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Evidence of cryptic diversity in *Podarcis peloponnesiacus* and re-evaluation of its current taxonomy; insights from genetic, morphological, and ecological data

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Abstract

The Peloponnese wall lizard, Podarcis peloponnesiacus, is endemic to the Peloponnese. Although the phylogeny and species diversity of the Balkan species of Podarcis have been extensively studied, the intraspecific relationships of P. peloponnesiacus are not yet well defined. The aim of this study was to investigate the intraspecific diversity in this species and clarify its taxonomic status by analyzing eight gene fragments (two mitochondrial and six nuclear) and several morphological traits, typically used for systematic inferences within the genus Podarcis. Together with ecological niche modeling, we provided an integrative evaluation of the differentiation between lineages. The combination of several phylogenetic, species delimitation, and chronophylogenetic analyses revealed the existence of two highly supported and divergent clades with a distinct geographical and parapatric distribution and high niche overlap. The differentiation of the two clades dates back to the Pleistocene and is probably correlated with the paleogeography of the Peloponnese. These clades also differed in several phenotypic traits, which, however, exhibit extensive overlap and are not fully diagnostic. The combination of the above results allowed us to identify the two revealed clades as distinct species.

KEYWORDS

mitochondrial DNA, nuclear DNA, phylogeny, phylogeography, southern Balkans, species delimitation, systematics

1 | INTRODUCTION

The Peloponnese (south continental Greece) is an important area for biodiversity, both in terms of landscape and species diversity (Valakos et al., 2008). It is considered one of the most important speciation centers in the Balkan Peninsula (Gkontas et al., 2016) with high levels of endemism for plants, invertebrates, and vertebrates (Jablonski et al., 2016). It is home to endemic reptile taxa, such as the species *Podarcis peloponnesiacus* (Bibron and Bory de Saint-Vincent, 1833) and Anguis cephallonica (Werner, 1894). There is even endemism there at the genus level, in the case of *Hellenolacerta graeca* (Bedriaga, 1886) (Valakos et al., 2008).

The high diversity of this region is related to the complex paleogeographical history of southern Greece, including the Peloponnese (submergence and re-emergence of landmasses, due to tectonic, volcanic, and eustatic events; Creutzburg, 1963), in combination with the climatic changes of the Tertiary and Quaternary (Zachos et al., 2001). Several tectonic faults, which became active in the Corinthian

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Gulf during the Pliocene, caused the isolation of the Peloponnese from continental Greece (3-4 Mya; Collier & Dart, 1991; Creutzburg, 1963; Zelilidis et al., 1998), turning it into an island, smaller in size than today, and closer to the coast (Dermitzakis, 1990). This isolation has been assumed to be the main cause of allopatric differentiation and speciation for several reptile and amphibian species, including the lizards P. peloponnesiacus (Poulakakis et al., 2005), L. trilineata (Sagonas et al., 2014), A. cephallonica (Jablonski et al., 2016), and Algyroides moreoticus (Strachinis et al., 2021), the nose-horned viper Vipera ammodytes (Ursenbacher et al., 2008), the alpine newt Ichthyosaura alpestris (Recuero et al., 2014; Sotiropoulos et al., 2007), and the tortoise, Testudo hermanni (Fritz et al., 2006), as well as, for several invertebrates, such as the snails [Codringtonia (Kotsakiozi et al., 2012) and Josephinella (Psonis et al., 2015)], the isopods [Trachelipus (Parmakelis et al., 2008)] and the beetle, Gnaptor boryi (Gkontas et al., 2016), all of which have differentiated lineages in the Peloponnese.

Lacertid lizards of the genus Podarcis have been proven to be a good model for biodiversity studies, as they have undergone a remarkable radiation, exhibiting high levels of differentiation in southern Europe (Oliverio et al., 2000), which is characterized by a complex geological history, high biodiversity, and a high percentage of endemism (Lymberakis & Poulakakis, 2010). This genus currently comprises 25 recognized species (Uetz et al., 2020), forming the predominant and most taxonomically diverse reptile group in southern Europe (Harris & Sá-Sousa, 2002). The southern Balkans host 10 native *Podarcis* species, five of which are endemic to Greek islands and the Peloponnese: P. cretensis (Wettstein, 1952) on the island of Crete, P. gaigeae (Werner, 1930) on the Skyros island group, P. levendis Lymberakis et al., 2008, on Pori and Lagouvardos islets, P. milensis (Bedriaga, 1882) on the Milos island group and P. peloponnesiacus on the Peloponnese (Lymberakis & Poulakakis, 2010; Pafilis, 2010; Speybroeck et al., 2020; Uetz et al., 2020); additionally, two alien Podarcis species (P. vaucheri and P. siculus) have also been found in Greece (Adamopoulou, 2015; Spilani et al., 2018). The species found in the Balkans (excluding the alien ones) are divided into three groups (Psonis et al., 2021). These are the P. tauricus group, including P. tauricus (Pallas, 1814), P. gaigeae, P. milensis, P. melisellensis (Braun, 1877), and P. ionicus (Lehrs, 1902), the P. erhardii group, which encompasses P. erhardii (Bedriaga, 1882), P. cretensis, P. levendis, and P. peloponnesiacus, and finally, P. muralis (Laurenti, 1868), which is widely distributed across the whole northern part of the range of the genus and is hypothesized to belong to the Italian group (Harris & Arnold, 1999). However, its position within this group is disputed (Psonis et al., 2018; Salvi et al., 2021). Moreover, two very recent studies based on genome data supported the phylogenetic relationship of P. muralis with the Iberian group of species (Garcia-Porta et al., 2019; Yang et al., 2021). It is surprising that based on these studies, the temporal diversification of the P. cretensis, P. levendis, and P. peloponnesiacus group coincides with the end of the Messinian Salinity Crisis (Krijgsman et al., 1999), so their divergence can be attributed to vicariant events, in contrast to the speciation events between other lineages of the genus Podarcis, which are attributed to the interactions of regional topography, climate, and geological

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history events (Salvi et al., 2021). This is in full agreement with previously published studies on the *Podarcis* species of the Balkans (Poulakakis et al., 2005; Psonis et al., 2018, 2021; Spilani et al., 2019), identifying the isolation of Crete (*P. cretensis*) from the Peloponnese (*P. peloponnesiacus*) and Pori (*P. levendis*) as the major vicariant event that led to diversification of those species at the end of the Miocene.

The focal species of this study, P. peloponnesiacus, commonly known as the Peloponnese wall lizard, is the most common lizard species of the Peloponnese (Valakos et al., 2008). It exhibits a snout-vent length (SVL) of up to 8.5 cm and a tail that can be twice as long. Males are larger than females, and the dorsum has striped markings in both sexes. Females are brown in color with yellowish dorsolateral stripes from the neck until the tail base, while males are more colorful, with greenish-brown backs and blue spots between the flanks and the fore limbs. On each side of the head, there is one postnasal scale and 0-7 supraciliary granules (Valakos et al., 2008). To date, three subspecies of P. peloponnesiacus have been recognized: P. p. peloponnesiacus (Bibron and Borv de Saint-Vincent, 1833), distributed in the Provinces of Laconia, Messenia, and Arcadia (Southern Peloponnese); P. p. lais (Buchholz, 1960), in the Provinces of Achaia and perhaps parts of Ilis (Northern Peloponnese); and P. p. thais (Buchholz, 1960), in the Province of Argolis (Northeast Peloponnese) and the islands of the Argosaronic gulf (Bringsøe, 1986; Chondropoulos, 1986). Their respective type localities noted in figure 2 of Buchholz (1960) initially designated four subspecies based exclusively on color patterns and coloration differences. This approach has been reviewed by Bringsøe (1986 and references therein) who restricted the subspecies to the aforementioned three, sinking the fourth subspecies of Buchholz (1960), P. p. phryne, in synonymy with P. p. lais. The species has a continuous range in the Peloponnese, with the exception of the northwestern part, where it has not been found (Bringsøe, 1986). Recently, the first occurrence of P. peloponnesiacus outside the Peloponnese was reported (in a southeastern district of Sterea Ellada, see locality 15 in Figure 1; Hedman et al., 2017). However, it is not clear whether this individual was an autochthonous specimen or one that was introduced by humans. As for its conservation status, P. peloponnesiacus is classified as Least Concern according to the IUCN criteria (Böhme & Lymberakis, 2009). At present, there are no phylogenetic studies focusing on P. peloponnesiacus, but in the studies of Lymberakis et al. (2008), Spilani et al. (2019), and Psonis et al. (2021), which used molecular phylogenetic methods, there were preliminary indications that P. peloponnesiacus was splitting into two distinct lineages. However, these two lineages have not been investigated in detail to date.

These findings prompted us to investigate the phylogeny of *P. peloponnesiacus* further, in order to provide an accurate description of the intraspecific diversity of the species and to clarify the taxonomic status of different evolutionary units (see also Speybroeck et al., 2020). By performing several analyses, we aim to shed light on the taxonomic status of the species. We aim to test the hypothesis of the existence of two distinct species; and, if these two species exist, we aim to estimate the time of their divergence and investigate the biogeographic context that stimulated their differentiation.



FIGURE 1 The geographical localities of all specimens used for the phylogenetic analyses. Numbers refer to the serial number of specimens (a/a) given in Table S1

2 | MATERIALS AND METHODS

2.1 | Specimens, DNA extraction, PCR amplification, and sequencing

For this study, a total of 193 specimens of P. peloponnesiacus were used, which were collected from 51 geographical localities. Additionally, two specimens of P. levendis and four specimens of P. cretensis were also included for comparative reasons and two P. erhardii specimens were used as the outgroup. All specimens had been deposited in the collections of the National History Museum of Crete-University of Crete, where they were conserved in 95% ethanol or were frozen (-86°C). For 142 specimens, we conducted total genomic DNA extraction from muscle tissue using a typical ammonium acetate protocol (Bruford et al., 1998), while the remaining 51 extractions were obtained from previous studies (Lymberakis et al., 2008; Spilani et al., 2019). Double-stranded PCR was used to amplify two mitochondrial gene fragments [large subunit of ribosomal RNA (16S) and cytochrome b (cyt b)] and six nuclear gene fragments [melanocortin 1 receptor (MC1R), recombination activating gene 1 (Rag1), natural killer tumor recognition receptor (NKTR), ubinuclein 1 protein (UBN1), and two anonymous loci Pod55 and Pod15b (Pereira et al., 2013)]. The total number of samples used, their code, their location, and the genetic loci amplified are presented in Table S1 (Accession

numbers MW832559 to MW832696, MW846641 to MW846854, MW880774 to MW880855, and MW880857 to MW880888). The geographical localities of the samples used are illustrated in Figure 1.

Primers used for each genetic locus and their PCR conditions are shown in Table S2. Each PCR reaction was performed in 20 μ l volume, in which 1 μ l template DNA was mixed with 2.5 units Taq polymerase (Dream Taq DNA Polymerase, Thermo Scientific), 1x PCR Buffer, 1.5–3 mM MgCl₂, 0.2 mM dNTPs, and 0.2 mM of each primer. The PCR cycles comprised a 10-min pro-incubation at 94°C, followed by 35 cycles of 1-min denaturation at 94°C, 1-min annealing temperature of each primer, and 1-min extension at 72°C, and then the cycling terminated with a 10-min extension at 72°C.

Double-stranded sequencing was conducted in an automated sequencer ABI3730XL (CeMIA Company; Larissa, Greece) using the Big-Dye Terminator v.3.1 Cycle Sequencing kit[®], following the manufacturer's protocol and using the same primers as in the PCR reactions.

2.2 | Alignment, genetic divergence, and model selection

Sequences were edited in a Codon Code Aligner (v. 3.7.1; Codon Code Corporation[®]), and the homology of the targeted loci was

verified with the BLAST algorithm (https://blast.ncbi.nlm.nih.gov/ Blast.cgi). Alignment was performed for each locus separately. For the mitochondrial gene fragments *cyt b* and *16S*, the alignment was performed using the ClustalW algorithm, which is embedded in the MEGA program (v. 7.0.26; Kumar et al., 2016). The nuclear loci were aligned with MAFFT (v. 7; Katoh & Standley, 2013) based on the FFT-NS-2 algorithm (Fast: Progressive method). Alignment gaps were inserted to resolve length differences between noncoding sequences (*16S*, *Pod15b*, *Pod55*). *Cytochrome b*, *MC1R*, *RAG1*, *NKTR*, and *UBN1* sequences were translated into amino acids prior to further analysis, in order to ensure the absence of stop codons. PHASE v.2.1.1 (Stephens et al., 2001) was used for nuclear gene fragments as it is implemented in DnaSP v.5.10.01 (Librado & Rozas, 2009) prior to alignment, in order to statistically infer the allelic sequences.

Genetic distances were calculated with MEGA (v. 7) based on the Tamura-Nei model of evolution.

For the phylogenetic, chronophylogenetic, and species delimitation analyses, three datasets were prepared. A mitochondrial dataset (mtDNA) comprised of the two mtDNA gene fragments for all P. peloponnesiacus, P. levendis, P. cretensis, and P. erhardii specimens. The second dataset (nuDNA) was created using the six nuclear gene markers (Pod55, MC1R, Rag1, Pod15b, NKTR, and UBN1). For this dataset, representatives from each one of the major evolutionary lineages that were identified from the phylogenetic tree produced from the initial mtDNA dataset were selected. The selection of the representatives was based on the results of the multi-rate Poisson Tree Processes (mPTP) analysis (v. 0.2.4; Kapli et al., 2017) on the phylogenetic tree produced from the mtDNA dataset. Based on this analysis (see Section 3), three groups were recognized within P. peloponnesiacus. Finally, a concatenated dataset was constructed, including all loci (mtDNA and nuDNA). Gene matrices are available on TreeBASE (http://purl.org/phylo/treebase/phylows/study/ TB2:S27763?x-access-code=38e8a3d614ca6d44fc62c4e7b3e081 e&format=html).

The nucleotide substitution model selection tests were carried out separately for the two types of genomes used in this study (mtDNA and nuDNA). The mtDNA alignment was subdivided into four pre-defined blocks; three of them corresponded to each codon position for cyt b and the fourth to 16S (non-coding genetic locus). The nuclear loci were subdivided into 14 blocks corresponding to the 1st, 2nd, and 3rd codon positions for the genes MC1R, Rag1, NKTR, UBN1, and two blocks for Pod55 and Pod15b. The alignments and the pre-defined blocks were then analyzed in PartitionFinder2 (PF) v.2.1.1 (Lanfear et al., 2017) to find the bestfit partitioning scheme and evolutionary models for each downstream analysis, evaluating the models that were implemented in each type of software (RAxML, MrBayes). Data blocks had linked branch lengths, and the model selection was based on the Bayesian information criterion, ignoring the evolutionary models that contained both gamma distribution and invariable sites (Yang, 2006). The optimal combination of block sequences was done with the "greedy" algorithm.

2.3 | Phylogenetic analyses

Phylogenetic analyses were performed separately for each dataset, based on maximum likelihood (ML) and Bayesian inference (BI). ML analysis was performed using the RAxML program (v. 8.1.21; Stamatakis, 2014). The best ML tree for each dataset was selected from 50 ML searches, and the statistical support of the branches was evaluated based on 1000 thorough bootstraps. BI analysis was performed in MrBayes (v. 3.2.6; Ronquist et al., 2012), based on the partition results and models revealed in PF2. Four runs were performed with eight independent sampling chains for each run. Each chain "ran" for 10⁷ generations for each dataset, except the mitochondrial dataset, which "ran" for 1.5×10^7 generations, sampling every 5000 generations. Four MCMC diagnostics were analyzed in Tracer v.1.6. (Rambaud et al., 2014) to check for convergence and stabilization of the analysis, such as the average standard deviation of split frequencies, the plot of the generation versus the log probability of the data (the log likelihood values), the average potential scale production factor (PSRF), and the estimated sample size (ESS). The first 25% of trees were discarded as burn-in, as a measure to sample from the stationary distribution and avoid the possibility of including random, sub-optimal trees. A 50% majority rule consensus tree was then produced from the posterior distribution of trees, and the posterior probabilities were calculated as the percentage of samples recovering any particular clade. Posterior probabilities ≥0.95 indicate statistically significant support (Huelsenbeck & Ronguist, 2001).

For nuclear loci, the relationships among haplotype sequences were determined using a haplotype network and a median joining model implemented in NETWORK 10.2 (Bandelt et al., 1999). The analysis was performed for each gene fragment separately.

2.4 | Species delimitation

The evaluation of the putative species' boundaries was performed using four different approaches: the mPTP, the Assemble Species by Automatic Partitioning (ASAP; Puillandre et al., 2021), the Bayesian Phylogenetics and Phylogeography—BPP v.4.3.8 (Flouri et al., 2018), and the Species Tree And Classification Estimation, Yarely—STACEY v.1.2.2 (Jones, 2017) implemented in BEAST2.

The ASAP builds species partitions from single-locus sequence alignments. For this reason, we performed this analysis based on the mtDNA alignment (*cyt b* and 165). The analysis was run using all of the three distance methods available (Jukes-Cantor, Kimura 2-parameter and simple p-distances) under default parameters (Split groups below 0.001 probability and highlighting results between 0.005 and 0.05 genetic distances).

In mPTP, the species were delimited using the mPTP ML approach. Given that mPTP analysis is restricted to a single locus, we used the ML phylogenetic tree produced by the mtDNA dataset.

Bayesian species delimitation was conducted in BP&P to explore different species delimitation models (A11 analysis). For the priors

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on population sizes (θ) and divergence times (τ), we used inverse-Gamma priors with $\alpha = 3$. The β parameter was adjusted according to the mean estimate of nucleotide diversity for θ ($\beta = 0.2$) and node height for τ ($\beta = 0.09$). We performed the analyses using the reversible-jump MCMC algorithm 0 ($\varepsilon = 2$). The analysis ran in duplicate to check for convergence. Analyses were run for 200,000 MCMC steps, with samples drawn every five steps and with the first 20% of samples discarded as burn-in. Assignment was based on the mtDNA phylogeny, and the maximum number of mtDNA potential species (seven species; see Section 3) revealed from the single-locus species delimitation analysis (mPTP). Following the suggestion of the authors of BP&P, our analysis was based on nuclear loci only, and not in combination with the mitochondrial ones (see manual of BP&P).

