Mammal Research (2026) 71:11
https://doi.org/10.1007/s13364-025-00822-0

ORIGINAL ARTICLE

Comparative mitogenome sequences and phylogenetic relationships of two mongooses (*Herpestes ichneumon* and *Urva auropunctata*) from Türkiye and Iraq

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Received: 11 October 2024 / Accepted: 2 September 2025 / Published online: 4 December 2025

Abstract

Mongoose species (Herpestidae) exhibit a wide geographic distribution across Africa, Asia, and several island regions, yet mitogenomic data remain scarce for many taxa and regions. In this study, the complete mitochondrial genomes of the Egyptian mongoose (*Herpestes ichneumon*) from Türkiye and the small Indian mongoose (*Urva auropunctata*) from Iraq are analyzed for the first time to explore their genetic structure and phylogenetic relationships within the Herpestidae. The mitogenomes are similar in overall organization and size (16,660 bp in *H. ichneumon* and 16,761 bp in *U. auropunctata*), with variations primarily found in the *D-loop* (control region), which influences genome length through repeated motifs. The Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic analyses using complete mitochondrial genome and cytochrome *b* (*CYTB*) sequences reinforce the previous findings on Herpestidae phylogeny. Results support the division of Herpestidae into two subfamilies (Herpestinae and Mungotinae), confirm the monophyly of *Urva*, and highlight the paraphyly of *Herpestes*. Based on the complete mitogenome sequences, the Iraqi *U. auropunctata* specimens are clustered with Japanese and Fijian specimens, indicating low level of intraspecific variation. *Herpestes ichneumon* is clustered with the *Galerella sanguine* based on the mitogenome sequences. Additionally, *H. ichneumon* haplotypes are grouped into three haplogroups (Iberian, Levantine, and South African) based on the *CYTB* sequences, reflecting regional genetic differentiation. Molecular dating estimated Herpestidae diverges from Eupleridae ~ 30.76 million years ago (Mya), with subfamily divergence occurring in the Early Miocene (~ 19.87 Mya). Within *Urva*, species begin diverging around 12.5 Mya, with *U. javanica* and *U. auropunctata* separating ~ 4.67 Mya. Recent divergence is also noted between *H. ichneumon* specimens from Türkiye and Lebanon (~ 150 Kya) and among *U. auropunctata* populations from Iraq, Japan, and Fiji (~ 600 Kya), supporting ongoing intraspecific diversification within both species. This study provides valuable insights into the phylogeny and evolutionary history of two mongoose species by comparing the structural and organizational features of their mitogenomes from biogeographically related regions, along with phylogenetic and evolutionary dating analyses based on complete mitogenome and *CYTB* sequences.

Keywords Egyptian mongoose · Small Indian mongoose · Phylogeny · Herpestidae · Mitochondrial DNA

Introduction

Mongooses (Carnivora, Herpestidae) are widely distributed in Africa and Asia and adapted to various habitats, feeding on vertebrate and invertebrate animals (Corbet and Hill 1992; Gilchrist et al. 2009). Mongooses are terrestrial carnivores with a small body and represented with 34 species classified within two subfamilies (Herpestinae; *Atilax, Xenogale, Herpestes, Cynictis, Galerella, Ichneumia, Paracynictis, Bdeogale, Rhynchogale,* Mungotinae; *Suricata, Crossarchus, Helogale, Dologale, Liberiictis, Mungos*) (Perez et al. 2006). As a result of numerous studies based

Communicated by: Astrid V. Stronen

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on different markers including morphological (Pocock 1916; Gregory and Hellman 1939; Petter 1969; Hendey 1974; Stains 1983; Wozencraft 1989; Veron 1995; Taylor and Matheson 1999; Egi et al. 2011), karyological (Fredga 1972), and molecular markers (Veron et al. 2006; Patou et al. 2009; Veron and Jennings 2017; Boukhdoud et al. 2021; Hassanin et al. 2021), there have been changes in taxonomic status of species due to polyphyletic groups observed within the Herpestidae (Perez et al. 2006; Patou et al. 2009). In the last decade, the Asian mongooses, previously classified within the genus *Herpestes,* have been classified within the genus *Urva* (*Urva auropunctata, U. fusca, U. brachyura, U. edwardsii, U. javanica, U. semitorquata, U. smithii, U. urva,* and *U. vitticolla*) (Patou et al. 2009; Egi et al. 2011; Veron et al. 2015; Veron and Jennings 2017). In this context, the name *Urva* was used for Asian Mongooses due to the latest classification of Mongooses suggested by Veron and Jennings (2017) in the current study. Additionally, because the African mongoose species *Herpestes naso* and *H. ichneumon* occupy a paraphyletic position within the genus *Herpestes* (Veron et al. 2004; Perez et al. 2006; Patou et al. 2009), Patou et al. (2009) suggested that *H. naso* should be reclassified under the genus *Xenogale*.

Herpestes ichneumon (the Egyptian mongoose) is the only mongoose species natively found in Türkiye. Its distribution also includes South Africa, the Levant region, and the Iberian Peninsula (Palomares and Delibes 1993; Zapata et al. 2007; Riquelme-Cantal et al. 2008; Do Linh San et al. 2016). Three different *Urva* species are found in Iraq, a country that is biogeographically similar to Türkiye: *Urva auropunctata* (small Indian mongoose, native to Iraq), *U. edwardsii* (Indian grey mongoose), and *U. javanica* (Javan mongoose) (Veron et al. 2006; Patou et al. 2009; Al-Sheikhly and Mallon 2013; Veron and Jennings 2017). Although several studies have focused on the morphological (Atay and Yeşiloğlu 2012; Al-Sheikhly and Mallon 2013), karyological (Özkurt 2015), and molecular (Gaubert et al. 2011) markers of the Turkish and the Iraqi mongooses, molecular studies for the Turkish and the Iraqi mongooses are scarce and based on partial mitochondrial DNA sequences. In a phylogeographic study based on two regions of mitochondrial DNA, cytochrome *b* and the control region, which included two specimens from Türkiye, Gaubert et al. (2011) concluded that *H. ichneumon* may have expanded from Africa to Europe, likely via the Sahara Desert, since the Middle Pleistocene. It was concluded that the Middle East clade, which includes the Turkish specimens of *H. ichneumon*, genetically diverged from the other clades approximately 256,000 years ago. Although partial mitochondrial DNA sequences have provided some insights into the evolutionary history of *H. ichneumon*, the complete mitochondrial genome of the Egyptian mongoose (*H. ichneumon*) from Türkiye remains unavailable. Including the full mitogenome of *H. ichneumon* from this region in mitochondrial genome-based analyses would significantly enhance our understanding of the phylogeny, genetic diversity, and evolutionary history of the Herpestidae.

Herpestes ichneumon and *Urva auropunctata* are important carnivorous species that have a considerable impact on the natural ecosystems (Courchamp et al. 2003; Doherty et al. 2016). In addition to their broad natural geographic range, mongooses have been intentionally introduced by humans to various regions—including islands in the Pacific and Indian Oceans, parts of Japan, the West Indies, the Caribbean, the Adriatic Sea, South America, and mainland Europe—beyond their native range, primarily as biological control agents targeting species such as rats and venomous snakes (Veron et al. 2006; Barun et al. 2011). Considering the habitat components of the areas they currently occupy, both species demonstrate a strong ability to adapt to diverse environments and are therefore classified as invasive (Barun et al. 2013; Louppe et al. 2021). Their diets are broad, including not only numerous invertebrate species but also various vertebrates such as reptiles, birds, and mammals (Berentsen et al. 2017; Mahmood and Adil 2017). As such, they pose a significant ecological pressure on native biodiversity, especially in interconnected ecosystems like those of Türkiye and Iraq. The spread of such invasive species beyond their natural habitats presents a significant challenge to global efforts aimed at protecting and sustaining biodiversity (Bellard et al. 2016; Holmes et al. 2019; Louppe et al. 2021). Given that these species are themselves part of biodiversity, understanding their genetic structure and assessing their impact on other species should be regarded as a key conservation priority (Sher and Primack 2020). Since they have been introduced to regions outside their natural habitats through human activity, these species are likely to exhibit a complex genetic structure on a global scale, similar to patterns observed in reintroduced large mammals or domesticated livestock (Kolbe et al. 2004; Dlugosch and Parker 2008; Şeker 2024). This is also an important problem for tracing their geographical origins, which are closely linked to their high adaptability and invasive nature, and for better understanding their present-day distribution patterns (Louppe et al. 2021). It is essential to uncover the genetic structures of these species and to analyze the geographical distribution of their genetic patterns. Such insights will provide a clearer understanding of the current distribution of these species and help assess their ecological impacts and potential threats to existing biodiversity. To this end, the analysis of the structure, organization, and sequence of mitochondrial DNA -a key microevolutionary phylogenetic marker- has been widely

used to determine the geographical distribution patterns of species' maternally inherited genetic structures (Avise 2000).

The mitochondrial genome (mitogenome) is maternally inherited, and it is approximately 16 kb in length and encodes 37 genes for mammalian species (Boore 1999). When compared to the results obtained from single gene data, whole mitogenomes provide phylogenetically more accurate and reliable results (Li et al. 2016; Yuan et al. 2016). In the recent years, whole mitogenome sequences have been commonly used as an important molecular marker in studies focused on phylogenetics, population genetics, and evolutionary history of mammalian species (de Abreu-Jr et al. 2020; Hassanin et al. 2021; Sosale et al. 2023). Although whole mitogenomes of 14 species within the Herpestidae (*Atilax paludinosus*, *Bdeogale nigripes*, *Crossarchus platycephalus*, *Cynictis penicillate*, *Galerella sanguinea*, *Herpestes ichneumon*, *H. semitorquata*, *H. naso*, *Ichneumia albicauda*, *Mungos mungo*, *Suricata suricatta*, *Urva auropunctata*, *U. brachyura*, *U. javanica*) are available from different geographical regions registered in the GenBank database (NCBI: https://www.ncbi.nlm.nih.gov/), whole mitogenomes of the Turkish and the Iraqi mongooses are unavailable yet.

