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National and Kapodistrian University of Athens

NATIONAL AND KAPODISTRIAN UNIVERSITY OF ATHENS

POSTGRADUATE PROGRAMME

ECOLOGY AND BIODIVERSITY CONSERVATION

MASTER THESIS

THE PHYLOGEOGRAPHY OF *ARMADILLO OFFICINALIS* (ISOPODA: ONISCIDEA) IN CYPRUS

IOANNIS ALEXIOU

BSc IN AGRICULTURE

SUPERVISOR: ARISTEIDIS PARMAKELIS

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ATHENS, 2019

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ΠΕΡΙΛΗΨΗ

Η Κύπρος αποτελεί ένα εξαιρετικά ενδιαφέρον μεσογειακό νησί ως προς την οικολογία, τη γεωλογία και τη γεωγραφία της. Μαζί με τη Νότια Ανατολία, αναγνωρίζεται ως ένα θερμό σημείο βιοποικιλότητας στη Μεσογειακή Λεκάνη. Ακόμη, παρουσιάζει πολύπλοκη γεωλογική εξέλιξη, συμπεριλαμβανομένου του σχηματισμού παλαιο-νησιών, καθώς και πολυάριθμα μοναδικά γεωγραφικά χαρακτηριστικά, όπως το μεγάλο μέγεθος και η υψηλή γεωγραφική απομόνωση. Ωστόσο, τα πρότυπα της βιοποικιλότητας στο νησί δεν είναι επαρκώς μελετημένα, ενώ η επιρροή των παρελθοντικών γεωλογικών γεγονότων και της γεωγραφίας στη βιοποικιλότητα της Κύπρου παραμένει αδιευκρίνιστη.

Με δεδομένη την αποσπασματική γνώση σχετικά με τους ιστορικούς και οικολογικούς παράγοντες που καθορίζουν τα πρότυπα της βιοποικιλότητας της Κύπρου, η παρούσα έρευνα προσπαθεί να προσφέρει μερικά στοιχεία προς αυτή την κατεύθυνση μέσα από τη μελέτη της κατανομής των γενεαλογικών γραμμών του *Armadillo officinalis* στην Κύπρο. Το *Armadillo officinalis* (Isopoda: Oniscidea: Armadillidae), καθώς και άλλα χερσαία ισόποδα, προσφέρεται ως οργανισμός-μοντέλο για τέτοιου είδους προσεγγίσεις σε νησιωτικά συστήματα, καθώς εμφανίζει εκτεταμμένη κατανομή, βρίσκεται σε μεγάλη ποικιλία βιοτόπων, παρουσιάζει μεγάλα μεγέθη πληθυσμών και ταυτόχρονα χαρακτηρίζεται από χαμηλή ικανότητα διασποράς.

Στην παρούσα έρευνα χρησιμοποιήθηκαν μιτοχονδριακές νουκλεοτιδικές αλληλουχίες προκειμένου: α) να εκτιμηθεί το επίπεδο της γενετικής ποικιλότητας των πληθυσμών του *Armadillo officinalis*στο νησί, β) να διερευνηθούν οι φυλογενετικές σχέσεις των πληθυσμών του είδους και γ) να αποσαφηνιστεί κατά πόσο οι πληθυσμοί του νησιού ανήκουν σε μία η περισσότερες γενεαλογικές γραμμές και πιθανά διαφορετικά είδη. Επιπρόσθετα, με χρήση γεωχωρικών δεδομένων έγινε προσπάθεια να διαπιστωθεί ποια είναι η επίδραση της γεωλογικής εξέλιξης του νησιού και των περιβαλλοντικών συνθηκών στην κατανομή των γενεαλογικών γραμμών του είδους. Ειδικότερα, εφαρμόστηκαν φυλογενετικές αναλύσεις, αναλύσεις φυλογεωγραφικής διάχυσης, μέθοδοι οριοθέτησης ειδών, αναλύσεις χρονολόγησης και μοντέλα

κατανομής ειδών, χρησιμοποιώντας τους μιτοχονδριακούς μοριακούς δείκτες 16S, COI και cytb, περιβαλλοντικά δεδομένα και γεωχωρικά δεδομένα θέσης.

Τα αποτελέσματα υποδεικνύουν αδιαμφισβήτητα το υψηλό επίπεδο της γενετικής ποικιλότητας του *Armadillo officinalis* στο νησί, καθώς και την παρουσία δύο συμπάτριων γενεαλογικών γραμμών του είδους στην Κύπρο: τη γενεαλογική γραμμή Α, η οποία περιλαμβάνει πληθυσμούς από όλη την έκταση της Κύπρου και τη γενεαλογική γραμμή Β, η οποία περιλαμβάνει πέντε πληθυσμούς από το βορειοανατολικό τμήμα της Κύπρου. Η γενεαλογική γραμμή Β συνδέεται πολύ στενά με πληθυσμούς προερχόμενους από άλλες μεσογειακές περιοχές που συμπεριλήφθηκαν στην μελέτη. Δια μέσου της χρονολόγησης, προκύπτει ότι οι δύο γενεαλογικές γραμμές διαφοροποιήθηκαν μεταξύ τους κατά το Ύστερο Μειόκαινο και διαφοροποιήθηκαν περαιτέρω κυρίως κατά το Πλειστόκαινο. Η κατανομή των δυο γενεαλογικών γραμμών στο νησί φαίνεται να επηρεάζεται από τη θερμοκρασία. Η γενεαλογική γραμμή Α αποτελεί πιθανότατα διακριτή μορφή, γεγονός που πιθανόν να οφείλεται στη μακροχρόνια γεωγραφική απομόνωση του νησιού. Η μικρότερη γεωγραφική κατανομή της γενεαλογικής γραμμής Β στην Κύπρο σε σχέση με τη γενεαλογική γραμμή Α, πιθανά να οφείλεται στην απομόνωση της πρώτης στο ανατολικό τμήμα της Ζώνης του Πενταδάκτυλου, η οποία, σε συνδυασμό με την περιορισμένη ικανότητα διασποράς του *Armadillo officinalis*, λειτούργησε ως γεωγραφικό αδιέξοδο. Επιπροσθέτως, η ανύψωση των παλαιο-νησιών που συνέθεταν την Κύπρο κατά το Ύστερο Μειόκαινο (σήμερα, ο Οφιόλιθος του Τροόδους και η Οροσειρά της Κερύνειας) φαίνεται να αποτελεί την κύρια γεωλογική διεργασία που διαμόρφωσε την κατανομή των γενεαλογικών γραμμών του *Armadillo officinalis* στο νησί. Τέλος, η κατανομή των δύο γενεαλογικών γραμμών στην Κύπρο είναι πιθανό να έχει επηρεαστεί από την ανθρώπινη δραστηριότητα.

Η παρούσα έρευνα αποτελεί το πρώτο βήμα για την εξερεύνηση της σχέσης μεταξύ της γεωλογικής εξέλιξης της Κύπρου και των οργανισμών του νησιού, ενώ ταυτόχρονα υπογραμμίζει τους κύριους παράγοντες που καθορίζουν τη βιοποικιλότητα της Κύπρου. Μελλοντικά, προτείνεται η μελέτη της συστηματικής των δύο γενεαλογικών γραμμών του *Armadillo officinalis* με τη χρήση μορφομετρικών δεδομένων και πυρηνικών μοριακών δεικτών. Ακόμη, προτείνεται η χρήση της παρούσας μεθοδολογίας σε διαφορετικές ταξινομικές ομάδες στο νησί και

λαμβάνοντας υπόψη διαφορετικές πηγές δεδομένων, ώστε παρόμοια ευρήματα να αναλυθούν υπό το πρίσμα της συγκριτικής μεθόδου.

ABSTRACT

Cyprus is regarded as an extremely interesting Mediterranean island in terms of ecology, geology and geography. Together with South Anatolia, it is considered as a biodiversity hotspot in the Mediterranean Basin. Moreover, it demonstrates a complex geological evolution, including the formation of paleoislands, as well as numerous exceptional geographical characteristics, such as the large island size and the high level of geographical isolation. However, the patterns of genetic diversity in the island are understudied, while the effect of past historical geological parameters and geography on the biodiversity of Cyprus remains unknown.

Considering the limited information regarding the historical and ecological parameters that rule the patterns of biodiversity in Cyprus, the present study attempts to shed light on that matter through the study of the distribution of the lineages of *Armadillo officinalis* in Cyprus. *Armadillo officinalis* (Isopoda: Oniscidea: Armadillidae), as well as other terrestrial isopods, is an ideal model-organism for such approaches in island systems, as it demonstrates a large distribution, it is located in a variety of habitats, displays large population sizes, and at the same time it is characterized by a limited dispersal ability.

In the present study, mitochondrial nucleotide sequences were used to: a) estimate the level of genetic diversity of the populations of *Armadillo officinalis* in the island, b) investigate the phylogenetic relationships between the populations of the species and c) clarify whether the island populations belong to one or more lineages and potentially different species. Furthermore, using geospatial data, an attempt was made to estimate the effect of the geological evolution and the environmental conditions of the island on the distribution of the lineages of the species. More specifically, phylogenetic analysis, phylogeographic diffusion analysis, species delimitation, estimation of divergence times and species distribution models were applied, using the mitochondrial molecular markers 16S, COI and cytb, environmental data and geospatial data.

The results clearly demonstrate the high level of genetic diversity of *Armadillo officinalis* in the island, as well as the presence of two sympatric lineages of *Armadillo officinalis* in Cyprus: lineage A, which includes populations from all over Cyprus, and lineage B, which includes five populations from the northeastern part of Cyprus. Lineage B is strongly associated with the populations from other Mediterranean areas that were included in the study. Through the estimation of the divergence times, it came into a conclusion that the two lineages were differentiated during the Late Miocene and further diversified during the Pleistocene. The distribution of the two lineages in the island seems to be affected by temperature. Lineage A is probably a distinct unit, which is possibly the result of the long-time geographical isolation of the island. The smaller geographical distribution of lineage B in Cyprus in comparison to lineage A is probably due to the isolation of the first one in the the eastern part of Pentadactylos Zone which, combined with the limited dispersal ability of *Armadillo officinalis*, acted as a geographical culs-de-sac. Furthermore, the uplift of paleoislands that consisted of Cyprus by the Late Miocene (nowadays, Troodos Ophiolite and Kyrenia Range) seems to be the main geological process that shaped the distribution of the lineages of *Armadillo officinalis* in the island. Lastly, the distribution of the two lineages in Cyprus probably has been affected by the human activity.

The present study acts as a first step for the exploration of the relationship between the geological evolution of Cyprus and Cypriot biota and highlights the main factors that affect the biodiversity of the island. In the future, the study of the systematics of the two lineages is suggested, using morphometric data and nuclear molecular markers. Moreover, it is suggested to apply the same methodology in different organisms and using various data sources, to analyze such foundings in a comparative way.

CONTENTS

List of abbreviations

The following list describes all acronyms, symbols and abbreviations used in the present study in alphabetical order.

16S: 16S ribosomal RNA

ABGD: Automatic Barcode Gap Discovery

ALT: altitude

ANN: Artificial Neural Networks

bGMYC: Bayesian implementation of the Generalized Mixed Yule Coalescent model

BI: Bayesian Inference

BIC: Bayesian Information Criterion

BIO: bioclimatic variable

bp: base pairs

bPTP: Bayesian implementation of the Poisson Tree Processes model

COI: cytochrome c oxidase I

CTAB: cetyl trimethyl ammonium bromide

Cytb: cytochrome b

DNA: deoxyribonucleic acid

ESM: ensembles of small models

ESS: Effective Sample Size

G: GAMMA

GMYC: Generalized Mixed Yule Coalescent

GTR: General Time-Reversible model

HKY: Hasagawa et al. (1985) model

HPD: highest posterior density

I: Invariant

K80: (Kimura 1980) model

Max: maximum

MCMC: Markov chain Monte Carlo

Min: minimum

MJ: Median-joining

ML: Maximum Likelihood

mPTP: multi-rate Poisson Tree Processes model

mtDNA: mitochondrial DNA

Mya: million years ago

NH_4OAc: ammonium acetate

NO.: number of

PA: pseudo-absences

PCA: principal component analysis

PCR: polymerase chain reaction

Pop.: population

pp: posterior probability

PTP: Poisson Tree Processes model

RF: Random Forest

RNA: ribonucleic acid

SDM: species distribution modeling

S.r.: substitution rate

T: temperature

TRI: terrain ruggedness index

TSS: True Skill Statistic

v.: version

vif: variance inflation factor

ya: years ago

Introduction

Islands as evolutionary laboratories

Islands are nature's evolutionary laboratories, providing numerous 'experiments' in the factors controlling biodiversity (Whittaker et al., 2017). Moreover, they highly contribute to the global biodiversity, containing 15-20 % of all terrestrial species (Whittaker et al., 2017). Mainland and island taxa are fundamentally different in evolutionary terms: on the mainland, species' ranges are often large and sensitive to range shifts as a result of a changing climate, geology and the subtle shifts in environmental tolerance; however, islands, provide comparatively smaller land areas that are geographically isolated, thus maintaining a remarkable diversity (Casquet et al., 2015).

The Mediterranean Sea contains more than 12000 islands, demonstrating exceptional species richness and level of endemism, as a result of a unique combination of paleogeography, paleoclimatology and geological history (Thanou et al., 2017). The Mediterranean Basin is considered as one of Earth's biodiversity hotspots, as its species richness is comparable to the tropics' (Médail et al., 2019). Furthermore, unexpected genetic diversity and complex phylogeographic histories have been found within Mediterranean islands for several species, such as *Trachelipus aegaeus* in the Aegean islands (Kamilari et al., 2014), *Podarcis filfolensis* in Malta (Salvi et al., 2014), *Metacrangony longipes* in the Balearic archipelago (Bauzà-ribot et al., 2011) and *Cyrtocarenum cunicularium* in Crete (Thanou et al., 2017).

However, the biodiversity patterns and genetic structure of populations and species within islands remain understudied in comparison to the mainland ones (Thanou et al., 2017). As a result, the patterns of genetic diversity in several Mediterranean islands remain understudied, despite their significance in biodiversity.

The study area: Cyprus

Cyprus is an example of an understudied Mediterranean island, even though it is characterized by a remarkable biodiversity, geology and geography. According to IUCN (2019), 1178 plant and animal species of Cyrpus have been assessed until today. Furthermore, Cyprus combined with South Anatolia, is regarded as one of the ten biodiversity hotspots in the Mediterranean Basin (Trias-Blasi et al., 2017). Moreover, Cyprus is considered to be a very important area for birds, as they use the island as a stop during their migrations between Europe and Africa (Giosa et al., 2018), and for plants, displaying a high plant diversity (Trias-Blasi et al., 2017).

Cyprus is also characterized by a complex geological evolution (Figure 1). The genesis of the island is the result of the subduction of the African plate beneath the Eurasian plate and the formation of Troodos Ophiolite (90 Mya), continued with the attachment of Mammonia Zone (230-75 million year old rocks) in its southwestern part (Unit of Environmental Studies, Research and Development Center-Intercollege, 2004). By the Late Miocene, Cyprus consisted of two paleoislands: the low-lying Troodos Ophiolite and Kyrenia Range, which began to rise as well (Poulakakis et al., 2013). Cyprus became a single insular entity for the first time during the Pleistocene, when Mesaoria basin, Kyrenia Range and Troodos Ophiolite were uplifted together (Poulakakis et al., 2013). As a result of its geological evolution, Cyprus consists of four geological zones: Pentadaktylos (Kyrenia) Zone; Troodos Zone or Troodos Ophiolite; Mamonia Zone or Complex; and, Zone of the autochthonous sedimentary rocks (Unit of Environmental Studies, Research and Development Center-Intercollege, 2004). However, the way the paleogeographical events have affected the biodiversity patterns in Cyprus remains unclear.

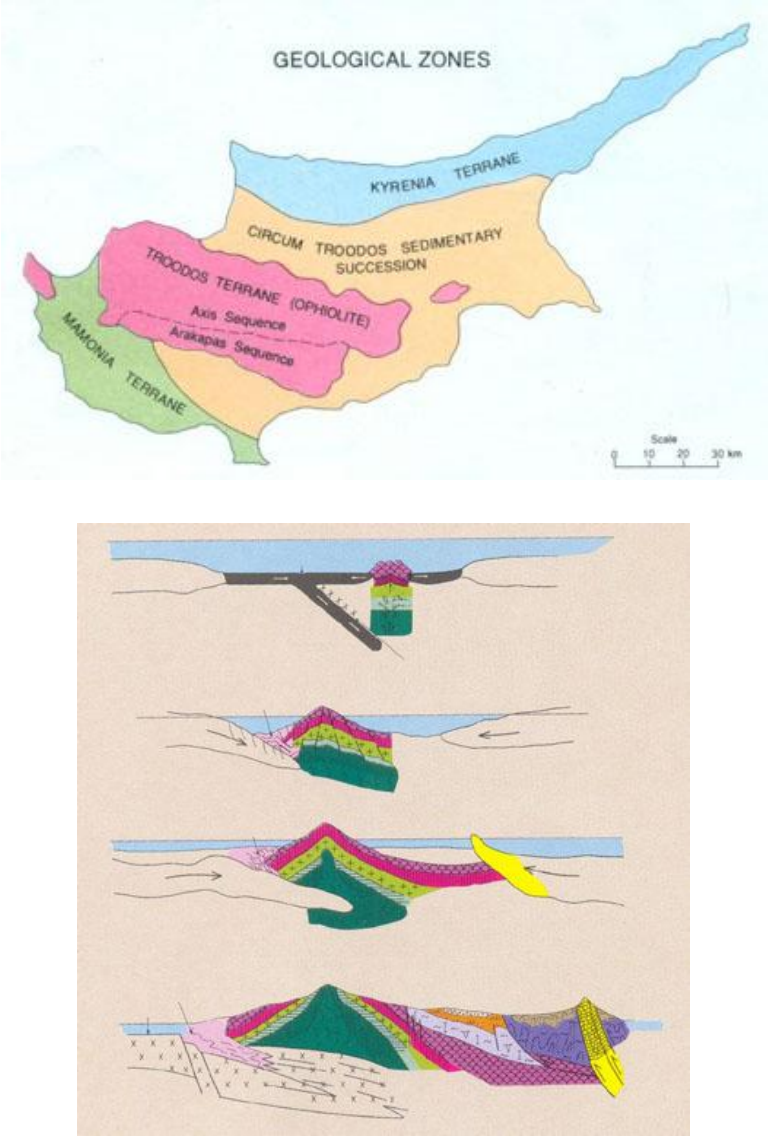


Figure 1. Geological structure (top) and evolution (bottom) of Cyprus. Retrieved from Unit of Environmental Studies, Research and Development Center-Intercollege, (2004).