In STACEY, BEAUti v. 2.4.7 (which is also included in BEAST2 v. 2.4.7) (Bouckaert et al., 2014), was used to prepare the input files. All loci were included in the analysis (the two mtDNA genes were considered a single locus). Each individual was considered as a distinct species a priori. For the selection of the most appropriate substitution model, we used the bModelTest tool. Ploidy values were fit to 2.0 and 0.5 for nuclear and mitochondrial genes, respectively, and the species tree was estimated with a Yule model with collapsed height nodes of $\varepsilon = 1 \times 10^{-4}$, and birth diff rate of 100 *a priori*. The collapse weight parameter (ω), which affects the number of clusters, was given a flat prior bound from 0 to 1.0, and thus, any possible grouping scheme received the same initial probability. As for other priors, the strict clock model for describing the molecular clock was used. The analysis was run twice with 5×10^8 generations. Results from the STACEY runs were summarized with the species delimitation analysis tool provided along with the STACEY package (speciesDA.iar) using collapse height = 0.001 and sim cutoff = 1.0 (no cluster similarity binning; Jones et al., 2015).

2.5 | Species tree construction and divergence time estimation

All loci (mtDNA and nuDNA) were used to estimate a species tree and divergence times, with the StarBeast2 package included in BEAST2. The required import file (xml) was created using the BEAUti program. As in the case of STACEY, the two mtDNA gene fragments were considered a single locus (the two mtDNA genes were unlinked in site and clock models and linked in trees). Nucleotide substitution models were given a priori based on the PF analysis. Priors were used in advance: "Birth Death Model" for the species tree, "Linear with Constant Root Populations" for the population model, and "Uncorrelated Lognormal" for the molecular clock description. The separation between the Peloponnese and Crete and the island group of Pori (P. levendis), and therefore the divergence between P. peloponnesiacus from P. cretensis and P. levendis, was used as a calibration point and defined at 5.3 million years ago (Normal distribution with a mean value of 5.3 and a standard deviation of 0.15; see Dermitzakis, 1990 and Introduction above). The MCMC analysis ran for 10⁹ generations, extracting results every 5000 generations and rejecting

the first 25% of them (burn-in). The resulting log files were analyzed with Tracer (v. 1.6) to determine that convergence of the analysis had occurred and a satisfactory effective sample size (ESS) was recovered (>200). Next, Tree Annotator v. 2.4.7, included in BEAST2, was used to estimate the species tree, calculating the maximum clade credibility tree that best represented the posterior distribution.

2.6 | Morphological data

2.6.1 | Recorded traits

To investigate the morphological differentiation of the two divergent evolutionary clades of *P. peloponnesiacus* (see Section 3), we examined a total of 332 specimens, which included museum specimens from the herpetological collections of the Natural History Museum of Crete (NHMC), the Natural History Museum, London (NHMUK), and the Natural History Museum, Vienna (NMW), and specimens sampled in the field. Specimens were collected from 43 geographical localities. We examined both linear biometric and pholidotic traits. Biometric variables were only considered in adult specimens (N = 305) and were always recorded by AK to reduce sources of measurement error. The total number of samples used, their code, their location, and the morphological traits recorded for each one are presented in Table S3, while the geographical localities of the samples used are illustrated in Figure S1.

Each of the specimens examined for morphological analyses was assigned to one of the two phylogenetic clades (1 or 2) based on (1) the genetic analyses of samples from the same population, when available; or (2) the geographical location of the population of origin well within the inferred range of each clade, when such assignment could be done without doubt. Specimens for which their assignment to one of the clades was ambiguous were excluded altogether. Note that for specimens from Stymfalia Lake, where both clades are found in syntopy (Spilani et al., 2019; see also results below), we only included genetically identified individuals, which could be unambiguously assigned to one of the two clades.

For each specimen examined, we measured nine biometric characters to the closest 0.01 mm using electronic calipers: SVL, trunk length (TRL, defined as the closest distance between anterior and posterior limbs), head length (HL), pileus length (PL), head width (HW), head height (HH), mouth opening (MO) measured from the tip of the snout to the posterior border of the last supralabial scale, forelimb length (FLL), and hindlimb length.

In addition, we recorded several pholidotic traits typically used for systematic inferences in lacertids (Kaliontzopoulou et al., 2012; Lymberakis et al., 2008), including both meristic and presence/ absence characters. Specifically, for each specimen, we recorded collar scales number (CSN), gular scales number (GSN), the number of transversal rows of ventral scales (VSN), femoral pores number (FPN), subdigital lamellae number under the 4th toe (SDLN), supratemporal scales number (STSN), supraciliary scales number (SCSN), supraciliary granules number (SCGN), the number of supralabial

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scales (SLAB), and the number of supralabial scales before the subocular (SLAB_suboc). Furthermore, we recorded the presence/ absence of the masseteric (MASS) and the tympanic scale (TYMP); the fragmentation of the tympanic scale (TYMPfr); the presence/ absence of contact between the internasal and frontal scales (IN_F), between the occipital and interparietal scales (O_IP), and between the rostral and internasal scales (R_IN); and the presence/absence of a third scale between the aforementioned pairs of scales (3rdIN_F, 3rdO_IP, 3rdR_IN). All bilateral characters were recorded on the right side of the lizard body when possible.

2.6.2 | Statistical analyses

All biometric traits were log-transformed prior to data analyses to better approximate the normal distribution. In order to test for differences in linear biometry between both evolutionary clades considered, we used AN(C)OVA comparisons, where we first tested for differences in body size, as represented by SVL; and in continuation, we used SVL as the covariate to compare variation in the remaining traits while taking size variation into account. The significance of examined AN(C)OVA models was evaluated through 1000 permutations of randomized residuals as implemented in the R-package RRPP (Collyer & Adams, 2018, 2019). To further investigate the biometric differentiation of both clades and identify those traits that contributed the most to discriminating them, we performed linear discriminant analyses, with a leave-one-out cross-validation procedure. For this, we first used a linear regression on SVL to remove size effects from the remaining biometric traits. Due to the existence of marked sexual dimorphism in body size and shape in Podarcis wall lizards (Kaliontzopoulou et al., 2015; Kaliontzopoulou et al., 2006, 2010), and since sexual differentiation was not the focus of this study, we performed all aforementioned analyses in each sex separately.

The analysis of pholidotic traits focused on different character sets, depending on whether they could be treated as continuous, or should rather be considered as categorical, variables. This provided three sets of pholidotic variables: (1) continuous meristic traits, including CSN, GSN, VSN, FPN, and SDLN; (2) meristic traits thatdue to their reduced variation range-were considered as ordinal categorical (STSN, SCSN, SCGN, SLAB, SLAB_suboc); and (3) binary traits (i.e., presence/absence ones, as described above). To test for differences in continuous pholidotic traits between both clades, we followed the same procedures as for linear biometric traits described above, including the evaluation of ANOVA models through randomized residuals on a permutation procedure and discriminant analyses, applied separately to members of each sex. To evaluate the differentiation of both clades in ordinal and binomial variables, we used logistic-regression models with a Poisson and a binomial error distribution respectively. For those traits found to be significantly different between clades, we then inspected the frequency of occurrence of each character state to gain insights with respect to traits that could be diagnostic.

2.7 | Species distribution modeling and niche similarity analyses

Species distribution modeling analyses test the impact of ecological factors on the current distribution of the lineages. Presence only datasets for the two clades of *P. peloponnesiacus* were analyzed. All the presence points used in the analyses were extracted from the NHMC collections database. In total, we used 193 points, 91, and 102 for each of the identified clades, resulting from the phylogenetic analyses. After the clean-up of the dataset for duplicate records and the spatial thinning of the occurrence data, the number of records was reduced to 41 for clade 1 and 17 for clade 2. The area of the modeling was based on the current species distribution (Böhme & Lymberakis, 2009) along with an extension in part of the central Greece and Attiki region due to a record in Athens (Hedman et al., 2017) (Figure S2).

Environmental data, at 1×1 km spatial resolution, from the CHELSA database were used (Bobrowski & Udo, 2017: Karger et al., 2017). The spThin R package (Aiello-Lammens et al., 2015) with an occurrence thinner radius of 2 km was used for the minimization of the effects of sampling bias (Boria et al., 2014) and the USDM R package (Naimi et al., 2014) for the calculation of variance inflation factor (VIF) for the set of selected predictors and in order to exclude the highly correlated variables from the set through a stepwise procedure (VIF values < 10). The Wallace R package (Kass et al., 2018) was used for the modeling, allowing the fine tune (Hao et al., 2020) of the MaxEnt algorithm using the ENMeval R package (Muscarella et al., 2014). The "random k-fold" partition scheme of ENMeval was selected for all the analyses (Muscarella et al., 2014) for training/validation. ENMeval allowed us to evaluate models using a spatial partitioning scheme and to "fine-tune" two parameters of MaxEnt that affect model complexity and predictive power. These parameters are the regularization multiplier (RM) or beta values and the feature classes (FCs). The RM penalizes overly complex models, whereas the FCs are functions of the raw environmental data (Morales et al., 2017). All FCs (L = Linear, Q = Quadratic, H = Hinge, P = Product) were selected, and the RM was set between 1 and 5 with steps of 0.5 allowing for model complexity and model tuning for each clade. Basically, all predictor variable coefficients were shrunk progressively until some reached 0, when they dropped out of the model. Only those variables with the greatest predictive contribution were retained in the model. Model selection was based on the average test area under the curve value (avg.test.AUC) along with the lowest delta corrected Akaike information criterion (delta.AICc; Leroy et al., 2018), calculated for each model following the method by Warren and Seifert (2011). In total, 45 different models were built, run, and tested for each clade. The final models selected to best approximate the niche of clades 1 & 2 were then used for the calculation of the niche overlap between clades. To this end, the relevant indices for niche overlap, D and I, based on Schoener's D and modified Hellinger I distances, respectively, as proposed by Warren et al. (2008) were calculated using the dismo R package (Hijmans et al., 2011). Values with ranges from 0 to 0.2 correspond to "no or limited" niche overlap,

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0.2 to 0.4 correspond to "low" overlap, 0.4 to 0.6 correspond to "moderate" overlap, 0.6 to 0.8 correspond to "high" overlap, and 0.8 to 1.0 correspond to "very high" overlap (Rödder & Engler, 2011).

2.8 | Diagnostic characters based on molecular data

Regarding the use of molecular data as diagnostic characters, we adopt the position of Nygren and Pleijel (2011). To this end, that is, to recover diagnostic combinations of nucleotides (DNCs) for predefined groups of DNA sequences, we used the program MoID (Molecular Diagnoses) v. 1.3 (Fedosov et al., 2019). A pure composite nucleotide character-that is, a combination of nucleotides at specific positions in the DNA alignment that are shared by all members of a focus taxon, and by none of the non-focus taxa members, is termed a primary diagnostic nucleotide combination (pDNC), whereas a diagnostic nucleotide combination, which combines several pDNCs (or characters from several pDNCs) aiming for an increased robustness of a diagnosis, is termed a secondary DNC (sDNC). MoID is designed to retrieve pDNCs and sDNCs for the pre-defined assemblages of DNA sequences that correspond to taxa (which may range from species, subspecies, or even populations to any higher level). The most polymorphic gene fragment (cyt b) was used for this analysis, aiming to identify sDNCs for the two major clades of P. peloponnesiacus (see Section 3). The numbering was based on the complete cytochrome b sequence of P. muralis, which is available in GenBank (MT027220).

3 | RESULTS

3.1 | Phylogenetic reconstruction

For the mtDNA dataset, a total of 982 base pairs (bp) were aligned (426 bp for *cyt b* and 556 bp for 165), 190 (19.3%) of which were variable, 160 (16.3%) when the outgroup was excluded. For the nuDNA dataset, a total of 3874 bp were aligned (426 bp for *Pod55*, 670 bp for *MC1R*, 983 bp for *Rag1*, 541 bp for *Pod15b*, 590 bp for *NKTR*, and 664 bp for *UBN1*), 130 sites (3.4%) of which were variable, 115 sites (2.9%) when the outgroup was excluded. Finally, for the concatenated dataset, a total of 4799 bp were aligned (417 bp for *cyt b*, 508 bp for 165, 426 bp for *Pod55*, 670 bp for *MC1R*, 983 bp for *Rag1*, 541 bp for *Pod15b*, 590 bp for *NKTR*, and 664 bp for *UBN1*).

The best-fit partitioning scheme for each downstream analysis and the selected nucleotide substitution models are given in Table S4.

Both phylogenetic analyses (ML and BI) on the mtDNA dataset produced trees with fairly similar topologies. The ML analysis resulted in a topology with lnL = -2979.33, while the BI analysis resulted in a topology with mean lnL = -3166.40. Phylogenetic analyses recovered two main very well-supported clades within *P. peloponnesiacus*, the sister group relationship of which has low statistical support (pp = 0.75, bs = 49; Figure 2). On the other hand, the monophyly of *P. cretensis* and

P. levendis was well supported. The phylogenetic analyses of the nuDNA dataset produced trees with similar topologies (InL = -6464.78 for ML and InL = -6487.52 for BI), in which *P. peloponnesiacus* was divided into two main clades, with higher statistical support (pp = 1, bs = 62) compared to the mtDNA dataset. Of these two clades, clade 1 is distributed in western and central Peloponnese (hereinafter *Podarcis peloponnesiacus* West or 1_ and clade 2 in eastern Peloponnese (hereinafter *Podarcis peloponnesiacus* East or 2_ (Figure S3), showing sympatry in the area of lakes Stymfalia and Doxa, where individuals from both clades were found. More specifically, we analyzed 97 individuals from Lake Stymfalia, 24 of which belonged to clade 1 and 73 to clade 2. For the concatenated dataset, both phylogenetic analyses produced a resolved phylogenetic tree (Figure 3; InL = -9039.30 for ML and InL = -9086.09 for BI), with two major clades within *P. peloponnesiacus*.

The results of haplotype network analysis for each nuclear gene separately suggested the distinction of the two clades of *P. peloponnesiacus* identified in the gene trees (Figure S4).

3.2 | Genetic distances

Pairwise genetic distances (Tamura-Nei model) between individuals varied up to 7.8% for 16S (up to 6.4% without the outgroup and up to 5.6% within P. *peloponnesiacus*) and up to 18.4% for *cyt b* (up to 12.2% without the outgroup and up to 11.6% within P. *peloponnesiacus*). Sequence divergence ranged up to 1.4% for Pod55, up to 1.8% for MC1R, up to 4.9% for Rag1, up to 1.5% for Pod15b, up to 1.7% for NKTR, and up to 2.6% for UBN1. Genetic distances among the major phylogenetic lineages are presented in Table 1.

3.3 | Species delimitation, species tree, and divergence times estimations

The mPTP analysis revealed seven clusters (potential species) in the phylogenetic tree of the mtDNA dataset with the best score for multi coalescent rate of 408.29. Three of them correspond to *P. peloponnesiacus* (one to the west clade, and two to the east clade; see Figure 2), two to *P. cretensis*, and the last two to each one of the remaining species (*P. levendis* and *P. erhardii*).

In all cases of ASAP analyses (using Jukes-Cantor, Kimura 2-parameter, and *p* distance), the best partition, which means the partition with the lowest ASAP-score, was that with six potential species (*P. erhardii*, *P. levendis*, two in *P. cretensis*, and two in *P. peloponnesiacus* (east and west clades).

In STACEY analysis, the SpeciesDelimitationAnalyser found classification with five clusters (species) as the one with the highest posterior probability (0.86); *P. cretensis*, *P. levendis*, *P. erhardii*, and the two clades of *P. peloponnesiacus* (east and west) as distinct species. The species tree obtained as part of species delimitation is given in Figure S5, indicating the presence of two potential species within *P. peloponnesiacus* with very high posterior probabilities (1.00).



represent the number of distinct entities (potential species) based on mPTP (seven in total) and ASAP (six in total) analyses. On the right side, the two main clades of *P. peloponnesiacus* are FIGURE 2 The ML mitochondrial gene tree (cyt b & 16S rRNA). The posterior probabilities and bootstrap supports (BI/ML) are presented on the branches. To clades, the vertical bars shown in detail WILEY JOURNAL®

The model estimated with BP&P (PP = 0.77) supported the presence of five species as in the case of STACEY, in which the posterior probabilities for the potential species in *P. peloponnesiacus* were 1.00 for the west clade and 0.97 for the east clade.

The species tree (Figure 4) resulting from StarBEAST2 showed high posterior ESS values (>342) for all parameters Topologically speaking, this species tree obtained from StarBEAST2 and STACEY and the gene trees from ML and BI analyses on the complete dataset led to similar conclusions regarding the relationships among the major clades (species) with the distinction of *P*. *peloponnesiacus* into two major clades (east and west) with high posterior probability [pp = 0.99 in StarBEAST2 (Figure 3) and 0.96 in STACEY (Figure S5)].

According to the chronophylogenetic analysis (Figure 4), the time of divergence between the two clades of *P. peloponnesia-cus* was estimated at 1.72 million years ago (the beginning of the Pleistocene), with the range from 0.92 to 2.57 million years ago (95% HPD). The differentiation between *P. levendis* and *P. peloponnesiacus* dates back to 3.55 MYA, with a range from 1.65 to 3.8 million years.