In this study, we aimed to: (a) determine the structure and organization of the mitogenomes of the *H. ichneumon* from Türkiye and *U. auropunctata* from Iraq for the first time by comparing them with available mitogenomes of other mongoose species, and (b) contribute to elucidating the phylogenetic relationships of the Turkish and Iraqi mongooses within the Herpestidae. Therefore, characterizing the genetic structure and geographical distribution of these genetic patterns of mongooses -an invasive species that exerts pressure on natural ecosystems- and determining their phylogenetic relationships can provide a valuable foundation for future efforts to document global biodiversity, a core objective of conservation biology (Sher and Primack 2020).

Material and methods

Sampling and gDNA extraction

Muscle tissues were collected from road-killed individuals of two Egyptian mongooses (*Herpestes ichneumon*) found in Mersin (N36° 55', E34° 57') and Adana (N37° 25', E35° 47'), Türkiye, as well as from three small Indian mongooses (*Urva auropunctata*) from Al-Nel Babil, South Babil, and Ad-Diwaniyah, Iraq. The tissue samples were deposited in the Mammal Collection of the Department of Biology, Faculty of Sciences, Erciyes University, Kayseri, Türkiye. Genomic DNA (gDNA) was extracted from the tissue samples using the QIAGEN DNeasy® Blood & Tissue Kit, following the manufacturer's protocol, and stored at −20 °C. The concentration of extracted gDNA was measured using a Qubit® 2.0 Fluorometer and the Qubit™ dsDNA BR Assay Kit. DNA quality was assessed by electrophoresing 5 µL of each gDNA sample on a 1% agarose gel, followed by visualization under UV light. All gDNA samples were subsequently stored at −20 °C until PCR amplification.

Long-range PCR amplification of complete mitogenomes

The complete mitogenomes were amplified from gDNA using two specific primer pairs (Table 1) and a Long-Range PCR procedure with NEB LongAmp® Taq 2X Master Mix (M0287S, NEB), following the method described by İbiş et al. (2020). The PCR mixtures contained 12.5 µL of 1X NEB LongAmp® Taq 2X Master Mix, 1.5 µL of each

Table 1 The specific primer pairs and Long-Range PCR conditions used for the amplification of mitogenomes

		Duration	Temperature	
Long-Range PCR Conditions	***Pre-denaturation***	1 minute	94°C	
	Denaturation	30 seconds	94°C	30 cycles
	Annealing	45 seconds	57°C (CrocAL1-2024L-CrocBH1-13002H) 55°C (ScVu-11712L-LuLu-2503H)	
	Extension	11 minutes (CrocAL1-2024L-CrocBH1-13002H) 7,5 minutes (ScVu-11712L-LuLu-2503H)	65°C	
	Final Extension	10 minute	65°C	
Primer Pairs	**CrocAL1-2024L**	5'-GACCGTGCAAAGGTAGCATAATC-3' (Forward 1)		
	CrocBH1-13002H	5'-TAATTAAAAGGGCTCAGGCGTTG-3' (Reverse 1)		
	ScVu-11712L	5'-AGAAGTAATCCATTGGTCTTAGGA-3' (Forward 2)		
	LuLu-2503H	5'-CTCAGATCACGTAGGACTTTAATC-3' (Reverse 2)		

primer (0.6 µM), 1 µL gDNA (~30 ng), and 8.5 µL ddH_2O. A mixture without gDNA was also included in the reactions as a negative control. The Long-Range PCR program was set up as shown in Table 1 and whole mitogenomes were obtained in two overlapping fragments (~11 kb and ~7.1 kb in length). The obtained PCR amplicons were run on an agarose gel of 1% (Fig. S1) and quantified by means of the Qubit™ dsDNA BR Assay Kit. All the PCR products were standardized to 1 ng (0.2 ng/5 µL) by diluting with ddH_2O for preparation of the sequencing library.

Library construction, sequencing, and bioinformatic analysis

Nextera XT DNA Library Prep Kit (Illumina, San Diego, USA) and Nextera XT DNA Library Preparation Index Kit v2 Set A (Cat. No: FC-131–nnn2001, Illumina, San Diego, USA) were used for the construction of sequencing libraries. The quantity of each library was normalized employing a bead-based method. Loading concentration of libraries was determined via the Qubit™ dsDNA HS Kit and sequencing steps were performed with MiSeq Reagent Kit v2 (500 cycles) (Illumina) and Illumina-MiSeq platform at Genome and Stem Cell Centre (GENKOK), Erciyes University.

The obtained raw data was assembled and analyzed by transferring it separately into Geneious Prime® 2020.1.2 software (Kearse et al. 2012). BBDuk v38.84 Trimming Tool in Geneious Prime was used to filter adapters, short reads (<50 bp), ambiguous nucleotides (N), and low-quality bases (Q-score<25). The remaining reads were assembled and annotated to the whole mitogenome of *Urva auropunctata* (*H. javanicus* in NCBI: NC_006835). Assembly operations were initially conducted by using the Geneious Mapper algorithm (Sensitivity: Highest sensitivity/Medium; and Fine Tuning: iterate up to 25 times) and checked manually by using the MITOS2 web server (Bernt et al. 2013). The repeat motifs in the control region (D-loop) were detected using the Tandem Repeats Finder web server (Benson 1999). AT skew and GC skew parameters were calculated with the following formulas: AT skew = [A-T]/[A+T] and GC skew = [G-C]/[G+C]. A graphical mitogenome map was created by means of CGView Server (Grant and Stothard 2008). The codon usage (Count) and relative synonymous codon usage (RSCU) data were determined in MEGA 12 software (Kumar et al. 2024).

Phylogenetic analyses

This study utilized two mitochondrial datasets for phylogenetic analyses: (i) A mitogenome phylogeny was constructed using complete mitochondrial genomes (excluding the *D-loop* region) from species representing seven mammalian families -Felidae, Prionodontidae, Nandiniidae, Viverridae, Herpestidae, Eupleridae, and Hyaenidae- sourced from both the NCBI database and the present study. *Cuon alpinus* (Canidae) was used as the outgroup (Table S1); (ii) A mitochondrial *CYTB* phylogeny was constructed to investigate phylogenetic relationships within the Herpestidae, using *CYTB* gene sequences. *Mungotictis decemlineata* (Eupleridae) and *Nandinia binotata* (Nandiniidae) served as outgroups (Table S2). All sequences were aligned using MAFFT v.7.450 a multiple sequence alignment program (Katoh et al. 2002).

To evaluate evolutionary relationships and estimate divergence times, two separate phylogenetic analyses based on nucleotide substitution models were conducted: Maximum Likelihood (ML) analysis using RAxML v8.2.11 (Stamatakis 2014) in Geneious Prime (Algorithm: Rapid hill-climbing with RELL, 1000 replicates, Model: GTR GAMMA I). and Bayesian Inference (BI) using BEAST v1.8.0 (Drummond et al. 2012). The best-fit nucleotide substitution model for the mitogenome datasets was identified as GTR+G+I based on the Bayesian Information Criterion (BIC), using jmodeltest2 v.2.1.10 (Darriba et al. 2012). Using the same criteria applied to the mitogenome dataset, the HKY+G+I nucleotide substitution model was identified as the best fitting model for the *CYTB* dataset. To assess the stability of the inferred tree topologies, nonparametric bootstrap analysis with 1000 replicates and Bayesian posterior probability (BPP) tests were performed. To estimate evolutionary divergence within Herpestidae based on the mitogenome data set, a Yule tree prior was selected, and a strict molecular clock model was applied in BI analysis. One independent Markov Chain Monte Carlo (MCMC) run was conducted in BEAST v1.8.0 (Drummond et al. 2012), consisting of 10,000,000 generations with sampling every 1000 generations. Tracer v1.6 was used to assess whether the effective sample size (ESS) exceeded the recommended threshold of 200 in the log file. TreeAnnotator v1.8.0 (part of the BEAST software package) was used to discard the first 10% (1000 trees) of the 10,000-tree file as burn-in and to generate a 50% majority-rule consensus tree for calculating Bayesian posterior probabilities (BPPs) and divergence times of the nodes. A calibration point proposed by Patou et al. (2009) (mean = 21.8 million year ago (Mya) and st. dev. = 3.6 Mya) was used to estimate divergence times within Herpestidae based on mitogenome data. The trees generated from the ML and BI analysis were visualized and edited using FigTree v1.4.0 (included in the BEAST software package). Genetic distances were estimated with the Kimura 2-Parameter (K2P) model using 1000 bootstrap replicates in MEGA 12 (Kumar et al. 2024).

Results

H. ichneumon and *U. auropunctata* mitogenomes

In the present study, we sequenced and analyzed the complete mitochondrial genomes of two *H. ichneumon* individuals from Türkiye and three *U. auropunctata* individuals from Iraq, with coverage depths ranging from 4,500X to 5,700X. The two Turkish *H. ichneumon* specimens shared a single haplotype (GenBank accession: MW401775; 16,660 bp), while the three *U. auropunctata* specimens each represented distinct haplotypes (GenBank accession: MW401772–MW401774; 16,761 bp). All mitogenomes comprised the standard set of 37 genes, including 22 transfer RNAs (tRNAs), 2 ribosomal RNAs (rRNAs), 13 protein-coding genes (PCGs), as well as a control region (*D-loop*) and an origin of light-strand replication (O_L). Of these, the *ND6* gene and eight tRNAs ($tRNA^{Gln}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, $tRNA^{Ser\ (UCN)}$, $tRNA^{Glu}$ and $tRNA^{Pro}$) were located on the light (*L*) strand, while the remaining 12 PCGs, 14 tRNAs, both rRNAs, the O_L, and control region (*D-loop*) were situated on the heavy (*H*) strand (Fig. 1; Table 2). Across all mitogenomes, nine overlapping regions and eleven intergenic spacers were identified. The longest overlap (43 bp) occurred between the *ATP8* and *ATP6* genes, whereas the longest intergenic spacer was found between $tRNA^{Trp}$ and $tRNA^{Ala}$. Additionally, the *ND2* and *COX1* genes in the mitogenomes of *H. ichneumon* and *U. auropunctata* shared a few nucleotides with their adjacent tRNAs (Table 2). Codon usage analysis revealed that the first, second, and third codon positions of the *H. ichneumon* PCGs were A+T rich, though less so compared to *U. auropunctata* (Fig. 2). Skew analysis showed a negative G/C skew and a positive A/T skew in both species (Table 3).