From a geographical point of view, Cyprus is exceptional in terms of size and geographical isolation. Indeed, Cyprus is the third larger Mediterranean island after Sicily and Sardinia (Fuller et al., 2016). Furthermore, it is one of the most isolated Mediterranean islands (Moores et al., 1984). The connection between Cyprus and its surrounding mainland areas has been a matter of conflict: some researchers suggest that the island has never been connected to the mainland, while others argue that the island was at some point connected to the surrounding mainland areas (Syria, South

Anatolia) by a land bridge (Poulakakis et al., 2013). In any case, it is generally accepted that Cyprus remains isolated from the mainland since the end of the Messinian Salinity Crisis, when the drastic sea-level drop led to the connection of Cyprus to the mainland (Poulakakis et al., 2013). Thus, the biogeographical history of most Cypriot biota remains unclear. Poulakakis et al. (2013) identified three colonizer categories in Cyprus: old colonizers during the Late Miocene or Early Pliocene (by geodispersal or transmarine dispersal); younger colonizers from the Middle East (transmarine dispersal); and new settlers due to human-induced introductions.

To sum up, Cyprus is a biodiversity hotspot and is characterized by a complex geology and geography. At the same time, the patterns of genetic diversity in the island remain understudied, while it is unknown what the imprint of the island's geological evolution on Cypriot biodiversity.

The organism under study: *Armadillo officinalis*

The order Isopoda includes more than 10300 terrestrial, freshwater and marine species; however, the assumed monophyletic suborder Oniscidea is almost exclusively composed of terrestrial species, representing one of the most successful conquerors of the land (Broly et al., 2013). More than 3700 Oniscidea species (see Sfenthourakis and Taiti 2015) have been found in numerous moist and arid terrestrial regions, highlighting their autonomy from aquatic environments, according to Schmidt (2008). The majority of Oniscidea species use decaying plant material as a food source and thus they represent an irreplaceable component of the soil fauna (Schmidt, 2008).

Even though the Oniscidea are found in variable terrestrial habitats, they are usually characterized by a narrow environmental niche and a low dispersal ability; due to this, they often demonstrate increased morphological and genetic variation (Gentile and Argano, 2005; Sfenthourakis and Taiti, 2015). In addition, terrestrial isopods are highly affected by habitat heterogeneity (Gentile and Argano, 2005) and display high levels of endemism (Sfenthourakis, 1996). Taking everything into account, Oniscidea

species represent valuable model organisms when applying evolutionary studies on insular taxa (Gentile and Argano, 2005).

Genus *Armadillo* (Isopoda: Armadillidae) was described by Duméril (1816). It includes several species, while it is distributed in the Mediterranean basin and western Asia (Schmalfuss, 1996). While several diagnostic characters of this genus are also present in other genera of Armadillidae (such as the ability to conglobate, or the hour-glass-shaped telson), the stridulatory scale ledge on the propodus of pereopods IV and V are found exclusively on genus *Armadillo* (Schmalfuss, 1996). The great morphological similarity between the *Armadillo* species in the eastern Mediterranean basin and the Near East implies a recent speciation, probably as a result of Pleistocene climatic changes (Schmalfuss, 1996).

Armadillo officinalis (Figure 2) is a terrestrial isopod that is largely distributed in the Mediterranean basin and the western Black Sea (Boyko et al., 2008). Ecologically, it is considered as a nocturnal, xeric and iteroparous species, while its reproductive period depends on the geographic area (Montesanto and Cividini, 2017). *Armadillo officinalis* lives in various habitats with different substrates and plant communities (Montesanto and Cividini, 2017), however it is mostly found in coastal Mediterranean regions with Mediterranean-type vegetation, such as maquis and olive trees (Schmalfuss, 1996). The morphology of *Armadillo officinalis,* as well as the morphological differences between *Armadillo officinalis* and other species of the genus *Armadillo,* is thoroughly described in Schmalfuss (1996).

Figure 2. *Armadillo officinalis* sample from Cyprus. Additional information on its morphology can be found in Schmalfuss (1996).

Scope of the present study

Taking into account the limited information regarding the historical and ecological parameters that rule the patterns of biodiversity in Cyprus, the present study aims to:

- study the genetic diversity of *Armadillo officinalis* in Cyprus,
- investigate the phylogenetic relationships between the populations of *Armadillo officinalis* in the island,
- identify the number of lineages regarding the Cypriot populations of *Armadillo officinalis* and
- explore the effect of the geological evolution of Cyprus and environmental factors on the distribution of the genetic diversity of *Armadillo officinalis*

To answer the above, a combined approach using molecular and geospatial data methods was applied. At first, *Armadillo officinalis* was analyzed as a whole. That way, the intraspecific relationships within the species were investigated and used as a basis for the study. For this purpose, several phylogenetic analyses and phylogeographic diffusion analysis methods were used. Afterwards, *Armadillo*

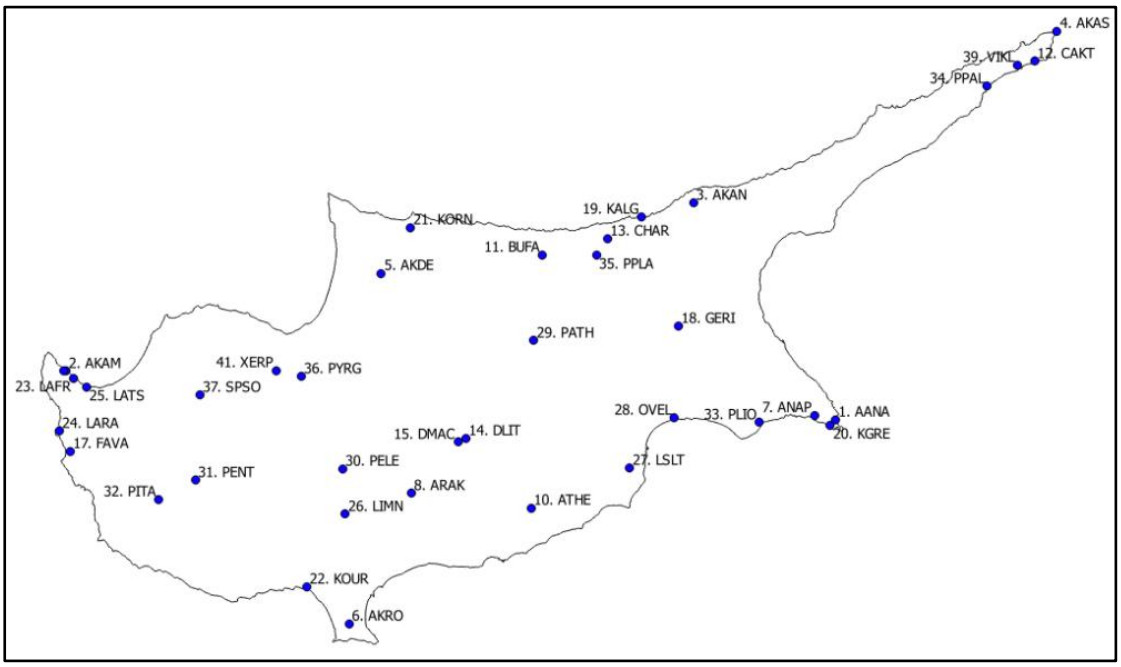
officinalis was split into a number of lineages, in order to associate each unit to the various paleogeographical events that have taken place in Cyprus. The identification of lineages was the result of numerous species delimitation methods, which led to the discovery of the *Armadillo officinalis* lineages in Cyprus. The relationship between the geological evolution of the island and the presence of the lineages *Armadillo officinalis* was further investigated through the study of their divergence times and their comparison in terms of genetics and environmental niche.

Materials and methods

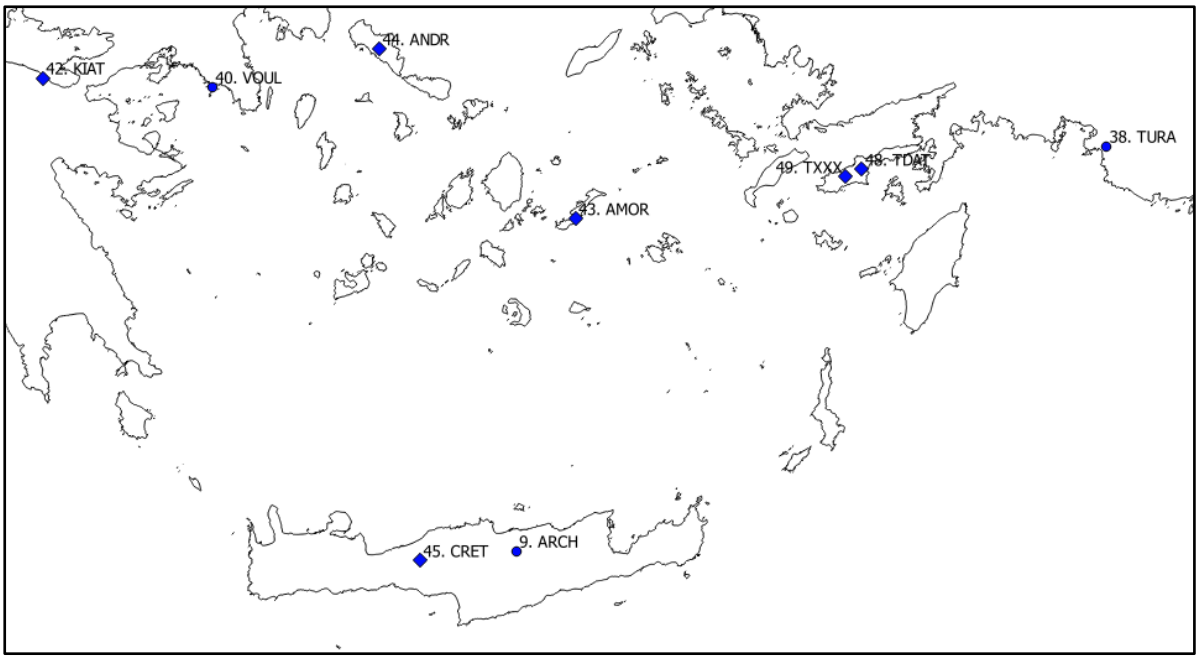
Sample collection, DNA extraction, PCR and sequence analysis

A total of 90 *Armadillo officinalis* specimens were included in this study, representing 38 populations in Cyprus, 1 in Tunisia, 1 in Italy, 6 in Greece, 4 in Turkey and 1 in Israel (Figure 3). 1-3 specimens were analyzed per population. Samples were preserved in 100% ethanol and stored in -20 ^{o}C. DNA extraction was performed as described in (Parmakelis et al., 2005), which is a modification of the protocol by (Winnepenninckx et al., 1993). Fragments of the mitochondrial loci Cytochrome c oxidase subunit I (COI), 16S ribosomal RNA (16S) and Cytochrome b (cytb) were PCR-amplified. These three molecular markers were chosen based on three reasons: their wide use in phylogenetic studies; their suitability for intraspecific phylogeographic studies; and their use in other case studies regarding Isopoda. PCR conditions, primers and master mixes used in the amplification of each marker are described in Appendix III. PCR products were purified using ammonium acetate and both strands of the PCR amplicon were sequenced via Sanger sequencing. The sequences were edited Διusing CodonCode Aligner v.2.0.6 (Codon Code Corporation) and aligned in MEGA v.7.0.26 (Kumar et al., 2015) using MUSCLE. The two coding genes (COI and cytb) were visually inspected for stop codons. Mean pairwise genetic distances for each marker and lineage were calculated in MEGA using the p-distance method. The number of haplotypes per gene fragment (Appendix II) was estimated using DnaSP v.6 (Rozas et al. 2017).

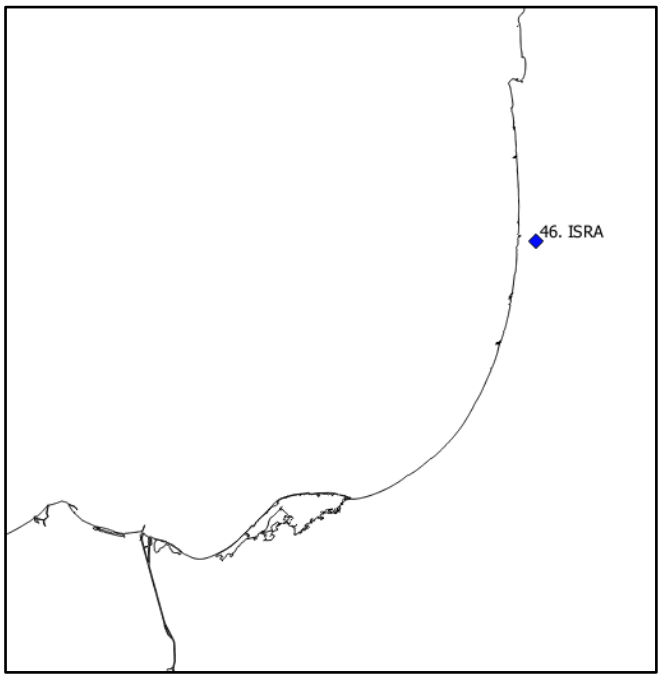
I. Cyprus



II. Greece and Turkey



III. Israel



IV. Italy and Tunisia

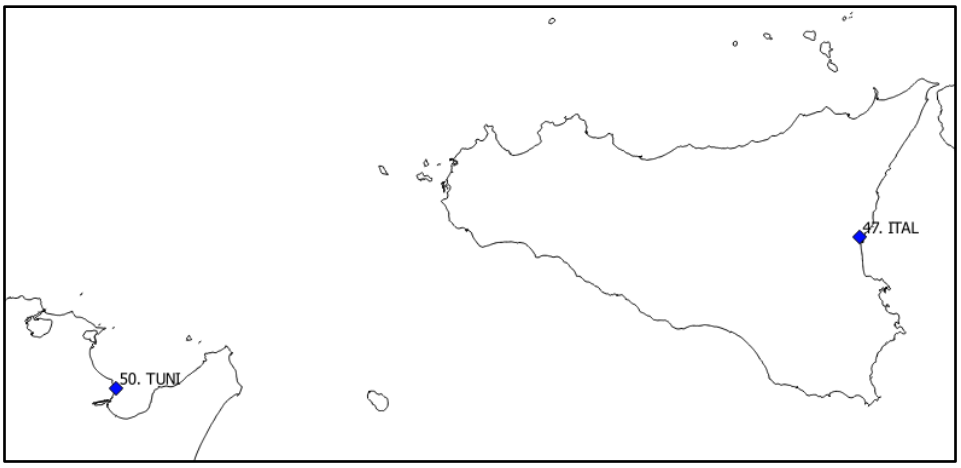


Figure 3. Population locations of the *Armadillo officinalis* individuals used in this study. Populations with questionable coordinates are marked by a diamond shape.

Phylogenetic analysis

In order to investigate the phylogenetic relationships of the *Armadillo officinalis* populations, a concatenated dataset was assembled containing all three molecular markers. The selection of the outgroups in the present phylogenetic analysis was challenging due to the absence of other species of the genus *Armadillo* available in GenBank. Thus, several sequences from terrestrial isopods belonging to the same family as *Armadillo officinalis* (family Armadillidae) were retrieved from GenBank and tested as outgroups in a preliminary phylogenetic analysis. Out of these, *Spherillo dorsalis* and *Spherillo obscurus* demonstrated the best results and one individual from each species was used in the present phylogenetic analysis.

Phylogenetic analysis was performed using Maximum Likelihood and Bayesian Inference frameworks. In the present phylogenetic analysis, the topologies inferred from the two phylogenetic analyses were compared to ensure phylogenetic credibility. Moreover, a concatenated molecular marker phylogenetic analysis was employed in order to investigate possible discrepancies in the topologies inferred from the three markers. In both analyses, the concatenated dataset was partitioned by molecular marker and by codon position for the protein-coding genes (COI, cytb). Partition was performed using PartitionFinder v.2.1.1 (Lanfear et al. 2016) with the following parameters: branch lengths = linked; models = BEAST; model selection = BIC; search = greedy. ML analysis was performed with RAxML v.8.2.10 (Stamatakis, 2014) using GTR+GAMMA model and 1000 bootstrap replicates. BI analysis was performed in BEAST v.1.8.4 (Drummond et al., 2012) with the following priors: HKY+G+I for all partitions (PartitionFinder results); uncorrelated lognormal relaxed clock; Coalescent: Constant size tree prior; Length of chain:$3x10^7$; Log parameters every: Length of chain/10^4. Tracer 1.6 (Rambaut et al., 2014) was used to confirm convergence (all ESS > 200). The BI phylogenetic tree was annotated in TreeAnnotator v.1.8.4 (provided with BEAST) and 25% of the trees were discarded as burn-in. The main clades in each phylogenetic tree were identified based on node support values: > 70 % bootstrap values for ML and > 0.95 posterior probability values for BI (Hillis and Bull, 1993; Huelsenbeck and Rannala, 2004).

Phylogeographic diffusion analysis

In most cases, the addition of phylogeographic reconstructions in phylogeographic studies helps to fully comprehend the phylogeographic patters under study (Collevatti et al., 2015). These phylogeographic reconstructions are usually based on a given phylogeny under various approaches (Lemey et al., 2010). Several models have been proposed to conduct such analyses, either in continuous or discrete space. In the case of continuous variables, the phylogeographic diffusion takes place in a given 2D or 3D landscape, where the locations are distributed; on the contrary, discrete models are based on pre-defined geographic discrete regions and focus on the transition between these regions (Ronquist et al., 2011). Continuous models work better in cases of short time scales, dense sampling and in studies that concentrate on the populations, as continuous diffusion progressively moves in the local areas, ultimately summing up discontinuities (Ronquist et al., 2011). This is the reason why some researchers tend to use discrete models; however, discrete models largely depend on the appropriate definition of discrete areas (Ronquist et al., 2011). Whereas it is easy to identify discrete areas when analyzing species distributed in insular systems, it is not feasible to do so when studying species that theoretically have a continuous distribution in space. The latter is the case in the present study and therefore continuous analysis was implemented.

Two interesting probabilistic methodologies regarding such analyses were proposed (Lemey et al., 2009; Lemey et al., 2010). Lemey et al. (2009) described a Bayesian inference framework, which models the diffusion between locations when they are treated as discrete states. However, the discrete phylogeographic diffusion is not suitable for diffusion processes in continuous landscapes, where locations are continuously distributed and cannot be categorized in discrete regions (Lemey et al., 2010). As a response to this challenge, Lemey et al. (2010) described a Bayesian inference framework which models the phylogeographic diffusion processes in continuous landscapes.

Since the populations of *Armadillo officinalis* in Cyprus are distributed in continuous space, as the island as a whole acts as a single area which cannot be divided in further discrete regions, a phylogeographic diffusion model in continuous space was applied.

The input data for this analysis were the phylogeny of *Armadillo officinalis*, using the concatenated dataset, and the locations of the populations of *Armadillo officinalis* in Cyprus, described as continuous traits. The analysis was performed in BEAST with the same parameters, evaluation and burn-in as the BI analysis, apart from the following: Continuous trait model: Cauchy RRW model; Length of chain: 10^8. The spatial diffusion results were visualized in SPREAD3 v.0.9.6 (Bielejec et al., 2016) using 'MCC tree with continuous traits' function, with a 80% HPD level.

