Journal of Species Research 15(1):83-116, 2026
https://doi.org/10.12651/JSR.2026.15.1.083

Open Access

Two new subspecies of the red-tongued pit viper *Gloydius ussuriensis* (Emelianov, 1929) (Viperidae, Crotalinae) in the Republic of Korea: Genetics, morphology, and ecology

Min Seock Do[1,#], Hye Sook Jeon[1,#], Yun Sun Lee[1,#], Hyung-Kyu Nam[1], Mu-Yeong Lee[2], Jung A Kim[1], Ji Hwa Jung[3], Yoonjee Hong[1], Myoung Chan Cha[4], Il Nam Kim[5], Woojin Choi[6], Seon-Mi Park[7], Sumin Lim[8], Nakyung Yoo[9], Jae-Hwa Suh[1], Sang-Cheol Lee[5,*], Hong Shik Oh[7,*] and Junghwa An[1,*]

[1]*National Institute of Biological Resources, Incheon 22689, Republic of Korea*
[2]*DNA Analysis Division, Seoul Institute, National Forensic Service, Seoul 08036, Republic of Korea*
[3]*Honam National Institute of Biological Research, Mokpo 58762, Republic of Korea*
[4]*Department of Biology, Kyung Hee University, Seoul 02453, Republic of Korea*
[5]*Department of Biology, Incheon National University, Incheon 22012, Republic of Korea*
[6]*Department of Biology, Kangwon National University, Chuncheon 24341, Republic of Korea*
[7]*Faculty of Science Education, Jeju National University, Jeju 63243, Republic of Korea*
[8]*Department of Applied Biology, Chungnam National University, Daejeon 34134, Republic of Korea*
[9]*Research Center for Endangered Species, National Institute of Ecology, Yeongyang 36531, Republic of Korea*

[#]*Co-first authors: Min Seock Do, Hye Sook Jeon, and Yun Sun Lee*
**Correspondent: 3881103@hanmail.net (S-C.Lee), sciedu@jejunu.ac.kr (H.S.Oh), safety@korea.kr (J.An)*

This red-tongued pit viper (*Gloydius ussuriensis*) inhabits the Korean Peninsula, including inland areas as well as Baengnyeongdo, Jeju-do, and Gapado Islands. However, the taxonomic status of *Gloydius ussuriensis* populations, including their subspecies classification, remains unclear, as few phylogenetic or taxonomic studies have compared inland and island populations. To address this gap, we analyzed 513 individuals sampled between 2018 and 2022. Mitochondrial DNA revealed two major lineages: (1) inland, Baengnyeongdo, and Chinese populations and (2) Jeju-do and Gapado populations. Nuclear DNA analysis (K = 3) identified three genetic groups, namely, inland, Baengnyeongdo, and Gapado, whereas the Jeju-do population exhibited an admixture of the inland and Gapado groups. Discriminant analysis of the 11 morphological traits indicated clear differences among the Baengnyeongdo, Gapado, Jeju-do, and inland populations. The snout-vent length was the longest in Baengnyeongdo and the shortest in the Gapado group. The ecological niche overlap between the populations was low (PI = 0.4075). Based on these findings, three subspecies have been identified: *G. ussuriensis ussuriensis*, *G. ussuriensis baengnyeongensis*, and *G. ussuriensis jejuensis*. The Tsushima Island pit viper (*G. tsushimaensis*) from Japan, although classified as a separate species, showed genetic and morphological similarities to the Jeju-do-Gapado group. Further phylogenetic and taxonomic studies are needed for *G. ussuriensis* island populations in southwestern Korea, which were not included in this study.

Keywords: Asian herpetology, island population, isolated evolution, mtDNA, pit viper

All content in the Journal of Species Research (JSR), published by the National Institute of Biological Resources (NIBR), is Open Access, meaning it is freely accessible online to everyone without fees or the need for authors' permission. Open Access articles are automatically archived in the Korea Institute of Science and Technology Information (KISTI)'s Open Access repository, AccessON. All JSR content is published and distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License (CC BY-NC-ND 4.0). This license permits non-commercial use, distribution, and reproduction in any medium, provided the original author and source are properly credited. However, no modifications or derivative works are allowed.

©2026 National Institute of Biological Resources.
This article was authored by [Min Seock Do, Hye Sook Jeon, Yun Sun Lee, Hyung-Kyu Nam, Mu-Yeong Lee, Jung A Kim, Ji Hwa Jung, Yoonjee Hong, Myoung Chan Cha, Il Nam Kim, Woojin Choi, Seon-Mi Park, Sumin Lim, Nakyung Yoo, Jae-Hwa Suh, Sang-Cheol Lee, Hong Shik Oh and Junghwa An] and is published by the National Institute of Biological Resources under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License (CC BY-NC-ND 4.0). Non-commercial use, distribution, and reproduction in any medium are permitted, provided the original authors are properly credited and the work is not modified in any way.

Introduction

Taxonomically, a subspecies is defined as a population within a species that is isolated by geographical barriers, such as mountain ranges or oceans, and exhibits genetic, morphological, or ecological differences. Such populations are in the process of speciation but have not yet undergone reproductive isolation (Pianka, 2011; Grant, 2017). Islands serve as important spaces for understanding species differentiation in evolutionary biology and have gained widespread attention in zoology, taxonomy, geography, ecology, and genetics (Shine *et al*., 2002; Coonan *et al*., 2005; Phillimore and Owens, 2006). The Korean Peninsula, surrounded by the sea on three sides, contains approximately 3,300 large and small islands, with the majority located in the South and West Seas (Cho *et al*., 2013). Many organisms on these islands became isolated due to rapid changes in sea level from the last glacial maximum (LGM) to the Holocene (Bloom and Park, 1985; Pirazzoli, 1991; Cho *et al*., 2013). Phylogenetic studies have elucidated the evolutionary history of various flora and fauna (Isogawa *et al*., 1994; Koh *et al*., 2000; Shine *et al*., 2002), particularly in the southwestern islands, which have yielded important geographical and evolutionary insights and led to the discovery of new species and subspecies (Koh *et al*., 2000; Wagner *et al*., 2016; Asadi *et al*., 2019).

Reptile species are less conspicuous than mammals, fish, and amphibians, which can limit sample collection, genetics, and evolutionary analysis (Friars and Diamond, 2011; Asadi *et al*., 2019; Morales-Martínez *et al*., 2021; Wagner *et al*., 2021). In particular, species of the family Viperidae are less active than others of the Serpentes suborder, exhibit a narrower range of behavior, and therefore have a narrower distribution range. They provide a useful model for studying the extent of genetic variation caused by geographical barriers and isolation (Reinert and Rupert, 1999; Gibbons *et al*., 2000; Wang *et al*., 2015; Do *et al*., 2017). Vipers are difficult subjects for research because of the relative lethality of their venom (Shim *et al*., 1998; Debono *et al*., 2019; Zhang *et al*., 2022). Nevertheless, over the past two decades, considerable efforts have been made in China, Japan, Russia, and other countries to elucidate the taxonomic intricacies and evolutionary history of Viperidae in Asia (Isogawa *et al*., 1994; Ding *et al*., 2011; Wang *et al*., 2015; Asadi *et al*., 2019; Zhang *et al*., 2022). However, few phylogenetic and taxonomic studies have considered Viperidae inhabiting the Korean Peninsula (Lee *et al*., 2022).

At least 23 species of the genus *Gloydius* (Viperidae) have been described (Orlov and Barabanov, 1999; Zhao, 2006; David and Vogel, 2015; Shi *et al*., 2017; 2018). The genus is taxonomically divided into two major groups. The red-tongued pit viper (*Gloydius ussuriensis*) belongs to the Brevicaudus group and is characterized by four palatine teeth and 21 dorsal scales. In contrast, the intermedius group is characterized by three palatine teeth and 23 dorsal scales (Gloyd and Conant, 1982; Guo and Zhang, 2002). The distribution of *G. ussuriensis* extends from Jeju-do Island in the Republic of Korea (southern limit) to North Korea, northeastern China, and the Russian Far East. In China, its geographical distribution range is very narrow, leading to its designation as an endangered species and legal protection (Emelianov, 1929; Zhao, 1998; Orlov and Barabanov, 1999). In the Republic of Korea, *G. ussuriensis* is widely distributed across the entire inland Korean Peninsula, as well as Jeju-do Island and several other large and small islands in the southwest. It is primarily found in mountainous areas at elevations of 0−1,200 m, as well as in adjacent rivers, valleys, and farmlands (Do and Yoo, 2014; Do *et al*., 2016; Do and Lee, 2023). This species exhibits greater morphological variation than the other vipers, particularly in terms of regional body size and head shape. However, few studies have compared specific morphological characteristics between regions (Kim *et al*., 2010; Kim and Oh, 2014b; David and Vogel, 2015; Do *et al*., 2023). Therefore, further research is needed to clarify regional differences and resolve the phylogenetic classification system of *G. ussuriensis* through genetic research.

This study examined the genetic, morphological, and ecological characteristics of *G. ussuriensis* populations from inland Korea and Baengnyeongdo, Jeju-do, and Gapado Islands. We aimed to elucidate the genetic variation and taxonomic status of populations isolated from geographical barriers. The phylogenetic relationships of *G. ussuriensis* were examined using mitochondrial DNA (mtDNA), while nuclear DNA was used to analyze the genetic diversity, structure, and differentiation levels. Major morphological factors, such as body length and scale number, were measured to distinguish the morphological characteristics of each group. Climatic and geomorphological environmental data for the study area were used to determine the ecological characteristics and niche of each population. The findings make a valuable contribution to clarifying the phylogenetic classification system of *G. ussuriensis* inhabiting the Republic of Korea, focusing on its genetic, morphological, and ecological characteristics.

Materials and Methods

Sample collection

Biological tissue samples for morphological and genetic analyses were obtained from the Biobanks of the National Institute of Biological Resources (NIBR BIOBANK) and Jeju National University. From 2018 to 2022, individuals were captured from forest valleys, rivers, and graveyards

Table 1. Genetic, morphological, and ecological information for *G. ussuriensis* by region.

Topography	Site	Code name				Number of information			
		mtDNA	ssrDNA	Morphology	Ecology	mtDNA	ssrDNA	Morphology	Ecology
Island	Baengnyeongdo	BI	BI	BI	BI	35	35	28	35
Korean Peninsula	Chungcheongbuk-do	CN	CN	KP	KP		27	7	48
Korean Peninsula	Chungcheongnam-do	CS	CS	KP	KP	28	42	18	59
Korean Peninsula	Gyeonggi-do	GG	GG	KP	KP	12	28		28
Island	Gapado	GI	GI	GI	GI	30	34	33	55
Korean Peninsula	Gyeongsangbuk-do	GN	GN	KP	KP	28	39	2	41
Korean Peninsula	Gyeongsangnam-do	GS	GS	KP	KP	20	28	1	30
Korean Peninsula	Jeju-do	JI	JI	JI	JI	18	31	35	66
Korean Peninsula	Jeollanam-do	JS	JS	KP	KP			7	46
Korean Peninsula	Northern Gangwon-do	KN	KN	KP	KP	34	33	7	34
Korean Peninsula	Southern Gangwon-do	KS	KS	KP	KP	54	55	2	55
Island	Heuksando	SHI	SHI	–	SHI		4	–	4
Island	Jangdo	SJI	SJI	–	SJI		9	–	9
					Total	259	365	140	510

Korean Peninsula (KP) Baengnyeongdo Island (BI), Chungcheongbuk-do (CN), Chungcheongnam-do (CS), Gyeonggi-do (GG), Gapado Island (GI), Gyeongsangbuk-do (GN), Gyeongsangnam-do (GS), Jeju-do Island (JI), Northern Gangwon-do (KN), Southern Gangwon-do (KS), Heuksando Island (SHI), and Jangdo Island (SJI).

across Korea using snake tongs or hooks (Do and Yoo, 2014). For genetic analysis, 0.2 cm of tail tip tissue was excised and preserved in 75% alcohol. Morphological information was collected only for adults with a total length of $\geq$40 cm (Kim and Oh, 2014b; Do *et al*., 2023). In total, 513 individuals were examined for genetic, morphological, and ecological characteristics and classified according to inland mountainous areas, administrative districts, and island regions (Table 1; Appendix). All animals were handled in accordance with legal regulations and released at the capture site and all procedures were approved by the Institutional Animal Care and Use Committee of the National Institute of Biological Resources (No. NIBR IACUC 20220001).

mtDNA testing was conducted on 259 individuals divided into five groups: Baengnyeongdo Island (BI; n = 35), inland (Group A; n = 105), inland (Group B; n = 71), Gapado Island (GI; n = 30), and Jeju-do Island (JI; n = 18). Nuclear DNA analysis was performed on 365 individuals divided into 12 groups: Chungcheongbuk-do (CN; n = 27), Chungcheongnam-do (CS; n = 42), Gyeonggi-do (GG; n = 28), Gyeongsangbuk-do (GN; n = 39), Gyeongsangnam-do (GS; n = 28), Gangwon-do Northern Region (KN; n = 33), Gangwon-do Southern Region (KS; n = 55), Jeju-do (JI; n = 31), Baengnyeongdo (BI; n = 35), Gapado Island (GI; n = 34), Heuksando Island (SHI; n = 4), and Jangdo Island (SJI; n = 9). Morphological analyses were conducted on 140 individuals divided into four groups: Korean Peninsula KP (n = 44), BI (n = 28), JI (n = 35), and GI (n = 33). Ecological characteristics were assessed using 510 samples divided into five groups: KP (n = 341), JI (n = 66), BI (n = 35), GI (n = 55), and SHI and SJI (n = 13).

Genetic characteristics

For the genetic analysis (Appendix), all tissue samples were extracted using a QIAamp® Micro kit (QIAGEN) according to the manufacturer's protocol.

mtDNA. PCR amplification of the mitochondrial cytochrome b gene (cytb, 936 bp) was performed using a specific forward primer L14724 (5′-TGACTTGAAGAACCACCGTTG-3′) and reverse primer H16064 (5′-CTTTGGTTTACAAGAACAATGCTTTA-3′) (Eskandar *et al*., 2018). The PCR reaction mixture (total volume: 20 µL) contained 1 µL template DNA (20–50 ng/µL), 10 µL 2X Bioneer PreMix (containing 100 µM of dNTP, 1.5 mM of $MgCl_2$, and 1 unit of Taq polymerase), and 1 µL each of the forward and reverse primers (10 × concentration). The PCR reaction conditions were as follows: denaturation at 95°C for 5 min, followed by 35 cycles of 1 min at 95°C, 1 min at 55°C, and 1 min at 72°C, with a final extension step at 72°C for 5 min.

The amplified cytb gene product was purified using ethanol (Genorech Corp., Republic of Korea) and the base sequence was analyzed using an ABI PRISM 3730XL (Applied Biosystems, Foster, CA, USA).

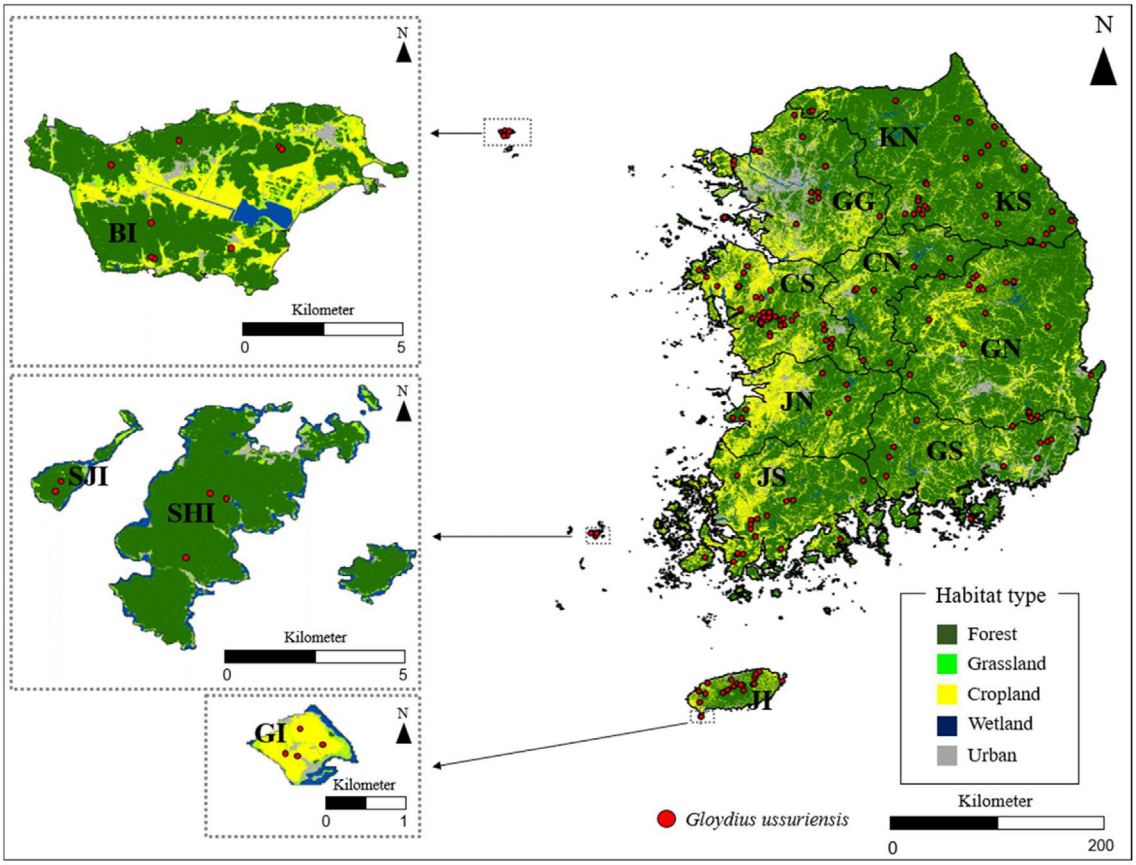


Fig. 1. Topography of the Republic of Korea, including regions and islands such as Baengnyeongdo Island (BI), Chungcheongbuk-do (CN), Chungcheongnam-do (CS), Gyeonggi-do (GG), Gapado Island (GI), Gyeongsangbuk-do (GN), Gyeongsangnam-do (GS), Jeju-do Island (JI), Northern Gangwon-do (KN), Southern Gangwon-do (KS), Heuksando Island (SHI), and Jangdo Island (SJI).

