



## Correspondence

# Molecular evidence reveals human-mediated dispersals of snake species in the Aegean Islands

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With almost 10,000 islands and islets, the Aegean Archipelago lies between the southern Balkan Peninsula (Greece) and Anatolia (Turkey) (Fig. 1). This region harbours one of the most species-rich herpetofaunas of Europe, mainly due to its position at the meeting point of Europe and Asia, and its old and intense geoclimatic history (see KORNILIOS et al. 2016 and references therein). On the other hand, the continuous human presence in this region for at least 9,000 years (KNAPP & BLAKE 2005) has also contributed to an important extent to the formation of the present Aegean fauna. Some human activities have actively modified the landscape, while others, such as the development of commercial trade routes in land and sea, have facilitated the accidental or intentional displacement of terrestrial animals, altering species' distributions (GIPPOLITI & AMORI 2006).

Greece is home to 23 species of snakes (PAFILIS & MARAGOU 2020). With few exceptions (e.g., *Vipera berus*, *V. graeca*), most species are also encountered on many Aegean islands, but in most instances, these occurrences have been recorded from shelf-islands situated very close to the mainland of the Balkan Peninsula in the west and Anatolia in the east. These islands used to be connected again and again to the neighbouring mainland until as recently as a few thousand years ago, e.g., during glacial maxima when the sea level was lower by as much as 140 m than today (PERISSORATIS & CONISPOLIATIS 2003) (Fig. 1). Hence, whether through vicariance or dispersal, the isolation times of these insular populations are very recent, and they exhibit very little genetic differentiation from their mainland conspecifics (e.g., KORNILIOS et al. 2012, KYRIAZI et al. 2013). However, twelve snake species are distributed on the central and southern Aegean islands that constitute independent biogeographic areas and have older and more complex geological histories, such as the Cyclades island

group in the centre of the Aegean Sea, and the Kasos-Karpathos group and Crete in the south (Fig. 1).

During the past two decades several phylogeographic studies have shed light on the biogeographic patterns of most of these species, describing their diversification history and explaining, to some extent, their presence (and absence) on Aegean islands. However, some insular occurrences still stand out and have not been investigated so far in a phylogeographic framework. In this study we utilise DNA sequences to investigate the phylogenetic position of specific insular populations of two species complexes, namely *Telescopus fallax* (FLEISCHMANN, 1831) and *Natrix tessellata* (LAURENTI, 1768), both being members of the family Colubridae. We have built on published phylogenies by adding unrepresented populations, including the insular ones of interest, and draw conclusions on their biogeographic history and origin.

The European Cat Snake *T. fallax* has a wide distribution in the eastern Mediterranean that includes the Balkan Peninsula and Anatolia, but also in large parts of western Asia (KYRIAZI et al. 2013, ŠMÍD et al. 2019; Fig. 1A). In the Aegean, it occurs on Crete, several central islands of the Cyclades (but with some interesting “absences”, e.g., on Naxos), also on Kasos but not the neighbouring island of Karpathos. The Dice Snake *N. tessellata* has a very large geographic distribution throughout Europe, Asia, and even in North Africa (KYRIAZI et al. 2013; Fig. 1B). In the Aegean, it occurs on Crete and the island of Serifos in the western Cyclades.

Samples, mitochondrial sequences,  
and phylogenetic analyses

A total of 252 sequences were included in our analyses, with 20 new sequences generated here and the remain-

ing ones retrieved from GenBank. Specifically, the *T. fallax* dataset included 69 sequences that replicate the phylogenies presented in KYRIAZI et al. (2013) and ŠMÍD et al. (2019), with the addition of 13 new sequences. The *N. tessellata* dataset included 183 sequences that replicate the phylogeny presented in KYRIAZI et al. (2013), with 7 new additional sequences. Specimen data (codes, sampling localities, and GenBank Accession Numbers) are given in the Supplementary Tables S1 and S2, while the sampling localities of the specimens that were analysed here are specified in Figure 1. Tissue samples have been deposited in the collections of the Zoological Museum of the University of Patras (ZMUP).