Protein coding genes

The protein-coding genes (PCGs) in the mitogenomes of *H. ichneumon* and *U. auropunctata* had a total length of 11,409 bp, accounting for 68.48% and 68.07% of their respective mitochondrial genomes. Across both species, the 13 PCGs encoded a total of 3,792 amino acids, excluding termination codons. The start codon ATG was used by 10 PCGs in both species, specifically for *ATP6*, *ATP8*, *COX1*, *COX2*, *COX3*, *CYTB*, *ND1*, *ND4*, *ND4L*, and *ND6* (Table 2). In *H. ichneumon*, the *ND2* and *ND5* genes started with ATC and ATT, respectively, while in *U. auropunctata*, these genes used ATT and ATA as start codons (Table 2). Regarding termination codons, *ATP6*, *ATP8*, *COX1*, *COX2*, *ND1*, *ND4L*, *ND5*, and *ND6* ended with TAA, while *ND2* and *CYTB* terminated with TAG and AGA, respectively. The *COX3*, *ND3*, and *ND4* genes concluded with incomplete stop codons (T–) (Table 2). Relative synonymous codon usage (RSCU) and overall codon usage patterns were illustrated in Fig. 3. Among the amino acids, Leucine, Serine, and Threonine were the most frequently encoded, while Cysteine, Arginine, and Tryptophan had the lowest frequencies. The most used codons included CUA, AUA, AUU, and UCA, whereas CGU, CGG, CGC, and GCG were among the least frequently used (Fig. 3).

Transfer RNA and ribosomal RNA genes

The 22 transfer RNA (tRNA) genes in the mitogenomes ranged in length from 59 to 75 bp and exhibited a high A+T content (Table 3). Most tRNAs displayed the typical cloverleaf secondary structure (Fig. 4), with the exception of $tRNA^{Ser1}$, which lacked a DHU arm. The tRNA structures were largely conserved among the three *U. auropunctata* mitogenomes. However, one haplotype (MW401772) exhibited a unique point mutation in the $T_{\Psi}C$ arm of $tRNA^{Ser1}$. While $tRNA^{Asn}$ and $tRNA^{Met}$ were identical between *H. ichneumon* and *U. auropunctata*, the remaining tRNAs showed species-specific variations across different structural regions (Fig. 4). The ribosomal RNA genes, *12S rRNA* (959 bp in *H. ichneumon*; 956 bp in *U. auropunctata*) and *16S rRNA* (1,576 bp in *H. ichneumon*; 1,570 bp in *U. auropunctata*), were located between $tRNA^{Phe}$ and $tRNA^{Leu2}$, with $tRNA^{Val}$ positioned in between. These rRNA genes exhibited a relatively higher positive AT-skew compared to other regions of the mitogenomes (Table 3).

OL Region and *D–loop*

The origin of light-strand replication (O_L) in the *H. ichneumon* and *U. auropunctata* mitogenomes was located within the WANCY region, specifically between, $tRNA^{Asn}$ and $tRNA^{Cys}$, and measured 37 bp in length (Table 2). Both species exhibited a conserved stem–loop structure within the O_L region, characterized by the motif 5′–CTTCT–3′. The control region (*D-loop*) was situated between $tRNA^{Pro}$ and $tRNA^{Phe}$ and displayed relatively higher G+C content compared to the rest of the mitogenome (Table 3). The *D-loop* measured 1,318 bp in *U. auropunctata* and 1,204 bp in *H. ichneumon* (Table 2). Tandem repeat motifs within the *D-loop* and their comparative patterns across Herpestidae representatives were presented in Fig. 5 and Table S3.

Phylogeny and divergence of Herpestidae

The BI (Fig. 6) and ML (Fig. S2) phylogenetic trees generated by using PCGs in this study exhibited consistent topologies, supporting a similar evolutionary framework for the Herpestidae. At the base of the phylogenetic trees, the

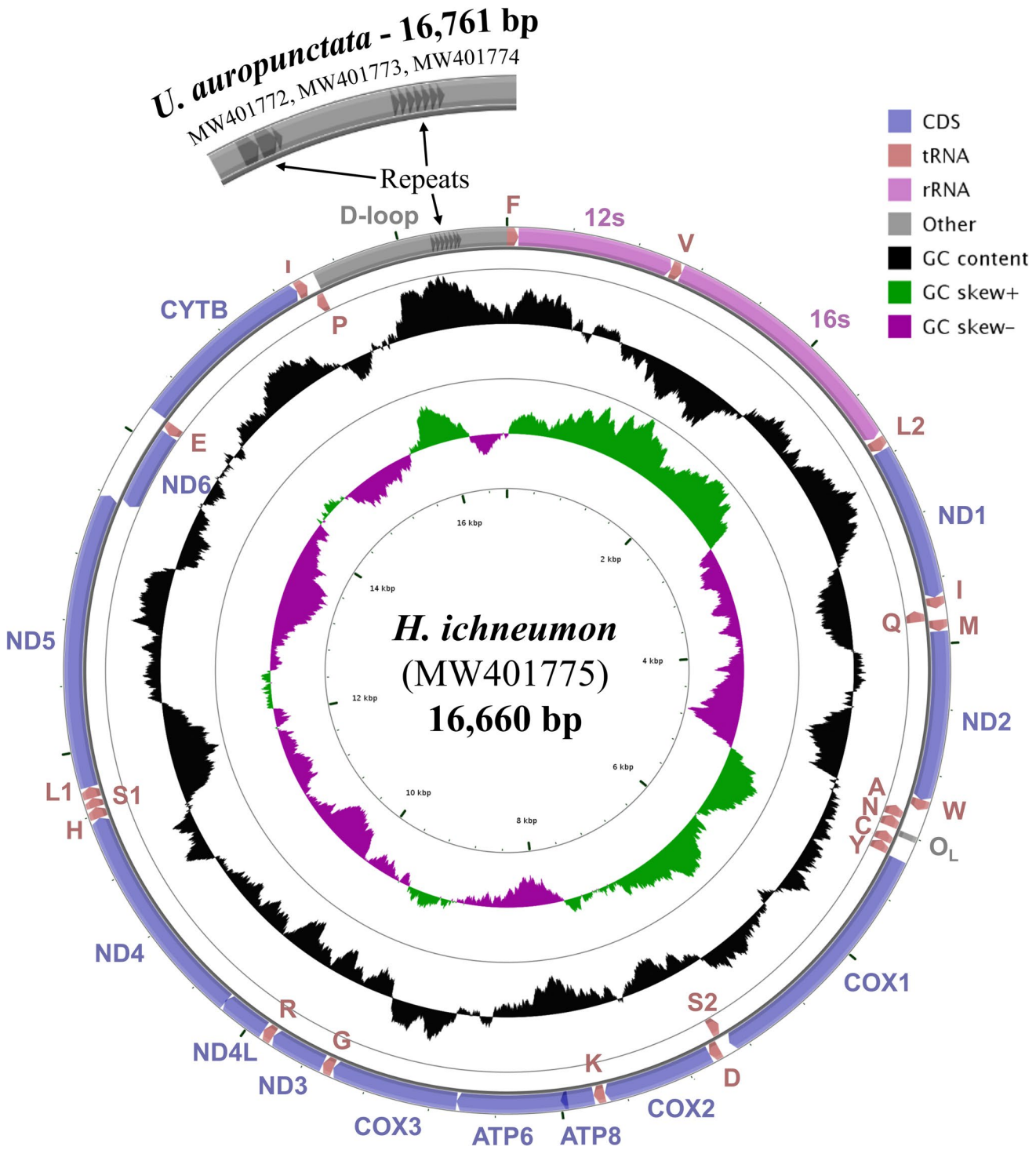

Fig. 1 Circular mitogenome structure of *H. ichneumon* (1 specimen) and *U. auropunctata* (3 specimens)

outgroup *Cuon alpinus* was positioned. Outside the Herpestidae clade, the Eupleridae occupied the most basal position in both phylogenetic trees. However, the relationships among the remaining Feliformia families differed between the BI and ML analyses, primarily due to the unstable placement of Viverridae. The Herpestidae was classified into two subfamilies: Herpestinae and Mungotinae (bootstrap support: 100%). Within the subfamily Herpestinae, two main clades were formed, Clade 1 (*Bdeogale, Rhynchogale, Cynictis, Ichneumia*, *Herpestes ichneumon*, and *Galerella*) and Clade 2 (*Urva, Atilax paludinosus*, and *Herpestes naso*), with the 100% bootstrap support. The genus *Urva* formed a

Table 2 Annotation and organizations of genes in mitogenomes of *H. ichneumon* and *U. auropunctata*

