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Genetic affiliation and origin of the European Cat Snake, *Telescopus fallax* (Fleischmann, 1831), in the Maltese archipelago

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SUMMARY

The snake fauna of the Mediterranean islands has been shaped by multiple processes, including both natural and human-mediated dispersal. Various past human cultures and recent changes in trade and transportation have played a crucial role in the expansion of some species into insular environments. The snakes present on the Maltese archipelago are particularly emblematic of this complex mix of dispersal events. The European Cat Snake, *Telescopus fallax* (Fleischmann, 1831), forms a species complex widespread from the Balkans to the Middle East and across many eastern Mediterranean islands, regarded in most of the literature as introduced on the Maltese archipelago. Here we genetically investigated the Maltese populations of *T. fallax* using the mitochondrial marker Cytochrome b, with the aim of properly identifying their genetic affiliation and tracing their possible origin. The eight sequences obtained from the populations of Malta and Gozo shared the same mitochondrial haplotype and clustered together with the Balkan clade of *T. fallax*, thereby supporting their affiliation to the currently recognized nominotypical subspecies. The haplotype of the Maltese Cat Snake is identical to that of populations from the western Peloponnese and the island of Skyros (Sporades, Greece). The lack of variability found between the studied populations and some from southern Greece supports the hypothesis that this snake was introduced during historical times. The succession of many small Hellenic communities on the Maltese archipelago over the last few millennia suggests a possible Greek-mediated introduction; however, precisely because of the repeated presence of these influences over time, it is difficult to pinpoint the exact timing of introduction.

INTRODUCTION

The Maltese archipelago comprises a group of islands located approximately 96 km south of Sicily, with which it has repeatedly shared land bridges during the Quaternary (Thake 1985). The squamate fauna of the Maltese archipelago includes biogeographically diverse elements such as: i) endemics, as *Podarcis filfolensis* (Bedriaga, 1876), ii) species that probably originated from Sicily, e.g. *Hierophis viridiflavus* (Lacépède, 1789) and *Zamenis situla* (Linnaeus, 1758), iii) species recently introduced from North Africa, as *Hemorrhois algirus* (Jan, 1863), iv) species with multiple sources of introduction, i.e. *Chamaeleo chamaeleon* (Linnaeus, 1758) (see Basso et al. 2019), v) species of Asian origin recently introduced, as *Indotyphlops braminus* (Daudin, 1803) (see Vella et al. 2020); and, finally, vi) reptiles probably introduced from the Balkans or the eastern Mediterranean area, as *Telescopus fallax* (Fleischmann, 1831), currently considered a possible species complex with unresolved taxonomy, following some studies on its genetic variation across its large geographic range (cf. Šmíd et al. 2019; Kornilios and Thanou 2024).

The snake fauna of the Mediterranean islands has been shaped by a complex interplay of natural and human-mediated processes (Bonardi et al. 2022). Natural dispersal may occur through active movements facilitated by past land connections during marine regression events (Faraone et al. 2022) or through active or passive transmarine spreading (Thanou et al. 2020). Human-mediated dispersal, in contrast, may result from deliberate introductions (Masseti and Zuffi 2011) or from unintentional transport, where propagules are introduced as 'contaminants' of traded goods (Silva-Rocha et al. 2015), a common pattern of the squamate fauna in these geographic areas (Mori et al. 2022; Sherpa et al. 2024).

Snakes belonging to *Telescopus fallax* complex are medium-sized nocturnal colubrids, which are among the most widespread snakes across the eastern Mediterranean islands, with an isolated presence in Malta (Giglioli 1894; Bonardi et al. 2022; Kornilios and Thanou 2024). Their continental distribution extends from northeastern Italy to Iran, covering the Balkans, Anatolia, the Levant and part of Mesopotamia (Sindaco et al. 2013).

Populations of *Telescopus fallax* from Malta were long considered rare and localised (Giglioli 1894; Lanfranco 1955). However, recent works show this snake to be quite widespread on the main island (Dobbs et al. 2025), while it is scarcely present on the neighbouring island of Gozo (A. Sciberras, unpublished data; Dobbs et al. 2022). Moreover, genetic data from Maltese samples are lacking, and their phylogenetic relationship to other populations of *T. fallax* complex from the Eastern Mediterranean remains unresolved

Recently, the *Telescopus fallax* complex has been the subject of several studies providing a large dataset on its genetic variation (Kyriazi et al. 2013; Šmíd et al. 2019; Kornilios and Thanou 2024), supporting the possibility of testing the origin of the Maltese population. Thus, we analyse the Maltese populations based on a mitochondrial DNA marker to clarify its possible origin and genetic affiliation.

MATERIALS AND METHODS

Fieldwork was conducted exclusively by car, through opportunistic visual sampling along randomly selected routes, with the aim of detecting freshly road-killed individuals. Geographic coordinates were recorded using a GPS device, and small tissue samples were collected and preserved in 96% ethanol directly in the field.

DNA extraction was performed using the BIORON GmbH 'Ron's Tissue DNA Mini Kit'. The fragment of the mitochondrial gene Cytochrome b (Cytb) was selected for amplification by polymerase chain reaction (PCR). The primer pair L14919/H16064 (Burbrink et al. 2000; de Queiroz et al. 2002) was used to amplify the Cytb mitochondrial fragment.