The complete sequence of the mitochondrial marker *cytochrome b* (*cytb*) was targeted for phylogenetic analyses, since this approach has been successfully used to reconstruct phylogenetic relationships in many snakes, including our two target species (e.g., KYRIAZI et al. 2013, KORNILOS et al. 2014, THANOU et al. 2023). It is also the sole

common genetic marker used in the published phylogenies we have built upon in the current study. PCR-amplification and sequencing were performed as described by THANOU et al. (2020). Sequences were aligned in the software ClustalX v. 2.0.12 (LARKIN et al. 2007) with default parameters to generate two separate datasets for the respective target species.

The genetic divergences among sequences and groups were estimated in MEGA7 (KUMAR et al. 2015) as uncorrected p-distances. For each species, a Neighbor-Joining (NJ) tree was calculated in MEGA7 as well, with the statistical support of the nodes tested via 1,000 bootstrap replicates (FELSENSTEIN 1985).

We built Maximum Likelihood (ML) trees with IQ-TREE v. 1.4.3 (NGUYEN et al. 2015, CHERNOMOR et al. 2016, TRIFINOPOULOS et al. 2016). Analyses were run using the “partitionfinder” and “Auto” options to determine the best partitioning schemes and best-fit substitution models for each partition (codon position). Nodal support was tested

