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Reconstruction of the phylogeny for the genus *Naemorhedus*: samples from Northeast and North China provide new evidence for taxonomic status

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ABSTRACT

The gorals (*Naemorhedus*), widely distributed ungulates across Asia, are facing significant threats from habitat fragmentation and human disturbance. Phylogenetic studies facilitate taxonomic revisions by revealing evolutionary relationships and phylogenetic distinctiveness among species, thereby informing the prioritization of conservation efforts to sustain genetic diversity, maintain ecological functions and formulate effective population protection strategies. However, taxonomic controversies persist within this genus. Previous studies lacked genetic samplings from northern China, resulting in unresolved discrepancies in the taxonomic status of the Chinese goral (*Naemorhedus griseus*). In this study, we added new samples from Northeast and North China. We analyzed all currently available complete sequences of mitochondrial cytochrome *b* (1 140 bp), the control region (1 127 bp), and cytochrome c oxidase subunit I (1 545 bp) to verify the phylogenetic status of this genus. Phylogenetic trees consistently supported the validity of six species: *Naemorhedus evansi*, *Naemorhedus baileyi*, *Naemorhedus cranbrooki*, *N. griseus*, *Naemorhedus goral*, and *Naemorhedus caudatus*. This finding was consistent with morphological and geographical evidence and further revealed that *N. griseus* populations distributed in China were subdivided into northeastern and southwestern subclades. Our results establish a robust foundation for further research into the genetic differentiation among isolated subpopulations of the Chinese goral, while providing critical scientific support for the management and conservation of genetic resources. This study contributes to the maintenance of gene pool diversity and offers actionable insights for advancing scientific conservation efforts targeting this species.

Keywords: Goral; Mitochondrion DNA; Phylogeny; Northeast and North China

INTRODUCTION

The investigation of phylogenetic relationships is a prerequisite for preserving biodiversity, particularly in assessing the level of threat faced by each taxon, which is essential for the management and conservation of endangered species (Schaller, 1977; Zachos et al., 2013). The gorals (*Naemorhedus*), distributed widely across Asia, spans diverse biogeographic and ecological zones (Dinerstein et al., 2017), adapting to diversified altitudes and habitats, with records in China, India, Pakistan, Myanmar, and South Korea (Bragina et al., 2020; Duckworth & MacKinnon, 2008; Hrabina, 2015; Jiang et al., 2015; Nijhawan, 2020). Vital to forest ecosystems, the conservation of gorals is crucial for maintaining regional biodiversity balance, especially for sustaining wild predator populations. However, natural environmental changes, alterations in land use, human disturbances, and illegal poaching have led to habitat destruction and fragmentation, population isolation and reduction, which threatened the survival of wild goral populations. Consequently, the goral was listed in the Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), prohibiting any international trade to protect it from human threats (Hemley, 1994; Wijnstekers, 2011). Despite extensive efforts to classify and evaluate the genus over recent decades, the taxonomic status remains controversial, and a consensus has yet to be reached (Li et al., 2020; Mori et al., 2019; Shukla et al., 2018). Early researches described ten species of gorals based on geographic distribution, body length, pelage features, and skull morphology, namely *Naemorhedus arnouxianus*, *Naemorhedus baileyi,* *Naemorhedus bedfordi*, *Naemorhedus caudatus*, *Naemorhedus cranbrooki*, *Naemorhedus evansi*,

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Naemorhedus griseus, *Naemorhedus goral*, *Naemorhedus hodgsoni*, *Naemorhedus raddeanus* (Dolan, 1963; Groves & Grubb, 1985, 2011; Grubb, 2005; Haltenorth, 1963; Hayman, 1961; Lydekker, 1913; Mead, 1989; Pucock, 1908). However, the International Union for Conservation of Nature (IUCN) recognized only three species: *N. goral*, *N. caudatus*, *N. baileyi*. Under the IUCN Red List criteria, *N. caudatus* and *N. baileyi* are classified as Vulnerable (VU), while *N. goral* is designated as Near Threatened (NT) (Bragina et al., 2020; Duckworth & MacKinnon, 2008; Nijhawan, 2020).

The distribution range of the Chinese goral (*N. griseus*) covers most of the mountainous areas in central and eastern China, as well as in southwestern regions. The Catalogue of Mammals in China (2021), Red List of China's Vertebrates, and Catalogue of Life China 2024 Annual Checklist all confirmed the validity of the Chinese goral (Lin et al., 2024; Ministry of Ecology and Environment of the People's Republic of China, 2020; Wei et al., 2021). Wang (2003) recorded gorals in North and Northeast China as the northeast subspecies of *N. caudatus caudatus*. Hrabina (2015) considered Chinese goral to be a local species in China with a broad but discontinuous distribution. Mori et al. (2019), for the first time, proposed reclassifying the genus from seven species to three species using complete mitochondrial data, namely *N. goral*, *N. baileyi*, *N. caudatus*, and suggested that *N. griseus*, *N. bedfordi* and *N. evansi* should be merged into *N. goral*. Li et al. (2020) divided gorals into five species based on the complete mitochondrial sequences and confirmed the validity of *N. evansi* and *N. cranbrooki*. This study also proposed that *N. baileyi* and *N. cranbrooki* were independent species, while *N. griseus* is a synonym of *N. goral*. Joshi et al. (2022) proposed new insights based on specimens from the Indian Himalayas, emphasizing the distinction between *N. goral* and *N. griseus,* and suggesting the division of the genus into six species, namely *N. baileyi*, *N. caudatus*, *N. cranbrooki*, *N. evansi, N. goral*, *N. griseus*. They pointed out that *N. goral* was a highly differentiated species containing two evolutionarily significant units (ESUs) distributed in the central and western Himalayas. Hrabina et al. (2023) supported this proposal after adding specimens from Pakistan.