Nuclear DNA. Seventeen species-specific simple sequence repeat (SSR) markers (Kim *et al*., 2023; Jeon *et al*., 2024a) were amplified according to QIAGEN® Multiplex PCR Kit protocols to amplify multiplex panel DNA fragments (Jeon *et al*., 2024b). Each forward primer (5′) was tagged with a universal dye-labeled primer (M13-6FAM, Hill-VIC, Neomycin-PET, and T3-NED) for annealing. The reaction mixture (total volume: 50 µL) comprised 2 µL template DNA (10 ng/µL), 18 µL RNase-free water, 25 µL 2X QIAGEN Multiplex PCR Master Mix (QIAGEN® Multiplex PCR Kit), and 5 µL 10X primer mix. All primers were diluted with TE (10 mM Tris, 1 mM EDTA, pH 8.0) to prepare a 100 µM stock solution. Each marker, consisting of three primer stocks, was prepared as a 2 µM primer mix (labeled forward primer : reverse primer : dye-labeled universal primer = 1 : 4 : 4). Multiplex PCR was performed using combinations of two to four primers. The PCR reaction conditions were as follows: denaturation at 95°C for 15 min; 10 cycles of 95°C for 30 s, 60−50°C for 90 s (with annealing temperature decreased by 1°C per cycle), and 72°C for 60 s; 25 cycles of 95°C for 30 s, 50°C for 90 s, and 72°C for 60 s; and a final extension step at 60°C for 30 min using touchdown PCR.

※Universal dye-labeled primer used in the SSR marker multiplex panel
M13: 6FAM-5′-GGATAACAATTTCACACAGG-3′
Hill: VIC-5′-TGACCGGCAGCAAAATTG-3′
Neomycin: PET-5′-AGGTGAGATGACAGGAGATC-3′
T3: NED-5′-AATTAACCCTCACTAAAGGG-3′

PCR products amplified using SSR markers were subjected to DNA fragment analysis using GeneScan 500 LIZ Size Standard (Applied Biosystems) and an ABI PRISM 3730XL Analyzer (Applied Biosystems). Raw data were used to identify key alleles using Geneious Pro v8.1.9 (Kearse *et al*., 2012).

Morphological characteristics

Morphological differences between groups were determined based on head, body, and tail lengths, and scale counts, as previously described for *Gloydius* (Isogawa *et al*., 1994; Shi *et al*., 2018; Wang *et al*., 2019). However,

Table 2. mtDNA information for domestic samples of *G. ussuriensis* and GenBank accession numbers for each individual.

Locality	N	H	Haplotype	GenBank accession no.
Chungcheongnam-do	28	4	Hap9–10, Hap12–13	MZ770931–MZ770932, MZ770934–MZ770935, MZ770922, MZ770930, MZ770933 PV867537–PV867547, PV867552–PV867561
Gangwon-do	88	9	Hap8, Hap16–20, Hap24–26	MZ770966–MZ770999, PV867588–PV867589, PV867513–PV867534, PV867536, PV867580–PV867586, PV867588–PV867593, PV867596–PV867601, PV867604–PV867609, PV867611–PV867614, PV867620–PV867621
Gyeonggi-do	12	3	Hap8, Hap11–12	MZ771010–MZ771011, PV867535, PV867548–PV867566
Gyeongsangbuk-do	32	6	Hap15, Hap18–19, Hap21–23	MZ770895, MZ770936–MZ770948, MZ770965, PV867568, PV867569, PV867575, PV867576, PV867578, PV867579, PV867587, PV867594, PV867595, PV867602, PV867603, PV867610, PV867615–PV867619
Gyeongsangnam-do	16	2	Hap14–15	MZ770949, MZ770957–MZ770964, PV867567, PV867570–PV867574, PV867577
Incheon Ongjin-gun (BI)	35	3	Hap5–7	MZ770896–MZ770921, PV867504–PV867512
Jeju Jeju-si (JI)	18	3	Hap28–30	MZ771002–MZ771004, PV867644–PV867658
Jeju Seogwipo-si (GI)	30	2	Hap27, 31	PV867622–PV867643, PV867659–PV867666

N, sample size; H, number of haplotypes.

as the number of dorsal scales was 21 across the groups, this trait was excluded from the analysis. The following traits were measured: total length (TTL; length from the tip of the snout to the tail tip), snout-vent length (SVL; length from the tip of the snout to the cloaca), tail length (TL; length from the cloaca to the tail tip), head length (HL; length from the tip of the snout to the temporomandibular joint), head width (HW; width of the head at the widest point near the temporomandibular joint), interorbital space (IOS; widest distance between two points on either side), and ventral scales (V; number of ventral scales) were measured. TTL, SVL, and TL were measured using a tape measure in increments of 0.1 cm and converted to 1 mm increments, whereas HL, HW, and IOS were measured using a caliper (CD-15APX; Mitutoyo, Kawasaki, Japan) in increments of 0.01 mm. The TL/TTL, TL/SVL, HL/TTL, HL/SVL, HL/HW, and HW/HL ratios were used to minimize errors in individual body size measurements and verify differences between groups (Shi *et al*., 2018; Wang *et al*., 2019).

Ecological characteristics

Ecological characteristics were analyzed using ArcGIS (Ver. 10.3; ESRI, Redlands, CA, USA). The coordinates of each individual were projected onto climate maps to extract pertinent environmental factors (Do *et al*., 2016; Do *et al*., 2022a). An elevation map was created using a digital elevation model provided by the National Geographic Information Institute (cell size: 10 m). A habitat map was created using Global Land Cover 2021 v 2.0, provided by the European Space Agency (cell size: 10 m). Climate data were obtained from WorldClim v.1.4, using 19 climate maps (cell size: 1 km) representing the current climate (average 1960–1990) (Fig. 1).

Statistical analysis

Genetic characteristics. The individual consensus sequences of the mtDNA cytb gene of *G. ussuriensis* and the nucleotide sequences of closely related species and other groups registered in NCBI were assembled using Geneious Pro v8.1.9 (Kearse *et al*., 2012). Genetic distance and phylogenetic tree analyses were performed using the assembled 936 bp sequence; cytb sequences from 259 individuals were registered in GenBank (Table 2). Haplotype diversity (h), nucleotide diversity (π), and polymorphic sites (P) of domestic copperhead snakes and related species were calculated using DNAsp v6. The assembled nucleotide sequences (saved as FASTA files) were used to construct a phylogenetic tree using Kimura's two-parameter model (Kimura, 1980) through neighbor-joining (Saitou and Nei, 1987) and the Hasegawa-Kishino-Yano model through maximum likelihood (ML) estimation in MEGA X v10.1.8 (Kumar *et al*., 2018). For maximum accuracy, 1,000 bootstraps were

Table 3. Reference sequence information for *G. ussuriensis*, *G. tsushimaensis*, *G. blomhoffi*, *G. brevicauda*, and *G. saxatilis* registered in GenBank.

Species	Locality	Haplotype	GenBank accession no.
G. ussuriensis	China	Hap3	HS11054
	China	Hap1	HS11204
	China	Hap3	HS11212
	China	Hap4	SYNU21
	China	Hap2	SYNU23
	China	Hap3	WS029
	China	Hap3	GP1326
	China	Hap3	Wbh11002
G. tsushimaensis	Japan	Hap32	JN870203
G. blomhoffi	China	–	EU913477
G. brevicauda	China	–	KF997885
G. saxatilis	South Korea	–	MZ770876

performed. The degree of differentiation between each nucleotide sequence was calculated in terms of genetic distance using Kimura's two-parameter model in MEGA X v10.1.8. Reference sequences for 12 *Gloydius* individuals were obtained from GenBank (Table 3) and analyzed using GenAlex v6.5 (Peakall and Smouse, 2006) for the number of alleles (N_A), number of effective alleles (N_E), predicted heterozygosity (H_E), and observed heterozygosity (H_O) using species-specific SSR markers. The genetic structures of the *G. ussuriensis* groups were analyzed using STRUCTURE v2.3.4 (Pritchard *et al*., 2000) with the following parameters: length of burn-in period = 10,000, number of MCMC reps after burn-in = 100,000, K = 1 to 5, and iterations = 3. A structure Harvester was used to calculate the optimal genetic structure. The Hardy-Weinberg exact test was applied using marker-specific and group-specific heterozygote and allele frequencies in GENEPOP v4.2 (Raymond and Rousset, 1995). The linkage disequilibrium (LD) between each gene pair was verified as previously described (Weir, 1979).

Morphological characteristics. SVL was compared between groups using one-way ANOVA. The main traits distinguishing the groups were quantitatively verified using linear discriminant analysis (LDA), as previously described (Mitteroecker and Bookstein, 2011; Tepos-Ramírez *et al*., 2021).

Gloydius ussuriensis is sexually dimorphic in the Republic of Korea. We compared the morphology of females and males within each group (Kim and Oh, 2014b; Do *et al*., 2023). Since body and head shape vary depending on the body length of each individual, SVL was set as a covariate and the remaining traits were used as the main factors for the analysis of covariance (Bradshaw *et al*., 2004; Strine *et al*., 2015; Do *et al*., 2023). The Bonferroni correction was performed for group-specific traits. All morphological characteristics are presented as mean± standard deviation (numerical range).

Ecological characteristics. Because the 19 climate variables showed high correlations, we extracted three principal components (PCs) with eigenvalues >1 according to Kaiser's criteria using principal component analysis (PCA) (Table 4). A kernel probability density plot was used to verify the degree of overlap between the altitudes and climatic environments of each group in both the inland and island areas.

We assessed the degree of ecological niche overlap among the *G. ussuriensis* groups using the Pianka index (PI), calculated using the geographic and climatic variables of each group in EcoSim (Entsminger, 2012). A PI of 1.0 indicates complete ecological niche overlap, whereas 0 indicates complete niche separation. The statistical significance of the ecological niche overlap was calculated using a random algorithm in EcoSim (Entsminger, 2012). All statistical tests of morphological and ecological characteristics were performed using R v4.1.3 (R Core Team, 2024).

Results

Genetic characteristics

mtDNA. A total of 259 domestic *G. ussuriensis* were used to determine the base sequence of Cytb. Diversity analysis showed that the Chinese *G. ussuriensis* (8 individuals) had 4 haplotypes, whereas the domestic *G. ussuriensis* (259 individuals) had 27 (Table 2). Three haplotypes were observed on three islands (Baengnyeongdo, Jeju-do, and Gapado) that were geographically distinct from the Chinese and domestic groups, except for four domestic inland haplotypes: Hap8 (Gangwon-do, Gyeonggi-do), Hap12 (Chungcheongnam-do, Gyeonggi-do), Hap18 (Gangwon-do, Gyeongsangbuk-do), and Hap19 (Gangwon-do, Gyeongsangbuk-do). Chinese *G. ussuriensis* showed high haplotype diversity (h = 0.964) and relatively low nucleotide diversity (π = 0.0021) (Table 5). Among the domestic groups, inland regions showed relatively high haplotype diversity (h = 0.835, 0.868) and nucleotide diversity (π = 0.0037, 0.0043). However, the Baengnyeongdo and Gapado Island groups showed low haplotype diversity (h = 0.519, 0.405) and nucleotide diversity (π = 0.0011, 0.0017). To determine the phylogenetic status of the South Korean *G. ussuriensis*, we constructed an ML tree that included its closest relatives, the Chinese copperhead, *G. tsushimaensis*, *G. blomhoffi*, *G. brevicauda*, and *G. saxatilis* (Fig. 2). Two major lineages of *G. ussuriensis* were identified. The domestic inland, Baengnyeongdo,

Table 4. PCA of 19 bioclimatic variables associated with red-tongued pit viper (*G. ussuriensis*) occurrence in South Korea.

Climatic variable		PC1	PC2	PC3
Eigenvalue		3.1301	2.2446	1.7094
% Variance explained		51.57	26.52	15.38
bio1	Annual mean temperature (°C)	**0.259**	0.204	0.207
bio2	Mean diurnal range (°C)	−0.260	−0.023	**0.268**
bio3	Isothermality (%)	−0.166	−0.066	**0.367**
bio4	Temperature seasonality (SD × 100; °C)	**−0.312**	0.045	0.057
bio5	Max temperature of warmest month (°C)	0.052	0.314	**0.400**
bio6	Min temperature of coldest period (°C)	**0.309**	0.099	0.018
bio7	Temperature annual range (°C)	**−0.307**	0.018	0.138
bio8	Mean temperature of wettest quarter (°C)	0.060	0.302	**0.401**
bio9	Mean temperature of driest quarter (°C)	**0.310**	0.063	0.066
bio10	Mean temperature of warmest quarter (°C)	0.152	0.307	**0.308**
bio11	Mean temperature of coldest quarter (°C)	**0.302**	0.116	0.101
bio12	Annual precipitation (mm)	0.188	**−0.329**	0.181
bio13	Precipitation of wettest month (mm)	−0.102	**−0.305**	0.295
bio14	Precipitation of driest month (mm)	**−0.250**	0.245	0.047
bio15	Precipitation seasonality (%CV; mm)	**−0.289**	0.086	0.043
bio16	Precipitation of wettest quarter (mm)	−0.003	**−0.379**	0.282
bio17	Precipitation of driest quarter (mm)	**0.266**	−0.227	0.013
bio18	Precipitation of warmest quarter (mm)	−0.058	**−0.349**	0.308
bio19	Precipitation of coldest quarter (mm)	**0.267**	−0.226	0.003

The first four PCs with eigenvalues >1 are presented here. The percentages in parentheses indicate the amount of variation explained by each PC and the components that were loaded most highly for *G. ussuriensis*.

and Chinese groups formed one lineage, whereas the Jeju-do and Gapado Island groups formed another. Multiple clades were identified in the former lineage. The domestic inland group was further divided into the A-group (KN, KS, GN, GS, GG, and CN) and B-group clades (KN, KS, GG, and CS). The Chinese group belonged to the same clade as the B group but formed a single branch within the clade. The Baengnyeongdo Island group formed a single clade in a country close to China. Based on the phylogenetic tree, a genetic distance analysis was performed for domestic *G. ussuriensis* (A-group, B-group, Baengnyeongdo, Jeju-do Island, and Gapado Island), Chinese *G. ussuriensis*, and Japanese *G. tsushimaensis* (Table 6). The Chinese group was genetically similar to the Baengnyeongdo (0.0104) and the domestic inland groups (A: 0.0147, B: 0.0140). The Jeju-do and Gapado Island groups showed a very close genetic distance (0.003), while both island groups showed a notable genetic distance (≥0.0459) from the inland, Baengnyeongdo, and Chinese groups. The Japanese group was genetically closer to the Jeju-do (0.0220) and Gapado Island groups (0.0246) than to the Chinese (0.0320), domestic inland (A: 0.0309, B: 0.0333), and Baengnyeongdo Island groups (0.0302).

Genetic diversity. The H_O and H_E values for domestic *G. ussuriensis* were 0.672 and 0.673, respectively. The genetic diversity within populations was lowest in the Gapado Island population (H_O: 0.33 0.339, H_E: 0.316), followed by Jeju-do Island (H_O: 0.606, H_E: 0.595), Heuksando Island (H_O: 0.618, H_E: 0.636), Jangdo Island (H_O: 0.634, H_E: 0.603), and Baengnyeongdo Island (H_O: 0.689, H_E: 0.669), all of which exhibited higher genetic diversity than the average (Table 7). The N_A and N_E values were highest in the Chungcheongnam-do group (10,824 and 6,666, re-

Table 5. Genetic diversity of mtDNA cytb base sequences in *G. ussuriensis*.

Locality	N	H	h	π(%)
China	8	7	0.964	0.0021
BI	35	4	0.519	0.0011
Group-A	105	24	0.868	0.0043
Group-B	71	17	0.835	0.0038
GI	30	2	0.404	0.0017
JI	18	6	0.745	0.0015

N, sample size; H, number of haplotypes; h, haplotype diversity; π, nucleotide diversity.

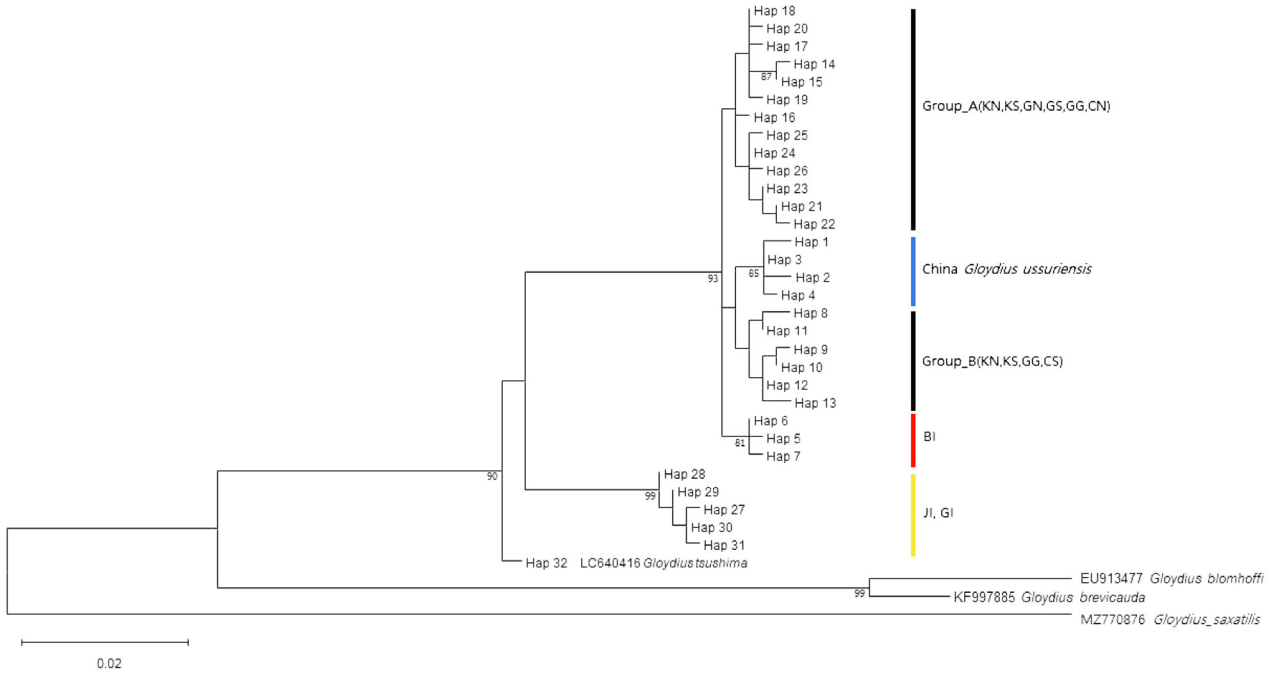


Fig. 2. Phylogenetic tree of *G. ussuriensis* haplotypes based on mtDNA cytochrome b gene (ML) Group_A: Gangwon-do, Gyeongsangbuk-do, Gyeongsangnam-do, Gyeonggi-do, Chungcheongnam-do; Group_B: Gangwon-do, Gyeonggi-do, Chungcheongnam-do, BI: Baengnyeongdo Island, JI: Jeju-do Island, GI: Gapado Island.

