

# Pan-mitochondrial genomic analysis of *Felis catus*: Insights into cat domestication

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## Abstract

Despite the popularity and diversity of domestic cats (*Felis catus*), the genetic adaptations resulting from their domestication remain largely unknown. To address this, we sequenced the complete mitochondrial genomes of five Chinese domestic cats and combined them with 126 publicly available sequences to create a comprehensive dataset. Phylogenomic analyses revealed significant genetic diversity within domestic cat lineages, distinct from their wild relatives (*F. silvestris*). Selective pressure analysis indicated that all 13 mitochondrial protein-coding genes are under purifying selection in domestic cats. We identified 16 stable variations differentiating domestic cats from wildcats, including a non-synonymous mutation in *nad5*, which encodes a subunit of mitochondrial respiratory complex I and is crucial for energy metabolism. Notably, *nad5* is under purifying selection in both groups, with domestic cats experiencing stronger selection pressure. Our findings illuminate the impact of domestication on mitochondrial genome evolution in cats, particularly selection on the respiratory gene *nad5*, providing insights into adaptive responses to human-modified environments.

**Keywords:** adaptive evolution, mitochondrial genome, *nad5*, phylogenomic analyses

## Introduction

Domestic cats (*Felis catus*) are among the most cherished companion animals globally. They have

coexisted with humans for approximately 10,000 years, distinguished by their unique domestication processes (Vigne et al., 2004; Hu et al., 2014; Bouma et al., 2021). These early human-cat interactions, particularly within the agricultural hubs of the Fertile Crescent, likely facilitated the initial domestication of cats for pest control (Menotti-Raymond et al., 2007). Cat breeding has shifted focus in recent years from functional roles to aesthetic traits. This shift has resulted in a wide variety of coat colors and patterns in contemporary breeds (Montague et al., 2014; Yu et al., 2021), showcasing significant phenotypic variation (Menotti-Raymond et al., 2008).

Over the course of domestication, cats have undergone significant adaptations, transitioning from solitary hunters to companions accustomed to human-provided resources. These shifts are reflected in their genetic and morphological traits. Studies comparing domestic cats to wildcats have revealed distinct physical differences across traits such as fur patterns, cranial dimensions, and intestine lengths. For example, Ragni et al., (1996) identified differences in coat coloration between domestic cats and European wildcats in Italy, while Krüger et al., (2009) found variations in cranial volume and intestinal morphology. Puzachenko et al., (2002) further demonstrated that skull morphology could serve as a useful tool in distinguishing wildcats from their domestic counterparts. However, despite these differences, extensive interbreeding and hybridization between domestic and wildcats have resulted in significant morphological overlap, complicating accurate identification based on physical attributes alone (O'Connor, 2007; Li et al., 2016). This observation has highlighted the importance of genetic tools to improve species differentiation and to provide deeper insights into the evolutionary adaptations of domestic cats.

Mitochondrial genes, essential for the electron transport chain and energy production, provide over 90% of cellular energy in animals (Rackham & Filipovska, 2022). Studies have shown that flightless birds, such as Pavo, Gallus, and Numida, experience relaxed selection pressure on their mitogenomes compared to flying species, as their reduced energy demands make minor mitochondrial mutations less detrimental (Shen et al., 2009). Similar patterns have been observed in insects and mammals, where groups with limited locomotion exhibit significantly lower evolutionary constraints on their mitogenomes compared to those with high locomotive abilities (James et al., 2016; Chang et al., 2020). Previous research has employed mtDNA to study the genetic diversity and evolutionary trajectories of cat populations. For example, the *cob* and *nad5* mitochondrial markers have been utilized to examine Iranian wildcats' genetic structure, while

similar markers reveal European wildcats' biogeographic histories (Mousavi et al., 2022; Velli et al., 2023). Patterson et al. (2023) utilized next-generation sequencing to reconstruct complete mitochondrial genomes of 119 European domestic cats, revealing patterns of tandem repeat variation and mitochondrial mutation dynamics. Despite these advances, studies often overlook the genetic differentiation between domestic and wildcat lineages. This oversight is especially pronounced in Asian populations, where data on mitochondrial diversity in domestic cats remains sparse.

Understanding the genetic variations between domestic and wildcats across different regions is vital for unraveling the molecular mechanisms of domestication and the adaptations that have enabled cats to thrive in human-dominated environments. This study addresses this gap by utilizing next-generation sequencing to map the complete mitochondrial genomes of five Chinese domestic cats, integrating these with 121 additional mitochondrial genomes from public databases to construct a comprehensive pan-mitochondrial genome, conceptualized as a composite representation of mitochondrial genetic diversity within a population or a group of related species. This pan-genomic resource encompasses a substantial fraction of observed DNA sequence variants. Furthermore, we conducted comparative analyses between domestic and wildcats to discern mitochondrial sequence variations and explore their domestication-related adaptations.

## **Material and methods**

### **Sample Collection and DNA Extraction**

We utilized mitochondrial genome data from 126 cats and their close relatives retrieved from public databases, predominantly of European origin, particularly from the United Kingdom. To improve the geographical representation, we also sequenced five Chinese (Asian) cat samples. In total, our analysis encompassed 131 cats and their close relatives (Table S1). The blood samples used for sequencing were collected from these five domestic cats during routine clinical examinations at a local pet hospital in Weihai, China. The genomic DNA was extracted by the DNeasy tissue kit (Qiagen, Beijing, China) following the instruction manual. DNA quality was assessed via 1% agarose gel electrophoresis and NanoDrop for subsequent experiments.

