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Complete mitochondrial genomes support the composition and rank of the American weasel genus *Neogale* (Carnivora: Mustelidae)

Bruce D. Patterson[1*], Héctor E. Ramírez Chaves[2], André Elias Rodrigues Soares[3], Júlio F. Vilela[4*] and Felix Grewe[5]

[1]*Negaunee Integrative Research Center, Field Museum of Natural History, Chicago IL 60605, USA*
[2]*Department of Biological Sciences, University of Caldas, Manizales, Caldas, Colombia*
[3]*Department of Medical Biochemistry and Microbiology, National Bioinformatics Infrastructure Sweden, Science for Life Laboratory, Uppsala University, Uppsala, Sweden*
[4]*Núcleo de História Natural da UFPI, Campus Amílcar Ferreira Sobral, Universidade Federal do Piauí – UFPI BR343, Km 3,5 - Bairro Meladão, 64808-605, Floriano, PI, Brazil 4*
[5]*Grainger Bioinformatics Center, Field Museum of Natural History, Chicago IL 60605, USA*
[*]*Corresponding authors: bpatterson@fieldmuseum.org; vilela@ufpi.edu.br*

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Abstract

Evidence that the endemic South American weasels are members of an American weasel clade has rested on a single mitochondrial gene sequence, cyt-*b* (1140 base pairs). We sequenced complete mitochondrial genomes of *Neogale africana* and *N. felipei* and reanalyzed their relationships to other mustelines. Both *Neogale* Gray and *Mustela* Linnaeus were securely recovered as reciprocally monophyletic in maximum likelihood and Bayesian analyses. *Neogale africana* and *N. felipei* are sisters, joined sequentially by *N. vison* and then *N. frenata.* This topology differs from prior ones based solely on cyt-*b*, where the panamerican species *N. frenata* is sister to the South American endemics. This finding suggests a different biogeographic scenario for the genus and offers a contrasting view of their life-mode evolution.

Key words: Biogeography, classification, Carnivora, mitogenomes, phylogeny

Introduction

The family Mustelidae (weasels and their allies) is the largest and most ecologically diversified family of Carnivora (Law et al., 2018). Extant members of the family include 22 genera and 68 species (Mammal Diversity Database, 2025), which are arrayed in eight clades of subfamily rank (Koepfli et al., 2008; Law et al., 2018). The most speciose of these clades with 21 species is the Mustelinae ("weasels and stoats"), a group that is sister to the Lutrinae ("otters"; Koepfli et al., 2008; Yu et al., 2011). Until recently, all musteline species were usually allocated to the genus *Mustela* Linnaeus, 1758, with the sole exception being American mink, often recognized in the separate genus *Neovison* Baryshnikov and Abramov, 1997 (Abramov, 2000; Wozencraft, 2005).

Molecular phylogenetic investigations of Mustelinae using a variety of markers routinely recovered a basal clade consisting of the American mink and long-tailed weasel (Sato et al., 2004; Fulton and Strobeck, 2006; Koepfli et al., 2008). Analyses that also included the two weasel species endemic to South America indicated their membership in this basal group (Harding and Smith, 2009; Law et al., 2018). The earliest name for this American clade of weasels is *Neogale* Gray, 1865, which contains the four extant species *N. vison*, *N. frenata*, *N. felipei*, and *N. africana* (Patterson et al., 2021). Using a 46 gene dataset with 74 fossil priors for the superfamily

Musteloidea, Law and colleagues (2018) estimated a Late Miocene split of *Neogale* from *Mustela* (ca. 8.69 Ma) and the crown divergences of *Neogale* species during the Pliocene and Pleistocene.