Table 6. Genetic distance of mtDNA cytb base sequences in *G. ussuriensis*.

	China	BI	B-group	A-group	GI	JI	Japan
China							
BI	0.0104						
B-group	0.0140	0.0115					
A-group	0.0147	0.0102	0.0085				
GI	0.0507	0.0459	0.0463	0.0459			
JI	0.0523	0.0476	0.0479	0.0475	0.0030		
Japan	0.0320	0.0302	0.0333	0.0309	0.0246	0.0220	

BI, Baengnyeongdo Island; GI, Gapado Island; JI, Jeju-do Island; A group (Northern Gangwon-do, Southern Gangwon-do, Gyeongsangbuk-do, Gyeongsangnam-do, Gyeonggi-do, Chungcheongbuk-do), B group (Northern Gangwon-do, Southern Gangwon-do, Gyeonggi-do, Chungcheongbuk-do).

spectively) and lowest in the Gapado Island group (3,059 and 1,811, respectively; Table 7). The genetic structures of the groups could be classified into three distinct groups (K = 3): Baengnyeongdo Island, Gapado Island, inland, and other island groups. The Baengnyeongdo and Gapado Island groups showed different genetic structures from those of the inland group, whereas the Jeju-do Island group had genetic structures similar to those of both the inland and Gapado Island groups (Fig. 3). The PCA of the genetic relationships between groups clustered eight of the 13 inland groups, whereas the Gapado and Baengnyeongdo Island groups were clustered separately. In contrast, the Jeju-do, Heuksando, and Jangdo Island groups clustered closer to the inland group than to the Gapado and Baengnyeongdo Island groups (Fig. 4A). In addition, individuals from inland areas, Heuksando Island, and Jangdo Island formed a single group, whereas those from Gapado Island, Baengnyeongdo, and Jeju-do Island formed separate groups (Fig. 4B). The level of genetic differentiation among the inland groups was low (Fst $\leq$ 0.0230), whereas the Gapado Island group was significantly differentiated from the inland groups (Fst $\geq$ 0.2745), much like the Baengnyeongdo and Jeju-do Island groups (Fst = 0.0886 and 0.1092, respectively; Table 8).

Table 7. Genetic diversity of *G. ussuriensis* by group.

Site	N	N_A	N_E	H_o	H_E	F_{IS}
BI	35	5.941	3.770	0.689	0.669	−0.031
CN	27	8.765	6.050	0.762	0.757	−0.024
CS	42	10.824	6.666	0.755	0.768	0.012
GG	28	9.645	6.145	0.742	0.758	−0.002
GI	34	3.059	1.811	0.339	0.316	−0.067
GN	39	10.294	6.483	0.736	0.757	0.027
GS	28	10.353	6.419	0.731	0.754	0.032
JI	31	7.765	4.276	0.606	0.595	−0.017
KN	33	8.941	5.940	0.737	0.720	−0.009
KS	55	10.529	6.341	0.711	0.739	0.039
SHI	4	4.294	3.626	0.618	0.636	0.019
SJI	9	4.294	3.093	0.634	0.603	−0.051
Total	365	7.892	5.052	0.672	0.673	−0.005

N_A, number of alleles relative to the number of individuals included in the analysis for genotype determination (N); N_E, effective number of alleles; H_O, observed heterozygosity; H_E, estimated heterozygosity; F_{IS}, fixation index; BI, Baengnyeongdo; CN, Chungcheongbuk-do; CS, Chungcheongnam-do; GG, Gyeonggi-do; GI, Gapado; GN, Gyeongsangbuk-do; GS, Gyeongsangnam-do; JI, Jeju-do Island; KN, northern Gangwon-do; KS, southern Gangwon-do; SHI, Heuksando Island; SJI, Jangdo Island.

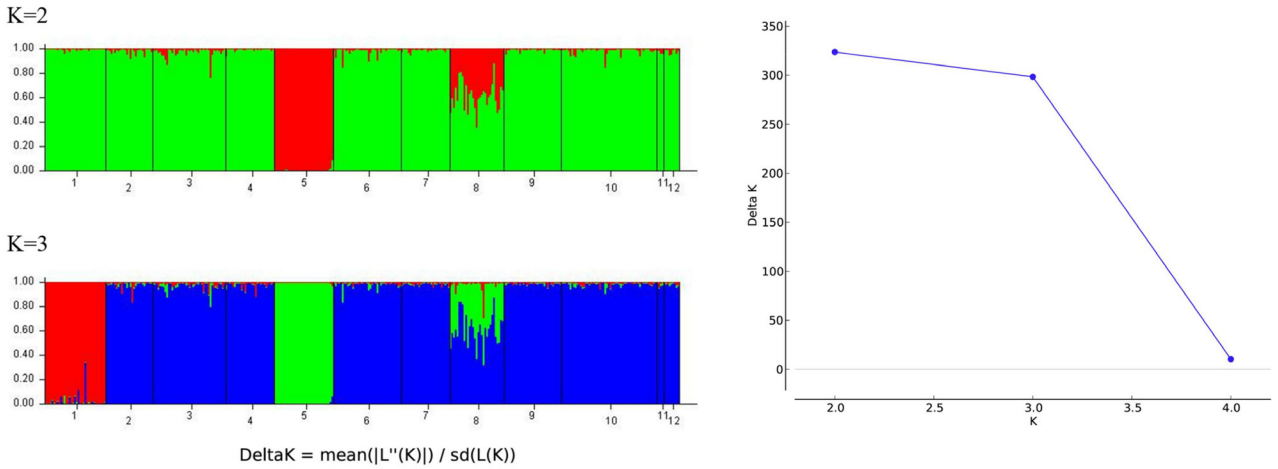


Fig. 3. Results of genetic population structure analysis for *G. ussuriensis* pop1: Baengnyeongdo Island, pop2: Chungcheongbuk-do, pop3: Chungcheongnam-do, pop4: Gyeonggi-do, pop5: Gapado Island, pop6: Gyeongsangbuk-do, pop7: Gyeongsangnam-do, pop8: Gyeongsangbuk-do, pop9: Northern Gangwon-do, pop10: Southern Gangwon-do, pop11: Heuksando Island, pop12: Jangdo Island.

Morphological characteristics

The SVL of *G. ussuriensis* was highest in the Baengnyeongdo and Jeju-do Island groups, followed by the inland group, whereas it was lowest in the Gapado Island group ($F = 27.810$, $p < 0.001$; Table 9). LDA showed that the four groups differed in terms of form (kappa = 0.845, $p < 0.0001$; Fig. 5). The explanatory power for the two axes was 94.2%, with axis 1 representing TL/SVL, HL/TTL, and HL/SVL and axis 2 representing TTL, HL/TTL, and HL in order of importance (Table 10).

Males in the Baengnyeongdo Island group had the highest SVL, followed by the inland and Jeju-do Island groups, with the Gapado Island population exhibiting the lowest size ($F = 19.500$, $p < 0.001$; Table 9). Body shape traits TL ($F = 14.438$, $p < 0.001$) and TTL ($F = 8.755$, $p < 0.01$); head shape traits HL ($F = 51.498$, $p < 0.001$) and IOS ($F = 23.644$, $p < 0.001$); body scale trait V ($F = 967.199$, $p < 0.001$); and body and head ratios TL/TTL ($F = 52.890$, $p < 0.001$), TL/SVL ($F = 36.143$, $p < 0.001$), HL/TTL ($F = 476.159$, $p < 0.001$), HL/SVL ($F = 497.390$, $p < 0.001$), and HW/HL ($F = 12.649$,

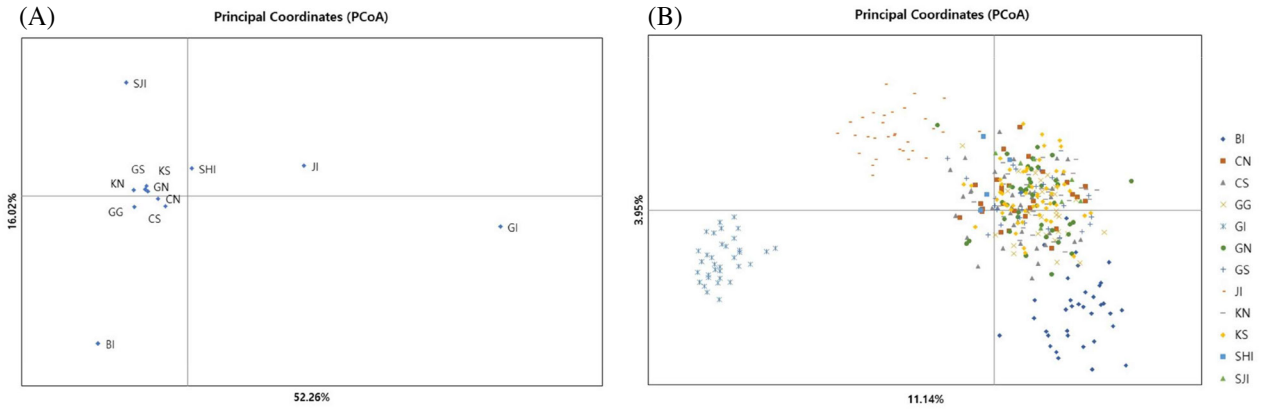


Fig. 4. PCA of regional *G. ussuriensis* populations (A, B). BI: Baengnyeongdo Island, CN: Chungcheongbuk-do, CS: Chungcheongnam-do, GG: Gyeonggi-do, GI: Gapado Island, GN: Gyeongsangbuk-do, GS: Gyeongsangnam-do, JI: Gyeongsangbuk-do, KN: Northern Gangwon-do, KS: Southern Gangwon-do, SHI: Heuksando Island, SJI: Jangdo Island.

Table 8. Level of genetic differentiation between *G. ussuriensis* groups.

	BI	CN	CS	GG	GI	GN	GS	JS	KN	KS	SHI	SJI
BI	0	*	*	*	*	*	*	*	*	*	*	*
CN	0.1037	0	*	*	*	*	*	*	*	*	NS	*
CS	0.0929	0.0048	0	*	*	*	*	*	*	*	NS	*
GG	0.0886	0.0089	0.0110	0	*	*	*	*	*	*	NS	*
GI	0.4021	0.3046	0.2745	0.3245	0	*	*	*	*	*	*	*
GN	0.1025	0.0072	0.0089	0.0108	0.2975	0	NS	*	*	*	NS	*
GS	0.0987	0.0050	0.0048	0.0139	0.3151	0.0066	0	*	*	*	NS	*
JI	0.2206	0.1161	0.1092	0.1363	0.2663	0.1302	0.1232	0	*	*	*	*
KN	0.1096	0.0130	0.0210	0.0117	0.3302	0.0087	0.0230	0.1420	0	NS	*	*
KS	0.1074	0.0105	0.0184	0.0076	0.2895	0.0070	0.0165	0.1252	0.0028	0	NS	*
SHI	0.1370	0.0329	0.0205	0.0314	0.3969	0.0332	0.0216	0.0952	0.0489	0.0303	0	NS
SJI	0.1758	0.0981	0.0936	0.0915	0.4526	0.0831	0.0825	0.2120	0.0976	0.0887	0.1059	0

BI, Baengnyeongdo; CN, Chungcheongbuk-do; CS, Chungcheongnam-do; GG, Gyeonggi-do; GI, Gapado; GN, Gyeongsangbuk-do; GS, Gyeongsangnam-do; JI, Jeju-do Island; KN, northern Gangwon-do; KS, southern Gangwon-do; SHI, Heuksando Island; SJI, Jangdo Island; P values obtained after 1320 permutations; adjusted nominal level (5%) for multiple comparisons: 0.000758; NS, not significant

$p < 0.001$) varied significantly between groups (Table 11).

Females had the highest SVL in the Baengnyeongdo Island group, followed by those in the Jeju-do Island and inland groups, with the Gapado Island population exhibiting the lowest size ($F = 8.416$, $p < 0.01$; Table 9). Head shape traits HL ($F = 9.752$, $p < 0.001$) and IOS ($F = 4.753$, $p < 0.05$); body scale trait V ($F = 1638.668$, $p < 0.001$); and body and head ratios TL/TTL ($F = 190.027$, $p < 0.001$), TL/SVL ($F = 146.787$, $p < 0.001$), HL/TTL ($F = 249.160$, $p < 0.001$), HL/SVL ($F = 270.559$, $p < 0.001$), and HW/HL ($F = 21.817$, $p < 0.001$) varied significantly between groups (Table 12).

Ecological characteristics

The Gapado Island group was distributed exclusively in Cropland (100.00%), whereas all other groups were observed most frequently in tree cover areas (Baengnyeongdo: 88.57%, inland: 84.59%, Heuksando: 100.00%, Jeju-do: 70.58%) (Fig. 6A). The Jeju-do Island group occurred at the highest mean elevation (391.98±304.47 m; range: 0–990 m), followed by the inland group (320.53±230.24 m; range: 6–950 m), the Heuksando Island group (139.23±41.76 m; range: 60–183 m), the Baengnyeongdo Island group (43.86±29.04 m; range: 15–103 m), and the Gapado Island group, which occurred at the lowest elevations (12.04±1.99 m; range: 10–14 m) (Fig. 6B).

Among the 19 climatic variables analyzed, the mean annual temperature was highest in the Gapado Island group (18.00±0.00°C; range: 18.00–18.00°C), followed by the Heuksando Island group (15.30±0.09°C; range: 15.10–15.39°C), Jeju-do Island group (13.80±2.12°C;

Table 9. Sample sizes (N) and mean±standard deviation (range: minimum−maximum) SVL of red-tongued pit viper (*G. ussuriensis*) populations and sex in South Korea.

SVL	N	BI	N	KP	N	JI	N	GI
All	28	473.64±54.89^{a} (388−575)	44	415.22±36.13^{bc} (343−480)	35	419.77±30.07^{b} (350−467)	33	361.00±17.92^{d} (338−430)
				F = 27.810, p < 0.001				
Female	16	488.25±54.15^{a} (388−575)	24	431.17±28.31^{bc} (372−480)	21	420.05±26.37^{c} (365−461)	13	364.69±10.86^{d} (350−390)
				F = 19.500, p < 0.001				
Male	12	454.17±51.70^{a} (395−545)	20	396.10±35.77^{b} (343−460)	14	419.36±35.97^{ab} (350−467)	20	358.60±21.24^{c} (338−430)
				F = 8.416, p < 0.01				
SSD		0.075		0.089		0.002		0.016

SVL, snout vent length; KP, Korean Peninsula; BI, Baengnyeongdo Island; GI, Gapado Island; JI, Jeju-do Island.

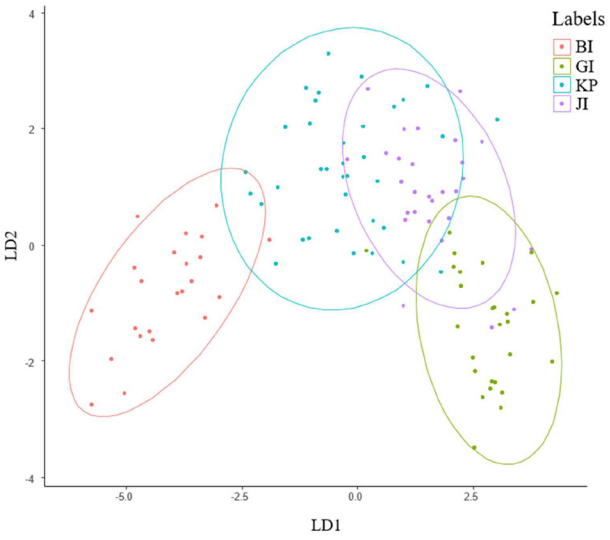


Fig. 5. Scatterplot based on LDA for red-tongued pit viper (*G. ussuriensis*) populations in the Republic of Korea, including Baengnyeongdo Island (BI), Korean Peninsula (KP), Jeju-do Island (JI), and Gapado Island (GI).

Table 10. LDA loadings of morphological characteristics for different red-tongued pit viper (*G. ussuriensis*) populations in South Korea.

Morphological variable	Axis 1	Axis 2
% explained variance	77.0	17.2
SVL	−2.491	2.161
TL	2.327	3.569
TTL	−0.959	**−15.610**
HL	0.457	**8.093**
HW	−0.026	0.198
IOS	0.578	0.491
V	−1.291	−0.105
TL/TTL	7.663	−1.601
TL/SVL	**−12.153**	−1.629
HL/TTL	**−13.048**	**−14.462**
HL/SVL	**12.418**	5.035
HW/HL	−0.432	−0.906

Total length; SVL: snout-vent length; TL: tail length; HL: head length; HW: head width; IOS: interorbital space; V: ventral scale.

range: 11.89−17.39°C), Baengnyeongdo Island group (13.40±0.08°C; range: 13.30−13.60°C), and inland group (12.97±1.61°C; range: 8.39−16.00°C). The mean annual precipitation was highest in the Jeju-do Island group (1928.18±100.65 mm; range: 1709−2010 mm), followed by the Gapado Island group (1740.00±0.00 mm; range: 1740−1740 mm), inland group (1342.19± 62.66 mm; range: 1136−1597 mm), Heuksando Island group (1164.92±11.28 mm; range: 1154−1187 mm), and Baengnyeongdo Island group (793.23±5.13 mm; range: 786−807 mm).

The PCA of the climate variables associated with the habitats of *G. ussuriensis* identified three PCs with eigenvalues >1, explaining 93.47% of the total variance (Table 4). PC1 best explained the seasonal variations in the average annual temperature, winter temperature, precipitation, and other climatic factors. As PC1 increased, the annual average temperature, winter temperature, and precipitation increased, and seasonality decreased. PC2 correlated with annual average precipitation and summer precipitation. As PC2 increased, annual average

Table 11. Sample sizes (N) and mean±standard deviation (range: minimum-maximum) of morphological characteristics for female red-tongued pit viper (*G. ussuriensis*) populations in the Republic of Korea.

