, the purified PCR products were analyzed with an automated DNA Sequencer (Perkin Elmer 377) at Bioneer Co. (Seoul, Korea).

Cytochrome *b* complete sequences were obtained from 91 specimens of *A. agrarius* across Eurasia, as listed in Table 1, and these sequences were compared to nine complete sequences of Eurasian *A. agrarius*, obtained from GenBank, as given in Table 2. Sequence alignment, detection of parsimonious informative sites, model selection, calculation of nucleotide distances, tree constructions with 1000 bootstrapped replications, and estimation of coefficient of evolutionary differentiation (Gst) were conducted using MEGA5 (Tamura *et al*. 2011). The Jukes-Cantor (JC) model, which showed the lowest Bayesian information criterion score, was chosen as the best model for our data by the program, and maximum likelihood and neighbor-joining trees were constructed by the JC model. *Apodemus sylvaticus* (AF159395), *A. peninsulae* (AB032850), and *A. argenteus* (AB032848) were used as outgroups. Additionally, cytochrome *b* partial sequences (402 bp; site nos 1 to 402), obtained from our complete sequence data, were used for the construction of maximum likelihood tree, and these results were compared to the results from complete sequences in order to determine whether or not the tree from partial sequences is congruent to the trees from complete sequences.

RESULTS

From the 91 cytochrome *b* complete sequences of *A. agrarius* in Eurasia, 57 haplotypes were identified, as listed in Table 1, and their GenBank accession numbers are KJ081981 to KJ081989 (9 haplotypes from Jeju Island), KJ081990 to KJ082205 (16 haplotypes from mainland Korea), KJ082006 to KJ082008 and KJ082011 to KJ082024 (17 haplotypes from China), KJ082009 and KJ082010 (2 haplotypes from far-eastern Russia), KJ082025 to KJ082027 (3 haplotypes from western Russia), KJ082028 and KJ082029 (2 haplotypes from Hungary), and KJ082030 to KJ082037 (8 haplotypes from Taiwan). Within the 66 cytochrome *b* haplotypes of *A. agrarius* (57 haplotypes from this study and nine haplotypes from GenBank), 162 sites (14.2%) were variable, and 92 sites (8.1%) were parsimony informative.

From maximum likelihood tree with the 66 haplotypes of cytochrome *b* partial sequences (402 bp) of *A. agrarius* (we did not show the tree in this paper), two clades were found [eight haplotypes from Taiwan (Gp 1) and other 58 haplotypes from Jeju and continental Eurasia (Gp 2)], and 28 (42%) of the

Table 1. Location, specimen number, and cytochrome *b* haplotypes of *Apodemus agrarius*, used in this study. Complete sequences of 57 haplotypes (1140 bp) were obtained from 91 specimens at 29 locations in Eurasia, as shown in Figure 1, and their GenBank accession numbers are KJ081981 to KJ082037.