Species delimitation and divergence times

Species delimitation was used as a way to split *Armadillo officinalis* into independent lineages. In general, species delimitation methods require multiple loci in order to be considered as accurate. In the present study, all molecular markers used are mitochondrial, thus representing a single locus. Therefore, the resulted lineages will be strictly refered to as mtDNA lineages. To identify the distinct *Armadillo officinalis* mtDNA lineages, various single-locus species delimitation methods were applied for each molecular marker, using different backgrounds to ensure delimitation credibility. For this purpose, five tree-based and one distance-based methods were chosen. Regarding the tree-based methods, the General Mixed Yule Coalescent model (Pons et al., 2006) and its Bayesian implementation (Reid and Carstens, 2012) use the branch lengths in the provided ultrametric phylogenetic trees (Pons et al., 2006), while Poisson Tree Processes model, Bayesian Poisson Tree Processes model (Zhang et al., 2013) and multi-rate Poisson Tree Processes model (Kapli et al., 2017) directly use the number of substitutions (Zhang et al., 2013). As for the distance-based method, Automatic Barcode Gap Discovery, it assigns individuals into species based on a barcode gap, which is found when the intraspecific divergence is lower than the interspecific one (Puillandre et al., 2011).

To assess GMYC and bGMYC, phylogenetic trees per molecular marker were inferred in BEAST as described above. Substitution rates per My for 16S (0.14%) and COI (1.64%) were used (Kamilari et al., 2014); unfortunately, terrestrial isopod cytb substitution rate was not available. For GMYC, the 'splits' package (Ezard et al.,

2009) in R v.3.4.3 (R Core Team, 2017) was used, applying the single threshold approach. bGMYC was performed in 'bGMYC' package (Reid and Carstens, 2012) in R, using 100 random trees, 10^3 generations and 80% burn-in. The 'bgmyc.point' function was used to investigate the species' limits, using a threshold of 0.05.

For PTP, mPTP and bPTP methods, phylogenetic trees per molecular marker were also inferred in BEAST as described above. mPTP and PTP were performed in the online server 'http://mptp.h-its.org' using the multi rate poisson tree processes method and the single rate poisson tree processes method (p-value < 0.001) respectively. bPTP was performed in the online server 'https://species.h-its.org' using No. MCMC generations=500000, thinning=100 and burn-in=10%.

ABGD was performed in the online server 'https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html', using all three datasets seperately. The analysis was performed as follows: Pmax=0.01; Kimura (K80) TS/TV model; and every other parameter were set as the default. The analysis was re-run with a lower relative gap width (X) whenever necessary.

The various species delimitation methods can lead to quite different results. This is why an evaluation method is necessary in order to validate the species demitation results, using all three molecular markers. Thus, the results from the species delimitation methods described above were evaluated using *BEAST (Heled and Drummond, 2010) function in BEAST v.1.8.4, which is a Bayesian MCMC method that uses multiple molecular markers and multi-individual data to group individuals into species in a single species tree ancestral reconstrucrion approach (Heled and Drummond, 2010). The use of different molecular markers and individuals through *BEAST can be helpful when estimating phylogenies, as the modeling of the incomplete lineage sorting and the intraspecific polymorphism in a given concatenated dataset can lead to the minimization of the inconsistency between gene trees and the species tree (Castelin et al., 2017).

In the present study, the assignation of individuals into species in the species tree was based on the partitions obtained from the several single-locus species delimitation results. The species tree was constructed in BEAST using the same dataset and partition as the BI analysis with the following priors: Species Tree: Yule Process; Size

Model: Piecewise linear & constant root; Ploidy type: mitochondrial; Ancestral State Reconstruction: Reconstruct all states at all ancestors for the species partition; MCMC: 10^8 generations. The trees were checked for convergence and annotated as mentioned above. The tips of the species tree were considered as a distinct lineage only for > 0.95 posterior probability support values in order to include only statistically important partitions.

After the identification of the distinct *Armadillo officinalis* lineages in Cyprus using the various species delimitation methods, the next step was to estimate the divergence times between them in an effort to identify the more likely paleogeographical events that have affected the diversification of the species in the island. Due to the high number of non-Cypriot populations exclusively represented by COI sequences, the highly informative COI dataset was used. Three substitution rates were tested to estimate the divergent times of the *Armadillo officinalis* lineages: 1.64 % My^{-1}, as estimated for *Orthometopon* (Poulakakis and Sfenthourakis, 2008); 2.3 % My^{-1}, or the 'standard mtDNA clock' (Papadopoulou et al., 2010); and 3.54 % My^{-1}, as calculated for tenebrionid beetles (Papadopoulou et al., 2010). The analysis was conducted in BEAST, using the same methodology as the BI analysis.

Species distribution modeling

A species distribution modeling framework was applied based on the species delimitation results. Species distribution models combine species occurrence data with environmental variables in order to predict distributions across landscapes (Elith and Leathwick, 2009). In the present study, a SDM was made for each lineage using the same environmental variables and the geographical locations of the populations of each lineage. The occurrence data for each lineage were not thinned, due to the low number of populations. The environmental variables used in the present study, all at the highest resolution, are the following: the current 19 bioclimatic variables from WorldClim (Hijmans et al. 2005); and terrain ruggedness index and altitude from EarthEnv (Amatulli et al., 2018). As seen in Table 1, the bioclimatic variables are associated to temperature and precipitation, while TRI and altitude are related to

topography. Thus, the chosen environmental variables cover several aspects of the ecology of *Armadillo officinalis.* However, not every environmental variable was retained: based on a multicollinearity assessment in 'usdm' package (Naimi et al., 2014) in R, only not highly correlated (vif < 0.7) variables were kept in the analysis.

The climatic niche of each lineage was modeled with 'biomod2' (Thuiller et al., 2009) package in R, using Random Forest and Artificial Neural Networks algorithms in an ensemble modeling scheme to avoid the uncertainties related to each model. Among other available models in 'biomod2' package, RF and ANN were selected for the analysis as they were able to cope with the low number of populations used. As these models require the use of pseudo-absences, the number of PA was set as equal to the number of presences. Minimum and maximum distance between presence and PA data was estimated in 'blockCV' package (Valavi et al., 2018) in R. PA generation and model calibration was repeated 100 times to guarantee no PA bias. The predictive performance of each model was evaluated by the TSS criterion, based on 10 evaluation runs, where 80 % of the data was used for training and 20% for evaluation. Models were considered as statistically important only for TSS > 0.9. The resulted probabilistic maps were transformed into binary presence/absence maps based on the TSS criterion.

Table 1. The environmental variables selected for the SDM (Hijmans et al., 2005; Amatulli et al., 2018). The variables in bold represent the retained variables.

BIO1	Annual Mean T
BIO2	Mean Diurnal Range (Mean of monthly (max T - min T))
BIO3	**Isothermality (BIO2/BIO7) (* 100)**
BIO4	T Seasonality (s.d. *100)
BIO5	Max T of Warmest Month
BIO6	Min T of Coldest Month
BIO7	T Annual Range (BIO5-BIO6)
BIO8	Mean T of Wettest Quarter
BIO9	Mean T of Driest Quarter
BIO10	Mean T of Warmest Quarter
BIO11	Mean T of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	**Precipitation Seasonality (Coefficient of Variation)**
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter
ALT	Altitude
TRI	**Mean of the absolute differences in elevation between a focal cell and its 8 surrounding cells**

Results

The resulted 1633 bp concatenated dataset consisted of 496 bp of 16S (70 sequences), 731 bp of COI (95 sequences) and 406 bp of cytb (67 sequences). The 16S, COI and cytb fragments resulted in 6, 31 and 33 haplotypes respectively (Appendix II). The genetic distances results are presented in Appendix IV and Table 2. Overall, the mean genetic distance per molecular marker was 5 %, 8 % and 8 % for 16S, COI and cytb respectively. The genetic distances within populations varied from 0-4 % for 16S, 0-5 % for COI and 0-4 % for cytb. Between populations, the genetic distances ranged from 0-17 % for 16S and cytb and 0-15 % for COI.

Table 2. Sequence data information and genetic distances of *Armadillo officinalis*

		16S	COI	Cytb
Sites (bp)	Conserved	375	519	274
	Variable	116	212	131
	Parsimony-infomative	90	167	105
	Singleton	26	45	25
	Total	496	731	406
No. of sequences		70	95	67
Overall mean genetic distance (%)		5	8	8
Within-population genetic distance (min-max) (%)		0-4	0-5	0-4
Between-population mean genetic distance (min-max) (%)		0-17	0-15	0-17
Within-lineage genetic distance (%)	Lineage A	4	7	7
	Lineage B	1	2	1
Between-lineage genetic distance (%)		9	10	13
Distance to *S. dorsalis* (%)	Lineage A	-	22	-
	Lineage B	-	23	-
Distance to *S. obscurus* (%)	Lineage A	-	24	-
	Lineage B	-	25	-

The results of ML (Figure 4) and BI (Figure 5) phylogenetic analysis produced trees with similar topologies and two major clades, supported by a 100% bootstrap value and posterior probability support value respectively. In the BI analysis, clade A further splits into further subclades (A1 and A2) with pp values > 0.95. However, the division of clade A into subclades is not well supported by the bootstrap support values in the ML analysis.

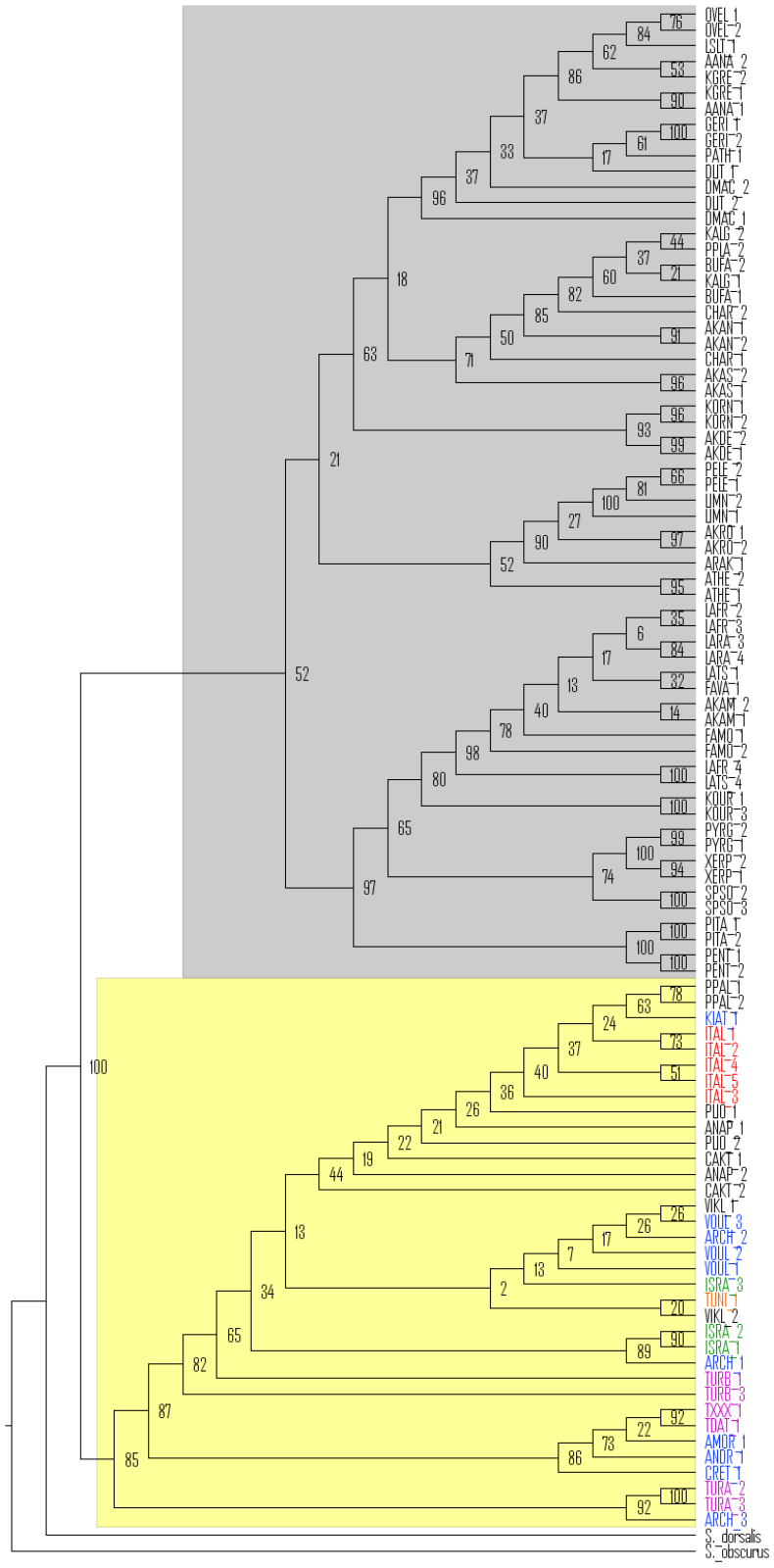


Figure 4. ML phylogenetic analysis results. Branch color corresponds to clade/lineage A (grey) and clade/lineage B (yellow). Node labels indicate bootstrap support values. Tip colours represent: **Cyprus, Greece, Israel, Italy, Tunisia and Turkey**.

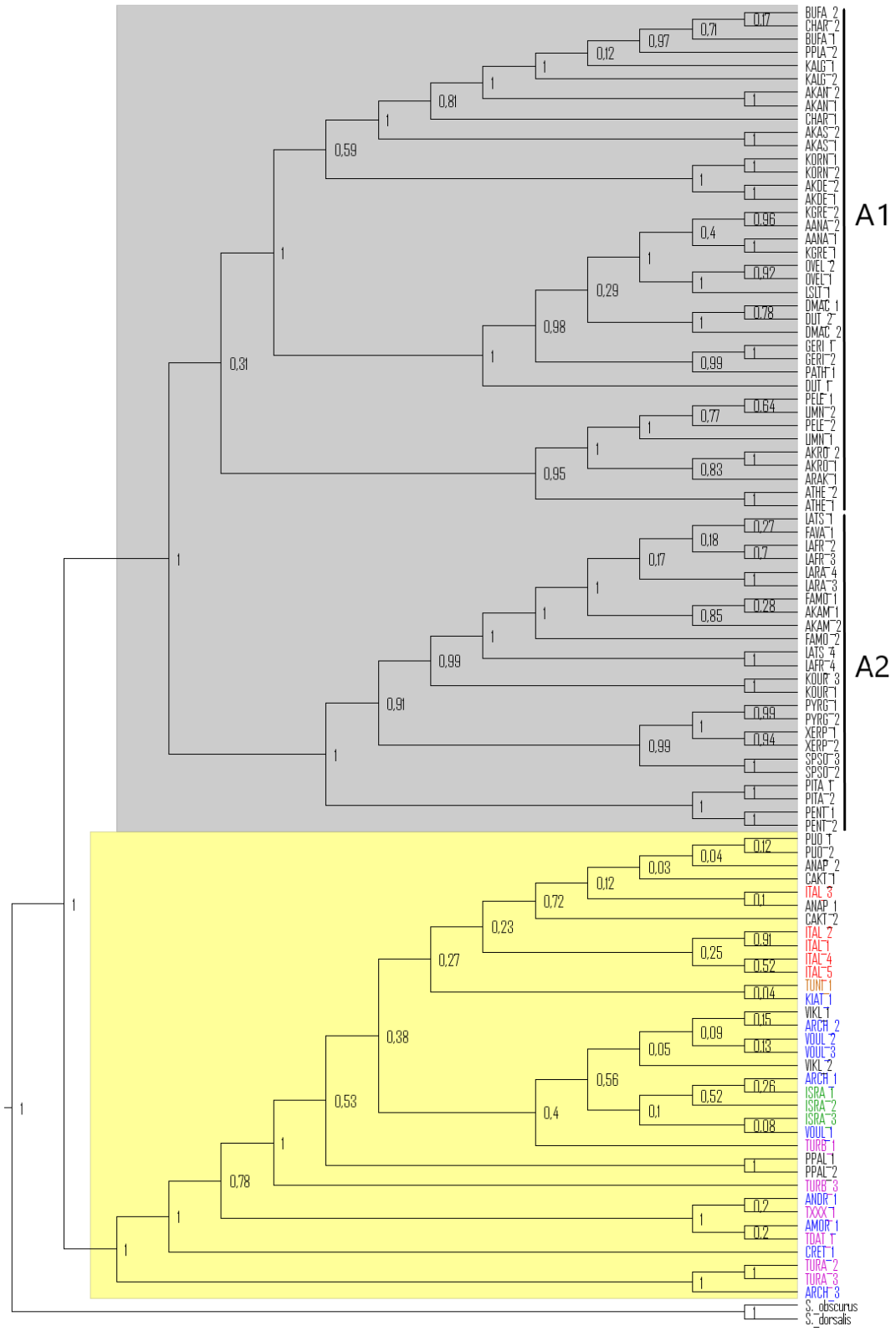


Figure 5. BI phylogenetic analysis results. Branch color corresponds to clade/lineage A (grey) and clade/lineage B (yellow). Node labels indicate posterior probability support values. Tip colours represent: **Cyprus, Greece, Israel, Italy, Tunisia and Turkey**.