Morphological variable	BI (N = 16)	KP (N = 24)	JI (N = 21)	GI (N = 13)	F-Value	p
	Mean±SD (range)	Mean±SD (range)	Mean±SD (range)	Mean±SD (range)		
TL	83.00±11.62 (60−106)[a]	66.79±9.40 (50−83)[b]	64.24±5.02 (55−73)[b]	54.00±4.56 (41−61)[c]	14.438	<0.001
TTL	**567.69±64.23 (443−666)[a]**	**496.63±36.16 (421−561)[b]**	**484.29±29.70 (423−528)[b]**	**418.69±13.53 (401−451)[c]**	**8.755**	**<0.01**
HL	**23.68±1.93 (18.9−26.8)[ab]**	**23.09±1.51 (20.2−26.45)[b]**	**24.41±1.64 (21.36−27.49)[a]**	**22.42±0.80 (21.54−24.68)[b]**	**51.498**	**<0.001**
HW	17.62±1.86 (14.25−20.52)[a]	14.05±1.92 (11.34−18.80)[c]	16.42±1.17 (14.79−18.52)[ab]	15.06±1.03 (12.98−16.94)[bc]	0.105	0.746
IOS	9.28±0.95 (7.6−11.11)[a]	8.87±0.87 (7.7−12)[ab]	9.44±0.55 (8.53−10.31)[a]	8.49±0.36 (7.77-9.16)[b]	23.644	<0.001
V	153.38±3.03 (149−162)[a]	149.50±2.83 (145−156)[b]	144.86±3.14 (139−150)[c]	143.46±1.71 (140−147)[c]	967.199	<0.001
TL/TTL	14.60±0.88 (13.45−16.08)[a]	13.40±1.2 (11.06−14.95)[b]	13.27±0.72 (11.97−14.32)[b]	12.89±0.88 (10.15−13.53)[b]	52.890	<0.001
TL/SVL	**16.98±1.20 (15.18−18.87)[a]**	**15.45±1.59 (12.44−17.44)[b]**	**15.31±0.96 (13.60−16.71)[b]**	**14.80±1.13 (11.29−15.64)[b]**	**36.143**	**<0.001**
HL/TTL	**4.19±0.23 (3.85−4.64)[d]**	**4.66±0.26 (3.86−5.15)[c]**	**5.04±0.22 (4.65−5.45)[b]**	**5.36±0.18 (5.04−5.66)[a]**	**476.159**	**<0.001**
HL/SVL	**4.87±0.28 (4.48−5.4)[d]**	**5.36±0.27 (4.51−5.82)[c]**	**5.81±0.24 (5.33−6.22)[b]**	**6.15±0.18 (5.82−6.35)[a]**	**497.390**	**<0.001**
HW/HL	74.45±5.55 (64.22−84.27)[a]	60.98±8.65 (49.22−85.45)[c]	67.38±4.31 (60.26−76.97)[b]	67.20±4.27 (56.76−76.27)[b]	12.649	<0.001

TTL, total length; SVL, snout-vent length; TL, tail length; HL, head length; HW, head width; IOS, interorbital space; V, ventral scales; BI, Baengnyeongdo Island; KP, Korean Peninsula; JI, Jeju-do Island; GI, Gapado Island.

Table 12. Sample sizes (N) and mean±standard deviation (range: minimum−maximum) of morphological characteristics for male red-tongued pit viper (*G. ussuriensis*) populations in the Republic of Korea.

Morphological variable	BI (N = 12)	KP (N = 20)	JI (N = 14)	GI (N = 20)	F-Value	p
	Mean±SD (range)	Mean±SD (range)	Mean±SD (range)	Mean±SD (range)		
TL	90.50±10.62 (79−112)[a]	71.65±7.71 (59−86)[bc]	74.57±4.75 (64−82)[b]	66.75±4.41 (62−82)[c]	0.497	0.483
TTL	**540.00±61.97 (475−651)[a]**	**467.80±41.24 (410−540)[b]**	**493.93±40.01 (418−544)[b]**	**425.35±25.13 (400−512)[c]**	**0.384**	**0.537**
HL	**22.69±2.16 (20.24−26.24)[ab]**	**21.62±2.41 (17.3−26.8)[b]**	**24.58±2.16 (20.54−28.27)[a]**	**21.52±0.91 (20.18−24.1)[b]**	**9.752**	**<0.001**
HW	16.48±1.49 (13.95−19.2)[ab]	14.19±2.99 (9.8−21.9)[b]	17.00±1.96 (13.93−20.66)[a]	14.41±1.54 (12.58−18.75)[b]	1.661	0.202
IOS	9.00±1.00 (7.6−10.54)[a]	8.55±1.20 (6.98−11.5)[b]	9.60±0.86 (7.8−10.92)[ab]	8.60±0.41 (7.85−9.61)[b]	4.753	<0.05
V	151.17±2.44 (148−157)[a]	147.50±2.33 (143−152)[b]	142.93±1.86 (140−147)[c]	141.35±1.69 (138−144)[c]	1638.668	<0.001
TL/TTL	16.76±0.47 (16.07−17.33)[a]	15.32±1.00 (13.78−17.49)[b]	15.13±0.62 (14.15−16.27)[b]	15.69±0.44 (14.71−16.47)[b]	190.027	<0.001
TL/SVL	**19.93±0.74 (18.75−21.01)[a]**	**18.11±1.38 (15.97−21.20)[b]**	**17.83±0.87 (16.49−19.43)[b]**	**18.62±0.62 (17.24−19.72)[b]**	**146.787**	**<0.001**
HL/TTL	**4.21±0.21 (3.93−4.46)[c]**	**4.62±0.34 (3.91−5.29)[b]**	**4.98±0.18 (4.62−5.22)[a]**	**5.07±0.19 (4.71−5.39)[a]**	**249.160**	**<0.001**
HL/SVL	**5.01±0.25 (4.58−5.36)[c]**	**5.46±0.40 (4.61−6.20)[b]**	**5.86±0.23 (5.38−6.15)[a]**	**6.01±0.23 (5.60−6.39)[a]**	**270.559**	**<0.001**
HW/HL	72.83±5.27 (65.93−82.02)[a]	65.56±10.54 (51.47−86.13)[a]	69.09±3.55 (61.53−74.15)[a]	66.96±6.29 (57.02−79.08)[a]	21.817	<0.001

TTL, total length; SVL, snout-vent length; TL, tail length; HL, head length; HW, head width; IOS, interorbital space; V, ventral scales; BI, Baengnyeongdo Island; KP, Korean Peninsula; JI, Jeju-do Island; GI, Gapado Island.

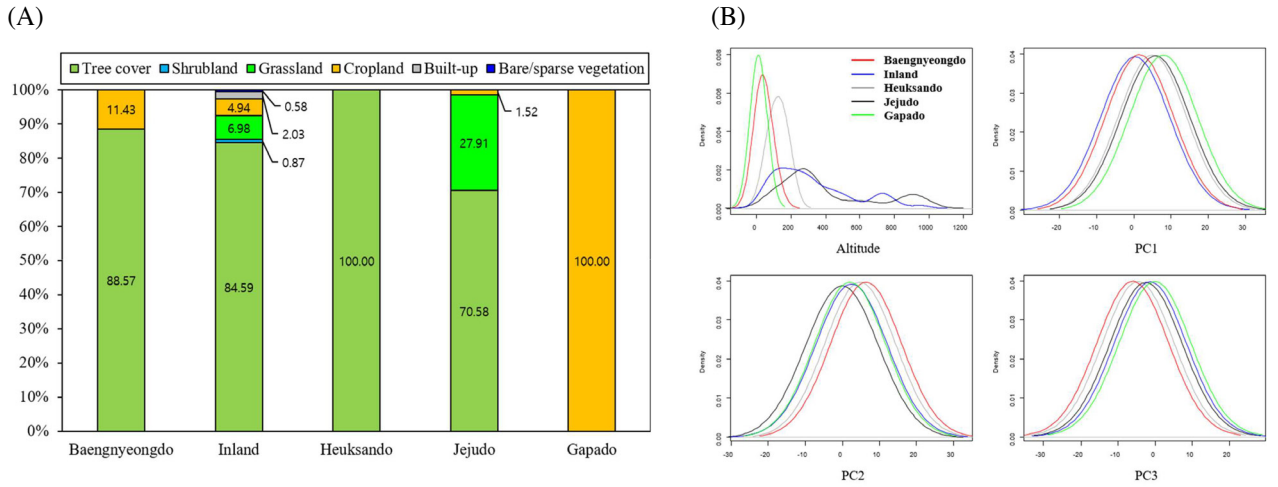


Fig. 6. (A) Occurrence of red-tongued pit viper (*G. ussuriensis*) populations according to habitat type. (B) Smoothed frequency distributions (kernel density plot) of altitudes and principal components (PC1, PC2, and PC3) associated with red-tongued pit viper (*G. ussuriensis*) in the Republic of Korea, including Baengnyeongdo (BI), Korean Peninsula (KP), Jeju-do Island (JI), Gapado Island (GI), Heuksando Island (SHI), and Jangdo Islands (SJI).

precipitation and summer precipitation decreased. PC3 explained the variables related to summer temperature and temperature variability, and was positively correlated with summer temperature, annual temperature range, and daily temperature range (Table 4).

The ecological niches of *G. ussuriensis* showed overlap among groups according to their specific climatic environments (PI = 0.4075). In terms of habitat (PI = 0.5673, $p < 0.01$), the Gapado Island group had lower PI values than the other groups, whereas for altitude (PI = 0.3225, $p < 0.05$), the PI values between the Baengnyeongdo and Gapado Island groups were relatively high but still lower than those of other groups. PC3 (PI = 0.3065, $p < 0.05$) indicated low PI values between most groups, except for the Baengnyeongdo and Heuksando Island groups and the inland and Jeju-do Island groups (Table 13). The degree of intergroup overlap was also reflected in the habitat distribution ratio, altitude, and probability density estimated for the three PCs (Fig. 6B).

Discussion

This study investigated the genetic, morphological, and ecological characteristics of *G. ussuriensis* inhabiting inland and island regions of the Republic of Korea. Island groups exhibited lower genetic diversity than the inland group, with the Gapado Island group exhibiting the lowest diversity among the island groups. The genetic structure was divided into three groups: Baengnyeongdo, inland, and Gapado Island. The genetic structure of the Jeju-do Island group was shared by both the inland and Gapado Island groups. The genetic characteristics were consistent with the morphological trends. Notably, the Jeju-do and Gapado Island groups showed no major morphological differences compared with the inland group in either females or males. In terms of climatic environment, the Baengnyeongdo and Gapado Island groups showed low overlap with other populations for most environmental factors.

Genetic characteristics

The genetic diversity of *G. ussuriensis* was lower in island groups than in inland groups, with genetic structure revealing differentiation between the Baengnyeongdo, inland, and Gapado Island groups. Similar patterns of reduced diversity in island populations have been observed in many other taxa (Grazziotin *et al*., 2006; Hurston *et al*., 2009; Lee *et al*., 2022; Wen *et al*., 2022). Geographic isolation affects the distribution of genes and promotes differentiation. Owing to the small size of the islands and the high density of island populations, island species are particularly vulnerable (Simberloff, 2000). For example, a study using nuclear DNA found that *G. shedaoensis* on Shetang Island, China, has low genetic diversity owing to its limited distribution range (Wen *et al*., 2022). Previous mtDNA studies on *G. ussuriensis* in the Republic of Korea also reported that island populations, such as Jeju-do and Baengnyeong Island, had lower genetic diversity than inland populations, with the latter particularly vulnerable to population decline due to its low genetic diversity (Lee *et al*., 2022). Together, these results emphasize that Korean island populations of *G. ussuriensis* have lower genetic diversity than inland populations. Detailed genetic studies (e.g., inbreeding) are required to verify their vulnerability

Table 13. Pinaka index (PI) showing degree of overall niche overlap according to environmental variables for red-tongued pit viper (*G. ussuriensis*) populations in the Republic of Korea.

Environmental variable	Species	PI	Mean of PI		ES[2]	p
			Observed	Simulated[1]		
Land	BI VS KP	0.9938	0.5673	0.2156	3.2825	**< 0.01**
	BI VS SHI and SJI	0.9917				
	BI VS JI	0.8110				
	BI VS GI	0.1279				
	KP VS SHI and SJI	0.9945				
	KP VS JI	0.8593				
	KP VS GI	0.0581				
	SHI and SJI VS JI	0.8149				
	SHI and SJI VS GI	0.0000				
	GI VS JI	0.0214				
Altitude	BI VS KP	0.3516	0.3225	0.1697	2.8395	**< 0.05**
	BI VS SHI and SJI	0.1670				
	BI VS JI	0.1319				
	BI VS GI	0.9622				
	KP VS SHI and SJI	0.6001				
	KP VS JI	0.5792				
	KP VS GI	0.2180				
	SHI and SJI VS JI	0.1790				
	SHI and SJI VS GI	0.0000				
	GI VS JI	0.0360				
PC1	BI VS KP	0.3700	0.4745	0.4914	−0.1541	N/A
	BI VS SHI and SJI	0.8479				
	BI VS JI	0.7682				
	BI VS GI	0.0000				
	KP VS SHI and SJI	0.3138				
	KP VS JI	0.2843				
	KP VS GI	0.0000				
	SHI and SJI VS JI	0.9907				
	SHI and SJI VS GI	0.5299				
	GI VS JI	0.6401				
PC2	BI VS KP	0.4511	0.3667	0.4455	−0.6587	N.A
	BI VS SHI and SJI	0.9998				
	BI VS JI	0.0000				
	BI VS GI	0.0000				
	KP VS SHI and SJI	0.4561				
	KP VS JI	0.4841				
	KP VS GI	0.8778				
	SHI and SJI VS JI	0.0000				
	SHI and SJI VS GI	0.0000				
	GI VS JI	0.3987				
PC3	BI VS KP	0.0247	0.3065	0.4417	1.0989	**< 0.05**
	BI VS SHI and SJI	0.9997				
	BI VS JI	0.0610				
	BI VS GI	0.0000				
	KP VS SHI and SJI	0.0247				
	KP VS JI	0.9623				
	KP VS GI	0.5865				
	SHI and SJI VS JI	0.0610				
	SHI and SJI VS GI	0.0000				
	GI VS JI	0.3460				

KP: Korean Peninsula; BI: Baengnyeongdo Island; JI: Jeju-do Island; GI: Gapado Island; SHI: Heuksando Island; SJI: Jangdo Island.

Table 14. Ratios of head to snout-vent length (HL/SVL) and head length to width (HL/HW) for red-tongued pit viper *G. ussuriensis*, *G. brevicaudus*, *G. intermedius*, and *G. tsushimaensis*.

Species	N	HL/SVL			HL/HW			Ref.
		Range	Mean	SD	Range	Mean	SD	
G. brevicaudus	40	4.44–7.07	5.67	0.61	1.08–2.56	1.81	0.33	Do *et al*. (2024)
G. intermedius	28	4.14–6.25	5.14	0.42	1.32–2.70	1.68	0.32	Do *et al*. (2024)
G. tsushimaensis	32	5.10–6.60	5.90	0.36	1.30–1.77	1.46	0.11	Isogawa *et al*. (1994)
G. ussuriensis								
KP group	49	5.30–6.70	6.00	0.25	1.26–1.73	1.42	0.11	Isogawa *et al*. (1994)
BI group	**28**	**4.48–5.40**	**4.93**	**0.27**	**1.19–1.56**	**1.36**	**0.10**	**Present study**
KP group	44	4.52–6.20	5.41	0.34	1.16–2.03	1.62	0.23	Present study
JI group	**35**	**5.33–6.22**	**5.83**	**0.24**	**1.30–1.66**	**1.48**	**0.09**	**Present study**
GI group	**33**	**5.60–6.39**	**6.07**	**0.22**	**1.26–1.76**	**1.50**	**0.12**	**Present study**

KP, Korean Peninsula; BI, Baengnyeongdo Island; JI, Jeju-do Island; GI, Gapado Island.

and inform the conservation of island populations.

Morphological characteristics

The body length (SVL) and total length (TTL) of *G. ussuriensis* varied among populations, with the longest individuals recorded in the Baengnyeongdo Island group (SVL: 388–575 mm, TTL: 443–666 mm). The Gapado Island population were the smallest group (SVL: 338–430 mm), whereas the inland (SVL: 343–480 mm, TTL: 400–561 mm) and Jeju-do Island groups (SVL: 350–467 mm, TTL: 418–544 mm) exhibited similar characteristics (Tables 9, 11, and 12). Consistent with previous findings for *G. ussuriensis*, the Baengnyeongdo Island group had consistently longer TTLs than inland groups. Conversely, the Gapado Island group exhibited a shorter body length than the Jeju-do Island group (Kim *et al*., 2010; Kim and Oh, 2014b).

The length of a snake's body is proportional to the size of the food resources (Pough and Groves, 1983; Shine, 1991; King, 2002). Among the three *Gloydius* species identified in the Republic of Korea, *G. brevicaudus* (mean SVL: 47.35±5.34 cm) and *G. ussuriensis* (44.38±2.96 cm) primarily prey on frogs, lizards, and small invertebrates, whereas *G. intermedius* (56.13±9.03 cm) primarily preys on rodents, which are comparatively larger prey resources (Mori *et al*., 1989; Choi *et al*., 2022; Do and Nam, 2021). Previous studies indicated that *G. ussuriensis* of the inland and Jeju-do Island regions feed on amphibians, whereas the Gapado Island population feeds only on small centipedes and lizards (Do and Yoo, 2014; Kim and Oh, 2014a). This could be attributed to the different distributions of available food sources associated with the distinct eco-geological characteristics of the islands, promoting the evolution of morphological differences between regions (Lomolino, 2005; Oh and Banjade, 2021). The number of amphibian species (23 species in the mainland, seven species in Jeju, and two species in Gapado Island) serving as the primary food source for *G. ussuriensis* may vary geographically. Given the higher species diversity on Jeju-do Island and the inland regions compared to Gapado Island, the primary food sources of *G. ussuriensis* inhabiting Jeju-do Island and the inland regions are also expected to differ (Kim and Oh, 2014a; Do *et al*., 2022b). Because only three amphibian species have been recorded on Baengnyeongdo Island, further research on the food sources and their sizes is needed (Park *et al*., 2019). The Gapado and Baengnyeongdo Island groups exhibited distinct morphologies compared to the other groups. The disparities in body size among these groups were likely associated with the types and quantities of available food sources. Future studies on the ecological niche of food resources used between groups will be important for elucidating the evolutionary causes of morphological differences.

The morphological characteristics of *G. ussuriensis* varied among groups, with HL/SVL and V demonstrating the most significant disparities between females and males. HL/TTL was identified as a significant morphological factor for distinguishing populations (Tables 11 and 12). HL/SVL was lowest in the Baengnyeongdo Island group (4.48–5.40), followed by the inland (4.51–5.82), Jeju-do Island (5.33–6.22), and Gapado Island groups (5.82–6.35). In males, the ratio was lowest in the Baengnyeongdo Island (4.58–5.36) and inland (4.61–6.20) groups and highest in the Gapado (5.60–6.39) and Jeju-do Island groups (5.38–6.15). The HL/SVL ratio of Baengnyeongdo Island was lower than that of the South Korean inland group, as well as the phylogenetically similar *G. brevicaudus*, *G. intermedius*, and *G. tsushimaensis* groups. HL/HW was also the lowest in this group (Emelianov, 1929; Isogawa *et al*., 1994; Do *et al*., 2024, Table 14). However, since

Table 15. Ratios of tail to total body length (TL/TTL) and number of ventral scales for red-tongued pit viper *G. ussuriensis*, *G. brevicaudus*, *G. intermedius*, and *G. tsushimaensis*.