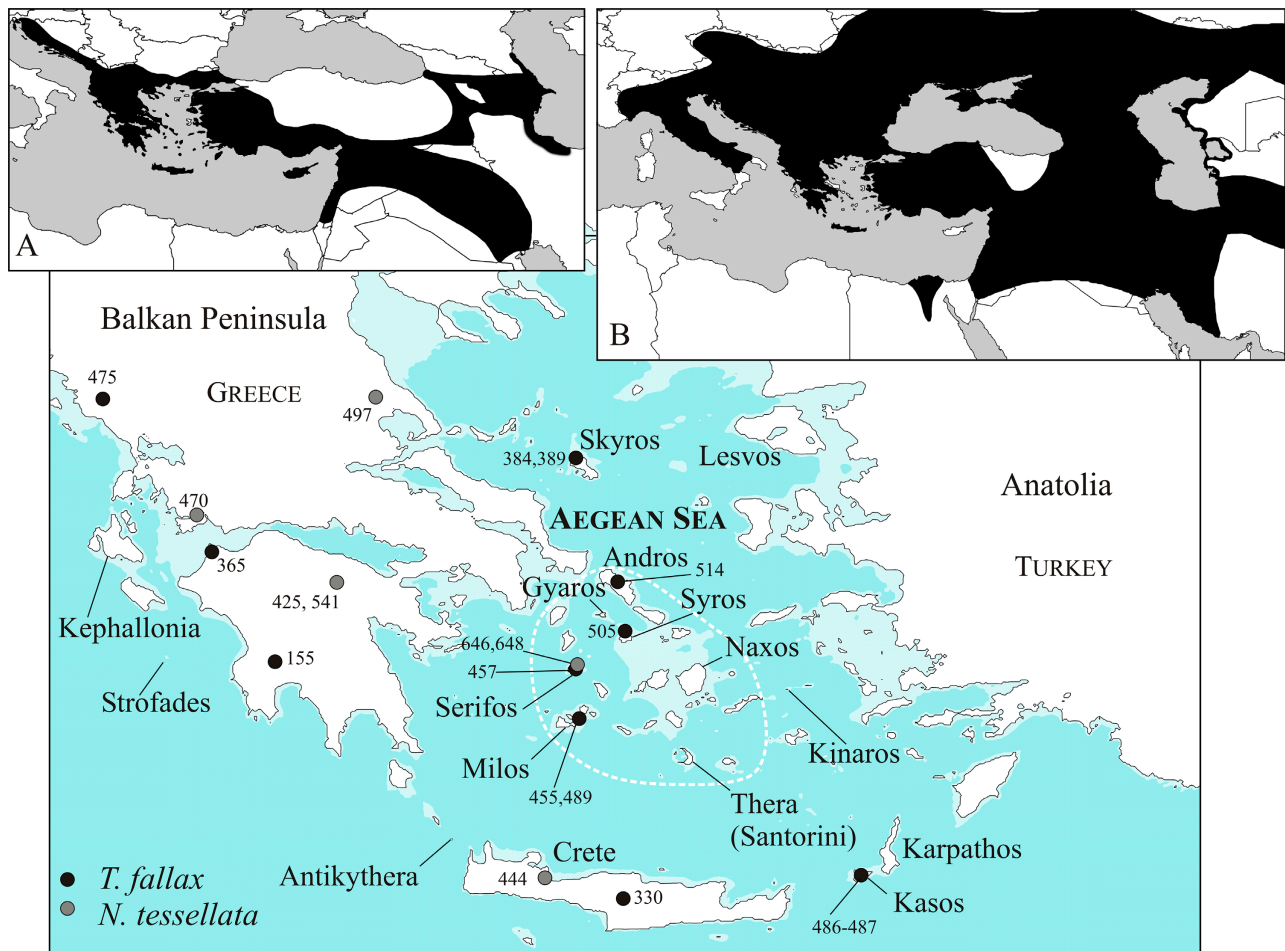


Figure 1. Map of the Aegean region showing the collection localities of the samples analysed in the current study outlining various geographic features mentioned in the text (e.g., island names), and the 140-m isobath (in light blue) that indicates connected islands and the mainland during glacial maxima (PERISSORATIS & CONISPOLIATIS 2003). The Cyclades island group is highlighted with a white dashed line. Inset A: approximate geographic distribution of *Telescopus fallax*. Inset B: approximate geographic distribution of *Natrrix tessellata* (after KYRIAZI et al. 2013).

via SH-aLRT tests with 10,000 replicates (GUINDON et al. 2010), 10,000 ultrafast bootstrap alignments (MINH et al. 2013), and 1,000 standard bootstrap alignments (FELSENSTEIN 1985). For the analysis of *T. fallax*, the “*T. f. syriacus*” clade (ŠMÍD et al. 2019) or “Easternmost” clade (KYRIAZI et al. 2013) was used as an outgroup, and for *N. tessellata* we used *N. helvetica* to root the tree.

For both ML analyses, the best partitioning scheme was the one with three partitions, one for each codon position. For *T. fallax*, the best-fit substitution model for each partition was TN+F+I, while for *N. tessellata*, it was TN+F+I+G4 (TAMURA & NEI 1993). The p-distance values between all clades and subclades of both phylogenies are shown in the Supplementary Tables S3 and S4.

### Cat Snake: phylogenetic tree topology and levels of divergence

There are two published mitochondrial phylogenies for *T. fallax* (KYRIAZI et al. 2013, ŠMÍD et al. 2019). However, the two datasets have not been combined into a single analysis up to now. The updated phylogeny based on the common marker *cytb* and the geographic distribution of the major clades and subclades are presented in Figure 2. The phylogenetic tree shows the early split of a clade that includes samples from Iran and east Turkey named “Easternmost Clade” (KYRIAZI et al. 2013) and “*T. f. syriacus*” (ŠMÍD et al. 2019). This clade presents high genetic distance values of 6.6–7.7% compared with all other major clades of the phylogeny. The