	Direction	*Start Position*		*End Position*		*Length (bp)*	*Intergenic Spacer*	*Initiation Codons*	*Terminal Codons*	*Anticodon*
	All	MW401772 MW401773 MW401774	MW401775	MW401772 MW401773 MW401774	MW401775	MW401772 MW401773 MW401774 ⟶ MW401775	MW401772 MW401773 MW401774 ⟶ MW401775	MW401772 MW401773 MW401774 ⟶ MW401775	All	All
tRNA-Phe	H	1	1	70	70	70	0			GAA
12S rRNA	H	71	71	1026	1029	956/959	0			
tRNA-Val	H	1027	1030	1094	1097	68	0			TAC
16S rRNA	H	1095	1098	2664	2673	1570/1576	+7/+8			
tRNA-Leu2	H	2672	2682	2746	2756	75	+2			TAA
ND1	H	2749	2759	3705	3715	957	−1	ATG	TAA	
tRNA-Ile	H	3705	3715	3773	3783	69	−3			GAT
tRNA-Gln	L	3771	3781	3843	3853	73	+1			TTG
tRNA-Met	H	3845	3855	3913	3923	69	0			CAT
ND2	H	3914	3924	4957	4967	1044	−2	ATT/ATC	TAG	
tRNA-Trp	H	4956	4966	5023	5033	68	+11/+13			TCA
tRNA-Ala	L	5035	5047	5103	5115	69	+1			TGC
tRNA-Asn	L	5105	5117	5177	5189	73	0			GTT
O_L	H	5178	5190	5214	5226	37	−3			
tRNA-Cys	L	5212	5224	5278	5290	67	0			GCA
tRNA-Tyr	L	5279	5291	5345	5357	67	1			GTA
COX1	H	5347	5359	6891	6903	1545	−3	ATG	TAA	
tRNA-Ser2	L	6889	6901	6957	6969	69	+6			TGA
tRNA-Asp	H	6964	6976	7030	7043	67/68	0			GTC
COX2	H	7031	7044	7714	7727	684	+3	ATG	TAA	
tRNA-Lys	H	7718	7731	7784	7797	67	+1			TTT
ATP8	H	7786	7799	7989	8002	204	−43	ATG	TAA	
ATP6	H	7947	7960	8627	8640	681	−1	ATG	TAA	
COX3	H	8627	8640	9410	9423	784	0	ATG	T–	
tRNA-Gly	H	9411	9424	9479	9492	69	0			TCC
ND3	H	9480	9493	9825	9838	346	+1	ATA	T–	
tRNA-Arg	H	9827	9840	9895	9908	69	0			TCG
ND4L	H	9896	9909	10192	10205	297	−7	ATG	TAA	
ND4	H	10186	10199	11563	11576	1378	0	ATG	T–	
tRNA-His	H	11564	11577	11633	11646	70	0			GTG
tRNA-Ser1	H	11634	11647	11692	11705	59	0			GCT
tRNA-Leu1	H	11693	11706	11762	11775	70	0			TAG
ND5	H	11763	11776	13583	13596	1821	−17	ATA/ATT	TAA	
ND6	L	13567	13580	14094	14107	528	0	ATG	TAA	
tRNA-Glu	L	14095	14108	14163	14176	69	+3			TTC
CYTB	H	14167	14180	15306	15319	1140	0	ATG	AGA	
tRNA-Thr	H	15307	15320	15376	15389	70	0			TGT
tRNA-Pro	L	15377	15390	15442	15455	66	+1			TGG
D-loop	H	15444	15457	16761	16660	1318/1204	0			

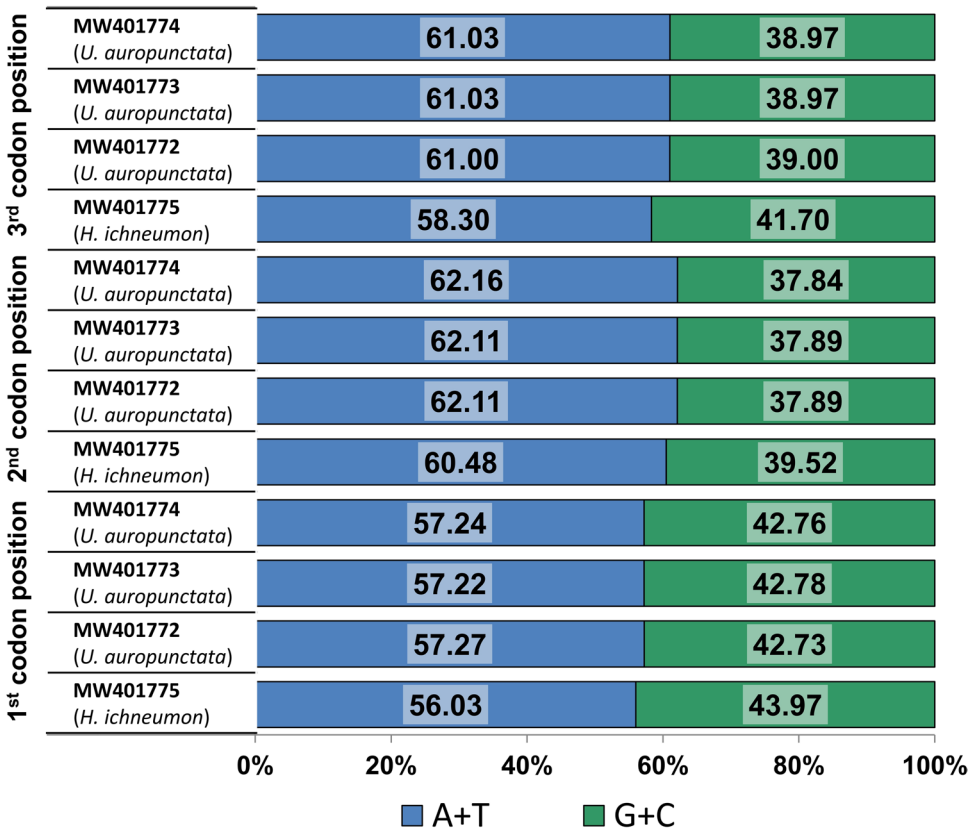

Fig. 2 A+T and G+C contents of PCGs in *H. ichneumon* and *U. auropunctata* mitogenomes

Table 3 Nucleotide composition of *H. ichneumon* and *U. auropunctata* mitogenomes

		Size	A (%)	C (%)	G (%)	T (%)	A+T%	G+C%	AT Skew	GC Skew	Total %
Whole genome	**MW401775**	16,660	33.09	27.65	13.95	25.31	58.40	41.60	0.133	−0.329	
	MW401772	***16761***	***33.32***	***26.06***	***13.72***	***26.91***	***60.22***	***39.78***	***0.106***	***−0.310***	
	MW401773	***16761***	***33.32***	***26.06***	***13.72***	***26.91***	***60.22***	***39.78***	***0.106***	***−0.310***	
	MW401774	***16761***	***33.32***	26.04	***13.72***	26.93	60.25	39.75	***0.106***	***−0.310***	
PCGs	**MW401775**	***11409***	32.47	29.13	12.60	25.80	58.27	41.73	0.114	−0.396	68.48
	MW401772	***11409***	32.53	***27.37***	12.50	***27.60***	60.13	39.87	***0.082***	***−0.373***	***68.07***
	MW401773	***11409***	32.52	***27.37***	12.51	***27.60***	60.12	39.88	***0.082***	***−0.373***	***68.07***
	MW401774	***11409***	32.54	27.36	12.49	27.61	60.15	39.85	***0.082***	***−0.373***	***68.07***
rRNA genes	**MW401775**	2535	36.53	23.91	17.95	21.62	58.15	41.85	0.256	−0.142	15.22
	MW401772	***2526***	***37.17***	***23.04***	***17.42***	***22.37***	***59.54***	***40.46***	***0.249***	***−0.139***	***15.07***
	MW401773	***2526***	***37.17***	***23.04***	***17.42***	***22.37***	***59.54***	***40.46***	***0.249***	***−0.139***	***15.07***
	MW401774	***2526***	***37.17***	23.00	***17.42***	22.41	59.58	40.42	0.248	−0.138	***15.07***
tRNA genes	**MW401775**	1514	34.87	21.53	15.65	27.94	62.81	37.19	0.110	−0.158	9.09
	MW401772	***1513***	***35.03***	20.75	***15.40***	28.82	63.85	36.15	0.097	−0.148	***9.03***
	MW401773	***1513***	***35.03***	***20.69***	***15.40***	***28.88***	***63.91***	***36.09***	***0.096***	***−0.147***	***9.03***
	MW401774	***1513***	***35.03***	***20.69***	***15.40***	***28.88***	***63.91***	***36.09***	***0.096***	***−0.147***	***9.03***
D-loop	**MW401775**	1204	30.15	28.99	15.37	25.50	55.65	44.35	0.084	−0.307	7.23
	MW401772	***1318***	31.26	26.33	14.57	27.85	***59.10***	***40.90***	0.058	−0.288	***7.86***
	MW401773	***1318***	31.34	26.40	14.49	27.77	***59.10***	***40.90***	0.060	−0.291	***7.86***
	MW401774	***1318***	31.18	26.25	14.64	27.92	***59.10***	***40.90***	0.055	−0.284	***7.86***

monophyletic clade and was sister to the clade comprising *Atilax paludinosus* and *Herpestes naso* (=*Xenogale naso*) (bootstrap support: 94%). The *U. auropunctata* mitogenomes clustered with those of three other *Urva* species: *U. javanica* (MW257214), *U. brachyura* (KY117547), and *U. semitorquata* (MH464789). *Urva auropunctata* was identified as the sister species to *Urva javanica* from Thailand, followed by a clade consisting of *U. brachyura* and *U. semitorquata* (for all, bootstrap support: 100%). The Iraqi mitogenomes of *U. auropunctata* clustered with the