Species	Female				Male				Ref.
	N	Range	Mean	SD	N	Range	Mean	SD	
Ventral scales									
G. brevicaudus	23	138–150	144.13	3.40	17	140–154	145.76	3.87	Do *et al.* (2024)
G. intermedius	12	152–167	159.17	4.93	16	149–164	156.31	3.77	Do *et al.* (2024)
G. tsushimaensis	18	144–153	147.50	2.10	14	140–151	145.30	2.80	Isogawa *et al.* (1994)
G. ussuriensis									
Russian group	18	149–157	153.20	2.40	14	146–152	149.50	2.10	Emelianov (1929)
Russian and Chinese groups	23	149–157	152.70	–	19	146–153	149.60	–	Gloyd and Conant (1990)
BI group	**16**	**149–162**	**153.38**	**3.03**	**12**	**148–157**	**151.17**	**2.44**	**Present study**
KP group	57	142–151	147.20	3.50	52	142–150	147.00	2.20	Paik *et al.* (1979)
KP group	24	145–156	149.50	2.83	20	143–152	147.50	2.33	Present study
JI group	**21**	**139–150**	**144.86**	**3.14**	**14**	**140–147**	**142.93**	**1.86**	**Present study**
GI group	**13**	**140–147**	**143.46**	**1.71**	**20**	**138–144**	**141.35**	**1.69**	**Present study**
TL/TTL									
G. brevicaudus	23	9.68–12.77	11.17	0.93	17	13.07–19.22	14.64	1.68	Do *et al.* (2024)
G. intermedius	12	10.14–14.62	11.79	1.33	16	11.01–13.55	12.36	0.57	Do *et al.* (2024)
G. tsushimaensis	17	11.80–14.30	13.20	0.80	14	14.00–17.50	15.50	1.00	Isogawa *et al.* (1994)
G. ussuriensis									
Russian group	18	12.10–14.70	13.50	0.60	14	11.60–17.40	14.80	1.40	Emelianov (1929)
Russian and Chinese groups	22	12.00–15.00	13.80	–	19	12.00–17.00	15.10	–	Gloyd and Conant (1990)
BI group	**16**	**13.45–16.08**	**14.60**	**0.88**	**12**	**16.07–17.33**	**16.76**	**0.47**	**Present study**
KP group	57	11.00–16.00	13.20	–	52	8.00–16.00	13.80	–	Paik *et al.* (1979)
KP group	24	11.06–14.95	13.40	1.20	20	13.78–17.49	15.32	1.00	Present study
JI group	**21**	**11.97–14.32**	**13.27**	**0.72**	**14**	**14.15–16.27**	**15.13**	**0.62**	**Present study**
GI group	**13**	**10.15–13.53**	**12.89**	**0.88**	**20**	**14.71–16.47**	**15.69**	**0.44**	**Present study**

KP, Korean Peninsula; BI, Baengnyeongdo Island; JI, Jeju-do Island; GI, Gapado Island.

the HL/SVL of the lectotype (ZISP 13327) of *Gloydius ussuriensis* recorded in Russia is very low at 3.98, further comparative studies with the Russian population are required to verify the major morphological traits of the Baengnyeongdo population (Orlov and Barabanov, 1999).

The Baengnyeongdo Island group (F: 149–162, M: 148–157) exhibited the highest number of scales, whereas the Jeju-do (F: 139–150, M: 140–147) and Gapado Island groups (F: 140–147, M: 138–144) exhibited the lowest. Both inland females (145–156) and males (143–152) differed from the other groups (Table 15). The Jeju-do and Gapado Island groups had fewer abdominal scales on average in both females and males than the other *G. ussuriensis* groups, and the phylogenetically similar *G. tsushimaensis* and *G. intermedius*. The Baengnyeongdo Island group had more abdominal scales than other *G. ussuriensis* groups, *G. tsushimaensis*, and *G. brevicaudus* (Emelianov, 1929; Gloyd and Conant, 1990; Isogawa *et al.*, 1994; Do *et al.*, 2024, Table 15). Meanwhile, the Baengnyeongdo Island group (F: 13.45–16.08, M: 16.07–17.33) had a higher TL/TTL than the inland (F: 11.06–14.95, M: 13.78–17.49), Jeju-do Island (F: 11.97–14.32, M: 14.15–16.27), and Gapado Island groups (F: 10.15–13.53, M: 14.71–16.47). The Baengnyeongdo Island group had a higher average TL/TTL for both females and males than all other *G. ussuriensis* groups, as well as *G. tsushimaensis*, *G. intermedius*, and *G. brevicaudus* (Emelianov, 1929; Gloyd and Conant, 1990; Isogawa *et al.*, 1994; Do *et al.*, 2024, Table 15).

In conclusion, the morphological characteristics of the Baengnyeongdo Island group were distinct from those of other groups and phylogenetically similar species. The inland, Jeju-do, and Gapado Island groups exhibited some overlapping morphological factors (e.g., TL/TTL and TL/SVL), whereas the Jeju-do and Gapado Island groups demonstrated greater similarities (e.g., V, HL/

TTL, and HL/SVL) than the inland group. These similarities were reflected in the LDA results; the Baengnyeongdo Island group was independent, the inland group exhibited a significant overlap with the Jeju-do Island group, and the Jeju-do Island group partially overlapped with the Gapado Island group (Fig. 5).

Ecological characteristics

The environmental niche of *G. ussuriensis* differed between the inland and island areas. The Baengnyeongdo, Gapado, and Heuksando Island groups inhabited lower altitudes than the inland and Jeju-do Island groups. In general, *G. ussuriensis* prefers valleys, rivers, and grasslands at altitudes of 0−1302 m within forested regions (Do *et al*., 2016; 2022b). However, on Gapado Island, all individuals were observed in cultivated fields (Kim *et al*., 2010). Island geography helps explain these differences. Gapado Island (0.84 km^2), located 5.5 km south of Jeju-do Island, is characterized by flat land, including grasslands and farmland, with no mountains (Koh and Park, 2010). Gapado and Baengnyeongdo Island (45.84 km^2), located in the northwest sea, and Heuksando (19.70 km^2) and Jangdo Island (2.23 km^2), located in the southwest sea, comprise low mountain ranges ($\leq$200 m). In contrast, inland regions include the Jirisan Mountain (elevation: 1915 m) and Taebaeksan Mountains, while Jeju-do Island contains Hallasan Mountain (elevation: 1947 m) (Song *et al*., 2006; Kim *et al*., 2013; Woo and Lee, 2016).

Climatic conditions also varied by latitude and altitude. For example, the average annual temperature, winter temperature, and precipitation were the highest on Gapado Island, which has the lowest latitude, and the lowest inland, which has a relatively high altitude. The average annual and summer precipitation was highest on Jeju-do Island (low latitudes) and lowest on Baengnyeongdo Island (highest latitude). The summer temperature, annual temperature range, and daily temperature range were the highest on Gapado Island and lowest on Baengnyeongdo Island.

Because of these habitat differences between the inland and island regions, ecological niches between populations overlapped, although to a lesser degree than in previous studies on the ecological niches of Viperidae species (PI 0.95) (Do *et al*., 2016; Do and Nam, 2021). Consequently, each *G. ussuriensis* group tended to have separate ecological niches depending on the climate and habitat associated with their location, with the Baengnyeongdo and Gapado Island groups showing the greatest separation from other groups.

Taxonomic implications

Understanding the evolution, origin, and boundaries of a species requires evidence from biogeography, genetics, morphometrics, and ecology (Padial *et al*., 2010; Shi *et al*., 2018; Wang *et al*., 2019). The *G. halys* complex, which extends from Azerbaijan and Iran to various countries in Central Asia, Eastern Siberia, Mongolia, and China, is classified into five distinct subspecies, largely shaped by geographical barriers (Orlov and Barabanov, 1999; Wagner *et al*., 2016; Asadi *et al*., 2019): (1) *G. h. halys* (Pallas, 1776), (2) *G. h. boehmei* Nilson, 1983, (3) *G. h. caraganus* Eichwald, 1831, (4) *G. h. cognatus* Gloyd, 1977, and (5) *G. h. stejnegeri* Rendahl, 1933. These subspecies share some traits (e.g., 23 dorsal fin rays) but differ in morphological characteristics (e.g., size, number of pelvic fins, and body color), distribution ranges, and habitat characteristics (altitude range and habitat) (Wagner *et al*., 2016). For example, *G. h. halys*, distributed from eastern Kazakhstan through southern Siberia to Mongolia, has a maximum length of 750 mm and 164−178 abdominal scales, whereas *G. h. stejnegeri*, distributed from southeastern Inner Mongolia to the Shaanxi and Hebei provinces in China, has a maximum length of 625 mm and 147−165 abdominal scales. The smallest, *G. h. boehmei*, endemic to high mountainous regions (2500 m) in eastern Afghanistan, has a maximum length of 487 mm and 155 abdominal scales (Orlov and Barabanov, 1999; Wagner *et al*., 2016). In addition, *Gloydius shedaoensis* in China is classified into two subspecies: *G. s. shedaoensis* (Zhao, 1979), which inhabits Shedao Island located approximately 8 km offshore from the mainland, and *G. s. qianshanensis* Li, 1999, which inhabits Liaoning Province on the mainland (Uetz *et al*., 2025). The two subspecies are clearly distinguished morphologically and ecologically. *G. s. shedaoensis* reaches a maximum total length of 850 mm, has 153−162 ventral scales, and inhabits mountainous areas below 215 m in elevation, whereas *G. s. qianshanensis* attains a smaller maximum total length of 742 mm but has more ventral scales (153−170) and inhabits mountainous areas above 400 m in elevation (Li, 1999; Qiu *et al*., 2023).

Previous studies reported that *G. ussuriensis* has a maximum length of 650 mm and 139−161 abdominal scales (Orlov and Barabanov, 1999). The morphological characteristics of *G. ussuriensis* in the Republic of Korea fell within this range but the Baengnyeongdo, Jeju-do, and Gapado Island groups differ in key morphological traits such as head length ratio and number of abdominal scales. In addition, the Gapado Island group has unique habitat preferences. These patterns are consistent with historical isolation: during the LGM, the Yellow Sea was approximately 120 m lower than today. The subsequent Holocene sea level rise created islands such as Baengnyeongdo and Gapado Island groups (Bloom and Park, 1985; Pirazzoli, 1991), leading to genetic isolation and niche differentiation (Pirazzoli, 1991; Cho *et al*., 2013).

Our findings also indicate morphological affinities between Japanese *G. tsushimaensis* (Isogawa *et al*., 1994) and the Jeju-do and Gapado Island populations (e.g., HL/SVL, HL/HW, and TL/TTL) (Figs. 2 and 6, Tables 14 and 15). Further research is needed to reclassify the taxonomy of *G. ussuriensis* and *G. tsushimaensis* through divergence time estimation and to confirm their origin and distribution patterns using phylogenetic analysis.

Taken together, the results suggest that the Baengnyeongdo Island and Jeju-do-Gapado Island region populations represent a new subspecies. We therefore propose recognizing three subspecies: *G. ussuriensis ussuriensis*, *G. ussuriensis baengnyeongensis*, and *G. ussuriensis jejuensis*, as part of the *G. ussuriensis* complex. Nuclear DNA analysis indicates that the Gapado Island group may have undergone recent differentiation. Further ecological studies are needed to investigate the habitat preferences between groups. Furthermore, we recommend conducting taxonomic studies on *G. ussuriensis* inhabiting various island regions in the southwestern part of the country that were not included in the present study.

This study has several taxonomic limitations. First, genetic comparisons with specimens from the type locality were not conducted, and the diversity of genetic markers was limited. Future studies should include type locality specimens and apply a wider range of mitochondrial and nuclear DNA markers for more precise phylogenetic analyses (e.g., Shi *et al*., 2017; Wang *et al*., 2019). Second, morphological comparisons should be expanded to include detailed and quantitative traits not addressed in this study, such as scale counts from specific regions, hemipenial morphology, X-ray—based skeletal structures, and coloration and pattern characteristics, to better clarify interpopulation morphological differences (e.g., Shi *et al*., 2018; Qiu *et al*., 2023). Finally, to elucidate ecological correlates of subspecific differentiation, more detailed data on ecological factors such as microhabitat use and preferred prey resources are needed (e.g., Li, 1999). Such information would help to refine our understanding of ecological differences among populations and provide essential baseline data for interpreting the background and evolutionary pathways of subspecies differentiation.

Taxonomic Account

Viperidae Gray, 1825
Gloydius Hoge and Romano-Hoge, 1981
Gloydius ussuriensis (Emelianov, 1929)

***Gloydius ussuriensis baengnyeongensis*, Do and Lee, ssp. nov.**

Etymology. *Gloydius ussuriensis baengnyeongensis* ssp. (Fig. 7A, B) is named after Baengnyeongdo, an island



Fig. 7. Individuals observed on (A) August 26, 2021, during the day; (B) May 25, 2019, at night by Min Seock Do and Sang-Cheol Lee on Baengnyeongdo Island. (C) Forest area and paddy field wetlands; (D) field inhabited by *G. ussuriensis baengnyeongensis* ssp. nov.

located in the West Sea of the Korean Peninsula, where it occurs. The English name is "Baengnyeon red-tongued pit viper" and the Korean name is "백령쇠살모사" in Korean.

Description of the holotype. *Gloydius ussuriensis baengnyeongensis* ssp. nov. holotype, deposited in the National Institute of Biological Resources (NIBR), Species Diversity Research Division, Incheon (catalog number NIBRRP0000101143). Adult male preserved in 75% ethanol. Total length 605 mm (SVL: 506 mm, TL: 99 mm). Head length 25.40 mm, head width 15.51 mm, ventral scales 152. Ratio of head length to head width (HL/HW) 1.64; ratio of head length to snout-vent length (HL/SVL) 5.02; ratio of tail length to total length (TL/TTL) 16.36. Collected from Baengnyeong-do, Ongjin, Incheon, Gyeonggi Province, South Korea (37°55′42.18″N, 124°39′19.72″E) on 26 August 2021 by Min Seock Do and Sang-Cheol Lee.

Comparison. The holotype differs from the lectotype of *G. ussuriensis* (ZISP 13327; adult male) by having a shorter total length (605 mm vs. 645 mm) and body length (506 mm vs. 570 mm), but a longer tail (99 mm vs. 75 mm) and head length (25.40 mm vs. 22.7 mm), a wider head (15.51 mm vs. 14.5 mm), and more ventral scales (152 vs. 145). In addition, the ratios HL/HW (1.64 vs. 1.57), HL/SVL (5.02 vs. 3.98), and TL/TTL (16.36 vs. 11.63) are all greater in the holotype than in the lectotype.

Diagnosis. The new subspecies, *G. ussuriensis baengnyeongensis* ssp., is assigned to *Gloydius* because of its small body size and bilateral pit holes between the eyes and nose. The brevicaudus classification is based on 21 dorsal scales; Guo and Zhang, 2002). The specimen has a light pink tongue and brown or blackish-brown tail, consistent with the taxonomic classification of the *G. ussuriensis* complex. This new subspecies differs from *G. ussuriensis* in the following morphological characteristics: (1) long body and tail, (2) long tail length relative to body length (15.18%−21.01%), and (3) high number of ventral scales (148−162).

Coloration. Both eyes have distinct white-yellow stripes behind them, and the tongue is light pink. The dorsal region exhibits a predominantly reddish-brown hue accompanied by brown and yellow tones. Distinct circular patterns extend from the neck to the tail on the left and right sides. The circular patterns may be blurred in some individuals or integrated on both sides to form a single pattern. The centers of the circular patterns are light grayish brown and the edges are dark blackish brown. The ventral region is characterized by white or yellowish-white pigmentation and occasionally marked by small blackish-brown spots distributed in an irregular pattern. No discernible patterns are present. The tail is brown or blackish-brown.



Fig. 8. Individuals observed on (A) September 26, 2020; (B) October 13, 2022, during the day by Min Seock Do and Sang-Cheol Lee on Jeju-do and Gapado Islands. (C) Geumoreum, Jeju-do Island, and (D) grassland of Gapado Island, where *G. ussuriensis jejuensis* ssp. nov. individuals were observed.

Distribution and ecology. *Gloydius ussuriensis baengnyeongensis* is endemic to the Republic of Korea and is found only in Baengnyeongdo. It primarily inhabits forested areas (Fig. 6A). Within 1 km of the main habitat are rice paddies, fields, greenhouses, residential areas, and roads. The area is rich in water resources, including rivers, valleys, and reservoirs (Fig. 7C, D). Individuals are mainly observed between April and October and are more active at night than during the day.

***Gloydius ussuriensis jejuensis*, Do and Oh, ssp. nov.**

Etymology. *Gloydius ussuriensis jejuensis* ssp. is named after the Jeju-do and Gapado Islands in the South Sea of the Korean Peninsula where it occurs (Fig. 8A, B). It is named "Jeju red-tongued pit viper" in English and "제주 쇠살모사" in Korean.

Description of the holotype. *Gloydius ussuriensis jejuensis* ssp. nov. holotype, deposited in the National Institute of Biological Resources (NIBR), Species Diversity Research Division, Incheon (catalog number NIBR RP0000101144). Adult male preserved in 75% ethanol. Total length 400 mm (SVL: 338 mm, TL: 62 mm). Head length 20.18 mm, head width 12.58 mm, ventral scales 143. Ratio of head length to head width (HL/HW) 1.60; ratio of head length to snout-vent length (HL/SVL) 5.97; ratio of tail length to total length (TL/TTL) 15.50. Collected from Gapa-do, Daejeong, Seogwipo, Jeju-do, South Korea (33°10′19.32″N, 126°16′12.01″E) on 13 October 2022 by Min Seock Do and Hong Shik Oh.

Comparison. The holotype differs from the lectotype of *G. ussuriensis* (ZISP 13327; adult male) by having a shorter total length (400 mm vs. 645 mm), shorter body length (338 mm vs. 570 mm), and shorter tail length (62 mm vs. 75 mm). The head is also shorter (20.18 mm vs. 22.7 mm) and narrower (12.58 mm vs. 14.5 mm), with fewer ventral scales (143 vs. 145). In contrast, the ratios HL/HW (1.60 vs. 1.57), HL/SVL (5.97 vs. 3.98), and TL/TTL (15.50 vs. 11.63) are all greater in the holotype than in the lectotype.