Location	Specimen number (cytochrome *b* haplotype)
Jeju Island, Korea	
Kwaneumsa (1)	K2231, K2233 (KJj01); K2100, K2103, K2232, K2234 (KJj03); K2102 (KJj04); K2235 (KJj05)
Seongpanak (2)	K2098 (KJj01); K2099 (KJj02)
Gozzawal (3)	K2160, K2164 (KJj06); K2166 (KJj07); K2167 (KJj08); K2168 (KJj09)
Mainland Korea	
Wan Island (4)	K0483 (KWd01); K2222-K2225 (KWd02); K2226 (KWd03); K2228 (KWd04)
Haenam (5)	K0480 (KHn01)
Mt. Jiri (6)	K2078 (KJr01)
Mt. Deokyu (7)	K2046 (KDy01); K2047, K2248 (KDy02)
Mt. Songri (8)	K1952, K1954 (KSr01); K1953 (KSr012)
Mt. Weolak (9)	K1967 (KWa01); K1968, K1969, K1971 (KWa02)
Mt. Chiak (10)	K1364 (KCa01)
Munsan (11)	K1591 (KMs01)
Mt. Odae (12)	K1372 (KOd01)
Uljin (13)	K0430 (KUj01)
China	
Longjiang (14), northeastern	C2072 (CLj01), C2073 (CLj02)
Shenyang (15), northeastern	C2094 (CSy01), C2124 (CSy02)
Changchun (16), northeastern	C2126 (CCc01)
Harbin (17), northeastern	C2131 (CHb01); C2132, C1233 (CHb02)
Daqing (18), northeastern	C2027 (CDq01)
Taishan (20), eastern	C2125 (CTs01)
Zibo (21), eastern	C0083 (CZb01); C0084 (CZb02); C0085, C0086 (CZb03); C0087 (CZb04); C0088 (CZb05)
Dongying (22), eastern	C2440, C2441, C2443, C2444, C2446, C2447 (CDySg01)
Shouguang (23), eastern	C2445 (CDySg01)
Tongzi (24), central	C2157 (CTz01), C2158 (CTz02)

Table 1 (continued)

| Location	Specimen number (cytochrome *b* haplotype)
Taiwan	
Hualien (25)	T2253 (THl01); T2255, T2254, T2250 (THl02); T2256, T2264 (THl03); T2257, T2261, T2262, T2263 (THl04); T2258, T2260 (THl05)
Dadushan (26)	T2482, T2485 (TDd01); T2481 (TDd02); T2484 (TDd03)
Hungary	
Ábrahámhegy (27)	H0002, H0027 (HAhBt01); H0003, H0004, H0015, H0032 (HAh02)
Balatonrendes (28)	H0033 (HAhBt01)
Russia	
Vladivostok (19), far-eastern	R2134 (RVv01), R2135 (RVv02)
Moscow (29), western	R0005 (RMc01), R0009 (RMc02), R0010 (RMc03)
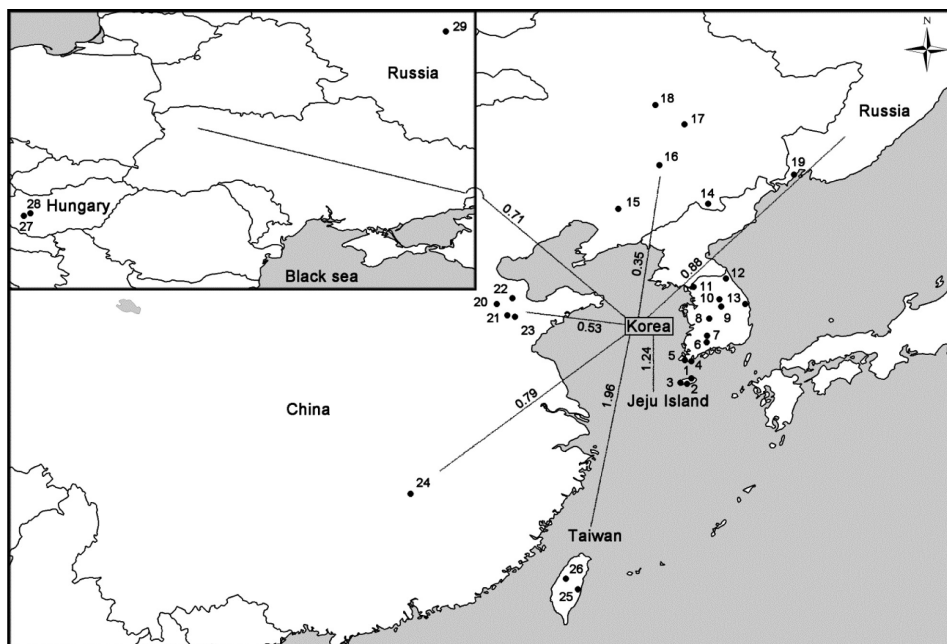
Fig. 1. Collection sites for 91 specimens from 29 locations of *Apodemus agrarius*, used in this study. The specimen number for each location are listed in Table 1, and minimum Jukes-Cantor distances between 17 haplotypes from mainland Korea and other 49 haplotypes from seven regions (Taiwan, Jeju, northeastern China, eastern China, central China, Far-eastern Russia, and Europe) based on the cytochrome *b* complete sequences are given above the lines, connecting mainland Korea and the seven regions.