FIGURE 3 Bayesian inference tree based on the concatenated (mtDNA & nuDNA) dataset. The posterior probabilities (>0.95) and bootstrap support (>50%) of both phylogenetic methods are given on top of the branches. The map within the tree shows the geographical distribution of specimens of the two clades of *P. peloponnesiacus*. The size of the circles indicates the number of specimens per 100 km². Black dots show the type localities of previously defined subspecies

TABLE 1Genetic distances using the Tamura-Nei model among major phylogenetic lineages: Cyt b/16S rRNA below diagonal-left,Pod55/MC1R/Rag1/Pod15b/NKTR/UBN1 above diagonal-right

	P. peloponnesiacus west	P. peloponnesiacus east	P. levendis	P. cretensis	P. erhardii
P. peloponnesiacus west		1/0.9/0.4/0.8/0.9/0.6	0.9/0.9/0.7/1.4/0.5/0.8	0.8/1/0.3/1.7/0.4/0.9	1.3/0.8/0.4/1.5/1.2/1.9
P. peloponnesiacus east	6.3/3.4		0.4/0.3/0.6/1/0.9/0.6	0.3/0.4/0.3/1.4/0.8/0.6	0.8/0.8/0.4/1/1.6/1.6
P. levendis	7.9/3.4	9.0/4.1		0.1/0.4/0.5/1.2/0.2/0.7	0.6/0.8/0.5/0.8/1/1.7
P. cretensis	8.0/3.9	8.6/4.5	9.4/5.1		0.5/0.9/0.1/1.3/0.9/1.4
P. erhardii	15.0/4.8	14.6/5.8	14.9/5.4	15.8/5.1	



FIGURE 4 The tree produced by the chronophylogenetic analysis. For the species tree, the posterior probabilities are given near the branches. Values >0.95 indicate statistical significance. For the divergence times, numbers showing arrows represent the divergence time in millions of years, while the parentheses indicate the uncertainty (95% HPD) of the time estimation. C.P. refers to the calibration point

3.4 | Morphological analyses

The morphological comparisons performed between individuals of the two clades observed within P. peloponnesiacus indicated the existence of significant differences in some-but not all-biometric and pholidotic traits, which were more prominent in males than in females. Individuals of the two clades did not differ in body size in either sex, but there were several body parts that did differ in females, namely relative TRL, PL, and MO; and all body dimensions relative to SVL in males, except for HH and FLL (Table 2). Similarly, we found significant differences between clades in the number of collar scales and femoral pores in both sexes, in addition to the number of gular and ventral scales only in males (Table 3). Indeed, individuals of clade 2 (eastern lineage) exhibited a lower number of collar scales (CSN), but a higher number of femoral pores (FPN) in both sexes, while males of clade 2 also exhibited a higher number of gular (GSN) and a higher number of ventral (VSN) scales (Figure 5). Despite these differences, however, the ranges of variation overlapped widely between both clades, not allowing the retrieval of unique diagnostic traits (Table S5).

Discriminant analyses performed to (size-corrected) biometric and continuous pholidotic traits reinforced the notion that, despite statistically significant morphological differentiation in both sexes, the morphological properties of the two clades are quite similar, yielding a relatively low capacity of their correct discrimination. Indeed, leave-one-out cross-validation of the discriminant functions constructed based on biometric variables resulted in moderate percentages of correct classification, which were lower for clade 2 (females: 63.04%; males: 42.37%) than for clade 1 (females: 86.36%; males: 86.60%). Examination of discriminant vector composition revealed that relative TRL and relative MO were the most relevant traits for the discrimination of eastern and western female individuals, while relative MO and elative FLL contributed the most for discriminating males (Table S6). Similarly, discriminant functions constructed based on continuous pholidotic traits resulted in relatively low percentages of correct classifications, with clade 2 being classified correctly at a lower percentage (females: 55.77%; males: 59.15%) than clade 1 (females: 88.30%; males: 81.74%). The number of collar scales (CSN) and femoral pores (FPN) was the most relevant variables

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TABLE 2 Results of AN(C)OVA comparisons of linear biometric traits between the two clades of *P. peloponnesiacus* for each sex separately

		Females (N = 1	33)			Males (N = 179)		
		SS	Z	р		SS	Z	р
SVL	clade	0.004	0.269	0.478	Clade	0.001	-0.377	0.751
TRL	SVL	2.223	3.490	0.001	SVL	1.496	3.414	0.001
	clade	0.061	2.118	0.001	Clade	0.030	1.586	0.002
	SVL: clade	0.001	0.245	0.498	SVL: clade	0.000	-0.759	0.833
HL	SVL	0.391	2.796	0.001	SVL	1.022	3.263	0.001
	Clade	0.002	0.535	0.340	Clade	0.037	1.779	0.001
	SVL: clade	0.009	1.105	0.072	SVL: clade	0.016	1.474	0.011
PL	SVL	0.532	3.309	0.001	SVL	0.902	3.081	0.001
	Clade	0.028	2.043	0.001	Clade	0.066	1.997	0.001
	SVL: clade	0.001	0.732	0.227	SVL: clade	0.009	1.139	0.082
HW	SVL	0.383	2.769	0.001	SVL	0.970	3.192	0.001
	Clade	0.012	1.212	0.051	Clade	0.045	1.805	0.001
	SVL: clade	0.000	-2.078	0.961	SVL: clade	0.000	-0.528	0.775
НН	SVL	0.595	2.944	0.001	SVL	0.944	2.881	0.001
	Clade	0.001	-0.129	0.644	Clade	0.016	1.038	0.113
	SVL: clade	0.000	-0.695	0.804	SVL: clade	0.001	-0.516	0.766
МО	SVL	0.582	3.462	0.001	SVL	1.065	3.320	0.001
	Clade	0.044	2.126	0.001	Clade	0.061	2.203	0.001
	SVL: clade	0.002	0.865	0.165	SVL: clade	0.000	-1.009	0.859
FLL	SVL	0.241	2.543	0.001	SVL	0.639	3.085	0.001
	Clade	0.008	0.927	0.116	clade	0.001	-0.041	0.621
	SVL: clade	0.007	0.953	0.125	SVL:clade	0.000	-2.398	0.971
HLL	SVL	0.275	3.055	0.001	SVL	0.596	3.162	0.001
	Clade	0.007	1.173	v	Clade	0.020	1.715	0.001
	SVL: clade	0.000	0.056	0.806	SVL: clade	0.001	0.177	0.521

Abbreviations: SS: sum of squares, Z: effect sizes, p: corresponding p-value based on 1000 residual randomizations. Significant effects are in bold text (see Section 2 for variable acronyms).

	FEMALES	(N = 145)		MALES (N	MALES (N = 185)				
	SS	Z	Pr(>F)	SS	Z	Pr(>F)			
CSN	0.320	2.143	0.001	0.242	1.868	0.001			
SDLNright	0.000	-0.919	0.844	0.001	0.045	0.581			
GSN	0.018	1.160	0.071	0.061	1.635	0.001			
VSN	0.000	-0.942	0.848	0.018	1.936	0.001			
FPN	0.171	2.129	0.001	0.179	2.120	0.001			

TABLE 3 Results of ANOVA comparisons of continuous pholidotic traits between the two clades of *P. peloponnesiacus* for each sex separately

Abbreviations: SS: sum of squares, Z: effect sizes, *p*: corresponding *p*-value based on 1000 residual randomizations. Significant effects are in bold text (see Materials & Methods for variable acronyms).

contributing to clade discrimination, in addition to the number of gular scales (GSN) in males (Table S7).

Finally, GLMs comparing the frequency distributions for categorical pholidotic traits revealed differences between clades in the number of supraciliary granules (SCGN), the probability of the presence of the masseteric scale (MASS), and the occurrence of contact between the rostral and internasal scales (R_IN; Table 4). Despite statistically identifiable differences between clades, however, none of these traits were strictly diagnostic, as all character states occurred in both clades (Figure 6).

FIGURE 5 Means and confidence intervals for males (M) and females (F) of each clade (1 or 2) for continuous pholidotic traits (Numbers of: collar scales (CSN), gular scales (GSN), ventral scales (VSN), and femoral pores (FPN) for which significant differences between clades were identified)



TABLE 4 Results of GLMs applied to ordinal and binary pholidotic traits to test for differences between the two clades of P. peloponnesiacus

	Coef	SE	z	p
Ordinal				
STSN	-0.087	0.057	-1.515	0.130
SCSN	-0.069	0.049	-1.391	0.164
SCGN	-0.809	0.112	-7.235	4.67*10 ⁻¹³
SLAB	-0.029	0.039	-0.748	0.455
SLAB_suboc	0.000	0.054	-0.009	0.993
Binary				
MASS	-1.545	0.363	-4.252	2.11*10 ⁻⁰⁵
TYMP	1.644	1.160	1.417	0.157
TYMPfr	-0.946	0.920	-1.028	0.304
O_IP	-0.346	0.245	-1.409	0.159
X3rdO_IP	-0.048	0.582	-0.082	0.935
IN_F	-0.015	0.739	-0.020	0.984
X3rdIN_F	-0.043	0.464	-0.092	0.927
R_IN	1.447	0.550	2.631	8.50*10 ⁻⁰³
X3rdR_IN	0.872	1.124	0.776	0.438

Abbreviations: Coef, estimated regression coefficient; SE, standard error; Z, effect sizes; p, corresponding p-value. Significant effects are in bold text (see Materials & Methods for variable acronyms).

Species distribution modeling and niche 3.5 similarity analyses

Based on the VIF analysis, six out of 19 initial predictors were retained in the models, including temperature seasonality (BIO4), the maximum temperature of the warmest month (BIO5), the mean temperature of the wettest guarter (BIO8), precipitation seasonality (BIO15), precipitation of the warmest quarter (BIO18), and precipitation of the coldest guarter (BIO19). Four and two random folds for calibration/validation were created for clades 1 and 2 respectively. The difference was due to the final dataset (41 points for clade 1 and 17 for clade 2), for which 4100 and 1700 pseudoabsence points were randomly created following the recommendations of Barbet-Massin et al. (2012). Forty-five models have been run consecutively for each clade, and the model with the lowest delta corrected Akaike information criterion (delta.AICc) has been selected (Tables S8-S11). For clade 1, the selected model used the L, Q, and H features with a beta value of 1.5 (hereafter LQH_1.5) (Table S8) and clade 2 used the L, Q, and a beta value of 1 (LQ_1) (Table S9; Figure 7). Clade 1 had a training AUC of 0.8 and avg.test.AUC of 0.74, whereas clade 2 a train.AUC of 0.87 and avg.test.AUC of 0.6. For clade 1 (Table S10), the mean temperature of the wettest quarter (BIO8), the precipitation seasonality (BIO15), and the precipitation of the warmest quarter (BIO18) predictors seemed to contribute the



FIGURE 6 Relative frequencies of distribution observed in each clade (1 or 2) for the number of supraciliary granules (SCGN), the presence of a masseteric scale (MASS), and the presence of contact between the rostral and internasal scales (R_IN)



FIGURE 7 Model output for the western clade (clade 1) on the left and the eastern clade (clade 2) on the right of P. peloponnesiacus

most to the model, with 95% (cumulatively) of permutation importance. For clade 2 (Table S11), the mean temperature of the wettest quarter (BIO8), the precipitation seasonality (BIO15), the precipitation of the warmest quarter (BIO18), and the precipitation of the coldest quarter (BIO19) contributed with 92% of permutation importance.

Pairwise evaluation of niche similarity between the two clades indicated "moderate" to "high" niche overlap according to both indices (D = 0.6, I = 0.86).

3.6 | Diagnostic characters based on cyt b

For the two major clades of *P. peloponnesiacus* revealed in phylogenetic analyses (east and west), which were recognized as potential species by species delimitation analyses (STACEY, ASAP, and BP&P), there exist several diagnostic nucleotide sites in cyt *b*. For the western clade, these are: position 165, nucleotide 'C', 247: 'T', 261: 'G', 288: 'C', 294: 'T', 345: 'T', and for the eastern clade these are: 171: 'T', 192: 'T', 318: 'T'. As we mentioned before, this numbering is based on the complete cytochrome *b* sequence of *P. muralis* retrieved from GenBank (MT027220).

4 | DISCUSSION

This study constitutes the first integrative research on *P. peloponnesiacus*, analyzing genetic, phenotypic, and environmental data. The main question addressed through this integration of different evidence is whether the existence of two differentiated lineages identified within *P. peloponnesiacus* in previous studies (Lymberakis et al., 2008; Spilani et al., 2019, 2020) is confirmed with the inclusion of a larger number of samples and a more comprehensive representation of the geographical distribution of the species. To this end, we analyzed a great number of genetic loci and carried out an assessment of morphological variation. We performed phylogenetic and species delimitation analyses together with species distribution modeling, and morphological (biometric and pholidotic) analyses. Ultimately, our main objective was to evaluate whether this subspecific divergence merits taxonomic distinction as different species, and whether these are morphologically and ecologically differentiated.

4.1 | Phylogenetic relationships within Podarcis peloponnesiacus

Phylogenetic analyses of the mtDNA dataset alone recovered two main clades within the species, with limited statistical support (p.p. = 0.75, b.s. = 49). However, analyses of the nuDNA dataset showed the same topology, with higher support values (p.p. = 1, b.s. = 62), which were further enhanced when using the concatenated (mtDNA and nDNA) dataset (p.p. = 1, b.s. = 92), which produced a completely resolved phylogeny. The inferred species tree, based on the combined dataset, showed the same topology (p.p. = 0.99) with that produced based on the concatenated dataset. In agreement with all of the above, the three different species delimitation approaches that were used to evaluate species' boundaries clearly supported the distinction of two differentiated groups of lineages within P. peloponnesiacus, with high posterior probabilities, while the two clades of *P. peloponnesiacus* are distinct at the nuclear level, as it is shown on the haplotype networks, but the discrimination is based on a limited number of samples compared to mitochondrial data. Equally important is the observation that the two groups of lineages are geographically separated, consisting of individuals from the western/central (clade 1) and the eastern (clade 2) Peloponnese (Figure 3). Similar distribution patterns in the area of the Peloponnese, that divide populations between the western and the eastern part of the peninsula, have also been found in other lizards of the family Lacertidae, such as Hellenolacerta graeca (unpublished data), in other groups of organisms such as spiders (Kornilios et al., 2016) and in isopods (Kamilari et al., 2014). Of particular interest is the fact that Lakes Stymfalia and Doxa form the intersection point of these clades, where individuals of both clades live in sympatry. Sympatric occurrence has also been confirmed for the same areas for the slow worms A. graeca and A. cephallonica (Jablonski et al., 2016).

Here, we should highlight that in the study of Spilani et al. (2019), where the population structure of *P. peloponnesiacus* was examined using microsatellite data, all the examined individuals of *P. peloponnesiacus* (they analyzed a total of 52 individuals, all of which are included in our study) were unequivocally assigned to two geographically distinct clusters, West and East Peloponnese. These findings, together with the evidence provided here, indicate that there is no genetic flow between individuals of the two clades and, probably, there are no hybrids. In the same study, phylogenetic analysis recovered two distinct subclades within *P. peloponnesiacus*, whose monophyly was well supported, and species delimitation analysis also revealed the existence of two species within *P. peloponnesiacus*.

Another very recent paper (Psonis et al., 2021), using genomic data (SNPs data through ddRADseq), revealed the splitting of *P. pelopon-nesiacus* into two clades that coincide with the east and west clade of our study. The same study also uncovered the relationships between *P. peloponnesiacus*, *P. cretensis*, and *P. levendis*, where *P. levendis* is more closely related to *P. peloponnesiacus* than to *P. cretensis*, a fact that is also affirmed from our phylogenetic tree revealed from the concatenated dataset.

Genetic distances between the two clades of *P. peloponnesiacus* (6.3% for *cyt b* and 3.4% for 16S) are of a similar order of magnitude to those found between species of the same genus, such as between *P. peloponnesiacus*, *P. levendis*, and *P. cretensis* (present study), or among members of the *P. tauricus* species group (Psonis et al., 2017, 2018) while they are very close to those of the species of the genus *Mesalina* (Kapli et al., 2008). Moreover, they are equivalent to those found between other species of the genus *Podarcis* outside Balkans, such as between *P. siculus* and *P. waglerianus* (6.6% for *cyt b* and 2.2% for 16S; Psonis et al., 2017).

4.2 | Species divergence and biogeography

The "moderate" to "high" niche overlap between the two clades, in combination with the high overlap of the bioclimatic variables that most contribute to each model (BIO8, BIO15, and BIO18 for clade 1 and BIO8, BIO15, BIO18, and BIO19 for clade 2), suggest that the distinct distribution of the two clades is probably not related to ecological differentiation. Instead, it may be due to biogeographical events. Given that individuals of the two clades, in the areas where they are found in sympatry, retain their identities, we could assume that they are currently excluding each other, although our data are not enough to support it. The strong geographical cohesiveness of both the nuclear and mitochondrial genetic signal within P. peloponnesiacus suggests a history of parapatric divergence of the two clades. The chronophylogenetic analysis estimated the time of divergence between the two clades of *P. peloponnesiacus* to be about 1.72 Mya, a time that corresponds to the lower Pleistocene period, which is very close to the estimation of previously published studies (1.86 Mya) (Spilani et al., 2020). This divergence is also consistent with the most intraspecific divergences in the genus Podarcis, that have occurred within the Pleistocene, and imply a major role for climatic and sea-level changes during this epoch (Salvi et al., 2021).

From a biogeographical point of view, the Peloponnese's mountain massifs constitute an extension of the Pindos Mountain range and consequently of the External Hellenides [the western and southernmost part of the Hellenic Orogenic belt, that run from western continental Greece to the Peloponnese and Crete (Dornsiepen et al., 2001)], which expanded during the Pliocene (van Andel et al., 1993; Papanikolaou, 2010), while, by the same period, extensive lowland areas throughout the Peloponnese were inundated by the sea (Dermitzakis, 1990). Moreover, during the Pliocene, there was a series of tectonic rearrangements, which resulted in an important size reduction, with the present

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mountainous areas becoming the only non-submerged land surfaces (Creutzburg, 1963). In the Upper Pliocene and Pleistocene, in the area around Megalopolis, there was a large deep freshwater lake (Falniowski & Szarowska, 2016), which may have been the initial geographical barrier that gradually isolated populations. Sea intervening between mountains also acted as a biogeographic barrier that prevented gene flow among populations (Psonis et al., 2018). In the Pleistocene, the Peloponnese was reconnected to mainland Greece, with paleogeographic illustrations showing wide land bridges between them (Ferentinos et al., 2012; Perissoratis & Conispoliatis, 2003) due to a major drop of sea level during the last glacial maximum (van Andel & Shackleton, 1982). In the middle Pleistocene, there were two sea introgressions throughout the Peloponnese (Siavalas et al., 2009), with populations probably surviving in higher altitudes. The high mountains of the Peloponnese (e.g., Helmos, Killini and Taygetos) had already attained their current altitude during the Pleistocene (Dimopoulos, 1993), providing suitable environments, for the survival of P. peloponnesiacus during ice ages. As for the contact zones of the two clades, lakes Stymfalia and Doxa, they formed at the end of the Pleistocene, with the separation of Killini from Mainalo and of Helmos from Killini respectively (Dimopoulos, 1993).

