

Lack of genetic divergence between *Mogera wogura coreana* from Korea and *M. w. robusta* from Northeastern China and adjacent Russia (Soricomorpha: Mammalia), reexamined from 12S rRNA and cytochrome *b* sequences

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To reexamine taxonomic status of endemic *Mogera wogura coreana* from Korea, we first obtained partial 12S rRNA sequences (893 bp) and complete cytochrome *b* gene sequences (1140 bp) of this subspecies, and these sequences and partial cytochrome *b* sequences (402 bp) were compared to the corresponding haplotypes of *M. wogura* from East Asia, obtained from GenBank. The one of three 12S rRNA haplotypes in *M. w. coreana* was identical to one 12S rRNA haplotype of *M. w. robusta* from East Asia: 10 complete and 13 partial cytochrome *b* haplotypes of *M. w. coreana* formed a single clade with one complete and four partial cytochrome *b* haplotypes of *M. w. robusta*, respectively. We considered that *M. w. coreana* from Korea is an endemic subspecies with only morphological differences, although it is necessary to reexamine the subspecies status of *M. w. coreana*. Additionally, in the 12S rRNA and complete cytochrome *b* sequences, *M. wogura* from Japan was distinct from the two continental subspecies of *M. w. coreana* and *M. w. robusta* with average distances of 1.76 and 5.65%, respectively; insular *M. wogura*, with within-group distances of 2.09 and 4.38%, respectively, was also genetically more divergent than the mainland *M. wogura*, with within-group distances of 0.08 and 0.57%, respectively. Thus, we considered that insular *M. wogura* of Japan dispersed into neighboring East Asian continent, which is opposite to the traditional hypothesis on the origin of Japanese *M. wogura*.

Keywords: DNA systematics; 12S rRNA; cytochrome *b* gene; Japanese mole; *Mogera wogura*

Introduction

Hutterer (2005) noted that the geographic distribution of the Japanese mole (*Mogera wogura* Temmink, 1842) extends from Korea to Japan through northeastern China and adjacent Siberia. He noted that among nine nominal subspecies, two subspecies are recognizable (*M. w. wogura* Thomas from Japan and *M. w. robusta* Nehring from Korea, northeastern China, and nearby Russia). However, *Mogera wogura coreana* from Korea was found to be distinct in morphological characters from *M. w. robusta* in northeastern China and far-eastern Russia (Jones and Johnson 1960), and four subspecies (*robusta*; *coreana*; *kobeae* from southwestern Honshu and Shikoku; and *kiusiuana* from Kyushu) were treated as a different species of *M. robusta* (Corbet 1978), indicating that the classification of *M. wogura* is still confused.

Molecular genetic studies for taxonomic reconsideration have become widespread during the past decade, and mitochondrial DNA (mtDNA) is a highly sensitive genetic marker suitable for studies of closely related taxa or populations of a variety of species (Sunnucks 2000). A population genetic analysis of

M. wogura was performed from partial cytochrome *b* sequences (402 bp) from Korea, Japan, and far-eastern Russia (Tsuchiya et al. 2000), and investigators reported that four sequences from Korea (*M. w. coreana*) and six sequences from far-eastern Russia (*M. w. robusta*) formed a continent clade-1 within *M. wogura*, and that one haplotype of *M. w. coreana* was identical to two haplotypes of *M. w. robusta* from far-eastern Russia, indicating that it is necessary to reexamine the taxonomic status of *M. w. coreana* from Korea by using complete cytochrome *b* sequences (1140 bp), with finer resolution.

In addition, complete cytochrome *b*, partial 12S rRNA, and partial RAG-1 sequences were analyzed for the examination of biogeography in Talpidae (Shinohara et al. 2004), and complete cytochrome *b* and partial 12S rRNA sequences were examined for the revision of *Mogera* (Kawada et al. 2007). They, however, used only two complete sequences of *M. wogura* from Japan to far-eastern Russia, indicating that it is necessary to obtain complete cytochrome *b* and partial 12S rRNA sequences of *M. w. coreana* from Korea in order to investigate the genetic diversity within *M. wogura*.