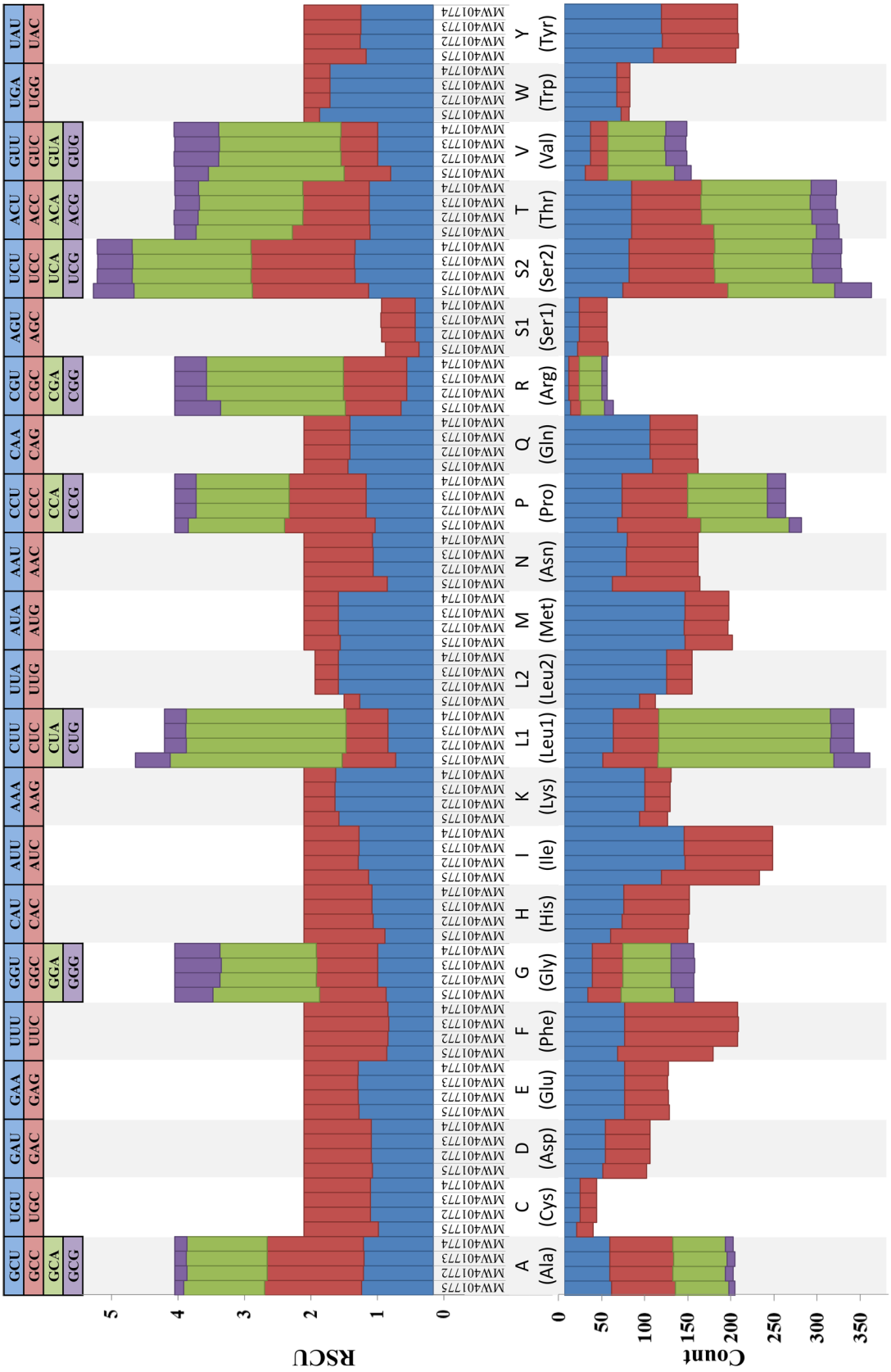

Fig. 3 RSCU and codon usage counts of *H. ichneumon* and *U. auropunctata* mitogenomes

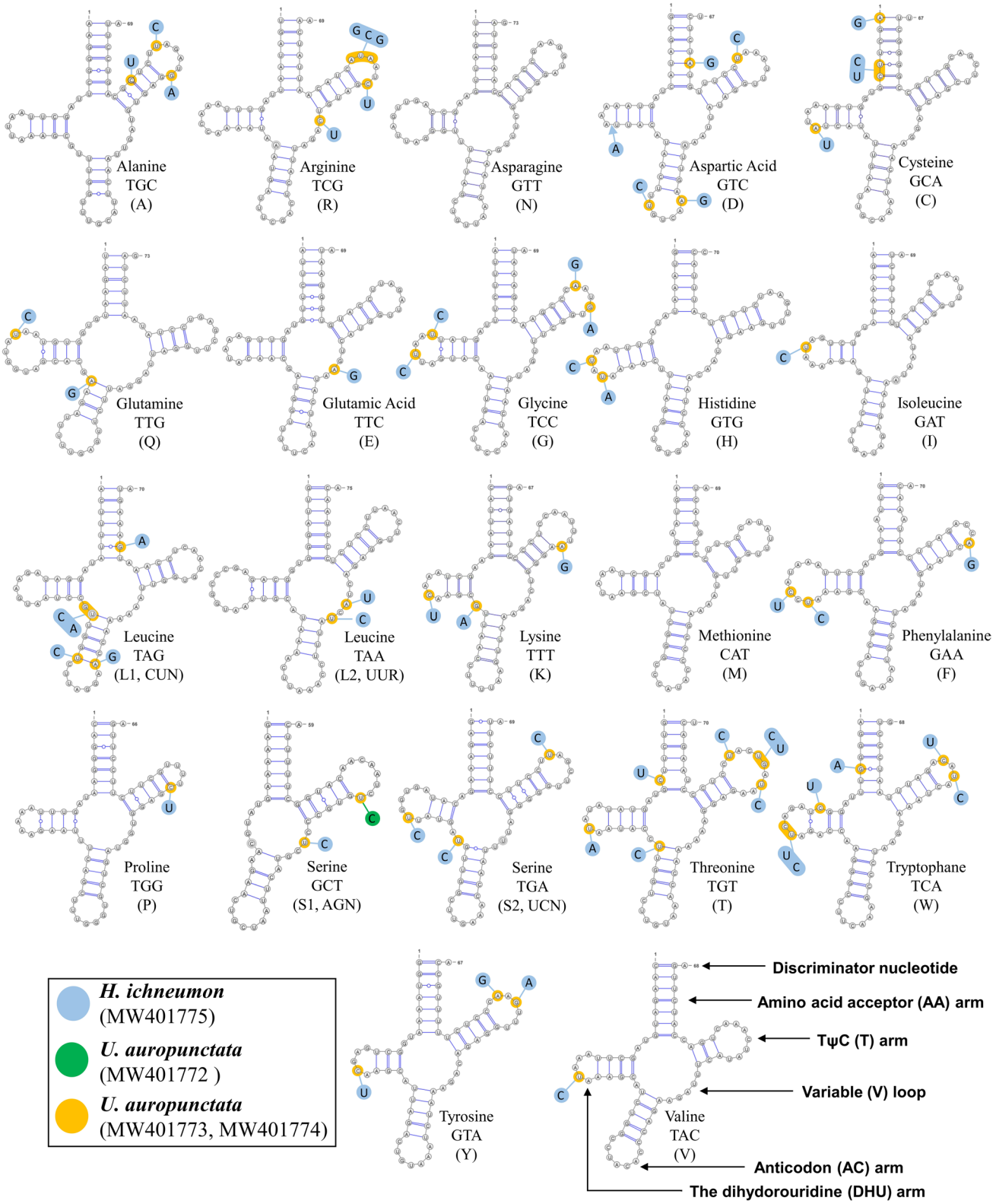

Fig. 4 Secondary structure prediction for tRNAs in the mitogenomes of *U. auropunctata* and *H. ichneumon*. Baseline structures represented the consensus structure for *U. auropunctata* while green nucleotides indicated the variation for MW401772 (*U. auropunctata*), and blue nucleotides indicate the variations for *H. ichneumon* (MW401775) sequences

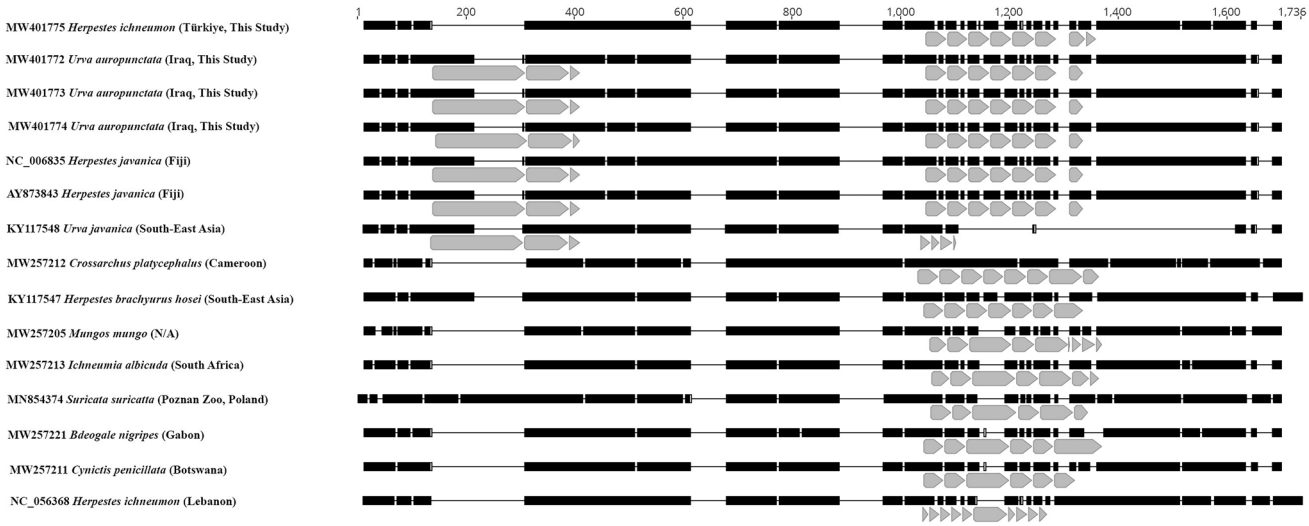

Fig. 5 A comparative map showing the location of Tandem repeats in the *D-loop* region of the mitogenomes of *H. ichneumon*, *U. auropunctata* and other Herpestidae species

Japanese (LC642815) and Fijian mitogenome labeled as *U. javanica* (=*Herpestes javanicus*, AY873843) (bootstrap support: 100%). The genus *Herpestes* was grouped with the genus *Galerella* in the phylogenetic tree (bootstrap support: 100%). *Herpestes ichneumon* was distinct from the *Urva* species and formed a sister relationship with *Galerella sanguinea* (bootstrap support: 100%), followed by the clade with the 100% bootstrap support (*Bdeogale nigripes*, *Rhynchogale melleri*, *Cynictis penicillata*, *Ichneumia albicauda*). The Turkish mitogenome of *H. ichneumon* from this study clustered closely with the Lebanese mitogenome (MW019668) of the same species (bootstrap support: 100%).