### **DNA Library Construction and Sequencing**

DNA was sonicated to fragments of 300~500 bp using the Covaris M220 platform. DNA libraries were constructed using the DNA Library Prep Kit for Illumina, with 1 µg of DNA per sample. Sequencing was performed on the Illumina NovaSeq 6000 platform (Biozeron, Shanghai, China)

in paired-end mode.

### **Mitochondrial Genome Assembly and Annotation**

The quality of raw sequencing data was assessed using FastQC v0.12.0, and Trimmomatic v0.39, was employed to trim low-quality bases, adapters, and short reads (Bolger et al., 2014). The preprocessing steps included: (1) removing adapter sequences from reads; (2) trimming non-AGCT bases at the 5' end; (3) removing read ends with quality scores below Q20; (4) discarding reads containing  $\geq 10\%$  Ns; and (5) eliminating fragments shorter than 75 bp after adapter removal and quality filtering. Clean reads were assembled using GetOrganelle v1.7.5, which employs a seed database to cyclically retrieve target reads and subsequently calls SPAdes to assemble the genome (Jin et al., 2020), and scaffolds with high coverage were identified by BLAST against the Nucleotide Sequence Database (Camacho et al., 2009). Selected scaffolds were then assembled into complete mitochondrial genomes. Annotation was conducted using MITOS (Bernt et al., 2013) for protein-coding genes (PCGs), tRNA, and rRNA genes, with manual verification of start and stop codons. The annotated mitochondrial genome was visualized using Proksee Software (Grant et al., 2023). The GC and AT skews were calculated using the following formulas: GC skew =  $(G - C) / (G + C)$  and AT skew =  $(A - T) / (A + T)$  (Nguyen et al., 2017). The complete mitochondrial genomes have been submitted to GenBank with accession numbers ranging from PP070530 to PP070534 (Table S1).

### **Phylogenomic Analyses**

The phylogenetic relationships among *Felis* species were reconstructed by combining the five new mitochondrial genomes with 126 published genomes (Table S1). *F. nigripes* (GenBank accession No. NC\_028309.1) was selected as the outgroup based on earlier phylogenetic studies of *Felis* (Yu et al., 2021). Alignment was performed using MAFFT v7 (Nakamura et al., 2018) and BioEdit 7.0.9.1 (Hall, 1999). Hypervariable regions were removed using Gblocks (Castresana 2000) in PhyloSuite (Zhang et al., 2020), yielding a conserved mitochondrial matrix. Maximum likelihood (ML) analysis was conducted with RAxML v8.2.12 (Stamatakis, 2014) using the GTRGAMMA model and 1000 bootstrap replicates. The phylogenetic tree was visualized with iTOL v6 (Letunic & Bork, 2021).

### **Selection Analysis Between Domestic Cats and Wildcats**

Selection between domestic cats and wildcats was assessed through analyses of relative synonymous codon usage (RSCU), selection pressure, and specific variants using the PhyloSuite

software (Zhang et al., 2020). RSCU values were calculated to assess codon preference, where  $RSCU > 1$  indicates increased usage,  $< 1$  implies decreased usage, and 1 denotes unbiased usage (Sharp et al., 1987). Protein-coding sequences from all 131 cats were extracted, and selection pressures were evaluated using the Ka/Ks ratio calculated in Dnasp5 (Librado & Rozas, 2009). A  $Ka/Ks > 1$  suggests positive selection,  $= 1$  indicates neutral selection, and  $< 1$  signifies purifying selection (Isabelle et al., 2020). SNP-sites were used to analyze DNA variation, identifying SNPs and InDels (Page et al., 2016). Mutation rates and nucleotide variation across 13 PCGs were visualized using OriginPro 2021 (Stevenson, 2011). Differences in amino acids corresponding to codons were identified using the vertebrate mitochondrial codon table.

### Protein structure prediction

The protein structures were predicted using the SWISS - MODEL online website (<https://swissmodel.expasy.org>; Waterhouse et al., 2018). The process involved identifying a suitable template, constructing the optimal model, selecting the model with the highest GMQE score, and downloading the PDB format file. Subsequently, analysis was performed using PyMOL v3.0.0 (<https://pymol.org/>).

## Results

### Mitochondrial Genome Characteristics and Base Composition

The mitochondrial genomes of the five newly sequenced domestic cats from China contained 37 genes: 13 protein-coding genes (PCGs), 22 tRNAs, and 2 rRNAs (Table S2). The genome sizes ranged from 16,977 to 17,048 bp, with an average base composition of 32.65% A, 27.09% T, 26.23% C, and 14.04% G (Table 1). The AT content was higher than the GC content, varying between 59.58% and 59.88%. Base skewness analysis revealed positive AT skew and negative GC skew, indicating a higher proportion of A and C bases. Twelve of the 13 PCGs were located on the heavy (H) chain with the exception of *nad6*, which was on the light (L) chain (Table S2). All three start codons (ATG, ATC, ATA) were observed across the PCGs, with ATG being the most predominant. Most PCGs ended with the stop codon TAA, while *cob* uniquely ended with AGA. Consistent with previous studies (Ojala et al. 1981), five PCGs had incomplete stop codons, represented as T-- or TA- (Table S2).