The PCR was carried out following Thanou et al. (2020). PCR products were checked using a UV transilluminator (Wealtec). Amplicons showing a single clear band of the expected size were purified using the Exo-SAP-IT® kit (Affymetrix USB). Sequencing was carried out by Macrogen Europe (Milan, Italy) on an ABI 3130xL sequencer (Applied

Table 1. Geographic origins of the collected *Telescopus fallax* (Fleischmann, 1831) samples from Maltese Archipelago and their Cytb GenBank Accession Numbers (A.N). Geographical decimal coordinates are reported according to the WGS84 datum.

#	Locality	Region	Latitude N	Longitude E	GenBank A.N.
1	Birżebbuġa	E Malta	35.837	14.520	PZ160441
2	Siġġiewi	S Malta	35.840	14.408	PZ160442
3	Siġġiewi	S Malta	35.834	14.422	PZ160443
4	Żabbar	N Malta	35.929	14.433	PZ160444
5	Fort Campbell	NW Malta	35.963	14.387	PZ160445
6	Fort Campbell	NW Malta	35.963	14.386	PZ160446
7	Marsalforn	N Gozo	36.071	14.253	PZ160447
8	Gebel Ciantar	S Malta	35.845	14.398	PZ160448

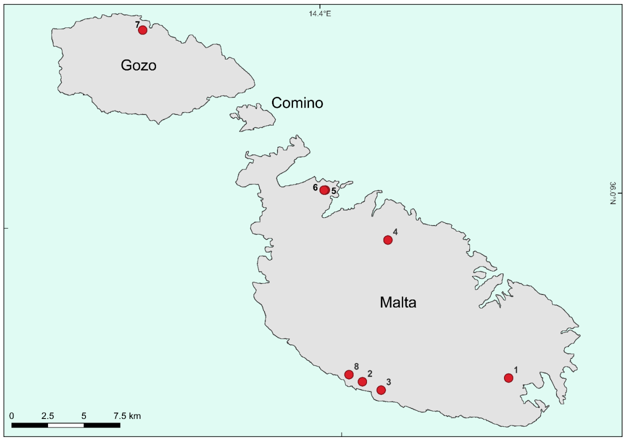

Figure 1. Distribution of *Telescopus fallax* (Fleischmann, 1831) samples across the Maltese archipelago. Numbers refer to those reported in Table 1.

Biosystems). Chromatograms were evaluated based on their Phred quality scores (Richterich 1998) and only sequences with continuous high-quality reads (QV > 20) were retained for subsequent analyses.

The newly generated Cytb sequences from Maltese *Telescopus fallax* were deposited in the public database GenBank (see Table 1). With the aim of comparing the newly generated Cytb sequences with those of other populations from the *T. fallax* complex [including *T. hoogstraali* Schmidt and Marx, 1956 and *T. nigriceps* (Ahl, 1924)], 64 published Cytb sequences were downloaded from the GenBank and included in our analyses (see Nagy et al. 2003; Eimermacher 2012; Kyriazi et al. 2013; Šmíd et al. 2019; Kornilios and Thanou 2024; see also Appendix 1). In addition, *T. dhara* (Forskål, 1775) (GenBank Accession number, A.N., "MK373067") was used as an outgroup.

The final dataset was aligned using MEGA12 (Kumar et al. 2024) using the ClustalW algorithm (Thompson et al. 1994). All sequences were translated into amino acids to check stop codons. The final phylogenetic tree was inferred using Maximum Likelihood (ML) analysis implemented in MEGA12, with the "Use all sites" option selected for the treatment of gaps and missing data. Node support was assessed through bootstrap analysis (Felsenstein 1985) with 1000 replicates. The best-fitting models of nucleotide substitution were selected using PartitionFinder v.1.0.1 (Lanfear et al. 2012) under the Akaike information criterion (AIC). The best-fit model for the study data set proved to be a Generalised Time-Reversible model of sequence evolution with gamma-distributed rate variation among sites (GTR + Γ).

RESULTS

Eight road-killed *Telescopus fallax*, four from Malta, and one from Gozo (Fig. 1; Table 1), were sampled between September 2025 and March 2026 and processed for DNA extraction. Eight newly generated Cytb sequences (1,117 bp) were obtained and included in the analyses (Table 1).

The phylogenetic tree, rooted on *Telescopus dhara*, showed a strongly structured topology, consistent with the most recent phylogenetic frameworks proposed for the *T. fallax* complex (Šmíd et al. 2019; Kornilios and Thanou 2024) (Fig. 2).

