



# Assessing the Taxonomic Status and Evolutionary History of *Acomys cilicicus*: Insights from mtDNA Analysis

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**Abstract:** The spiny mouse *Acomys cilicicus* is confined to a ~120 km<sup>2</sup> coastal strip between Silifke and Erdemli in southern Turkey. The species has long been of uncertain taxonomic status. We sequenced a 950-bp fragment of the mitochondrial cytochrome b (CYTB) gene from 16 individuals of *A. cilicicus* across five localities and integrated these data with published CYTB sequences of *A. minous*, *A. nesiotes* and *A. cahirinus*. Median-joining network and Kimura-2-parameter distance analyses revealed two geographically structured haplotypes of *A. cilicicus* within an overall low diversity background (< 2% divergence). Phylogenetic reconstructions, using maximum likelihood and Bayesian relaxed-clock approaches, identified *A. cilicicus* as a strongly supported, monophyletic sister clade to *A. minous*. Divergence dating placed the split between *A. cilicicus* and *A. minous* at ~0.17 million years ago (95% highest posterior density: 0.03-0.37 Mya). Coalescent-based migration modelling (MIGRATE) supports a two-stage colonisation scenario: an ancestral dispersal of *A. cahirinus* into Crete giving rise to *A. minous*, followed by Pleistocene maritime colonisation from Crete to southern Anatolia, yielding *A. cilicicus*. These results validate the distinct species status of *A. cilicicus* as a discrete conservation unit and highlight the need for multilocus nuclear markers to resolve incomplete lineage sorting in this recently diverged Mediterranean clade.

**Key words:** Anatolian spiny mouse, introduced species, phylogeography, species status

## Introduction

*Acomys cilicicus* is currently known only from a ~120 km<sup>2</sup> coastal strip between Silifke and Erdemli in southern Turkey, likely as a result of a human-mediated introduction rather than a long-standing

native lineage (Çetintaş et al. 2017, Kaya Özdemirel et al. 2022). Its restricted distribution and putative recent establishment make it an ideal system for investigating how founder events and subsequent demographic shifts influence genetic diversity and evolutionary trajectories in novel environments.

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Populations founded by few individuals commonly experience pronounced founder effects and genetic bottlenecks that reduce allelic richness and heterozygosity, potentially compromising fitness and increasing extinction risk (Abdelkrim et al. 2005). Even when establishment succeeds, genetic drift in the new habitat can further erode diversity; alternatively, strong selective pressures may drive rapid phenotypic and genetic divergence (Lee 2002). Thus, assessing the genetic diversity of an introduced species is crucial for understanding both its evolutionary potential and long-term persistence.

The *Acomys* comprises 19 species distributed across the Arabian Peninsula, Africa, southern Turkey, Cyprus and Crete (Bates 1994; Wilson and Reeder 2005). Aghova et al. (2019) grouped these into five main clades: *subspinosus*, *spinosissimus*, *russatus*, *wilsoni* and *cahirinus* and noted that Mediterranean taxa (including *A. cilicicus*) fall within the *cahirinus* group, where species boundaries remain uncertain and warrant detailed investigation.

Historical and recent studies illustrate this taxonomic ambiguity. The first Turkish record from Silifke was reported by Lehmann (1966), initially as *A. cahirinus* and later reassigned to *A. nesiotus*. Spitzenberger (1978) then identified Silifke specimens as a distinct taxon, *A. cilicicus*, based on dental and morphometric differences. Barome et al. (2001) and Giagia-Athanasopoulou et al. (2011) highlighted low mitochondrial divergence among *A. nesiotus*, *A. minous* and *A. cilicicus* and cautioned that karyotypic characters alone are insufficient for delimitation. More recently, Frynta et al. (2010) and Renaud et al. (2020), using D-loop data showed that Mediterranean introductions of *Acomys* occurred at different times, consistent with human-assisted dispersal. Together, these studies underscore sparse sampling ( $n < 10$  for *A. cilicicus*) and reliance on single-locus markers, leaving phylogeographic history and unresolved species status.

To address these gaps, we sequenced the mitochondrial *CYTB* from 16 individuals of *A. cilicicus* across five localities and applied a relaxed-clock Bayesian framework. Our aims were to (1) infer phylogenetic relationships and estimate separation time within the *cahirinus* complex, (2) evaluate the genetic distinctiveness of *A. cilicicus* against its congeners and (3) explore plausible human-mediated introduction routes into Anatolia. We adopted measured phrasing throughout, explicitly acknowledging potential gene-tree/species-tree discordance inherent to single-locus data and the resulting uncertainties in our inferences.