**Table 1** Basic characteristics of five complete mitochondrial genomes of domestic cat in China

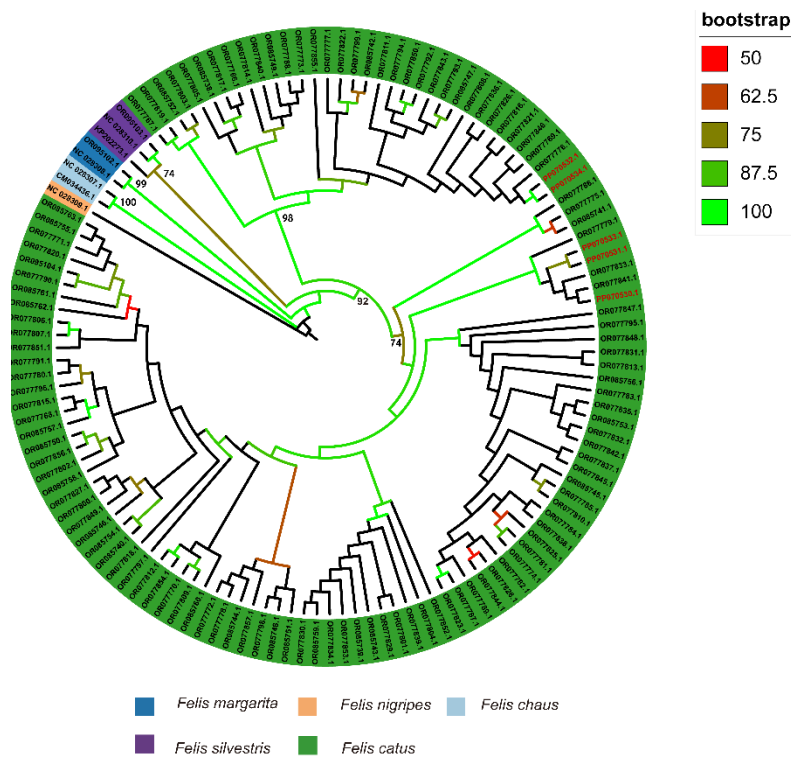
| Accession No. | Length(bp) | T%    | C%    | A%    | G%    | AT%   | GC%   | AT-skew | GC-skew |
|---------------|------------|-------|-------|-------|-------|-------|-------|---------|---------|
| PP070530      | 17026      | 27.13 | 26.17 | 32.67 | 14.03 | 59.80 | 40.20 | 0.093   | -0.302  |

|                 |       |       |       |       |       |       |       |       |        |
|-----------------|-------|-------|-------|-------|-------|-------|-------|-------|--------|
| <b>PP070531</b> | 16977 | 27.19 | 26.13 | 32.69 | 14.00 | 59.88 | 40.12 | 0.092 | -0.302 |
| <b>PP070532</b> | 17048 | 26.98 | 26.33 | 32.61 | 14.08 | 59.59 | 40.41 | 0.095 | -0.303 |
| <b>PP070533</b> | 16978 | 27.16 | 26.16 | 32.68 | 14.00 | 59.84 | 40.16 | 0.092 | -0.303 |
| <b>PP070534</b> | 17048 | 26.97 | 26.34 | 32.61 | 14.08 | 59.58 | 40.42 | 0.095 | -0.303 |
| <b>Average</b>  | 17015 | 27.09 | 26.23 | 32.65 | 14.04 | 59.74 | 40.26 | 0.093 | -0.303 |

The 22 tRNAs span a total length of 1,515 to 1,516 bp across the genomes of the five newly sequenced cats. The tRNA organization was consistent across all individuals, with 14 tRNAs located on the H strand and eight on the L strand. Both rRNAs were encoded on the H strand, with *rrnS* positioned between *trnF*-tta and *trnV*-gta, and *rrnL* located between *trnV*-gta and *trnL2*-tta. The length of *rrnS* was 962 bp, while *rrnL* ranged from 1,576 to 1,577 bp.

### Phylogenomic Analyses

The phylogenomic analysis of cat species based on mitochondrial genomes revealed five primary branches corresponding to *F. catus* (domestic cat), *F. silvestris* (wildcat), *F. margarita* (sand cat), *F. chaus* (jungle cat), and *F. nigripes* (black-footed cat), highlighting the utility of mitochondrial genomes as a powerful tool for species identification (Fig. 1). The newly sequenced Chinese cats were distributed across these branches, with individuals PP070530, PP070531, and PP070533 clustering together in one subclade, while PP070532 and PP070534 grouped within other lineages. This distribution indicates diverse origins and substantial lineage differences among Chinese cats. Additionally, domestic cats and wildcats were shown to be closely related, forming well-supported clusters, reflecting their close evolutionary relationship.