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In this study, to reexamine taxonomic status of endemic *M. w. coreana* from Korea and genetic divergence within *M. wogura* populations, we first obtained partial sequences of mtDNA 12S rRNA (893 bp) and complete sequences (1140 bp) of cytochrome *b* gene of *M. w. coreana* from Korea, and these sequences were compared to the corresponding haplotypes of *M. wogura*, available from GenBank. The partial cytochrome *b* sequences (402 bp) of *M. wogura*, obtained from this study and GenBank, were also analyzed, and the results were compared to the results based on complete sequences.

Materials and methods

For this analysis, we collected 15 specimens from four locations in Korea (three specimens from Cheongju, two specimens from Mt. Songri, nine specimens from Mt. Weolak, and one specimen from Mt. Seolak), and the specimen number from each location is listed in Table 1. Small pieces of muscle were taken and preserved in a deep freezer.

Total cellular DNA was extracted using a genomic DNA extraction kit (Intron Co., Seoul, Korea). The 12S rRNA was PCR-amplified using primers L651 and 12GH, designed by Adkins et al. (2001). The PCR thermal cycle for 12S rRNA was as follows: 95°C for 10 min, 94°C for 45 sec, 62°C for 45 sec, 72°C for 45 sec (30 cycles), and 72°C for 5 min. For DNA amplification of the cytochrome *b* gene, the primers L14724 and H15149 (Irwin et al. 1991) were used, and the PCR thermal cycle was as follows: 94°C for 5 min, 94°C for 1 min, 58°C for 1 min, 72°C for 1 min (32 cycles), and 72°C for 5 min. To remove primer and unincorporated nucleotides, the amplified product was purified using a DNA PrepMate kit with a silica-based matrix (Intron Co.). The purified PCR products were analyzed using an automated DNA sequencer (Perkin Elmer 377) at Bioneer Co. (Seoul, Korea).

The partial sequences (893 bp) of 12S rRNA were obtained from *M. w. coreana* in Korea, and these sequences were compared to three corresponding haplotypes of *M. wogura*, obtained from GenBank:

AB106238 (*M. w. robusta*) from Kedorovaya, far-eastern Russia, two haplotypes of *M. wogura* from Japan (AB106237 from Mishima, Honshu, and AB032846 from Kyushu). Two 12S rRNA haplotypes (AB106236, *M. imaizumii*; and AB181633, *M. insularis*) of *Mogera* were used for comparison. The complete sequences of cytochrome *b* (1140 bp) were obtained from *M. w. coreana* in Korea, and these sequences were compared to four corresponding haplotypes of *M. wogura*, obtained from GenBank: AB037646 (*M. w. robusta*) from Primorye, far-eastern Russia, three haplotypes of *M. wogura* from Japan (AB037623 from Mishima, Honshu; AB033612 from Kyushu; and NC005035, Honshu). Two complete cytochrome *b* haplotypes (AB037613, *M. imaizumii*; and AB181618, *M. insularis*) were used for comparison.

In addition, from the complete cytochrome *b* gene sequences of *Mogera*, obtained from this study and GenBank, mentioned above, partial cytochrome *b* sequences (402 bp) were used to analyze together with the 13 corresponding partial sequences of *M. wogura*, obtained from GenBank: three haplotypes (AB037639, AB037641, and AB037642) of *M. w. coreana* from Korea, four haplotypes (AB037644, AB037645, AB037647, and AB037648) of *M. w. robusta* from far-eastern Russia, three haplotypes (AB037631, AB037632, and AB037638) of *M. wogura* from Kyushu, Japan, two haplotypes (AB037624 and AB037624) of *M. wogura* from Shikoku, Japan, and one haplotype (AB036628) of *M. wogura* from Honshu, Japan.

Sequence alignment, detection of parsimonious informative sites, model selection, calculation of nucleotide distances, and tree constructions with 1000 bootstrapped replications were performed using MEGA5 (Tamura et al. 2011). The Jukes Cantor model, which showed the lowest Bayesian information criterion scores, was selected, and neighbor-joining and maximum likelihood trees were constructed. Two trees were congruent, and maximum likelihood trees are shown in this paper. *Talpa europaea* (12S rRNA, NC002391; cytochrome *b* gene, AB076829) was used as outgroup.