Based on the above, we could assume that *P. peloponnesiacus* was originally a single evolutionary unit, distributed throughout the Peloponnese, when it was still a continuous land mass. During the Pliocene, the species may have started to subdivide into diverging populations due to biogeographical barriers. Populations would then have been isolated in separate glacial refugia, resulting in reproductive isolation, leading to genetic differentiation due to drift (Abellán & Svenning, 2014). The Peloponnese could have served as an area with multiple subrefugia (Jablonski et al., 2016; Jesse et al., 2010). More specifically, the northern mountain ranges of Killini, Oligyrtos, Trachi, and Lyrkio, as well as Parnonas mountain in the southern part of the Peninsula, form a high-elevation line. This separates the western and eastern Peloponnese and could represent a geographical barrier (For a geographical map showing the mountain ranges of the Peloponnese, see Figure S6). At the end of the Pleistocene, when climatic conditions became favorable, western and eastern lineages could subsequently come into secondary contact.

4.3 | Morphological distinctiveness

In order to explore the phenotypic differentiation between the two clades of *P. peloponnesiacus*, we performed an extensive investigation of biometric and pholidotic traits. Unfortunately, none of these characters could be considered as diagnostic between clades, because even if there were some that had significant differences between two populations, their ranges of variation overlapped. However, it is not the first time that diagnostic characters have failed to be defined; the same has been observed in other species of the genus *Podarcis*, between closely related lineages that have experienced high genetic differentiation (Bruschi et al., 2006;

Kaliontzopoulou et al., 2012; Rodríguez et al., 2017), where the range of scale counts among species largely overlap. It is well documented that *Podarcis* lizards, although exhibiting high phenotypic variation between populations and individuals of the same species (Carretero, 2008; Kaliontzopoulou et al., 2018), are characterized by a generally conserved morphology, leading to high levels of cryptic diversity (Kaliontzopoulou et al., 2011, 2012), and the study of these species has revealed that speciation is not always coupled with morphological change (Bickford et al., 2007).

4.4 | Taxonomy

Despite years of study, the taxonomy of the genus Podarcis is complex and continuously under reconsideration leading to repeated revisions and/or identifications of new species (Carretero, 2008; Harris et al., 2002; Kaliontzopoulou et al., 2011; Lima et al., 2010: Lymberakis et al., 2008: Pinho et al., 2007: Poulakakis et al., 2005; Psonis et al., 2017; Rodríguez et al., 2017; Salvi et al., 2017; Sá-Sousa & Harris, 2002; Senczuk et al., 2019). There are several cases of Podarcis species that were raised from subspecies to species rank (for a review see Senczuk, Harris, et al., 2019; Speybroeck et al., 2020) or that are considered species complexes due to high levels of cryptic genetic diversity (Bellati et al., 2011; Harris et al., 2005; Harris & Sá-Sousa, 2001; Pinho et al., 2006; Podnar, Mayer, & Tvrtković, 2004, 2005; Poulakakis et al., 2003, 2005; Psonis et al., 2017). Very recently, a new species (Podarcis galerai) was discovered in the P. hispanicus complex (Bassitta et al., 2020), based exclusively on molecular analyses, without any morphological differentiation from its closest lineage (P. hispanicus).

Although the monophyly of *P. peloponnesiacus* has been strongly supported by previous studies (Lymberakis et al., 2008; Poulakakis et al., 2005; Spilani et al., 2019), our data showed that a rearrangement of the taxonomic status of this monophyly is needed. Recapitulating essential relevant parts of the information presented above, there are three main issues to consider:

1. During recent years, there has been an accumulation of data from various sources indicating that the monophyletic species P. peloponnesiacus, consists of two distinct clades, which began diverging ~1.8 Mya. Specifically, presence data in numerous localities, combined with data of molecular markers (mtDNA, nuDNA, and microsatellites) in Spilani et al. (2019), phylogenomic data (ddRADseq) in Psonis et al. (2021), and molecular markers (mtDNA, nuDNA), together with morphological data in the present study, were statistically analyzed in a series of approaches including sequence relationships, chronophylogenetic analysis, species delimitation techniques, morphological comparisons, and niche similarity models. These produced overwhelmingly congruent data from distinct realms and are unequivocal in recognizing two distinct taxa, mostly parapatric, except for a single point of syntopic coexistence, nevertheless, with no evidence of genetic admixture whatsoever.

- 2. The data on which the designation of subspecies was initially based in Buchholz (1960) were rather weak in a taxonomic sense, as the author worked exclusively on coloration patterns and colors, for which he mentions overlap among the taxa recognized. This was combined with somewhat vague descriptions of the subspecies distributions. Bringsøe (1986) altered this view, sinking one of Buchholz's (1960) subspecies (*P. p. phryne*) in synonymy with *P. p. lais*. Nevertheless, distributions restricted in Bringsøe (1986) were still not based on defined limits among the taxa, but rather attributed to respective secondary divisions (Provinces) of the Greek administrative system (see Introduction).
- 3. The distributions of the two new taxa mentioned in the first point partially (inasmuch as their distribution areas were never strictly defined) coincide with the ones of previously designated subspecies as described in point 2. The relationships and distributions of the two groups of taxa (the three of Bringsøe (1986) and the two proposed in this study) are explicitly presented below in the description of the new taxa.

Following the reasoning above, we propose splitting the species *Podarcis peloponnesiacus* to two taxa, specifically:

Podarcis peloponnesiacus (Bibron and Bory de Saint-Vincent, 1833).

Synonymy: Lacerta peloponnesiaca peloponnesiaca Bibron and Bory de Saint-Vincent, 1833.

Podarcis peloponnesiacus peloponnesiacus (Bibron and Bory de Saint-Vincent, 1833).

Lacerta peloponnesiaca lais Bucholz, 1960 ("Kalavrita, Nordwest-Peloponnes").

Lacerta peloponnesiaca phryne Bucholz 1960 ("Berg Velia, südlich Kalavrita, oberhalb de Waldgürtels").

Type locality

"Mistras bei Sparti (Peloponnes)" restricted by Buchholz (1960). Holotype: MNHN-RA 2706 with the paratype series designated by the same author, including the nominotypical subspecies.

Distribution

The western part of the Peloponnese as presented in Figure 2.

Description

The description of the species follows Buchholz (1960) and is completed by the morphological data presented here (paragraph 3.4). However, there is no combination of morphological characters adequate to safely discriminate *P. peloponnesiacus* from the new taxon described at the species level below, *P. thais*.

Differential diagnosis

A differential diagnosis of the species regarding closely related congenerics is provided in Lymberakis et al. (2008). However, neither the latter nor the morphological characters examined here provide an unequivocal diagnosis with respect to *P. thais* (see below). Hence, WILEY

we restrict our differential diagnosis exclusively to molecular characters: In our *Cyt b* alignment, nucleotide position 165 is occupied by base 'C'; nucleotide position 247 is occupied by base 'T'; nucleotide position 261 is occupied by base 'G'; nucleotide position 288 is occupied by base 'C'; nucleotide position 294 is occupied by base 'T'; and nucleotide position 345 is occupied by base 'T'.

Podarcis thais (Buchholz, 1960) **stat. nov**. *Synonymy: Lacerta peloponnesiaca thais* Buchholz, 1960 *Podarcis peloponnesiacus thais* (Buchholz, 1960).

Type locality

"Aesculap-Heiligtum (400 m), Argolis".

Holotype

ZFMK-H 12261, and the type series designated by Buchholz (1960).

Distribution

The eastern part of the Peloponnese as presented in Figure 2. A discrepancy between the distribution proposed by Bringsøe (1986) and the one adopted here, regarding the specimens of the eastern slopes of Mt. Parnon and southwards from there (Figure 2). According to the present work, these populations fall unequivocally under the new taxon *P. thais*, which is elevated here.

Description

The description of the species follows Buchholz (1960) and is completed by the morphological data presented here (paragraph 3.4).

Differential diagnosis

In accordance with the reasoning of the differential diagnosis for *P. peloponnesiacus*, the differential diagnosis of *P. thais* is also exclusively based on molecular characters: In our *Cyt b* alignment, nucleotide position 171 is occupied by base 'T'; nucleotide position 192 is occupied by base 'T'; and nucleotide position 318 is occupied by base 'T'. The differential diagnosis with molecular characters supports differentiating the species from *P. peloponnesiacus*. For other closely related congenerics, the differential diagnosis in Lymberakis et al. (2008) of the former parent taxon (*P. peloponnesiacus*) is also valid for the new species.

4.5 | Conclusions

In this study, we showed there to be high intraspecific genetic variation within *P. peloponnesiacus*, highlighted the existence of a cryptic lineage with reproductive isolation [we combined our results with those of Spilani et al. (2019)] and a west-east geographical pattern. We also suggested, in accordance with many previous studies, that landscape and environmental events in the southern Balkan Peninsula (including the Peloponnese) were most probably major factors in species diversification processes. The revealed genetic structure of *P. peloponnesiacus* has considerable

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implications for the taxonomy of the species and subsequently for its conservation. We proposed that the two clades within *P. peloponnesiacus* constitute two different taxa, and thus, we elevated *P. p. thais* to species level. Although *P. peloponnesiacus* has been suggested to be a species whose population and habitat are not threatened, it is now necessary to properly evaluate population sizes and revaluate possible threats to both these endemic taxa. Finally, our results clearly show that the general pattern of possible speciation events in *P. peloponnesiacus* is comparable to those of other taxa in the Peloponnese and the presence of divergent clades matches the historical biogeography of the Peloponnese peninsula.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the correspondig author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Supporting Information

Evidence of cryptic diversity in *Podarcis peloponnesiacus* and re-evaluation of its current taxonomy; insights from genetic, morphological and ecological data

Phylogeny of Podarcis peloponnesiacus

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Figure S1. Geographic origin of the the specimens used in morphometrics. Left: Geographical localities of all specimens used for biometric traits. Right: Geographical localities of all specimens used for pholidotic traits.



Figure S2. Geographic origin of the reference points used in SDM analyses. Circles correspond to the western clade (clade 1) and crosses to the eastern clade (clade 2). The green polygon highlights the area of modelling.



Figure S3. BI tree based on nuDNA. The gene tree of all nuclear loci

(*Pod55/MC1R/Rag1/Pod15b/NKTR/UBN1*) produced by the BI analysis. The posterior probabilities and bootstrap supports (BI/ML) are presented on the branches.



Figure S4. Haplotype network for each nuclear locus separately for *P. peloponnesiacus*.



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0.008

Figure S5. The species tree produced by STACEY analysis. Posterior probabilities are shown in the branches.



Figure S6. A geographical map of Peloponnese with the main mountains and Lake Stymfalia.

Table S1. List of specimens used in molecular analyses. Table shows the serial number of specimens (a/a), the NHMC code (code given in samples of Natural History Museum of Crete), the species name, the location of the specimens, the field code (FC, code specifying the exact locality of specimens), the molecular code used for each sample for convenience in this study, and the genetic loci amplified in this study (x) (*cyt b, 16S, MC1R, Pod55, Pod15b, Rag1, NKTR, UBN1*).

a/a	Species	NHMC Code	Location	Field Code	Molecular Code	cyt b	16S	MC1R	Pod55	Pod15b	Rag1	NKTR	UBN1
1	P. peloponnesiacus	80 3 54 112	Polydroso (Tsintzina)	13859	1220	MW846724	MW832640	MW880775	MW846816	MW846786		MW880813	MW880873
2	P. peloponnesiacus	80.3.54.132	Gerolimenas	16879	944	MK905680	MK929220	MW880810	MW846854	MW846813	MW880871	MW880832	MW880888
3	P. peloponnesiacus	80.3.54.131	Kiveri	16866	913	MK905668	MK929208	MK929646	MK926662	MK926626	MK941385	MK941417	MK941444
4	P. peloponnesiacus	80.3.54.116	Panachaiko mountain	13017	1224	MW846728	MW832644	MW880777	MW846818	MW846788	MW880837		
5	P. peloponnesiacus	80.3.54.136	Loutsa	16884	918	MK905673	MK929213	MW880808	MW846852	MK926615	MW880869	MW880831	MW880887
6	P. peloponnesiacus	80.3.54.137	Voidokoilia	16886	919	MK905674	MK929214	MW880809	MW846853		MW880870		
7	P. peloponnesiacus	80.3.54.154	Artemisia	20349	909	MK905664	MK929204	MW880804	MW846848	MW846809	MW880865	MW880829	
8	P. peloponnesiacus	80.3.54.153	Chora Gaitson	20348	908	MK905663	MK929203	MW880803	MW846847		MW880864	MW880828	
9	P. peloponnesiacus	80.3.54.151	Skoutari	20346	906	MK905661	MK929201	MW880801	MW846845		MW880862	MW880826	MW880883
10	P. peloponnesiacus	80.3.54.152	Avramianika	20347	907	MK905662	MK929202	MW880802	MW846846	MW846808	MW880863	MW880827	MW880884
11	P. peloponnesiacus	80.3.54.135	Petalidi	16882	917	MK905672	MK929212	MW880807	MW846851	MW846811	MW880868	MW880830	
12	P. peloponnesiacus	80.3.54.184	Achladocampos	24531	1255	MW846758	MW832672		MW846825				
13	P. peloponnesiacus	80.3.54.208	Alevrou	24548	1279	MW846771	MW832681						
14	P. peloponnesiacus	80.3.54.25	Pyrgos	5660	160	AY896117.1	AY896174.2*	MK929626	MK926642	MK926606	MW880853	MK941401	
15	P. peloponnesiacus	80.3.54.133	Korydalos	21757	429	MW846783	MW832694	MW880799	MW846842	MW846805	MW880858	MW880822	
16	P. peloponnesiacus	80.3.54.206	Karytaina	24547	1277	MW846770	MW832680	MW880791	MW846833	MW846799	MW880847		
17	P. cretensis	80.3.51.177	Samaria	1859	71	AF486204.1	AY896161.1	MK929617.1	MK926633.1	MK926597.1	MK941355.1	MK941390.1	MK941419.1
18	P. cretensis	80.3.51.2067	Balos	10335	389	MK905602.1	MK929151.1	MK929641.1	MK926657.1	MK926621.1	MK941378.1	MK941410.1	MK941439.1
19	P. cretensis	80.3.51.277	Marmara isl.	1552	92	AF486208.1	AY896150.1	MK929621.1	MK926637.1	MK926601.1	MK941358.1	MK941393.1	MK941422.1
20	P. cretensis	80.3.51.327	Koufonisi isl.	2998	93	AF486213.2	AY896147.1	KX658530	KX658583		MK941359.1	MK941394.1	MK941423.1
21	P. erhardii	80.3.51.2389	Astakida isl.	15979	380	MK905593.1	MK929142.1	MK929640.1	MK926656.1	MK926620.1	MK941377.1		MK941438.1
22	P. erhardii	80.3.51.2390	Astakida isl.	15979	235	MK905556.1	MK929105.1	MK929629.1	MK926645.1	MK926609.1	MK941368.1	MK941403.1	MK941431.1
23	P. peloponnesiacus	80.3.54.17	Stymfalia lake	613	1141	MW846650	MW832568						
24	P. peloponnesiacus	80.3.54.22	Stymfalia lake	5617	1144	MW846653	MW832571						
25	P. peloponnesiacus	80.3.54.19	Lafka	615	9	AY896122.1	MW832695	MK929612	MK926628	MK926591			
26	P. peloponnesiacus	80.3.54.16	Stymfalia lake	613	1140	MW846649	MW832567						
27	P. peloponnesiacus	80.3.54.20	Lafka	615	10	AY896123.1	MW832559	MK929613	MK926629	MK926593	MW880833	MW880811	MW880872
28	P. peloponnesiacus	80.3.54.9	Stymfalia lake	3826	127	AF486231.1	MK929103	MK929625	MK926641	MK926605	MK941365	MK941400	MK941429
29	P. peloponnesiacus	80.3.54.21	Stymfalia lake	5617	1143	MW846652	MW832570						
30	P. peloponnesiacus	80.3.54.18	Stymfalia lake	613	1142	MW846651	MW832569						
31	P. peloponnesiacus	80.3.54.23	Stymfalia lake	5617	1145	MW846654	MW832572						
32	P. peloponnesiacus	80.3.54.52	Stymfalia lake	7746	1165	MW846672	MW832588						
33	P. peloponnesiacus	80.3.54.34	Stymfalia lake	5887	1150	MW846658	MW832575						
34	P. peloponnesiacus	80.3.54.47	Stymfalia lake	5595	1160	MW846667	MW832583						
35	P. peloponnesiacus	80.3.54.39	Stymfalia lake	5887	404	MK905613	MK929160		MW846841		MW880857		
36	P. peloponnesiacus	80.3.54.49	Stymfalia lake	7748	1162	MW846669	MW832585						
37	P. peloponnesiacus	80.3.54.54	Stymfalia lake	7746	1167	MW846674	MW832590						
38	P. peloponnesiacus	80.3.54.51	Stymfalia lake	7746	1164	MW846671	MW832587						
39	P. peloponnesiacus	80.3.54.41	Stymfalia lake	5887	401	MK905610	MK929159						
40	P. peloponnesiacus	80.3.54.32	Stymfalia lake	5887	375	MK905588	MK929137	MK929635	MK926651	MW846812	MW880855	MW880821	
41	P. peloponnesiacus	80.3.54.42	Stymfalia lake	5887	385	MK905598	MK929147						
42	P. peloponnesiacus	80.3.54.45	Stymfalia lake	5595	1158	MW846665	MW832582						