## Materials and Methods

Specimens of *Acomys cilicicus* ( $n=16$ ) were collected from Mersin (Table 1, Fig. 1); the specimens used are those collected for the paper by Çetintaş et al. 2017. Tissue was collected from the ear and liver. Later, DNA samples were isolated from the tissues using a 5-Prime DNA isolation kit.

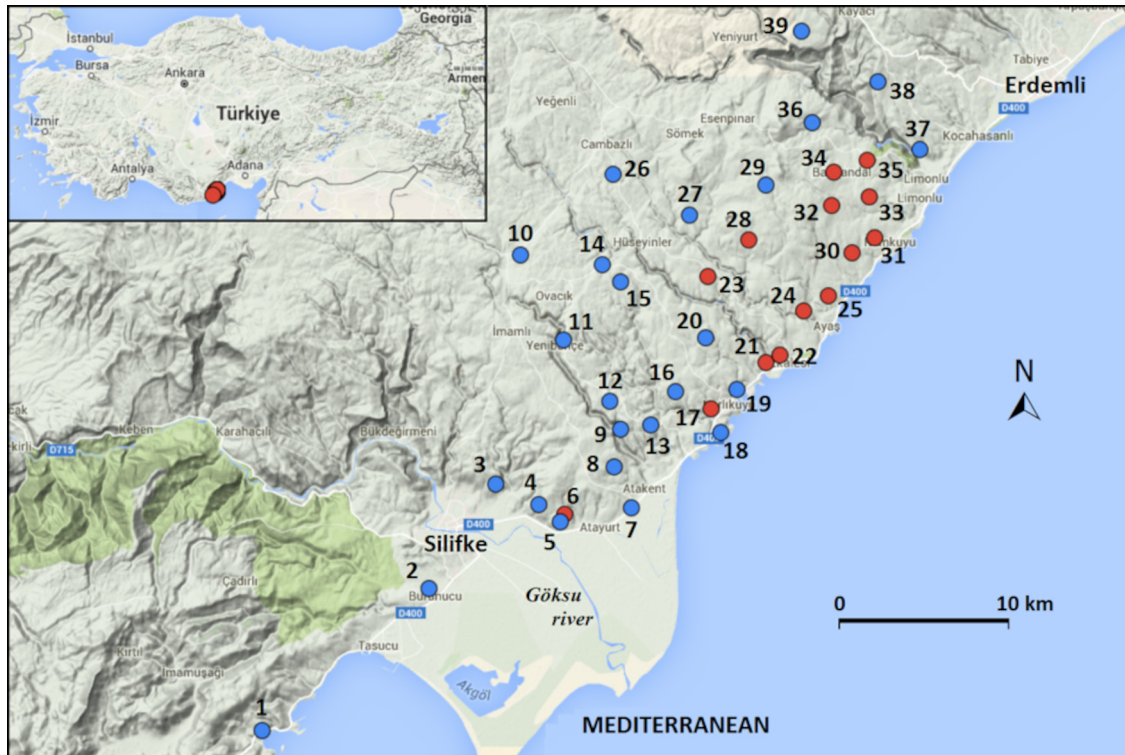
We sequenced *CYTBs* from mtDNA using primers L14724 5'-GATATGAAAAACCATCGTTG-3' and H15915 5'-TCTCCATTCTGGTTACAA-GAC-3' (Irwin et al. 1991). Raw *CYTB* sequences were corrected and a consensus sequence was generated for each individual sample using Geneious R9 (<http://www.geneious.com/>); mismatches or misreads were corrected manually. We also used previously published sequences of the other species to align the sequences (Supplement Table 1). All sequences were aligned using Clustal X with BioEdit (Hall, 1999). After alignment, some parts of the sequences were deleted, as most of them covered gaps and were manually misread. We uploaded 16 sequences to GenBank (accession numbers from OP791973 to OP791988), with a length of 950 bp (Supplement Table 1). A median-joining network (Bandelt et al. 1999) was constructed using Network (<https://www.fluxus-engineering.com/sharenet.htm>). To draw networks, Röhl data files were prepared in DNAsp (Librado & Rozas 2009). Sequences from GenBank were also included in the network to better understand the relationships between *cilicicus* (Supplement Table 2). We also provide a Kimura-2 model distance calculated in MEGA 11 (Tamura et al. 2011).