Table 1. Location, specimen number, and 12S rRNA and complete cytochrome *b* haplotypes of 15 specimens from *Mogera wogura coreana* in Korea used in this study. Three 12S rRNA and 10 cytochrome *b* haplotypes were identified from *M. w. coreana*.

| Location | Specimen number (12S rRNA ¹ and cytochrome <i>b</i> ² haplotypes) |
|------------|--|
| Cheongju | KM09 and KM17 (CBKc01 ²); KM012 (12SKcKsoKw01 ¹ , CBKc02 ²) |
| Mt. Songri | KM13 (12SKcKsoKw01 ¹ , CBKso01 ²), KM61 (CBKso01 ²) |
| Mt. Weolak | KM01 (CBKw01 ²); KM02 and KM06 (CBKw02 ²); KM003 (12SKw02 ¹ , CBKw03 ²); KM04 (CBKw04 ²); KM05, KM08, and KM11 (CBKw05 ²); KM014 (12SKcKsoKw01 ¹ , CBKw06 ²) |
| Mt. Seolak | KM007 (12SKse01 ¹ , CBKse01 ²) |

Results

Three 12S rRNA haplotypes were identified from partial sequences (893 bp) of five specimens of *M. w. coreana* from four locations in Korea, as shown in Table 1: haplotype 12SKcKsoKw01, three specimens from Cheongju, Mt. Songri, and Mt. Weolak; 12SKw02, one specimen from Mt. Weolak; and 12SKse01, one specimen from Mt. Seolak. Within six haplotypes of *M. wogura* (three haplotypes from this study and three haplotypes from GenBank), 69 sites (7.72%) were variable, and 23 sites (2.57%) were parsimoniously informative. The average nucleotide distance among the three haplotypes of *M. w. coreana* from Korea was 0.08%.

Maximum likelihood tree with the six 12S rRNA haplotypes from *M. wogura* is shown in Figure 1. One haplotype (12SKcKsoKw01) of *M. w. coreana* from three locations in Korea was identical to one haplotype (AB106238) of *M. w. robusta* from Kedorovaya, far-eastern Russia, and four haplotypes from the two continental subspecies (*coreana* from Korea and *robusta* from far-eastern Russia) formed one clade (Gp 1), with a within-group average distance of 0.08%. In addition, the clade (Gp 1), composed of four haplotypes of the two continental subspecies, was distinct from two haplotypes (AB106237 and AB032846) of *M. wogura* in Japan, with an average distance of 1.76% (range 1.59–2.09%), although the two haplotypes from Japan were variable, with an average distance of 2.09%.

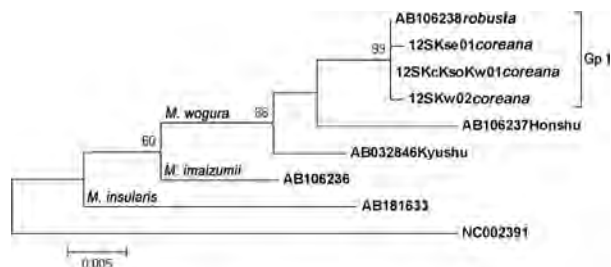


Figure 1. Maximum likelihood tree with six 12S rRNA haplotypes (893 bp) from *Mogera wogura*. Three haplotypes of *M. w. coreana* were obtained from this study, and three haplotypes of *M. wogura* were obtained from GenBank. The tree was constructed with 1000 bootstrapped replications, and the bootstrap values $>50\%$ are reported at the internodes. For three haplotypes of *M. w. coreana*, location and specimen number are listed in Table 1, and subspecies name follows haplotype name in each haplotype. In one haplotype (AB106238) of *M. w. robusta*, the subspecies name of *robusta* follows the accession number, whereas in the other two Japanese haplotypes (AB106237 and AB032846), the location name in Japan follows the accession number. Two 12S rRNA haplotypes of *Mogera* (AB106236, *M. imaizumii*; AB181633, *M. insularis*) were used for comparison, and *Talpa europaea* (NC002391) was used as outgroup.