Table 2. Location and accession number of *Apodemus agrarius*, obtained from GenBank. Nine cytochrome *b* complete sequences from Eurasia were used for this study.

Location	GenBank accession number
Mainland Korea	AB303225
Ussurisky, far-eastern Russia	AB032851
Taishan, eastern China	AY389012
Shanghai, eastern China	AB096815
Xi'an, central China	AY389011
Tongzi, central China	AB096809
Lubeck, Germany, Europe	AB096817
Italy, Europe	AB303226
Serbia, Europe	AF159390

66 haplotypes were found to be identical in their sequences. However, based on maximum likelihood and neighbor-joining trees, with the 66 haplotypes of cytochrome *b* complete sequences of *A. agrarius*, as shown in Figure 2, three clades were recognized: eight haplotypes (Gp 1) from Taiwan (Taiwan clade), nine haplotypes (Gp 2) from Jeju (Jeju clade), and 49 haplotypes (Gp 3) from continental Eurasia (continental Eurasian clade), ranging from mainland Korea to Germany. Only two haplotypes (CZb05 and AB389011) were similar in their sequences, indicating that 2 (3%) of the 66 haplotypes are identical in their sequences.

The Taiwan clade (Gp 1) was divergent from the continental Eurasian clade (Gp 3), with average JC distance of 2.79%, ten fixed site differences (site nos 46, 114, 312, 318, 735, 909, 1059, 1065, 1122, and 1125), and the Gst value of 0.36 between the two clades. The Jeju clade (Gp 2) was also divergent from the continental Eurasian clade (Gp 3), with average JC distance of 1.83%, six fixed site differences (site nos 561, 564, 735, 990, 1086, and 1116), and the Gst value of 0.32 between the two clades. Additionally, the Taiwan clade (Gp 1) was composed of two subclades (western and eastern), with average JC distance of