The phylogeny was reconstructed using maximum likelihood (ML) methods. The reconstruction substitution model (TIM2+I) was selected using jModelTest 2 (Darriba et al. 2012), with corrected Akaike Information Criterion (AICc) weights as the selection criterion, via the Cypres online tools portal (<https://www.phylo.org/>). The ML tree was reconstructed using the web server PHYML (Guindon et al. 2010), which was used as an online tool <http://www.atgc-montpellier.fr/phyml/>. All trees were visualised using FigTree v.1.4 (Rambaut 2009).

Two calibration points from Aghova et al. (2019) were used in the analysis: the separation time between *spinosissimus-subspinosus* (7.04 my) and between *cahirinus* (Arabian region, cah10 in Aghova et al. 2019) and north-eastern *cahirinus* (Saharan region, cah9 in Aghova et al. 2019) (1.59 my). Separation time estimates were obtained using BEAST v2.5 (Bouckaert et al. 2019) and the best-fitting substitution model was selected using

**Table 1.** Sampling locations within the distribution area of *Acomys cilicicus*, including coordinates, altitudes (m a.s.l.), localities (+) and Haplotypes revealed from *CYTB* sequences.

Localities (No in Figure 1)	Coordinates	Altitude (m)	N	Haplotype			
				H1	H2	H3	H4
Karahmetli (27, 28, 29)	36°31'38.82"N, 34°7'26.52"E	483-630	3	1	1	1	0
Narlıkuyu (17,19)	36°27'7.89"N, 34°6'59.17"E	81-108	7	5	1	0	1
Hüseyinler (15)	36°30'59.02"N, 34°1'50.75"E	720 m	1	1	0	0	0
Ayaş (24)	36°29'33.21"N, 34°9'44.65"E	117-196	3	3	0	0	0
Kumkuyu (32)	36°32'51.17"N,34°10'35.28"E	347-387	2	2	0	0	0



**Fig. 1.** Trapping localities to determine the distribution area of *Acomys cilicicus*. The numbers correspond to those given in Table 1. Blue dots indicate the localities where specimens of *Acomys* could not be captured and red dots indicate the localities where specimens were captured (The map is modified from Çetintaş et al. 2017).

jModeltest-2 (Darriba et al. 2012: via the online tool phylo.org/cipres). Estimation parameters were optimised in BEAUTI 2.5. The analysis was performed with an optimised relaxed molecular clock and a calibrated Yule prior. Ten replicate MCMC chains were run for 100 million generations each; with an effective sample size (ESS) greater than 200 for each parameter. Posterior distributions of MRCAs and other model parameters were checked using TRACER 1.5 (Rambaut & Drummond 2009) and posterior samples from all chains were combined in LogCombiner, using the BEAST package. The Maximum Clade Credibility (MCC) tree was constructed using TreeAnnotator, also part

of the BEAST package, while plotting was done in FigTree 1.4 (<http://tree.bio.ed.ac.uk/software/figtree/>) to show the species status of our sampling of *Acomys* in the Mediterranean basin. We estimated the direction and magnitude of gene flow between pairs of populations of different sizes using a coalescent-based maximum likelihood approach to estimate long-term gene flow (Beerli and Felsenstein 2001) using Migrate 3.6.6 (Beerli 2009). Parameters were estimated from the data. We set the number of recorded steps in a chain to 1,000. Three possible scenarios were tested for three populations: *A. minous*-Crete as 1st, *A. cilicicus*-Turkey as 2nd and *A. cahirinus*-Egypt as 3rd.

## Results

The network analysis revealed that there were two haplotypes that appear to be endemic due to their clear separation from others in the network (Fig. 2, Tables 1 and Supplement Table 2). It also showed that Cyprus spiny mice and Silifke spiny mice grouped with different haplotypes from Crete: *minous*, became an ancestral species for *A. cilicicus* and *A. nesiotis*. Kimura-2 distance also determined genetic distances within *cilicicus*-like networks (Supplement Table 3). The K-2P distance analysis showed a low genetic distance among all three species of *Acomys*. The distance between groups of *A. spinosissimus* and *A. cahirinus* was also smaller than expected.