The two main phylogenetic clades correspond to lineages A (grey) and B (yellow), as identified from the species delimitation results and evaluated by *BEAST (Figure 6). *BEAST results were statistically important (posterior probability > 0.95) only for partitions that corresponded to the two major phylogenetic clades. Lineage A exclusively consists of Cypriot populations, while lineage B includes five populations from Cyprus (ANAP, CAKT, PLIO, PPAL and VIKL) and all populations from other Mediterranean areas. The results of the several single-locus species delimitation methods varied by molecular marker and by method. ABGD resulted in two partitions for 16S, three for COI and two for cytb. GMYC indicated five partitions for 16S and four for COI. bGMYC presented two partitions for both 16S and COI. PTP and bPTP both resulted in two partitions for 16S, but displayed an oversplit in COI and cytb markers. mPTP demonstrated one single lineage for 16S, four for COI and five for cytb. In general, the fewer number of partitions was observed in ABGD, bGMYC and mPTP methods, while 16S always resulted in less oversplitted results in comparison to COI and cytb. The populations in Cyprus, grouped by lineage, are presented in Figure 7. According to Table 2, the within-lineage genetic distances are lower in lineage B (1 %, 2 % and 1 % for 16S, COI and cytb respectively) than in lineage A (4 %, 7 % and 7 % for 16S, COI and cytb respectively). The genetic distances between lineages range from 9 % for 16S to 10 % for COI and 13 % for cytb. As for the outgroups, their genetic distance from lineage A is 22 % for *Spherillo dorsalis* and 24 % for *Spherillo obscurus* and from lineage B is 23 % for *Spherillo dorsalis* and 25 % for *Spherillo obscurus.*

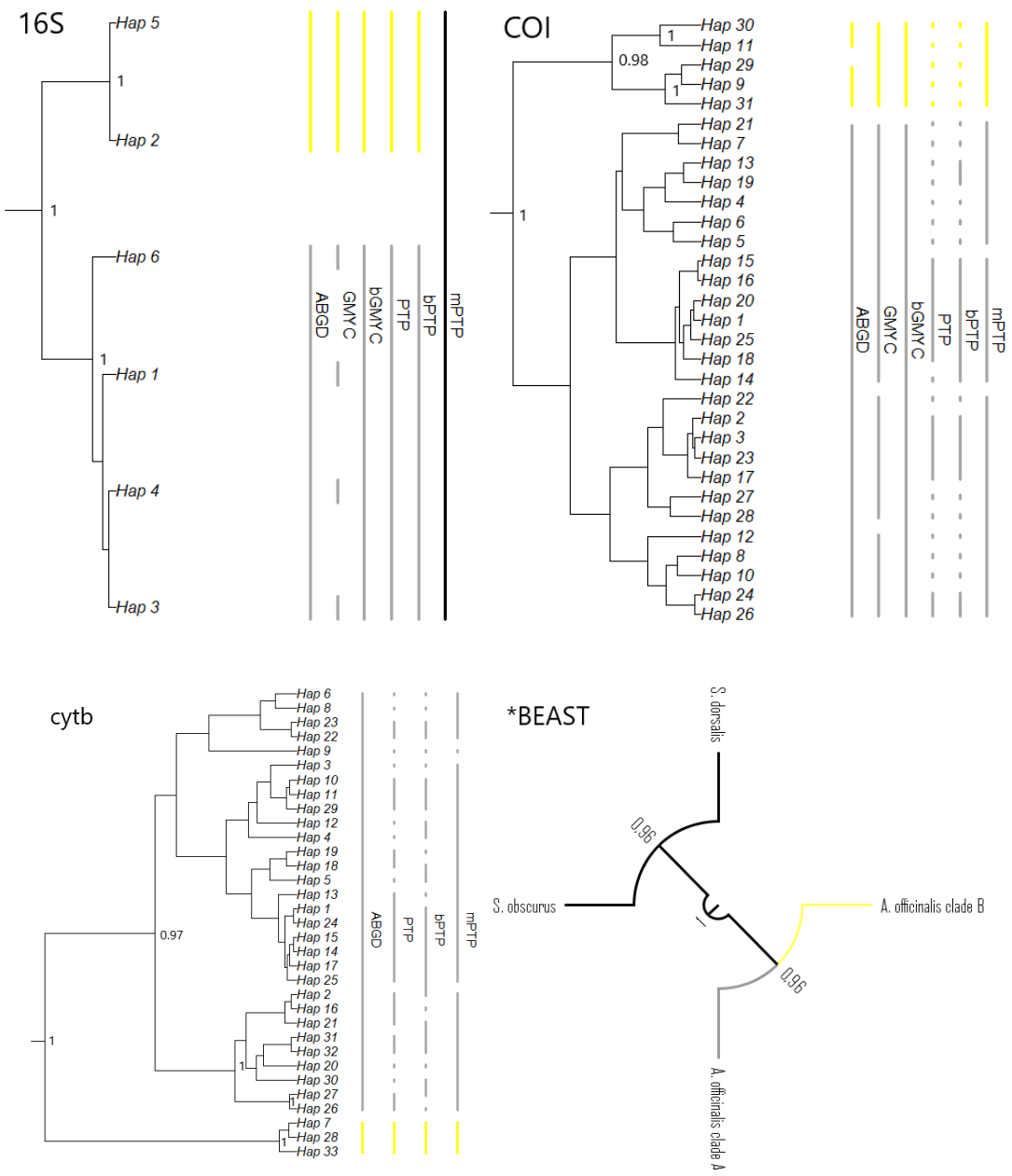


Figure 6. Species delimitation results. Tip labels correspond to the haplotype names. Each bar represents a separate single-locus species delimitation method, while the bar fragments indicate the resulted number of partitions of each method. Bar colors and branch colors correspond to the lineage colors. Node labels correspond to posterior probability values (only for pp > 0.95).

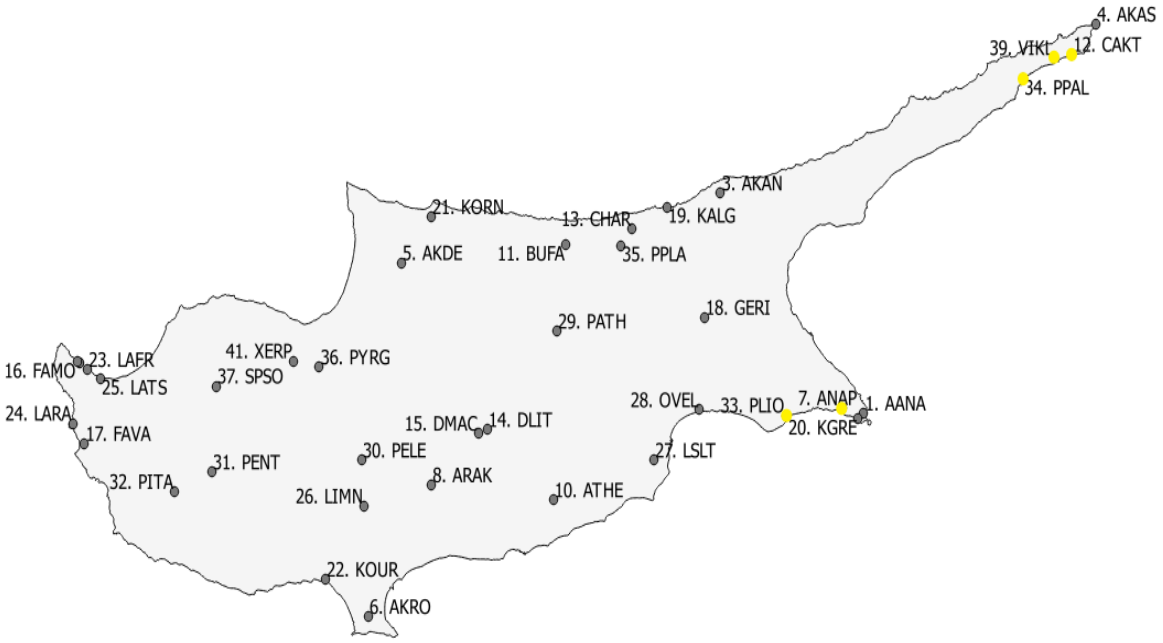
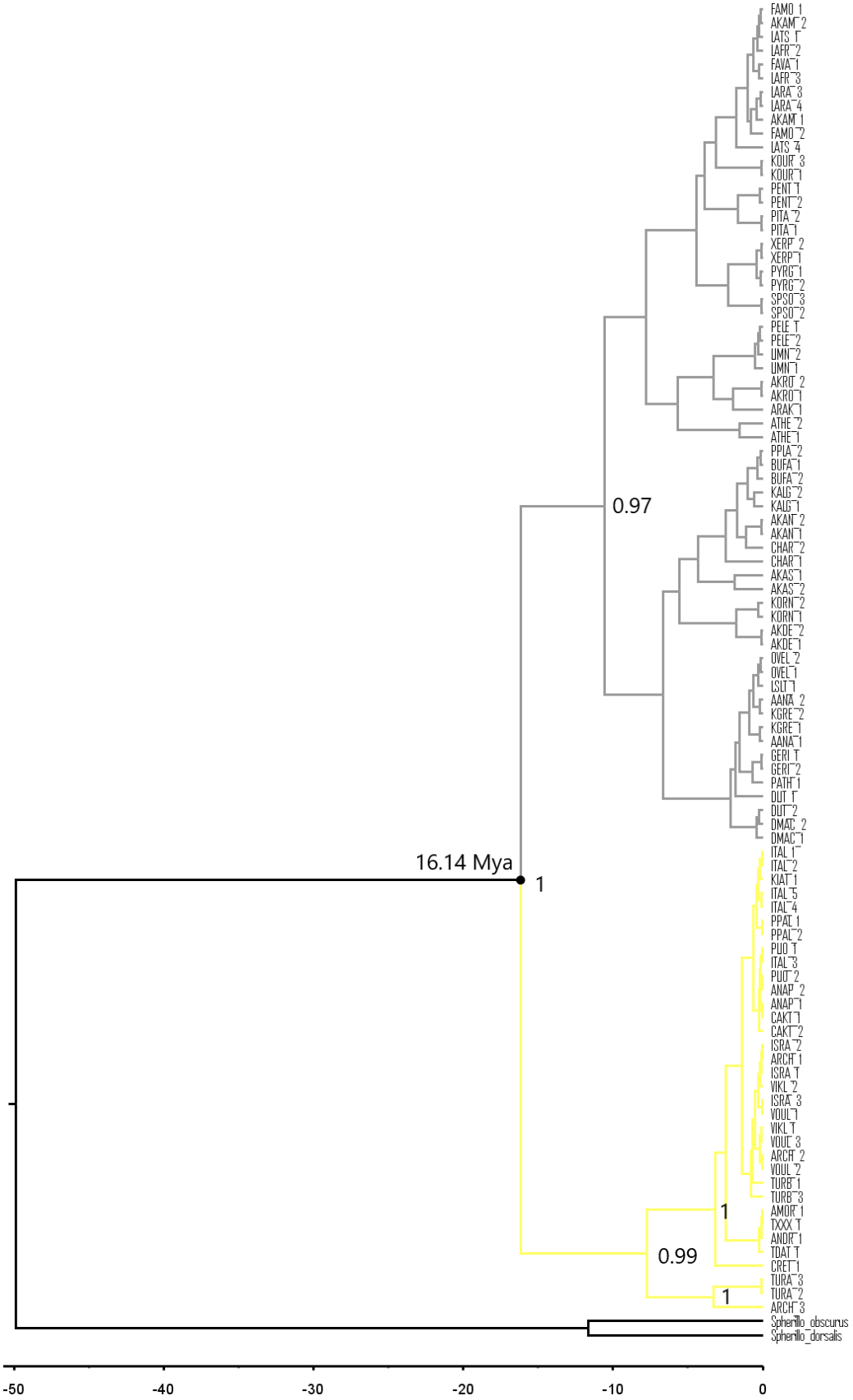


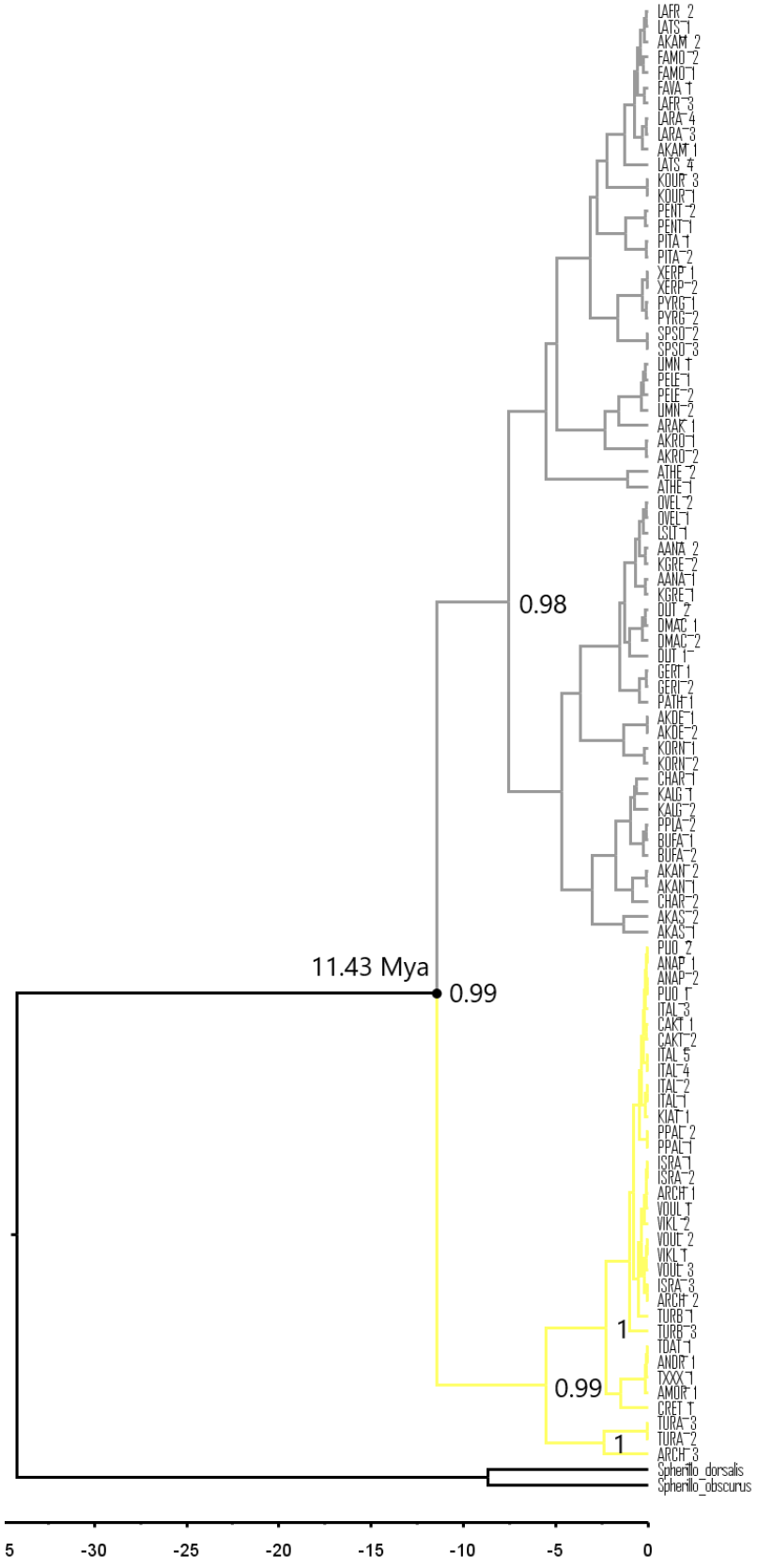
Figure 7. Locations of *Armadillo officinalis* populations in Cyprus, grouped by lineage. Population colors represent lineage colors.

As for the divergent times of *Armadillo officinalis* (Figure 8), the results were quite different based on the three substitution rates used. The divergence time between the two *Armadillo officinalis* lineages was estimated at 16.14 Mya, 11.43 Mya and 7.42 Mya based on the 1.64 % My^{-1} , 2.3 % My^{-1} and 3.54 % My^{-1} substitution rate respectively, during the Late Meiocene. In all three dated phylogenies, the two lineages further diverged during the Pliocene and Pleistocene. In the case of the 3.54 % substitution rate, the lineages highly diversified during the Pleistocene.

I. S.r.: 1.64 % My^{-1}


FAMO_1
AKAM_2
LATS_1
LAFR_2
FAVA_1
LAFR_3
LARA_3
LARA_4
AKAM_1
FAMO_2
LATS_4
KOUR_3
KOUR_1
PENT_1
PENT_2
PITA_2
PITA_1
XERP_2
XERP_1
PYRG_1
PYRG_2
SPSO_3
SPSO_2
PELE_1
PELE_2
LIMN_2
LIMN_1
AKRO_2
AKRO_1
ARAK_1
ATHE_2
ATHE_1
PPLA_2
BUFA_1
BUFA_2
KALG_2
KALG_1
AKAN_2
AKAN_1
CHAR_2
CHAR_1
AKAS_1
AKAS_2
KORN_2
KORN_1
AKDE_2
AKDE_1
OVEL_2
OVEL_1
LSIT_1
AANA_2
KGRE_2
KGRE_1
AANA_1
GERI_1
GERI_2
PATH_1
OUT_1
OUT_2
DMAC_2
DMAC_1
ITAL_1
ITAL_2
KIAT_1
ITAL_5
ITAL_4
PPAL_1
PPAL_2
PUO_1
ITAL_3
PUO_2
ANAP_2
ANAP_1
CAKT_1
CAKT_2
ISRA_2
ARCH_1
ISRA_1
VIKL_2
ISRA_3
VOUL_1
VIKL_1
VOUL_3
ARCH_2
VOUL_2
TURB_1
TURB_3
AMOR_1
TXXX_1
ANDR_1
TOAT_1
CRET_1
TURA_3
TURA_2
ARCH_3
Sphenillo_obscurus
Sphenillo_dorsalis
0.97
16.14 Mya
1
1
0.99
1
-50
-40
-30
-20
-10
0

II. S.r.: 2.3 % My^{-1}


11.43 Mya
0.98
0.99
1
0.99
1
Sphenillo_dorsalis
Sphenillo_obscurus
5
-30
-25
-20
-15
-10
-5
0

III. S. r.: 3.54 % My^{-1}

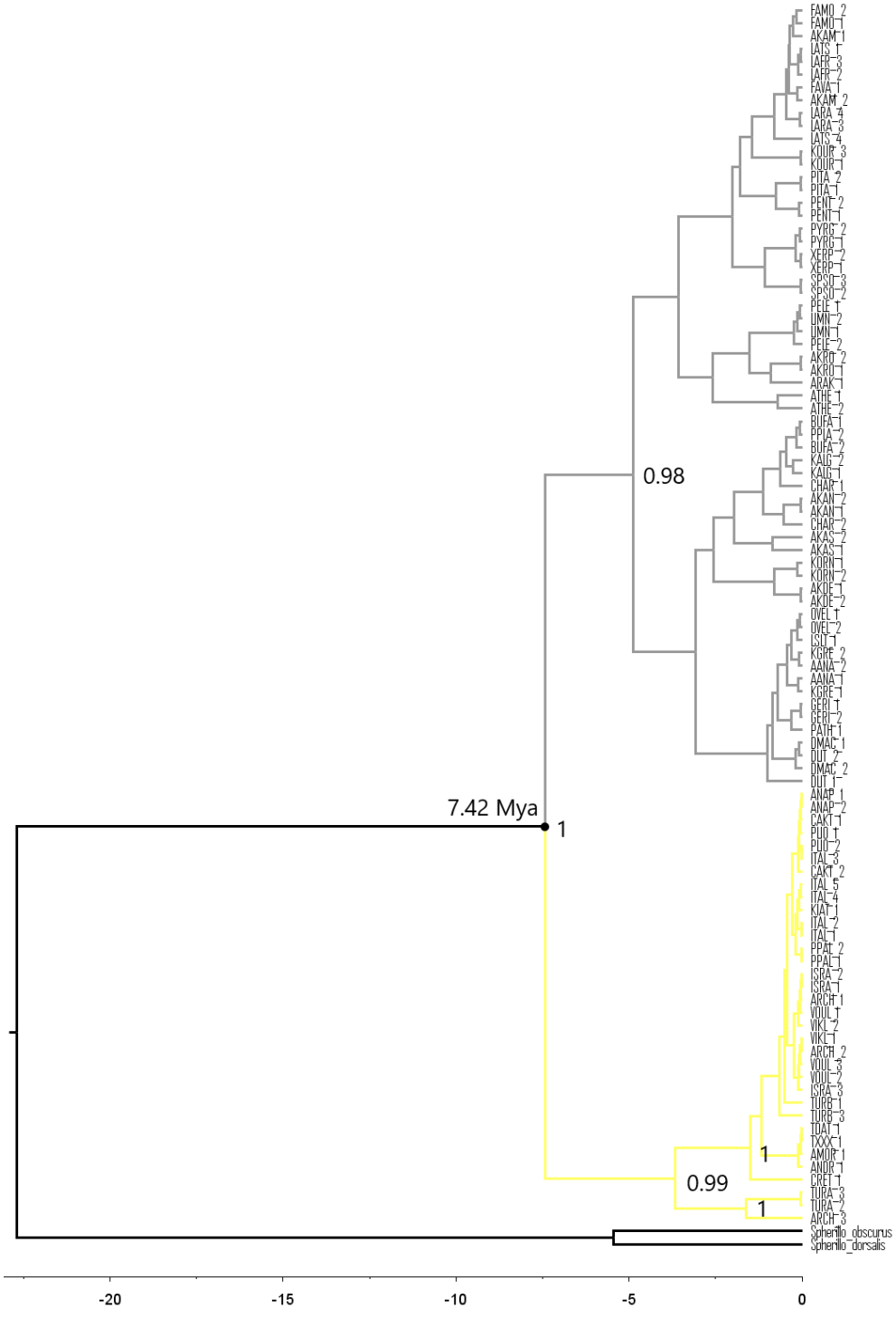


Figure 8. The estimated divergence times of *Armadillo officinalis*. Branch color corresponds to the lineage colors. Node labels correspond to posterior probability values (only for pp > 0.95). The scale axis represents the time scale (in million years).