Fig. 2. Phylogenetic trees with 66 haplotypes of cytochrome *b* complete sequences (1140 bp) from Eurasian *Apodemus agrarius*. For maximum likelihood (A) and neighbor-joining (B) trees 57 haplotypes were obtained from this study, and nine haplotypes were obtained from GenBank. The trees were constructed with 1000 bootstrapped replications, and the bootstrap values greater than 50% are reported at the internodes. *Apodemus sylvaticus* (AF159395), *A. peninsulae* (AB032850), and *A. argenteus* (AB032848) were used as outgroups. The location and specimen number for each haplotype, obtained from this study, are listed in Table 1, and collection site follows haplotype name in each haplotype, whereas the location and accession number for each haplotype, obtained from GenBank, are listed in Table 2, and collection site follows accession number in each haplotype.
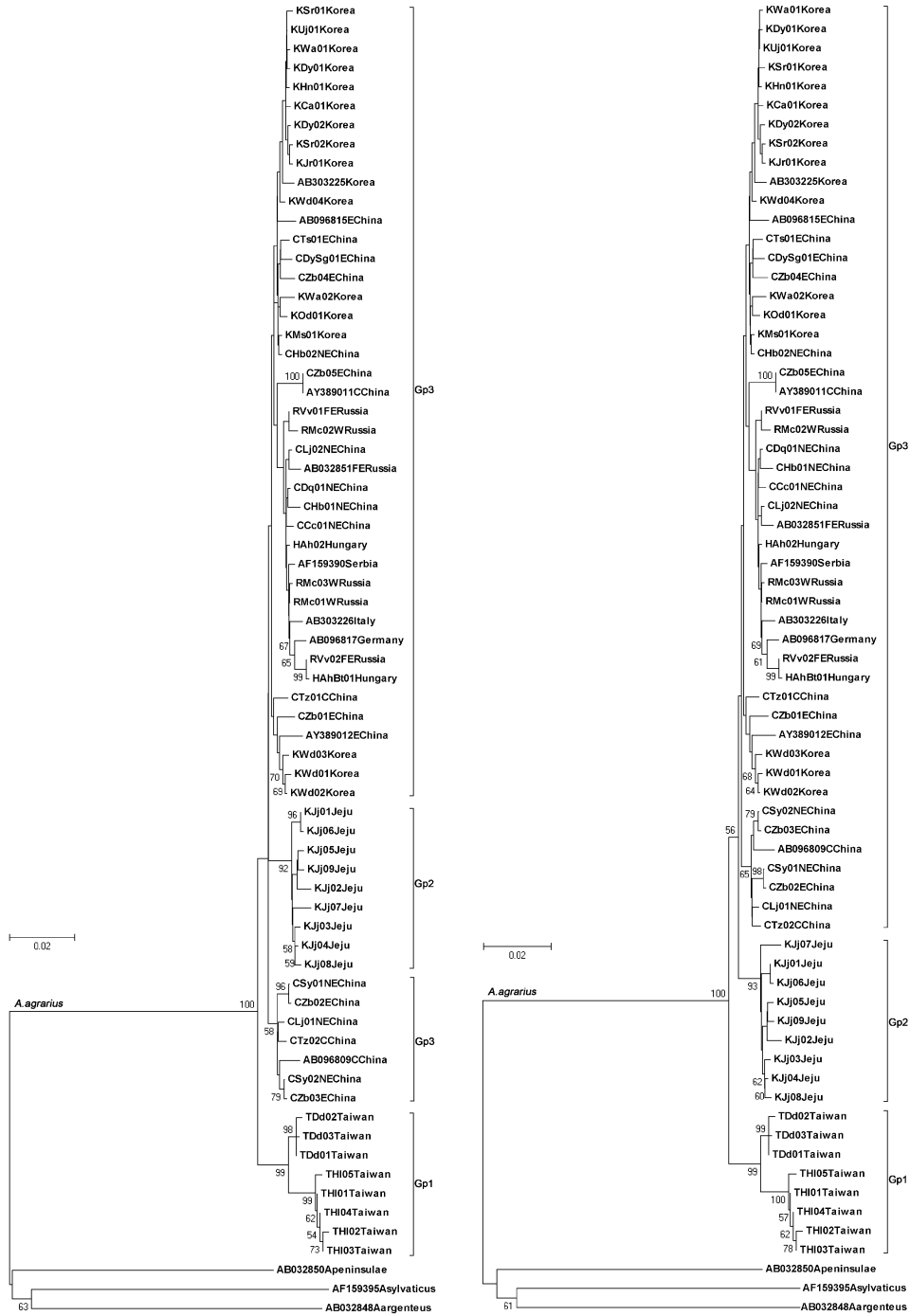
1.34%, six fixed site differences (site nos 831, 843, 897, 918, 990, and 1000), and the Gst value of 0.73 between them. Average JC nucleotide distances within Gps 1, 2, and 3 were 0.85%, and 0.65%, and 1.10%, respectively.

The minimum JC distances between 17 haplotypes from mainland Korea and other 49 haplotypes from seven regions in Eurasia (eight from Taiwan, nine from Jeju, eight from northeastern China, nine from eastern China, four from central China, three from far-eastern Russia, and eight from Europe) were 1.96%, 1.24%, 0.35%, 0.53%, 0.79%, 0.88%, and 0.71%, respectively, and these distances are shown above the line, connecting mainland Korea and the seven regions, in Figure 1.