Ten cytochrome *b* haplotypes were identified from complete sequences (1140 bp) of 15 specimens of *M. w. coreana* from four locations in Korea, as shown in Table 1; two haplotypes (CBKc01 and CBKc02) from Cheongju, CBKso01 from Mt. Songri, six haplotypes (CBKw01–CBKw06) from Mt. Weolak, and CBKse01 from Mt. Seolak were recognized. Within 14 haplotypes (1140 bp) of *M. wogura* (10 haplotypes from this study and four haplotypes from GenBank), 84 sites (7.37%) were variable, and 61 sites (5.35%) were parsimoniously informative. The average nucleotide distance among 10 haplotypes of *M. w. coreana* from Korea was 0.43% (range 0.09–0.97%), and an average distance between 10 haplotypes of *M. w. coreana* and one haplotype (AB037646) of *M. w. robusta* from far-eastern Russia was 0.57%.

Maximum likelihood tree with 14 cytochrome *b* haplotypes from *M. wogura*, based on complete sequences (1140 bp), is shown in Figure 2, and 11 haplotypes from two continental subspecies (*coreana* from Korea and *robusta* from far-eastern Russia) formed a clade (Gp 1). In addition, the clade (Gp 1) from 11 haplotypes of the two continental subspecies was distinct from three haplotypes of *M. wogura* (AB037623, NC005035, and AB033612) in Japan, with an average distance of 5.65% (range 5.17–6.51%); the three haplotypes from Japan were also variable, with an average distance of 4.38% (range 2.14–5.74%).

In addition, maximum likelihood tree with 27 partial cytochrome *b* haplotypes (402 bp) of *M. wogura* is shown in Figure 3, and 17 haplotypes from the two continental subspecies formed one clade (Gp 1), with an average distance of 0.49% between the two subspecies. The clade (Gp 1), composed of 17 haplotypes of the two continental subspecies, was distinct from nine haplotypes of *M. wogura* from Japan, with an average distance of 5.36%, and one haplotype of *M. w. robusta* from Ussuriysky, far-eastern Russia, with an average distance of 5.45%.

In summary, in this 12S rRNA and cytochrome *b* sequence analyses, the subspecies *coreana* from Korea was not divergent from the subspecies *robusta* from far-eastern Russia, whereas these two continental subspecies, with low divergence, were distinct from other *M. wogura* from Japan, with high divergence. Additionally, the partial cytochrome *b* sequence (402 bp) from Ussuriysky, far-eastern Russia, is peculiar among the other haplotypes of *M. wogura*.

Discussion

Tsuchiya et al. (2000) considered, based on partial sequence (402 bp) of cytochrome *b* gene, one haplotype of *M. w. robusta* from one specimen at Ussuriysky in