Yet the membership of *N. africana* (Desmarest) and *N. felipei* (Izor and de la Torre) in *Neogale* rests on evidence from a single mitochondrial gene (cyt-b). Both the recently elevated *Neogale* and the reconstituted *Mustela* lack robust morphological diagnoses and are in need of revision (Patterson et al., 2021), which heightens the reliance of group classification on genetic evidence. We sought to expand genetic characterization of the group by isolating complete mitochondrial genomes of *N. africana* and *N. felipei* from museum specimens. Both species are poorly known and infrequently encountered, even in museums (Ramírez-Chaves et al., 2014; Ramírez-Chaves and Patterson, 2014).

Material and Methods

Sampling

Tissue samples of *Neogale africana* and *N. felipei* were collected from museum skin or skeleton vouchers at the Field Museum of Natural History, Chicago. The *N. africana* specimen (FMNH 106488) is a male from Brazil: Acre; Rio Jurua (-8.3537, -72.6225) collected by L. E. Hill and the *N. felipei* specimen (FMNH 86745) is a male from Colombia: Cauca; Popayán (2.45, -76.6) collected by K. von Sneidern, both collected in the mid-20th century. Our taxonomy follows that of the Mammal Diversity Database (2025).

DNA extraction and sequencing

For the historical samples DNA extraction was performed at a sterile laboratory according to the protocols previously established for ancient DNA work (Poinar and Cooper, 2000). The DNA extraction followed the protocol described in Dabney and Meyer (2019). This protocol uses a stable solution of proteinase K, SDS, and DTT to perform an initial lysis step, followed by a treatment with a strong chaotropic agent, guanidine hydrochloride, designed to maximize the recovery of shorter, damaged DNA fragments. The DNA was then purified with the use of a SPRI beads-based purification strategy (Thermo Fisher Scientific). Sequencing libraries were prepared following Meyer and Kircher (2010). Quality and concentration of all DNA and sequencing libraries were assessed using a Qubit® DNA Assay Kit on the Qubit® 3.0 Fluorometer (Life Technologies). All sequencing libraries were sequenced on an Illumina MiSeq machine at the Paleogenomics Laboratory, University of California, Santa Cruz.

Mitogenome assembly

Paired-end Illumina reads for each sample were merged using SeqPrep (https://github.com/jstjohn/SeqPrep). Standard parameters were used with SeqPrep with the exceptions that merged reads were set to have a minimum length of 10 bp (-l 10) and that within the overlapping alignment, only mismatches with a quality score higher than 20 were counted (-q 20). Merged reads were assembled with SPAdes v3.1.1 (Nurk et al., 2013) using default parameters. Mitogenome contigs were filtered and sorted using abacas (http://abacas.sourceforge.net/) with the *Mustela nigripes* mitogenome (NC_024942) as a query sequence file. The tab, gaps.tab, and fasta output files from abacas were merged into a single embl file by a custom script and imported into Geneious Prime v2025.0.3 (https://www.geneious.com) for further processing. In Geneious, gaps in the mitogenome sequences were manually removed when contig ends were overlapping (Supplementary Table 1). The remaining gaps were adjusted to sizes so that they aligned with the *Mustela nigripes* reference sequence. Raw reads were mapped back to the adjusted mitogenomes with Bowtie2 (Langmead and Salzberg, 2012) to verify closed gaps. In addition, minor sequence changes were made based on the read mapping information. Annotation features were propagated to the mitogenomes from *Mustela nigripes* using the Geneious annotation function by similarity.