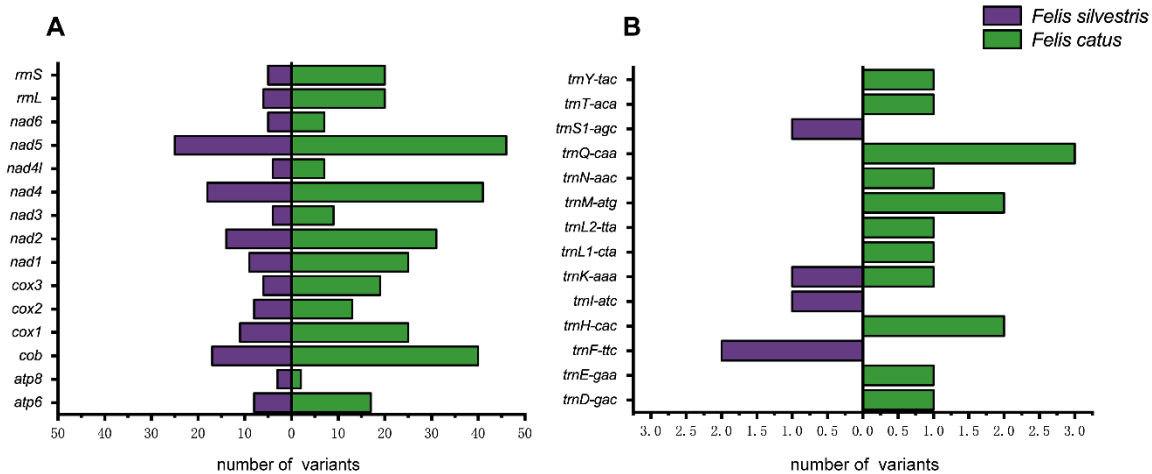


**Figure 1.** The ML tree of *Felis* inferred from the complete mitochondrial genome. The terminal branch numbers represent GenBank accession numbers, while the color blocks designate different species. Degree of bootstrap is displayed by color grades from red (low support) to green (high support).

### Nucleotide Variation Between Domestic and Wildcats

To gain insights into the mitochondrial genome variations between and within domestic cats and their wild relatives, we conducted a pan-mitochondrial genome nucleotide variation analysis encompassing three wildcat species and 123 domestic cats (Fig. 2). A total of 580 variants were identified, comprising 97% single-nucleotide variants (SNVs) and 3% indels (Table S3). Most variants were located in PCG regions (72%), followed by control regions and gene spacers (16%), rRNA regions (9%), and tRNA regions (3%). Among the individual PCGs, the *cob* gene exhibited the highest mutation rate, while *nad6* had the lowest (Fig. S1).

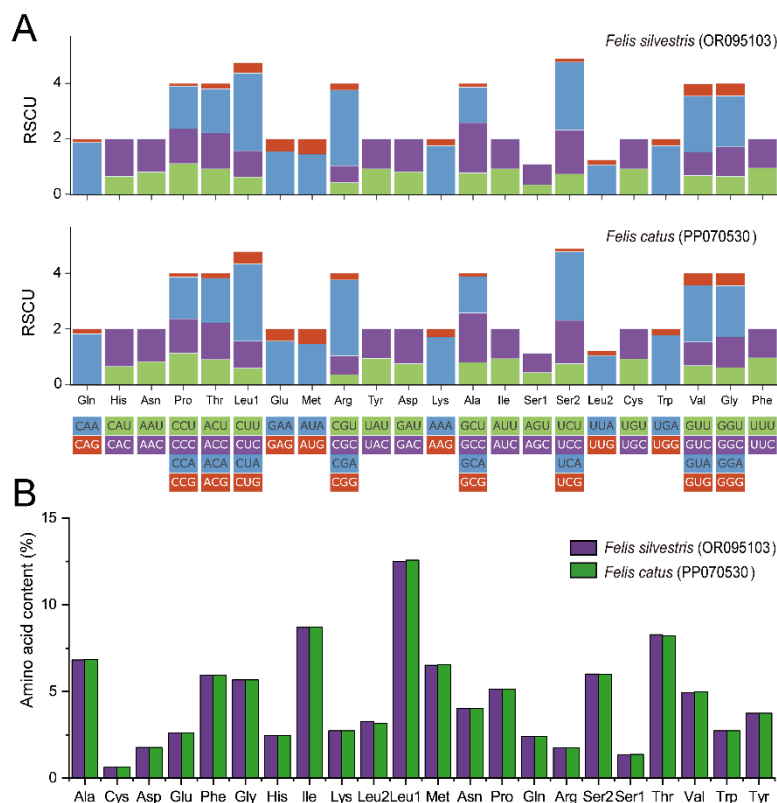




**Figure 3.** Comparison the nucleotide variants of the mitochondrial regions between the domestic and wildcats. The horizontal coordinate represents the number of variants and the vertical coordinate represents the genic regions.