In the ML (Fig. 7) and BI (Fig. S3) phylogenetic trees based on the *CYTB* dataset *H. ichneumon* was closely related to species of the genus *Galerella* (bootstrap support: 64%, BPP: 0.97), while *U. auropunctata* clustered closely with two other *Urva* species: *U. edwardsii* and *U. javanica* (bootstrap support: 99%, BPP: 1). Several *CYTB* sequences originally labeled as *U. javanica* -from Bangladesh, Fiji, Guyana, Japan, Madagascar, Myanmar, Pakistan, and unknown localities- were considered to belong to *U. auropunctata*. The clade consisting of "*Urva javanica* (from China, Hong Kong, Java, Thailand, and unknown localities)" and "*Urva edwardsii* (from Bahrain, Bangladesh, Iran, and the UAE)" was grouped together with *U. auropunctata*. Notably, the Iraqi sequences (MW401772, MW401773, and MW401774) and the Pakistani sequences (DQ519071 and DQ519068) of *U. auropunctata* formed a well-supported clade (bootstrap supports: 73%, BPP: 0.99). *Herpestes ichneumon* clade was divided into three main haplogroups: Haplogroup 1 included sequences from South Africa, Haplogroup 2 comprised sequences from Iberia and Spain, and Haplogroup 3 contained sequences from Lebanon and Türkiye. According to the ML phylogenetic tree, Haplogroups 1 and 2 formed a sister group (bootstrap support: 55%), with Haplogroup 3 occupying the most basal position (bootstrap support: 100%). Conversely, in the BI tree, Haplogroup 1 was outside (BPP: 0.88), while Haplogroups 2 and 3 were inferred to be more closely related (BPP: 1).

Evolutionary dating analyses based on the mitogenome dataset indicated that divergence events within the Herpestidae began approximately 19.87 Mya (95% HPD: 12.28–26.95 Mya; BPP: 1) during the Early Miocene, marked by the split between the subfamilies Herpestinae and Mungotinae (Fig. 6). Evolutionary differentiation within the subfamily Mungotinae began approximately 17.83 Mya (95% HPD: 11.07–24.33 Mya; BPP: 1), while divergence within Herpestinae commenced around 14.55 Mya (95% HPD: 8.98–19.74 Mya; BPP: 1). The clade, comprising *Ichneumia*, *Cynictis*, *Rhynchogale*, *Bdeogale*, *Galerella*, and *Herpestes ichneumon*, began diverging around 13.32 Mya (95% HPD: 8.4–18.29 Mya; BPP: 1). The Clade 2, consisting of *Urva*, *Atilax* and *Herpestes naso*, began to diverge approximately 13.89 Mya (95% HPD: 8.65–18.9 Mya; BPP: 1). The divergence between *Urva* and the *Atilax*+*Herpestes naso* clade was dated to approximately 13.89 Mya (95% HPD: 8.65–18.9 Mya; BPP: 1). *Atilax* diverged from *Herpestes naso* approximately 9.8 Mya (95% HPD: 6.19–13.55 Mya; BPP: 1). The Iraqi population of *U. auropunctata* diverged from the clade containing the Japanese and Fijian populations approximately 600 kilo years ago (Kya) (95%HPD: 037–0.86 Kya, BPP: 1). Meanwhile, the Turkish and Lebanese populations of *H. ichneumon* began to diverge around 150 Kya (95%HPD: 0.08–0.25 Kya).

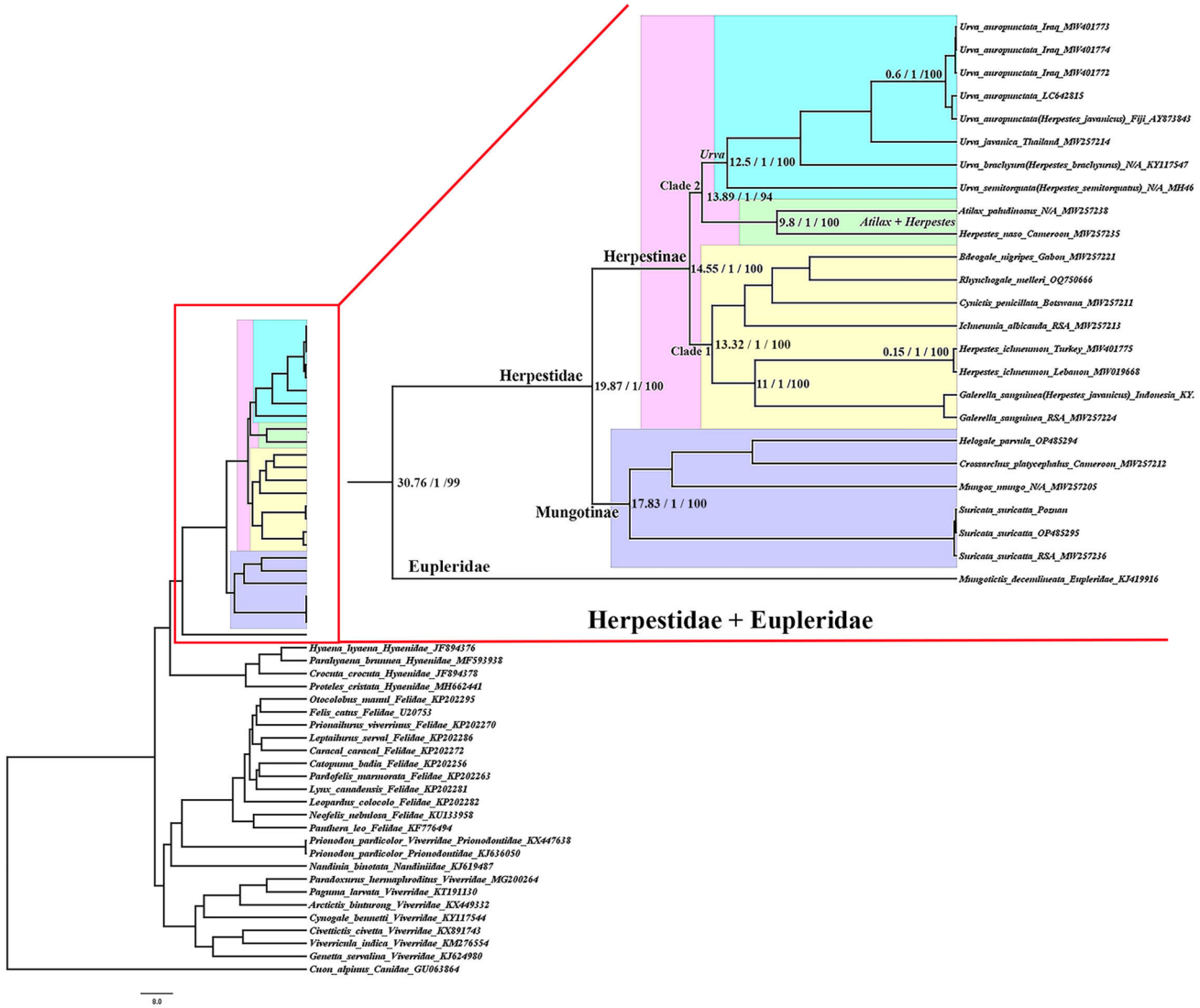

Fig. 6 BI phylogenetic tree and divergence dating results based on the complete mitogenome sequences. Numbers at the nodes from left to the right represent estimated divergence times, Bayesian posterior probabilities (BPPs), and bootstrap support values from ML analysis, respectively, for the major clades. For detailed explanations of the main nodes, please refer to the main text

The mean K–2P genetic distance based on the PCGs between the Iraqi mitogenomes (MW401772, MW401773, and MW401774) and the Fijian mitogenome (AY873843) of *U. auropunctata* was 0.68%, while the distance to the Japanese mitogenome was 0.63%. The genetic distance between the Turkish (MW401775) and Lebanese (MW019668) mitogenomes of *H. ichneumon* was approximately 1.66%. On the other hand, based on the *CYTB* sequences, the mean K–2P genetic distance between the Turkish specimen of *H. ichneumon* (MW401775) and the Iberian specimens (AF511059, EF689049, EF689050, EF689052, and EF689051) was 1.1%. In contrast, the mean K–2P genetic distance between the Turkish specimen and the South African specimen (AF522337) was 2.1%.

Discussion

Mitogenome structure and organization of both species

The complete mitochondrial genomes of the Egyptian mongoose (*H. ichneumon*) from Türkiye and the small Indian mongoose (*U. auropunctata*) from Iraq were characterized in the current study to compare them with available mitogenomes of other mongoose species and to contribute to understanding the phylogenetic relationships of the Turkish and Iraqi mongooses within the Herpestidae. The mitogenome of *Herpestes ichneumon* from Türkiye was 16,660 bp in length, while the mitogenome of *Urva auropunctata* from Iraq was 16,761 bp. The length of the mitogenome