Phylogenetic analyses

The mitogenome sequences were aligned with all complete RefSeq mitogenomes of *Mustela* (n= 10) and *Neogale* (n= 2) available on Genbank, as well as to *M. haidarum* (MK603009.1), *M. furo* (KT693383.1), and *M. richardsonii cicognanii* (MK603895.1), for which no RefSeq exists (Table 1). The complete mitochondrial genomes of several otters (*Hydrictis maculicollis* (NC_046485.1), *Lutra lutra* (NC_062277.1), *L. sumatrana* (NC_035810.1), and *Lontra canadensis* (NC_071788.1)) and ictonychines (*Galictis vittata* (NC_053973.1), *Ictonyx libycus* (NC_065092.1), *I. striatus* (NC_053979.1), and *Poecilogale albinucha* (NC_053975.1)) were used to assess the sisterhood of Mustelinae + Lutrinae and to root the phylogeny (cf. Law et al., 2018). Sequences were aligned using MAFFT v7.490 (Katoh et al., 2002; Katoh and Standley, 2013) with default parameter settings as implemented in Geneious. The alignments of the complete mitogenomes (excluding the divergent D-loop) and concatenated coding sequences (both nucleotides and amino acid translations) were used for phylogenetic reconstruction. Maximum likelihood (ML) trees were inferred with IQ-TREE v2.2.0 (Minh et al., 2020). For each dataset, the best-fit substitution model was selected using ModelFinder as implemented in IQ-TREE (Kalyaanamoorthy et al., 2017). ML trees were then inferred under the selected models. Support values were estimated with 1000 ultrafast bootstrap replicates using the fast bootstrapping option (Hoang et al., 2018).

Table 1: Taxa and reference samples used in this analysis; taxonomy follows Mammal Diversity Database (2025).

Species	Subfamily	Accession	Sequence Length (bp)	% GC
Galictis vittata	Ictonychinae	NC_053973.1	16495	40.80%
Ictonyx libycus	Ictonychinae	NC_065092.1	16549	39.50%
Ictonyx striatus	Ictonychinae	NC_053979.1	16541	40.30%
Poecilogale albinucha	Ictonychinae	NC_053975.1	16518	38.90%
Hydrictis maculicollis	Lutrinae	NC_046485.1	16308	41.30%
Lontra canadensis	Lutrinae	NC_071788.1	16500	42.80%
Lutra lutra	Lutrinae	NC_062277.1	16536	41.90%
Lutra sumatrana	Lutrinae	NC_035810.1	16586	41.70%
Mustela altaica	Mustelinae	NC_021751.1	16521	39.70%
Mustela erminea	Mustelinae	NC_025516.1	16471	39.90%
Mustela eversmannii	Mustelinae	NC_028013.1	16463	40.00%
Mustela haidarum	Mustelinae	MK603009.1	16007	39.80%
Mustela itatsi	Mustelinae	NC_034330.1	16027	39.50%
Mustela kathiah	Mustelinae	NC_023210.1	16552	38.90%
Mustela lutreola	Mustelinae	NC_056132.1	16504	39.90%
Mustela nigripes	Mustelinae	NC_024942.1	16556	39.90%
Mustela nivalis	Mustelinae	NC_020639.1	16512	40.00%
Mustela putorius	Mustelinae	NC_020638.1	16523	39.80%
Mustela furo	Mustelinae	KT693383.1	16525	39.80%
Mustela richardsonii cicognanii	Mustelinae	MK603895.1	16007	39.80%
Mustela sibirica	Mustelinae	NC_020637.1	16559	39.80%
Neogale africana	Mustelinae	FMNH 106488	16679	38.20%
Neogale felipei	Mustelinae	FMNH 86745	16405	39.30%
Neogale frenata	Mustelinae	NC_020640.1	16543	39.20%
Neogale vison	Mustelinae	NC_020641.1	16552	38.60%

To complement the ML analyses, we performed Bayesian inference (BI) phylogenetics using MrBayes v3.2.7a (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012). For nucleotide data sets, we used the GTR+G model (lset nst= 6 rates=gamma), and for the amino acid alignment, we used the JTT+G model (prset aamodelpr=fixed(jones); lset rates=gamma), reflecting the best-fit models selected by IQ-TREE. Each MrBayes analysis was run for 1,000,000 generations with four Markov chains (one cold, three hot), sampling every 500 generations from the posterior distribution, and the first 25% of all sampled trees were discarded as the burn-in. We ensured MCMC convergence using the average standard deviation of split frequencies (ASDSF) and the potential scale reduction factor (PSRF) in MrBayes. All runs achieved ASDSF = 0.000 and PSRF ~ 1.0, indicating convergence. Effective sample sizes (ESS) for all parameters exceeded 200. All alignment files and scripts used in this project are available at https://github.com/felixgrewe/mustela_mito. The mitogenomes of *N. africana* and *N. felipei* were uploaded to GenBank with the accession numbers PV658327 and PV658326, respectively.