According to the maximum likelihood tree, *A. cilicicus* was represented as the main branch separated from *A. minous*, *A. nesiotis* and *A. cahirinus* (Fig. 3). Four sequences, originally deposited as *A. minous* (GenBank accessions AJ2333955–AJ2333958), unexpectedly nested within the clade of *A. cilicicus* in our CYTB ML tree (Fig. 2). We attribute this to (i) the very recent divergence of Mediterranean lineages of *Acomys*, (ii) the inherently slow mitochondrial mutation rate in this genus and (iii) incomplete lineage sorting, whereby ancestral polymorphisms persist across speciation events.

We also calculated the separation time of *A. cilicicus*, as no previous data were available for *A.*

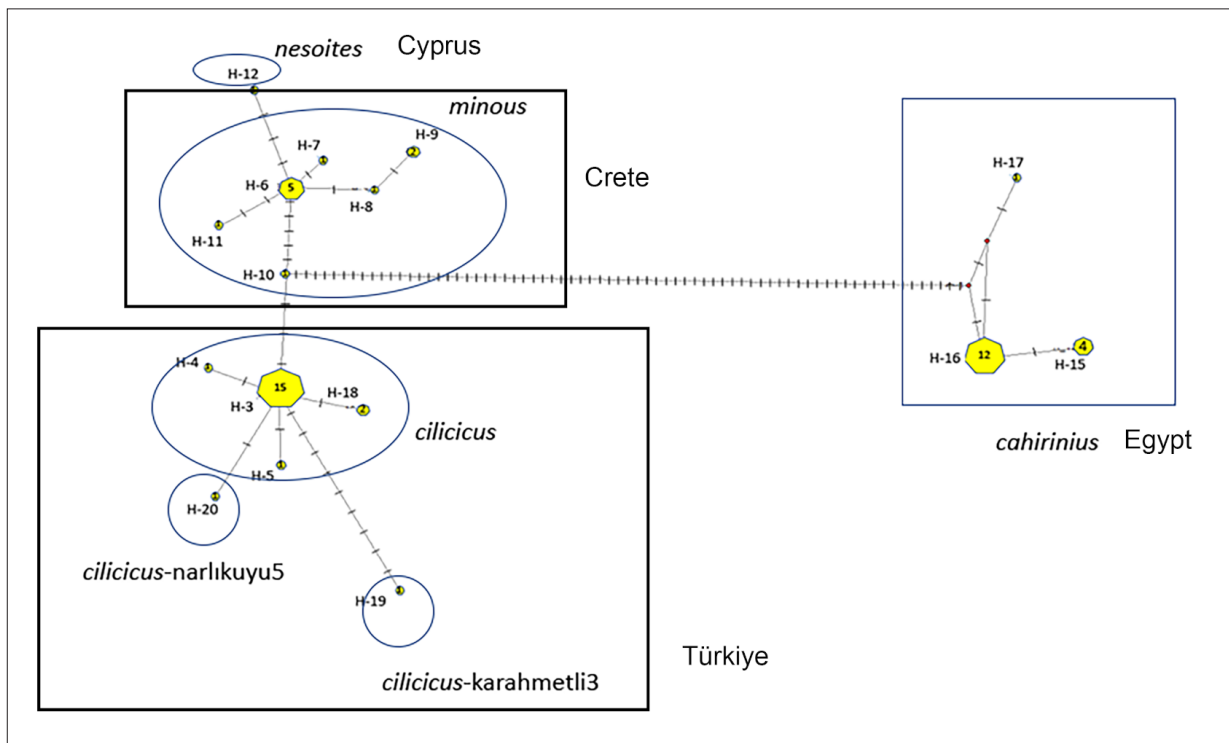
*cilicicus* on its separation time or phylogeographic pattern. Our estimates showed that the separation time between *cilicicus* and its closest ancestor, *minous*, was approximately 170 k years (Table 2).

We tested three possible migration routes using MIGRATE (Fig. 4). They were all based on the hypothesis that *A. cahirinus* was the ancestral species and that Silifke, Crete and Cyprus were invaded by *Acomys* at different times.