## RSCU, Amino Acid Content, and Selection Pressure Between Domestic Cats and Wildcats

Mitochondrial PCGs from a representative domestic cat (PP070530) and wildcat (OR095103) were analyzed. Most frequently observed codons were CUA (Leu1), followed by AUA (Met), AUC (Ile), AUU (Ile), and ACA (Thr) (Fig. 4A, Table S5). RSCU values ranged from 0.11 to 2.77 in domestic cats and from 0.1 to 2.8 in wildcats, indicating similar codon preference. Codons with RSCU > 2 were highly frequent and predominantly ended in adenine. Leu1 was the most abundant, while Cys was the least represented (Fig. 4B). Ka/Ks ratios were calculated for each PCG to assess selection pressure, yielding values between 0.01 and 0.15. These ratios were significantly below 1, indicating pervasive purifying selection in both domestic and wildcats (Fig. 5; Table S6).



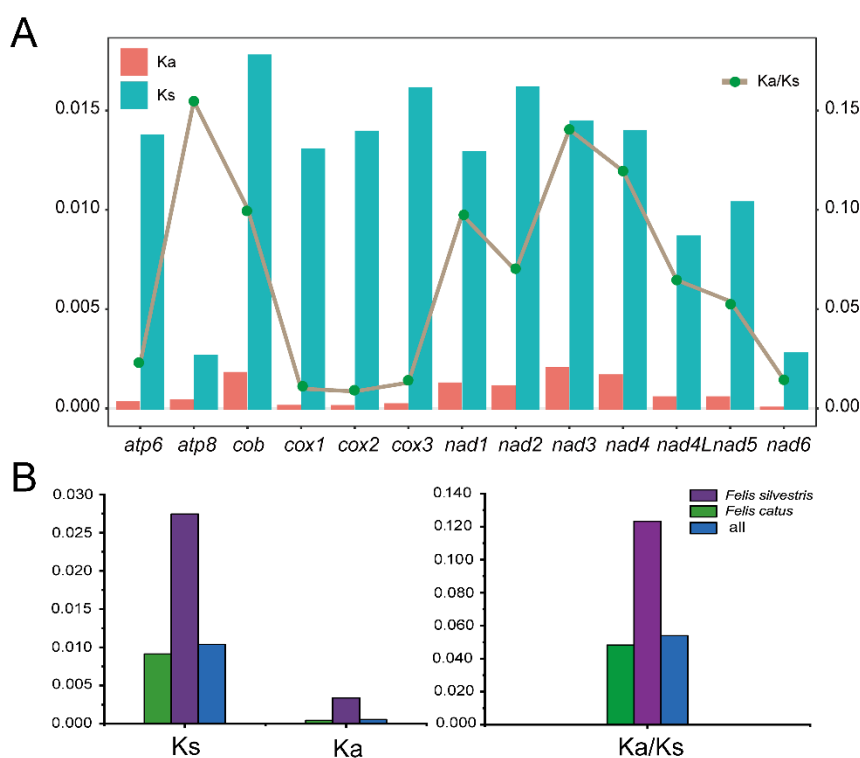
**Figure 4.** Comparison of codon and amino acid usage in the mitochondrial genome of domestic and wildcats. (A) Compares the codon and codon usage for each amino acid, while (B) Compares the amino acid content in the two types of mitochondrial genomes.

**Table 2.** Completely differentiated loci between domestic cats and wildcats

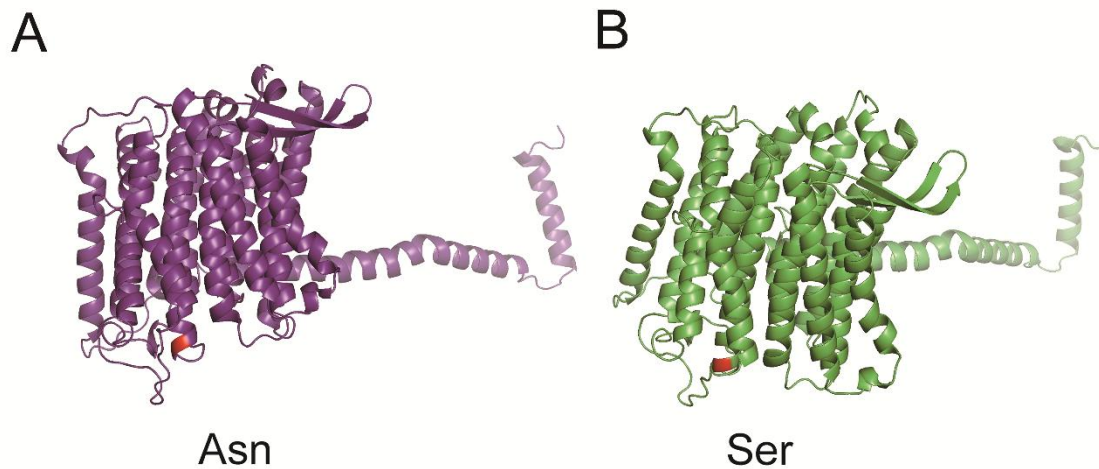
| Codon      | Gene | Site | Amino Acid | Coding protein |
|------------|------|------|------------|----------------|
| TAC/TAT    | nad1 | 342  | Tyr/ Tyr   | complex I      |
| TAC/TAT    | nad1 | 426  | Tyr / Tyr  | complex I      |
| CTA/CTT    | nad1 | 729  | Leu/ Leu   | complex I      |
| AAC/AAT    | nad2 | 231  | Asn/ Asn   | complex I      |
| TTG/T(C)TA | nad4 | 135  | Leu/ Leu   | complex I      |
| TTA/CTA    | nad4 | 790  | Leu/ Leu   | complex I      |
| CTA/CTG    | nad4 | 831  | Leu/ Leu   | complex I      |
| ATT/ATC    | nad5 | 447  | Ile/ Ile   | complex I      |
| AAT/AGT    | nad5 | 1046 | Asn/Ser    | complex I      |
| ATT/AGT    | nad5 | 1377 | Ile/ Ile   | complex I      |
| GGT/GGC    | cox1 | 1296 | Gly/ Gly   | complex IV     |
| GAG/GAA    | cox1 | 1497 | Glu/ Glu   | complex IV     |
| GAC/GAT    | cox2 | 264  | Asp/ Asp   | complex IV     |
| CTA/TTA    | atp6 | 505  | Leu/ Leu   | ATP synthase   |
| CTA/CTG    | atp6 | 648  | Leu/ Leu   | ATP synthase   |
| AAC/AAT    | cob  | 45   | Asn/ Asn   | complex III    |