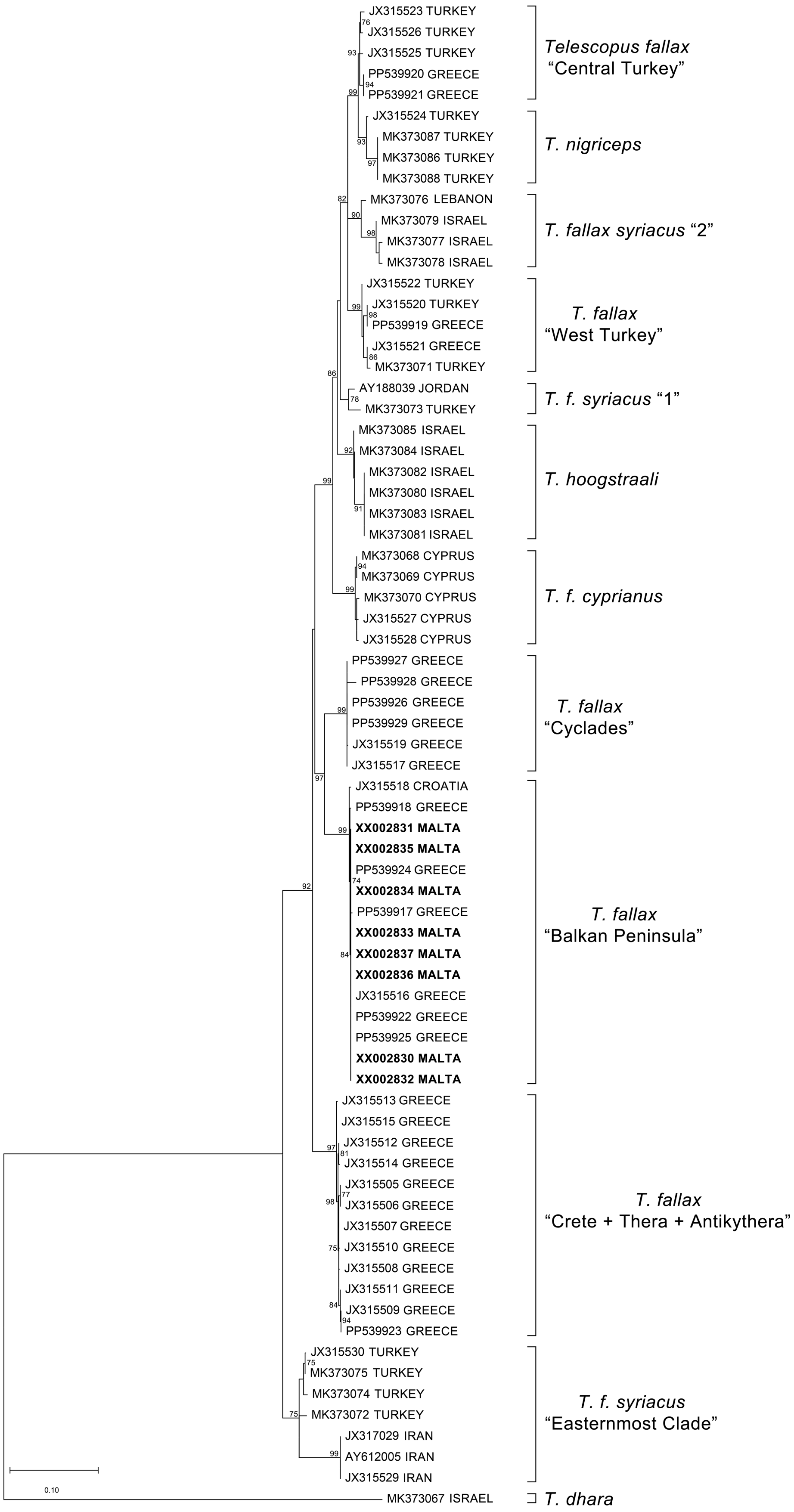

Figure 2. Maximum likelihood phylogenetic tree of *Telescopus fallax* complex based on a 1117-bp-long fragment of the mitochondrial Cytb gene. *Telescopus dhara* (Forskål, 1775) (GenBank A.N., MK373067) was used as outgroup. Bootstrap values are indicated at the nodes to represent statistical support. Our newly generated sequences are reported in bold. The clades are named following Kornilios and Thanou (2024).