43	P. peloponnesiacus	80.3.54.37	Stymfalia lake	5887	1153	MW846661	MW832578		MW846815		MW880835		
44	P. peloponnesiacus	80.3.54.38	Stymfalia lake	5887	1154	MW846662	MW832579						
45	P. peloponnesiacus	80.3.54.50	Stymfalia lake	7746	1163	MW846670	MW832586						
46	P. peloponnesiacus	80.3.54.36	Stymfalia lake	5887	1152	MW846660	MW832577						
47	P. peloponnesiacus	80.3.54.33	Stymfalia lake	5887	374	MK905587	MW832693	MK929634	MK926650	MK926614	MK941373	MK941407	MW880878
48	P. peloponnesiacus	80.3.54.53	Stymfalia lake	7746	1166	MW846673	MW832589						
49	P. peloponnesiacus	80.3.54.44	Stymfalia lake	5595	1157	MW846664	MW832581						
50	P. peloponnesiacus	80.3.54.55	Stymfalia lake	7746	1168	MW846675	MW832591						
51	P. peloponnesiacus	80.3.54.24	Stymfalia lake	5617	1146	MW846655	MW832573						
52	P. peloponnesiacus	80.3.54.40	Stymfalia lake	5887	1155	MW846663	MW832580						
53	P. peloponnesiacus	80.3.54.31	Stymfalia lake	5887	1149	MW846657	MW832574						
54	P. peloponnesiacus	80.3.54.30	Stymfalia lake	5888	1148	MW846656							
55	P. peloponnesiacus	80.3.54.35	Stymfalia lake	5887	1151	MW846659	MW832576						
56	P. peloponnesiacus	80.3.54.46	Stymfalia lake	5595	1159	MW846666							
57	P. peloponnesiacus	80.3.54.48	Stymfalia lake	7747	1161	MW846668	MW832584						
58	P. peloponnesiacus	80.3.54.73	Stymfalia lake	5672	1203	MW846708	MW832624						
59	P. peloponnesiacus	80.3.54.81	Stymfalia lake	5672	1210	MW846714	MW832630						
60	P. peloponnesiacus	80.3.54.60	Stymfalia lake	7746	1173	MW846680	MW832596						
61	P. peloponnesiacus	80.3.54.74	Stymfalia lake	5672	1204	MW846709	MW832625						
62	P. peloponnesiacus	80.3.54.67	Stymfalia lake	5672	1180	MW846686	MW832602						
63	P. peloponnesiacus	80.3.54.65	Stymfalia lake	5672	1178	MW846684	MW832600						
64	P. peloponnesiacus	80.3.54.69	Stymfalia lake	5672	1199	MW846705	MW832621						
65	P. peloponnesiacus	80.3.54.75	Stymfalia lake	5672	1205	MW846710	MW832626						
66	P. peloponnesiacus	80.3.54.80	Stymfalia lake	5672	1209	MW846713	MW832629						
67	P. peloponnesiacus	80.3.54.63	Stymfalia lake	5672	1176	MW846682	MW832598						
68	P. peloponnesiacus	80.3.54.83	Stymfalia lake	5672	1212	MW846716	MW832632						
69	P. peloponnesiacus	80.3.54.62	Stymfalia lake	5672	1175	MW846681	MW832597						
70	P. peloponnesiacus	80.3.54.76	Stymfalia lake	5672	1206	MW846711	MW832627						
71	P. peloponnesiacus	80.3.54.84	Stymfalia lake	5672	1213	MW846717	MW832633						
72	P. peloponnesiacus	80.3.54.77	Stymfalia lake	5672	1207	MW846712	MW832628						
73	P. peloponnesiacus	80.3.54.71	Stymfalia lake	5672	1201	MW846706	MW832622						
74	P. peloponnesiacus	80.3.54.66	Stymfalia lake	5672	1179	MW846685	MW832601						
75	P. peloponnesiacus	80.3.54.68	Stymfalia lake	5672	1181	MW846687	MW832603						
76	P. peloponnesiacus	80.3.54.82	Stymfalia lake	5672	1211	MW846715	MW832631						
77	P. peloponnesiacus	80.3.54.58	Stymfalia lake	7746	1171	MW846678	MW832594						
78	P. peloponnesiacus	80.3.54.64	Stymfalia lake	5672	1177	MW846683	MW832599						
79	P. peloponnesiacus	80.3.54.72	Stymfalia lake	5672	1202	MW846707	MW832623						
80	P. peloponnesiacus	80.3.54.59	Stymfalia lake	7746	1172	MW846679	MW832595						
81	P. peloponnesiacus	80.3.54.57	Stymfalia lake	7746	1170	MW846677	MW832593						
82	P. peloponnesiacus	80.3.54.78	Stymfalia lake	5672	1223	MW846727	MW832643						
83	P. peloponnesiacus	80.3.54.56	Stymfalia lake	7746	1169	MW846676	MW832592						
84	P. peloponnesiacus	80.3.54.87	Stymfalia lake	5672	1216	MW846720	MW832636						
85	P. peloponnesiacus	80.3.54.103	Stymfalia lake	9404	1190	MW846696	MW832612						
86	P. peloponnesiacus	80.3.54.120	Stymfalia lake	16964	851	MK905651	MK929195						
87	P. peloponnesiacus	80.3.54.108	Stymfalia lake	9404	1195	MW846701	MW832617						
88	P. peloponnesiacus	80.3.54.106	Stymfalia lake	9404	1193	MW846699	MW832615						
89	P. peloponnesiacus	80.3.54.102	Stymfalia lake	9404	1189	MW846695	MW832611						
90	P. peloponnesiacus	80.3.54.96	Stymfalia lake	9404	1183	MW846689	MW832605						
91	P. peloponnesiacus	80.3.54.110	Stymfalia lake	9404	1197	MW846703	MW832619						
92	P. peloponnesiacus	80.3.54.105	Stymfalia lake	9404	1192	MW846698	MW832614						
93	P. peloponnesiacus	80.3.54.86	Stymfalia lake	5672	1215	MW846719	MW832635						

94	P. peloponnesiacus	80.3.54.89	Stymfalia lake	8629	1218	MW846722	MW832638						
95	P. peloponnesiacus	80.3.54.88	Stymfalia lake	8629	1217	MW846721	MW832637						
96	P. peloponnesiacus	80.3.54.111	Stymfalia lake	9404	1198	MW846704	MW832620						
97	P. peloponnesiacus	80.3.54.98	Stymfalia lake	9404	1185	MW846691	MW832607						
98	P. peloponnesiacus	80.3.54.95	Stymfalia lake	9404	1182	MW846688	MW832604						
99	P. peloponnesiacus	80.3.54.121	Stymfalia lake	16964	850	MK905650	MK929194						
100	P. peloponnesiacus	80.3.54.99	Stymfalia lake	9404	1186	MW846692	MW832608						
101	P. peloponnesiacus	80.3.54.97	Stymfalia lake	9404	1184	MW846690	MW832606						
102	P. peloponnesiacus	80.3.54.109	Stymfalia lake	9404	1196	MW846702	MW832618						
103	P. peloponnesiacus	80.3.54.85	Stymfalia lake	5672	1214	MW846718	MW832634						
104	P. peloponnesiacus	80.3.54.104	Stymfalia lake	9404	1191	MW846697	MW832613						
105	P. peloponnesiacus	80.3.54.122	Stymfalia lake	16964	849	MK905649	MK929193			MW846807	MW880860	MW880824	
106	P. peloponnesiacus	80.3.54.100	Stymfalia lake	9404	1187	MW846693	MW832609						
107	P. peloponnesiacus	80.3.54.90	Stymfalia lake	8629	1219	MW846723	MW832639						
108	P. peloponnesiacus	80.3.54.101	Stymfalia lake	9404	1188	MW846694	MW832610						
109	P. peloponnesiacus	80.3.54.107	Stymfalia lake	9404	1194	MW846700	MW832616						
110	P. peloponnesiacus	80.3.54.166	Stymfalia lake	23017	1237	MW846741	MW832657						
111	P. peloponnesiacus	80.3.54.162	Stymfalia lake	23017	1233	MW846737	MW832653						
112	P. peloponnesiacus	80.3.54.123	Stymfalia lake	16964	848	MK905648	MK929192						
113	P. peloponnesiacus	80.3.54.165	Stymfalia lake	23017	1236	MW846740	MW832656						
114	P. peloponnesiacus	80.3.54.159	Stymfalia lake	23017	1230	MW846734	MW832650						
115	P. peloponnesiacus	80.3.54.160	Stymfalia lake	23017	1231	MW846735	MW832651						
116	P. peloponnesiacus	80.3.54.167	Stymfalia lake	23017	1238	MW846742	MW832658						
117	P. peloponnesiacus	80.3.54.158	Stymfalia lake	23017	1229	MW846733	MW832649						
118	P. peloponnesiacus	80.3.54.124	Stymfalia lake	16964	847	MK905647	MK929191	MK929644	MK926660	MK926624	MK941383	MK941415	MK941442
119	P. peloponnesiacus	80.3.54.163	Stymfalia lake	23017	1234	MW846738	MW832654						
120	P. peloponnesiacus	80.3.54.161	Stymfalia lake	23017	1232	MW846736	MW832652						
121	P. peloponnesiacus	80.3.54.164	Stymfalia lake	23017	1235	MW846739	MW832655						
122	P. peloponnesiacus	80.3.54.155	Doxa lake	20341	910	MK905665	MK929205						
123	P. peloponnesiacus	80.3.54.130	Doxa lake	16963	1227	MW846731	MW832647						
124	P. peloponnesiacus	80.3.54.157	Doxa lake	20341	912	MK905667	MK929207						
125	P. peloponnesiacus	80.3.54.129	Doxa lake	16963	1226	MW846730	MW832646	MW880779	MW846820	MW846790	MW880839		MW880875
126	P. peloponnesiacus	80.3.54.128	Doxa lake	16963	1003	MW846644	MW832563						
127	P. peloponnesiacus	80.3.54.156	Doxa lake	20341	911	MK905666	MK929206						
128	P. peloponnesiacus	80.3.54.193	Kyllini	24534	1264	MW846761	MW832675	MW880785	MW846827		MW880843		
129	P. peloponnesiacus	80.3.54.194	Kyllini	24534	1265	MW846762							
130	P. peloponnesiacus	80.3.54.195	Mati beach, Feneos	24535	1266	MW846763		MW880786	MW846828	MW846794			
131	P. peloponnesiacus	80.3.54.202	Galatas	24543	1273	MW846766	MW832678	MW880787	MW846829	MW846795	MW880844		
132	P. peloponnesiacus	80.3.54.196	Mati beach, Feneos	24535	1267	MW846764	MW832676						
133	P. peloponnesiacus	80.3.54.203	Kandila	24544	1274	MW846767	MW832679	MW880788	MW846830	MW846796	MW880845		
134	P. peloponnesiacus	80.3.54.218	Feneos	24555	1289	MW846780	MW832690	MW880797	MW846839	MW846804	MW880852		
135	P. peloponnesiacus	80.3.54.219	Feneos	24555	1290	MW846782	MW832692						
136	P. peloponnesiacus	80.3.54.214	Lykouria	24553	1285	MW846777	MW832687	MW880795	MW846837	MW846803			
137	P. peloponnesiacus	80.3.54.29	Feneos	5801	219	AY896116.1	AY896173.1	MK929628	MK926644	MK926608	MK941367	MK941402	MK941430
138	P. peloponnesiacus	80.3.54.27	Peloponnesos	5662	41	AY896119.1	AY896176.1						
139	P. peloponnesiacus	80.3.54.7	Stoupa	780	8	AY896124.1	AY896179.2*	MK929611	MK926627	MK926592	MK941352	MK941386	MW880881
140	P. peloponnesiacus	80.3.54.6	Stoupa	780	129	MW846781	MW832691						
141	P. peloponnesiacus	80.3.54.14	Stoupa	780	1139	MW846648	MW832566						
142	P. peloponnesiacus	80.3.54.5	Stoupa	780	1136	MW846646							
143	P. peloponnesiacus	80.3.54.134	Agios Dimitrios	16881	916	MK905671	MK929211	MW880806	MW846850	MW846810	MW880867		MW880885
144	P. peloponnesiacus	80.3.54.114	Erymanthos	13020	396	KX657922	KX658224	KX658498	KX658604	KX658551	MK941379	MK941411	MK941440

145	P. peloponnesiacus	80.3.54.115	Erymanthos	13022	1222	MW846726	MW832642						
146	P. peloponnesiacus	80.3.54.126	Olymbia	20031	1002	MW846643	MW832562						
147	P. peloponnesiacus	80.3.54.125	Olymbia	20031	1001	MW846642	MW832561	MW880774	MW846814	MW846785	MW880834	MW880812	
148	P. peloponnesiacus	80.3.54.210	Platiana	24550	1281	MW846773	MW832683	MW880792	MW846834	MW846800	MW880848		
149	P. peloponnesiacus	80.3.54.211	Aspra spitia	24551	1282	MW846774	MW832684	MW880793	MW846835	MW846801	MW880849		
150	P. peloponnesiacus	80.3.54.117	Egaleo	13081	397	KX657923	KX658225	KX658499	KX658605	KX658552	MK941380	MK941412	MK941441
151	P. peloponnesiacus	80.3.54.113	Lykovounia, Chora Trifillias	14135	1221	MW846725	MW832641	MW880776	MW846817	MW846787	MW880836	MW880814	
152	P. peloponnesiacus	80.3.54.168	Gargalianoi	14508	1239	MW846743	MW832659						
153	P. peloponnesiacus	80.3.54.171	Raptopoulo	14525	1242	MW846746	MW832662	MW880781	MW846822	MW846791	MW880841	MW880817	MW880877
154	P. peloponnesiacus	80.3.54.169	Kryoneri	14522	1240	MW846744	MW832660	MW880780	MW846821		MW880840	MW880816	MW880876
155	P. peloponnesiacus	80.3.54.170	Kryoneri	14522	1241	MW846745	MW832661						
156	P. peloponnesiacus	80.3.54.204	Tripoli	24545	1275	MW846768		MW880789	MW846831	MW846797	MW880846		
157	P. peloponnesiacus	80.3.54.205	Megalopoli	24546	1276	MW846769		MW880790	MW846832	MW846798	MW880851		
158	P. peloponnesiacus	80.3.54.189	Sparti	24533	1260	MW846759	MW832673	MW880784	MW846826		MW880866		
159	P. peloponnesiacus	80.3.54.190	Sparti	24533	1261	MW846760	MW832674						
160	P. peloponnesiacus	80.3.54.142	Monemvasia	20282	924	MK905679	MK929219						
161	P. peloponnesiacus	80.3.54.138	Monemvasia	20282	898	MK905654	MK929198						
162	P. peloponnesiacus	80.3.54.140	Monemvasia	20282	914	MK905669	MK929209						
163	P. peloponnesiacus	80.3.54.141	Monemvasia	20282	915	MK905670	MK929210	MW880805	MW846849				MW880886
164	P. peloponnesiacus	80.3.54.3	Kalavryta	775	1135	MW846645	MW832564						
165	P. peloponnesiacus	80.3.54.15	Kalavryta	610	2	AY896120.1	MK929091	MW880798	MW846840		MW880854		
166	P. peloponnesiacus	80.3.54.1	Kalavryta	775	400	MK905609	MK929158						
167	P. peloponnesiacus	80.3.54.4	Kalavryta	777	128	MW846772	MW832682						
168	P. peloponnesiacus	80.3.54.2	Kalavryta	775	7	AY896121.1	AY896177.1	MW880800	MW846843	MW846806	MW880859	MW880823	MW880880
169	P. peloponnesiacus	80.3.54.217	Argos	24554	1288	MW846779	MW832689						
170	P. peloponnesiacus	80.3.54.146	Argos	20344	901	MK905656							
171	P. peloponnesiacus	80.3.54.216	Argos	24554	1287	MW846778	MW832688	MW880796	MW846838				
172	P. peloponnesiacus	80.3.54.145	Argos	20344	900	MK905655							
173	P. peloponnesiacus	80.3.54.147	Argos	20344	902	MK905657	MK929199	MK929645	MK926661	MK926625	MK941384	MK941416	MK941443
174	P. peloponnesiacus	80.3.54.13	Taygetos mountain	602	399	MK905608	MK929157						
175	P. peloponnesiacus	80.3.54.172	Taygetos mountain	14536	1243	MW846747	MW832663						
176	P. peloponnesiacus	80.3.54.173	Taygetos mountain	14536	1244	MW846748	MW832664	MW880782	MW846823	MW846792	MW880842	MW880818	
177	P. peloponnesiacus	80.3.54.11	Taygetos mountain	602	384	MK905597	MK929146						
178	P. peloponnesiacus	80.3.54.176	Taygetos mountain	14536	1247	MW846751	MW832667						
179	P. peloponnesiacus	80.3.54.10	Taygetos mountain	602	1138	MW846647	MW832565						
180	P. peloponnesiacus	80.3.54.12	Taygetos mountain	602	398	MK905607	MK929156	MK929642	MK926658	MK926622	MK941381	MK941413	MW880879
181	P. peloponnesiacus	80.3.54.198	Nea Figaleia	24536	1269	MW846765	MW832677						
182	P. peloponnesiacus	80.3.54.182	Kato Figaleia	24530	1253	MW846756	MW832671						
183	P. peloponnesiacus	80.3.54.181	Kato Figaleia	24530	1252	MW846755							
184	P. peloponnesiacus	80.3.54.183	Kato Figaleia	24530	1254	MW846757							
185	P. peloponnesiacus	80.3.54.150	Kosmas	20339	905	MK905660			MW846844		MW880861	MW880825	MW880882
186	P. peloponnesiacus	80.3.54.149	Kosmas	20339	904	MK905659							
187	P. peloponnesiacus	80.3.54.148	Leonidio	20345	903	MK905658	MK929200						
188	P. peloponnesiacus	80.3.54.213	Doxa lake	24552	1284	MW846776	MW832686						
189	P. peloponnesiacus	80.3.54.212	Doxa lake	24552	1283	MW846775	MW832685	MW880794	MW846836	MW846802	MW880850		
190	P. peloponnesiacus	80.3.54.119	Epidavros	16783	1000	MW846641	MW832560						
191	P. peloponnesiacus	80.3.54.127	Epidavros	16783	1225	MW846729	MW832645	MW880778	MW846819	MW846789	MW880838	MW880815	MW880874
192	P. peloponnesiacus	80.3.54.118	Epidavros	16783	999	MW846784	MW832696						
193	P. peloponnesiacus	80.3.54.143	Mavrovouni	16100	1228	MW846732	MW832648						
194	P. peloponnesiacus	80.3.54.174	Moni Panagias Malevis	14553	1245	MW846749	MW832665						

195	P. peloponnesiacus	80.3.54.175	Moni Panagias Malevis	14553	1246	MW846750	MW832666	MW880783	MW846824	MW846793		MW880819	
196	P. peloponnesiacus	80.3.54.26	Agios Petros, Parnonas	5661	161	AY896118.1	AY896175.2*	MK929627	MK926643	MK926607	MK941366	MW880820	
197	P. peloponnesiacus	80.3.54.177	Megalopoli	24528	1248	MW846752	MW832668						
198	P. peloponnesiacus	80.3.54.179	Megalopoli	24528	1250	MW846754	MW832670						
199	P. peloponnesiacus	80.3.54.178	Megalopoli	24528	1249	MW846753	MW832669						
200	P. levendis	80.3.51.288	Pori isl.	2409	96	AF486222.2	AY896171.2	KX658538	KX658591	KX658538.1	MK941362.1	MK941397.1	MK941426.1
201	P. levendis	80.3.51.279	Pori isl.	2409	94	AF486221.2	AY896170.2	KX658537	KX658590	KX658537.1	MK941360.1	MK941395.1	MK941424.1

Table S2. Primers used for the amplification of mtDNA and nuDNA loci.Primers used for each locus, their sequences, the length (base pairs) of the amplicon, the concentration of MgCl₂, and the annealing temperature applied to each pair.