As shown in Figure 9, the phylogeographic diffusion of *Armadillo officinalis* started at the central-eastern part of Cyprus (black dot in Fig 9.A). From there, the two *Armadillo officinalis* lineages followed opposite directions: lineage A moved to Troodos Ophiolite, which served as a focal point for the distribution of the species to Pentadactylos Zone, Mamonia Zone and the Zone of the autochthonous sedimentary rocks; on the other hand, lineage B remained isolated in the eastern Pentadactylos Zone and later moved to the eastern coast of the Zone of the autochthonous sedimentary rocks.

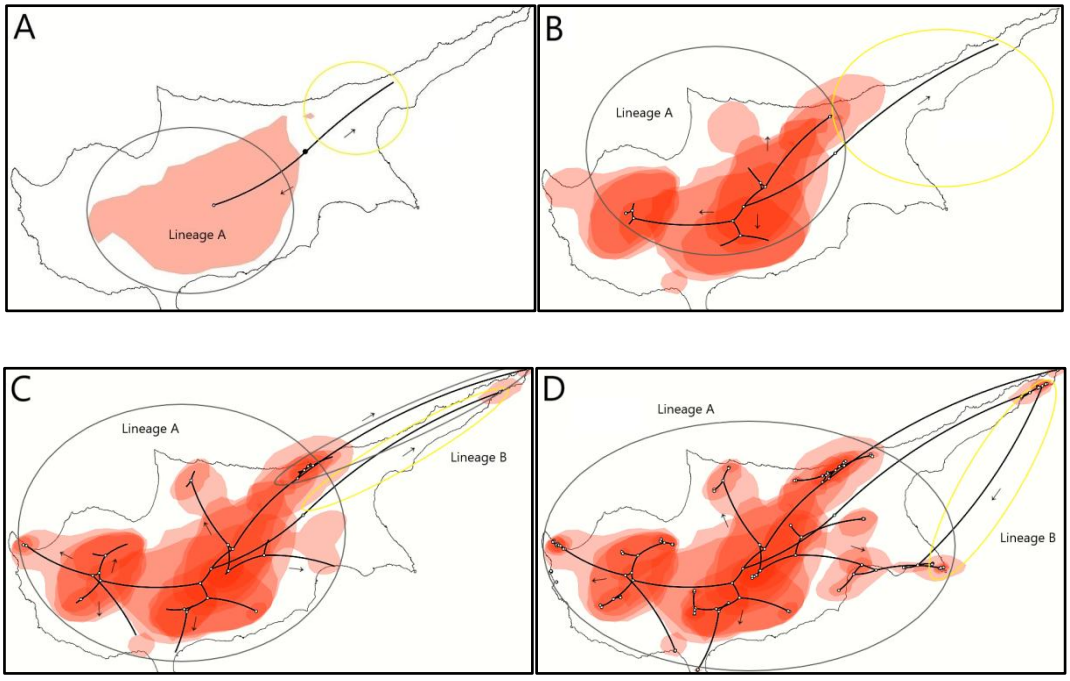


Figure 9. Phylogeographic diffusion analysis results. Points indicate intervals and population locations. Lines indicate the phylogeographic diffusion processes. Polygons represent HPD 80% level.

Species distribution modeling results (both TSS > 0.9) are presented in Figure 10 as presence/absence maps, transformed from probabilistic maps based on the TSS criterion. Based on the multicollinearity test (vif < 0.7), only three variables were retained: BIO3 (isothermality), BIO15 (seasonal precipitation) and TRI (terrain

ruggedness index). The minimum distance between presences and pseudo-absences was set on 34511 m, according to 'blockCV' results. Based on environmental niche and occurrence data, lineage A distributes all over Cyprus apart from the eastern Pentadactylos Zone, while lineage B distributes in the northeastern parts of the island. SDM results are in accordance to the locations of the Cypriot populations grouped by lineage (see Figure 7). Furthermore, the environmental variable that mostly contributes on the modeling of each lineage is BIO3 for lineage A and BIO3+TRI for lineage B. The environmental variables used in Cyprus are presented in Figure 11.

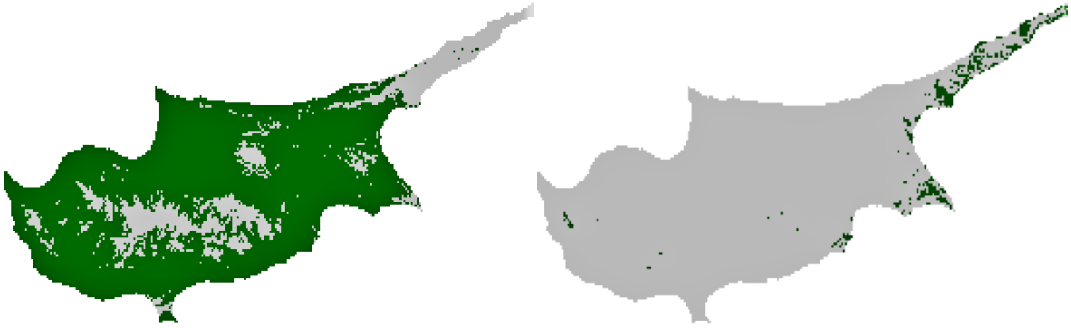


Figure 10. Species distribution modeling results for *Armadillo officinalis* lineage A (left) and B (right). Map color indicates presence/absence binary data.

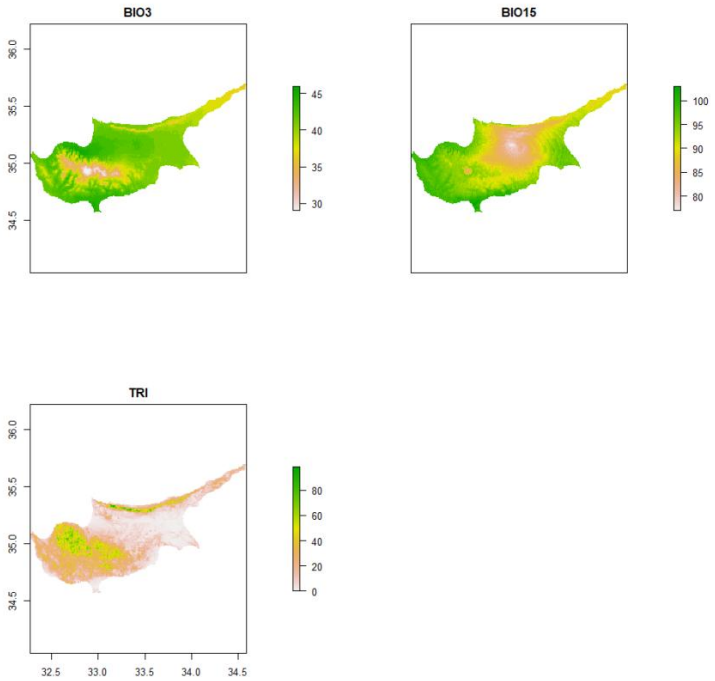


Figure 11. Retained environmental variables used for SDM in Cyprus. Color gradient represents the intensity of each variable.

Discussion

The genetic diversity of *Armadillo officinalis*

As described above, terrestrial isopods are characterized by a high degree of genetic diversity. For instance, in a phylogeographic study on the family Porcellionidae (Dimitriou et al., 2018), the range of genetic variation between the different genera was estimated at 16.9–50.3 % for COI and 16.9–36.5 % for 16S. In the same study, the genetic distances between two species of the genus *Porcellio, Porcellio laevis* and *Porcellio nasutus*, were estimated at 20.6 % for 16S and 20.9 % for COI. Thus, this is an example of the high level of genetic diversity in terrestrial isopods, both in the family and genus level.

Similar results in the genus level were presented in three case studies in the Mediterranean basin. In the phylogenetic study on the Greek populations of the genus *Ligidium* (Klossa-Kilia et al., 2006), the main genetic distance between the defined species belonging to the genus *Ligidium* ranged from 7.6 % to 24.4 % for 16S and 14.4 % to 23.3 % for COI. Furthermore, the divergence between the populations of *Ligidium beieri* ranged from 0.3 % to 7.2 % for 16S and 5.9 % to 15.6 % for COI. In a similar phylogenetic study (Parmakelis et al., 2008) on two species of the genus *Trachelipus* (*Trachelipus kytherensis* and *Trachelipus aegaeus*), the mean genetic distances varied from 7.2 % (between *Trachelipus kytherensis* and *Trachelipus aegaeus*) to 10.5 % (between *Trachelipus kytherensis* and a new undescribed *Trachelipus* species). Accordingly, based on the study of the Greek populations of the genus *Orthometopon* (Poulakakis and Sfenthourakis, 2008), the genetic distances between the different *Orthometopon* clades ranged from 0 to 18.4 %. Taking everything into account, the genetic variation in terrestrial isopods highly varies between the different terrestrial isopod genera.

Terrestrial isopods also demonstrate a high level of genetic diversity in the intraspecific level. For instance, according to the intraspecific phylogeography of

Spherillo grossus (Isopoda: Armadillidae) on the west coast of Australia (Lee et al., 2014), the between-population genetic distances ranged from 0 to 15 % for 16S and from 0 to 14 % for COI, while the maximum estimated within-population genetic distances were 3.5 % for 16S and 5.4 % for COI. At the same time, despite the great genetic variation observed in *Spherillo grossus*, the species demonstrated a limited morphological variation. Thus, the case study of *Spherillo grossus* proves that there are cases of terrestrial isopods that are characterized by high genetic distances in the intraspecific level, which can be comparable to the genetic distances between taxa in higher taxonomic levels.

Taking everything into account, it seems that the genetic diversity of *Armadillo officinalis* is in agreement with the one of other terrestrial isopods. To begin with, both the within-population and between-population genetic distances in *Armadillo officinalis* are comparable to the ones estimated in *Spherillo grossus*. Also, the genetic distance between *Armadillo officinalis* and the outgroups used in the phylogenetic analysis (*Spherillo obscurus* and *Spherillo dorsalis*, both belonging to the family Armadillidae) falls into the genetic distance ranges estimated for the family Porcellionidae (Dimitriou et al., 2018).

However, due to the lack of sufficient case studies regarding cytb in terrestrial isopods, a comparison could not be made between the cytb dataset of *Armadillo officinalis* and other species of terrestrial isopods. In response to this challenge, a cytb dataset was assembled using several cytb sequences from GenBank and the cytb sequences of *Armadillo officinalis*. The genetic distances tables and the sequences retrieved from GenBank are further analysed in Appendix IV. As a result of this analysis, the within-lineage genetic distances of *Armadillo officinalis* are in agreement with the one of other isopods, which range from 0 to 22 %. Additionally, the genetic distance between lineages A and B (13 %) are lower than the ones between other species, even though it is close to the 17 % genetic distance estimated between *Ligia hawaiensis* and *Ligia perkinsi*, as well as the 18 % genetic distance between *Tylos chilensis* and *Tylos spinulosus.*

The *Armadillo officinalis* lineages in Cyprus

According to the phylogenetic analysis (ML and BI trees), *Armadillo officinalis* consists of two main phylogenetic clades: clade A, which consists of populations from all over Cyprus; and clade B, which consists of five populations in Cyprus (ANAP, CAKT, PLIO, PPAL, VIKL) and every population in other Mediterranean areas (Tunisia, Italy, Greece, Turkey and Israel). In the BI analysis, clade A further divides into two subclades: subclade A1, which consists of populations in the Troodos Zone, the Zone of the autochthonous sedimentary rocks and Pentadactylos Zone; and subclade A2, which includes populations located in the Mamonia Zone and Troodos Zone. However, the three BI subclades are not well supported by the bootstrap support values in the ML analysis; thus, *Armadillo officinalis* is considered to be consisted of the two main phylogenetic clades that are well-supported by both the ML and BI analysis.

Based on the species delimitation results, the two main clades identified by the phylogenetic analysis correspond to two distinct mitochondrial lineages. The differentiation between the two mitochondrial lineages is supported by a 100 % support value in both phylogenetic trees, while *BEAST validated the delimitation results from the several single-locus species delimitation methods. As mentioned above, the use of species delimitation methods require multiple loci in order to be taken into account. However, the species delimitation results in the present study can be considered as accurate, as the two lineages are highly differentiated, as seen in the phylogenetic analysis results. In any case, the resulted lineages in the present study are strictly refered to as mtDNA lineages.

Additionally, regarding the genetic distances results of the two mitochondrial lineages, the genetic variation is much higher in lineage A is comparison to lineage B. On top of that, the genetic distances between lineage A and lineage B are comparable to the genetic distances between the different species of the genera *Ligidium* (Klossa-Kilia et al., 2006) and *Trachelipus* (Parmakelis et al., 2008). As a result, the genetic distances between lineages A and B are as high as the ones between different species in other terrestrial isopod species.

As for the divergence times of the two distinct *Armadillo officinalis* lineages, all three dated phylogenies seem questionable. To begin with, the use of 1.64 % and 2.3 % substitution rates led to unrealistically old ages, which are inconsistent with the emergence and geological evolution of Cyprus. On the other hand, the 3.54 % substitution rate is better fitted to the paleogeography of the island in comparison to the other two substitution rates: the divergence time between the lineages A and B (7.42 Mya) takes place while the paleoisland formation has already taken place (Late Miocene), while most of the diversification of the two lineages has occurred during the Pleistocene, after the uplift of Cyprus as a single unit. Overall, it seems that the uplift of the Troodos Ophiolite paleoisland during the Miocene marked the start of the divergence between lineages A and B and, ultimately, enhanced the diversification of *Armadillo officinalis*. However, based on the rest of the results in the present study, it is expected that the divergence times of *Armadillo officinalis* are even more recent than the ones estimated with the 3.54 % substitution rate, implying that the substitution rate of COI for *Armadillo officinalis* could be even greater than 3.54 %. In a phylogeographic study of the spider genus *Cyrtocarenum* in the Aegean region (Kornilios et al., 2016), the use of published spider substitution rates also resulted in unrealistically old ages in some cases, while the estimated substitution rates were significantly higher in comparison. Thus, it seems that the use of all the three substitution rates above is improper for the estimation of the divergence times of *Armadillo officinalis* and it is suggested that the present analysis is in need of revision, using a suitable substitution rate.

The phylogeographic diffusion analysis results clearly indicate the different diffusion processes between the two lineages. During their early divergence, lineage A was located on the Troodos Ophiolite, while lineage B on the eastern Pentadactylos Zone. These two areas correspond to the two paleoislands that Cyprus consisted of by the Late Miocene. After the uplift of Cyprus as a single unit, lineage A continued distributing in the surrounding areas (Mamonia Zone, Zone of the autochtonous sedimentary rocks and Pentadactylos Zone), while lineage B remained isolated in the eastern Pentadactylos Zone and the eastern coast of the Zone of the autochthonous sedimentary rocks. Overall, the phylogeographic diffusion analysis results are in agreement with the paleogeography of Cyprus, as they correspond to the formation of Troodos and Pentadactylos paleoislands and the latter uplift of the island as a whole.

Regarding the environmental niche parameters of *Armadillo officinalis* in Cyprus, SDM results clearly indicate that the two lineages distribute in opposite parts of the island: lineage B is located in northeastern Cyprus (eastern Pentadactylos Zone and eastern coast of the Zone of the autochthonous sedimentary rocks), while lineage A distributes in every geological zone of the island. SDM results are in agreement with the locations of the populations of each lineage. Moreover, in both cases, the main environmental parameter that contributed significantly in the two lineages was BIO3 (isothermality), which is a variable related to temperature. Temperature as the main contributor in the SDM of *Armadillo officinalis* is no surprise, as *Armadillo officinalis* is regarded as a xeric terrestrial isopod species. Thus, it is reasonable to see the two lineages are absent from areas with low BIO3 values, such as those in the central Troodos Zone and in the Pentadactylos Zone. On top of that, TRI (a topography-related variable) also contributed in the SDM of lineage B. Taking a look into the locations of the populations belonging to lineage B (eastern Pentadactylos Zone and eastern Zone of the autochthonous sedimentary rocks), it is clear that lineage B is absent from locations with rough topographic characteristics, such as the mountainous Kyrenia Range and Troodos Ophiolite, where lineage A is present. However, due to the low number of populations of lineage B in Cyprus and the significant contribution of temperature to both lineages, it would be overconfident to suggest that topography may have affected the distribution of lineage B in a different way than lineage A. Thus, temperature is considered as the main environmental niche parameter that affected the distribution of the two lineages.

Factors shaping the distribution of *Armadillo officinalis'* lineages in Cyprus

Overall, the factors affecting the differentiation of lineages A and B are quite complex. As mentioned above, Cyprus is one of the most isolated Mediterranean islands, since it hasn't been directly connected to the mainland since the end of the MSC (5.33 Mya). Since lineage A exclusively consists of Cypriot populations, it is considered to be the result of the great geographical isolation of Cyprus. On the other hand, populations ANAP, CAKT, PLIO, PPAL and VIKL represent lineage B in

Cyprus, which is considered as the lineage of *Armadillo officinalis* that is commonly present in several Mediterranean areas. However, the distribution of lineage B in Cyprus is much smaller in comparison to the one of lineage A. This phenomenon is observed probably due to geographical and ecological reasons: starting its diffusion from Troodos Ophiolite, lineage A had plenty of space to distribute and diversify in every geological zone of the island, while lineage B isolated in the northeastern part of Pentadactylos Zone, which acted as a geographical culs-de-sac; in addition, the limited dispersal ability of *Armadillo officinalis* further contributed to the geographical isolation of lineage B.