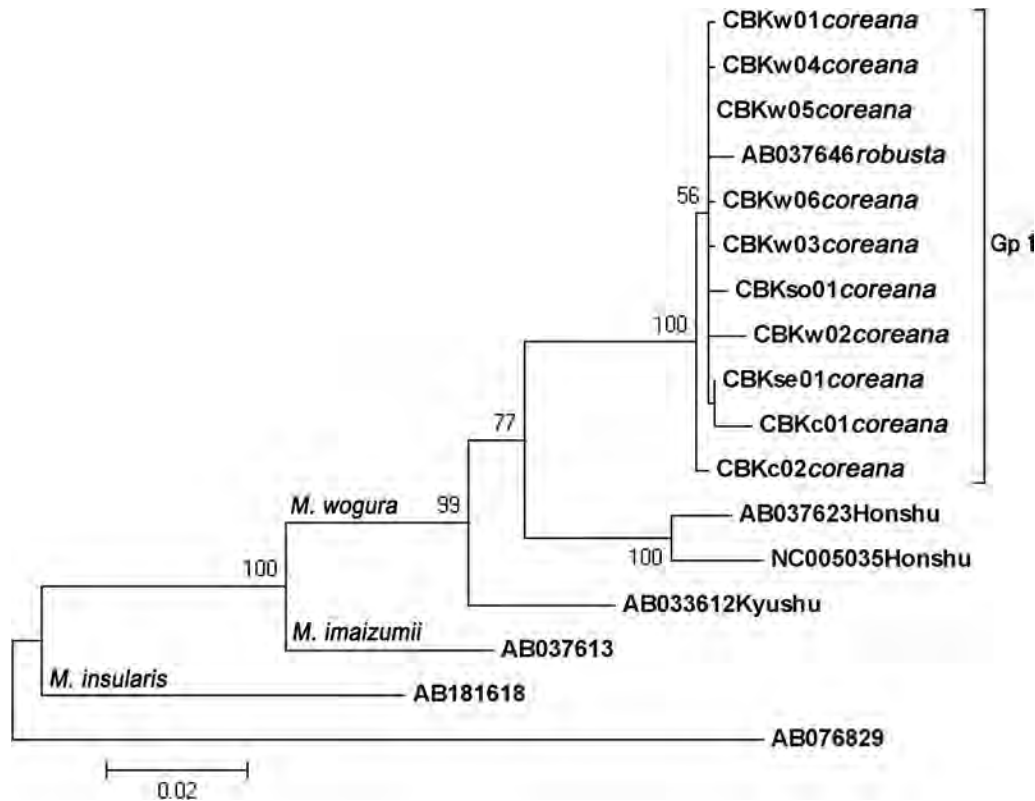


Figure 2. Maximum likelihood tree with 14 complete cytochrome *b* haplotypes (1140 bp) from *Mogera wogura*. Ten haplotypes of *M. w. coreana* were obtained from this study, and four haplotypes of *M. wogura* were obtained from GenBank. The tree was constructed with 1000 bootstrapped replications, and the bootstrap values >50% are reported at the internodes. For 10 haplotypes of *M. w. coreana*, location and specimen number are listed in Table 1, and subspecies name follows haplotype name. In one haplotype (AB037646) of *M. w. robusta* from far-eastern Russia, the subspecies name of *robusta* follows the accession number, whereas in the other three Japanese haplotypes (AB037623, NC005035, and AB033612) the location name in Japan follows the accession number. Two complete cytochrome *b* haplotypes of *Mogera* (AB037613, *M. imaizumii*; and AB181618, *M. insularis*) were used for comparison, and *Talpa europaea* (AB076829) was used as outgroup.

far-eastern Russia as a clade (continent-2). In this analysis from the partial cytochrome *b* sequences (402 bp) with additional specimens from Korea (Figure 3), we confirmed that one Ussuriysky haplotype is distinct from the other 26 haplotypes of *M. wogura* in Korea, far-eastern Russia, and Japan, with an average distance of 5.45%. Dubey et al. (2009) noted that typical features of pseudogene are (1) the presence of stop codon and frame-shift mutations, (2) an accumulation of nonsynonymous mutations, and (3) the presence of chimeric sequences. We could not recognize any characteristics of pseudogene from the Ussuriysky cytochrome *b* sequence, and we considered that the Ussuriysky sequence is not an artifact.

Tsuchiya et al. (2000) also noted that 10 cytochrome *b* partial sequences of *M. wogura* from Korea and far-eastern Russia formed the other continent clade (continent-1), and they found that the diversity between the two clades (continent-1 and continent-2) from Korea and far-eastern Russia was greater than the

diversity among the three clades (Honshu, Shikoku, and Kyushu) from Japanese islands. In this analysis (Figure 3), the average nucleotide distance between 18 continental haplotypes (1 Ussuriysky haplotype and 17 haplotypes from Korea and far-eastern Russia) was greater than the average distance among nine insular haplotypes from Japanese islands, indicating that the continental *M. wogura* dispersed into Japanese islands, as noted by Tsuchiya et al. (2000).

However, Tsuchiya et al. (2000) designated only one distinct haplotype of the Ussuriysky as a continent-2 clade, without examination of the specimens from across *M. wogura*'s distribution range, including north-eastern China and interior far-eastern Russia. In this study with additional specimens from Korea (Figure 3), we could not find the specimens which belonged to the continent-2 clade, and we found identical 12S rRNA sequences from three specimens in Korea and one specimen in Kedorovaya, far-eastern Russia. Tsuchiya et al. (2000) had already found identical cytochrome *b*