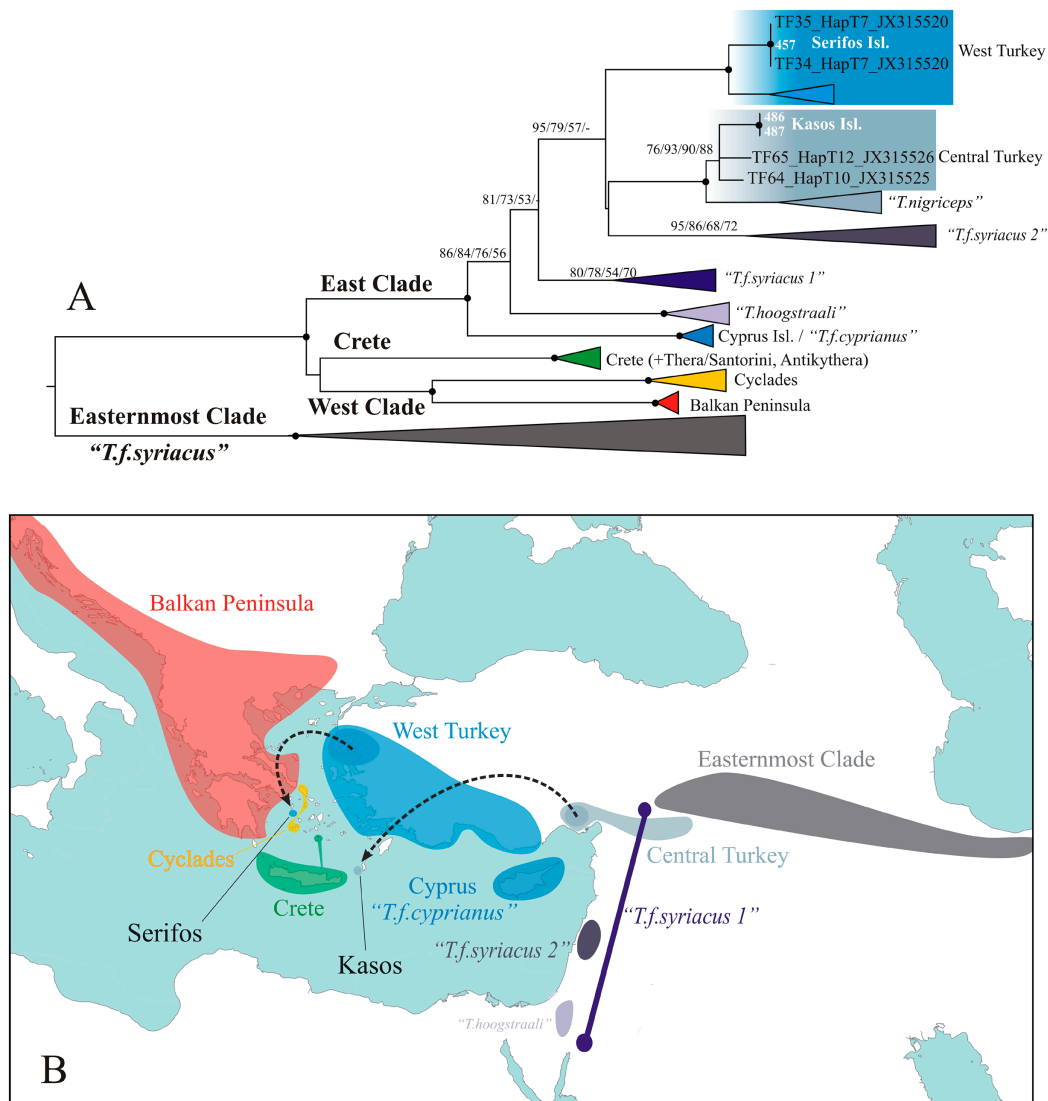


Figure 2. (A) The mitochondrial gene tree as constructed from our Maximum-Likelihood (ML) analysis for *Telescopus fallax*. The major phylogenetic clades are collapsed except for the ones of interest. Nodal support is based on SH-aLRTs/ultrafast bootstraps/standard bootstraps from ML/standard bootstraps from Neighbor-Joining (NJ). Only values >50 are shown, while absolute support is marked with a black dot. The sample codes and geographical locations of the individuals correspond to those in Fig. 1 and Table S1. (B) Map of the approximate distribution of each mitoclade, using the same colour coding. Long-distance translocations are indicated as arrows.

remaining populations, in turn, form three distinct clades: the East Clade (east of the Aegean: Anatolia, eastern Aegean islands, Cyprus, the Levant), the West Clade (west of the Aegean: Balkan Peninsula and Aegean islands), and Crete (including the islands of Antikythera and Thera-Santorini). Based on our *cytb* analyses, these three clades form a polytomy with genetic distances of 5.3–6.6% between them. Populations from west of the Aegean and Crete were not included by ŠMÍD et al. (2019), while in the phylogeny proposed by KYRIAZI et al. (2013) there was only very weak support for a relationship between the West Clade and Crete that is not supported here. The West Clade is further diversified into two subclades, with one corresponding to the Cyclades islands and one to the continental parts of Greece and the Balkan Peninsula (Fig. 2). The East Clade presents a more complicated situation with several subclades distributed in Turkey, Cyprus, Syria, Jordan, Lebanon and Israel (Fig. 2). These were previously identified by KYRIAZI et al. (2013) or ŠMÍD et al. (2019) or both. Among them, some subclades correspond to other species, namely *T. hoogstraali* and *T. nigriceps*, which is indicative of a need for a taxonomic revision of this group (ŠMÍD et al. 2019). Based on the taxonomic inconsistencies and the old age of the *T. fallax* diversification (6–11 Mya as per KYRIAZI et al. 2013 and 6–9.5 Mya according to ŠMÍD et al. 2019), *T. fallax* most probably represents a species complex rather than a single species.