Results

Genome assembly and annotation

Total DNA sequencing of *Neogale africana* and *N. felipei* on an Illumina MiSeq platform generated 4,506,890 and 2,676,068 forward and reverse sequences, respectively, with lengths ranging from 35 to 76 bp. By trimming and merging overlapping reads using SeqPrep, we obtained 3,511,589 reads for *N. africana* (lengths from 10 to 137 bp) and 2,526,301 reads for *N. felipei* (lengths from 13 to 137 bp). All reads were utilized for an assembly with SPAdes, yielding a whole genome assembly size of 1,170,458 bp, an average k-mer coverage of 2.83 (SD= 24.09), and a largest contig of 11,174 bp for *N. africana* (Supplementary Table 1). The assembly for *N. felipei* showed similar results, with a total size of 863,246 bp and a largest contig of 10,664 bp. However, its average k-mer coverage was 29.6 (SD= 180.61), indicating a more complete assembly than for *N. africana*. This improved assembly quality was also evident after running abacas to identify mitogenome contigs, resulting in 17 contigs (totaling 15,888 bp) for *N. africana* and three more complete contigs (totaling 16,477 bp) for *N. felipei*. Overlaps were identified before and after reads mapping to merge these contigs, leading to final mitogenome assembly sizes of 16,679 bp for *N. africana* and 16,405 bp for *N. felipei* (Fig. 1, Supplementary Table 2). Consequently, the assemblies of *N. africana* and *N. felipei* had 10 gaps and one unclosed gap, respectively. Annotations revealed no unexpected features, with the typical 13 protein-coding genes, two ribosomal RNA genes, 22 transfer RNA genes, and the canonical D-loop region all identified (Supplementary Table 3).

A. *Neogale africana* (FMNH 106488)

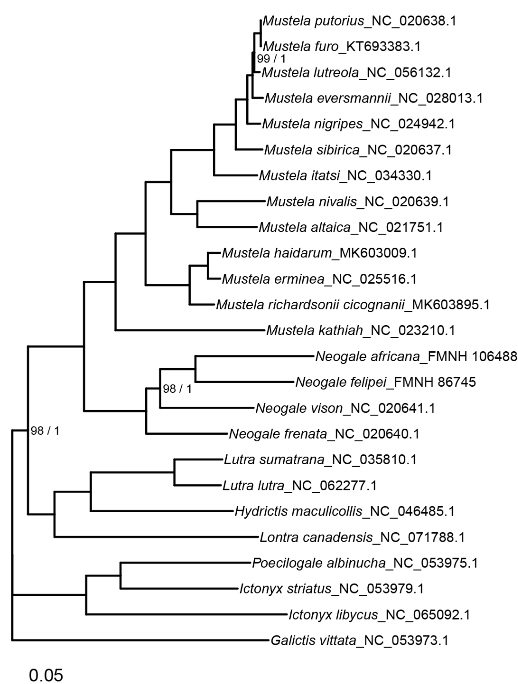
B. *Neogale felipei* (FMNH 86745)

Figure 1: Genome annotations, assembly continuity, and re-mapping of raw reads to the mitogenomes of (A) *Neogale africana* and (B) *Neogale felipei*. The mitogenomes are represented linearly, starting with the tRNA-Phe gene. The top row indicates a typical mammalian mitogenome gene content of 13 protein-coding genes (magenta), two ribosomal RNA genes (red), 22 transfer RNA genes (not shown), and the canonical D-loop region (yellow). The middle row highlights the individual contigs of the assembly in red. The lower row displays the merged reads mapped onto the assembled mitogenome (black).