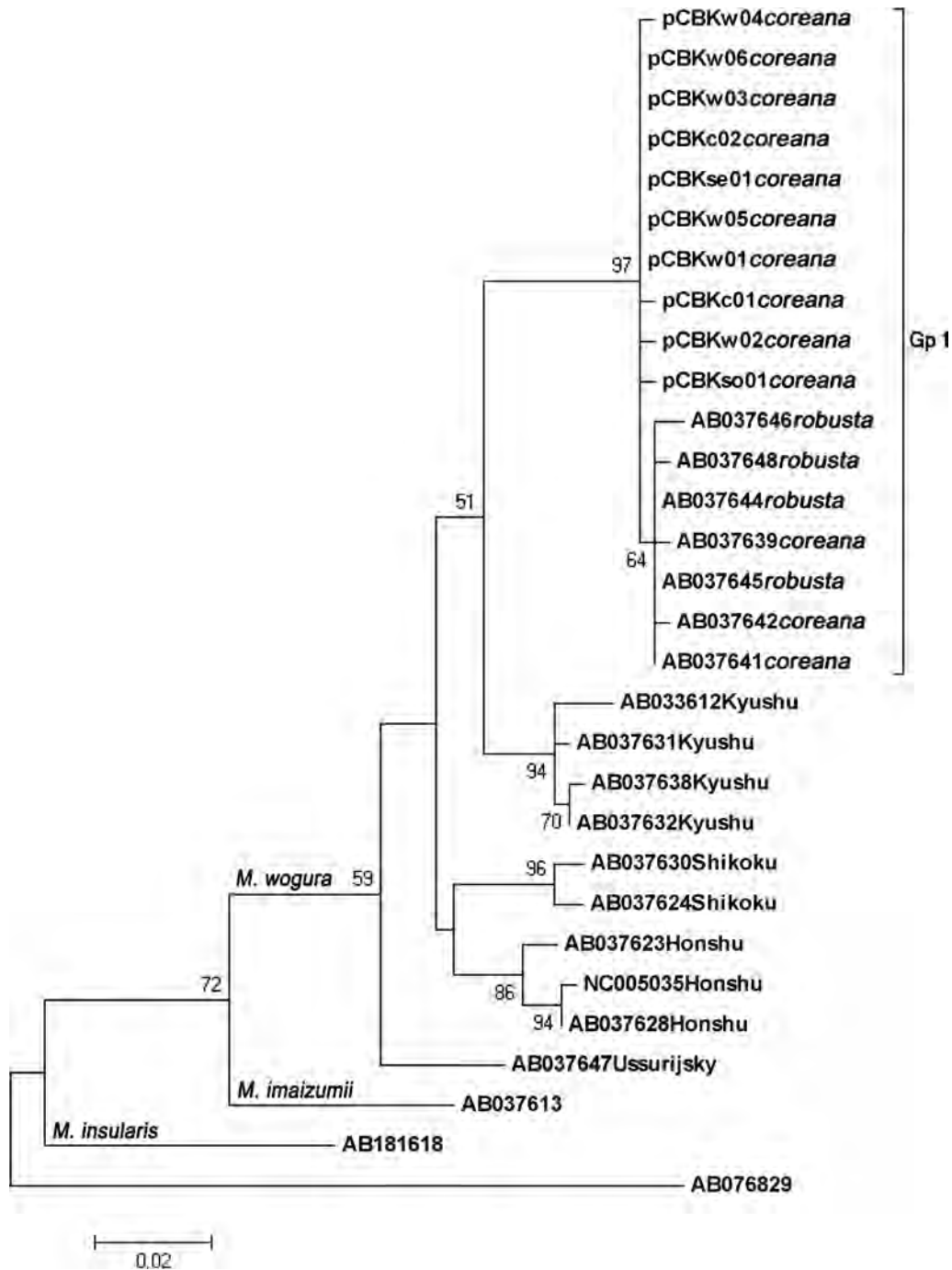


Figure 3. Maximum likelihood tree with 27 partial cytochrome *b* haplotypes (402 bp) from *Mogera wogura*. Ten haplotypes of *M. w. coreana* were obtained from this study, and 17 haplotypes of *M. wogura* were obtained from GenBank. The tree was constructed with 1000 bootstrapped replications, and the bootstrap values > 50% are reported at the internodes. For 10 haplotypes of *M. w. coreana*, location and specimen number are listed in Table 1, and subspecies name follows haplotype name in each haplotype. In seven haplotypes of *M. w. coreana* and *M. w. robusta*, the subspecies name of *coreana* or *robusta* follows the accession number, whereas in one haplotype (AB037647) from Ussuriysky and the other 10 Japanese haplotypes, the location name follows the accession number. Two cytochrome *b* haplotypes of *Mogera* (AB037613, *M. imaizumii*; and AB181618, *M. insularis*) were used for comparison, and *Talpa europaea* (AB076829) was used as outgroup.

sequences from one specimen in Korea and one specimen in Kedorovaya, which is not far from the Ussuriysky in far-eastern Russia. Thus, for our further

discussions in our present paper, we decided to exclude the continent-2 clade, which was recognized from only one, ‘mysterious’ Ussuriysky haplotype and from

insufficient sampling by Tsuchiya et al. (2000), although it is needed to examine the nature of this haplotype by further studies.