Diagnosis. The new subspecies *G. ussuriensis jejuensis* ssp. is assigned to *Gloydius* because of its small body size and bilateral pit holes between the eyes and nose. The Brevicaudus classification is based on 21 dorsal scales (Guo and Zhang, 2002). It has a light pink tongue and brown or blackish-brown tail, consistent with the taxonomic classification of the *G. ussuriensis* complex. It differs from *G. ussuriensis* in the following morphological characteristics: (1) longer head length relative to body length (5.33−6.39) and (2) fewer ventral scales (138−150).

Coloration. Both eyes have distinct white-yellow stripes behind them, and the tongue is light pink. The dorsal region exhibits a predominantly reddish-brown hue accompanied by brown and yellow tones. Distinct circular patterns extend from the neck to the tail on the left and right sides. The centers of the circular patterns are light grayish brown and the edges are dark blackish brown. The ventral region is characterized by white or yellowish-white pigmentation and occasionally marked by small blackish-brown spots distributed in an irregular pattern. No discernible patterns are observed. The tail is brown or blackish-brown.

Distribution and ecology. *Gloydius ussuriensis jejuensis* is endemic to the Republic of Korea and is found on the Gapado and Jeju-do islands. On Jeju-do Island, this species mainly inhabits forested areas (Fig. 6A). Within 1 km of the main habitat, there are cultivated areas, such as grasslands and fields, residential areas, roads, rivers, and valleys, with abundant water resources. On Gapado Island, it mainly inhabits grasslands, graveyards, and barley fields (Fig. 8C, D). It is mainly observed between April and October and is more active at night than during the day.

Conflicts of Interest

The author of this paper have no affiliation with any interests and are solely responsible for the paper.

Acknowledgements

We express our gratitude to Dr. Jae-Han Shim, Dr. Jin-Won Lee, Dr. Hye-Kyoung Moon, Dr. Ki-Baek Nam, Dr. Kyo-Soung Koo, Chang-Deuk Park, and Jongsun Kim for their assistance in securing *G. ussuriensis* samples and conducting this research. This work was supported by grants from the National Institute of Biological Resources funded by the Ministry of Environment, Republic of Korea [NIBR No.202104102, No.202206102].

References

Asadi, A., C. Montgelard, M. Nazarizadeh, A. Moghaddasi, F. Fatemizadeh, E. Simonov, H.G. Kami and M. Kaboli. 2019. Evolutionary history and postglacial colonization of an Asian pit viper (*Gloydius halys caucasicus*) into Transcaucasia revealed by phylogenetic and phylogeographic analyses. Scientific Reports 9(1):1224.

Bloom, A.L. and Y.A. Park. 1985. Holocene sea-level history and tectonic movements, Republic of Korea. Quaternary Research Japan 24(2):77-84.

Bradshaw, D., A. Fabien, S. Maumelat, T. Schwaner and X. Bonnet. 2004. Diet divergence, jaw size and scale counts in two neighbouring populations of tiger snakes (*Notechis scutatus*). Amphibia-Reptilia 25(1):9-17.

Cho, M., E. Lee, H. You, N.G. Kang and D.G. Yoo. 2013. Late

Quaternary sedimentation in the Yellow Sea off Baegryeong Island, Korea. Geophysics and Geophysical Exploration 16(3):145-153.

Choi, W., J. Park, J. Kim, M.S. Do, S.J. Rhim, A. Grajal-Puche and D. Park. 2022. Diets of four snake species in South Korean mountain forests. Journal of Asia-Pacific Biodiversity 15(4):495-499.

Coonan, T.J., C.A. Schwemm, G.W. Roemer, D.K. Garcelon and L. Munson. 2005. Decline of an island fox subspecies to near extinction. The Southwestern Naturalist 50(1):32-41.

David, P. and G. Vogel. 2015. An updated list of Asian pitvipers and a selection of recent publications. In: Asian Pitvipers, Edition Chimaira, Frankfurt am Main, pp. 545-557.

Debono, J., M.H. Bos, M.S. Do and B.G. Fry. 2019. Clinical implications of coagulotoxic variations in Mamushi (Viperidae: *Gloydius*) snake venoms. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology 225:108567.

Ding, L.I., X.N. Gan, S.P. He and E.M. Zhao. 2011. A phylogeographic, demographic and historical analysis of the short?tailed pit viper (*Gloydius brevicaudus*): evidence for early divergence and late expansion during the Pleistocene. Molecular Ecology 20(9):1905-1922.

Do, M.S. and J.C. Yoo. 2014. Distribution pattern according to altitude and habitat type of the Red-tongue viper snake (*Gloydius ussuriensis*) in the Cheon-ma mountain. Journal of Wetlands Research 16(2):193-204.

Do, M.S. and K.B. Nam. 2021. Distribution patterns and ecological niches of the red-tongued pit viper (*Gloydius ussuriensis*) and the central Asian pit viper (*Gloydius intermedius*) in Cheonmasan Mountain, South Korea. Russian Journal of Herpetology 28(6):348-354.

Do, M.S. and S.C. Lee. 2023. First record of a tapeworm (genus *Spirometra*) in the oral cavity of a viper *Gloydius ussuriensis* in South Korea. Herpetology Notes 16:373-376.

Do, M.S., J. Kim and J.H. Choi. 2024. Sexual size dimorphism of the three pit viper species (*G. brevicaudus*, *G. ussuriensis*, *G. intermedius*) in South Korea. Russian Journal of Herpetology 31(3):127-138.

Do, M.S., J.W. Lee, H.J. Jang, D.I. Kim and J.C. Yoo. 2016. Interspecific competition and spatial ecology of three species of vipers in Korea: An application of ecological niche-based models and GIS. Korean Journal of Environment and Ecology 30(2):173-184.

Do, M.S., K.B. Nam and J.C. Yoo. 2017. Distribution and movement tendencies of short-tailed viper snakes (*Gloydius saxatilis*) by altitude. Asian Herpetological Research 8(1):39-47.

Do, M.S., S. Choi, H.J. Jang and J.H. Suh. 2022a. Predicting the distribution of three Korean pit viper species (*Gloydius brevicaudus*, *G. ussuriensis*, and *G. intermedius*) under Climate Change. Russian Journal of Herpetology 29(5): 262-274.

Do, M.S., S.J. Son, G. Choi, N. Yoo, D.I. Kim, K.S. Koo and H.K. Nam. 2022b. The establishment of ecological conservation for herpetofauna species in hotspot areas of South Korea. Scientific Reports 12(1):1-13.

Do, M.S., S.J. Son, J.H. Jung, S.C. Lee, G. Choi and H.K. Nam. 2023. Effects of environmental factors and intraspecific niche overlap on the body and ecological characteristics of red-tongued pit vipers (*Gloydius ussuriensis*). Scientific Reports 13(1):21310.

Emelianov, A.A. 1929. Snakes of the far eastern district. Memoirs of the Vladivostok Section. of the Russian State Geographical Society 3(20):1-208.

Entsminger, G.L. 2012. EcoSim Professional: Null Modeling Software for Ecologists, Version 1. http://www.garyentsminger.com/(Acquired Intelligence, Inc., Montrose, USA, 2014).

Friars, K.A. and A.W. Diamond. 2011. Predicting the sex of Atlantic Puffins, *Fratercula arctica*, by discriminant analysis. Waterbirds 34(3):304-311.

Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. BioScience 50(8):653-666.

Gloyd, H.K. and R. Conant. 1982. The classification of the *Agkistrodon halys* complex. Japanese Journal of Herpetology 9(3):75-78.

Gloyd, H.K. and R. Conant. 1990. Snakes of the *Agkistrodon* Complex - A Monographic Review. Society for the Study of Amphibians and Reptiles, New York. pp. 18-38.

Grant, P.R. 2017. Ecology and Evolution of Darwin's Finches (Princeton Science Library Edition). In: Ecology and Evolution of Darwin's Finches (Princeton Science Library Edition), Princeton University Press, Princeton.

Grazziotin, F.G., M. Monzel, S. Echeverrigaray and S.L. Bonatto. 2006. Phylogeography of the *Bothrops jararaca* complex (Serpentes: Viperidae): past fragmentation and island colonization in the Brazilian Atlantic Forest. Molecular Ecology 15:3969-3982.

Guo, P. and F.J. Zhang. 2002. Phylogenetic and biogeographic studies on *Deinagkistrodon* and *Gloydius* in China. Journal-Sichuan University Natural Science Edition 39(2):378-381.

Hurston, H., L. Voith, J. Bonanno, J. Foufopoulos, P. Pafilis, E. Valakos and N. Anthony. 2009. Effects of fragmentation on genetic diversity in island populations of the Aegean wall lizard *Podarcis erhardii* (Lacertidae, Reptilia). Molecular Phylogenetics and Evolution 52(2):395-405.

Isogawa, K., A. Moriya and S.I. Mitsui. 1994. A new snake of the genus *Agkistrodon* (Serpentes: Viperidae) from Tsuishima Island, Nagasaki prefecture, Japan. Japanese Journal of Herpetology 15:101-111.

Jeon, H.S., M.S. Do, J.A. Kim, Y. Hong, C.E. Lim, J.H. Suh

and J. An. 2024a. First complete mitogenome sequence of Korean *Gloydius ussuriensis* (Viperidae: Crotalinae). Journal of Species Research 13(2):127-130.

Jeon, H.S., M.Y. Lee, J.A. Kim, M.S. Do, I.N. Kim, W.J. Choi and J. An. 2024b. Characterization of 23 microsatellite markers and development of multiplex PCRs for the Amur viper *Gloydius saxatilis* (Viperidae) and cross-species amplification in other *Gloydius* species. Genetics and Molecular Research 23(1):gmr19095.

Kearse, M., R. Moir, A. Wilson, A. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes and A. Drummond. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28(12):1647-1649.

Kim, B.S. and H.S. Oh. 2014a. Foods use of the red-tongued viper snake (*Gloydius ussuriensis*). Korean Journal of Environment and Ecology 28(6):657-663.

Kim, B.S. and H.S. Oh. 2014b. Sexual size dimorphism in the red-tongued viper snake (*Gloydius ussuriensis*) of population. Korean Journal of Environment and Ecology 28(5):542-549.

Kim, B.S., M.H. Jang and H. Ota. 2010. A study on size of Ussuri mamushi *Gloydius ussuriensis* inhabiting at small islet Gapado in Jeju Island, Korea. In: Proceedings of the Korean Society of Environment and Ecology Conference, Korean Society of Environment and Ecology, Seoul. pp. 131-134.

Kim, J.A., M.Y. Lee, H.S. Jeon, M.S. Do, K.S. Koo, S.C. Lee, J.H. Jung, Y.J. Hong and J. An. 2023. Development of microsatellite markers to assess the genetic diversity of the red-tongue viper, *Gloydius ussuriensis* (Reptilia: Viperidae) on the Korean Peninsula. Journal of Species Research 12(4):281-285.

Kim, J.H., G.H. Nam, S.Y. Kim, J.S. Kim, J.E. Choi and B.Y. Lee. 2013. A floristic study of Baengnyeongdo (Isl.) in Korea. Korean Journal of Plant Resources 26(2):178-213.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16(2):111-120.

King, R.B. 2002. Predicted and observed maximum prey size-snake size allometry. Functional Ecology 16:766-772.

Koh, G.W. and J.B. Park. 2010. The study on geology and volcanism in Jeju Island (II): Petrochemistry and 40Ar/39Ar absolute ages of the volcanic rocks in Gapado-Marado, Jeju Island. Economic and Environmental Geology 43(1): 53-66.

Koh, H.S., W.J. Lee and T.D. Kocher. 2000. The genetic relationships of two subspecies of striped field mice, *Apodemus agrarius coreae* and *Apodemus agrarius chejuensis*. Heredity 85(1):30-36.

Kumar, S., G. Stecher, M. Li, C. Knyaz and K. Tamura. 2018. MEGA X: Molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35(6):1547-1549.

Lee, Y.S., M.S. Do, W. Kim, H.S. Jeon, S.C. Lee, J.H. Jung and J. An. 2022. Phylogenetic relationships between three Korean pit viper *Gloydius* (Serpentes: Crotalinae) species using mitochondrial DNA genes. Genes & Genomics 44(5):517-526.

Li, J. 1999. Infraspecific classification of two species of *Gloydius* (Serpentes: Crotalinae). Acta Zootaxonomica Sinica 4:454-460.

Lomolino, M.V. 2005. Body size evolution in insular vertebrates: Generality of the island rule. Journal of Biogeography 32:1683-1699.

Mitteroecker, P. and F. Bookstein. 2011. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. Evolutionary Biology 38:100-114.

Morales-Martínez, D.M., M.E. Rodríguez-Posada and H.E. Ramírez-Chaves. 2021. A new cryptic species of yellow-eared bat *Vampyressa melissa* species complex (Chiroptera: Phyllostomidae) from Colombia. Journal of Mammalogy 102(1):90-100.

Mori, A., D. Ji, H. Moriguchi and M. Hasegawa. 1989. Food habits of snakes in East Asia: A biogeographical approach to resource partitioning. In: M. Matsui, T. Hikida and R.C. Goris (eds.), Current Herpetology in East Asia, Herpetological Society of Japan, Kyoto. pp. 433-436.

Oh, H.S. and M. Banjade. 2021. Ecology of red-tongue viper (*Gloydius ussuriensis*) in Jeju Island, South Korea. Snake Venom and Ecology. IntechOpen.

Orlov, N.L. and A.V. Barabanov. 1999. Analysis of nomenclature, classification, and distribution of the Agkistrodonhalys-Agkistrodonintermedius complexes: A critical review. Russian Journal of Herpetology 6(3):167-192.

Padial, J.M., A. Miralles, I. De la Riva and M. Vences. 2010. The integrative future of taxonomy. Frontiers in Zoology 7(1):1-14.

Paik, N.K., Y.J. Kim and S.Y. Yang. 1979. Biochemical variation and systematic status of the genus *Agkistrodon* (Crotalidae) in Korea. The Korean Journal of Zoology 22(4):153-164.

Park, C.D., M.S. Do, J.H. Lee and J.H. Suh. 2019. Herpetofauna in Socheong, Daecheong and Baengnyeong islands, Korea. Korean Journal of Herpetology 10:1-7.

Peakall, R.O.D. and P.E. Smouse. 2006. GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6(1):288-295.

Phillimore, A.B. and I.P. Owens. 2006. Are subspecies useful in evolutionary and conservation biology? Proceedings of the Royal Society B: Biological Sciences 273(1590):1049-1053.

Pianka, E.R. 2011. Evolutionary ecology: seven edition - ebook. Eric. R. Pianka.

Pirazzoli, P.A. 1991. World Atlas of Holocene Sea-Level Changes. Elsevier, Amsterdam.

Pough, F.H. and J.D. Groves. 1983. Specializations of the body form and food habits of snakes. American Zoologist 23(2):443-454.

Pritchard, J.K., M. Stephens and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945-989.

Qiu, X.C., X.P. Wang, S. Qi, J.Z. Wang, Z.Y. Xia, H.T. Wang, S.B. Zhou, G.X. Yu, Z.X.X. Wu, J.S. Shi and P.P. Li. 2023. Neotype designation and redescription of *Gloydius shedaoensis qianshanensis* Li, 1999 (Squamata: Serpentes: Viperidae). Herpetozoa 36:297-306.

R Core Team. 2024. R: A language and environment for statistical computing. http://www.R-project.org/(R Foundation for Statistical Computing, Vienna, Austria, 2024).

Raymond, M. and F. Rousset. 1995. GENEPOP (version 1.2): Population genetic software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

Reinert, H.K. and R.R. Rupert. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. Journal of Herpetology 33:45-61.

Saitou, N. and M. Nei. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4(4):406-425.

Shi, J.S., D.C. Yang, W.Y. Zhang, L.F. Peng, N. Orlov, F. Jiang, L. Ding, M. Hou, X.L. Huang, S. Huang and P.P. Li. 2018. A new species of the *Gloydius strauchi* complex (Crotalinae: Viperidae: Serpentes) from Qinghai, Sichuan, and Gansu, China. Russian Journal of Herpetology 25(2):126-138.

Shi, J.S., G. Wang, X.E. Chen, Y.H. Fang, L. Ding, S. Huang, M. Hou, J. Liu and P.P. Li. 2017. A new moth-preying alpine pitviper species from Qinghai-Tibetan Plateau (Viperidae, Crotalinae). Amphibia-Reptilia 38(4):517-532.

Shim, J.H., Y.J. Son, S.S. Lee, K.S. Park, H.B. Oh and Y.D. Park. 1998. Ecological study on poisonous snake and investigation of the venom characteristics, snakebiting frequency in Korea. Korean Journal of Environment and Ecology 12(1):58-77.

Shine, R. 1991. Why do larger snakes eat larger prey items? Functional Ecology 5:493-502.

Shine, R., L.X. Sun, E. Zhao and X. Bonnet. 2002. A review of 30 years of ecological research on the Shedao Pitviper, *Gloydius shedaoensis*. Herpetological Natural History 9(1):1-14

Simberloff, D. 2000. Extinction-proneness of island species-causes and management implications. Raffles Bulletin of Zoology 48:1-9.

Song, H.K., G.S. Park, H.R. Park, S.K. So, H.J. Kim and M.Y. Kim. 2006. Vegetation and soil properties of a forest wetland in Jangdo, Sinan-Gun. Korean Journal of Environment and Ecology 20(4):407-414.

Strine, C., I. Silva, B. Nadolski, M. Crane, C. Barnes, T. Artchawakom, J. Hill and P. Suwanwaree. 2015. Sexual dimorphism of tropical green pit viper *Trimeresurus* (*Cryptelytrops*) *macrops* in Northeast Thailand. Amphibia-Reptilia 36(4):327-338.

Tepos-Ramírez, M., O. Flores-Villela, J.A. Velasco, C.P. Lara, O.R. García Rubio and R.C. Jadin. 2021. Molecular phylogenetics and morphometrics reveal a new endemic jumping pitviper (Serpentes: Viperidae: *Metlapilcoatlus*) from the Sierra Madre Oriental of Mexico. Journal of Herpetology 55(2):181-191.

Uetz, P., P. Freed and J. Hošek. 2025. The Reptile Database. *Gloydius shedaoensis* (Zhao, 1979). Available at: https://reptile-database.reptarium.cz/Gloydius/shedaoensis (accessed 1 October 2025).

Wagner, M., M. Kovačić and S. Koblmüller. 2021. Unravelling the taxonomy of an interstitial fish radiation: Three new species of *Gouania* (Teleostei: Gobiesocidae) from the Mediterranean Sea and redescriptions of *G. willdenowi* and *G. pigra*. Journal of Fish Biology 98(1):64-88.

Wagner, P., A. Tiutenko, G. Mazepa, L.J. Borkin and E. Simonov. 2016. Alai! Alai! - a new species of the *Gloydius halys* (Pallas, 1776) complex (Viperidae, Crotalinae), including a brief review of the complex. Amphibia-Reptilia 37(1):15-31.