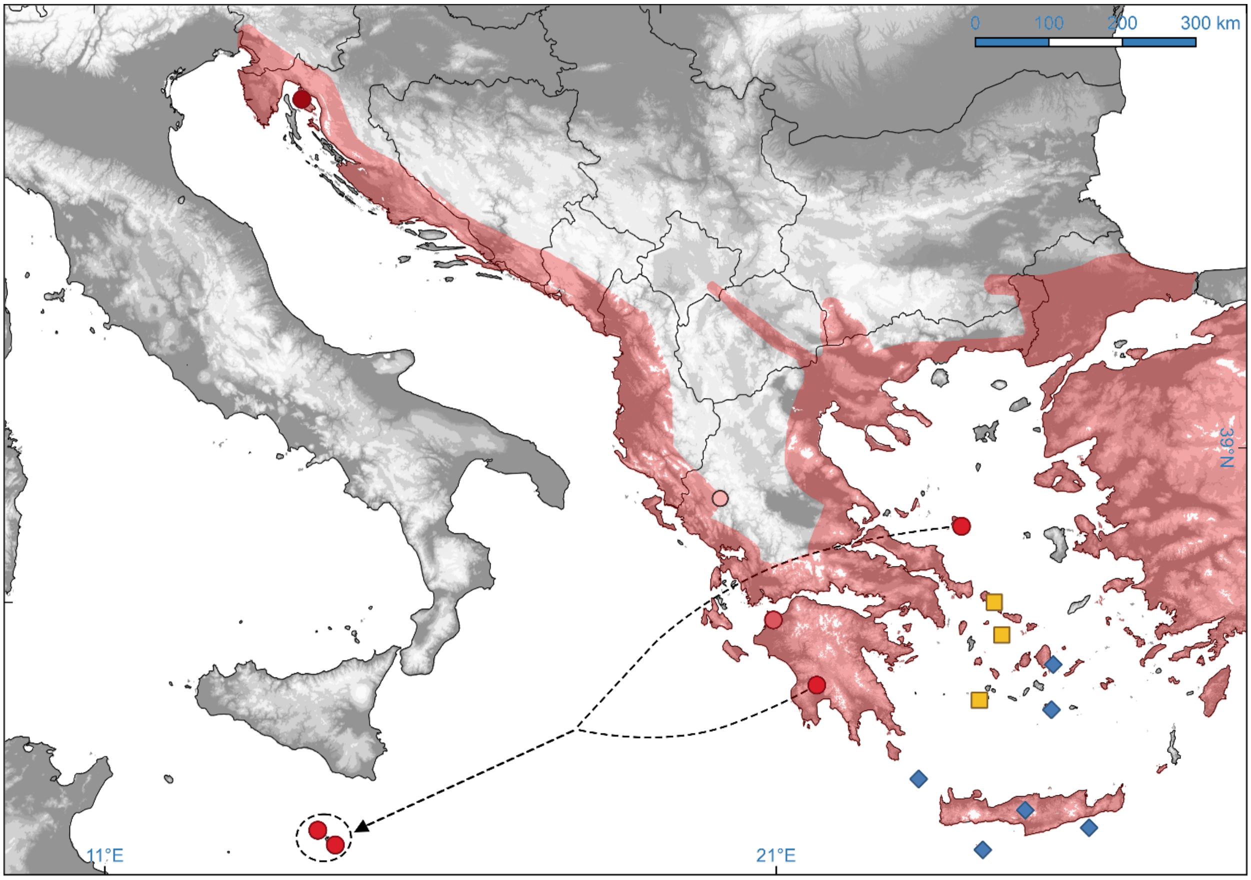

Figure 3. European Cat Snake, *Telescopus fallax* complex approximate western distribution (pink area) obtained from Sindaco et al. (2013). The symbols represent the major clades reported by Kornilios and Thanou (2024): Balkan Peninsula clade (dots), Crete + Thera + Antikythera clade (blue diamonds), Cyclades clade (yellow squares). The haplotypes are reported as different colours only for the Balkan Peninsula clade.

The sample with GenBank accession number "JX315524", labelled as *Telescopus fallax* in its GenBank account, cluster within the *T. nigriceps* clade, whereas "MK373071", reported as *T. fallax fallax*, falls into the *T. f.* "West Turkey" clade (Fig. 2; Appendix 1). The Maltese samples cluster within the "Balkan Peninsula" clade (*sensu* Kornilios and Thanou 2024), showing a sister clade relationship with the lineage from the Cyclades islands. Furthermore, all the newly generated Maltese *T. fallax* Cytb sequences share the same haplotype, which is identical to that recorded in mainland Greece and on the island of Skyros (Sporades, Greece).

DISCUSSION

Our results clearly show that the Maltese populations of *Telescopus fallax* belong to the so-called "Balkan Peninsula clade" (*sensu* Kornilios and Thanou 2024), which includes sequences from Croatia (Krk Island) and Greece (Epirus, the Peloponnese, and Skyros; see Fig. 3). The type locality of the species remains historically controversial. While Mertens and Müller (1928) restricted the *terra typica* to Trieste in north-eastern Italy, a population that has not yet been studied genetically, Fleischmann (1831) stated in the original description that the holotype was collected in Dalmatia (see dall'Asta 2011). However, both regions are most likely associated with the Balkan Peninsula clade based on currently available genetic evidence. Therefore, the Maltese population can be assigned to *T. fallax sensu stricto* and to the nominate subspecies. This conclusion agrees with the previous treatment of the Maltese populations as *T. f. fallax* (Mertens 1921; Lo Cascio and Sciberras 2020). However, earlier studies of phenotypic variation did not provide clear support for this subspecific attribution, which may instead have been based largely on the general habitus of the Maltese European Cat Snake, closely resembling that of Balkan populations (Fig. 4).

Figure 4. European Cat Snakes, *Telescopus fallax* (Fleischmann, 1831), newborn (A) and adult (B) individuals from Il-Blata l-Bajda (Malta).

Some authors have cautiously hypothesised that *Telescopus fallax* could be native on the Maltese archipelago (Lanza 1973; Schembri 1984; Schembri and Lanfranco 1996). However, the lack of genetic variability, the shared haplotype with most sequences of the "Balkan peninsula" clade and the absence of direct land connection between the Maltese archipelago and the Balkans strongly support a recent origin of *T. fallax* populations in Malta, likely via human-mediated dispersal processes, as suggested by several authors (Borg 1939; Lanfranco 1955; Lo Cascio and Sciberras 2020). Borg (1939) assumed that *T. fallax* was introduced to Malta with firewood transported to Floriana (Porto region) during the First World War, in the same way as *Hemorrhois algirus*, which remains confined around the Floriana area (Dobbs et al. 2025). However, Giglioli (1894) first mentioned *T. fallax* for Malta more than twenty years before the WWI. The literature on the reptiles of the Maltese archipelago prior to Giglioli (1894) is scarce (Adams 1870; De Betta 1874; Giglioli 1880; Gulia 1890) and only partial information is provided, which does not allow us to trace a precise timing of introduction and diffusion of *T. fallax* in Malta. Nevertheless, alternative hypotheses can also be considered, beyond those involving a recent introduction or multiple introduction waves between the late 19th and early 20th century.