Apart from the ecological and geographical parameters affecting the distribution of the two lineages in the island, the geological evolution of Cyprus seems to have left an imprint on *Armadillo officinalis* as well. In Cyprus, Troodos Zone and Pentadactylos Zone seem to act as two focal points where lineages A and B respectively isolate geographically and genetically. These two geological zones correspond to the two paleoislands that Cyprus consisted of by the late Miocene; thus, the formation of Cyprus' paleoislands seems to be the main geological process affecting the phylogeography of *Armadillo officinalis*. A similar relationship was observed between paleoislands and the genetic diversity of *Cyrtocarenum cunicularium* in Crete (Thanou et al., 2017). As a result, paleoisland formation seems to be a major factor affecting the genetic diversity of insular taxa.

Another factor that might have played a significant role in the distribution of the two *Armadillo officinalis* lineages in Cyprus is the human presence. In the Aegean archipelago, various human activities, such as the introduction of domestic animals and the application of agricultural practices, seem to have affected biodiversity in the Aegean islands (Sfenthourakis and Triantis, 2017). For instance, human-aided dispersal seems to have affected the population clustering of the terrestrial isopod *Trachelipus aegaeus* in the Aegean islands (Kamilari et al., 2014). As for the island under study, Cypriot biodiversity seems to have been affected by humans as well, as Poulakakis et al. (2013) identified reptile species that are thought to have arrived in Cyprus through human-induced introductions. Hence, *Armadillo officinalis* is likely to have been affected by the human presence in Cyprus in some level. For instance, the distributions of the two *Armadillo officinalis* lineages in Cyprus have been probably

affected by human activities in the island. Moreover, it is possible that lineage B (considering both the Cypriot populations and the populations in other Mediterranean areas) has also been affected by the human activity as well, given its low within-lineage genetic distances. However, such hypothesis cannot be further explored using the present data. In the future, the study of the anthropogenic factors affecting *Armadillo officinalis* in the island is proposed, using population genetics methodologies and taking into account more populations from other Mediterranean areas apart from Cyprus.

Undeniably, the use of islands as model systems can lead to the discovery of unexpected diversity, justifying their role as natural evolutionary laboratories. In the case of Cyprus, the complex geological evolution –especially paleoisland formation processes-, the great geographical isolation, the human activity and the limited dispersal ability of *Armadillo officinalis* are likely the main reasons affecting the genetic differentiation and the distribution of the two *Armadillo officinalis* lineages. However, the systematics of lineage A remains unclear: since all molecular markers used in the present study are of mitochondrial origin, lineage A can only be described as a mitochondrial lineage; in addition, the present study does not include any morphological data. Thus, further research is essential to address this topic, including the morphological comparison between the two lineages and the use of nuclear molecular markers.

Despite some phylogeographic case studies in Cyprus (Poulakakis et al., 2013), the present study is the first one to focus on some of the factors that have a significant effect on Cypriot biodiversity. On top of that, it led to the discovery of a hidden mitochondrial lineage in the island. In the future, it is promising to apply the same methodology across different taxa to study the island's biodiversity patterns in a comparative way. However, it is suggested to include different sources of data (e.g. morphological, molecular and environmental) to explore biodiversity in a holistic perspective. That way, one can fully understand the true ecological significance of Cyprus, one of the most biologically diverse areas in the Mediterranean basin.

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Appendices

Appendix I. Information on the *Armadillo officinalis* individuals and outgroups used in this study.

Samples	16S	COI	cytb	Population	Pop. No.	Latitude	Longitude	Location	Accession
AANA_1	X	X	X	AANA	1	34.97655	34.07148	Cyprus	
AANA_2	X	X	X	AANA	1	34.97655	34.07148	Cyprus	
AKAM_1	X	X	X	AKAM	2	35.06965	32.32673	Cyprus	
AKAM_2	X	X	X	AKAM	2	35.06965	32.32673	Cyprus	
AKAN_1	X	X	X	AKAN	3	35.38288	33.75302	Cyprus	
AKAN_2	X	X	X	AKAN	3	35.38288	33.75302	Cyprus	
AKAS_1	X	X	X	AKAS	4	35.69462	34.58743	Cyprus	
AKAS_2	X	X	X	AKAS	4	35.69462	34.58743	Cyprus	
AKDE_1		X	X	AKDE	5	35.25428	33.04264	Cyprus	
AKDE_2	X	X	X	AKDE	5	35.25428	33.04264	Cyprus	
AKRO_1	X	X	X	AKRO	6	34.60115	32.96917	Cyprus	
AKRO_2	X	X	X	AKRO	6	34.60115	32.96917	Cyprus	
AMOR_1		X		AMOR	43			Greece	
ANAP_1	X	X	X	ANAP	7	34.98518	34.02329	Cyprus	
ANAP_2	X	X	X	ANAP	7	34.98518	34.02329	Cyprus	
ANDR_1		X		ANDR	44			Greece	
ARAK_1	X	X	X	ARAK	8	34.84417	33.10959	Cyprus	
ARCH_1		X		ARCH	9	35.23476	25.15234	Greece	
ARCH_2		X		ARCH	9	35.23476	25.15234	Greece	
ARCH_3		X		ARCH	9	35.23476	25.15234	Greece	
ATHE_1	X	X	X	ATHE	10	34.81644	33.38065	Cyprus	
ATHE_2	X	X		ATHE	10	34.81644	33.38065	Cyprus	
BUFA_1	X	X	X	BUFA	11	35.28750	33.40944	Cyprus	
BUFA_2	X	X	X	BUFA	11	35.28750	33.40944	Cyprus	
CAKT_1	X	X	X	CAKT	12	35.63898	34.53423	Cyprus	
CAKT_2	X	X	X	CAKT	12	35.63898	34.53423	Cyprus	

CHAR_1	X	X	X	CHAR	13	35.31715	33.55677	Cyprus	
CHAR_2	X	X	X	CHAR	13	35.31715	33.55677	Cyprus	
CRET_1		X		CRET	45			Greece	
DLIT_1	X	X	X	DLIT	14	34.94615	33.23383	Cyprus	
DLIT_2	X	X	X	DLIT	14	34.94615	33.23383	Cyprus	
DMAC_1	X	X	X	DMAC	15	34.93941	33.21534	Cyprus	
DMAC_2	X	X	X	DMAC	15	34.93941	33.21534	Cyprus	
FAMO_1	X	X	X	FAMO	16	35.07113	32.32238	Cyprus	
FAMO_2	X	X	X	FAMO	16	35.07113	32.32238	Cyprus	
FAVA_1	X	X	X	FAVA	17	34.92057	32.33797	Cyprus	
GERI_1	X	X	X	GERI	18	35.15341	33.71695	Cyprus	
GERI_2	X	X	X	GERI	18	35.15341	33.71695	Cyprus	
ISRA_1		X		ISRA	46			Israel	
ISRA_2		X		ISRA	46			Israel	
ISRA_3		X		ISRA	46			Israel	
ITAL_1		X		ITAL	47			Italy	FN824106.1
ITAL_2		X		ITAL	47			Italy	FN824107.1
ITAL_3		X		ITAL	47			Italy	FN824108.1
ITAL_4		X		ITAL	47			Italy	FN824109.1
ITAL_5		X		ITAL	47			Italy	FN824110.1
KALG_1	X	X		KALG	19	35.35750	33.63360	Cyprus	
KALG_2	X	X	X	KALG	19	35.35750	33.63360	Cyprus	
KGRE_1	X	X	X	KGRE	20	34.96621	34.05929	Cyprus	
KGRE_2		X	X	KGRE	20	34.96621	34.05929	Cyprus	
KIAT_1		X		KIAT	42			Greece	
KORN_1	X	X	X	KORN	21	35.33932	33.10881	Cyprus	
KORN_2	X	X	X	KORN	21	35.33932	33.10881	Cyprus	
KOUR_1	X	X	X	KOUR	22	34.66985	32.87377	Cyprus	
KOUR_3	X	X	X	KOUR	22	34.66985	32.87377	Cyprus	
LAFR_2	X	X	X	LAFR	23	35.05708	32.34472	Cyprus	
LAFR_3	X	X	X	LAFR	23	35.05708	32.34472	Cyprus	
LAFR_4	X	X	X	LAFR	23	35.05708	32.34472	Cyprus	

LARA_3	X	X	X	LARA	24	34.95805	32.31267	Cyprus	
LARA_4	X	X	X	LARA	24	34.95805	32.31267	Cyprus	
LATS_1	X	X	X	LATS	25	35.04030	32.37372	Cyprus	
LATS_4	X	X	X	LATS	25	35.04030	32.37372	Cyprus	
LIMN_1	X	X	X	LIMN	26	34.80515	32.96094	Cyprus	
LIMN_2	X	X	X	LIMN	26	34.80515	32.96094	Cyprus	
LSLT_1	X	X	X	LSLT	27	34.88972	33.60452	Cyprus	
OVEL_1		X	X	OVEL	28	34.98273	33.70572	Cyprus	
OVEL_2	X	X	X	OVEL	28	34.98273	33.70572	Cyprus	
PATH_1	X	X	X	PATH	29	35.12777	33.38851	Cyprus	
PELE_1	X	X	X	PELE	30	34.88979	32.95444	Cyprus	
PELE_2	X	X	X	PELE	30	34.88979	32.95444	Cyprus	
PENT_1	X	X	X	PENT	31	34.86794	32.62110	Cyprus	
PENT_2	X	X	X	PENT	31	34.86794	32.62110	Cyprus	
PITA_1	X	X	X	PITA	32	34.83190	32.53938	Cyprus	
PITA_2	X	X	X	PITA	32	34.83190	32.53938	Cyprus	
PLIO_1	X	X		PLIO	33	34.97288	33.89863	Cyprus	
PLIO_2	X	X	X	PLIO	33	34.97288	33.89863	Cyprus	
PPAL_1	X	X		PPAL	34	35.59372	34.42598	Cyprus	
PPAL_2	X	X	X	PPAL	34	35.59372	34.42598	Cyprus	
PPLA_2	X	X	X	PPLA	35	35.28628	33.53122	Cyprus	
PYRG_1	X	X	X	PYRG	36	35.06178	32.86050	Cyprus	
PYRG_2	X	X	X	PYRG	36	35.06178	32.86050	Cyprus	
SPSO_2	X	X	X	SPSO	37	35.02673	32.63098	Cyprus	
SPSO_3	X	X	X	SPSO	37	35.02673	32.63098	Cyprus	
TDAT_1		X	X	TDAT	48			Turkey	
TUNI_1				TUNI	50			Tunisia	AJ388094.1
TURA_2		X		TURA	38	36.557	29.15958	Turkey	
TURA_3		X		TURA	38	36.557	29.15958	Turkey	
TURB_1		X		TURB	51			Turkey	
TURB_3		X		TURB	51			Turkey	
TXXX_1		X		TXXX	49			Turkey	

VIKL_1	X	X	X	VIKL	39	35.63274	34.49475	Cyprus	
VIKL_2	X	X	X	VIKL	39	35.63274	34.49475	Cyprus	
VOUL_1		X		VOUL	40	37.48328	23.47027	Greece	
VOUL_2		X		VOUL	40	37.48328	23.47027	Greece	
VOUL_3		X		VOUL	40	37.48328	23.47027	Greece	
XERP_1	X	X	X	XERP	41	35.07310	32.80300	Cyprus	
XERP_2	X	X	X	XERP	41	35.07310	32.80300	Cyprus	
S. obscurus		X		Outgroup					AB861896_1
S. dorsalis		X		Outgroup					AB861897_1

Appendix II. Information on the haplotype distribution per molecular marker.

- *16S haplotypes (number of haplotypes = 6)*

Hap 1: 53 (AANA_1 AANA_2 AKAM_1 AKAM_2 AKAN_1 AKAN_2 AKDE_2 AKRO_1 AKRO_2 ARAK_1 ATHE_1 ATHE_2 BUFA_1 CHAR_1 CHAR_2 DLIT_1 DLIT_2 DMAC_1 DMAC_2 FAMO_1 FAMO_2 FAVA_1 GERI_1 GERI_2 KALG_1 KALG_2 KGRE_1 KORN_1 KOUR_1 KOUR_3 LAFR_2 LAFR_3 LARA_3 LARA_4 LATS_1 LATS_4 LIMN_1 LIMN_2 LSLT_1 OVEL_2 PATH_1 PELE_1 PELE_2 PENT_1 PENT_2 PITA_1 PITA_2 PPLA_2 PYRG_1 PYRG_2 SPSO_3 XERP_1 XERP_2)

Hap 2: 11 (TUNI_1 ANAP_1 ANAP_2 CAKT_1 CAKT_2 PLIO_1 PLIO_2 TDAT_1 TXXX_1 VIKL_1 VIKL_2)

Hap 3: 3 (AKAS_1 AKAS_2 BUFA_2)

Hap 4: 1 (KORN_2)

Hap 5: 2 (PPAL_1 PPAL_2)

Hap 6: 1 (SPSO_2)

- *COI haplotypes (number of haplotypes = 31)*

Hap 1: 5 (AANA_1 AANA_2 KGRE_1 LSLT_1 OVEL_1)

Hap 2: 1 (AKAM_1)

Hap 3: 7 (AKAM_2 FAMO_1 FAVA_1 LAFR_2 LAFR_3 LARA_3 LATS_1)

Hap 4: 6 (AKAN_1 AKAN_2 BUFA_1 BUFA_2 CHAR_2 PPLA_2)

Hap 5: 1 (AKAS_1)

Hap 6: 1 (AKAS_2)

Hap 7: 2 (AKDE_1 AKDE_2)

Hap 8: 2 (AKRO_1 AKRO_2)

Hap 9: 26 (ANAP_1 ANAP_2 ARCH_1 ARCH_2 CAKT_1 CAKT_2 ITAL_1 ITAL_2 ITAL_3 ITAL_4 ITAL_5 ISRA_1 ISRA_2 ISRA_3 PLIO_1 PLIO_2 PPAL_1 PPAL_2 TURB_1 TURB_3 VIKL_1 VIKL_2 VOUL_1 VOUL_2 VOUL_3 KIAT_1)

Hap 10: 1 (ARAK_1)

Hap 11: 1 (ARCH_3)

Hap 12: 2 (ATHE_1 ATHE_2)

Hap 13: 2 (CHAR_1 KALG_1)

Hap 14: 1 (DLIT_1)

Hap 15: 1 (DLIT_2)

Hap 16: 2 (DMAC_1 DMAC_2)

Hap 17: 1 (FAMO_2)

Hap 18: 3 (GERI_1 GERI_2 PATH_1)

Hap 19: 1 (KALG_2)

Hap 20: 1 (KGRE_2)

Hap 21: 2 (KORN_1 KORN_2)

Hap 22: 6 (KOUR_1 KOUR_3 PENT_1 PENT_2 PITA_1 PITA_2)

Hap 23: 2 (LARA_4 LATS_4)

Hap 24: 3 (LIMN_1 LIMN_2 PELE_1)

Hap 25: 1 (OVEL_2)

Hap 26: 1 (PELE_2)

Hap 27: 4 (PYRG_1 PYRG_2 XERP_1 XERP_2)

Hap 28: 2 (SPSO_2 SPSO_3)

Hap 29: 4 (TDAT_1 TXXX_1 AMOR_1 ANDR_1)

Hap 30: 2 (TURA_2 TURA_3)

Hap 31: 1 (CRET_1)

- *Cytb haplotypes (number of haplotypes = 33)*

Hap 1: 5 (AANA_1 AANA_2 KGRE_1 KGRE_2 LSLT_1)

Hap 2: 9 (AKAM_1 AKAM_2 FAMO_1 FAMO_2 LAFR_2 LAFR_3 LARA_3 LARA_4 LATS_1)

Hap 3: 2 (AKAN_1 AKAN_2)

Hap 4: 2 (AKAS_1 AKAS_2)

Hap 5: 2 (AKDE_1 AKDE_2)

Hap 6: 2 (AKRO_1 AKRO_2)

Hap 7: 8 (ANAP_1 ANAP_2 CAKT_1 CAKT_2 LSLT_2 PLIO_2 VIKL_1 VIKL_2)

Hap 8: 1 (ARAK_1)

Hap 9: 1 (ATHE_1)

Hap 10: 1 (BUFA_1)

Hap 11: 3 (BUFA_2 CHAR_2 KALG_2)

Hap 12: 1 (CHAR_1)

Hap 13: 1 (DLIT_1)

Hap 14: 2 (DLIT_2 DMAC_1)

Hap 15: 1 (DMAC_2)

Hap 16: 1 (FAVA_1)

Hap 17: 2 (GERI_1 GERI_2)

Hap 18: 1 (KORN_1)

Hap 19: 1 (KORN_2)

Hap 20: 2 (KOUR_1 KOUR_3)

Hap 21: 1 (LATS_4)

Hap 22: 1 (LIMN_1)

Hap 23: 3 (LIMN_2 PELE_1 PELE_2)

Hap 24: 1 (OVEL_1)

Hap 25: 1 (PATH_1)

Hap 26: 2 (PENT_1 PENT_2)

Hap 27: 2 (PITA_1 PITA_2)

Hap 28: 1 (PPAL_2)

Hap 29: 1 (PPLA_2)

Hap 30: 4 (PYRG_1 PYRG_2 XERP_1 XERP_2)

Hap 31: 1 (SPSO_2)

Hap 32: 1 (SPSO_3)

Hap 33: 1 (TDAT_1)

Appendix III. PCR primers, conditions and master mix examples.

(Simon et al., 1994)	F: 16S AR_LR_N13398	16S
	R: 16S_BR_LR_J12887	
	F: C1-J-1718	COI
	R: C1-N-2191	
(Folmer et al., 1994)	F: HCOI2198	
	R: LCOI1490	
(Barraclough et al., 1999)	F: CB3	cytb
	R: CB4	

	Stage	16S		COI		Cytb	
		◦C	Time	◦C	Time	◦C	Time
PCR conditions	Pro-incubation	95	3'	95	3'	94	2'
	Denaturation	94	15"	94	15"	94	30"
	Annealing	52	1'	40	1'	45	30"
	Extension	72	1.5'	72	1.5'	70	1'
	Another step	72	10'	72	10'	72	10'
	Standby T	16	∞	16	∞	16	∞
	Number of cycles	35		39		39	

16S example master mix			
	Stock	Concentration	25uL
Taq buffer	5X	1X	5
$MgCl_2$	25mM	3.8mM	3.8
dNTPs	10mM	0.2mM	0.5
PrimerA	10mM	0.4mM	1
Primer B	10mM	0.4mM	1
Taq polymerase	5u/ul	0.02	0.1
BSA	10mg/ml	1μg/μl	2.5
ddH2O			10.1

COI example master mix			
	Stock	Concentration	25uL
Taq buffer	10X	1X	2.5
$MgCl_2$	25mM	4mM	2.5
dNTPs	10mM	0.2mM	0.5
Primer A	10mM	0.4mM	1
Primer B	10mM	0.4mM	1
Taq polymerase	5u/ul	0.02	0.1
BSA	10mg/ml	1µg/µl	2.5
ddH2O			11.6

cytb example master mix			
	Stock	Concentration	25uL
Taq buffer	10X	1X	2.5
$MgCl_2$	25mM	5.5mM	4
dNTPs	10mM	0.2mM	0.5
Primer A	10mM	0.4mM	1
Primer B	10mM	0.4mM	1
Taq polymerase	5u/ul	0.02	0.1
BSA	10mg/ml	1µg/µl	2.5
ddH2O			14.9

Appendix IV. Genetic distances results (p-distance method).