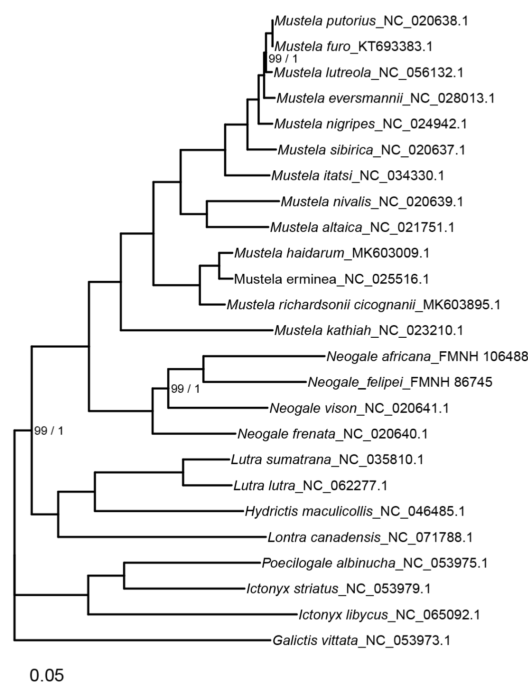
Mitogenome phylogenies

We used four datasets to examine the phylogenetic relationships of the sampled taxa: (1) nucleotide sequences of all coding sequences and rRNA genes, (2) nucleotide coding sequences excluding the rRNA genes, (3) complete mitogenomes excluding the D-loop region, and (4) amino acid sequences of all translated coding sequences. Each dataset was analyzed independently using IQ-TREE to infer ML phylogenies under best-fit models selected by ModelFinder, and with MrBayes for Bayesian analyses using approximate model equivalents (Supplementary Table 4). All resulting trees exhibited the same topology; all recovered both *Neogale* and *Mustela* as reciprocally monophyletic clades across all datasets and analyses (Fig. 2).