The eastern Mediterranean islands have witnessed multiple cases of snake translocations, both in ancient and recent times (Pafilis 2010; Kyriazi et al. 2013; Mahtani-Williams et al. 2020), in a context where both Greek and Minoan civilisations held snakes in high ritual and symbolic regard (Håland 2011; Kornilios and Thanou 2024). *Zamenis situla* exemplifies this pattern: its distribution across certain Aegean islands appears to result from a recent dispersal from the Peloponnese and aligns with the distribution of ancient Hellenic colonies (Kyriazi et al. 2013), where it was traditionally regarded as the "snake of the house" (Pafilis 2010). A similar scenario applies to *Telescopus fallax* complex, whose insular distribution may partly reflect anthropochory associated with both Greek and Christian civilisations (Pafilis 2010; Kornilios and Thanou 2024). Indeed, *T. fallax* has been used on the Ionian Islands for Christian rites, probably of pagan origin, since at least the late 17th century (Gittenberger and Hoogmoed 1985; Warnecke 1988 and references therein). Although Malta was not directly colonised by the Hellenic world, it was repeatedly influenced and inhabited by Greek communities from ancient times, beginning with possible Mycenaean contacts in the 13th-12th century B.C. (Bonanno 1994). The Maltese archipelago underwent further Greek influences during the Byzantine period (Bonanno 1994) and subsequently, from the Middle Ages until the 19th century A.D., was affected by the settlement of many small Greek communities, linked to trade, religion and to events of exile and diaspora (Buxton 1922; Gardika 1972; Nicholas 2005; Mifsud Montanaro 2010). Given these multiple historical interactions between Maltese and Greek cultures, it is difficult to precisely assess the timing of colonisation of the Maltese archipelago by *T. fallax*. A Greek-mediated introduction nevertheless appears highly plausible. However, given the species' widespread distribution on the main island of Malta (Dobbs et al. 2025) and the limited literature available on species' record from the archipelago before the 20th century, an ancient introduction cannot be completely ruled out. Conversely, regarding the recently detected presence of *T. fallax* in Gozo (A. Sciberras, unpublished data; Dobbs et al. 2022), our data support the hypothesis of a human-mediated secondary colonisation from the nearby island of Malta, as previously reported by Dobbs et al. (2022).

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REFERENCES

Adams, A.L. (1870) Notes of a naturalist in the Nile Valley and Malta. Edmonston & Douglas, Edinburgh.

Basso, R., Vannuccini, M.L., Nerva, L., Mazza, G., Seno, M., & Mori, E. (2019) Multiple origins of the common chameleon in southern Italy. Herpetozoa, 32, 11–19. DOI: 10.3897/herpetozoa.32.e35611

Bonanno, A. (1994) Malte antique. Revue du Monde Musulman et de la Méditerranée, 71, 39–47. DOI: 10.3406/remmm.1994.1633

Bonardi, A., Ficetola, G.F., Razzetti, E., Canedoli, C., Falaschi, M., Lo Parrino, E., Rota, N., Padoa-Schioppa, E., & Sindaco, R. (2022) ReptIslands: Mediterranean islands and the distribution of their reptile fauna. Global Ecology and Biogeography, 31, 840–847. DOI: 10.1111/geb.13490

Borg, J. (1939) Our insect visitors. Archivium Melitense, 10, 191–197.

Burbrink, F.T., Lawson, R., & Slowinski, J.B. (2000) Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. Evolution, 54, 2107–2118. DOI: 10.1554/0014-3820(2000)054[2107:MDPOTP]2.0.CO;2

Buxton, L.H.D. (1922) The Ethnology of Malta and Gozo. The Journal of the Royal Anthropological Institute of Great Britain and Ireland, 52, 164–211. DOI: 10.2307/284373

dall'Asta, A. (2011) *Telescopus fallax* (Fleischmann, 1831) In: Fauna d'Italia, Reptilia, vol. XLV. (ed. by C. Corti, M. Capula, L. Luiselli, E. Razzetti and R. Sindaco), pp. 578–582. Edizioni Calderini, Bologna.

De Betta, E.C. (1874) Parte quarta. Rettili ed Anfibi (107 pp.). In: Fauna d'Italia (ed by Cornalia E.), pp. 1870–1874. Vallardi, Milano.

de Queiroz, A., Lawson, R., & Lemos-Espinal, J.A. (2002) Phylogenetic relation-ships of North American garter snakes (*Thamnophis*) based on fourmitochondrial genes: how much DNA sequence is enough? MolecularPhylogenetics and Evolution, 22, 315–329. DOI: 10.1006/mpev.2001.1074

Dobbs, E.G.S., Griffiths, R.A., Dobbs, N.R., Kell, C., Caruso, C. & Lofaro, A. (2022) Distribution of the native and naturalised snake species in the Maltese Archipelago. British Herpetological Society Reports, 2, 11–13.

Dobbs, E.G.S., Dobbs, N.R., Griffiths, R.A., Kell, C., Caruso, C. & Lofaro, A. (2025) An analysis of the distributions of the native and naturalised snake species in the Maltese archipelago. Nature Trust Malta, Malta.

Eimermacher, T.G. (2012) Phylogenetic Systematics Of Dispholidine Colubrids (Serpentes: Colubridae). PhD Thesis, UT Arlington.