I. Within-population genetic distances

- 16S

1.AANA	0.00
2.AKAM	0.00
3.AKAN	0.02
4.AKAS	0.00
5.AKDE	-
6.AKRO	0.00
7.ANAP	0.00
8.ARAK	-
10.ATHE	0.02
11.BUFA	0.00
12.CAKT	0.00
13.CHAR	0.03
14.DLIT	0.01
15.DMAC	0.01

16.FAMO	0.01
17.FAVA	-
18.GERI	0.00
19.KALG	0.01
20.KGRE	-
21.KORN	0.00
22.KOUR	0.01
23.LAFR	0.02
24.LARA	0.01
25.LATS	0.04
26.LIMN	0.00
27.LSLT	-
28.OVEL	-
29.PATH	-

30.PELE	0.00
31.PENT	0.00
32.PITA	0.00
33.PLIO	0.00
34.PPAL	0.02
35.PPLA	-
36.PYRG	0.00
37.SPSO	0.01
39.VIKL	0.00
41.XERP	0.00
48.TDAT	-
49.TXXX	-
50.TUNI	-

- COI

1.AANA	0.01
2.AKAM	0.01
3.AKAN	0.00
4.AKAS	0.04
5.AKDE	0.00
6.AKRO	0.00
7.ANAP	0.00
8.ARAK	-
9.ARCH	0.05
10.ATHE	0.02
11.BUFA	0.00
12.CAKT	0.00
13.CHAR	0.04
14.DLIT	0.02
15.DMAC	0.00
16.FAMO	0.01
17.FAVA	-

18.GERI	0.00
19.KALG	0.01
20.KGRE	0.02
21.KORN	0.00
22.KOUR	0.00
23.LAFR	0.00
24.LARA	0.00
25.LATS	0.02
26.LIMN	0.01
27.LSLT	-
28.OVEL	0.00
29.PATH	-
30.PELE	0.01
31.PENT	0.00
32.PITA	0.00
33.PLIO	0.00
34.PPAL	0.00

35.PPLA	-
36.PYRG	0.00
37.SPSO	0.00
38.TURA	0.00
39.VIKL	0.00
40.VOUL	0.00
41.XERP	0.00
42.KIAT	-
43.AMOR	-
44.ANDR	-
45.CRET	-
46.ISRA	0.00
47.ITAL	0.00
48.TDAT	-
49.TXXX	-
51.TURB	0.01

- cytb

1.AANA	0.00
2.AKAM	0.00
3.AKAN	0.00
4.AKAS	0.00
5.AKDE	0.00
6.AKRO	0.01
7.ANAP	0.00
8.ARAK	-
10.ATHE	-
11.BUFA	0.01
12.CAKT	0.00
13.CHAR	0.04
14.DLIT	0.02

15.DMAC	0.01
16.FAMO	0.00
17.FAVA	-
18.GERI	0.00
19.KALG	-
20.KGRE	0.01
21.KORN	0.01
22.KOUR	0.00
23.LAFR	0.00
24.LARA	0.00
25.LATS	0.01
26.LIMN	0.01
27.LSLT	-

28.OVEL	-
29.PATH	-
30.PELE	0.00
31.PENT	0.00
32.PITA	0.00
33.PLIO	-
34.PPAL	-
35.PPLA	-
36.PYRG	0.00
37.SPSO	0.01
48.TDAT	-
39.VIKL	0.00
41.XERP	0.00

- Terrestrial isopod cytb dataset

Species	**Genetic distance**	**Accession number**
A. officinalis lineage A	0.07	
A. officinalis lineage	0.01	
T. punctatus	0.00	KF007725-26, KF007731, KF007735, KF007736, KF007738, KF007741
L. hawaiensis	0.12	KF546703-18, KF546720-21
L. perkinsi	0.14	KF546719, KF546722-23
L. vitiensis	0.22	KF546724, KF546727
L. exotica	-	KF546726
L. occidentalis	-	KF546728
L. baudiniana	0.16	KF555656, KF555658-752, KF555755-63
L. oceanic	-	KF555657
L. italic	-	KF555753
T. albidus	-	KJ468127
T. capensis	-	KJ468128
T. chilensis	-	KJ468129
T. europaeus	0.05	KJ468130-31
T. exiguus	-	KJ468132
T. granulatus	-	KJ468133
T. granuliferus	0.00	KJ468134-5
H. brevicornis	-	KJ468136
T. maindroni	-	KJ468137
T. marcuzzii	-	KJ468138
T. neozelanicus	-	KJ468139
T. opercularis	0.17	KJ468140-41
T. ponticus	0.13	KJ468142-44
T. spinulosus	-	KJ468145
T. wegeneri	-	KJ468146
L. dentipes	0.13	MF805556-59, MF805561-63

Between-population genetic distances

- 16S

AANA																																						
AKAM	0.04																																				
AKAN	0.04	0.07																																			
AKAS	0.01	0.05	0.03																																		
AKDE	0.03	0.07	0.05	0.03																																	
AKRO	0.03	0.05	0.06	0.03	0.02																																
ANAP	0.07	0.09	0.09	0.08	0.09	0.07																															
ARAK	0.03	0.05	0.06	0.03	0.03	0.00	0.08																														
ATHE	0.02	0.05	0.05	0.03	0.03	0.02	0.08	0.03																													
BUFA	0.03	0.06	0.02	0.03	0.05	0.05	0.08	0.05	0.04																												
CAKT	0.07	0.09	0.09	0.08	0.09	0.07	0.00	0.09	0.08	0.08																											
CHAR	0.02	0.06	0.03	0.03	0.04	0.04	0.08	0.05	0.03	0.02	0.08																										
DLIT	0.01	0.05	0.04	0.02	0.03	0.03	0.07	0.04	0.03	0.04	0.07	0.02																									
DMAC	0.00	0.04	0.03	0.02	0.03	0.03	0.07	0.04	0.02	0.03	0.07	0.02	0.01																								
FAMO	0.04	0.00	0.07	0.05	0.07	0.05	0.09	0.05	0.05	0.06	0.09	0.06	0.05	0.04																							
FAVA	0.08	0.00	0.12	0.10	0.10	0.07	0.15	0.07	0.09	0.13	0.15	0.10	0.08	0.08	0.01																						
GERI	0.01	0.05	0.04	0.02	0.04	0.03	0.08	0.03	0.02	0.03	0.08	0.03	0.01	0.01	0.05	0.09																					
KALG	0.03	0.06	0.03	0.03	0.05	0.05	0.08	0.05	0.04	0.01	0.08	0.02	0.03	0.02	0.06	0.12	0.03																				
KGRE	0.00	0.04	0.03	0.01	0.03	0.03	0.07	0.03	0.02	0.03	0.07	0.02	0.01	0.00	0.04	0.08	0.01	0.03																			
KORN	0.02	0.05	0.03	0.01	0.03	0.03	0.08	0.04	0.03	0.03	0.07	0.03	0.02	0.02	0.05	0.09	0.02	0.03	0.01																		
KOUR	0.03	0.03	0.06	0.05	0.06	0.04	0.09	0.04	0.04	0.05	0.09	0.04	0.04	0.04	0.03	0.06	0.04	0.05	0.03	0.04																	
LAFR	0.05	0.01	0.08	0.06	0.07	0.05	0.10	0.05	0.06	0.07	0.10	0.07	0.06	0.05	0.01	0.00	0.06	0.07	0.05	0.06	0.04																
LARA	0.05	0.00	0.08	0.06	0.07	0.05	0.09	0.06	0.05	0.07	0.09	0.06	0.05	0.05	0.01	0.01	0.05	0.07	0.05	0.05	0.03	0.01															
LATS	0.05	0.02	0.08	0.06	0.08	0.05	0.11	0.05	0.06	0.08	0.11	0.07	0.06	0.05	0.02	0.02	0.06	0.08	0.05	0.06	0.04	0.02	0.02														
LIMN	0.04	0.04	0.06	0.04	0.05	0.02	0.08	0.01	0.03	0.06	0.09	0.05	0.05	0.04	0.05	0.06	0.03	0.06	0.03	0.04	0.04	0.04	0.05	0.04													
LSLT	0.03	0.08	0.06	0.03	0.04	0.05	0.08	0.06	0.04	0.06	0.09	0.05	0.03	0.03	0.08	0.08	0.04	0.05	0.02	0.04	0.07	0.07	0.08	0.07	0.06												
OVEL	0.00	0.07	0.05	0.02	0.05	0.03	0.10	0.03	0.03	0.05	0.10	0.04	0.02	0.01	0.07	0.08	0.02	0.05	0.00	0.03	0.06	0.07	0.08	0.07	0.03	0.00											
PATH	0.01	0.05	0.04	0.02	0.03	0.02	0.08	0.02	0.01	0.03	0.07	0.02	0.01	0.00	0.05	0.09	0.01	0.03	0.01	0.02	0.04	0.05	0.05	0.06	0.03	0.02	0.01										
PELE	0.03	0.04	0.07	0.05	0.05	0.03	0.09	0.02	0.04	0.06	0.09	0.05	0.03	0.03	0.04	0.06	0.03	0.06	0.03	0.03	0.04	0.04	0.05	0.05	0.00	0.03	0.03	0.03									
PENT	0.04	0.04	0.06	0.05	0.07	0.03	0.11	0.03	0.06	0.05	0.11	0.05	0.05	0.04	0.04	0.05	0.05	0.06	0.04	0.04	0.05	0.04	0.04	0.05	0.02	0.06	0.06	0.05	0.03								
PITA	0.03	0.03	0.05	0.04	0.06	0.03	0.08	0.04	0.04	0.05	0.07	0.04	0.04	0.03	0.03	0.06	0.03	0.05	0.03	0.03	0.03	0.04	0.03	0.05	0.03	0.06	0.05	0.04	0.03	0.00							

PLIO	0.07	0.08	0.08	0.07	0.09	0.07	0.00	0.08	0.08	0.07	0.00	0.08	0.07	0.07	0.08	0.15	0.08	0.08	0.07	0.07	0.09	0.09	0.09	0.11	0.08	0.09	0.10	0.08	0.09	0.10	0.07										
PPAL	0.09	0.10	0.11	0.09	0.12	0.10	0.01	0.11	0.10	0.09	0.01	0.10	0.10	0.09	0.10	0.17	0.11	0.10	0.09	0.09	0.11	0.11	0.11	0.13	0.10	0.13	0.14	0.10	0.12	0.12	0.09	0.01								
PYRG	0.03	0.03	0.05	0.04	0.06	0.03	0.08	0.03	0.04	0.05	0.08	0.04	0.03	0.03	0.03	0.05	0.04	0.05	0.03	0.03	0.02	0.04	0.03	0.04	0.03	0.06	0.05	0.04	0.04	0.04	0.03	0.08	0.09							
SPSO	0.03	0.03	0.06	0.04	0.05	0.03	0.09	0.02	0.03	0.05	0.08	0.04	0.03	0.03	0.02	0.05	0.03	0.05	0.03	0.03	0.02	0.03	0.03	0.04	0.02	0.05	0.05	0.03	0.02	0.03	0.02	0.08	0.11	0.02						
TDAT	0.08	0.10	0.11	0.08	0.09	0.07	0.02	0.08	0.09	0.10	0.02	0.10	0.08	0.08	0.10	0.13	0.09	0.10	0.08	0.08	0.10	0.10	0.11	0.11	0.08	0.08	0.09	0.08	0.09	0.12	0.08	0.02	0.05	0.08	0.09					
TUNI	0.08	0.10	0.10	0.09	0.09	0.06	0.00	0.08	0.08	0.09	0.00	0.09	0.08	0.08	0.10	0.15	0.09	0.09	0.08	0.08	0.10	0.10	0.10	0.11	0.08	0.09	0.10	0.08	0.09	0.11	0.08	0.00	0.01	0.08	0.09	0.02				
TXXX	0.07	0.09	0.08	0.08	0.08	0.07	0.02	0.08	0.08	0.08	0.02	0.08	0.07	0.07	0.09	0.13	0.08	0.08	0.06	0.07	0.08	0.09	0.09	0.10	0.07	0.06	0.09	0.07	0.08	0.10	0.07	0.02	0.04	0.07	0.08	0.00	0.01			
VIKL	0.08	0.09	0.09	0.08	0.09	0.07	0.00	0.09	0.08	0.08	0.00	0.08	0.08	0.08	0.09	0.15	0.08	0.08	0.07	0.07	0.09	0.09	0.09	0.11	0.09	0.09	0.11	0.08	0.09	0.10	0.07	0.00	0.01	0.08	0.09	0.02	0.00	0.02		
XERP	0.03	0.03	0.05	0.04	0.06	0.04	0.08	0.04	0.04	0.05	0.08	0.04	0.04	0.04	0.03	0.05	0.04	0.05	0.03	0.03	0.02	0.04	0.04	0.04	0.04	0.06	0.06	0.04	0.04	0.04	0.03	0.08	0.09	0.00	0.02	0.09	0.08	0.08	0.08	

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AANA																																												
AKAM	0.10																																											
AKAN	0.06	0.09																																										
AKAS	0.07	0.09	0.06																																									
AKDE	0.06	0.10	0.05	0.07																																									
AKRO	0.06	0.08	0.07	0.08	0.07																																							
AMOR	0.09	0.10	0.09	0.11	0.10	0.09																																						
ANAP	0.10	0.11	0.10	0.12	0.11	0.10	0.02																																					
ANDR	0.09	0.10	0.09	0.11	0.10	0.09	0.00	0.02																																				
ARAK	0.10	0.07	0.08	0.09	0.09	0.05	0.11	0.12	0.11																																			
ARCH	0.10	0.11	0.09	0.12	0.10	0.11	0.04	0.03	0.04	0.11																																		
ATHE	0.08	0.09	0.07	0.09	0.08	0.06	0.10	0.11	0.10	0.07	0.11																																	
BUFA	0.05	0.09	0.02	0.05	0.06	0.06	0.10	0.10	0.10	0.10	0.11	0.08																																

CAKT	0.09	0.10	0.09	0.12	0.11	0.10	0.02	0.00	0.02	0.12	0.03	0.11	0.10																				
CHAR	0.06	0.09	0.03	0.06	0.06	0.07	0.09	0.10	0.09	0.08	0.10	0.07	0.02	0.10																			
CRET	0.12	0.15	0.13	0.13	0.13	0.12	0.03	0.06	0.03	0.13	0.08	0.13	0.12	0.06	0.13																		
DLIT	0.03	0.10	0.05	0.06	0.06	0.07	0.09	0.10	0.09	0.08	0.08	0.08	0.06	0.09	0.06	0.13																	
DMAC	0.02	0.09	0.04	0.06	0.06	0.06	0.09	0.09	0.09	0.07	0.08	0.08	0.05	0.09	0.05	0.12	0.01																
FAMO	0.10	0.01	0.09	0.09	0.11	0.08	0.10	0.11	0.10	0.07	0.11	0.09	0.09	0.10	0.09	0.14	0.10	0.10															
FAVA	0.09	0.01	0.09	0.09	0.10	0.07	0.09	0.10	0.09	0.06	0.11	0.08	0.08	0.10	0.09	0.13	0.09	0.09	0.01														
GERI	0.02	0.10	0.04	0.06	0.05	0.06	0.08	0.09	0.08	0.08	0.08	0.07	0.05	0.09	0.05	0.12	0.02	0.01	0.10	0.09													
ISRA	0.10	0.11	0.09	0.12	0.09	0.11	0.03	0.00	0.03	0.12	0.02	0.11	0.11	0.00	0.10	0.08	0.09	0.09	0.11	0.11	0.09												
ITAL	0.10	0.11	0.09	0.12	0.10	0.10	0.02	0.00	0.02	0.12	0.03	0.10	0.10	0.00	0.10	0.06	0.09	0.09	0.11	0.11	0.09	0.01											
KALG	0.06	0.09	0.03	0.06	0.07	0.06	0.09	0.10	0.09	0.10	0.11	0.07	0.01	0.09	0.03	0.12	0.06	0.05	0.09	0.08	0.05	0.11	0.10										
KGRE	0.01	0.10	0.06	0.07	0.06	0.07	0.08	0.10	0.08	0.11	0.10	0.08	0.05	0.09	0.06	0.12	0.03	0.03	0.10	0.09	0.02	0.10	0.10	0.06									
KIAT	0.09	0.11	0.09	0.12	0.10	0.09	0.02	0.00	0.02	0.12	0.04	0.10	0.10	0.00	0.10	0.05	0.09	0.09	0.10	0.10	0.09	0.01	0.00	0.10	0.09								
KORN	0.07	0.10	0.05	0.07	0.03	0.08	0.10	0.11	0.10	0.08	0.10	0.08	0.06	0.11	0.06	0.13	0.06	0.06	0.10	0.09	0.05	0.09	0.10	0.07	0.07	0.11							
KOUR	0.08	0.05	0.08	0.08	0.09	0.06	0.10	0.10	0.10	0.08	0.10	0.08	0.08	0.10	0.08	0.12	0.08	0.07	0.06	0.04	0.07	0.10	0.10	0.08	0.08	0.10	0.09						
LAFR	0.09	0.00	0.09	0.09	0.09	0.07	0.10	0.10	0.10	0.06	0.11	0.08	0.08	0.10	0.09	0.13	0.09	0.09	0.01	0.00	0.09	0.11	0.11	0.08	0.09	0.10	0.09	0.04					
LARA	0.09	0.01	0.08	0.08	0.08	0.08	0.09	0.10	0.09	0.05	0.09	0.08	0.09	0.10	0.09	0.14	0.08	0.08	0.01	0.01	0.08	0.09	0.10	0.09	0.09	0.10	0.08	0.06	0.01				
LATS	0.09	0.01	0.09	0.09	0.10	0.07	0.10	0.10	0.10	0.06	0.11	0.08	0.09	0.10	0.09	0.13	0.09	0.09	0.02	0.01	0.09	0.10	0.10	0.09	0.09	0.10	0.10	0.05	0.01	0.02			
LIMN	0.07	0.08	0.08	0.09	0.08	0.03	0.10	0.11	0.10	0.05	0.12	0.06	0.07	0.11	0.07	0.14	0.07	0.06	0.08	0.07	0.07	0.12	0.11	0.06	0.08	0.10	0.09	0.07	0.07	0.08	0.08		
LSLT	0.01	0.10	0.06	0.07	0.06	0.07	0.09	0.10	0.09	0.10	0.09	0.09	0.06	0.10	0.06	0.12	0.03	0.02	0.11	0.10	0.02	0.09	0.10	0.07	0.01	0.09	0.06	0.09	0.10	0.09	0.10	0.08	
OVEL	0.01	0.10	0.05	0.07	0.05	0.07	0.09	0.09	0.09	0.10	0.09	0.08	0.05	0.09	0.06	0.12	0.02	0.02	0.11	0.09	0.01	0.08	0.09	0.06	0.02	0.09	0.06	0.08	0.09	0.09	0.10	0.08	0.00