In the context of persistent taxonomic controversies, the selection of appropriate molecular markers is important to resolve phylogenetic relationships within the genus *Naemorhedus*. Mitochondrial cytochrome c oxidase subunit I (COI), cytochrome *b* (Cyt *b*), and the control region (D-loop) are established genetic markers for accurate species identification in mammals. Due to their appropriate evolutionary rates and demonstrated efficacy in resolving recent radiations, these mitochondrial genes have been widely adopted as robust markers for genus-level phylogenetic reconstructions (Brehm et al., 2003; Gray,1989; Schindel & Miller, 2005). Among them, COI, a canonical DNA barcode gene, exhibits broad taxonomic discriminative power and relatively conserved evolutionary rates, providing foundational signals for delineating closely related species within genera (Fišer Pečnikar & Buzan, 2014; Tobe et al., 2009, 2010). It is formally recognized as the optimal DNA barcode locus by the International Barcode of Life initiative (https://ibol.org/about/dna-barcoding/). Concatenated analysis of these three markers can synthesize genetic variation across temporal scales, mitigating the limitations of single-gene mitochondrial analyses while ensuring robust phylogenetic topology and nodal support (Zhang et al., 2020).

Notably, current taxonomic studies on gorals exhibit a pervasive geographic sampling bias. As a key distribution area of Chinese goral, genetic samples from diverse regions in China are highly valuable for clarifying the phylogenetic relationships within the genus. However, existing taxonomic frameworks lacked populations from northern China. This study focused on two critical habitats of Chinese goral: North China (Yunmengshan Nature Reserve, Beijing) and Northeast China (Saihanwula National Nature Reserve, Inner Mongolia). Due to the historical human disturbances, the local populations were in different isolation states (Zhou, 2015). Infrared camera monitoring data indicated effective population recovery (Zhu, 2018), with a density of 15.3 individuals/km^2 recorded in Yunmengshan Nature Reserve (Yu, 2023), demonstrating conservation efficacy. Nevertheless, conservation genetic studies revealed moderate genetic diversity in both populations, suggesting restricted gene flow due to geographic isolation (Yang et al., 2019). To fill these gaps, we collected goral samples from Northeast and North China. By integrating these specimens with all currently available complete sequences (COI, Cyt *b* and D-loop) for the genus, this study aimed to clarify the phylogeny of the genus and to re-examine the taxonomic status of the Chinese goral. We expected that our new data would provide a solid theoretical foundation for precise conservation and management of Chinese goral populations, which are in severe segregation.

MATERIALS AND METHODS

Sample collection

Field sampling was conducted in March 2017 at the Saihanwula National Nature Reserve, Inner Mongolia, where biological tissue samples from two Chinese goral individuals were collected, including one muscle tissue sample and one liver tissue sample. Additional sampling in April 2022 at the Yunmengshan Nature Reserve, Beijing, yielded biological tissues from three Chinese goral individuals, comprising two ear tissue samples and one muscle tissue sample (Figure 1). All individuals died naturally in the wild, and all samples were provided by the Saihanwula National Nature Reserve and Yunmengshan Nature Reserve. The samples were fixed in collection tubes with absolute ethanol, and then frozen at –20°C.

DNA extraction and primer design

The total DNA was exacted using the Tissue DNA Kit D3396 (Omega Bio-Tek, USA), and the DNA quality was verified using the NanoPhotometer (Thermo Fisher Scientific, China) and gel electrophoresis (Beijing Liuyi Biotechnology, China). In this study, three complete mitochondrial sequences were amplified using Polymerase Chain Reaction (PCR): 1) the complete mitochondrial COI of approximately 1 545 bp; 2) the complete mitochondrial Cyt *b* of approximately 1 140 bp; 3) the complete mitochondrial D-loop of approximately 1 127 bp.

Primer design was conducted using Primer Premier v.5.0 based on the complete mitochondrial genome of goral (accession number: NC020723) from the NCBI database. This software employs an automatic mode to select optimal primers by evaluating parameters including Tm, GC% content, degeneracy, presence of secondary structures, primer length, and thermodynamic profile, and assigns a comprehensive score to each primer pair (Lalitha, 2000; Ren et al., 2004).