#### Cat Snake: origin of the Serifos and Kasos populations

The target insular populations of our study, i.e., the Aegean islands of Serifos and Kasos, are both nested within the East Clade rather than the West Clade or the ones that corresponded to Crete or the Cyclades, despite the geographic proximity. Specifically, the Serifos population matched the haplotype T7 of KYRIAZI et al. (2013), being genetically identical to samples TF35 and TF34 from west Turkey and the island of Lesbos, respectively, more than 250 km distant and on the far side of the Aegean (Fig. 2B). Individuals from Kasos were genetically very close to samples TF64 and TF65 from central Turkey (KYRIAZI et al. 2013), almost 800 km distant, with 0.7% of genetic divergence for *cytb* (Fig. 2B). The extremely low genetic diversity and the very large geographic distances point to long-distance anthropogenic displacement. Our result also explains the Cat Snake's occurrence on Kasos but not on the neighbouring island of Karpathos.

#### Dice Snake: phylogenetic tree topology and levels of divergence

The Dice Snake's mitochondrial phylogeny is well known (GUICKING et al. 2009, KYRIAZI et al. 2013, JABLONSKI et al. 2023) and it includes several highly divergent lineages, indicating that it also represents a species complex rather than a single species. Its start of diversification dates back to more than 9 Mya (KYRIAZI et al. 2013, JABLONSKI et al.

2023). The mitochondrial phylogeny and the geographic distribution of this species' major clades and subclades are illustrated in Fig. 3. All published phylogenies, including the current one, agree in that an Iranian Clade branched off first. This clade exhibits genetic distances of between 7.1 and 8.1% from all others. The populations from the remaining geographic distribution of *N. tessellata* form three major clades, namely Greece (populations from the southern Balkan Peninsula), Jordan (populations from Jordan and Egypt), and a third clade that includes all remaining populations. The p-distances between these three major clades vary between 7.0 and 7.8%, and they seem to represent relict lineages of a much more widely distributed form that since became largely extinct and survived only in refugia (e.g., the southern Balkans and the southern Levant). The third clade in turn split into two major lineages, i.e., one distributed east of western Anatolia and as far east as China while diverging into two subclades, a Central Asian one and an Anatolian one (with the latter including the populations from the island of Cyprus). The other lineage is distributed west of west Anatolia, and as far west as central Europe: it split into a subclade ranging on Crete and a subclade that connects the populations from southwestern Turkey and populations from northwestern Turkey+Europe.

#### Dice Snake: origin of the Serifos and Crete populations

With regard to the Aegean islands, the Cretan populations are most probably a result of a rather old overseas dispersal from Anatolia: p-distances are quite high (2.7–2.8%), and the dispersal has been dated to some 2.3 Mya (KYRIAZI et al. 2013). The population on the Aegean island of Serifos is nested within the subclade of SW Turkey, showing very low p-distances of 1% from the samples NT34 and NT36 of KYRIAZI et al. (2013). These low values of genetic differentiation, the fact that this is the only known *N. tessellata* population from any central Aegean island, and the great distance between the Serifos and the source populations (> 400 km; Fig. 3B) lead us to conclude that the Serifos population has resulted from human-mediated displacement.

#### Implications on taxonomy and biodiversity

As already mentioned, the two studied snake species represent species complexes. It is expected that future studies (including molecular phylogenies based on multiple markers) will eventually recognise several distinct species within each of the groups. Here we have demonstrated the possibility that Greece and the Aegean region may harbour more than one (in fact up to three) different species of the *T. fallax* complex: the insular populations of Serifos and Kasos do not have any phylogenetic affinities with their neighbouring populations but they belong to the highly divergent East Clade that is naturally distributed in Anatolia and is probably a different species than the one found on the other islands of the central Aegean. The island of Crete

may also host an endemic *Telescopus* species. In a similar vein for *N. tessellata*, the Serifos population most probably represents a different species from the Greek mainland one, which is also highly divergent, as is suggested by the mitochondrial tree and the estimated genetic distances.