Wang, H., H. Wang, Y. Xiao, X. Wang, L. Sun, J. Shi, A. Lin, J. Feng and Y. Wu. 2015. Low genetic diversity and moderate inbreeding risk of an insular endemic pit viper (*Gloydius shedaoensis*): Implication for conservation. Journal of Herpetology 49(2):190-199.

Wang, K., J. Ren, W. Dong, K. Jiang, J. Shi, C.D. Siler and J. Che. 2019. A new species of plateau pit viper (Reptilia: Serpentes: *Gloydius*) from the upper Lancang (= Mekong) Valley in the Hengduan Mountain region, Tibet, China. Journal of Herpetology 53(3):224-236.

Weir, B.S. 1979. Inferences about linkage disequilibrium. Biometrics 35:235-254.

Wen, G., L. Jin, Y. Wu, X. Wang, J. Fu and Y. Qi. 2022. Low diversity, little genetic structure but no inbreeding in a high-density island endemic pit-viper *Gloydius shedaoensis*. Current Zoology 68(5):526-534.

Woo, I. and G.H. Lee. 2016. Geology and geography of uninhabited islands around Daeheuksando and Hongdo. Korean Journal of Nature Conservation 10(2):101-110.

Zhang, M.H., S.C. Shi, C. Li, P. Yan, P. Wang, L. Ding, J. Du, A. Plenković-Moraj, J.P. Jiang and J.S. Shi. 2022. Exploring cryptic biodiversity in a world heritage site: A new pitviper (Squamata, Viperidae, Crotalinae) from Jiuzhaigou, Aba, Sichuan, China. ZooKeys 1114:59.

Zhao, E. 1998. China red data book of endangered animals: Amphibia and Reptilia. Science Press, Beijing. pp. 120-121.

Zhao, E.M. 2006. Snakes of China (Volume I). Anhui Science and Technology Publishing House, Hefei, pp. 118-129.

Submitted: August 25, 2025
Revised: October 10, 2025
Accepted: December 2, 2025

Appendix. Sampling localities and genetic, morphological, and ecological data for each individual of *Gloydius ussuriensis*.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
1	IN06474	Chungcheongnam-do	Gongju-si	CS	○	○		○	C
2	IN06475	Chungcheongnam-do	Gongju-si	CS				○	C
3	IN06476	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
4	IN06477	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
5	IN06478	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
6	IN06479	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
7	IN06480	Incheon metropolitan city	Ongjin-gun	BI	○	○		○	C
8	IN06481	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
9	IN06482	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
10	IN06483	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
11	IN06484	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
12	IN06485	Incheon metropolitan city	Ongjin-gun	BI	○	○		○	C
13	IN06486	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
14	IN06487	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
15	IN06488	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
16	IN06489	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
17	IN06490	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
18	IN06491	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
19	IN06492	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
20	IN06493	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
21	IN06494	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
22	IN06495	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
23	IN06496	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
24	IN06497	Incheon metropolitan city	Ongjin-gun	BI	○	○		○	C
25	IN06498	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
26	IN06499	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
27	IN06500	Incheon metropolitan city	Ongjin-gun	BI	○	○		○	C
28	IN06501	Incheon metropolitan city	Ongjin-gun	BI	○	○		○	C
29	IN06502	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
30	IN06503	Incheon metropolitan city	Ongjin-gun	BI	○	○		○	C
31	IN06504	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
32	IN06505	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
33	IN06506	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
34	IN06507	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
35	IN06508	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
36	IN06509	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
37	IN06510	Incheon metropolitan city	Ongjin-gun	BI	○	○	○	○	C
38	IN06511	Incheon metropolitan city	Ongjin-gun	BI	○	○		○	C
39	IN06539	Chungcheongnam-do	Buyeo-gun	CS	○	○		○	C
40	IN06540	Chungcheongnam-do	Buyeo-gun	CS		○		○	C
41	IN06541	Daejeon metropolitan city		CN			○	○	C
42	IN06542	Daejeon metropolitan city		CN			○	○	C
43	IN06543	Daejeon metropolitan city		CN				○	C
44	IN06544	Daejeon metropolitan city		CN			○	○	C
45	IN06545	Daejeon metropolitan city		CN			○	○	C
46	IN06546	Daejeon metropolitan city		CN				○	C
47	IN06547	Chungcheongnam-do	Gongju-si	CS				○	C
48	IN06548	Chungcheongnam-do	Gongju-si	CS				○	C

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
49	IN06549	Chungcheongnam-do	Gongju-si	CS				○	C
50	IN06550	Chungcheongnam-do	Hongseong-gun	CS	○	○		○	C
51	IN06551	Chungcheongnam-do	Seosan-si	CS	○	○	○	○	C
52	IN06552	Chungcheongnam-do	Seosan-si	CS	○	○		○	C
53	IN06553	Chungcheongnam-do	Seosan-si	CS	○		○	○	C
54	IN06554	Chungcheongnam-do	Seosan-si	CS			○	○	C
55	IN06555	Chungcheongnam-do	Seosan-si	CS	○		○	○	C
56	IN06556	Chungcheongnam-do	Seosan-si	CS			○	○	C
57	IN06557	Chungcheongnam-do	Seosan-si	CS	○	○	○	○	C
58	IN06558	Chungcheongnam-do	Seosan-si	CS	○	○	○	○	C
59	IN06559	Chungcheongnam-do	Seosan-si	CS	○	○		○	C
60	IN06560	Chungcheongnam-do	Seosan-si	CS	○	○	○	○	C
61	IN06561	Chungcheongnam-do	Seosan-si	CS	○	○	○	○	C
62	IN06562	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○	○	○	C
63	IN06563	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
64	IN06564	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
65	IN06565	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
66	IN06566	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
67	IN06567	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
68	IN06568	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
69	IN06569	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
70	IN06570	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
71	IN06571	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
72	IN06572	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
73	IN06573	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
74	IN06574	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
75	IN06575	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
76	IN06576	Gyeongsangnam-do	Yangsan-si	GS	○	○	○	○	C
77	IN06577	Jeollanam-do	Haenam-gun	JS			○	○	C
78	IN06578	Jeollanam-do	Haenam-gun	JS			○	○	C
79	IN06579	Jeollanam-do	Haenam-gun	JS			○	○	C
80	IN06580	Jeollanam-do	Haenam-gun	JS			○	○	C
81	IN06581	Jeollanam-do	Haenam-gun	JS			○	○	C
82	IN06582	Jeollanam-do	Haenam-gun	JS			○	○	C
83	IN06583	Jeollanam-do	Haenam-gun	JS				○	C
84	IN06584	Jeollanam-do	Haenam-gun	JS				○	C
85	IN06585	Jeollanam-do	Haenam-gun	JS				○	C
86	IN06586	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
87	IN06587	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
88	IN06588	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
89	IN06589	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
90	IN06590	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
91	IN06591	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
92	IN06592	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
93	IN06593	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
94	IN06594	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
95	IN06595	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○	○	○	C
96	IN06596	Gangwon-do	Gangneung-si	KN	○	○		○	C
97	IN06597	Gangwon-do	Gangneung-si	KN	○	○		○	C

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
98	IN06598	Gangwon-do	Gangneung-si	KN	○	○		○	C
99	IN06599	Gangwon-do	Gangneung-si	KN	○	○		○	C
100	IN06601	Gangwon-do	Gangneung-si	KN	○	○		○	C
101	IN06602	Gangwon-do	Gangneung-si	KN	○	○		○	C
102	IN06603	Gangwon-do	Gangneung-si	KN	○	○		○	C
103	IN06604	Gangwon-do	Gangneung-si	KN	○	○	○	○	C
104	IN06605	Gangwon-do	Gangneung-si	KN	○	○	○	○	C
105	IN06606	Gangwon-do	Gangneung-si	KN	○	○		○	C
106	IN06607	Gangwon-do	Gangneung-si	KN	○	○		○	C
107	IN06608	Gangwon-do	Gangneung-si	KN	○	○	○	○	C
108	IN06609	Gangwon-do	Gangneung-si	KN	○	○	○	○	C
109	IN06610	Gangwon-do	Gangneung-si	KN	○	○	○	○	C
110	IN06611	Gangwon-do	Gangneung-si	KN	○	○		○	C
111	IN06612	Gangwon-do	Gangneung-si	KN	○	○	○	○	C
112	IN06613	Gangwon-do	Gangneung-si	KN	○		○	○	C
113	IN06614	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
114	IN06615	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
115	IN06616	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
116	IN06617	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
117	IN06618	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
118	IN06619	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
119	IN06620	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
120	IN06621	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
121	IN06622	Gangwon-do	Hoengseong-gun	KS		○		○	C
122	IN06623	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
123	IN06624	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
124	IN06625	Gangwon-do	Jeongseon-gun	KS	○	○		○	C
125	IN06626	Gangwon-do	Jeongseon-gun	KS	○	○		○	C
126	IN06627	Gangwon-do	Jeongseon-gun	KS	○	○		○	C
127	IN06628	Gangwon-do	Jeongseon-gun	KS	○	○		○	C
128	IN06629	Gangwon-do	Samcheok-si	KS	○	○		○	C
129	IN06630	Gangwon-do	Samcheok-si	KS	○	○		○	C
130	IN06631	Gangwon-do	Samcheok-si	KS	○	○	○	○	C
131	IN06632	Gangwon-do	Samcheok-si	KS	○	○	○	○	C
132	IN06633	Gangwon-do	Wonju-si	KS	○	○		○	C
133	IN06634	Gangwon-do	Wonju-si	KS	○	○		○	C
134	IN06635	Gangwon-do	Wonju-si	KS	○	○		○	C
135	IN06636	Gangwon-do	Wonju-si	KS	○	○		○	C
136	IN06637	Gangwon-do	Wonju-si	KS	○	○		○	C
137	IN06638	Gangwon-do	Wonju-si	KS	○	○		○	C
138	IN06639	Gangwon-do	Wonju-si	KS	○	○		○	C
139	IN06640	Gangwon-do	Wonju-si	KS	○	○		○	C
140	IN06641	Gangwon-do	Wonju-si	KS	○	○		○	C
141	IN06642	Gangwon-do	Samcheok-si	KS	○	○		○	C
142	IN06643	Gangwon-do	Wonju-si	KS	○	○		○	C
143	IN06644	Jeollabuk-do	Buan-gun	JN			○	○	C
144	IN06645	Jeollabuk-do	Buan-gun	JN				○	C
145	IN06646	Jeju-do	Jeju-si	JI		○		○	C
146	IN06647	Jeju-do	Jeju-si	JI	○	○		○	C

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
147	IN06648	Jeju-do	Jeju-si	JI	○	○		○	C
148	IN06649	Jeju-do	Jeju-si	JI	○	○		○	C
149	IN06650	Jeju-do	Seogwipo-si	JI	○	○		○	C
150	IN06651	Jeollanam-do	Jangheung-gun	JS			○	○	C
151	IN06652	Jeollanam-do	Jangheung-gun	JS				○	C
152	IN06653	Jeollanam-do	Jangheung-gun	JS				○	C
153	IN06654	Jeollanam-do	Yeongam-gun	JS				○	C
154	IN06655	Jeollanam-do	Yeongam-gun	JS				○	C
155	IN06656	Gyeonggi-do	Gimpo-si	GG	○	○		○	C
156	IN06657	Gyeonggi-do	Gimpo-si	GG	○	○		○	C
157	IN06658	Jeollanam-do	Yeongam-gun	JS				○	C
158	IN06659	Jeollanam-do	Yeongam-gun	JS				○	C
159	IN06685	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
160	IN06686	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
161	IN06687	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
162	IN06688	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
163	IN06689	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
164	IN06690	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
165	IN06691	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
166	IN06692	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
167	IN06693	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
168	IN06694	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
169	IN06695	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
170	IN06697	Chungcheongbuk-do	Chungju-si	CN			○	○	C
171	IN06699	Chungcheongbuk-do	Danyang-gun	CN		○		○	C
172	IN06700	Chungcheongbuk-do	Danyang-gun	CN		○		○	C
173	IN06701	Chungcheongnam-do	Cheongyang-gun	CS		○	○	○	C
174	IN06702	Chungcheongnam-do	Taean-gun	CS	○		○	○	C
175	IN06703	Chungcheongnam-do	Taean-gun	CS	○	○		○	C
176	IN06704	Chungcheongnam-do	Taean-gun	CS	○		○	○	C
177	IN06705	Chungcheongnam-do	Taean-gun	CS		○		○	C
178	IN06706	Chungcheongnam-do	Taean-gun	CS			○	○	C
179	IN06707	Chungcheongnam-do	Yesan-gun	CS		○		○	C
180	IN06827	Jeollabuk-do	Buan-gun	JN			○	○	C
181	IN06828	Chungcheongnam-do	Cheongyang-gun	CS		○	○	○	C
182	IN06829	Chungcheongnam-do	Cheongyang-gun	CS	○	○	○	○	C
183	IN06830	Chungcheongnam-do	Cheongyang-gun	CS	○	○	○	○	C
184	IN06997	Gyeongsangbuk-do	Cheongdo-gun	GS	○	○		○	C
185	IN06998	Gyeonggi-do	Yeoncheon-gun	GG		○		○	C
186	IN07001	Gangwon-do	Wonju-si	KS	○	○		○	C
187	IN07002	Gangwon-do	Hoengseong-gun	KS	○	○		○	C
188	IN07003	Gangwon-do	Wonju-si	KS	○	○		○	C
189	IN07008	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
190	IN07009	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
191	IN07010	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
192	IN07011	Gangwon-do	Inje-gun	KN	○	○		○	C
193	IN07012	Gangwon-do	Yanggu-gun	KN	○	○		○	C
194	IN07013	Gangwon-do	Gangneung-si	KN	○	○		○	C
195	IN07017	Gangwon-do	Gangneung-si	KN	○	○		○	C

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
196	IN07018	Gangwon-do	Gangneung-si	KN	○	○		○	C
197	IN07019	Gangwon-do	Gangneung-si	KN	○	○		○	C
198	IN07020	Gangwon-do	Gangneung-si	KN	○	○		○	C
199	IN07021	Gangwon-do	Gangneung-si	KN	○	○		○	C
200	IN07022	Gangwon-do	Gangneung-si	KN	○	○		○	C
201	IN07025	Gyeongsangbuk-do	Cheongdo-gun	GS	○	○		○	C
202	IN07026	Ulsan metropolitan city	Ulju-gun	GS	○	○		○	C
203	IN07027	Ulsan metropolitan city	Ulju-gun	GS	○	○		○	C
204	IN07028	Ulsan metropolitan city	Ulju-gun	GS	○	○		○	C
205	IN07029	Ulsan metropolitan city	Ulju-gun	GS	○	○		○	C
206	IN07030	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
207	IN07031	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
208	IN07032	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
209	IN07033	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
210	IN07034	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
211	IN07035	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
212	IN07036	Jeollanam-do	Gangjin-gun	JS				○	C
213	IN07037	Jeollanam-do	Gangjin-gun	JS				○	C
214	IN07038	Jeollanam-do	Gangjin-gun	JS				○	C
215	IN07039	Jeollanam-do	Gangjin-gun	JS				○	C
216	IN07040	Jeollanam-do	Gangjin-gun	JS				○	C
217	IN07041	Jeollanam-do	Gangjin-gun	JS				○	C
218	IN07042	Jeollanam-do	Gangjin-gun	JS				○	C
219	IN07043	Jeollanam-do	Gangjin-gun	JS				○	C
220	IN07044	Jeollanam-do	Haenam-gun	JS				○	C
221	IN07045	Jeollanam-do	Haenam-gun	JS				○	C
222	IN07046	Jeollanam-do	Haenam-gun	JS				○	C
223	IN07047	Jeollanam-do	Haenam-gun	JS				○	C
224	IN07048	Jeollanam-do	Haenam-gun	JS				○	C
225	IN07049	Jeollanam-do	Haenam-gun	JS				○	C
226	IN07050	Jeollanam-do	Haenam-gun	JS				○	C
227	IN07051	Jeollanam-do	Haenam-gun	JS				○	C
228	IN07052	Jeollanam-do	Haenam-gun	JS				○	C
229	IN07053	Jeollanam-do	Yeongam-gun	JS				○	C
230	IN07054	Jeollanam-do	Hampyeong-gun	JS				○	C
231	IN07055	Jeollanam-do	Hampyeong-gun	JS				○	C
232	IN07056	Jeollanam-do	Hampyeong-gun	JS				○	C
233	IN07057	Jeollabuk-do	Buan-gun	JN				○	C
234	IN07059	Jeju-do	Jeju-si	JI		○		○	C
235	IN07060	Jeju-do	Jeju-si	JI	○	○		○	C
236	IN07061	Jeju-do	Jeju-si	JI		○		○	C
237	IN07062	Jeju-do	Jeju-si	JI		○		○	C
238	IN07063	Jeju-do	Jeju-si	JI		○		○	C
239	IN07064	Jeju-do	Jeju-si	JI		○		○	C
240	IN07065	Jeju-do	Jeju-si	JI	○	○		○	C
241	IN07066	Jeju-do	Jeju-si	JI		○		○	C
242	IN07067	Jeju-do	Jeju-si	JI	○	○		○	C
243	IN07068	Jeju-do	Jeju-si	JI		○		○	C
244	IN07069	Jeju-do	Jeju-si	JI		○		○	C