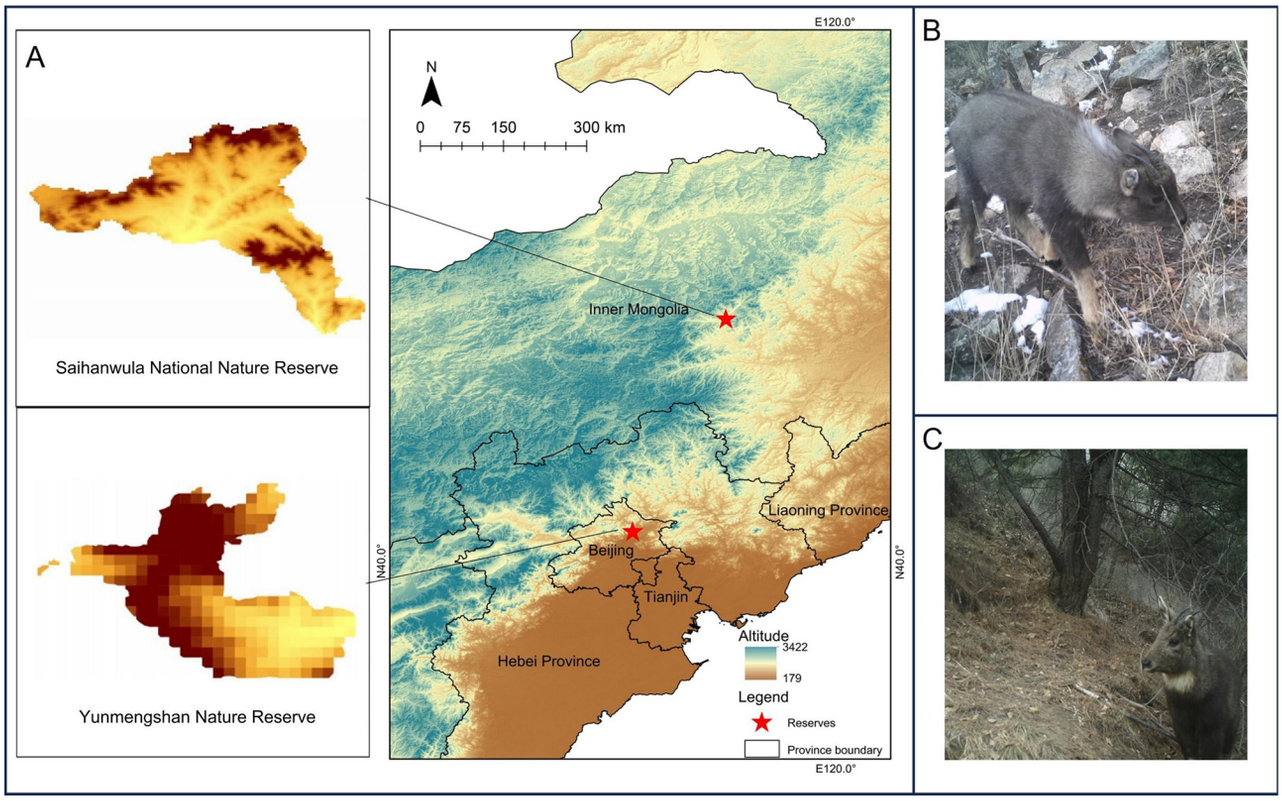

Figure 1 Geographical context of the study areas and photographic records of the Chinese goral.

A: Location of Beijing Yunmengshan Nature Reserve and Inner Mongolia Saihanwula National Nature Reserve. B: Camera trap photo of the Chinese goral (*Naemorhedus griseus*) from Saihanwula National Nature Reserve, Inner Mongolia. C: Camera trap photo of the Chinese goral (*N. griseus*) from Yunmengshan Nature Reserve, Beijing.

Due to the prolonged storage of some tissue samples, a multi-fragment amplification strategy was implemented for COI, Cyt *b*, and D-loop to ensure PCR amplification quality. The resulting amplicons were subsequently assembled into complete sequences. Target regions were set to 300–500 bp, and primer pairs with scores≥80 were prioritized for experimental validation. After empirical testing (gradient PCR and Sanger sequencing), the most efficient primers were selected for subsequent analyses. Detailed primer information was provided in Supplementary Table S1. PCR amplification system: the total system was 30 μl, including 2 μl of sample DNA (30–50 ng/μl), 15 μl of 2×T5 Super PCR Mix (Tsingke Biotechnology, China), 0.2 μl of Bovine serum albumin (NeoFroxx GmbH, Germany), 1 μl each of forward and reserve primers (Tsingke Biotechnology, China), with the rest of the system made up by DNase/RNase-free ddH_2O (Tsingke Biotechnology, China). Reaction conditions: pre-denaturation at 95°C for 5 min; denaturation at 94°C for 40 s; annealing at 50.5–55°C for 30 s (details were shown in Supplementary Table S1); extension at 72°C for 45 s, for 40 cycles; then, extension at 72°C for 8 min; and storage at 4°C.

To monitor potential contamination, each amplification included sequencing-validated muscle DNA as a positive control alongside a DNA-free negative control. The amplification results were detected using 2% agarose gel electrophoresis and visualized under the gel imaging system. The PCR products were sent to Beijing Tsingke Biotech Company for purification and bidirectional Sanger sequencing using the ABI 3730XL system (Appliosystems Inc., America). Raw sequences were initially visualized and edited using Chromos v.2.2.6 to inspect chromatogram peaks, followed by manual proofreading with the EditSeq module in DNASTAR v.7.1 (Burland, 2000). Sequence assembly was performed using the SeqMan module in DNASTAR v.7.1. The assembled sequences were then subjected to a BLAST analysis on the NCBI platform to confirm sequence identity as target fragments. The obtained sequences were submitted to GenBank under the accession numbers: PQ626689–PQ626693 (*N. griseus*, complete COI gene), PQ634329–PQ634333 (*N. griseus*, complete Cyt *b* gene), PQ634334–PQ634338 (*N. griseus*, complete D-loop).

Sequence alignment and dataset preparation

We referred to and summarized taxonomic revisions of the genus *Naemorhedus* established in previous studies (Hrabina et al., 2023; Joshi et al., 2022; Li et al., 2020), which were based on genetic distances, phenotypic features, phylogenetic relationships, and specific geographic origins (Table 1). Following these revisions, sequences originally annotated as *N. goral* in GenBank (MG865962, MG591488, KT878720, and JX188255) have been reclassified as *N. griseus*, while sequences previously assigned to *N. griseus* (JN632664 and MF155891) were reclassified as *N. evansi*. Within the framework of the revised dataset, the available mutilocus data for *N. goral* exclusively comprised the complete mitochondrial genome (accession numbers: MKH102) submitted by Sun et al. (2024) in the China National GeneBank DataBase (CNGBdb), which included sequences of Cyt *b*, COI, and D-loop. To comprehensively evaluate the phylogenetic relationships within *Naemorhedus*, we adopted a dual analytical strategy. First, we constructed the multilocus phylogenetic tree using Cyt *b*, COI, and D-loop sequences under the revised taxonomic framework. Second, we

Table 1 List of the revised complete mitochondrial genomes of *Naemorhedus*

Accession numbers	Original designation (GenBank)	Revised taxonomic assignments	Supporting references
MG865962	*Naemorhedus goral*	*Naemorhedus griseus*	Joshi et al., 2022 Hrabina et al., 2023
MG591488	*Naemorhedus goral*	*Naemorhedus griseus*	Joshi et al., 2022 Hrabina et al., 2023
KT878720	*Naemorhedus goral*	*Naemorhedus griseus*	Joshi et al., 2022 Hrabina et al., 2023
JX188255	*Naemorhedus goral*	*Naemorhedus griseus*	Hrabina et al., 2023
JN632664	*Naemorhedus griseus*	*Naemorhedus evansi*	Li et al., 2020 Joshi et al., 2022 Hrabina et al., 2023
MF155891	*Naemorhedus griseus*	*Naemorhedus evansi*	Li et al., 2020 Joshi et al., 2022 Hrabina et al., 2023

implemented a complementary single-locus COI phylogenetic analysis to incorporate critical lineage data. The single-locus dataset was augmented with *N. goral* COI sequences (OK244620–OK244622) from Hrabina et al. (2023), which exclusively focused on sequencing the COI gene. The dual-tree approach not only validated the topological stability of the classification system but also enhanced nodal support estimation at critical phylogenetic junctures through single-locus sample expansion, thereby optimizing the balance between data utilization and the robustness of phylogenetic inference. Complete details of all sequences employed in this study are provided in Supplementary Table S2.