Faraone, F.P., Melfi, R., Di Nicola, M.R., Giacalone, G. & Lo Valvo, M. (2022) Phylogenetic affinities of the Italian population of Eastern Montpellier Snake, *Malpolon insignitus* (Serpentes, Lamprophiidae). Herpetology Notes, 15, 711–715.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution; International Journal of Organic Evolution, 39, 783–791. DOI: 10.1111/j.1558-5646.1985.tb00420.x

Fleischmann, F.L. (1831) Dalmatiae nova serpentum genera. Inaugural Dissertation, Erlangen

Gardika, E. (1972) Η ίδρυση του ελληνικού προξενείου της Μάλτας (1827). Mnemon, 2, 118–134. DOI: 10.12681/mnimon.143

Giglioli, E.H. (1880) Elenco dei Mammiferi, degli Uccelli e dei Rettili ittiofagi od interessanti per la pesca, appartenenti alla fauna italiana, e catalogo degli Anfibi e dei Pesci italiani. N. 11. Esposizione Internazionale di Pesea in Berlino 1880. Sezione Catalogo degli espositori e delle co se esposte. Stamperia Reale, Firenze.

Giglioli, E.H. (1894) La fauna dell'Italia, specialmente in riguardo agli animali Vertebrati. In: La Terra. Trattato popolare di geografia universale. II (ed. by G. Marinelli), pp. 448–466. F. Vallardi, Milano.

Gittenberger, E. & Hoogmoed, M.S. (1985) Notizen zum christlichen Schlangenkult auf der ionischen Insel Kefallinia (Cephalonia). Salamandra, 21, 90–94.

Gulia, G. (1890) Erpetologia maltese. Il Naturalista Maltese, 1, 14–15.

Håland, E.J. (2011) Saints and Snakes: Death, Fertility, and Healing in Modern and Ancient Greece and Italy. Performance and Spirituality, 2, 111–151.

Kornilios, P., & Thanou, E. (2024) Molecular evidence reveals human-mediated dispersals of snake species in the Aegean Islands. Salamandra, 60, 201–207.

Kumar, S., Stecher, G., Suleski, M., Sanderford, M., Sharma, S. & Tamura, K. (2024) MEGA12: Molecular Evolutionary Genetic Analysis Version 12 for Adaptive and Green Computing. Molecular Biology and Evolution, 41, msae263. DOI: 10.1093/molbev/msae263

Kyriazi, P., Kornilios, P., Nagy, Z.T., Poulakakis, N., Kumlutaş¸ Y., Ilgaz, Ç., Avcı, A., Göçmen, B. & Lymberakis, P. (2013) Comparative phylogeography reveals distinct colonization patterns of Cretan snakes. Journal of Biogeography, 40, 1143–1155. DOI: 10.1111/jbi.12057

Lanfear, R., Calcott, B., Ho, S.Y.W., & Guindon, S. (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution, 29, 1695–1701. DOI: 10.1093/molbe v/ mss020

Lanfranco, G. (1955) Reptiles, Amphibians of the Maltese Islands. Snakes, geckos, lizards, turtles, frogs, found in Malta. In: Malta Year Book 1955, pp. 198–209. La Valletta.

Lanza, B. (1973) Gli Anfibi e i Rettili delle isole circumsiciliane. Lavori della Società italiana di Biogeografia, 3, 755–804. DOI: 10.21426/B63110065

Lo Cascio, P., & Sciberras, A. (2020) "Cold-blooded" travellers around Sicily: how introductions and extinctions have shaped the recent herpetofauna of Circum-Sicilian and Maltese islands. In: Life on islands. 1. Biodiversity in Sicily and surrounding islands. Studies dedicated to Bruno Massa. (ed. by T. La Mantia, E. Badalamenti, A. Carapezza, P. Lo Cascio and A. Troia), pp. 355–390. Edizioni Danaus, Palermo.

Masseti, M., & Zuffi, M.A.L. (2011) On the origin of the population of asp viper, *Vipera aspis hugyi* Schinz, 1833, of the island of Montecristo, in the Northern Tyrrhenian Sea (Tuscan archipelago, Italy). Herpetological Bulletin, 117, 1–9.

Mahtani-Williams, S., Fulton. W., Desvars-Larrive. A., et al. (2020) Landscape Genomics of a Widely Distributed Snake, *Dolichophis caspius* (Gmelin, 1789) across Eastern Europe and Western Asia. Genes 11, e1218. DOI: 10.3390/genes11101218

Mertens, R. (1921) Zur Kenntnis der Reptilienfauna von Malta. Zoologischer Anzeiger, 53, 236–240.

Mertens, R., & Müller, L. (1928) Die Amphibien und Reptilien Europas. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 41, 1–62.

Mifsud Montanaro, G. (2010) Orthodox Churches in Malta. Diocesan Ecumenical Commission, Malta.

Mori, E., Andreone, F., Viviano, A. et al. (2022) Aliens coming by ships: distribution and origins of the ocellated skink populations in peninsular Italy. Animals, 12, 1709. DOI: 10.3390/ani12131709

Nagy, Z.T., Joger, U., Wink, M., Glaw, F., & Vences, M. (2003) Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from nuclear and mitochondrial gene phylogenies. Proceedings of the Royal Society, Biological Sciences, 270, 2613–2621. DOI: 10.1098/rspb.2003.2547

Nicholas, N. (2005) A History of the Greek Colony of Corsica. Journal of the Hellenic Diaspora, 16, 33–78.