DISCUSSION

From the 66 haplotypes of cytochrome *b* partial sequences (402 bp) of *A. agrarius*, two subgroups (Gp 1 from Taiwan and Gp 2 from Jeju and continental Eurasia) were recognized, and 28 (42%) of the 66 haplotypes were identical in their sequences. However, based on the 66 haplotypes with complete sequences, three subgroups (Gp 1 from Taiwan, Gp 2 from Jeju, and Gp 3 from continental Eurasia) were detected (Fig. 2), and 2 (3%) of the 66 haplotypes were identical in their sequences. We found that the results based on cytochrome *b* partial sequences are less informative than the results from cytochrome *b* complete sequences. Thus, we concluded that cytochrome *b* partial sequences of *A. agrarius* have to be used in caution to infer its population subdivision or phylogenetic relationships, and in further discussions we excluded the sequencing results by SUZUKI *et al.* (2003) and SAKKA *et al.* (2010), based on cytochrome *b* partial sequences.

Based on nine cytochrome *b* complete sequences, one Taiwan *A. agrarius* haplotype was not distinctly divergent from other eight haplotypes in Eurasia (SUZUKI *et al.* 2008), but from this study based on cytochrome *b* complete sequences (Fig. 2) with the 57 cytochrome *b* haplotypes of *A. agrarius* in Eurasia, obtained in this study, the Taiwan clade (Gp 1) was one of three distinct clades and was divergent from the continental Eurasian clade (Gp 3), with average JC distance of 2.79% and ten fixed site differences, indicating that distinctiveness of the Taiwan population was evidently detected from this study based on more numerous cytochrome *b* complete sequences, with finer resolution.

Based on control region partial sequences of *A. agrarius*, KOH *et al.* (2000) found that most of Wan Island specimens are clustered with all Jeju specimens, whereas other Wan Island specimens belonged to the other subgroup with the specimens from mainland Korea. From our cytochrome *b* sequencing study (Fig. 2) we found that the Jeju clade (Gp 2) is one of three distinct clades and is divergent from the continental Eurasian clade (Gp 3), with average JC

distance of 1.83% and six fixed site differences, indicating that distinctness of the Jeju *A. agrarius* was recognized clearly from this study on the basis of more conservative cytochrome *b* gene.

Island populations should diverge over time (morphologically and genetically) from populations of respective mainland species (Johnson *et al*. 2000), although at the end of the last glacial period, large areas of continental shelf was dry land, allowing easy exchange of plant and animal species by land bridge connections to what are now isolated islands (Lomolino *et al*. 2010). The Gst value is equivalent to the Fst value (Halliburton 2004), and the Fst value above 0.25 indicate "very great" genetic differentiation between them (Wright 1978). From this study (Fig. 2), we found the Gst value of 0.35 between the Taiwan clade (Gp 1) and continental Eurasian clade (Gp 3) and the Gst value of 0.32 between the Jeju clade (Gp 2) and continental Eurasian clade (Gp 3). Thus, we considered that each of two insular *A. agrarius* populations has been in isolation in spite of land connection to continental East Asia during the last glacial period.

Additionally, a subspecies is an aggregate of phenetically similar populations of a species differing taxonomically from other populations of that species (Mayr & Ashlock 1991), and it was advocated that a classification should reflect all available characters distributed as widely and as evenly as possible over the organisms studied (Huelsenbeck *et al*. 1996). Corbet (1978) noted that insular forms (Taiwan and Jeju) of *A. agrarius* are rather large in size but are not very distinctive.

Based on a morphometric analysis with 31 external and cranial characters from 15 nominal subspecies of *A. agrarius* in Eurasia (Koh & Tikhonova 1998), *A. agrarius* from insular Jeju and Wan was a large-size form, and *A. agrarius* from North Korea, China, and Taiwan was a medium-size form. But, from the 66 cytochrome *b* haplotypes (Fig. 2) Taiwan and Jeju populations were two distinct clades (Gp 1, Taiwan clade; and Gp 2, Jeju clade), indicating that our sequencing results support the subspecies status of two insular subspecies (*A. a. insulaemus* Tokuda, 1941 from Taiwan and *A. a. chejuensis* Johnson et Jones, 1955 from Jeju).