MAFFT v.7.520 was used for aligning sequences due to its superior speed and accuracy (Ahola et al., 2006; Nuin et al., 2006; Pais et al., 2014). The algorithm was set as the iterative optimization algorithm for pairwise weight and coherence score, with the command line parameter specified as G-INS-i. The gap penalty and extension penalty were set to 1.53 and 0.123, respectively (Katoh et al., 2002; Katoh & Standley, 2013). The sequences were trimmed using Gblocks v.0.91b under the authors' recommended parameter settings to eliminate phylogenetic noise and retain phylogenetic signals (Talavera & Castresana, 2007). The trimmed sequences were subsequently concatenated into a dataset comprising COI, Cyt *b*, and D-loop sequences using PhyloSuite v.1.2.3 (Zhang et al., 2020). The multilocus dataset included 25 complete COI, Cyt *b*, and D-loop concatenated sequences, incorporating five novel sequences from our study and 18 published *Naemorhedus* sequences. Two outgroup taxa were selected: *Capricornis crispus* (NC012096) and *Rupicapra rupicapra* (NC020633).

The single-locus dataset encompassed 28 complete COI sequences from six goral species, including five novel sequences from our study, 21 published *Naemorhedus* sequences. Two outgroup taxa were selected: *C. crispus* (NC012096) and *R. rupicapra* (NC020633). All COI sequences were translated to amino acids using the vertebrate mitochondrial translation code in Mega v.11. No stop codons or gaps were detected, confirming that all protein-coding sequences were functional and no pseudogenes were amplified (Tamura et al., 2021).

Phylogenetic tree construction

The phylogenetic model selection and optimization workflow proceeded as follows: The optimal partitioning scheme and nucleotide substitution models were determined using ModelFinder v.2.2.0 (Lanfear et al., 2012), which addresses phylogenetic signal heterogeneity through partitioned modeling of loci with divergent evolutionary rates. Based on the Bayesian Information Criterion (BIC), the optimal partitioning schemes and substitution models were selected under “edge-linked” and “merge” partition modes for both IQ-TREE and MrBayes frameworks. For the multilocus concatenated dataset, the optimal partitioning scheme comprised two subsets: (COI+Cyt *b*) and D-loop. Under the IQ-TREE framework, the (COI+Cyt *b*) subset was best fitted by the TPM2u+F+G4 substitution model, while the D-loop subset was optimized under HKY+F+G4. Under the MrBayes framework, both subsets converged on HKY+F+G4 as the optimal model. For the single-locus COI dataset, the optimal evolutionary models differed between frameworks: HKY+F+R2 in IQ-TREE and HKY+F+I+G4 in MrBayes.

Phylogenetic analyses were constructed using the Maximum Likelihood (ML) in IQ-TREE v.1.6.8 (Nguyen et al., 2015) and Bayesian Inference (BI) in MrBayes v.3.2.7 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). For ML analyses, the robustness of the phylogenetic branches was assessed through 1 000 bootstrap replicates, with bootstrap values≥70% considered strongly supported. Bayesian phylogenetic analyses employed the Metropolis-coupled Markov chain Monte Carlo (MCMC) algorithm with the following parameters: 5 000 000 generations with 2 runs, 4 chains per run, sampling every 100th generation, and 10% burn-in fraction (Altekar et al., 2004). Convergence of MCMC analyses was assessed by the average standard deviation of split frequencies (ASDSF) in MrBayes v.3.2.7 and the effective sample size (ESS) values of traces in Tracer v.1.7.1 (Rambaut et al., 2018). The observed ASDSF values were all lower than 0.01, and the ESS for all parameters were all higher than 1 000, meeting the criteria for recommended convergence thresholds according to Lakner et al. (2008) and Fabreti & Höhna (2022). Bayesian posterior probabilities≥0.95 were deemed to indicate strong nodal support in BI analyses.

Divergence time analysis

To establish a temporal framework for the evolution of the genus *Naemorhedus*, we employed Bayesian MCMC methods in BEAST v.2.7.7 to estimate divergence times (Drummond et al., 2012). The analysis incorporated an uncorrelated lognormal relaxed molecular clock (Drummond et al., 2006) and a Yule tree prior (Gernhard, 2008). A temporal calibration point was applied to the most recent common ancestor (MRCA) of *Capricornis* and *Naemorhedus*, constrained by their intergeneric divergence time 12.2–7.3 million years ago (Ma) retrieved from the TimeTree database (Kumar et al., 2017). MCMC parameters were configured as follows: 50 000 000 generations, sampling every 1 000th generation, with 10% burn-in. Convergence was assessed in Tracer

v.1.7.1 (Rambaut et al., 2018), where all parameters exhibited ESS>500, indicating stationarity. Node divergence times are reported as posterior medians with 95% HPD intervals on the maximum clade credibility tree. Final tree visualization was conducted in FigTree v.1.4.4 (Rambaut, 2018).

RESULTS

The multilocus dataset comprising 25 sequences (3 776 bp) revealed substantial genetic variation, with 787 variable sites identified, including 514 parsimony-informative sites. Phylogenetic construction based on these concatenated sequences generated a topology, employing a dual-assessment framework for nodal support using ML bootstrap values and BI posterior probabilities (Figure 2). The majority of branches exhibited robust statistical support, indicating high confidence in the inferred phylogenetic relationships.

This dataset provided critical resolution for two groups defined by geographical distribution: Group 1, distributed across the Myanmar-southwestern China-Thailand biogeographic region, comprised *N. evansi*, *N. baileyi*, and *N. cranbrooki*, each forming strongly supported monophyletic lineages (99/1.00, 100/1.00, and 96/1.00, respectively), unequivocally validating their recognition as distinct species. Group 2, encompassing taxa from China and Korea region (*N. caudatus*, *N. goral*, and *N. griseus*), revealed *N. caudatus* as a monophyletic clade with full nodal support (100/1.00), suggesting early divergence within the genus. The *N. goral* and *N. griseus* complex formed a highly supported sister-clade relationship (99/1.00). Internal topology further resolved that *N. goral* clustered as sister to the southwestern subclade of *N. griseus* (distributed in southwestern China, e.g., Sichuan Province), while the northeastern subclade of *N. griseus*, which spanned central China (e.g., Hubei Province), northern China (e.g., Shanxi Province and Beijing), and northeastern China (Chifeng, Inner Mongolia), was recovered as a monophyletic lineage. Based on the divergence time analysis results (Figure 3), the split between *N. goral* and *N. griseus* occurred approximately 2.3Ma, while the divergence between *N. goral* and the southwestern subclade of *N. griseus* dated back to 1.1Ma. These findings suggested that *N. griseus* likely underwent a relatively recent population expansion or lineage diversification event.