Pafilis, P. (2010) A brief history of Greek herpetology. Bonn Zoological Bulletin, 57, 329–345.

Richterich, P. (1998) Estimation of errors in 'raw' DNA sequences: a validation study. Genome Research, 8, 251–259. DOI: 10.1101/gr.8.3.251

Schembri, P.J. (1984) Maltese snakes. Civilization, 13, 350–351.

Schembri, P.J., & Lanfranco, E. (1996) Introduced species in the Maltese Islands. In: Introduction of alien species of flora and fauna. (ed. by A.E. Baldacchino and A. Pizzuto), pp. 1–21. Environment Protection Department, Malta.

Sherpa, S., Salvi, D. Silva-Rocha, I., Capblancq, T., Paris, J.R., Carretero, M.A., & Ficetola, G.F. (2024) Reconstructing the Complex Colonisation Histories of Lizards Across Mediterranean Archipelagos. Journal of Biogeography, 51, 157–172. DOI: 10.1111/jbi.14739

Silva-Rocha, I., Salvi, D., Sillero, N., Mateo, J.A., & Carretero, M.A. (2015) Snakes on the Balearic Islands: an invasion tale with implications for native biodiversity conservation. PLoS ONE 10, e0121026. DOI: 10.1371/journal.pone.0121026

Sindaco, R., Venchi, A., & Grieco, C. (2013) The Reptiles of the Western Palearctic. 2. Annotated checklist and distributional atlas of the snakes of Europe, North Africa. Middle East and Central Asia, with an update to the, Vol 1, Edizioni Belvedere, Latina.

Šmíd J., Göçmen, B., Crochet, P.A., Trape, J.F., Mazuch, T., Uvizl, M., & Nagy Z.T. (2019) Ancient diversification, biogeography, and the role of climatic niche evolution in the Old World cat snakes (Colubridae, *Telescopus*). Molecular Phylogenetics and Evolution, 134, 35–49. DOI: 10.1016/j.ympev.2019.01.015

Thompson, J.D., Higgins, D.G., & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research, 22, 4673–4680. DOI: 10.1093/nar/22.22.4673

Thake, M. (1985) The biogeography of the Maltese islands, illustrated by the Clausiliidae. Journal of Biogeography, 12, 269–287. DOI: 10.2307/2844999

Thanou, E., Kornilios, P., Lymberakis, P., & Leaché, A.D. (2020) Genomic and mitochondrial evidence of ancient isolations and extreme introgression in the four-lined snake. Current Zoology, 66, 99–111. DOI: 10.1093/cz/zoz018

Vella, A., Vella, N., Mifsud, C.M., & Magro, D. (2020) First records of the Brahminy blindsnake, *Indotyphlops braminus* (Daudin, 1803) (Squamata: Typhlopidae) from Malta with genetic and morphological evidence. Natural and Engineering Sciences, 5, 122–135. DOI: 10.28978/nesciences.832967

Warnecke, H. (1988) *Telescopus fallax* (Fleischmann, 1831) auf den ozeanischen Strophaden-Inseln? (Serpentes: Colubridae). Salamandra, 24, 16–19.

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Appendix 1. Origin and source of the used Cytb sequences of the *Telescopus fallax* complex downloaded from GenBank. The clades are named following Kornilios and Thanou (2024) as also reported in Fig. 2. "*T. f.*", *Telescopus fallax*. The "Taxon" column refers to the taxonomic labels given in the respective GenBank records.