### Variation in Coding Regions Between Domestic Cats and Wildcats

Our analysis of eight PCGs identified sixteen distinct coding variations between domestic cats and wildcats (Table 2). Ten of these variations were found in the *nad1*, *nad2*, *nad4*, and *nad5* regions, which are crucial for the synthesis of NADH dehydrogenase (complex I). The remaining variations were found in the *cox1*, *cox2*, *atp6*, and *cob* genes, which are involved in the synthesis of complexes IV, ATP, and III. Notably, we discovered only one non-synonymous mutation: a codon-change from AAT to AGT in the *nad5* region, resulting in an amino acid substitution from Asparagine (Asn) to Serine (Ser). Selection pressure analysis revealed that the Ka/Ks value of *nad5* in domestic cats was approximately one-third of that in wildcats, indicating that *nad5* is under stronger purification selection in domestic cats (Fig. 5B, Table S7). Despite this, both Asn and Ser are hydrophilic, and the overall structure of the protein subunit encoded by the *nad5* gene remains largely unchanged (Fig. 6).



**Figure 5.** Comparative analysis of selective pressures exerted on coding genes between domestic and wildcats. (A) Ka/Ks value for all 13 PCGs. The blue histogram represents Ka values, while the orange histogram corresponds to Ks values. The solid green circle with gray denotes the Ka/Ks ratio. (B) Comparative analysis of Ka/Ks value for the non-synonymous mutation in *nad5* between domestic and wildcats.



**Figure 6.** Predictive three-dimensional structure of the protein encoded by the *nad5* gene in domestic and wildcats. (A) wildcat (B) domestic cat. Regions with amino acid changes highlighted in red.

## Discussion

Cats have lived with humans for around 10,000 years. Once valued for pest control, they are now mainly bred for aesthetic traits, leading to diverse coat patterns and significant phenotypic variation. This study presents a mitochondrial pangenome of domestic cats, highlighting genetic divergence between domestic and wildcats. On the phylogenomic tree, our newly sequenced Chinese cats clustered within European cats and were close to *F. silvestris* (Fig. 1), supporting the hypothesis of a shared ancestry of domestic cats with wildcats (Yu et al., 2021; Patterson et al., 2023).

The domestication of cats from wild to human-dominated environments has been accompanied by shifts in energy acquisition and metabolism. Given that mitochondria are the primary energy suppliers (Rackham & Filipovska, 2022), we hypothesize that the mitochondrial genome of domestic cats may reflect their domestication process. Our analysis of the mitochondrial pangenome shows that the Ka/Ks values for all 13 protein-coding genes are consistently below 1, indicating purifying selection. Interestingly, we found higher mutation rates in respiratory-related genes, such as *nad4*, *nad5*, and *cob*, in domestic cats compared to wildcats (Fig. 3). These findings suggest possible adaptations associated with the transition from wild habitats to human-dominated environments, where metabolic demands and energy utilization may have shifted due to changes in behavior, diet, and activity levels.

To explore genetic differences between domestic cats and wildcats, we identified 16 distinct differentiation sites in the mitochondrial genome—regions uniform within each group (domestic

vs. wild) but divergent between them. Of these, 15 sites had synonymous mutations, which do not alter protein structures but may indicate neutral evolution or regulatory adaptations. Notably, one site in the *nad5* gene had a non-synonymous mutation, changing asparagine to serine. This mutation affects NADH dehydrogenase, a key component of complex I in the mitochondrial electron transport chain, essential for aerobic respiration and ATP production (Wirth et al., 2016). The *nad5* mutation provides insights into how domestication may have influenced mitochondrial function. Previous studies showed that *nad5* gene expression is crucial for respiration regulation; mouse cells with *nad5* nonsense mutations exhibited impaired mitochondrial function compared to wild-type (Bai et al., 2000). Our selection pressure analysis indicates that both domestic and wildcats undergo purifying selection on *nad5*, with domestic cats experiencing stronger purifying selection. One explanation for increased purifying selection on *nad5* in domestic cats is their distinct ecological niches. Wildcats live in unpredictable environments, requiring high metabolic flexibility to cope with challenges like food scarcity and predation. In contrast, domestic cats rely on stable, human-provided resources and face fewer environmental stressors. This reduced ecological pressure may have led to fine-tuning of respiratory efficiency, as reflected in the *nad5* mutation and other genes. These differences highlight the divergent evolutionary paths of domestic cats, shaped by dependence on humans, versus the adaptive resilience of wildcats in natural habitats. The observed hypervariability in domestic cats, especially in *nad5*, is likely due to a complex interplay of factors. This includes substantial post-domestication population expansion, extensive admixture with wildcats introducing diverse haplotypes, and potential shifts in selective pressures. While domestication facilitated these conditions, the observed diversity is better explained as the combined outcome of demography, hybridization, and selection. Future comprehensive studies, integrating population genetics, ecological, and functional analyses, are therefore essential to disentangle the specific contributions of demographic history, admixture, and selective forces in shaping domestic cat mitochondrial diversity.