The COI single-locus dataset (28 sequences, 1 545 bp) revealed substantial genetic variation, containing 312 variable sites (104 parsimony-informative sites). Phylogenetic construction based on this dataset resolved a topology (Figure 4) that provided critical support for the taxonomic delineation of two groups within *Naemorhedus*, defined by their biogeographic distributions: Group 1, distributed across the Myanmar-southwestern China-Thailand biogeographic region, comprised *N. evansi*, *N. baileyi*, and *N. cranbrooki*, each forming strongly supported monophyletic clades (100/1.00, 92/1.00, and 97/1.00, respectively). Group 2 encompassed *N. caudatus*, *N. goral*, and *N. griseus* distributed from Pakistan to East Asia (China and Korea). In the phylogenetic topology, *N. caudatus* formed a monophyletic clade, suggesting an early genetic divergence event. *N. goral* and *N. griseus* constituted a composite evolutionary clade, within which *N. goral* clustered with the southwestern subclade of *N. griseus*. Further analysis of sequence variation revealed high similarity between KP878720 and MG865962, with limited variable sites. Notably, KT878720 exhibited convergent substitutions at eight nucleotide positions with *N. goral* populations (OK244620–OK244622). Remarkably, the

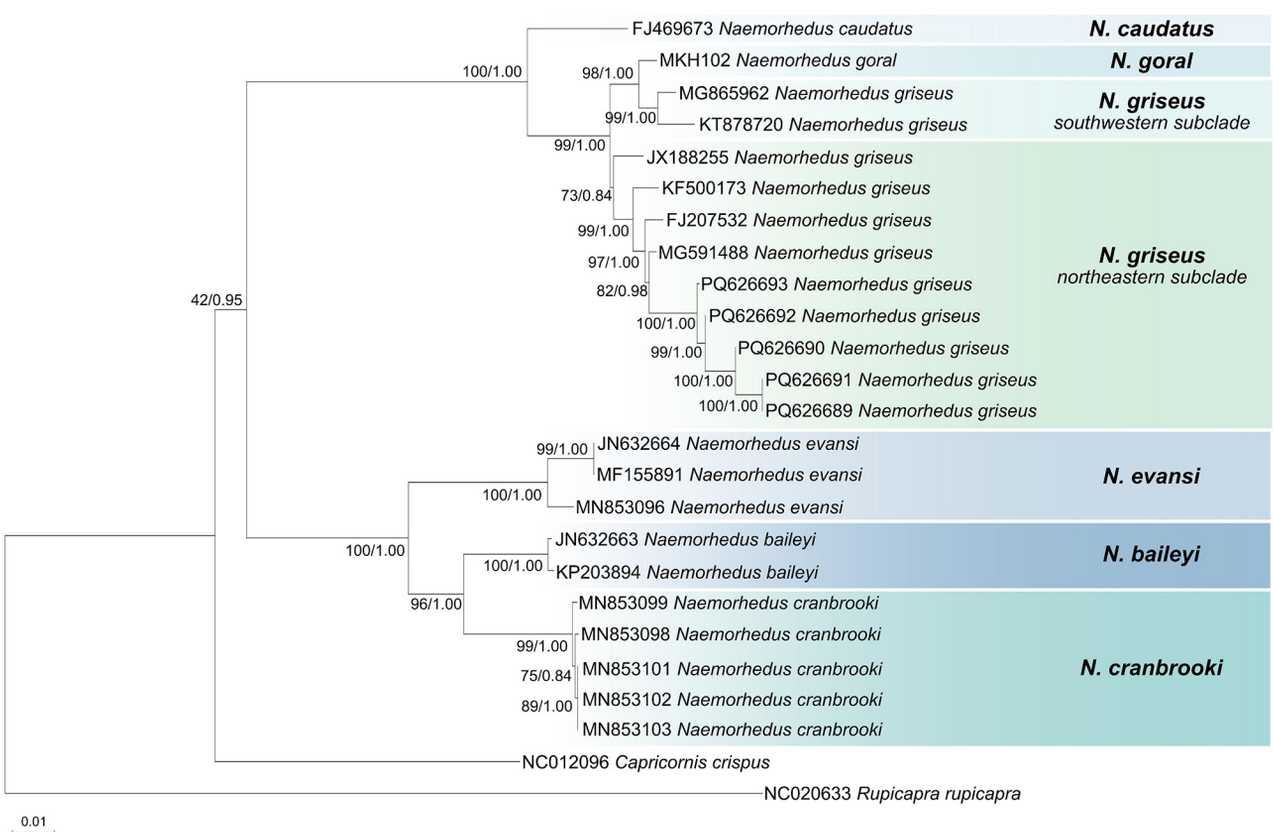

Figure 2 Phylogenetic tree of multilocus dataset for the genus *Naemorhedus*

Above the clades values represented the bootstraps supports and posterior probability: ML, maximum likelihood; BI, of Bayesian.