Genetic loci	Primers	Sequence (5'-3')	Length (Base Pairs)	MgCl ₂ Concentration (mM) Annealing Temperature (°C)	Reference
	GLUDG	TGA CTT GAA RAA CCA YCG TTG	425	3Mm	(Palumbi 1996)
	CB2	CCC TCA GAA TGA TAT TTG TCC TCA	120	42-48,6°C	(1 uuuuuu, 1990)
	I 1/18/11	AAA AAG CTT CCA TCC AAC ATC TCA GCA		3Mm	(Kocher et al., 1989)
Cyt b	CB2	TGA TGA AA	308	42-48.6°C	(,,
	CD2	CCC TCA GAA TGA TAT TTG TCC TCA		42-40,0 C	(Palumbi, 1996)
	L-Cyt b P.erh	AAA ACA TCA CCC CAT SAT WA	350	1,5Mm	(Spilani et al. 2010)
R-Cyt b P.erh		GGA CTC CAA TGT TTC ATG TT	350	44-47°C	(Sphan et al., 2019)
	16SAr-1	CGG CCG CCT GTT TAT CAA AAA CAT	- 530	3Mm	(Palumbi 1006)
16S	16SBr-h	GGA GCT CCG GTT TGA ACT CAG ATC	~550	47-48,4°C	(1 aumol, 1990)
rRNA	16S-65f	AGG GAC TAG AAT GAA CGG CT	270	1,5Mm	(Setter:
	16S-433r	GGG TGT CCT GAT CCA ACA TC	~370	57-58,6°C	(Sphani et al., 2019)
MC1P	MC1R-f	GGC NGC CAT YGT CAA GAA CCG GAA CC	649	1,5Mm	(Pinho et al. 2010)
MCIK	MC1R-r	CTC CGR AAG GCR TAA ATG ATG GGG TCC AC	049	57-59°C	(1 millo et al., 2010)
Dog1	RAG-fo	GAA AAG GGC TAC ATC CTG G	1020	1,5Mm	(Mayer & Pavlicev,
Ragi	RAG-R1	AAA ATC TGC CTT CCT GTT ATT G	1020	50-53,2°C	2007)
NKTD	NKTRf19	GAT GAC ATG GAG ATY TGY ACT CC	620	1,5Mm	(Townsond at al. 2011)
MAIN	NKTRr18	CTY CTD GAY CGA CTT CTT GAG TGA CT	050	47-52,2°C	(10wilsend et al., 2011)
LIDN1	UBN1_f1	CCY CTM AAT TTY CTG GCW GAR CAG GC	732	1,5Mm	(Townsend et al. 2011)
UDINI	UBN1_r2	GGT CAG YAA YTT KGC CAC HCC YT	152	50-55,1°C	(10wilsend et al., 2011)
Pod55	pod55f	GGA TCT TTA TAG GAG AGT GCA GGC C	123	1,5Mm	(Pereira et al. 2013)
r 0033	pod55r	TTC CAG ATT GTG TTT ATC CTG GTG G	423	57-59°C	(1 ciclia ci al., 2013)
Dod15h	pod15bf	AAT CCT GGC TAA ATG CAA GCC TTG G	420 422	1,5Mm	(Paraira at al. 2012)
rouisb	pod15br	GCC AGG AGA ATA AGC TAC TCC ATC C	420-455	55-59°C	(reiella et al., 2015)

References of table S2

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Table S3. List of specimens used for morphological analyses. Table shows the serial number of specimens (a/a), the **collection** to which the sample belongs (NHMC: Natural History Museum of Crete, NHMUK: Natural History Museum of London, NMW: Naturhistorisches Museum Wien and AK: specimens sampled in the field by Antigoni Kaliontzopoulou), the **code**, the **location**, and the morphological **traits** examined for each specimen (biometric, pholidotic or both).

Mor	ohological traits			
a/a	Collection	Code	Location	Traits
1	NHMC	NHMC80.3.54.1	Kalavryta	Biometric, Pholidotic
2	NHMC	NHMC80.3.54.2	Kalavryta	Biometric, Pholidotic
3	NHMC	NHMC80.3.54.3	Kalavryta	Biometric, Pholidotic
4	NHMC	NHMC80.3.54.4	Kalavryta	Biometric, Pholidotic
5	NHMC	NHMC80.3.54.5	Stoupa	Biometric, Pholidotic
6	NHMC	NHMC80.3.54.6	Stoupa	Biometric, Pholidotic
7	NHMC	NHMC80.3.54.7	Stoupa	Biometric, Pholidotic
8	NHMC	NHMC80.3.54.8	Stoupa	Biometric
9	NHMC	NHMC80.3.54.9	Stymfalia lake	Biometric, Pholidotic
10	NHMC	NHMC80.3.54.10	Taygetos mountain	Biometric, Pholidotic
11	NHMC	NHMC80.3.54.11	Taygetos mountain	Biometric, Pholidotic
12	NHMC	NHMC80.3.54.12	Taygetos mountain	Biometric, Pholidotic
13	NHMC	NHMC80.3.54.13	Taygetos mountain	Biometric, Pholidotic
14	NHMC	NHMC80.3.54.14	Stoupa	Pholidotic
15	NHMC	NHMC80.3.54.16	Stymfalia lake	Biometric, Pholidotic
16	NHMC	NHMC80.3.54.17	Stymfalia lake	Biometric, Pholidotic
17	NHMC	NHMC80.3.54.18	Stymfalia lake	Biometric, Pholidotic
18	NHMC	NHMC80.3.54.19	Lafka	Biometric, Pholidotic
19	NHMC	NHMC80.3.54.20	Lafka	Biometric, Pholidotic
20	NHMC	NHMC80.3.54.21	Stymfalia lake	Biometric, Pholidotic
21	NHMC	NHMC80.3.54.22	Stymfalia lake	Biometric, Pholidotic
22	NHMC	NHMC80.3.54.23	Stymfalia lake	Biometric, Pholidotic
23	NHMC	NHMC80.3.54.24	Stymfalia lake	Biometric, Pholidotic
24	NHMC	NHMC80.3.54.30	Stymfalia lake	Biometric, Pholidotic
25	NHMC	NHMC80.3.54.44	Stymfalia lake	Pholidotic
26	NHMC	NHMC80.3.54.45	Stymfalia lake	Pholidotic
27	NHMC	NHMC80.3.54.46	Stymfalia lake	Pholidotic
28	NHMC	NHMC80.3.54.47	Stymfalia lake	Pholidotic

29	NHMC	NHMC80.3.54.48	Stymfalia lake	Biometric, Pholidotic
30	NHMC	NHMC80.3.54.49	Stymfalia lake	Pholidotic
31	NHMC	NHMC80.3.54.50	Stymfalia lake	Biometric, Pholidotic
32	NHMC	NHMC80.3.54.51	Stymfalia lake	Biometric, Pholidotic
33	NHMC	NHMC80.3.54.52	Stymfalia lake	Biometric, Pholidotic
34	NHMC	NHMC80.3.54.53	Stymfalia lake	Biometric, Pholidotic
35	NHMC	NHMC80.3.54.54	Stymfalia lake	Biometric, Pholidotic
36	NHMC	NHMC80.3.54.55	Stymfalia lake	Biometric, Pholidotic
37	NHMC	NHMC80.3.54.56	Stymfalia lake	Biometric, Pholidotic
38	NHMC	NHMC80.3.54.57	Stymfalia lake	Biometric, Pholidotic
39	NHMC	NHMC80.3.54.58	Stymfalia lake	Biometric, Pholidotic
40	NHMC	NHMC80.3.54.59	Stymfalia lake	Biometric, Pholidotic
41	NHMC	NHMC80.3.54.60	Stymfalia lake	Biometric, Pholidotic
42	NHMC	NHMC80.3.54.62	Stymfalia lake	Pholidotic
43	NHMC	NHMC80.3.54.63	Stymfalia lake	Pholidotic
44	NHMC	NHMC80.3.54.65	Stymfalia lake	Pholidotic
45	NHMC	NHMC80.3.54.66	Stymfalia lake	Pholidotic
46	NHMC	NHMC80.3.54.67	Stymfalia lake	Pholidotic
47	NHMC	NHMC80.3.54.71	Stymfalia lake	Pholidotic
48	NHMC	NHMC80.3.54.72	Stymfalia lake	Pholidotic
49	NHMC	NHMC80.3.54.73	Stymfalia lake	Pholidotic
50	NHMC	NHMC80.3.54.76	Stymfalia lake	Pholidotic
51	NHMC	NHMC80.3.54.77	Stymfalia lake	Pholidotic
52	NHMC	NHMC80.3.54.89	Stymfalia lake	Pholidotic
53	NHMC	NHMC80.3.54.90	Stymfalia lake	Pholidotic
54	NHMC	NHMC80.3.54.112	Polydroso(Tzitzina)	Biometric, Pholidotic
55	NHMC	NHMC80.3.54.113	Lykovounia	Pholidotic
56	NHMC	NHMC80.3.54.114	Erymanthos mountain	Pholidotic
57	NHMC	NHMC80.3.54.115	Erymanthos mountain	Biometric, Pholidotic
58	NHMC	NHMC80.3.54.116	Panachaiko mountain	Biometric, Pholidotic
59	NHMC	NHMC80.3.54.117	Aigaleo mountain	Pholidotic
60	NHMC	NHMC80.3.54.131	Kiveri	Pholidotic
61	NHMC	NHMC80.3.54.133	Korydalos	Biometric, Pholidotic
62	NHMC	NHMC80.3.54.134	Agios Dimitrios	Pholidotic
63	NHMC	NHMC80.3.54.135	Petalidi	Pholidotic
64	NHMC	NHMC80.3.54.136	Loutsa	Pholidotic

65	NHMC	NHMC80.3.54.137	Voidokoilia	Pholidotic
66	NHMC	NHMC80.3.54.158	Stymfalia lake	Biometric, Pholidotic
67	NHMC	NHMC80.3.54.159	Stymfalia lake	Pholidotic
68	NHMC	NHMC80.3.54.160	Stymfalia lake	Pholidotic
69	NHMC	NHMC80.3.54.161	Stymfalia lake	Pholidotic
70	NHMC	NHMC80.3.54.162	Stymfalia lake	Biometric, Pholidotic
71	NHMC	NHMC80.3.54.163	Stymfalia lake	Biometric, Pholidotic
72	NHMC	NHMC80.3.54.164	Stymfalia lake	Biometric, Pholidotic
73	NHMC	NHMC80.3.54.165	Stymfalia lake	Pholidotic
74	NHMC	NHMC80.3.54.166	Stymfalia lake	Biometric, Pholidotic
75	NHMC	NHMC80.3.54.167	Stymfalia lake	Biometric, Pholidotic
76	NHMC	NHMC80.3.54.168	Gargalianoi	Biometric, Pholidotic
77	NHMC	NHMC80.3.54.169	Kryoneri	Biometric, Pholidotic
78	NHMC	NHMC80.3.54.170	Kryoneri	Biometric, Pholidotic
79	NHMC	NHMC80.3.54.171	Raptopoulo	Biometric, Pholidotic
80	NHMC	NHMC80.3.54.172	Taygetos mountain	Biometric, Pholidotic
81	NHMC	NHMC80.3.54.173	Taygetos mountain	Biometric, Pholidotic
82	NHMC	NHMC80.3.54.174	Moni Panagias Malevis	Biometric, Pholidotic
83	NHMC	NHMC80.3.54.175	Moni Panagias Malevis	Biometric, Pholidotic
84	NHMC	NHMC80.3.54.176	Taygetos mountain	Biometric, Pholidotic
85	NHMC	NHMC80.3.54.177	Megalopoli	Biometric, Pholidotic
86	NHMC	NHMC80.3.54.178	Megalopoli	Biometric, Pholidotic
87	NHMC	NHMC80.3.54.179	Megalopoli	Biometric, Pholidotic
88	NHMC	NHMC80.3.54.181	Kato Figaleia	Biometric, Pholidotic
89	NHMC	NHMC80.3.54.182	Kato Figaleia	Biometric, Pholidotic
90	NHMC	NHMC80.3.54.183	Kato Figaleia	Biometric, Pholidotic
91	NHMC	NHMC80.3.54.184	Achladocampos	Biometric, Pholidotic
92	NHMC	NHMC80.3.54.189	Sparti	Biometric, Pholidotic
93	NHMC	NHMC80.3.54.190	Sparti	Biometric, Pholidotic
94	NHMC	NHMC80.3.54.193	Kyllini	Biometric, Pholidotic
95	NHMC	NHMC80.3.54.194	Kyllini	Biometric, Pholidotic
96	NHMC	NHMC80.3.54.195	Mati beach, Feneos	Biometric, Pholidotic
97	NHMC	NHMC80.3.54.196	Mati beach, Feneos	Biometric, Pholidotic
98	NHMC	NHMC80.3.54.203	Kandila	Pholidotic
99	NHMC	NHMC80.3.54.204	Tripoli	Pholidotic
100	NHMC	NHMC80.3.54.205	Megalopoli	Pholidotic

101	NHMC	NHMC80.3.54.206	Karitaina	Pholidotic
102	NHMC	NHMC80.3.54.207	Alevrou	Pholidotic
103	NHMC	NHMC80.3.54.208	Alevrou	Pholidotic
104	NHMC	NHMC80.3.54.210	Platiana	Pholidotic
105	NHMC	NHMC80.3.54.211	Aspra Spitia	Pholidotic
106	NHMC	NHMC80.3.54.212	Doxa lake	Pholidotic
107	NHMC	NHMC80.3.54.213	Doxa lake	Pholidotic
108	NHMC	NHMC80.3.54.214	Likouria	Pholidotic
109	NHMC	NHMC80.3.54.215	Likouria	Pholidotic
110	NMW	11555.1	Olymbia	Pholidotic
111	NMW	11555.2	Olymbia	Biometric, Pholidotic
112	NMW	11555.3	Olymbia	Biometric, Pholidotic
113	NMW	11555.5	Olymbia	Biometric, Pholidotic
114	NMW	11557.1	Olymbia	Biometric, Pholidotic
115	NMW	11557.2	Olymbia	Biometric, Pholidotic
116	NMW	11557.3	Olymbia	Pholidotic
117	NMW	11557.4	Olymbia	Pholidotic
118	NMW	11560.1	Alagonia	Biometric, Pholidotic
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120	NMW	11560.3	Alagonia	Biometric, Pholidotic
121	NMW	11560.4	Alagonia	Biometric, Pholidotic
122	NMW	11560.5	Alagonia	Biometric, Pholidotic
123	NMW	11562.1	Kalamata	Biometric, Pholidotic
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126	NMW	11562.4	Kalamata	Biometric, Pholidotic
127	NMW	11562.5	Kalamata	Pholidotic
128	NMW	11562.6	Kalamata	Biometric, Pholidotic
129	NMW	11562.7	Kalamata	Biometric, Pholidotic
130	NMW	11562.8	Kalamata	Biometric, Pholidotic
131	NMW	11562.9	Kalamata	Biometric, Pholidotic
132	NMW	11562.10	Kalamata	Biometric, Pholidotic
133	NMW	11563	Kalamata	Biometric, Pholidotic
134	NMW	11564.1	Kalamata	Biometric, Pholidotic
135	NMW	11564.2	Kalamata	Biometric
136	NMW	11564.3	Kalamata	Biometric, Pholidotic