## Conclusion

In summary, domestication has significantly influenced mitochondrial genome evolution in cats, particularly in respiratory-related genes like *nad5*. The interplay between purifying selection and mutation rates in these genes sheds light on how domestic cats have adapted to human-altered environments. Future research should investigate the functional effects of these genetic changes on mitochondrial efficiency and energy metabolism, and examine their relationship to traits

specific to domesticated lifestyles. Additionally, comparative studies across diverse populations will clarify global patterns of cat domestication and the interaction between natural and artificial selection.

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## References

- Bai, Y.D., Shakeley, R. M., & Attardi, G. (2000). Tight control of respiration by NADH dehydrogenase ND5 subunit gene expression in mouse mitochondria. *Molecular and Cellular Biology*, 20(3), 805–815.
- Bernt, M., Donath, A., Juehling, F., Externbrink, F., Florentz, C., Frittsch, G., Puetz, J., Middendorf, M., & Stadler, P. F. (2013). MITOS: Improved de novo metazoan mitochondrial genome annotation. *Molecular Phylogenetics and Evolution*, 69(2), 313–319.
- Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics*, 30(15), 2114–2120.
- Bouma, E. M., Reijgwart, M. L., & Dijkstra, A. (2021). Family member, best friend, child or ‘just a pet’: Owners’ relationship perceptions and consequences for their cats. *International Journal of Environmental Research and Public Health*, 18(1), 193.
- Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., & Madden, T. L. (2009). BLAST plus: Architecture and applications. *BMC Bioinformatics*, 10(1), 421.
- Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17(4), 540–552.
- Chang, H., Qiu, Z., Yuan, H., Wang, X., & Huang, Y. (2020). Evolutionary rates of and selective constraints on the mitochondrial genomes of orthoptera insects with different wing types. *Molecular Phylogenetics and Evolution*, 145, 106734.
- Menotti-Raymond, M., Roca, A. L., Hupe, K., Johnson, W. E., Geffen, E., Harley, E. H., Delibes, M., Pontier, D., Kitchener, A. C., Yamaguchi, N., O’Brien, S. J., Macdonald, D. W., & Driscoll, C. A. (2007). The Near Eastern Origin of Cat Domestication. *Science*, 317(5837), 519–523. <https://doi.org/10.1126/SCIENCE.1139518>
- Grant, J. R., Enns, E., Marinier, E., Mandal, A., Herman, E. K., Chen, C. Y., Graham, M., Van Domselaar, G., & Stothard, P. (2023). Proksee: In-depth characterization and visualization of bacterial genomes. *Nucleic Acids Research*, 51(W1), gkad326.
- Hall, T. A. (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
- Hu, Y., Hu, S., Wang, W., Wu, X., Marshall, F. B., Chen, X., Hou, L., & Wang, C. (2014). Earliest evidence for commensal processes of cat domestication. *Proceedings of the National Academy of Sciences*, 111(1), 116–120.
- Isabelle, C., Abby, C., L. T. C., & Antonio, B. J. (2020). The complete mitochondrial genome of the red-jointed brackish-water fiddler crab *Minuca minax* (LeConte 1855) (Brachyura: Ocypodidae): New family gene order, and purifying selection and phylogenetic informativeness of protein coding genes. *Genomics*, 113(1), 565–572.
- James, J. E., Piganeau, G., & Eyre-Walker, A. (2016). The rate of adaptive evolution in animal