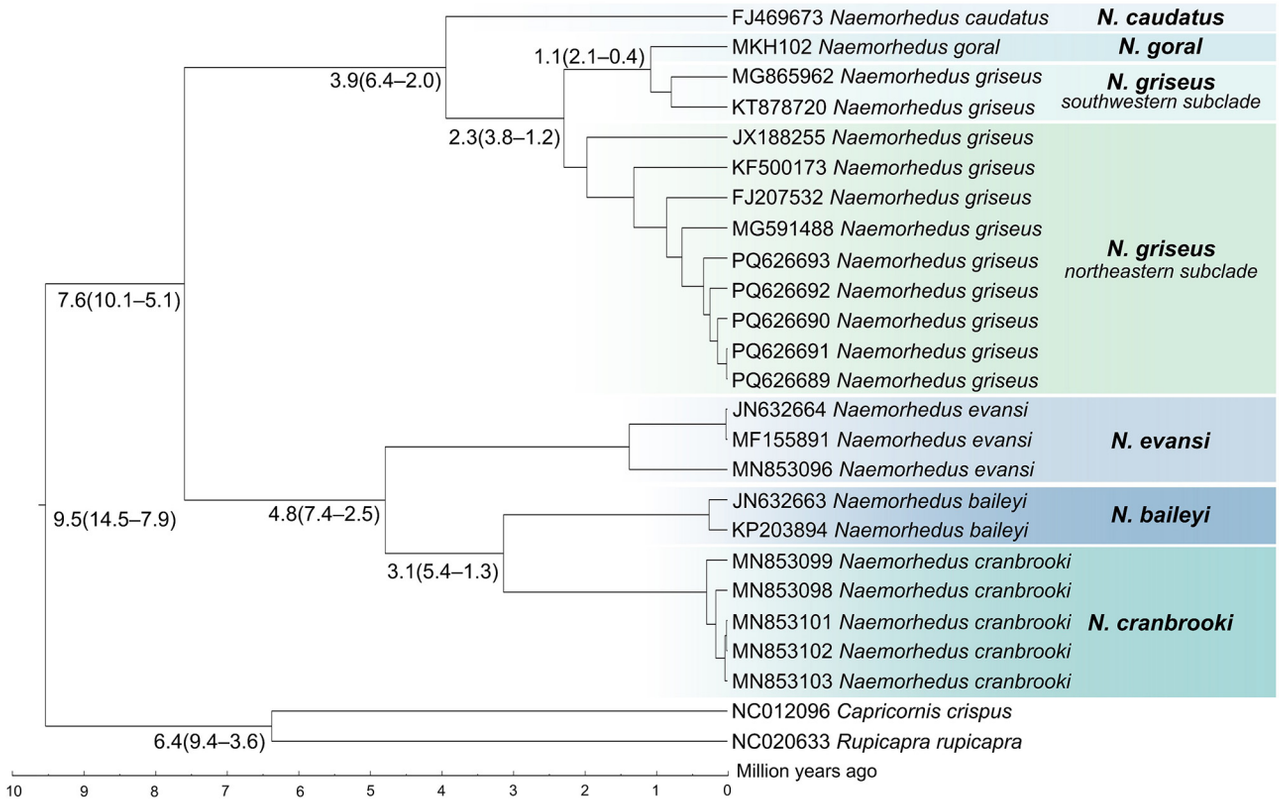

Figure 3 Divergence time estimation based on multilocus dataset for the genus *Naemorhedus*

Node ages represent estimated divergence times with 95% HPD intervals.

northeastern subclade of *N. griseus* formed a highly supported monophyletic group, with internal branches showing robust statistical support (Bootstrap values: 90–100%; posterior probabilities: 0.99–1.00). This indicated strong phylogenetic concordance and high genetic homogeneity within this lineage.

DISCUSSION

Concatenated alignments of multiple loci have several advantages, by concatenating multiple loci, the number of analyzed loci can be significantly increased, integrating differences in evolutionary rates and time for more comprehensive genetic information and enhancing the resolution of evolutionary relationship. This approach also reduces misleading information produced by a single gene, thereby improving the accuracy of phylogenetic trees (Ali et al., 2025; Heled & Drummond, 2010). The heterogeneity in single-gene evolutionary rates can only provide limited genetic information. To address the limitations, we analyzed three complete gene sequences (Cyt *b*, COI, and D-loop) using multilocus phylogenetic analyses. This method effectively compensated for the shortcomings of single-gene data. By combining information from multiple genes, our study not only increased the variation site numbers, but also balanced the differences in evolutionary rates among different genes, thereby significantly improving the accuracy and reliability of phylogenetic trees (Baker & DeSalle, 1997; Xiang et al., 2023; Zhang et al., 2020). Our study showed that multilocus phylogenetic trees, when compared to those based on single gene, displayed minor differences at the small branch level but maintained a high level of consistency in the larger branch structure, strongly demonstrating good stability of phylogenetic information (Figure 2; Figure 4). Overall, this approach further validates the potential and importance of multilocus phylogenetic analyses to enhance the accuracy of phylogenetic inference.

Based on the phylogenetic analysis of multiple loci, we identified two main branches within the genus: the *baileyi-cranbrooki-evansi* clade and the *caudatus-goral-griseus* clade. The bootstrap values and posterior probability values showed strong statistical support for all major branches and also demonstrated high support for most internal sub-branches (Figure 2; Figure 4). Aligning with previous studies that utilized mitochondrial single-gene or genomic data, our findings provided new comprehensive evidence for the phylogeny and taxonomy of the genus *Naemorhedus* (Hrabina et al., 2023; Joshi et al., 2022; Li et al., 2020). The results further confirmed the presence of six valid taxa of gorals, which agreed with traditional morphological findings (Groves & Grubb, 2011; Hrabina, 2015).

Mori et al. (2019) and Li et al. (2020) initially considered *N. griseus* and *N. goral* to be synonyms based on complete mitochondrial sequences. However, this view was later contested by Joshi et al. (2022) and Hrabina et al. (2023), who argued that it was a misidentification of *N. griseus*. In line with the taxonomic revisions proposed by Li et al. (2020), Joshi et al. (2022), and Hrabina et al. (2023), the classification of genetic samples from Chiang Mai, Guizhou, and Myanmar (JN632664, MF155891, and MN853096) has been revised *N. griseus* to *N. evansi*. Similarly, samples from Sichuan and Shanxi in China (MG865962, MG591488, KT878720, and JX188255) have been revised *N. goral* to *N. griseus.* Based on these revisions, the phylogenetic tree revealed a highly supported sister-group relationship between *N. goral* and the *N. griseus* complex (Figure 2). Internal topology further demonstrated that *N. goral* formed a sister clade to *N. griseus*