Central populations of a species range are relatively homogeneous (Eckert *et al*. 2008). From our previous studies the Siberian roe deer (*Capreolus pygargus ochraceus*) from Jeju Island was concordantly divergent from other populations of *C. pygargus* from continental East Asia in *IRBP*, cytochrome *b,* and control region sequences (Koh *et al*. 2013*a*), and the Asian lesser white-toothed shrew (*Crocidura shantungensis*) from Jeju was also divergent from other *C. shantungensis* from continental East Asia in cytochrome *b* sequences (Koh *et al*. 2013*b*).

Corbet (1978) classified *A. agrarius* from Europe and western and central Asia as *A. a. agrarius* and *A. agrarius* from eastern Asia as *A. a. ningpoensis,*

but Koh and Tikhonova (1998) reported that continental *A. agrarius* populations from mainland Korea to Europe are not distinct with one another in their morphometric characters. Moreover, based on cytochrome *b* complete sequences of *A. agrarius* eight *A. agrarius* haplotypes from continental Eurasia were not subdivided into subgroups on the basis of nine cytochrome *b* complete sequences (Suzuki *et al*. 2008). Based on fossil evidence from southwestern France Aguilar *et al*. (2008) noted that a much western expansion of *A. agrarius* lineage from Asia into west Europe occurs at the end of the last cold phase of the Pleistocene.

In this study with the 66 haplotypes of the cytochrome *b* complete sequences from Eurasian *A. agrarius* (Fig. 2), 49 haplotypes from continental Eurasia formed the continental Eurasian clade (Gp 3), and the minimum JC distances between 17 haplotypes from mainland Korea and other 32 haplotypes from five regions (northeastern China, eastern China, central China, far-eastern Russia, and Europe) were 0.35%, 0.53%, 0.79%, 0.88%, and 0.71%, respectively, as shown in Figure 1, indicating that the continental Eurasian form of *A. agrarius* can be classified into *A. a. agrarius*. Heckman *et al*. (2007) noted that multi locus strategy using nuclear and mitochondrial data provides independent estimates of genealogical history, and that congruence among estimates provides strong evidence of actual population divergence. We propose further genetic analyses with additional specimens across Eurasia to confirm our present findings.

Finally, the lowland to mid-elevation species in Taiwan exhibit a general pattern of eastern versus western allopatric subpopulations, separated by the central mountain range, which functions as a prominent geographical barrier to species movement and gene flow among populations since 1 to 2 Mya (Huang & Lin 2011). From this study (Fig. 2), we first found that the Taiwan clade (Gp 1) of *A. agrarius* is divided into two subclades (western subclade from Dadushan and eastern subclade from Hualien), with average JC distance of 1.34%, six fixed site differences, and the Gst value of 0.73, indicating that the Taiwan's central mountain range functions as a geographical barrier within Taiwan *A. agrarius*.

We also found that one haplotype from unrecorded collection site in Taiwan (GenBank accession no. AB096816) was identical in its sequences to the Taiwan TDd01 from this study, which belonged to the western subclade, and we used 16 specimens of *A. agrarius* from only two locations in Taiwan. In addition, from a phylogeographic study of the large Japanese wood mouse, *Apodemus speciosus*, on Sado Island, Japan, with the cytochrome *b* gene (Tomozawa *et al*. 2010), two well diverged lineages throughout the island were found, and we propose further genetic analyses with more specimens from various locations in Taiwan to confirm the genetic differentiation between the two Taiwan subclades, recognized in this study.