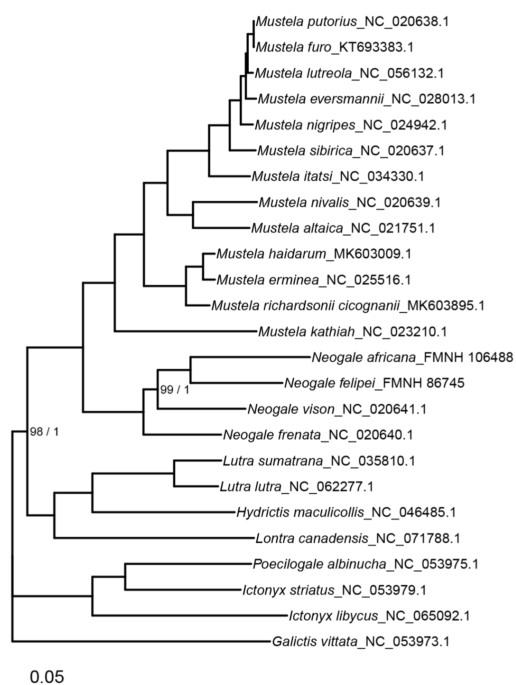
A. All coding sequences and rRNA genes



B. All coding sequences excluding rRNA genes



C. Complete mitogenomes excluding the D-loop



D. Amino acid sequences of translated coding sequences

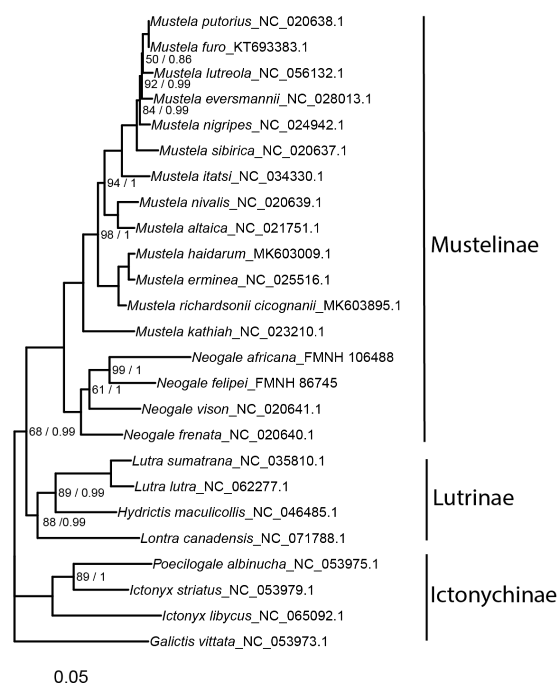


Figure 2: Phylogenetic relationships of the Mustelinae (*Mustela* and *Neogale*) based on mitogenome sequences. Maximum likelihood and Bayesian phylogenetic trees resulted in the same tree topology for all datasets, so only ML trees are shown. (A) nucleotide sequences of all coding sequences and rRNA genes, (B) nucleotide coding sequences excluding rRNA genes, (C) complete mitogenomes excluding the D-loop region, and (D) amino acid sequences of all translated coding sequences. Support values (ML bootstrap / Bayesian posterior probability) are shown for all informative nodes that lack 100/1.0 support.

These two clades together form a strongly supported clade constituting the subfamily Mustelinae. Sister to the Mustelinae is a well-supported clade of the four otter species, subfamily Lutrinae. Lacking an outgroup in our analysis, the basal subfamily Ictonychinae is recovered as paraphyletic, with *Ictonyx* and *Poecilogale* in one clade and *Galictis* in another, each clade appearing as sisters to Mustelinae + Lutrinae and each other. Phylogenetic relationships are strongly supported (BS > 70, pp > 0.99) across all trees and analyses, with three exceptions: in the ML tree based on amino acid sequences, the sister relationship between *N. vison* and *N. africana* + *N. felipei* and the sister relationship of Lutrinae and Mustelinae have bootstrap supports of only 61 and 68, respectively, while being strongly supported by the BI analyses. In addition, the sister relationship of *M. lutreola* to *M. putorius* + *M. furo* received only a 50 bootstrap and 0.86 posterior probability support.

Discussion

The two weasels endemic to South America (*N. africana* and *N. felipei*) were recovered as sisters, joined afterwards by *N. vison* and *N. frenata.* This group of four taxa was recovered in each of the ML and BI analyses on each of the data partitions and supports earlier phylogenetic studies based on cyt-*b* (Harding and Smith, 2009; Law et al., 2018). Harding and Smith (2009) first identified this group and proposed to call it *Vison* Gray, 1843, however the type species of that genus-group name, *Viverra lutreola* Linnaeus (= *Mustela lutreola*), is not a member of the group. In a 46-gene analysis using 74 fossil priors, Law et al. (2018) also recovered that grouping and dated its divergence from *Mustela sensu stricto* in the Late Miocene (~8.7 Ma). Although that divergence time predates the appearance of many other recognized mustelid genera including various otter genera, Law et al. (2018) retained all weasels in the genus *Mustela*, as did Burgin et al. (2020). Hassanin et al. (2021) used mitogenomes to analyze the evolutionary relationships of carnivorans; despite lacking mitogenomes for *N. felipei* and *N. africana*, they accepted the generic distinction of the group and argued that its name should be *Grammogale* Cabrera, 1940. Previously, we showed that the earliest name available for this group is *Neogale* Gray, 1864, *neo-* having been chosen by Gray to signal the American ("New World") membership of this group (Patterson et al., 2021).

The sisterhood of *Neogale felipei* and *N. africana* that is evident in the mitogenomes mirrors other evidence identified by Izor and de la Torre (1978): extensive interdigital webbing, ventral pelage markings, riparian distributions, and a remarkably different form of the baculum or penis bone. Their bacula possess a trifid distal tip, with the medial and right lateral processes joined by a thin, translucent layer of bone in *N. africana* (Izor and de la Torre, 1978; Izor and Peterson, 1985).