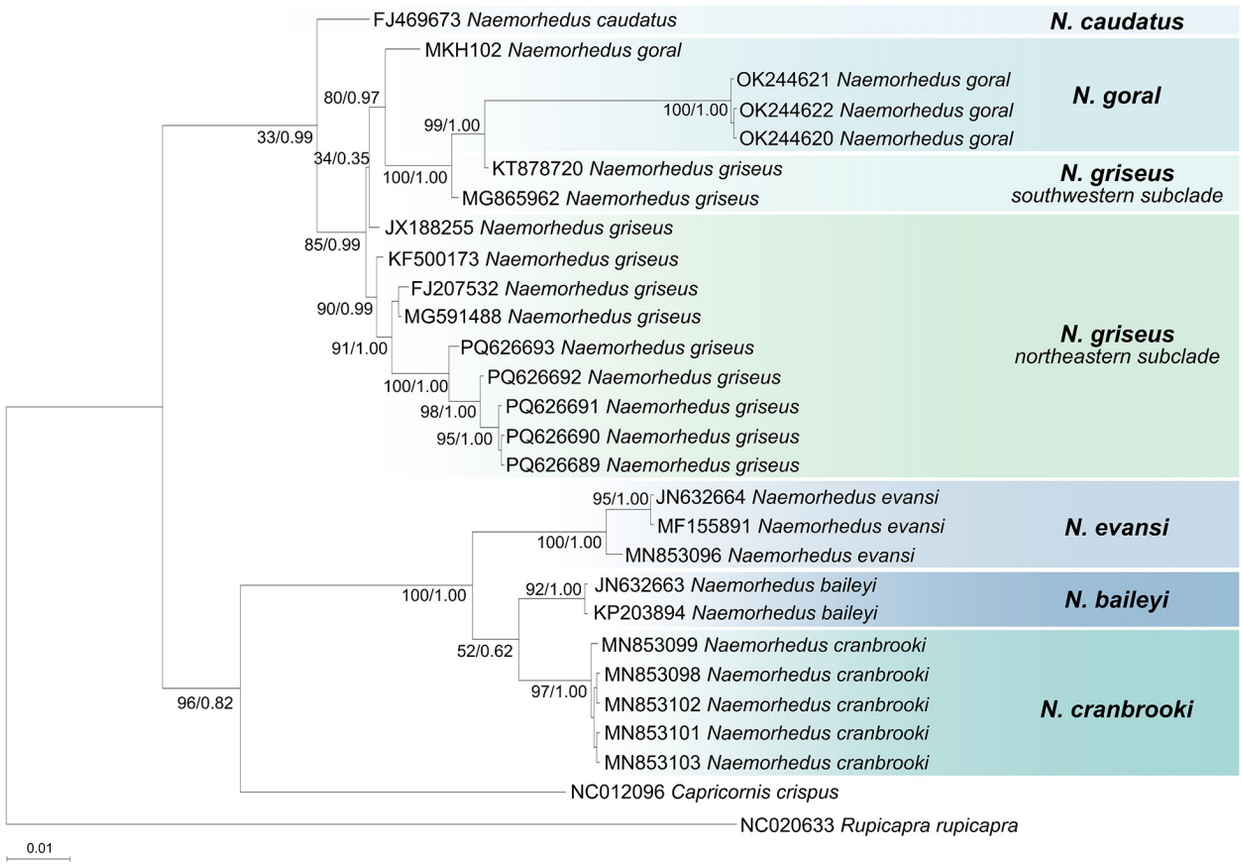

Figure 4 Phylogenetic tree of COI single-locus dataset for the genus *Naemorhedus*

Above the clades values represented the bootstraps supports and posterior probability: ML, maximum likelihood; BI, of Bayesian.

populations in Southwest China, whereas *N. griseus* from Northeast and North China constituted a monophyletic lineage. This geographic segregation likely drove intra-specific genetic differentiation within *N. griseus*. Furthermore, analysis of COI sequence polymorphisms revealed high similarity between KP878720 and MG865962 in *N. griseus*, with minimal variable sites. Notably, KP878720 shared eight convergent nucleotide sites with *N. goral* populations (OK244620–OK244622). This pattern may stem from either parallel evolution or gene introgression, suggesting unresolved taxonomic complexities or intricate evolutionary history in this lineage. Hrabina et al. (2023) documented a similar topology in their analysis, proposing it as an artefact arising from sequence similarity. Their findings emphasized the necessity to re-evaluate the sequence quality of KT878720 and its source population, particularly regarding ancestral polymorphisms, genetic drift, or possible introgression events in the past. Similarly, we proposed that future studies should expand the sampling scale and implement population genomic investigations to elucidate the underlying patterns of genetic polymorphism. Special emphasis should be placed on increasing *N. goral* sequences, as the limited availability of *N. goral* sequences likely influenced the current topological configuration. All sequences in our study comprised complete mitochondrial genes, consequently, partial mitochondrial gene fragments available in the NCBI database were not applicable to our dataset. Joshi et al. (2022) employed Cyt *b* (404 bp) and COI (225 bp) gene fragments to assess phylogenetic relationships within the genus *Naemorhedus*. Their analysis, incorporating *N. goral* sequences from Uttarakhand (India), resolved *N. goral* as a monophyletic group sister to other *Naemorhedus* species. To validate and extend present findings, future studies should prioritize comprehensive mitochondrial genome sequencing of populations in India Himalayan Region, particularly to complement the existing biogeographic framework established in this investigation.

Morphological identification remains indispensable in taxonomic classification. Integrative taxonomy, combining morphological and molecular evidence, is critical for accurate species delineation. Hrabina (2015) comprehensively documented morphological characteristics of *Naemorhedus* species using 979 field photographs and 84 pelage specimens from global collections. This study included detailed descriptions of the Chinese goral (*N. griseus*) in Sichuan, Shanxi, and Inner Mongolia, China, recording its geographic distribution and diagnostic traits such as pelage patterns and horn morphology. Photographic evidence from Sichuan's Tangjiahe Nature Reserve (source of sequence MG865962 in our study) and western Sichuan (origin of KT878720), both representing the southwestern subclade of *N. griseus*, strongly supported the morphological assignment of these populations to *N. griseus* rather than *N. goral*. Additionally, Hrabina (2015) provided images of *N. griseus* from the Saihanwula National Nature Reserve in Inner Mongolia, morphologically corroborating our newly sampled northeastern subclade. In contrast, photographic comparisons of *N. goral* from the Kashmir region of Pakistan in Hrabina's study revealed marked morphological distinctions from the southwestern *N. griseus*.