REFERENCES

AGUILAR, J., PELESSIE, T., SIGE, B. & MICHAUX, J. (2008) Occurrence of the striped field mouse lineage (Apodemus agrarius Pallas, 1711; Rodentia; Mammalia) in the late Pleistocene of southwestern France. *Comptes Rendus Palevol* **7**: 217–225.

BELLINIVA, E. (2004) A phylogenetic study of the genus Apodemus by sequencing the mitochondrial DNA control region. *Journal of Zoological Systematics and Evolutionary Research* **42**: 289–297.

BERRY, R. J. (1986) Genetics of insular populations of mammals, with particular reference to differentiation and founder effects in British small mammals. *Biological Journal of Linnean Society* **28**: 205–230.

CORBET, G. B. (1978) *The mammals of the Palaearctic region: a taxonomic review*. British Museum (Natural History), Cornell University Press, London, pp. 137–138.

ECKERT, C. G., SAMIS, K. E. & LOUGHEED, C. (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Molecular Ecology* **17**: 1170–1188.

HALLIBURTON, R. (2004) *Introduction to population genetics*. Pearson Education Inc., NJ, 325 pp.

HECKMAN, K. L., MARIAMI, C. L., RASOLOARISON, R. & YODER, A. D. (2007) Multiple nuclear loci reveal patterns of incomplete lineage sorting and complex species history within western mouse lemurs. *Molecular Phylogenetics and Evolution* **43**: 353–367.

HUANG, J. & LIN, C. (2011) Lineage-specific late Pleistocene expansion of an endemic subtropical gossamer-wing damselfly, *Eupha formosa*, in Taiwan. *BMC Evolutionary Biology* **11**: 94.

HUELSENBECK, J. P., BULL, J. J. & CUNNINGHAM, C. W. (1996) Combining data in phylogenetic analysis. *Trends in Ecology and Evolution* **11**: 152–157.

IRWIN, D. M., KOCHER, T. D. & WILSON, A. C. (1991) Evolution of the cytochrome *b* gene of mammals. *Journal of Molecular Evolution* **32**: 128–144.

JOHNSON, K. P., ADLER, F. R. & CHERRY, J. L. (2000) Genetic and phylogenetic consequences of island biogeography. *Evolution* **54**: 387–396.

JONES, J. K. & JOHNSON, D. H. (1965) Synopsis of the lagomorphs and rodents of Korea. *University of Kansas Publication, Museum Natural History* **16**: 357–407.

KOH, H. S. & TIKHONOVA, G. (1998) Morphometric analyses with 15 subspecies of striped field mice, Apodemus agrarius Pallas (Mammalia, Rodentia) from Eurasia. *Korean Journal of Systematic Zoology* **14**: 341–355.

KOH, H. S., LEE, W. J. & KOCHER, T. (2000) Genetic relationships between two subspecies of Apodemus agrarius from Korea. *Heredity* **76**: 563–570.

KOH, H. S., SETER, S., ZHANG, M., WANG, J., JANG, K. H. & BAZARSAD, D. (2011) Lack of mitochondrial DNA sequence divergence in two subspecies of the striped field mouse (Apodemus agrarius mantchuricus from northeastern China and nearby Russia and *A. a. coreae* from the Korean Peninsula). *Acta Theriologica Sinica* **31**: 84–89.

KOH, H. S., BAYARLKHAGVA, D., JANG, K. H., HAN, E. D., JO, J. E., HAM, E. J., JEONG, S. K., LEE, J. H., KIM, K. S., KWEON, G. H. & IN, S. T. (2013*a*) Genetic divergence of the Siberian roe deer from Korean Jeju Island (Capreolus pygargus ochraceus), reexamined from nuclear *IRBP* and mitochondrial cytochrome *b* and control region sequences of C. pygargus. *Journal of Biological Research, Thessaloniki* **19**: 46–55.