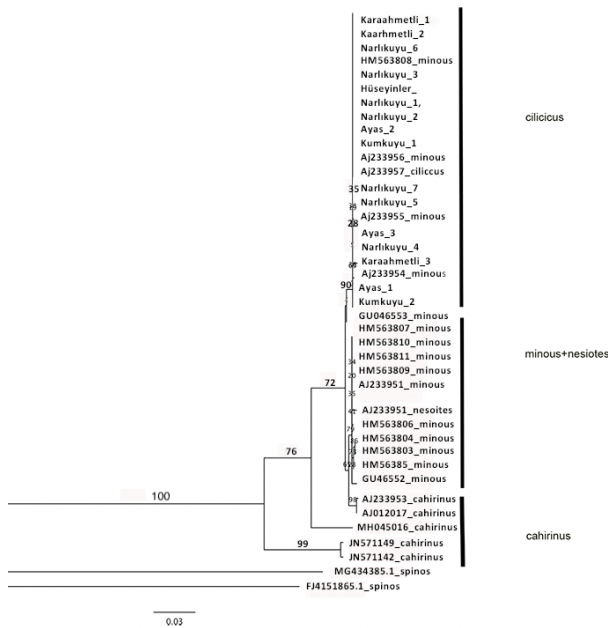
Our first model assumed that *cahirinus* spread separately to Crete and Silifke and that the speciation of *minous* and *cilicicus* at these localities occurred independently (Fig. 4: dashed arrows). The second model (Fig. 4: single arrow) accepted that *cahirinus* first moved to Crete, where it evolved into *minous* and later moved from Crete to Silifke and from Crete to Cyprus. The last model assumed that

**Table 2.** Separation times (mya) between species of *Acomys*. \* indicates calibration points.

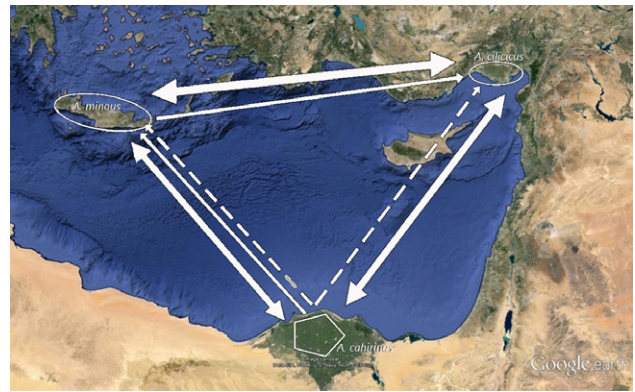
Separation point	Separation time (95%)
<i>cilicicus/minous</i>	0.17 (0.031, 0.368)
<i>minous/cahirinus</i>	0.26 (0.042, 0.58)
<i>spinosissimus/ subspinosus</i> *	7.04 (6.95, 7.17)
<i>cahirinus (cah9)/cahirinus (cah10)</i> *	1.57 (1.50, 1.64)



**Fig. 2.** Haplotypes relation as revealed using median-joining network. All haplotypes are listed in Supplement, Table 3.



**Fig. 3.** Maximum likelihood tree of species of *Acomys* inferred from *CYTB* sequences. Species, including *A. cilicicus*, are separated from each other with high branch probabilities.



**Fig. 4.** Schematic representation of the three possible migration routes tested by MIGRATE and showing all three localities (Silifke - *A. cilicicus*, Crete - *A. minous* and Egypt - *A. cahirinus*). Model 1 is shown with dashed arrows, model 2 with single headed arrows and model 3 with double headed arrows. According to model 3, migration paths are bidirectional and the ancestral status of *Acomys cahirinus* is doubtful. Models 1 and 2 were constructed with the assumption that *A. cahirinus* was an ancestral species for *A. nesiotes* and *A. cilicicus*. According to these models, migration routes are unidirectional.

**Table 3.** Log marginal likelihood results and Bayesian factors for the three models.

Model	Bezier lmL	Harmonic lmL	LBF (Bezier)	Choice (Bezier)	Model probability
1	-4904.276518	-4607.564427	-42.54	1	0.000
2	-4704.879579	-4489.106412	0.00	2 (best)	0.545
3	-4558.201211	-4392.242926	-3.22	3	0.123

all species moved bidirectionally; between Crete and Silifke, Silifke and Egypt and Egypt and Crete (Fig. 4: double-headed arrows). According to our results, the second model had the highest support of all three model probabilities (Table 3).

## Discussion

*Acomys cilicicus* was first described by Spitzenberger (1978) from Silifke, Mersin. However, its taxonomic status remains controversial (Spitzenberger 1978, Macholán et al. 1995, Kıvanç et al. 1997, Barome et al. 2001, Kryštufek & Vohralík 2009, Kıvanç et al. 2013, Aghova et al. 2019, Renaud et al. 2020). A recent survey confirmed its narrow distribution (Çetintaş et al. 2017) under ongoing anthropogenic pressure. Genetic distance analyses indicate limited divergence among populations within *A. cilicicus*, yet two distinct haplotypes (Karahmetli vs. Narlikuyu) differ consistently across network and phylogenetic analyses.