Divergence time estimation revealed that speciation events within the genus *Naemorhedus* predominantly occurred during the Late Miocene to Pleistocene epochs. Specifically, the

ancestral divergence of *Naemorhedus* was dated to approximately 7.6Ma, while interspecific divergences clustered between 2.3Ma and 6.4Ma. These temporal patterns correlate closely with the rapid uplift of the Qinghai-Xizang Plateau and the establishment of the Asian monsoon climate system, indicating that geotectonic and climatic events likely played pivotal roles in driving species divergence within this genus (Deng & Ding, 2015; Sun et al., 2024). The relatively close genetic distance and recent divergence between the southwestern subclade of *N. griseus* and *N. goral* may reflect a recent evolutionary isolation on geological time scales. Combined with the strongly supported phylogenetic topology (southwestern subclade node: 96/1.00), the monophyletic grouping of southwestern *N. griseus* with *N. goral* likely resulted from allopatric speciation driven by geographic isolation. The *N. goral* sequences (OK244620–OK244622) used in our study were collected by Hrabina et al. (2023) in Kashmir District, Pakistan, while the southwestern subclade of *N. griseus* (MG865962, KP787820) occurred in Sichuan Province, China (Liu & Jiang, 2017; Yao et al., 2019). Both were currently distributed in high-elevation zones flanking the Himalayas (western and eastern edge, respectively). The rapid uplift of the Qinghai-Xizang Plateau during the Pliocene-Pleistocene likely disrupted gene flow between the ancestral populations of *N. goral* and *N. griseus*. Geographical barriers, such as deep valleys and high mountain ridges, effectively isolated these populations, leading to their independent genetic evolution (Zhang et al., 2013). Subsequent geological activity caused significant topographic dissection and drainage reorganization, further promoting habitat fragmentation and environmental heterogeneity (Sun et al., 2024). This series of events ultimately shaped the current phylogenetic relationships observed. Notably, *N. griseus* exhibited deep genetic divergence between its southwestern and northeastern geographic subclades, with branch lengths and topological isolation exceeding some interspecific divergence levels (e.g., *N. goral* vs. southwestern subclade of *N. griseus*). This phylogeographic structure may reflect Quaternary glacial-interglacial cycles (2.58Ma to present) shaping population histories in East Asia's monsoon-dominated regions: the genetic distinctiveness of the southwestern subclade could stem from prolonged isolation in glacial refugia, while the northeastern subclade may have expanded during interglacial periods via forest-steppe ecotones, facilitating secondary contact (Hewitt, 2000). It is critical to note that the maternally inherited nature of mitochondrial markers may overestimate divergence time scales. Future studies integrating nuclear genomic data are warranted to validate these hypotheses.

Considering the geographical distribution and phylogenetic relationships, we hypothesized that there are two geographically separated clades of *N. griseus* in China. The southwestern subclade is mainly found in Southwest China (e.g. Sichuan), while the northeastern subclade is widely distributed in central China (e.g. Hubei), North China (e.g. Shanxi and Beijing), and Northeast China (e.g. Chifeng, Inner Mongolia). The geographic distribution pattern can also provide important insights for understanding the evolutionary history of *Naemorhedus* and for devising effective conservation strategies.

The habitat of Chinese goral (*N. griseus*) has been impacted by natural environment changes and human activities, leading to a fragmented population distribution. This species tends to inhabit steep rock terrain, and it displays a heightened level of vigilance towards both human influences and predation risk. These traits have greatly increased the difficulty of direct field investigation and animal tissue sampling (Chen et al., 2002). Yang et al. (2019) conducted a genetic study using fecal samples from the Chinese goral in Songshan National Nature Reserve in Beijing and Saihanwula National Nature Reserve in Inner Mongolia. Based on microsatellite and mitochondrial DNA, that study indicated significant spatial genetic structure and genetic differentiation between the two populations, recommending that each population should be considered as distinct ESUs for conservation and management. Our phylogenetic analyses integrating multilocus and COI single-locus datasets revealed distinct clustering patterns in *N. griseus* populations. Specimens from Yunmengshan Nature Reserve, Beijing (PQ626689–PQ626691) formed a clade, whereas those from Saihanwula National Nature Reserve, Inner Mongolia (PQ626692–PQ626693) occupied divergent phylogenetic branches. This topology provided molecular evidence for potential differentiation between these populations, suggesting either distinct subpopulations or geographic differentiation. Therefore, it is much better to use whole-genome data in future research to evaluate the genetic differentiation of gorals from different regions to accurately determine the degree of genetic differentiation.

CONCLUSIONS

In summary, the main inferences of this study are: (1) By utilizing all the currently available complete sequences of Cyt *b*, D-loop, and COI of gorals, we reclarified the taxonomic status of the genus *Naemorhedus*. The results consistently supported the validity of six species: *N. evansi*, *N. baileyi*, *N. cranbrooki*, *N. griseus*, *N. goral*, and *N. caudatus*. (2) Our findings confirmed that gorals distributed in Northeast China (eastern Inner Mongolia) and North China (Beijing) belong to *N. griseus*, and further proposed that *N. griseus* within China was subdivided into two distinct subclades: the northeastern subclade and the southwestern subclade.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Sample collections in the field were conducted following the Wildlife Protection Law of the People's Republic of China.

DATA AVAILABILITY

The obtained sequences were submitted to the Science Data Bank (https://doi.org/10.57760/sciencedb.zrdc.00033).

The obtained sequences were submitted to GenBank under the accession numbers: PQ626689–PQ626693 (*Naemorhedus griseus*, complete COI gene), PQ634329–PQ634333 (*Naemorhedus griseus*, complete Cyt *b* gene), PQ634334–PQ634338 (*Naemorhedus griseus*, complete D-loop).

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Z.L. and W.D.B. designed the experiments; Z.L. performed experiments and analyzed the data; Z.L. and R.H.W. made the figures; F.L.G, Y.Y.H and W.D.B. provided experimental guidance; All the authors contributed to the analyses and discussions of the results; Z.L. and W.D.B. wrote the manuscript. All authors read and approved the final version of the manuscript.

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