Taxon	**Locality**	**Country**	**GenBank A.N.**	**Clade**	**Source**
T. dhara	Horvot Shivta	Israel	MK373067	Outgroup	Šmíd et al. 2019
T. fallax	Thira island	Greece	JX315505	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Thira island	Greece	JX315506	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Chrysi island	Greece	JX315507	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Chrysi island	Greece	JX315508	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Crete island	Greece	JX315509	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Koufonisi island	Greece	JX315510	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Crete island	Greece	JX315511	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Antikythera island	Greece	JX315512	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Crete island	Greece	JX315513	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Antikythera island	Greece	JX315514	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Gaydos island	Greece	JX315515	*T. f.* Crete+Thera+Antikythera	Kyriazi et al. 2013
T. fallax	Skyros island	Greece	JX315516	*T. f.* Balkan Peninsula	Kyriazi et al. 2013
T. fallax	Milos island	Greece	JX315517	*T. f.* Cyclades	Kyriazi et al. 2013
T. fallax	Krk island	Croatia	JX315518	*T. f.* Balkan Peninsula	Kyriazi et al. 2013
T. fallax	Syros island	Greece	JX315519	*T. f.* Cyclades	Kyriazi et al. 2013
T. fallax	Manisa	Turkey	JX315520	*T. f.* West Turkey	Kyriazi et al. 2013
T. fallax	Kastelorizo island	Greece	JX315521	*T. f.* West Turkey	Kyriazi et al. 2013
T. fallax	Mersin	Turkey	JX315522	*T. f.* West Turkey	Kyriazi et al. 2013
T. fallax	Izmir	Turkey	JX315523	*T. f.* Central Turkey	Kyriazi et al. 2013
T. fallax	Kilis	Turkey	JX315524	*Telescopus nigriceps*	Kyriazi et al. 2013
T. fallax	Adana	Turkey	JX315525	*T. f.* Central Turkey	Kyriazi et al. 2013
T. fallax	Adana	Turkey	JX315526	*T. f.* Central Turkey	Kyriazi et al. 2013
T. fallax fallax	Bodrum	Turkey	MK373071	*T. f.* West Turkey	Šmíd et al. 2019
T. fallax	Ioannina Island, Lake Pamvotida	Greece	PP539917	*T. f.* Balkan Peninsula	Kornilios and Thanou 2024
T. fallax	Strofylia	Greece	PP539918	*T. f.* Balkan Peninsula	Kornilios and Thanou 2024
T. fallax	Serifos island	Greece	PP539919	*T. f.* Cyclades	Kornilios and Thanou 2024
T. fallax	Kasos island	Greece	PP539920	*T. f.* Central Turkey	Kornilios and Thanou 2024
T. fallax	Kasos island	Greece	PP539921	*T. f.* Central Turkey	Kornilios and Thanou 2024
T. fallax	Meligalas	Greece	PP539922	*T. f.* Balkan Peninsula	Kornilios and Thanou 2024
T. fallax	Crete island	Greece	PP539923	*T. f.* Crete+Thera+Antikythera	Kornilios and Thanou 2024
T. fallax	Skyros island	Greece	PP539924	*T. f.* Balkan Peninsula	Kornilios and Thanou 2024
T. fallax	Skyros island	Greece	PP539925	*T. f.* Balkan Peninsula	Kornilios and Thanou 2024
T. fallax	Milos island	Greece	PP539926	*T. f.* Cyclades	Kornilios and Thanou 2024
T. fallax	Milos island	Greece	PP539927	*T. f.* Cyclades	Kornilios and Thanou 2024
T. fallax	Syros island	Greece	PP539928	*T. f.* Cyclades	Kornilios and Thanou 2024
T. fallax	Andros island	Greece	PP539929	*T. f.* Cyclades	Kornilios and Thanou 2024
T. fallax	Cyprus island	Cyprus	JX315527	*T. f. cyprianus*	Kyriazi et al. 2013
T. fallax	Cyprus island	Cyprus	JX315528	*T. f. cyprianus*	Kyriazi et al. 2013
T. fallax cyprianus	Cyprus island	Cyprus	MK373068	*T. f. cyprianus*	Šmíd et al. 2019
T. fallax cyprianus	Cyprus island	Cyprus	MK373069	*T. f. cyprianus*	Šmíd et al. 2019
T. fallax cyprianus	Cyprus island	Cyprus	MK373070	*T. f. cyprianus*	Šmíd et al. 2019
T. fallax iberus	Estehard	Iran	AY612005	*T. f. syriacus* Easternmost Cl.	Nagy et al. 2003
T. fallax	Estehard	Iran	JX315529	*T. f. syriacus* Easternmost Cl.	Kyriazi et al. 2013
T. fallax iberus	Estehard	Iran	JX317029	*T. f. syriacus* Easternmost Cl.	Eimermacher 2012
T. fallax	Tasan	Jordan	AY188039	*T. f. syriacus* 1	Nagy et al. 2003
T. fallax syriacus	Sanliurfa	Turkey	JX315530	*T. f. syriacus* Easternmost Cl.	Kyriazi et al. 2013
T. fallax syriacus	Sanliurfa	Turkey	MK373073	*T. f. syriacus* 1	Šmíd et al. 2019
T. fallax syriacus	Sanliurfa	Turkey	MK373074	*T. f. syriacus* Easternmost Cl.	Šmíd et al. 2019
T. fallax syriacus	Sanliurfa	Turkey	MK373075	*T. f. syriacus* Easternmost Cl.	Šmíd et al. 2019
T. fallax syriacus	El Barouk	Lebanon	MK373076	*T. f. syriacus* 2	Šmíd et al. 2019
T. fallax syriacus	Gilboa Desert	Israel	MK373077	*T. f. syriacus* 2	Šmíd et al. 2019
T. fallax syriacus	Meral	Israel	MK373078	*T. f. syriacus* 2	Šmíd et al. 2019
T. fallax syriacus	Hare Gilboa	Israel	MK373079	*T. f. syriacus* 2	Šmíd et al. 2019
T. hoogstraali	Yeroham	Israel	MK373080	*Telescopus hoogstraali*	Šmíd et al. 2019
T. hoogstraali	Zomet HaNegev	Israel	MK373081	*Telescopus hoogstraali*	Šmíd et al. 2019

T. hoogstraali	Zin Bridge	Israel	MK373082	*Telescopus hoogstraali*	Šmíd et al. 2019
T. hoogstraali	Zomet Zipporim	Israel	MK373083	*Telescopus hoogstraali*	Šmíd et al. 2019
T. hoogstraali	Nahal Nizana	Israel	MK373084	*Telescopus hoogstraali*	Šmíd et al. 2019
T. hoogstraali	Mizpe Ramon	Israel	MK373085	*Telescopus hoogstraali*	Šmíd et al. 2019
T. nigriceps	Kilis	Turkey	MK373086	*Telescopus nigriceps*	Šmíd et al. 2019
T. nigriceps	Kilis	Turkey	MK373087	*Telescopus nigriceps*	Šmíd et al. 2019
T. nigriceps	Sanliurfa	Turkey	MK373088	*Telescopus nigriceps*	Šmíd et al. 2019