Tsuchiya et al. (2000) reported, based on partial cytochrome *b* sequences (402 bp), that 10 sequences of *M. wogura* from Korea and far-eastern Russia formed a continent clade-1, and one sequence of *M. w. coreana* from Mt. Seolak in Korea was identical to two sequences of *M. w. robusta* from Kedorovaya and Khasan in far-eastern Russia. In this study from partial cytochrome *b* sequences with additional specimens from Korea (Figure 3), we confirmed that 17 sequences of the two continental subspecies in *M. wogura* formed a clade (Gp 1), and that one haplotype of *M. w. coreana* from Seolak was identical to two haplotypes of *M. w. robusta* from far-eastern Russia. In addition, in this study with 14 complete cytochrome *b* haplotypes (1140 bp) of *M. wogura* (Figure 2), 11 haplotypes from the two continental subspecies formed a single clade (Gp 1); the average distance between 10 haplotypes of *M. w. coreana* and one haplotype of *M. w. robusta* was 0.57%.

Furthermore, in this study with six 12S rRNA haplotypes (893 bp) of *M. wogura* in East Asia (Figure 1), one haplotype of *M. w. coreana* from three locations (Cheongju, Mt. Songri, and Mt. Weolak) in Korea was identical to one haplotype of *M. w. robusta* from Kedorovaya: four haplotypes from two subspecies (*coreana* from Korea and *robusta* from far-eastern Russia) of *M. wogura* formed one clade (Gp 1), with a within-group average distance of 0.08%. Thus, we concluded that *M. w. coreana* from Korea is not genetically divergent from *M. w. robusta* in far-eastern Russia.

On the basis of morphological studies of eight external and cranial characters, Jones and Johnson (1960) reported that *M. w. coreana* from Korea is smaller in size than *M. w. robusta* from northeastern China and adjacent Russia, and Corbet (1978) also classified *M. w. coreana* as a different subspecies of *M. robusta*, although Hutterer (2005) listed *M. w. coreana* as a synonym of *M. w. robusta*. We found that this sequencing results for these two continental subspecies of *M. wogura* (Figures 1–3) does not support the subspecies classification based on morphological characters by Jones and Johnson (1960) and Corbet (1978), distinguishing the two subspecies, but does support the treatment by Hutterer (2005), recognizing only one subspecies of *M. w. robusta*.

A classification should be the product of all available characters distributed as widely and evenly as possible over the organisms studied (Huelsenbeck et al. 1996). Furthermore, most biologists would prefer to see DNA sequence information as a supplement to, rather than as a replacement for, morphological data (Mallet and Willmott 2003). Thus, we considered that

M. w. coreana from Korea is an endemic subspecies with only morphological differences, although it is necessary to reexamine the subspecies status of *M. w. coreana*.

Additionally, Johnson et al. (2000) noted that island populations should diverge over time (genetically and morphologically) from populations of respective mainland species, although at the end of the last glacial, large areas of continental shelf were dry land, facilitating exchange of plant and animal species by land bridge connections to what are now isolated islands (Lomolino et al. 2010). Tsuchiya et al. (2000) reported, based on cytochrome *b* partial sequences (402 bp), that one clade of continent-1 from Korea and far-eastern Russia was distinct from other three clades from Japan. In this study with partial cytochrome *b* sequences, with additional specimens from Korea (Figure 3), we confirmed that the clade composed of 17 sequences from Korea and far-eastern Russia (Gp 1) is distinct from other nine insular haplotypes from Japan, with an average distance of 5.36%.