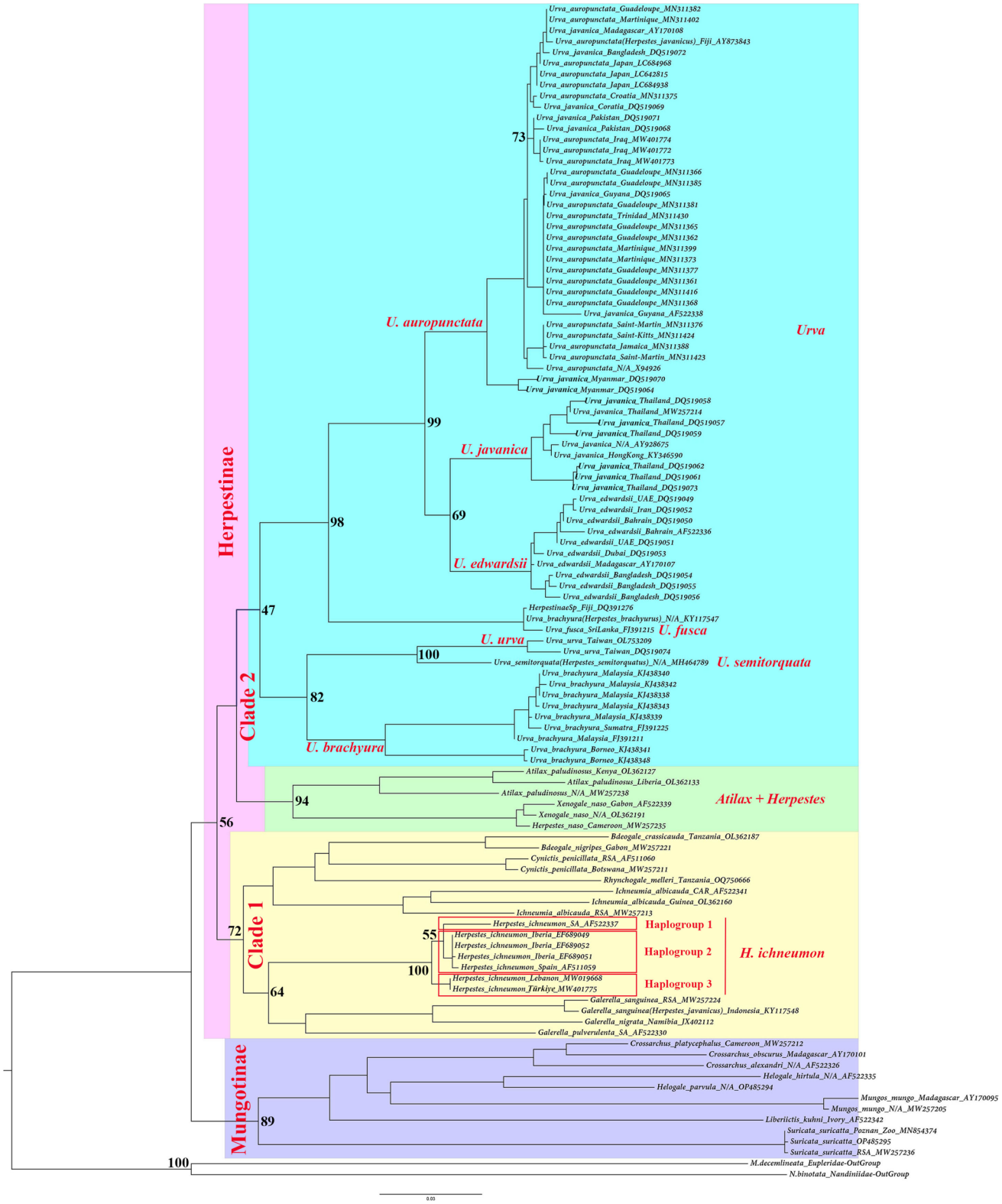

Fig. 7 ML phylogenetic tree of the Herpestidae reconstructed using the HKY+G+I substitution model based on the *CYTB* dataset. For detailed explanations of the main nodes, please refer to the main text

can vary, frequently due to differences in the number of repeated motifs in the control region (Krettek et al. 1995). The control region, or *D-loop* region, is a non-coding region that regulates the replication and transcription processes of the mitogenome (Lee et al. 1995). It can contain nucleotide repeats, which offer insights into intraspecific genetic differentiation (Xie et al. 2006). The *D-loop* region varies in length across many mammalian species (Sbisà et al. 1997; Pumo et al. 1998) and has a higher A+T content compared to G+C (Sbisà et al. 1997). The *D-loop* region of *U. auropunctata* and *H. ichneumon* was 1,318 bp and 1,204 bp in length, respectively. In the present study, the *D-loop* region was located between $tRNA^{Pro}$ and $tRNA^{Phe}$, and its G+C content was relatively higher than that of other regions in the mitogenomes. When compared to the tandem repeats in mitogenomes across the Herpestidae, the *U. auropunctata* from Iraq and *U. auropunctata* from Fiji (AY873843, labeled as *Herpestes javanicus* in GenBank) shared similar motifs and repeat structures (81 bp, 2.2 times, and 32 bp, 6.9 times). However, *H. ichneumon* from Türkiye exhibited only one motif (28 bp, 7.4 times). *Urva fusca* (KY117547, listed as *Herpestes brachyurus* in GenBank) shared a motif similar to that of *H. ichneumon* (MW401775), while *Suricata suricatta* (MN854374) had a similar motif, but with different length and repeat number (32 bp, 5.8 times). Therefore, the observed differences in mitogenome lengths are thought to result from variations in the number of repeated motifs within the *D-loop* regions of both species.

Like other species in the Herpestidae and many mammalian mitogenomes, the mitogenomes studied here exhibited similar structure and organization (Boore 1999; Derežanin et al. 2020; Boukhdoud et al. 2021). The mammalian mitogenome can contain overlapping or intergenic spacers between protein-coding genes (Fernández-Silva et al. 2003). Additionally, protein-coding genes (PCGs) and adjacent tRNAs in the mammalian mitogenome may share a few nucleotides (Curole and Kocher 1999). Consistent with these structural features of the mammalian mitogenome, the mitogenomes of *H. ichneumon* and *U. auropunctata* included nine overlapping regions and 11 intergenic spacers between genes. Moreover, *ND2* and *COX1* genes in the mitogenomes of *H. ichneumon* and *U. auropunctata* also shared a few nucleotides with the adjacent tRNAs. The mitogenome of *U. auropunctata* from Fiji (AY873843), originally submitted to GenBank under the name *Herpestes javanicus* (Penny and McLenachan 2005, unpublished), along with the mitogenomes of the same species from Iraq analyzed in the present study (MW401772–MW401774), exhibited a nucleotide composition ranking of A>T>C>G. In contrast, the mitogenomes of *H. ichneumon* from Lebanon (MW019668; Boukhdoud et al. 2021) and Türkiye analyzed in the current study (MW401775) displayed a different ranking pattern of A>C>T>G. Additionally, the mitogenomes of *H. ichneumon* and *U. auropunctata* characterized in this study showed a high A+T content (Table 3), consistent with the mitochondrial genome structure observed in other members of the Herpestidae (Hassanin et al. 2021). Compared to G+C content, the 1st, 2nd, and 3rd codon positions of the *H. ichneumon* PCGs were rich in A+T content, although this was relatively lower than that observed in *U. auropunctata* (Fig. 2). This pattern is a characteristic feature of vertebrate mitogenomes (Mayfield and McKenna 1978). Moreover, the negative G/C skew and positive A/T skew observed in the mitogenomes (Table 3) -resulting from asymmetrical directional mutational pressure (Perna and Kocher 1995; Reyes et al. 1998; Hassanin et al. 2005)- can serve as useful indicators for understanding the evolutionary dynamics of the mitogenome (Meganathan et al. 2012).

The total length of the PCGs in the mitogenomes of both species, as well as their proportion relative to the entire mitogenome, were consistent with those observed in typical mammalian mitogenomes (Krettek et al. 1995; Kim et al. 2017; İbiş et al. 2020; Şeker 2024). The observation that 10 of the 13 protein-coding genes in both species begin with the codons ATG or ATA reflects a common characteristic of mammalian mitogenomes (Xiufeng and Árnason 1994). On the other hand, the start codons for the *ND2* and *ND5* genes differed between the two species. In the *H. ichneumon* mitogenome, they were identified as ATC and ATT, while in the *U. auropunctata* mitogenome, they were ATT and ATA, respectively. The *COX3*, *ND3*, and *ND4* genes in the mitogenomes of both species were found to terminate with an incomplete stop codon (T–), a pattern consistent with the occurrence of truncated stop codons in mitochondrial protein-coding genes of other mammalian species (Ojala et al. 1981; Gissi et al. 1998; Zhong et al. 2010; Jiang et al. 2012; Hassanin et al. 2015; Yue et al. 2015). Furthermore, this structural feature supports the hypothesis that selective pressure may have favored the use of incomplete stop codons as a mechanism to reduce mitogenome size (Rand 1993). Unlike the other two mitogenomes, one *U. auropunctata* mitogenome (MW401772) exhibited a unique single mutation in the $T_{\Psi}C$ arm of $tRNA^{Ser1}$. The $tRNA^{Asn}$ and $tRNA^{Met}$ sequences of *H. ichneumon* were identical to those of *U. auropunctata*, whereas the remaining tRNAs showed species-specific variations across different regions (Fig. 4). In both species, the *12S rRNA* and *16S rRNA* genes were similar in length and occupied the same positions within the mitogenome. Additionally, these two genes exhibited higher positive AT-skew values compared to other regions of the mitogenome. The origin of light-strand replication (O_L) and the *D-loop* (control region) are essential elements of the mitogenome, playing key roles in its maintenance and replication (Annex and Williams 1990). As observed in many

vertebrates, the O_L region in the mitogenomes of *H. ichneumon* and *U. auropunctata* was located between $tRNA^{Asn}$ and $tRNA^{Cys}$ within the WANCY region and measured 37 bp in length (Table 2). While the O_L region typically begins with the 5′–GCCGG–3′ motif in many vertebrates (Zardoya et al. 1995), variations in this sequence have been reported (Ding et al. 2016). In the present study, the O_L region of both *H. ichneumon* and *U. auropunctata* mitogenomes displayed a conserved stem–loop motif of 5′–CTTCT–3′.

Phylogeny and divergence dating

Building on the results of previous molecular studies of the Herpestidae, the maximum likelihood (ML) and Bayesian inference (BI) phylogenetic analyses conducted in this study -using newly obtained complete mitochondrial genome sequences along with *CYTB* sequences from two mongoose species (*H. ichneumon* and *U. auropunctata*) found in Türkiye and Iraq- have contributed to a deeper understanding of Herpestidae phylogeny and reinforced earlier findings.