Notably, the pair-wise distance between these two localities exceeds that between *A. cilicicus* and *A. minous*, suggesting separate source populations; however, our mitochondrial *CYTB* data alone cannot resolve their precise origins. Although absolute genetic distances may fall below common speciation thresholds, *A. cilicicus* forms a well-supported clade in both maximum-likelihood and network reconstructions, and its coastal distribution, with no apparent natural corridor for gene flow, implies effective geographic and reproductive isolation. Comparisons with outgroup taxa (*A. subspinosus*, *A. spinosissimus*, *A. cahirinus*) yield divergences near 2%, which is a heuristic rodent speciation benchmark (Bradley and Baker 2001), a result indicating relatively slow genetic differentiation, consistent with the species’ sedentary behaviour in Anatolia.

Phylogeographic reconstruction aligns with the five-clade framework of Aghova et al. (2019) and suggests a multi-stage colonisation: ancestral

dispersal of *A. cahirinus* into Crete (yielding *A. minous*), a second wave from Crete to Anatolia and subsequent divergence of *A. cilicicus*. Our relaxed-clock estimates place the split between the Egyptian and Ethiopian lineages of *cahirinus* at ~1.57 mya, preceding the 0.65 mya estimate of Barome et al. (2001), and agree with the ~1.59 mya split reported by Aghova et al. (2019). Chromosomal and *CYTB* data (Giagia-Athanasopoulou et al. 2011) further support an early colonisation (>0.4 mya), reinforcing *A. cahirinus* as the Mediterranean ancestor.

The results of the migration analysis showed that both *A. cilicicus* and *A. nesiotetes* evolved from *minous*, thus all Mediterranean species in our tree were placed within the *cahirinus* clade, as shown by other studies (Barome et al. 2001, Aghová et al. 2019). The tree in Barome et al. (2001) also placed *minous* and *nesiotetes* in a group that was represented as a sister group to *minous* and *cilicicus*. Our molecular clock calculations have shown that *A. cilicicus* may have been introduced to Anatolia earlier. Gaffney (2021) reviewed the potential ports during the Pleistocene. Simmons (2012) findings from Crete point to 170,000 years ago. Early hominids in North Africa may have invaded the island in the Mediterranean, as suggested by our migration analysis (Fig. 4). Our findings suggest that *Acomys cilicicus* likely diverged from *A. minous* during the Middle Pleistocene. This divergence time overlaps with periods of intensified biogeographic connectivity across the Mediterranean but does not, by itself, confirm human-mediated dispersal. The potential role of human transport, including early maritime activity, remains speculative and should be explored through integrative archaeological and genetic approaches. The status of *A. nesiotetes* remains unresolved due to its very recent divergence and limited sampling; targeted genomic and expanded geographic surveys are needed to clarify its relationship to *A. minous* and *A. cilicicus*. The nesting of certain haplotypes of *A. minous* within the clade of *A. cilicicus* highlights a limitation of single-locus mitochondrial analyses in recently diverged taxa. Slow *CYTB* evolution and incomplete lineage sorting can cause retention of ancestral haplotypes across sister species, leading to apparent intermixing in gene trees. That may explain haplotypes of *minous* within the clade of *cilicicus*. To resolve these discordances and confirm species boundaries, future studies should incorporate multiple unlinked nuclear markers and broaden geographic sampling across the Mediterranean complex of *Acomys*.

## Conclusion

Our phylogeographic and migration analyses indicate that the colonisation of the Mediterranean by *Acomys* occurred within at least two distinct waves, with *A. cilicicus* and *A. nesiotetes* deriving from Cretan lineage. The monophyly of Turkish *A. cilicicus*, its unique mitochondrial haplotypes and its strict geographic isolation support its recognition as a distinct conservation unit. Nonetheless, multilocus and genomic-scale data are needed to confirm species boundaries, resolve introduction pathways and assess potential gene flow among Mediterranean taxa of *Acomys*. Given its narrow distribution, genetic uniqueness and ongoing anthropogenic threats, *A. cilicicus* merits targeted conservation efforts. Future work should integrate high-resolution molecular markers and ecological data to refine its evolutionary history and inform management strategies for this and other Mediterranean spiny mice.

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