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
245	IN07070	Jeju-do	Jeju-si	JI		○		○	C
246	IN07071	Jeju-do	Jeju-si	JI		○		○	C
247	IN07072	Jeju-do	Jeju-si	JI	○	○		○	C
248	IN07073	Jeju-do	Jeju-si	JI	○	○		○	C
249	IN07074	Jeju-do	Jeju-si	JI	○	○		○	C
250	IN07075	Jeju-do	Jeju-si	JI	○	○		○	C
251	IN07076	Jeju-do	Jeju-si	JI	○	○		○	C
252	IN07077	Jeju-do	Jeju-si	JI	○	○		○	C
253	IN07078	Jeju-do	Jeju-si	JI		○		○	C
254	IN07079	Jeju-do	Jeju-si	JI		○		○	C
255	IN07080	Jeju-do	Jeju-si	JI	○	○		○	C
256	IN07081	Jeju-do	Jeju-si	JI	○	○		○	C
257	IN07082	Jeju-do	Jeju-si	JI	○	○		○	C
258	IN07148	Gangwon-do	Gangneung-si	KN	○	○		○	C
259	IN07149	Gangwon-do	Jeongseon-gun	KS	○	○		○	C
260	IN07150	Gyeongsangnam-do	Yangsan-si	GS	○	○		○	C
261	IN07151	Chungcheongnam-do	Dangjin-si	CS	○	○		○	C
262	IN07152	Chungcheongnam-do	Seosan-si	CS	○	○		○	C
263	IN07153	Chungcheongnam-do	Seosan-si	CS	○	○		○	C
264	IN07154	Chungcheongnam-do	Seosan-si	CS		○		○	C
265	IN07155	Chungcheongnam-do	Seosan-si	CS	○	○		○	C
266	IN07156	Chungcheongnam-do	Seosan-si	CS	○	○		○	C
267	IN07157	Chungcheongnam-do	Seosan-si	CS	○	○	○	○	C
268	IN07158	Chungcheongnam-do	Hongseong-gun	CS		○		○	C
269	IN07159	Chungcheongnam-do	Hongseong-gun	CS	○	○		○	C
270	IN07160	Chungcheongnam-do	Buyeo-gun	CS		○		○	C
271	IN07161	Chungcheongnam-do	Gongju-si	CS	○	○		○	C
272	IN07162	Daejeon metropolitan city		CN				○	C
273	IN07163	Daejeon metropolitan city		CN				○	C
274	IN07164	Daejeon metropolitan city		CN				○	C
275	IN07165	Daejeon metropolitan city		CN				○	C
276	IN07166	Daejeon metropolitan city		CN				○	C
277	IN07167	Daejeon metropolitan city		CN				○	C
278	IN07168	Daejeon metropolitan city		CN				○	C
279	IN07169	Daejeon metropolitan city		CN				○	C
280	IN07170	Daejeon metropolitan city		CN				○	C
281	IN07171	Daejeon metropolitan city		CN				○	C
282	IN07220	Gyeonggi-do	Pocheon-si	GG		○		○	C
283	IN07221	Gyeonggi-do	Pocheon-si	GG		○		○	C
284	IN07222	Gyeonggi-do	Pocheon-si	GG		○		○	C
285	IN07223	Gyeonggi-do	Pocheon-si	GG		○		○	C
286	IN07224	Gyeonggi-do	Pocheon-si	GG		○		○	C
287	IN07225	Gyeonggi-do	Pocheon-si	GG		○		○	C
288	IN07226	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
289	IN07227	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
290	IN07228	Gyeongsangbuk-do	Bonghwa-gun	GN	○	○		○	C
291	IN07230	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
292	IN07231	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
293	IN07232	Chungcheongbuk-do	Cheongju-si	CN		○		○	C

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
294	IN07233	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
295	IN07234	Gyeongsangbuk-do	Sangju-si	GN		○		○	C
296	IN07242	Gangwon-do	Samcheok-si	KS	○	○		○	C
297	IN07243	Gangwon-do	Samcheok-si	KS	○	○		○	C
298	IN07244	Gangwon-do	Samcheok-si	KS	○	○		○	C
299	IN07245	Gangwon-do	Samcheok-si	KS	○	○		○	C
300	IN07246	Gangwon-do	Samcheok-si	KS	○	○		○	C
301	IN07247	Gangwon-do	Samcheok-si	KS	○	○		○	C
302	IN07248	Gangwon-do	Samcheok-si	KS	○	○		○	C
303	IN07249	Jeju-do	Jeju-si	JI	○	○		○	C
304	IN07250	Jeju-do	Jeju-si	JI	○	○		○	C
305	IN07251	Gyeongsangbuk-do	Cheongdo-gun	GS		○		○	C
306	IN07255	Chungcheongbuk-do	Cheongju-si	CN		○		○	C
307	IN07912	Gyeongsangbuk-do	Yecheon-gun	GN		○		○	C
308	IN07914	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
309	IN07915	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
310	IN07919	Jeollabuk-do	Wanju-gun	JN				○	C
311	IN07920	Jeollabuk-do	Jinan-gun	JN		○		○	C
312	IN07921	Chungcheongnam-do	Cheongyang-gun	CS	○	○		○	C
313	IN07922	Gyeongsangbuk-do	Cheongdo-gun	GS	○	○		○	C
314	IN07923	Gyeongsangbuk-do	Cheongdo-gun	GS	○	○		○	C
315	IN07924	Gyeongsangbuk-do	Andong-si	GN	○	○		○	C
316	IN07925	Gyeongsangbuk-do	Andong-si	GN	○	○		○	C
317	IN07926	Gyeongsangbuk-do	Andong-si	GN	○	○		○	C
318	IN07934	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
319	IN07935	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
320	IN07936	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
321	IN07937	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
322	IN07938	Chungcheongnam-do	Cheongyang-gun	CS	○	○		○	C
323	IN07939	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
324	IN07940	Chungcheongnam-do	Cheongyang-gun	CS	○	○		○	C
325	IN07941	Chungcheongnam-do	Cheongyang-gun	CS		○	○	○	C
326	IN07942	Chungcheongnam-do	Cheongyang-gun	CS		○		○	C
327	IN07943	Chungcheongnam-do	Cheongyang-gun	CS	○	○		○	C
328	IN07947	Gyeongsangbuk-do	Andong-si	GN	○	○		○	C
329	IN07948	Jeollanam-do	Gwangyang-si	JS				○	C
330	IN07949	Jeollanam-do	Gwangyang-si	JS				○	C
331	IN07955	Gyeongsangbuk-do	Yecheon-gun	GN		○		○	C
332	IN07956	Gyeongsangbuk-do	Yecheon-gun	GN		○		○	C
333	IN07970	Chungcheongnam-do	Cheongyang-gun	CS				○	C
334	IN07971	Chungcheongnam-do	Cheongyang-gun	CS				○	C
335	IN07972	Chungcheongnam-do	Cheongyang-gun	CS				○	C
336	IN07978	Gyeongsangbuk-do	Yecheon-gun	GN		○		○	C
337	IN07985	Gyeongsangbuk-do	Yecheon-gun	GN		○		○	C
338	IN07986	Gyeongsangbuk-do	Yecheon-gun	GN	○	○		○	C
339	IN07989	Chungcheongnam-do	Cheongyang-gun	CS				○	C
340	IN07990	Chungcheongnam-do	Cheongyang-gun	CS				○	C
341	IN07991	Chungcheongnam-do	Cheongyang-gun	CS				○	C

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
342	IN07992	Gyeongsangbuk-do	Yeongju-si	GN		○		○	C
343	IN07993	Gyeongsangbuk-do	Andong-si	GN	○	○		○	C
344	IN08206	Gyeongsangbuk-do	Mungyeong-si	GN		○		○	C
345	IN08207	Incheon metropolitan city	Ongjin-gun	CS		○			C
346	IN08208	Gangwon-do	Inje-gun	KN	○	○		○	C
347	IN08209	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
348	IN08210	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
349	IN08211	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
350	IN08212	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
351	IN08213	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
352	IN08214	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
353	IN08215	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
354	IN08216	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
355	IN08217	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
356	IN08218	Gangwon-do	Yanggu-gun	KN	○	○		○	C
357	IN08219	Jeollabuk-do	Jinan-gun	CN		○		○	C
358	IN08220	Jeollabuk-do	Jinan-gun	CN		○		○	C
359	IN08221	Jeollanam-do	Gangjin-gun	JS				○	C
360	IN08222	Jeollanam-do	Gangjin-gun	JS				○	C
361	IN08223	Jeollanam-do	Gangjin-gun	JS				○	C
362	IN08224	Jeollanam-do	Gangjin-gun	JS				○	C
363	IN08225	Jeollanam-do	Gangjin-gun	JS				○	C
364	IN08226	Gangwon-do	Inje-gun	KN	○	○		○	C
365	IN08227	Gyeongsangnam-do	Hadong-gun	GS		○		○	C
366	IN08228	Jeollanam-do	Gwangyang-si	JS				○	C
367	IN08229	Gyeonggi-do	Yeoncheon-gun	GG		○		○	C
368	IN08230	Gyeonggi-do	Dongducheon-si	GG		○		○	C
369	IN08231	Jeollanam-do	Jindo-gun	JS					C
370	IN08232	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
371	IN08233	Gangwon-do	Pyeongchang-gun	KS	○	○		○	C
372	IN08235	Gyeongsangnam-do	Miryang-si	GS	○	○		○	C
373	IN08236	Gyeonggi-do	Yeoncheon-gun	GG		○		○	C
374	IN08248	Gyeonggi-do	Namyangju-si	GG	○	○		○	D (N)
375	IN08249	Gyeonggi-do	Namyangju-si	GG	○	○		○	D (N)
376	IN08251	Gangwon-do	Yangyang-gun	KN	○	○		○	D (N)
377	IN08252	Gyeongsangbuk-do	Gumi-si	GN		○		○	D (N)
378	IN08253	Gyeongsangbuk-do	Gumi-si	GN		○		○	D (N)
379	IN08254	Gyeongsangbuk-do	Cheongsong-gun	GN	○	○		○	D (N)
380	IN08255	Gyeonggi-do	Yeoju-si	GG		○		○	D (N)
381	IN08256	Gangwon-do	Hongcheon-gun	KN	○	○		○	D (N)
382	IN08257	Jeollabuk-do	Imsil-gun	CN				○	D (N)
383	IN08258	Gangwon-do	Hongcheon-gun	KN	○	○		○	D (N)
384	IN08259	Jeollanam-do	Hwasun-gun	JS				○	D (N)
385	IN08260	Gyeongsangnam-do	Gimhae-si	GS		○		○	D (N)
386	IN08261	Gyeongsangnam-do	Gimhae-si	GS		○		○	D (N)
387	IN08262	Gyeongsangnam-do	Sancheong-gun	GS		○		○	D (N)
388	IN08263	Gyeongsangnam-do	Sancheong-gun	GS		○		○	D (N)
389	IN08264	Gyeongsangnam-do	Tongyeong-si	GS		○			D (N)
390	IN08265	Gyeonggi-do	Namyangju-si	GG	○	○		○	D (N)

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
391	IN08267	Gyeonggi-do	Namyangju-si	GG	○	○		○	D (N)
392	IN08268	Gyeonggi-do	Namyangju-si	GG	○	○		○	D (N)
393	IN08269	Gyeonggi-do	Gwangju-si	GG		○		○	D (N)
394	IN08270	Gyeonggi-do	Gwangju-si	GG		○		○	D (N)
395	IN08271	Gyeonggi-do	Gwangju-si	GG		○		○	D (N)
396	IN08272	Gyeonggi-do	Gwangju-si	GG		○		○	D (N)
397	IN08276	Gyeongsangnam-do	Hapcheon-gun	GS		○		○	D (N)
398	IN08277	Gyeonggi-do	Paju-si	GG	○	○		○	D (N)
399	IN08278	Gyeonggi-do	Paju-si	GG	○	○		○	D (N)
400	IN08279	Gyeonggi-do	Paju-si	GG	○	○		○	D (N)
401	IN08280	Gyeonggi-do	Hwaseong-si	GG		○		○	D (N)
402	IN08281	Jeollanam-do	Goheung-gun	JS				○	D (N)
403	IN08282	Jeollanam-do	Goheung-gun	JS				○	D (N)
404	IN08283	Gyeonggi-do	Seongnam-si	GG	○	○		○	D (N)
405	IN08284	Jeollanam-do	Hwasun-gun	JS				○	D (N)
406	IN08285	Gyeongsangbuk-do	Gimcheon-si	GN		○		○	D (N)
407	IN08286	Gangwon-do	Yangyang-gun	KN	○	○		○	D (N)
408	IN08288	Gyeongsangbuk-do	Pohang-si	GN	○	○		○	D (N)
409	IN08289	Gyeongsangbuk-do	Pohang-si	GN	○	○		○	D (N)
410	IN08290	Gyeonggi-do	Paju-si	GG	○	○		○	D (N)
411	IN09824	Jeju-do	Jeju-si	JI			○	○	D (J)
412	IN09825	Jeju-do	Jeju-si	JI			○	○	D (J)
413	IN09826	Jeju-do	Jeju-si	JI			○	○	D (J)
414	IN09827	Jeju-do	Jeju-si	JI			○	○	D (J)
415	IN09828	Jeju-do	Jeju-si	JI			○	○	D (J)
416	IN09829	Jeju-do	Jeju-si	JI			○	○	D (J)
417	IN09830	Jeju-do	Jeju-si	JI			○	○	D (J)
418	IN09831	Jeju-do	Jeju-si	JI			○	○	D (J)
419	IN09834	Jeju-do	Jeju-si	JI			○	○	D (J)
420	IN09835	Jeju-do	Jeju-si	JI			○	○	D (J)
421	IN09836	Jeju-do	Jeju-si	JI			○	○	D (J)
422	IN09837	Jeju-do	Jeju-si	JI			○	○	D (J)
423	IN09838	Jeju-do	Jeju-si	JI			○	○	D (J)
424	IN09839	Jeju-do	Jeju-si	JI			○	○	D (J)
425	IN09840	Jeju-do	Jeju-si	JI			○	○	D (J)
426	IN09841	Jeju-do	Jeju-si	JI			○	○	D (J)
427	IN09842	Jeju-do	Jeju-si	JI			○	○	D (J)
428	IN09844	Jeju-do	Jeju-si	JI			○	○	D (J)
429	IN09845	Jeju-do	Jeju-si	JI			○	○	D (J)
430	IN09846	Jeju-do	Jeju-si	JI			○	○	D (J)
431	IN09847	Jeju-do	Jeju-si	JI			○	○	D (J)
432	IN09848	Jeju-do	Jeju-si	JI			○	○	D (J)
433	IN09850	Jeju-do	Jeju-si	JI			○	○	D (J)
434	IN09851	Jeju-do	Jeju-si	JI			○	○	D (J)
435	IN09853	Jeju-do	Jeju-si	JI			○	○	D (J)
436	IN09854	Jeju-do	Jeju-si	JI			○	○	D (J)
437	IN09855	Jeju-do	Jeju-si	JI			○	○	D (J)
438	IN09857	Jeju-do	Jeju-si	JI			○	○	D (J)
439	IN09858	Jeju-do	Jeju-si	JI			○	○	D (J)

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
440	IN09859	Jeju-do	Jeju-si	JI			○	○	D (J)
441	IN09860	Jeju-do	Jeju-si	JI			○	○	D (J)
442	IN09861	Jeju-do	Jeju-si	JI			○	○	D (J)
443	IN09863	Jeju-do	Jeju-si	JI			○	○	D (J)
444	IN09864	Jeju-do	Jeju-si	JI			○	○	D (J)
445	IN09865	Jeju-do	Jeju-si	JI			○	○	D (J)
446	IN09875	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
447	IN09876	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
448	IN09880	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
449	IN09881	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
450	IN09882	Jeju-do	Seogwipo-si	GI	○		○	○	D (J)
451	IN09883	Jeju-do	Seogwipo-si	GI			○	○	D (J)
452	IN09884	Jeju-do	Seogwipo-si	GI			○	○	D (J)
453	IN09885	Jeju-do	Seogwipo-si	GI			○	○	D (J)
454	IN09886	Jeju-do	Seogwipo-si	GI			○	○	D (J)
455	IN09888	Jeju-do	Seogwipo-si	GI			○	○	D (J)
456	IN09891	Jeju-do	Seogwipo-si	GI			○	○	D (J)
457	IN09892	Jeju-do	Seogwipo-si	GI			○	○	D (J)
458	IN09893	Jeju-do	Seogwipo-si	GI			○	○	D (J)
459	IN09898	Jeju-do	Seogwipo-si	GI			○	○	D (J)
460	IN09899	Jeju-do	Seogwipo-si	GI			○	○	D (J)
461	IN09900	Jeju-do	Seogwipo-si	GI			○	○	D (J)
462	IN09902	Jeju-do	Seogwipo-si	GI			○	○	D (J)
463	IN09903	Jeju-do	Seogwipo-si	GI			○	○	D (J)
464	IN09905	Jeju-do	Seogwipo-si	GI			○	○	D (J)
465	IN09907	Jeju-do	Seogwipo-si	GI			○	○	D (J)
466	IN09908	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
467	IN09909	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
468	IN09910	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
469	IN09911	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
470	IN09912	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
471	IN09913	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
472	IN09914	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
473	IN09915	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
474	IN09916	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
475	IN09917	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
476	IN09918	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
477	IN09919	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
478	IN09920	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
479	IN09921	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
480	IN09922	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
481	IN09923	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
482	IN09924	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
483	IN09925	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
484	IN09926	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
485	IN09927	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
486	IN09928	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
487	IN09929	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
488	IN09930	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)

Appendix. Continued.

No.	ID	Province	District	Population code	Information				Note*
					mtDNA	ssrDNA	Morphology	Ecology	
489	IN09931	Jeju-do	Seogwipo-si	GI	○	○	○	○	D (J)
490	IN09932	Jeju-do	Seogwipo-si	GI	○	○		○	D (J)
491	IN09936	Jeju-do	Seogwipo-si	GI			○	○	D (J)
492	IN09937	Jeju-do	Seogwipo-si	GI			○	○	D (J)
493	IN09939	Jeju-do	Seogwipo-si	GI			○	○	D (J)
494	IN09945	Jeju-do	Seogwipo-si	GI			○	○	D (J)
495	IN09948	Jeju-do	Seogwipo-si	GI			○	○	D (J)
496	IN09951	Jeju-do	Seogwipo-si	GI		○		○	D (J)
497	IN10358	Jeollanam-do	Sinan-gun	SJI		○		○	C
498	IN10359	Jeollanam-do	Sinan-gun	SJI		○		○	C
499	IN10360	Jeollanam-do	Sinan-gun	SJI		○		○	C
500	IN10361	Jeollanam-do	Sinan-gun	SJI		○		○	C
501	IN10362	Jeollanam-do	Sinan-gun	SJI		○		○	C
502	IN10363	Jeollanam-do	Sinan-gun	SJI		○		○	C
503	IN10364	Jeollanam-do	Sinan-gun	SJI		○		○	C
504	IN10365	Jeollanam-do	Sinan-gun	SJI		○		○	C
505	IN10366	Jeollanam-do	Sinan-gun	SJI		○		○	C
506	IN10367	Jeollanam-do	Sinan-gun	SHI		○		○	C
507	IN10368	Jeollanam-do	Sinan-gun	SHI		○		○	C
508	IN10369	Jeollanam-do	Sinan-gun	SHI		○		○	C
509	IN10370	Jeollanam-do	Sinan-gun	SHI		○		○	C
510	IN10541	Jeju-do	Seogwipo-si	GI		○		○	C
511	IN10542	Jeju-do	Seogwipo-si	GI		○		○	C
512	IN10543	Jeju-do	Seogwipo-si	GI		○		○	C
513	IN10544	Jeju-do	Seogwipo-si	GI		○	○	○	C
Total					259	365	140	510	

C, collection; D(N), distribution (National Institute of Biological Resources); D(J), distribution (Jeju National University).