PATH	0.02	0.09	0.05	0.06	0.05	0.06	0.08	0.09	0.08	0.10	0.09	0.08	0.04	0.09	0.04	0.11	0.02	0.02	0.09	0.08	0.01	0.09	0.09	0.04	0.02	0.09	0.05	0.07	0.08	0.09	0.08	0.07	0.02	0.02															
PELE	0.07	0.08	0.08	0.09	0.08	0.03	0.10	0.11	0.10	0.06	0.12	0.06	0.07	0.11	0.07	0.13	0.07	0.06	0.08	0.07	0.07	0.12	0.11	0.06	0.08	0.10	0.08	0.07	0.07	0.08	0.07	0.01	0.08	0.08	0.07														
PENT	0.09	0.06	0.08	0.10	0.10	0.08	0.10	0.11	0.10	0.12	0.12	0.10	0.09	0.11	0.09	0.13	0.09	0.09	0.07	0.06	0.08	0.12	0.11	0.09	0.09	0.11	0.10	0.05	0.06	0.07	0.06	0.09	0.10	0.09	0.08	0.09													
PITA	0.07	0.05	0.07	0.09	0.08	0.07	0.09	0.10	0.09	0.09	0.11	0.09	0.08	0.09	0.08	0.12	0.08	0.08	0.05	0.05	0.07	0.10	0.10	0.08	0.08	0.10	0.08	0.05	0.04	0.05	0.05	0.08	0.08	0.08	0.07	0.08	0.03												
PLIO	0.10	0.11	0.10	0.12	0.10	0.10	0.02	0.00	0.02	0.12	0.03	0.11	0.10	0.00	0.10	0.06	0.09	0.09	0.11	0.10	0.09	0.00	0.00	0.10	0.09	0.00	0.10	0.10	0.10	0.10	0.10	0.11	0.10	0.09	0.09	0.11	0.11	0.10											
PPAL	0.09	0.11	0.09	0.12	0.10	0.09	0.02	0.01	0.02	0.12	0.03	0.10	0.10	0.01	0.10	0.06	0.09	0.08	0.11	0.10	0.09	0.01	0.01	0.10	0.09	0.00	0.10	0.10	0.10	0.10	0.10	0.11	0.10	0.09	0.09	0.11	0.10	0.10	0.01										
PPLA	0.05	0.09	0.02	0.05	0.06	0.07	0.09	0.10	0.09	0.10	0.12	0.08	0.00	0.10	0.02	0.12	0.06	0.05	0.09	0.09	0.05	0.11	0.10	0.01	0.06	0.10	0.06	0.08	0.09	0.10	0.09	0.07	0.06	0.06	0.04	0.07	0.09	0.08	0.10	0.10									
PYRG	0.08	0.06	0.06	0.09	0.08	0.07	0.08	0.09	0.08	0.06	0.09	0.08	0.07	0.09	0.06	0.11	0.07	0.06	0.06	0.05	0.07	0.09	0.09	0.06	0.08	0.09	0.08	0.05	0.05	0.06	0.05	0.07	0.08	0.08	0.06	0.07	0.06	0.05	0.09	0.09	0.07								
SPSO	0.08	0.05	0.08	0.09	0.09	0.07	0.10	0.10	0.10	0.07	0.10	0.09	0.08	0.10	0.08	0.12	0.08	0.08	0.06	0.05	0.08	0.10	0.11	0.08	0.09	0.11	0.09	0.06	0.04	0.06	0.05	0.08	0.09	0.09	0.07	0.07	0.06	0.05	0.10	0.10	0.08	0.03							
TDAT	0.09	0.11	0.09	0.11	0.09	0.09	0.00	0.02	0.00	0.11	0.04	0.10	0.09	0.02	0.10	0.04	0.09	0.09	0.11	0.10	0.08	0.03	0.02	0.09	0.09	0.02	0.10	0.09	0.10	0.09	0.10	0.11	0.09	0.09	0.08	0.11	0.10	0.09	0.02	0.02	0.10	0.08	0.10						
TURA	0.10	0.12	0.09	0.12	0.10	0.11	0.08	0.08	0.08	0.09	0.07	0.11	0.11	0.09	0.10	0.11	0.08	0.08	0.12	0.11	0.08	0.08	0.08	0.11	0.10	0.09	0.10	0.09	0.11	0.10	0.11	0.13	0.10	0.09	0.09	0.13	0.11	0.10	0.08	0.07	0.11	0.09	0.10	0.07					
TURB	0.09	0.11	0.08	0.12	0.09	0.10	0.02	0.01	0.02	0.12	0.03	0.11	0.11	0.01	0.10	0.07	0.08	0.08	0.11	0.11	0.08	0.01	0.01	0.11	0.09	0.00	0.09	0.10	0.11	0.09	0.10	0.12	0.09	0.08	0.09	0.12	0.11	0.10	0.01	0.01	0.11	0.09	0.11	0.02	0.07				
TXXX	0.09	0.11	0.10	0.11	0.10	0.09	0.00	0.02	0.00	0.11	0.04	0.10	0.10	0.02	0.10	0.04	0.09	0.09	0.11	0.10	0.09	0.03	0.02	0.09	0.09	0.02	0.10	0.09	0.10	0.10	0.10	0.11	0.10	0.09	0.08	0.11	0.10	0.09	0.02	0.02	0.10	0.08	0.10	0.00	0.07	0.02			
VIKL	0.10	0.11	0.09	0.12	0.09	0.11	0.03	0.01	0.03	0.12	0.02	0.11	0.11	0.01	0.10	0.08	0.09	0.09	0.11	0.11	0.09	0.00	0.01	0.11	0.10	0.01	0.09	0.10	0.11	0.09	0.10	0.12	0.09	0.09	0.09	0.12	0.12	0.10	0.01	0.02	0.12	0.09	0.11	0.03	0.07	0.01	0.03		
VOUL	0.10	0.11	0.09	0.12	0.09	0.11	0.03	0.00	0.03	0.12	0.02	0.11	0.11	0.01	0.10	0.08	0.09	0.09	0.11	0.11	0.08	0.00	0.01	0.11	0.10	0.01	0.09	0.10	0.11	0.09	0.10	0.12	0.09	0.08	0.09	0.12	0.12	0.10	0.00	0.02	0.11	0.09	0.10	0.03	0.07	0.00	0.03	0.00	
XERP	0.08	0.05	0.06	0.09	0.08	0.06	0.09	0.09	0.09	0.06	0.09	0.08	0.06	0.09	0.06	0.11	0.07	0.06	0.06	0.05	0.07	0.09	0.09	0.06	0.08	0.10	0.08	0.05	0.04	0.06	0.05	0.07	0.08	0.08	0.06	0.06	0.06	0.05	0.09	0.09	0.06	0.00	0.03	0.08	0.09	0.08	0.08	0.09	0.09

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AANA																																						
AKAM	0.09																																					
AKAN	0.07	0.10																																				
AKAS	0.05	0.09	0.04																																			
AKDE	0.03	0.07	0.04	0.04																																		
AKRO	0.08	0.07	0.08	0.08	0.06																																	
ANAP	0.13	0.13	0.13	0.13	0.12	0.12																																
ARAK	0.07	0.08	0.08	0.07	0.06	0.02	0.12																															
ATHE	0.11	0.11	0.12	0.11	0.10	0.08	0.16	0.08																														
BUFA	0.06	0.10	0.03	0.05	0.06	0.08	0.14	0.08	0.12																													
CAKT	0.13	0.13	0.13	0.13	0.12	0.12	0.00	0.12	0.16	0.13																												
CHAR	0.06	0.10	0.04	0.05	0.05	0.08	0.13	0.07	0.11	0.03	0.13																											
DLIT	0.02	0.09	0.07	0.06	0.03	0.08	0.13	0.07	0.11	0.06	0.13	0.06																										
DMAC	0.01	0.09	0.07	0.06	0.03	0.08	0.13	0.07	0.11	0.06	0.13	0.06	0.01																									
FAMO	0.09	0.00	0.10	0.09	0.07	0.07	0.13	0.08	0.11	0.10	0.13	0.10	0.09	0.09																								
FAVA	0.10	0.01	0.10	0.10	0.08	0.08	0.14	0.08	0.11	0.10	0.14	0.10	0.10	0.10	0.01																							
GERI	0.01	0.09	0.07	0.06	0.03	0.08	0.13	0.08	0.11	0.07	0.13	0.06	0.01	0.01	0.10	0.10																						
KALG	0.06	0.10	0.02	0.05	0.05	0.08	0.13	0.08	0.12	0.01	0.13	0.02	0.06	0.06	0.10	0.10	0.06																					
KGRE	0.00	0.09	0.07	0.06	0.03	0.08	0.14	0.07	0.10	0.07	0.13	0.06	0.02	0.01	0.09	0.10	0.01	0.06																				
KORN	0.04	0.08	0.05	0.05	0.02	0.07	0.13	0.07	0.10	0.06	0.13	0.05	0.04	0.04	0.08	0.09	0.04	0.05	0.04																			
KOUR	0.08	0.05	0.09	0.09	0.07	0.07	0.13	0.06	0.11	0.09	0.13	0.08	0.08	0.08	0.05	0.05	0.08	0.09	0.08	0.08																		
LAFR	0.09	0.00	0.10	0.09	0.07	0.07	0.14	0.07	0.10	0.10	0.13	0.09	0.09	0.09	0.01	0.01	0.09	0.10	0.09	0.08	0.04																	
LARA	0.09	0.00	0.10	0.09	0.07	0.07	0.14	0.07	0.11	0.10	0.13	0.09	0.09	0.09	0.00	0.01	0.09	0.10	0.09	0.08	0.04	0.00																
LATS	0.09	0.01	0.10	0.10	0.08	0.07	0.14	0.08	0.11	0.10	0.14	0.10	0.09	0.09	0.01	0.01	0.10	0.10	0.09	0.08	0.05	0.01	0.01															
LIMN	0.08	0.07	0.09	0.08	0.06	0.03	0.13	0.03	0.07	0.08	0.12	0.08	0.08	0.08	0.07	0.08	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.08														
LSLT	0.00	0.06	0.07	0.06	0.02	0.06	0.14	0.08	0.08	0.07	0.14	0.06	0.02	0.02	0.06	0.06	0.01	0.08	0.00	0.03	0.06	0.06	0.06	0.06	0.06													
OVEL	0.00	0.09	0.07	0.05	0.03	0.08	0.13	0.08	0.10	0.07	0.13	0.06	0.02	0.02	0.09	0.10	0.01	0.06	0.01	0.04	0.08	0.09	0.10	0.10	0.08	0.01												
PATH	0.01	0.09	0.06	0.05	0.03	0.08	0.13	0.08	0.11	0.06	0.13	0.06	0.01	0.01	0.09	0.10	0.01	0.06	0.01	0.04	0.08	0.09	0.10	0.10	0.08	0.01	0.01											
PELE	0.08	0.07	0.09	0.08	0.06	0.03	0.13	0.03	0.07	0.08	0.13	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.08	0.07	0.07	0.07	0.07	0.08	0.00	0.06	0.08	0.08										
PENT	0.10	0.06	0.11	0.10	0.08	0.09	0.14	0.08	0.13	0.11	0.14	0.11	0.10	0.10	0.07	0.07	0.10	0.11	0.10	0.09	0.06	0.06	0.06	0.06	0.08	0.11	0.10	0.10	0.08									
PITA	0.09	0.06	0.10	0.09	0.07	0.08	0.13	0.08	0.12	0.10	0.13	0.10	0.09	0.09	0.06	0.06	0.09	0.10	0.09	0.09	0.05	0.05	0.05	0.05	0.08	0.09	0.10	0.10	0.07	0.01								
PLIO	0.13	0.13	0.13	0.13	0.12	0.12	0.00	0.12	0.16	0.13	0.00	0.13	0.13	0.13	0.13	0.14	0.13	0.13	0.13	0.13	0.13	0.13	0.14	0.14	0.13	0.14	0.13	0.13	0.13	0.14	0.13							
PPAL	0.13	0.14	0.13	0.13	0.12	0.12	0.01	0.12	0.17	0.13	0.01	0.13	0.13	0.13	0.14	0.15	0.13	0.13	0.13	0.13	0.14	0.14	0.14	0.14	0.13	0.15	0.13	0.13	0.13	0.14	0.13	0.01						
PPLA	0.06	0.10	0.03	0.05	0.05	0.08	0.13	0.08	0.12	0.01	0.13	0.03	0.06	0.06	0.10	0.10	0.06	0.01	0.06	0.05	0.09	0.10	0.10	0.10	0.08	0.08	0.06	0.05	0.08	0.11	0.10	0.13	0.13					
PYRG	0.08	0.04	0.10	0.09	0.07	0.08	0.14	0.08	0.11	0.09	0.13	0.08	0.08	0.08	0.04	0.05	0.08	0.09	0.08	0.08	0.04	0.04	0.04	0.04	0.07	0.07	0.09	0.09	0.07	0.05	0.05	0.13	0.14	0.09				

SPSO	0.09	0.05	0.09	0.09	0.07	0.08	0.14	0.08	0.11	0.09	0.13	0.09	0.09	0.09	0.05	0.05	0.09	0.09	0.09	0.09	0.03	0.04	0.05	0.05	0.07	0.09	0.09	0.09	0.07	0.05	0.04	0.13	0.14	0.08	0.03			
TDAT	0.13	0.14	0.13	0.13	0.12	0.13	0.02	0.13	0.16	0.13	0.02	0.13	0.13	0.13	0.14	0.15	0.14	0.13	0.14	0.13	0.14	0.14	0.14	0.15	0.13	0.15	0.13	0.13	0.13	0.14	0.14	0.02	0.02	0.13	0.14	0.14		
VIKL	0.13	0.13	0.13	0.13	0.12	0.12	0.00	0.12	0.16	0.13	0.00	0.13	0.13	0.13	0.13	0.14	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.14	0.13	0.14	0.13	0.13	0.13	0.14	0.13	0.00	0.01	0.13	0.13	0.13	0.02	
XERP	0.09	0.04	0.09	0.10	0.07	0.07	0.13	0.07	0.11	0.09	0.13	0.09	0.09	0.08	0.04	0.05	0.09	0.09	0.09	0.08	0.04	0.04	0.04	0.04	0.07	0.07	0.09	0.09	0.07	0.05	0.05	0.13	0.14	0.09	0.00	0.03	0.14	0.13

- Terrestrial isopod cytb dataset

*A. officinalis*lineage A																												
*A. officinalis*lineageB	0.13																											
T. punctatus	0.35	0.35																										
L. hawaiensis	0.36	0.36	0.32																									
L. perkinsi	0.37	0.37	0.33	0.17																								
L. vitiensis	0.38	0.39	0.36	0.24	0.25																							
L. exotica	0.40	0.38	0.33	0.22	0.24	0.25																						
L. occidentalis	0.39	0.39	0.33	0.24	0.25	0.26	0.23																					
L. baudiniana	0.38	0.38	0.33	0.25	0.25	0.27	0.26	0.25																				
L. oceanica	0.39	0.39	0.37	0.28	0.28	0.28	0.28	0.26	0.29																			
L. italica	0.35	0.36	0.33	0.25	0.25	0.28	0.27	0.25	0.28	0.25																		
T. albidus	0.41	0.42	0.30	0.37	0.39	0.37	0.35	0.37	0.37	0.39	0.35																	
T. capensis	0.38	0.39	0.24	0.39	0.41	0.38	0.38	0.38	0.38	0.38	0.39	0.24																
T. chilensis	0.35	0.35	0.27	0.31	0.31	0.33	0.33	0.34	0.33	0.36	0.33	0.33	0.30															
T. europaeus	0.40	0.38	0.24	0.39	0.39	0.40	0.37	0.37	0.36	0.39	0.41	0.29	0.22	0.31														
T. exiguus	0.40	0.41	0.24	0.38	0.39	0.39	0.37	0.38	0.37	0.38	0.36	0.27	0.25	0.32	0.29													
T. granulatus	0.36	0.37	0.20	0.36	0.36	0.38	0.37	0.36	0.36	0.36	0.34	0.28	0.21	0.30	0.25	0.25												
T. granuliferus	0.40	0.39	0.26	0.35	0.36	0.34	0.39	0.36	0.35	0.34	0.33	0.29	0.27	0.31	0.27	0.28	0.22											
H. brevicornis	0.36	0.37	0.29	0.34	0.34	0.35	0.36	0.34	0.34	0.33	0.33	0.32	0.29	0.28	0.30	0.31	0.26	0.34										
T. maindroni	0.38	0.36	0.23	0.35	0.36	0.37	0.40	0.33	0.32	0.36	0.36	0.26	0.23	0.33	0.26	0.24	0.22	0.27	0.29									
T. marcuzzii	0.39	0.36	0.25	0.36	0.35	0.36	0.38	0.33	0.35	0.36	0.36	0.29	0.26	0.29	0.28	0.23	0.26	0.29	0.30	0.24								
T. neozelanicus	0.36	0.36	0.23	0.34	0.35	0.36	0.38	0.37	0.34	0.33	0.35	0.29	0.25	0.30	0.26	0.29	0.23	0.26	0.29	0.25	0.27							
T. opercularis	0.40	0.39	0.26	0.36	0.37	0.37	0.38	0.38	0.37	0.37	0.38	0.28	0.25	0.32	0.27	0.28	0.24	0.23	0.31	0.27	0.27	0.25						
T. ponticus	0.42	0.40	0.24	0.38	0.39	0.40	0.40	0.39	0.37	0.41	0.40	0.29	0.25	0.33	0.19	0.26	0.25	0.29	0.35	0.26	0.28	0.28	0.28					
T. spinulosus	0.38	0.37	0.27	0.34	0.33	0.35	0.33	0.32	0.34	0.36	0.36	0.33	0.27	0.18	0.32	0.31	0.30	0.32	0.29	0.34	0.31	0.25	0.31	0.34				
T. wegeneri	0.39	0.37	0.31	0.36	0.37	0.37	0.36	0.37	0.37	0.36	0.37	0.32	0.34	0.34	0.34	0.34	0.30	0.35	0.33	0.29	0.33	0.31	0.34	0.34	0.30			
L. dentipes	0.39	0.40	0.34	0.23	0.25	0.25	0.21	0.23	0.27	0.28	0.28	0.36	0.37	0.36	0.37	0.35	0.38	0.35	0.36	0.35	0.37	0.36	0.35	0.36	0.37	0.35		

«Δηλώνω ρητά ότι, το κείμενο της μεταπτυχιακής διπλωματικής εργασίας δεν αποτελεί προϊόν μερικής ή ολικής αντιγραφής, οι πηγές δε που χρησιμοποιήθηκαν περιορίζονται στις βιβλιογραφικές αναφορές και μόνον»

Ιωάννης Αλεξίου