Kawada et al. (2007) found that two complete cytochrome *b* haplotypes (1140 bp) of *M. wogura*, collected from Japan and far-eastern Russia, had a distance value of 5.3%. In this study with 12S rRNA and complete cytochrome *b* sequences (Figure 1 and 2), three haplotypes of *M. wogura* from Japan were distinct from the 11 haplotypes of the two continental subspecies, with average distances of 1.76 and 5.65%, respectively. We considered that insular *M. wogura* from Japan has been geographically isolated even during the last glacial and is genetically diverged from neighboring population in Korea and far-eastern Russia.

Tsuchiya et al. (2000) also noted that the ancestral *M. wogura* from East Asian continent invaded the Japanese islands. In this study with 12S rRNA and complete cytochrome *b* sequences, we found that Japanese *M. wogura*, with a within-group distance of 2.09 and 4.38%, respectively, was genetically much more heterogeneous than the continental *M. wogura* (Gp 1), with a within-group distance of 0.08 and 0.57%, respectively. We considered that an alternative hypothesis, that is, the dispersal of insular *M. wogura* of Japan into neighboring East Asian continent, can be the most plausible explanation for the lack of genetic divergence of the continental *M. wogura* from Korea and far-eastern Russia, compared with the divergent *M. wogura* from Japanese islands. Thus, we propose further analyses with morphological and DNA characters of additional *M. wogura* specimens from across its distributional range to reexamine evolutionary history within this species and the subspecies classification as well.

References

- Adkins RM, Gelke EL, Rowe D, Honeycutt RL. 2001. Molecular phylogeny and divergence time estimates for major rodent groups: evidence from multiple genes. *Mol Biol Evol.* 18:777–791.
- Corbet GB. 1978. The mammals of the Palaearctic region: a taxonomic review. London: British Museum (Natural History), Cornell University Press. p. 35–36.
- Dubey S, Michaux J, Brunner H, Hutterer R, Vogel P. 2009. False phylogenies on wood mice due to cryptic cytochrome-*b* pseudogene. *Mol Phylogenet Evol.* 50:633–641.
- Huelsenbeck JP, Bull JJ, Cunningham CW. 1996. Combining data in phylogenetic analysis. *Trends Ecol Evol.* 11: 152–157.
- Hutterer R. 2005. Order Soricomorpha. In: Wilson DE, Reeder DM, editors. *Mammal species of the world: a taxonomic and geographic reference*. 3rd ed. Baltimore: Johns Hopkins University Press. p. 306–307.
- Irwin DM, Kocher TD, Wilson AC. 1991. Evolution of the cytochrome *b* gene of mammals. *J Mol Evol.* 32:128–144.
- Johnson KP, Aler FR, Cherry JL. 2000. Genetic and phylogenetic consequences of island biogeography. *Evolution* 54:387–396.
- Jones JK, Johnson DH. 1960. Review of the insectivores of Korea. *Univ. of Kansas Publ., Mus. Nat. Hist.* 9: 549–578.
- Kawada S, Shinohara A, Kobayashi S, Harada M, Oda S, Lin L. 2007. Revision of the mole genus *Mogera* (Mammalia: Lipotyphla: Talpidae) from Taiwan. *Syst Biodiversity* 5:223–240.
- Lomolino MV, Riddle BR, Whittaker RJ, Brown JH. 2010. *Biogeography*. 4th ed. Sunderland, MA: Sinauer Associates Inc. p. 878.
- Mallet J, Willmott K. 2003. Taxonomy: renaissance or Tower of Babel. *Trends Ecol Evol.* 18:57–59.
- Shinohara A, Suzuki H, Tsuchiya K, Zhang Y, Luo J, Jiang X, Wang Y, Campbell KL. 2004. Evolution and biogeography of talpid moles from continental East Asia and the Japanese islands inferred from mitochondrial and nuclear gene sequences. *Zool Sci.* 21:1177–1185.
- Sunnucks P. 2000. Efficient genetic markers for population biology. *Trends Ecol Evol.* 15:199–203.
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: molecular evolutionary genetic analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol Biol Evol.* 28:2731–2739.
- Tsuchiya K, Sujuki H, Shinohara A, Harada M, Wakana S, Sakaizumi M, Han S, Lin L, Kryukov AP. 2000. Molecular phylogeny of East Asian moles inferred from the sequence variation of the mitochondrial cytochrome *b* gene. *Genes Genet Syst.* 75:17–24.