In both Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic trees constructed from complete mitochondrial genome sequences, the Iraqi *Urva auropunctata* mitogenomes clustered with those from Japan and Fiji. The mean Kimura 2-Parameter (K2P) genetic distances between the Iraqi sequences (MW401772, MW401773, MW401774) and the Japanese (LC642815) and Fijian (AY873843) sequences were 0.63% and 0.68%, respectively, indicating low intraspecific divergence and supporting their placement within a single species clade. These low divergence values are consistent with limited genetic differentiation, likely due to recent anthropogenic introductions of *U. auropunctata* to Japan and Fiji during the late 19th to early 20th centuries (Louppe et al. 2021). The Fijian mitogenome (AY873843), previously misidentified as *H. javanica*, is now classified as *U. auropunctata*, a species native to regions extending from the Arabian Peninsula to Southeast Asia and the northern Indian subcontinent (Gilchrist et al. 2009; Jennings and Veron 2011). *Urva auropunctata* has been introduced to several non-native regions, including the Caribbean Islands, Croatia, Fiji, Guyana, and Japan (Veron et al. 2006). Populations in the Caribbean and Fiji are believed to originate from India (Gorman 1975; Tvrtković and Kryštufek 1990), while the Japanese population likely derives from Bangladesh (Simberloff et al. 2000). The current findings are congruent with previous biogeographic and phylogenetic studies of the species (Gorman 1975; Tvrtković and Kryštufek 1990; Simberloff et al. 2000; Veron et al. 2006; Gilchrist et al. 2009; Jennings and Veron 2011).

Consistent with the topologies inferred from complete mitochondrial genome data, ML and BI phylogenetic analyses based on *CYTB* sequences also support a close relationship between *U. auropunctata* and the congeneric species *U. edwardsii* and *U. javanica*. *CYTB* sequences retrieved from GenBank and initially labeled as *U. javanica* from Bangladesh, Fiji, Guyana, Japan, Madagascar, Myanmar, Pakistan, and an unspecified locality were analyzed under the revised identification of *U. auropunctata*. These sequences, along with others labeled as *U. javanica* from China, Hong Kong, Java, Thailand, and unknown localities, and *U. edwardsii* from Bahrain, Bangladesh, Iran, and the United Arab Emirates, formed a well-supported clade with *U. auropunctata*. In both ML and BI *CYTB* phylogenetic trees, the Iraqi (MW401772, MW401773, MW401774) and Pakistani (DQ519071, DQ519068; Veron et al. 2007) *U. auropunctata* sequences clustered together with strong statistical support (bootstrap value: 73%, BPP: 0.99). The mean K2P genetic distance between the Iraqi and Pakistani specimens was 0.28%, indicative of low intraspecific variation (Bradley and Baker 2001; Baker and Bradley 2006), likely attributable to the geographical proximity of the two regions.

The *H. ichneumon* mitogenome sequenced from the Turkish specimen in this study clustered closely with the Lebanese mitogenome (MW019668; Boukhdoud et al. 2021), and this close genetic relationship was supported by a low mean K2P genetic distance of 0.16% between the two sequences. Phylogenetic analyses based on *CYTB* sequences, conducted using both ML and BI methods, revealed three distinct haplogroups within *H. ichneumon*. This pattern is consistent with the genetic structuring previously reported by Gaubert et al. (2011), who analyzed partial *CYTB* and control region sequences. The observed genetic distances among *H. ichneumon* haplogroups further reflect their biogeographical structuring. The relatively low divergence between the Turkish (Haplogroup 3) and Iberian (Haplogroup 2) specimens (K2P: 1.1%) compared to the higher divergence with the South African specimens (Haplogroup 1) (K2P: 2.1%) suggests intraspecific variation and also closer historical connectivity between populations within the Mediterranean basin (Bradley and Baker 2001; Baker and Bradley 2006). This pattern aligns with the species' preference for Mediterranean and wetland habitats, which are continuous or ecologically similar between Türkiye and the Iberian Peninsula, facilitating gene flow (Delibes 1999). In contrast, the greater genetic distance to the South African population likely reflects long-term geographical isolation imposed by the separation of distinct biogeographical regions and climatic zones (Gaubert et al. 2011). Additionally, the Anatolian region represents a biogeographical crossroads between the Afro-Tropical and Palearctic realms, potentially acting as a natural barrier to eastward dispersal into the arid environments of Iraq and

Iran, which lack suitable habitats for *H. ichneumon* (Delibes 1999; Palomares 2013). Together, these ecological and biogeographical factors contribute to the observed genetic differentiation among haplogroups and explain the species' current distribution.

Molecular dating analysis based on whole mitogenome sequences suggested that Herpestidae diverged from its sister clade, Eupleridae, in the Early Oligocene, approximately 30.76 Mya, consistent with the previous estimate reported by Eizirik and Murphy (2009). Also, it was estimated that the adaptive radiation within Herpestidae began in the Early Miocene, approximately 19.87 Mya, marked by the divergence of the two subfamilies, Herpestinae and Mungotinae. This estimate closely aligns with the divergence time of 21.8 Mya reported by Patou et al. (2009) based on partial mitochondrial and nuclear genes sequences or their combinations. However, the divergence time estimate proposed in the present study predates the previously reported divergence time of approximately 11.8 Mya between *Mungos mungo* (Mungotinae) and *Herpestes javanicus* (Herpestinae) within Herpestidae, as reported by Koepfli et al. (2006). The discrepancy in divergence times may be attributed to the limited sampling of Herpestidae in the study by Koepfli et al. (2006). The divergences within Mungotinae and within Herpestidae were estimated to have begun approximately 17.83 and 14.55 Mya, corresponding to the Early and Middle Miocene, respectively. Aligning with these results, a previous study by Patou et al. (2009) revealed that both subfamilies began to diversify around the same time. Two clades within Herpestinae diverged almost simultaneously, one comprising *Galerella*, *H. ichneumon*, *Ichneumia*, *Cynictis*, *Rhynchogale*, and *Bdeogale*, and the other including *A. paludinosus*, *H. naso*, and *Urva*. These divergences occurred approximately 13.32 and 13.89 Mya during Middle Miocene, respectively. Turkish and Iraqi specimens of *H. ichneumon* are estimated to have diverged from each other around 150,000 years ago, a timeframe that aligns with the evolutionary divergence estimate for the Middle East clade of *H. ichneumon*, which includes the Turkish specimens, as determined by Gaubert et al. (2011). The genetic distance of 0.16% between the two specimens corresponds to the lower bound of the confidence interval for their estimated divergence time, assuming a mitochondrial DNA mutation rate of 2% per million years (Taberlet et al. 1998; Johns and Avise 1998). Also, *Urva* began to diversify approximately 12.5 Mya, during the Middle Miocene. The onset of diversification within *Urva* aligns with the evolutionary divergence timeline proposed by Patou et al. (2009). According to the results of the Bayesian Inference (BI) analysis in the present study, *U. semitorquata* was the first to diverge, approximately 12.5 million years ago, followed by *U. brachyura* around 8.52 million years ago. This is consistent with the diversification events among Asian mongooses that occurred during the Late Miocene period (11–8 million years ago), as identified by Patou et al. (2009). Subsequently, *U. javanica* and *U. auropunctata* diverged approximately 4.67 million years ago within *Urva*. These findings suggest that species-level divergence within *Urva* continued into the Late Pliocene, rather than concluding in the Late Miocene as previously suggested by Patou et al. (2009). The evolutionary divergence of *U. auropunctata* specimens from Iraq, Japan, and Fiji -dated to approximately 600 Kyr ago- was found to align closely with the lower bound of the confidence interval for the 0.63% and 0.68% genetic distance calculated using the K-2P model, assuming a mitochondrial DNA mutation rate of 2% per million years (Taberlet et al. 1998; Johns and Avise 1998).

Conclusion

The comprehensive phylogenetic and molecular dating analyses presented in this study not only reinforces the monophyly of *Urva* and the paraphyly of *Herpestes* but also provide new insights into the evolutionary history and divergence patterns within the Herpestidae. The phylogenetic placements of *H. ichneumon* and *U. auropunctata* were consistent with previous molecular studies, while the inclusion of newly sequenced mitogenomes from Türkiye and Iraq added valuable geographic and genetic resolution. The low intraspecific genetic distances observed among geographically proximate populations supported recent divergence events, whereas broader interspecific divergence timelines aligned with major Miocene diversification events. These findings highlighted the significance of complete mitochondrial genomes in resolving evolutionary relationships and underscore the role of geographic isolation, human-mediated dispersal, and historical biogeography in shaping the genetic structure of Herpestidae species. Future studies incorporating nuclear genomic data and broader sampling across the distribution range will be essential to further refine these evolutionary timelines and clarify species boundaries within these ecologically diverse carnivore species within Herpestidae.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-025-00822-0.

Acknowledgements We would like to thank the Proofreading & Editing Office of the Dean's of Research at Erciyes University for the proofreading service.

Author contributions BY, AYS, PSŞ, CT and Oİ contributed to the study conception and design. The sample collection was performed by AYS, AQN and HAMAA. Data collection, Investigation, Valida-

tion and Visualization were performed by BY, AYS, PSŞ, MB, ST, HAMAA, and Oİ. The draft of the manuscript was written by BY, AYS, PSŞ, CT, and Oİ, and all authors commented on previous versions of the manuscript. CT and Oİ supervised the study. All authors read and approved of the final manuscript and agree to be accountable for all aspects of the work.

Funding This study was supported by the Research Fund of Erciyes University (Project Nr: FBAÜ-2023–12262).

Data availability The mitogenomes sequences of two mongooses (*U. auropunctata* and *H. ichneumon*) from Iraq and Türkiye were deposited into NCBI's GenBank under the accession numbers MW401772, MW401773, MW401774 and MW401775.

Declarations

Ethical approval Research ethics committee approval was provided for the capture of the animals, permission No. E-21264211–288.04–10822834 from The Republic of Türkiye Ministry of Agriculture and Forestry, General Directorate of Nature Conservation and National Parks in regard to 23/061 numbered in conjunction with Erciyes University Local Ethics Committee for Animal Experiments.

Conflict of interest The authors declare no competing interests.

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