137	NMW	11564.4	Kalamata	Biometric, Pholidotic
138	NMW	11567.1	Sparti	Biometric, Pholidotic
139	NMW	11567.2	Sparti	Biometric, Pholidotic
140	NMW	11567.3	Sparti	Pholidotic
141	NMW	17101.1	Olymbia	Biometric, Pholidotic
142	NMW	17101.2	Olymbia	Biometric, Pholidotic
143	NMW	26365.3	Achladokampos	Biometric, Pholidotic
144	NMW	26365.4	Achladocampos	Biometric
145	NMW	26365.5	Achladocampos	Biometric
146	NMW	26365.6	Achladokampos	Biometric, Pholidotic
147	NMW	26365.7	Achladokampos	Biometric, Pholidotic
148	NMW	26365.8	Achladokampos	Biometric, Pholidotic
149	NMW	26395.1	Kato Figaleia	Biometric, Pholidotic
150	NMW	26395.3	Kato Figaleia	Biometric, Pholidotic
151	NMW	26395.8	Kato Figaleia	Biometric, Pholidotic
152	NMW	26395.10	Kato Figaleia	Biometric, Pholidotic
153	NMW	26395.11	Kato Figaleia	Biometric, Pholidotic
154	NMW	26395.12	Kato Figaleia	Biometric, Pholidotic
155	NMW	26395.14	Kato Figaleia	Biometric, Pholidotic
156	NMW	26395.17	Kato Figaleia	Biometric, Pholidotic
157	NMW	26396.3	Kyllini mountain.	Biometric, Pholidotic
158	NMW	26396.5	Kyllini	Biometric
159	NMW	26396.6	Kyllini mountain.	Biometric, Pholidotic
160	NMW	26396.8	Kyllini	Biometric
161	NMW	26415.5	Kalavryta	Biometric, Pholidotic
162	NMW	26415.1	Kalavryta	Biometric, Pholidotic
163	NMW	26415.11	Kalavryta	Biometric, Pholidotic
164	NMW	26415.12	Kalavryta	Biometric, Pholidotic
165	NMW	26415.13	Kalavryta	Biometric, Pholidotic
166	NMW	26415.14	Kalavryta	Biometric, Pholidotic
167	NMW	26415.15	Kalavryta	Biometric, Pholidotic
168	NMW	26426.2	Monemvasia	Biometric, Pholidotic
169	NMW	26426.3	Monemvasia	Biometric, Pholidotic
170	NMW	26426.4	Monemvasia	Biometric, Pholidotic
171	NMW	26426.5	Monemvasia	Biometric, Pholidotic
172	NMW	26426.6	Monemvasia	Biometric, Pholidotic

173	NMW	26426.7	Monemvasia	Biometric, Pholidotic
174	NMW	26426.8	Monemvasia	Biometric, Pholidotic
175	NMW	26426.11	Monemvasia	Biometric, Pholidotic
176	NMW	26426.12	Monemvasia	Biometric, Pholidotic
177	NMW	26426.13	Monemvasia	Biometric, Pholidotic
178	NMW	26426.14	Monemvasia	Biometric, Pholidotic
179	NMW	26426.15	Monemvasia	Biometric, Pholidotic
180	NMW	26426.17	Monemvasia	Biometric, Pholidotic
181	NMW	26439.2	Olymbia	Biometric, Pholidotic
182	NMW	26439.3	Olymbia	Biometric, Pholidotic
183	NMW	26439.4	Olymbia	Biometric, Pholidotic
184	NMW	26439.5	Olymbia	Biometric, Pholidotic
185	NMW	26439.6	Olymbia	Biometric, Pholidotic
186	NMW	26439.8	Olymbia	Biometric, Pholidotic
187	NMW	26439.9	Olymbia	Biometric, Pholidotic
188	NMW	26439.1	Olymbia	Biometric, Pholidotic
189	NMW	26439.11	Olymbia	Biometric, Pholidotic
190	NMW	26439.14	Olymbia	Biometric, Pholidotic
191	NMW	26452.3	Megalopoli	Biometric, Pholidotic
192	NMW	26452.4	Megalopoli	Biometric, Pholidotic
193	NMW	26452.5	Megalopoli	Biometric, Pholidotic
194	NMW	26452.6	Megalopoli	Biometric, Pholidotic
195	NMW	26452.7	Megalopoli	Biometric, Pholidotic
196	NMW	26452.8	Megalopoli	Biometric, Pholidotic
197	NMW	26452.10	Megalopoli	Biometric, Pholidotic
198	NMW	26478.5	Sparti	Biometric, Pholidotic
199	NMW	26478.6	Sparti	Biometric, Pholidotic
200	NMW	26478.7	Sparti	Biometric, Pholidotic
201	NMW	26478.8	Sparti	Biometric, Pholidotic
202	NMW	26478.9	Sparti	Biometric, Pholidotic
203	NMW	26478.10	Sparti	Biometric, Pholidotic
204	NMW	26478.11	Sparti	Biometric, Pholidotic
205	NMW	26478.12	Sparti	Biometric, Pholidotic
206	NMW	26478.13	Sparti	Biometric, Pholidotic
207	NMW	28847.15	Mati beach, Feneos	Biometric, Pholidotic
208	NMW	28847.16	Mati beach, Feneos	Biometric, Pholidotic

209	NMW	28847.17	Mati beach, Feneos	Biometric, Pholidotic
210	NMW	28847.18	Mati beach, Feneos	Biometric, Pholidotic
211	NMW	28847.19	Mati beach, Feneos	Biometric, Pholidotic
212	NMW	28847.2	Mati beach, Feneos	Biometric, Pholidotic
213	NMW	28847.22	Mati beach, Feneos	Biometric, Pholidotic
214	NMW	28847.23	Mati beach, Feneos	Biometric, Pholidotic
215	NMW	28848.1	Achladokampos	Biometric, Pholidotic
216	NMW	28848.2	Achladokampos	Biometric, Pholidotic
217	NMW	28848.5	Achladokampos	Biometric, Pholidotic
218	NMW	28848.6	Achladokampos	Biometric, Pholidotic
219	NMW	28848.8	Achladokampos	Biometric, Pholidotic
220	NMW	28851.1	Megalopoli	Biometric, Pholidotic
221	NMW	28868.1	Kalavryta	Biometric, Pholidotic
222	NMW	28868.2	Kalavryta	Biometric, Pholidotic
223	NMW	28868.3	Kalavryta	Biometric, Pholidotic
224	NMW	28868.4	Kalavryta	Biometric, Pholidotic
225	NMW	31104.2	Kyllini mountain	Biometric, Pholidotic
226	NMW	31104.4	Kyllini mountain	Biometric, Pholidotic
227	NMW	31104.5	Kyllini mountain	Biometric, Pholidotic
228	NMW	31104.6	Kyllini mountain	Biometric, Pholidotic
229	NMW	31104.7	Kyllini mountain	Biometric, Pholidotic
230	NMW	31104.8	Kyllini mountain	Biometric, Pholidotic
231	NMW	31365.8	Mati beach, Feneos	Biometric, Pholidotic
232	NMW	31365.9	Mati beach, Feneos	Biometric, Pholidotic
233	NMW	31365.1	Mati beach, Feneos	Biometric, Pholidotic
234	NMW	36286.2	Olymbia	Biometric, Pholidotic
235	NMW	36286.3	Olymbia	Biometric, Pholidotic
236	NMW	36286.4	Olymbia	Biometric, Pholidotic
237	NMW	36286.8	Olymbia	Biometric, Pholidotic
238	NMW	36286.9	Olymbia	Biometric, Pholidotic
239	NMW	36286.10	Olymbia	Biometric, Pholidotic
240	NMW	36286.12	Megalopoli	Biometric, Pholidotic
241	NMW	36286.13	Megalopoli	Biometric, Pholidotic
242	NMW	36286.14	Megalopoli	Biometric, Pholidotic
243	NMW	36286.15	Megalopoli	Biometric, Pholidotic
244	NMW	36286.16	Megalopoli	Biometric, Pholidotic

245	NMW	36286.17	Megalopoli	Biometric, Pholidotic
246	NMW	36286.18	Megalopoli	Biometric, Pholidotic
247	NMW	36286.19	Megalopoli	Biometric, Pholidotic
248	NMW	36286.20	Vasses, Apollo Temple	Biometric, Pholidotic
249	NMW	36286.21	Methoni	Biometric, Pholidotic
250	NMW	36286.22	Methoni	Biometric, Pholidotic
251	NMW	36286.23	Methoni	Biometric, Pholidotic
252	NMW	36286.24	Methoni	Biometric, Pholidotic
253	NMW	36286.25	Methoni	Biometric, Pholidotic
254	NMW	36286.26	Methoni	Biometric, Pholidotic
255	NMW	36286.27	Methoni	Biometric, Pholidotic
256	NMW	36286.28	Methoni	Biometric, Pholidotic
257	NMW	26365.4	Achladocampos	Pholidotic
258	NMW	26365.5	Achladocampos	Pholidotic
259	NMW	26396.5	Kyllini mountain	Biometric
260	NMW	26396.8	Kyllini mountain	Biometric
261	NHMUK	1972.109	Tripi, Sparti	Biometric
262	NHMUK	1972.1322	Sparti	Biometric
263	NHMUK	1904.10.31.22	Kalamata	Biometric
264	NHMUK	1917.5.11.33	Kalamata	Biometric
265	NHMUK	1917.5.11.34	Kalamata	Biometric
266	NHMUK	83.7.30.1	Kalamata	Biometric
267	NHMUK	83.7.30.2	Kalamata	Biometric
268	NHMUK	92.9.19.13	Kalamata	Biometric
269	NHMUK	92.9.19.14	Kalamata	Biometric
270	NHMUK	1972.1087	Tripi, Sparti	Biometric
271	NHMUK	1972.1088	Tripi, Sparti	Biometric
272	NHMUK	1972.1089	Tripi, Sparti	Biometric
273	NHMUK	1972.1092	Mykenae	Biometric
274	NHMUK	1972.1093	Mykenae	Biometric
275	NHMUK	1972.1224	Sparti	Biometric
276	NHMUK	1904.10.21.23	Olymbia	Biometric
277	NHMUK	1904.10.21.24	Olymbia	Biometric
278	AK	pelEF1	Argos	Biometric, Pholidotic
279	AK	pelEF2	Argos	Biometric, Pholidotic
280	AK	pelEF3	Argos	Biometric, Pholidotic

281	AK	pelEF4	Argos	Biometric, Pholidotic
282	AK	pelEF5	Argos	Biometric, Pholidotic
283	AK	pelEF6	Argos	Biometric, Pholidotic
284	AK	pelEF7	Argos	Biometric, Pholidotic
285	AK	pelEF8	Argos	Biometric, Pholidotic
286	AK	pelEF9	Argos	Biometric, Pholidotic
287	AK	pelEF10	Argos	Biometric, Pholidotic
288	AK	pelEF11	Argos	Biometric, Pholidotic
289	AK	pelEF12	Argos	Biometric, Pholidotic
290	AK	pelEF13	Argos	Biometric, Pholidotic
291	AK	pelEF14	Argos	Biometric, Pholidotic
292	AK	pelEF15	Argos	Biometric, Pholidotic
293	AK	pelEF16	Argos	Biometric, Pholidotic
294	AK	pelEF17	Argos	Biometric, Pholidotic
295	AK	pelEF18	Argos	Biometric, Pholidotic
296	AK	pelEM1	Argos	Biometric, Pholidotic
297	AK	pelEM2	Argos	Biometric, Pholidotic
298	AK	pelEM3	Argos	Biometric, Pholidotic
299	AK	pelEM4	Argos	Biometric, Pholidotic
300	AK	pelEM5	Argos	Biometric, Pholidotic
301	AK	pelEM6	Argos	Biometric, Pholidotic
302	AK	pelEM7	Argos	Biometric, Pholidotic
303	AK	pelEM8	Argos	Biometric, Pholidotic
304	AK	pelEM9	Argos	Biometric, Pholidotic
305	AK	pelEM10	Argos	Biometric, Pholidotic
306	AK	pelEM11	Argos	Biometric, Pholidotic
307	AK	pelEM12	Argos	Biometric, Pholidotic
308	AK	pelEM13	Argos	Biometric, Pholidotic
309	AK	pelEM14	Argos	Biometric, Pholidotic
310	AK	pelEM15	Argos	Biometric, Pholidotic
311	AK	pelEM16	Argos	Biometric, Pholidotic
312	AK	pelEM17	Argos	Biometric, Pholidotic
313	AK	pelEM18	Argos	Biometric, Pholidotic
314	AK	pelEM19	Argos	Biometric, Pholidotic
315	AK	pelEM20	Argos	Biometric, Pholidotic
316	AK	pelEM21	Argos	Biometric, Pholidotic

317	AK	pelWF1	Doxa lake	Biometric, Pholidotic
318	AK	pelWF2	Doxa lake	Biometric, Pholidotic
319	AK	pelWF3	Doxa lake	Biometric, Pholidotic
320	AK	pelWF4	Doxa lake	Biometric, Pholidotic
321	AK	pelWF5	Doxa lake	Biometric, Pholidotic
322	AK	pelWF6	Doxa lake	Biometric, Pholidotic
323	AK	pelWF7	Doxa lake	Biometric, Pholidotic
324	AK	pelWF8	Doxa lake	Biometric, Pholidotic
325	AK	pelWF9	Doxa lake	Biometric, Pholidotic
326	AK	pelWF10	Doxa lake	Biometric, Pholidotic
327	AK	pelWF11	Doxa lake	Biometric, Pholidotic
328	AK	pelWF12	Doxa lake	Biometric, Pholidotic
329	AK	pelWF13	Doxa lake	Biometric, Pholidotic
330	AK	pelWF14	Doxa lake	Biometric, Pholidotic
331	AK	pelWF15	Doxa lake	Biometric, Pholidotic
332	AK	pelWF16	Doxa lake	Biometric, Pholidotic
333	AK	pelWF17	Doxa lake	Biometric, Pholidotic
334	AK	pelWF18	Doxa lake	Biometric, Pholidotic
335	AK	pelWM1	Doxa lake	Biometric, Pholidotic
336	AK	pelWM2	Doxa lake	Biometric, Pholidotic
337	AK	pelWM3	Doxa lake	Biometric, Pholidotic
338	AK	pelWM4	Doxa lake	Biometric, Pholidotic
339	AK	pelWM5	Doxa lake	Biometric, Pholidotic
340	AK	pelWM6	Doxa lake	Biometric, Pholidotic
341	AK	pelWM7	Doxa lake	Biometric, Pholidotic
342	AK	pelWM8	Doxa lake	Biometric, Pholidotic
343	AK	pelWM9	Doxa lake	Biometric, Pholidotic
344	AK	pelWM10	Doxa lake	Biometric, Pholidotic
345	AK	pelWM11	Doxa lake	Biometric, Pholidotic
346	AK	pelWM12	Doxa lake	Biometric, Pholidotic
347	AK	pelWM13	Doxa lake	Biometric, Pholidotic
348	AK	pelWM14	Doxa lake	Biometric, Pholidotic
349	AK	pelWM15	Doxa lake	Biometric, Pholidotic
350	AK	pelWM16	Doxa lake	Biometric, Pholidotic
351	AK	pelWM17	Doxa lake	Biometric, Pholidotic
352	AK	pelWM18	Doxa lake	Biometric, Pholidotic

353	AK	pelWM19	Doxa lake	Biometric, Pholidotic
354	AK	pelWM20	Doxa lake	Biometric, Pholidotic
355	AK	pelWM21	Doxa lake	Biometric, Pholidotic

Table S4. The selected models of nucleotide subsitutions. Models of nucleotide substitution for each block and for the 2 analyses of each dataset (mtDNA, nDNA and concatenated DNA).

mtDNA			
RaxML		MrBayes	
Partition name	Best subset	Partition name	Best subset
cytb_pos2	GTR	cytb_pos2	HKY+G
cytb_pos1, 16s, cytb_pos3	GTR+G	cytb_pos3, 16s	HKY+G
		cytb_pos1	JC
nDNA			
RaxML		MrBayes	
Partition name	Best subset	Partition name	Best subset

mc1r_pos2, pod55, mc1r_pos1, ubn1_pos2	GTR+I	nktr_pos1, nktr_pos2, rag1_pos2, nktr_pos3, rag1_pos3, pod55, rag1_pos1, mc1r_pos1, ubn1_pos2	HKY+I
mc1r_pos3, ubn1_pos3, ubn1_pos1	GTR	mc1r_pos3	HKY+I
pod15, nktr_pos1, rag1_pos2, nktr_pos2, rag1_pos3, rag1_pos1, nktr_pos3	GTR+I	mc1r_pos2 pod15 ubn1_pos1, ubn1_pos3	F81 JC HKY

Concatenated DNA			
RaxML		Bayes	
Partition name	Best subset	Partition name	Best subset
cytb_pos2, 16s, cytb_pos1	GTR+I	cytb_pos2	JC
cytb_pos3	СТР	cytb_pos3	HKY
	UIK	16s, cytb_pos1	HKY+I
mc1r_pos2, mc1r_pos1, ubn1_pos2, pod55	GTR+I	nktr_pos1, nktr_pos2, rag1_pos2, rag1_pos1, pod55, nktr_pos3, rag1_pos3, mc1r_pos1, ubn1_pos2	HKY+I
mc1r_pos3, ubn1_pos3,	СТР	mc1r_pos3	HKY
ubn1_pos1	GIR	mc1r_pos2	F81
pod15, nktr_pos1, rag1_pos2, nktr_pos2,	GTR+I	pod15	JC
rag1_pos5, nktr_pos5, rag1_pos1		ubn1_pos1, ubn1_pos3	HKY

	Cla	de 1	Cla	nde 2
	Females	Males	Females	Males
SVL	70.84 ± 1.28	74.30 ± 1.09	71.77 ± 2.05	73.95 ± 1.53
	56.51 - 82.73	56.27 - 86.14	57.25 - 86.91	60.34 - 85.89
TRL	37.51 ± 1.06	34.97 ± 0.69	39.93 ± 1.62	35.75 ± 0.96
	26.67 - 51.16	24.60 - 43.80	28.79 - 52.54	26.77 - 43.80
HL	21.53 ± 0.31	25.85 ± 0.39	21.52 ± 0.52	25.00 ± 0.66
	18.19 - 24.73	21.12 - 31.25	17.58 - 25.00	20.10 - 30.48
PL	15.39 ± 0.23	18.61 ± 0.30	15.06 ± 0.31	17.79 ± 0.41
	12.73 - 17.37	14.56 - 25.68	12.71 - 17.03	14.75 - 20.60
HW	9.66 ± 0.15	11.78 ± 0.20	9.54 ± 0.22	11.33 ± 0.26
	7.92 - 11.38	8.87 - 14.10	8.06 - 10.95	9.13 - 13.85
HH	7.84 ± 0.15	9.58 ± 0.19	7.86 ± 0.20	9.34 ± 0.23
	6.13 - 9.34	7.08 - 12.49	6.40 - 9.41	7.15 - 11.20
MO	13.76 ± 0.21	16.52 ± 0.26	13.36 ± 0.30	15.80 ± 0.35
	11.15 - 15.68	12.84 - 19.42	11.39 - 15.25	12.84 - 18.77
FLL	22.01 ± 0.32	25.25 ± 0.36	21.78 ± 0.42	25.25 ± 0.49
	17.32 - 25.33	18.68 - 28.74	18.40 - 24.60	20.90 - 28.66
HFL	38.42 ± 0.49	44.82 ± 0.58	38.07 ± 0.66	43.67 ± 0.80
	32.89 - 44.09	36.96 - 50.73	32.74 - 41.63	36.29 - 48.77
CSN	11.10 ± 0.26	11.09 ± 0.20	10.06 ± 0.29	10.31 ± 0.27
	8 - 14	8 - 14	8 - 12	7 - 13
GSN	29.95 ± 0.43	30.73 ± 0.41	30.67 ± 0.68	31.90 ± 0.55
	25 - 36	24 - 37	25 - 37	26 - 37
VSN	32.11 ± 0.21	29.63 ± 0.17	32.07 ± 0.29	30.23 ± 0.21
	29 - 35	28 - 33	29 - 34	28 - 32
FPN	20.99 ± 0.23	22.23 ± 0.28	22.60 ± 0.53	23.69 ± 0.35
	18 - 24	18 - 26	17 - 27	20 - 28
SDLN	28.91 ± 0.29	29.63 ± 0.24	28.86 ± 0.40	29.53 ± 0.44
	26 - 32	26 - 33	26 - 33	22 - 34

Table S5. Descriptive statistics for males and females of the two clades of *P. peloponnesiacus*, for biometric and continuous pholidotic traits. Values are mean \pm 95% confidence interval (top), and range (bottom) (see Materials & Methods for variable abbreviations).