#### A review of human-mediated dispersals of snakes in the Aegean Sea

Several ancient and more recent Mediterranean civilisations that have been active in the Aegean Sea, such as the Minoans, the ancient Greeks, the Romans, the Carthagi-

nians, and even the early Christians had strong cultural relationships with snakes. Island introductions of snakes have been attributed to religious rituals (e.g., Minoans, Romans, or Christians), war tactics such as launching terracotta jars filled with snakes against enemy ships to frighten the crews, traditions and beliefs such as keeping snakes in the house for good luck (MASSETI & ZUFFI 2011), and the mitigation of rodent populations (SCHÄTTI & SIGG 1989).

We have highlighted here several cases of insular snake populations as being products of very recent human-mediated dispersals (Figs 2B and 3B show the geographic positions of introduced insular populations and their sources). Faunistic studies, especially in combination with molecular

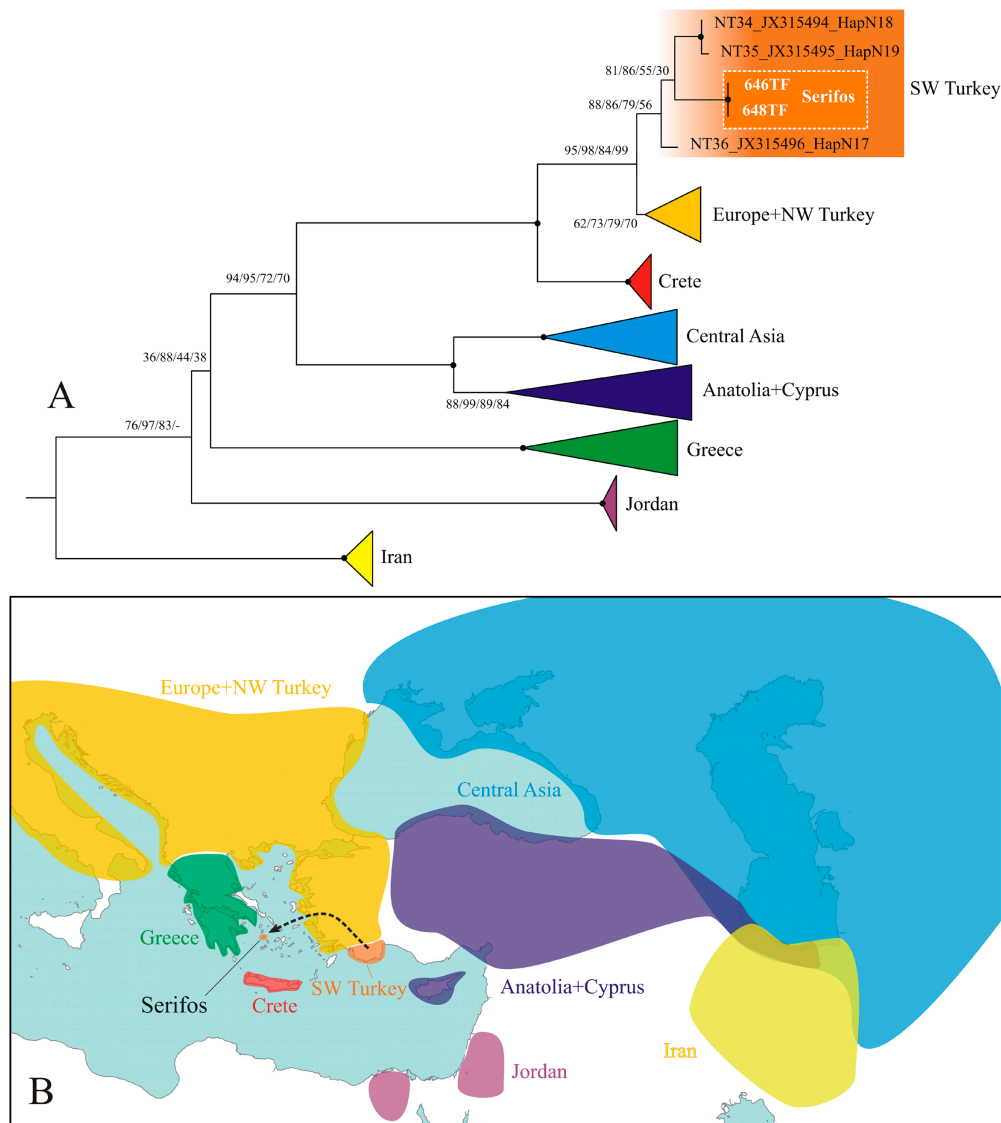


Figure 3. (A) The mitochondrial gene tree as constructed from our Maximum-Likelihood (ML) analysis for *Natrix tessellata*. The major phylogenetic clades are collapsed except for the ones of interest. Nodal support is based on SH-aLRTs/ultrafast bootstraps/standard bootstraps from ML/standard bootstraps from Neighbor-Joining (NJ). Only values >50 are shown, while absolute support is marked with a black dot. The sample codes and geographical locations of the individuals correspond to those in Fig. 1 and Table S1. (B) Map of the approximate distribution of each mitoclade, using the same colour coding. Long-distance translocations are indicated as arrows.

data, have identified similar patterns for other snake species and other Aegean islands. For several decades it was believed that the island of Gyaros in the northern Cyclades was home to the endemic *Coluber* (or *Hierophis*) *gyarosensis*. After the analysis of molecular genetic data, this turned out to be a human-mediated occurrence of *Hierophis viridiflavus* and specifically its eastern mitoclade, corresponding to the usually melanistic subspecies *H. v. carbonarius* (UTIGER & SCHÄTTI 2004). Assumingly, this snake population resulted from an intentional translocation during Roman times when Gyaros served as a place of exile (UTIGER & SCHÄTTI 2004). The extremely low genetic diversity of *Zamenis situla* in the Aegean region, in combination with the observation that its fragmented range coincides with the ancient Greek colonies, led to the conclusion that its occurrence on the Aegean islands, possibly including Crete, is also the result of multiple intentional human translocations (KYRIAZI et al. 2013). Especially for the island of Thera (Santorini), the volcanic eruption in 1650 BC led to extensive species extinctions (GRUBER 1979). The only two snake species found on the island today, i.e., *Z. situla* but also *T. fallax*, recolonised this island from Crete only in recent times (KYRIAZI et al. 2013). Thera once was a colony of the Cretan Minoan civilisation, in which snakes occupied a profound religious position. *Telescopus fallax* has also been moved to the small islets of Strofades by monks, quite possibly from Kephallonia, where these snakes have been used in Christian rituals to this day (WARNECKE 1988). The Caspian Whipsnake, *Dolichophis caspius*, can be found on the island of Karpathos, but not on the neighbouring island of Kasos, which is the pattern of that of the Cat Snake in reverse. Recent mitochondrial phylogenies furthermore show that *D. caspius* has reached Karpathos from northern Greece or even from the central Balkans in historical times (JAVORČÍK et al. 2024). As a result, the remote islands of Kasos and Karpathos do not host native snake species, with the possible exception of *Natrix natrix*. Albeit extremely rare, the latter is found on Karpathos (BOGAERTS et al. 2018), but it is unknown whether this is an “old inhabitant” or a “new arrival”. It was only very recently that a single dead individual was found on Kasos, assumed to be an anthropogenic arrival from Karpathos (GRANO & CATTANEO 2020). A new record of the Javelin Boa *Eryx jaculus* on the small island of Kinaros is probably likewise the result of a very recent human introduction (ROSSO et al. 2018). Due to its semifossorial habits, Javelin Boas can be unintentionally transported, meaning that its fragmented distribution in the Aegean may mask additional human-induced dispersals. The endemic Milos Viper is found on four islands of the archipelago of Milos. Genetics best support its status as a subspecies, i.e., as *Macrovipera lebetina schweizeri*, rather than a distinct species, which is the current accepted status (see SPEYBROECK et al. 2020). Specifically, Milos Viper populations are genetically almost identical to *M. lebetina* from south-central Turkey and Cyprus (STÜMPPEL 2012; P. KORNILIOS & E. THANOU unpubl. data). The extremely low level of genetic differentiation and the very large distance between Milos and neighbouring islands from

south-central Turkey, likely point to the very recent human-induced dispersal of this viper to Milos. It is extraordinary and worthy of note how much these insular populations have differentiated from their parental species in such a short time, maybe as a result of strong selection and drift.

Clearly, the list of human-mediated dispersals of snakes across the Aegean and eastern Mediterranean is not complete, and further instances of both old and very recent displacements will surely be revealed in future studies. Even with the current knowledge, it is evident that humans have played an important role in shaping snake species' distributions and have contributed to the high reptilian biodiversity found in Greece and adjacent regions.

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