- mitochondria. *Molecular Ecology*, 25(1), 67–78.
- Jin, J. J., Yu, W. B., Yang, J. B., Song, Y., de Pamphilis, C. W., Yi, T. S., & Li, D. Z. (2020). GetOrganelle: A fast and versatile toolkit for accurate de novo assembly of organelle genomes. *Genome Biology*, 21(1), 1–31.
- Krüger, M., Hertwig, S. T., Jetschke, G., & Fischer, M. S. (2009). Evaluation of anatomical characters and the question of hybridization with domestic cats in the wildcat population of Thuringia, Germany. *Journal of Zoological Systematics and Evolutionary Research*, 47(3), 268–282.
- Letunic, I., & Bork, P. (2021). Interactive Tree of Life (iTOL) v5: An online tool for phylogenetic tree display and annotation. *Nucleic Acids Research*, 49(W1), W293–W296.
- Li, G., Davis, B. W., Eizirik, E., & Murphy, W. J. (2016). Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). *Genome Research*, 26(1), 1–11.
- Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25(11), 1451–1452.
- Menotti-Raymond, M., David, V. A., Pflueger, S. M., Lindblad-Toh, K., Wade, C. M., O'Brien, S. J., & Johnson, W. E. (2008). Patterns of molecular genetic variation among cat breeds. *Genomics*, 91(1), 1–11.
- Montague, M. J., Li, G., Gandolfi, B., Khan, R., Aken, B. L., Searle, S. M., Minx, P., Hillier, L. W., Koboldt, D. C., & Davis, B. W. (2014). Comparative analysis of the domestic cat genome reveals genetic signatures underlying feline biology and domestication. *Proceedings of the National Academy of Sciences*, 111(48), 17230–17235.
- Mousavi, M., Naderi, S., Rezaei, H. R., & Adibi, M. A. (2022). Evolutionary history and distribution of African wildcat, *Felis lybica* in Iran. *Caspian Journal of Environmental Sciences*, 20(3), 637–648.
- Nakamura, T., Yamada, K. D., Tomii, K., & Katoh, K. (2018). Parallelization of MAFFT for large-scale multiple sequence alignments. *Bioinformatics*, 34(14), 2490–2492.
- Nguyen, H. D., Bui, T. A., Nguyen, P. T., Kim, O. T. P., & Vo, T. T. B. (2017). The complete mitochondrial genome sequence of the indigenous I pig (*Sus scrofa*) in Vietnam. *Asian-Australasian Journal of Animal Sciences*, 30(7), 930–937.
- O'Connor, T. P. (2007). Wild or domestic? Biometric variation in the cat *Felis silvestris* Schreber. *International Journal of Osteoarchaeology*, 17(6), 581–595.
- Ojala, D., Montoya, J., & Attardi, G. (1981). tRNA punctuation model of RNA processing in human mitochondria. *Nature*, 290(5806), 470–474.
- Page, A. J., Taylor, B., Delaney, A. J., Soares, J., Seemann, T., Keane, J. A., & Harris, S. R. (2016). SNP-sites: Rapid efficient extraction of SNPs from multi-FASTA alignments. *Microbial Genomics*, 2(4), e000056.
- Patterson, E. C., Lall, G. M., Neumann, R., Ottolini, B., Batini, C., Sacchini, F., Foster, A. P., Wetton, J. H., & Jobling, M. A. (2023). Mitogenome sequences of domestic cats demonstrate lineage expansions and dynamic mutation processes in a mitochondrial minisatellite. *BMC Genomics*, 24(1), 690.
- Puzachenko, A. Y. (2002). Hybrid syndrome and method for identification of hybrids in museum collections of *Felis silvestris* and *Felis lybica*. *Säugetierkundliche Informationen*, 26, 234–248.
- Rackham, O., & Filipovska, A. (2022). Organization and expression of the mammalian mitochondrial genome. *Nature Reviews Genetics*, 23(10), 606–623.
- Ragni, B., & Possenti, M. (1996). Variability of coat-colour and markings system in *Felis silvestris*. *Italian Journal of Zoology*, 63(3), 285–292.
- Sharp, P. M., & Li, W. H. (1987). The codon adaptation index—A measure of directional synonymous

- codon usage bias, and its potential applications. *Nucleic Acids Research*, 15(3), 1281–1295.
- Shen, Y. Y., Shi, P., Sun, Y. B., & Zhang, Y. P. (2009). Relaxation of selective constraints on avian mitochondrial DNA following the degeneration of flight ability. *Genome Research*, 19(10), 1760–1765.
- Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30(9), 1312–1313.
- Stevenson, K. J. (2011). Review of OriginPro 8.5. *Journal of the American Chemical Society*, 133(14), 5621.
- Velli, E., Caniglia, R., & Mattucci, F. (2023). Phylogenetic history and phylogeographic patterns of the European Wildcat (*Felis silvestris*) populations. *Animals*, 13(6), 953.
- Vigne, J.-D., Guilaine, J., Debue, K., Haye, L., & Gérard, P. (2004). Early taming of the cat in Cyprus. *Science*, 304(5668), 259.
- Waterhouse, A., Bertoni, M., Bienert, S., Studer, G., Tauriello, G., Gumienny, R., Heer, F. T., de Beer, T. A. P., Rempfer, C., & Bordoli, L. (2018). SWISS-MODEL: Homology modelling of protein structures and complexes. *Nucleic Acids Research*, 46(W1), W296–W303.
- Wirth, C., Brandt, U., Hunte, C., & Zickermann, V. (2016). Structure and function of mitochondrial complex I. *Biochimica et Biophysica Acta*, 1857(7), 902–914.
- Yu, H., Xing, Y. T., Meng, H., He, B., Li, W. J., Qi, X. Z., Zhao, J. Y., Zhuang, Y., Xu, X., & Yamaguchi, N. (2021). Genomic evidence for the Chinese mountain cat as a wildcat conspecific (*Felis silvestris bieti*) and its introgression to domestic cats. *Science Advances*, 7(26), eabg0221.
- Zhang, D., Gao, F., Jakovli, I., Zou, H., & Wang, G. T. (2020). PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Molecular Ecology Resources*, 20(1), 348–355.