KOH, H. S., KARTAVTSEVA, I. V., LEE, B. K., KWEON, G. H., YANG, B. G., HEO, S. W. & IN, S. T. (2013*b*) A preliminary study on genetic diversity of the Asian lesser white-toothed shrew Crocidura shantungensis (Mammalia: Soricomorpha) in mainland Korea, ad-

jacent islands, and continental East Asia: cytochrome *b* sequence analyses. *Russian Journal of Theriology* **12**(2): 71–77.

LIU, X., WEI, F., LI, M., JIANG, X., FENG, Z. & HU, J. (2004) Molecular phylogeny and taxonomy of wood mice (genus Apodemus Kaup, 1829) based on complete mtDNA cytochrome *b* sequence, with emphasis on Chinese species. *Molecular Phylogenetics and Evolution* **33**: 1–15.

LOMOLINO, M. V., RIDDLE, B. R., WHITTAKER, R. J. & BROWN, J. H. (2010). *Biogeography.* 4th ed. Sinauer Associates, Sunderland, MA, 878 pp.

LOPEZ, V. J., CULVER, M., STEPHENS, J. C., JOHNSON, W. E. & O'BRIEN, S. J. (1997) Rate of nuclear and cytoplasmic mitochondrial DNA sequence divergence in mammals. *Molecular Biology and Evolution* **14**: 277–286.

MAYR, E. & ASHLOCK, P. D. (1991) *Principles of systematic zoology.* McGraw-Hill, New York, 475 pp.

MUSSER, G. G. & CARLETON, M. D. (2005). Superfamily Muroidea. Pp. 1261–1262. *In*: WILSON, D. E. & REEDER, D. M. (eds): *Mammal species of the world: a taxonomic and geographic reference.* 3rd ed. Johns Hopkins University Press, Baltimore.

SAKKA, H., QUERE, J. P., KARTAVTSEVA, I., PAVLENKO, M., CHELOMINA, G., ATROKIN, D., BOGDANOV, A. & MICHAUX, J. (2010) Complete phylogeography of four *Apodemus* species (Mammalia: Rodentia) in the Asian Far East: evidence of Quaternary climatic changes in their genetic structure. *Biological Journal of Linnean Society* **100**: 797–821.

SUNNUCKS, P. (2000) Efficient genetic markers for population biology. *Trends in Ecology and Evolution* **15**: 199–203.

SUZUKI, H., Sato, J. J., TSUCHIYA, K., LUO, J., ZHANG, Y., WANG, Y. & JIANG, X. (2003) Molecular phylogeny of wood mice (Apodemus, Muridae) in east Asia. *Biological Journal of Linnean Society* **80**: 469–481.

SUZUKI, H., FILIPUCCI, M. G., CHELOMINA, G. N., SATO, J. J., SERIZAWA, K. & NEVO, E. (2008) A biogeographic view of Apodemus in Asia and Europe inferred from nuclear and mitochondrial gene sequence. *Biochemical Genetics* **46**: 329–346.

TAMURA, K., PETERSON, D., PETERSON, N., STECHER, G., NEI, M. & KUMAR, S. (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**: 2731–2739.

TOMOZAWA, M., TOMIDA, H., SUZUKI, H. & TSUCHIYA, K. (2010) Mitochondrial phylogeography and population history of the large Japanese wood mouse (Apodemus speciosus) on Sado Island, Japan. *Mammal Study* **35**: 93–97.

WANG, Y. (1985) Subspecific classification and distribution of Apodemus agrarius in Sichuan, China. Pp. 86–89. *In:* KAWAMICHI, T. (ed.): *Contemporary mammalogy in China and Japan.* Mammalian Society of Japan.

WRIGHT, S. (1978) *Evolution and the genetics of populations, IV. Variability within and among natural populations.* University of Chicago Press, Chicago, 85 pp.

ZHANG, Y., SANGKE, J., GUOQIANG, J., SHIBAU, L., ZHONGYAO, Y., GENGGUI, W. & MANLI, Z. (1997) *Distribution of mammalian species in China.* China Forestry Publishing House, Beijing, 280 pp.