Tables S6 & S7. Discriminant vector composition (Table S6) and percentages of correct classification based on a leave-one-out cross-validation procedure (Table S7) for the discrimination of the two clades of *P. peloponnesiacus* based on (size-corrected) linear biometric and continuous pholidotic traits, for each sex separately (see Materials and Methods for variable abbreviations).

LINEA	R BIOME	FRIC	CONTINUOUS PHOLIDOTIC					
	F	М		F	М			
SVL	-1.42	0.72	CSN	0.50	0.45			
cor_TRL	-18.17	-1.28	SDLN	0.05	0.12			
cor_HL	-11.25	2.61	GSN	-0.04	-0.06			
cor_PL	10.36	6.48	VSN	-0.02	-0.46			
cor_HW	-6.55	8.33	FPN	-0.51	-0.45			
cor_HH	-4.48	-6.30						
cor_MO	18.42	15.35						
cor_FLL	0.28	-9.84						
cor_HFL	-5.26	2.93						

Table S6

Table S7

LINEA	AR BI	OMETRI	С	CONTINUOUS PHOLIDOTIC					
F		classifie	ed as	F		classifie	ed as		
		1	2			1	2		
observed	1	86.36	13.64	observed	1	88.30	11.70		
	2	36.96	63.04		2	44.23	55.77		
Μ		classi	fied as	М		classi	fied as		
		1	2			1	2		
observed	1	86.61	13.39	observed	1	81.74	18.26		
	2	57.63	42.37		2	40.85	59.15		

	settings	features	rm	train. AUC	avg.test.	var.test.	avg.diff. AUC	var.diff. AUC	avg.test. or MTP	var.test. orMTP	avg.test. or10pct	var.test. or10pct	AICc	delta AICc	w.AIC	narameters
9	LOH 1.5	LOH	1.500	0.792	0.743	0.006	0.056	0.006	0.050	0.010	0.175	0.016	872.496	0.000	0.164	9
1	L 1	L	1,000	0,770	0,755	0,004	0,032	0,002	0,050	0,003	0,150	0,017	872,605	0,110	0,155	4
6	L_1.5	L	1,500	0,770	0,758	0,003	0,029	0,001	0,050	0,003	0,150	0,017	872,909	0,413	0,133	4
11	L_2	L	2,000	0,770	0,759	0,003	0,027	0,001	0,050	0,003	0,125	0,016	873,344	0,849	0,107	4
16	L_2.5	L	2,500	0,770	0,756	0,003	0,027	0,001	0,050	0,003	0,125	0,016	873,913	1,418	0,081	4
21	L_3	L	3,000	0,768	0,754	0,003	0,027	0,001	0,050	0,003	0,125	0,016	874,597	2,102	0,057	4
26	L_3.5	L	3,500	0,767	0,751	0,002	0,027	0,001	0,050	0,003	0,125	0,016	875,133	2,637	0,044	4
7	LQ_1.5	LQ	1,500	0,771	0,752	0,004	0,036	0,002	0,050	0,003	0,175	0,023	875,553	3,058	0,035	5
31	L_4	L	4,000	0,765	0,748	0,002	0,026	0,001	0,050	0,003	0,100	0,007	875,753	3,258	0,032	4
12	LQ_2	LQ	2,000	0,770	0,750	0,004	0,035	0,002	0,050	0,003	0,175	0,023	876,259	3,763	0,025	5
36	L_4.5	L	4,500	0,764	0,744	0,001	0,026	0,001	0,050	0,003	0,125	0,009	876,468	3,972	0,022	4
30	LQHP_3.5	LQHP	3,500	0,767	0,715	0,004	0,050	0,005	0,075	0,009	0,175	0,016	877,161	4,665	0,016	4
17	LQ_2.5	LQ	2,500	0,768	0,747	0,003	0,035	0,002	0,050	0,003	0,175	0,023	877,178	4,683	0,016	5
41	L_5	L	5,000	0,762	0,739	0,001	0,024	0,001	0,050	0,003	0,150	0,010	877,272	4,777	0,015	4
22	LQ_3	LQ	3,000	0,766	0,743	0,003	0,034	0,002	0,050	0,003	0,175	0,023	877,885	5,390	0,011	5
24	LQH_3	LQH	3,000	0,766	0,742	0,003	0,037	0,002	0,050	0,003	0,175	0,023	877,885	5,390	0,011	5
25	LQHP_3	LQHP	3,000	0,770	0,716	0,005	0,056	0,006	0,075	0,009	0,175	0,016	877,988	5,493	0,011	5
40	LQHP_4.5	LQHP	4,500	0,757	0,701	0,005	0,044	0,007	0,050	0,010	0,100	0,020	878,678	6,182	0,007	3
27	LQ_3.5	LQ	3,500	0,765	0,738	0,002	0,033	0,002	0,050	0,003	0,125	0,009	878,709	6,214	0,007	5
29	LQH_3.5	LQH	3,500	0,765	0,739	0,002	0,033	0,002	0,050	0,003	0,125	0,009	878,733	6,237	0,007	5
35	LQHP_4	LQHP	4,000	0,762	0,709	0,005	0,048	0,006	0,075	0,009	0,175	0,016	879,121	6,626	0,006	4
2	LQ_1	LQ	1,000	0,773	0,748	0,004	0,041	0,002	0,050	0,003	0,150	0,017	879,140	6,644	0,006	7
42	LQ_5	LQ	5,000	0,757	0,727	0,001	0,023	0,002	0,075	0,009	0,150	0,010	879,515	7,019	0,005	4

Table S8. SDM for *Podarcis peloponnesiacus* **west (Clade 1).** The results of the MaxEn Model using Wallace R package for *Podarcis peloponnesiacus* west (Clade 1). With yellow mark, the model with the lowest delta.AICc.

44	LQH_5	LQH	5,000	0,757	0,727	0,001	0,023	0,002	0,075	0,009	0,150	0,010	879,515	7,019	0,005	4
32	LQ_4	LQ	4,000	0,763	0,732	0,001	0,031	0,002	0,050	0,003	0,150	0,010	879,710	7,215	0,004	5
43	H_5	Н	5,000	0,725	0,723	0,000	0,010	0,001	0,025	0,003	0,125	0,023	879,803	7,307	0,004	1
39	LQH_4.5	LQH	4,500	0,760	0,729	0,001	0,028	0,002	0,050	0,003	0,150	0,010	880,867	8,371	0,002	5
38	H_4.5	Н	4,500	0,722	0,723	0,000	0,010	0,001	0,025	0,003	0,125	0,023	880,950	8,455	0,002	2
14	LQH_2	LQH	2,000	0,784	0,743	0,005	0,049	0,004	0,050	0,010	0,175	0,023	881,598	9,102	0,002	10
33	H_4	Н	4,000	0,731	0,723	0,000	0,011	0,001	0,025	0,003	0,100	0,013	881,910	9,415	0,001	3
19	LQH_2.5	LQH	2,500	0,777	0,742	0,004	0,046	0,003	0,050	0,003	0,175	0,023	882,241	9,746	0,001	8
34	LQH_4	LQH	4,000	0,763	0,732	0,001	0,031	0,002	0,050	0,003	0,150	0,010	882,488	9,992	0,001	6
45	LQHP_5	LQHP	5,000	0,752	0,698	0,006	0,042	0,007	0,050	0,010	0,100	0,020	883,245	10,750	0,001	4
37	LQ_4.5	LQ	4,500	0,760	0,729	0,001	0,028	0,002	0,050	0,003	0,150	0,010	883,601	11,105	0,001	6
28	H_3.5	Н	3,500	0,740	0,725	0,001	0,012	0,001	0,025	0,003	0,125	0,023	885,496	13,001	0,000	5
18	H_2.5	Н	2,500	0,783	0,728	0,000	0,047	0,002	0,075	0,009	0,175	0,016	885,937	13,441	0,000	9
20	LQHP_2.5	LQHP	2,500	0,778	0,717	0,006	0,065	0,007	0,100	0,020	0,175	0,016	886,229	13,733	0,000	9
15	LQHP_2	LQHP	2,000	0,783	0,726	0,006	0,063	0,007	0,100	0,020	0,175	0,016	886,515	14,019	0,000	11
8	H_1.5	Н	1,500	0,795	0,744	0,003	0,055	0,005	0,100	0,013	0,175	0,016	888,448	15,953	0,000	13
23	H_3	Н	3,000	0,755	0,727	0,001	0,026	0,001	0,075	0,009	0,125	0,023	890,625	18,129	0,000	8
13	H_2	Н	2,000	0,788	0,739	0,001	0,047	0,003	0,100	0,013	0,175	0,016	894,075	21,580	0,000	13
10	LQHP_1.5	LQHP	1,500	0,790	0,736	0,005	0,061	0,006	0,100	0,020	0,175	0,016	899,193	26,698	0,000	15
5	LQHP_1	LQHP	1,000	0,811	0,743	0,004	0,063	0,007	0,075	0,009	0,175	0,016	961,358	88,863	0,000	24
3	H_1	Н	1,000	0,812	0,746	0,003	0,064	0,006	0,075	0,009	0,175	0,016	974,984	102,488	0,000	25
4	LQH_1	LQH	1,000	0,811	0,742	0,004	0,064	0,007	0,075	0,009	0,175	0,016	1008,467	135,971	0,000	27

	settings	features	rm	train. AUC	avg.test. AUC	var.test. AUC	avg.diff. AUC	var.diff. AUC	avg.test. orMTP	var.test. orMTP	avg.test. or10pct	var.test. or10pct	AICc	delta.AICc	w.AIC	parameters
2	LQ_1	LQ	1,000	0,880	0,592	0,000	0,200	0,001	0,472	0,002	0,472	0,002	363,876	0,000	0,563	6
1	L_1	L	1,000	0,858	0,571	0,000	0,214	0,001	0,472	0,002	0,472	0,002	367,066	3,190	0,114	5
20	LQHP_2.5	LQHP	2,500	0,829	0,627	0,001	0,140	0,002	0,111	0,025	0,299	0,012	367,437	3,562	0,095	4
25	LQHP_3	LQHP	3,000	0,816	0,631	0,000	0,114	0,003	0,111	0,025	0,292	0,003	367,692	3,816	0,084	3
23	H_3	Н	3,000	0,777	0,631	0,000	0,114	0,003	0,111	0,025	0,292	0,003	370,521	6,645	0,020	3
24	LQH_3	LQH	3,000	0,777	0,579	0,005	0,152	0,008	0,222	0,099	0,403	0,047	370,521	6,645	0,020	3
12	LQ_2	LQ	2,000	0,796	0,575	0,006	0,142	0,009	0,278	0,154	0,403	0,047	372,271	8,395	0,008	4
19	LQH_2.5	LQH	2,500	0,822	0,608	0,002	0,158	0,004	0,167	0,056	0,410	0,002	372,599	8,723	0,007	5
11	L_2	L	2,000	0,705	0,565	0,007	0,143	0,009	0,278	0,154	0,403	0,047	373,181	9,305	0,005	2
22	LQ_3	LQ	3,000	0,705	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	373,395	9,519	0,005	2
34	LQH_4	LQH	4,000	0,720	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	373,467	9,591	0,005	2
33	H_4	Н	4,000	0,720	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	373,467	9,591	0,005	2
7	LQ_1.5	LQ	1,500	0,843	0,567	0,001	0,198	0,000	0,410	0,002	0,528	0,002	373,542	9,666	0,004	6
43	H_5	Н	5,000	0,682	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	373,560	9,684	0,004	1
44	LQH_5	LQH	5,000	0,682	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	373,560	9,684	0,004	1
45	LQHP_5	LQHP	5,000	0,682	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	373,560	9,684	0,004	1
31	L_4	L	4,000	0,500	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	373,622	9,746	0,004	0
36	L_4.5	L	4,500	0,500	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	373,622	9,746	0,004	0
41	L_5	L	5,000	0,500	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	373,622	9,746	0,004	0
28	H_3.5	Н	3,500	0,756	0,661	0,000	0,052	0,000	0,056	0,006	0,292	0,003	373,678	9,803	0,004	3
29	LQH_3.5	LQH	3,500	0,756	0,565	0,007	0,150	0,008	0,278	0,154	0,403	0,047	373,678	9,803	0,004	3
18	H_2.5	Н	2,500	0,805	0,627	0,001	0,140	0,002	0,111	0,025	0,299	0,012	373,983	10,107	0,004	5
27	LQ_3.5	LQ	3,500	0,704	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	374,393	10,518	0,003	2

Table S9. SDM for *Podarcis peloponnesiacus* **east** (Clade 2). The results of the MaxEn Model using Wallace R package for *Podarcis peloponnesiacus* west (Clade 2). With yellow mark, the model with the lowest delta.AICc.

16	L_2.5	L	2,500	0,704	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	374,615	10,739	0,003	2
38	H_4.5	Н	4,500	0,707	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	374,882	11,007	0,002	2
39	LQH_4.5	LQH	4,500	0,707	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	374,882	11,007	0,002	2
40	LQHP_4.5	LQHP	4,500	0,707	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	374,882	11,007	0,002	2
17	LQ_2.5	LQ	2,500	0,709	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	375,257	11,381	0,002	3
30	LQHP_3.5	LQHP	3,500	0,788	0,661	0,000	0,052	0,000	0,056	0,006	0,292	0,003	375,480	11,604	0,002	4
32	LQ_4	LQ	4,000	0,703	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	375,575	11,699	0,002	2
42	LQ_5	LQ	5,000	0,685	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	375,758	11,882	0,001	1
26	L_3.5	L	3,500	0,685	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	375,874	11,998	0,001	1
35	LQHP_4	LQHP	4,000	0,722	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	376,282	12,407	0,001	3
6	L_1.5	L	1,500	0,741	0,565	0,004	0,177	0,003	0,285	0,051	0,465	0,016	376,305	12,429	0,001	4
21	L_3	L	3,000	0,703	0,489	0,000	0,119	0,014	0,278	0,154	0,278	0,154	376,433	12,557	0,001	2
15	LQHP_2	LQHP	2,000	0,860	0,623	0,000	0,173	0,001	0,111	0,025	0,299	0,012	376,682	12,806	0,001	7
37	LQ_4.5	LQ	4,500	0,697	0,500	0,000	0,000	0,000	0,000	0,000	0,000	0,000	376,953	13,077	0,001	2
14	LQH_2	LQH	2,000	0,863	0,613	0,001	0,180	0,001	0,167	0,056	0,354	0,001	406,493	42,618	0,000	10
13	H_2	Н	2,000	0,862	0,623	0,000	0,173	0,001	0,111	0,025	0,299	0,012	406,860	42,984	0,000	10
8	H_1.5	Н	1,500	0,893	0,655	0,000	0,181	0,001	0,167	0,056	0,472	0,002	415,885	52,009	0,000	11
10	LQHP_1.5	LQHP	1,500	0,894	0,655	0,000	0,181	0,001	0,167	0,056	0,472	0,002	443,181	79,305	0,000	12
3	H_1	Н	1,000	0,944	0,715	0,001	0,194	0,000	0,472	0,002	0,583	0,014	NA	NA	NA	24
4	LQH_1	LQH	1,000	0,942	0,727	0,000	0,185	0,001	0,472	0,002	0,583	0,014	NA	NA	NA	22
5	LQHP_1	LQHP	1,000	0,941	0,715	0,001	0,194	0,000	0,472	0,002	0,583	0,014	NA	NA	NA	24
9	LQH_1.5	LQH	1,500	0,904	0,647	0,000	0,187	0,001	0,167	0,056	0,472	0,002	NA	NA	NA	16

	variable	percent.contribution	permutation.importance
1	bio_15	68,4505	52,4383
2	bio_18	8,8284	24,9571
3	bio_19	1,4822	0,3146
4	bio_4	0	0
5	bio_5	4,7125	4,1616
6	bio_8	16,5264	18,1284

Table S10. The results of the variable importance test for *Podarcis peloponnesiacus* west (Clade 1).

Table S11. The results of the variable importance test for *Podarcis peloponnesiacus* east (Clade 2).

	variable	percent.contribution	permutation.importance
1	bio_15	22,1589	27,018
2	bio_18	21,2251	25,9072
3	bio_19	19,3834	29,0275
4	bio_4	2,628	7,5827
5	bio_5	0	0
6	bio_8	34,6047	10,4646