Prior phylogenetic studies of *Neogale* using cyt-*b* recovered a monophyletic *Neogale* as sister to *M. strigidorsa* + *M. nudipes* (Harding and Smith 2009), so that *Mustela* is rendered paraphyletic. In addition, cyt-*b* sequences identify *N. frenata* as the sister of *N. africana* + *N. felipei* (Harding and Smith, 2009; Law et al., 2018). The geographic ranges of *Neogale* taxa in boreal North America (*N. vison*), North, Central and South America (*N. frenata*), Andean South America (*N. felipei*) and Amazonian South America (*N. africana*) suggested a history of speciation resulting from successive southward colonization (Harding and Smith, 2009). However, all permutations of our analyses with mitogenomes (Fig. 2)—ML and Bayesian analyses on all four data partitions—recover reciprocal monophyly of *Mustela* and *Neogale* and suggest an alternative topology for *Neogale*, where *N. vison,* not *N. frenata*, is recovered as sister to the South American endemics. The more weakly supported ML tree based on animo acids (Fig. 2D) likely just reflects the smaller dataset on which it is based.

In keeping with relationships shown by the mitogenome phylogeny, *N. vison*, *N. africana*, and *N. felipei* all show external adaptations to semi-aquatic habits and highly derived genitalia. On the other hand, *N. frenata* is more plesiomorphic in terms of life mode, body form (see Krupa and Everson, 2025), and bacular morphology; like *Mustela* species, the tip of its baculum resembles a hockey stick, not a trident. Bacular differences between *N. frenata* and the South American endemics were sufficiently great that Izor and de la Torre (1978) placed them in different subgenera before genetic data were available to unite them.

Mitogenomes confirm the integrity of *Neogale* and *Mustela* as monophyletic groups, and their early divergence in comparison with other mustelid taxa supports their recognition as genera. Shared ecological habits responsible for morphological convergence of members in each group (Law et al., 2018; Law et al., 2019)—such as the generalists *Neogale frenata* and *Mustela richardsonii* or the semi-aquatic minks, *N. vison* and *M. lutreola*—have long complicated efforts to diagnose these groups using morphology. Both *Neogale* and *Mustela* need thorough revisions and morphological diagnoses that will enable a clearer understanding of their evolutionary histories and the forces that have shaped them.

Our mitogenome analyses also support a phylogenetic pattern first noted by Koepfli et al. (2008). The earliest diverging branch in each of the subfamilies analyzed (Fig. 2) separates New World taxa from their Old World relatives, indicating the early colonization of the Americas by each via Beringia. In the case of Mustelinae, subsequent colonizations of the Americas appear to be responsible for the Holarctic (e.g. *M. erminea*, *M. nivalis*) and Nearctic (e.g., *M. nigripes*) species in the genus *Mustela*. The apparent paraphyly of

Ictonychinae in Figure 2 appears to be just that, an artifact of taxonomic sampling designed to test the integrity of *Mustela, Neogale*, and Mustelinae. Various studies utilizing both mitochondrial and nuclear evidence strongly support the monophyly of ictonychines and their sisterhood to Mustelinae + Lutrinae (Koepfli et al., 2008; Law et al., 2018; Hassanin et al., 2021).

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Author contributions

Bruce Patterson, Júlio Vilela and Felix Grewe conceived the study, with preliminary contributions from Héctor Ramírez Chaves. Vilela collected the tissue samples from museum specimens, Vilela and André Soares extracted the mitogenomes, and Grewe and Vilela performed the sequencing operations. Patterson and Grewe conducted the phylogenetic analyses and wrote the first draft of the manuscript with help from Soares. All authors read the article and approved its content.

Conflicts of interest

The authors declare that there are no conflicting issues related to this research article.

Supplementary data

https://jad.lu.ac.ir/article_725922.html

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