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Genetic and morphometric comparisons of populations of *Lacerta diplochondrodes* Wettstein, 1952 (Squamata: Lacertidae) in Türkiye

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The diverse climate types and geographical structures across Anatolia result in a high level of species diversity. Among these, the lizard species *Lacerta diplochondrodes* exhibits several distinct populations, with some of them recognized as subspecies. The primary objective of our study was to investigate whether populations from Thrace and the Western Black Sea region of Türkiye differ from other documented populations. For this purpose, we conducted a comprehensive analysis of genetic and morphometric parameters. For the genetic analysis, we utilized the *COI* and *cyt-b* gene regions as molecular markers. Principal Component Analysis (PCA) and Canonical Discriminant Analysis (CDA) were used for the morphometric analyses to differentiate populations. Our findings indicate that a population found in the Bolu region in Western Black Sea region of Turkey differs from the other populations both in morphometric and genetic traits. The *L. d. diplochondrodes* and *L. d. cariensis* populations represent sister lineages, and they are both genetically and morphologically only weakly differentiated. These two lineages are therefore referred to as *L. d. diplochondrodes*. Overall, four different lineages can be distinguished in Türkiye, out of which the lineage of the Western Black Sea region (Bolu lineage) is described for the first time.

Keywords: Anatolia; zoogeography; *COI; cyt-b;* lineages; morphometry; phylogeny

Introduction

Lacerta trilineata Bedriaga, 1886, the Balkan Green Lizard, is one of the largest species within the genus *Lacerta*, reaching up to 50 cm in total length (Anđelković et al., 2022). It is the most widespread lizard species in the Balkans (Sagonas et al., 2019) and occurs from northern Croatia along the Adriatic coast (including many islands) across Albania, North Macedonia, Serbia, Greece (including several of the larger Ionian and Aegean islands), Bulgaria, south-eastern Romania, to western Anatolia (Anđelković et al., 2022). Phylogenetic studies revealed that *Lacerta diplochondrodes* Wettstein, 1952 is a species distinct from *L. trilineata* (Kornilios et al., 2020). It took a long time to determine the taxonomic status of the populations found in Türkiye. Morphological (Baran, 1969; Bodenheimer, 1944; Çevik, 1999; Mertens, 1952; Mertens & Müller, 1940; Peters, 1964; Schmidtler, 1975) and genetic (Ahmadzadeh et al., 2013; Kornilios et al., 2019; Kornilios et al., 2020; Sagonas et al., 2014) studies in Anatolia and Thrace have been conducted on this species and many subspecies have been described. Based on morphological studies, the following subspecies of *Lacerta trilineata* were described: *L. t. cariensis* Peters, 1964, *L. t. ciliciensis* Schmidtler, 1975, *L. t. diplochondrodes* Wettstein, 1952, *L. t. dobrogica* Fuhn & Mertens, 1959, *L. t. galatiensis* Peters, 1964, *L.*

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t. isaurica Schmidtler, 1975, *L. t. media* Lantz & Cyrén, 1920, *L. t. pamphylica* Schmidtler, 1975, *L. t. trilineata* Bedriaga, 1886, and *L. t. wolterstorffi* Mertens, 1922 (Baran, 1969; Bodenheimer, 1944; Çevik, 1999; Mertens, 1952; Mertens & Müller, 1940; Peters, 1964; Schmidtler, 1975). *Lacerta t. media* and *L. t. pamphylica* were elevated to species rank in subsequent studies (Schmidtler, 1986) and *L. t. isaurica*, *L. t. media* and *L. t. wolterstorffi* were recognized as subspecies of *Lacerta media* Lantz & Cyrén, 1920 (Schmidtler, 1986). In a genetic study of the *L. trilineata*, samples from Ankara and Konya provinces in Türkiye were found to belong to *L. t. diplochondrodes* (Ahmadzadeh et al., 2013). *Lacerta trilineata* is thought to have originated in Anatolia, from where it passed to the Balkans (Ahmadzadeh et al., 2013; Kornilios et al., 2019; Sagonas et al., 2014). In a recent study, bioinformatics and phylogenetic analyzes of genomic "Single nucleotide polymorphisms" (SNP) sequences obtained with "Double digest restriction-site associated DNA" (ddRAD) data were used confirmed the presence of *L. diplochondrodes* in Türkiye (Kornilios et al., 2020). The Thrace population of *L. diplochondrodes* was assigned to *L. d. dobrogica*, the western Anatolian population to *L. d. cariensis*, the north-west and central Anatolia populations to *L. d. galatiensis*, and the Aegean population to *L. d. diplochondrodes* (Kornilios et al., 2020). The status of the Western Black Sea populations has so far not been examined. Our study aimed to find out, whether genetic differences between various populations of *L. diplochondrodes* are supported by morphometric data. For this purpose, we particularly analyzed the mitochondrial *COI* and c*yt-b* gene sequences of populations in the Western Black Sea and Western Taurus regions.

Material and Methods

Study area and sampling. A total of 46 samples were obtained from field surveys and museum collections (Table 1 in Supplementary material). Sampling was conducted between April and August 2016–2018 in western Anatolia (Bursa, Izmir, Konya, and Muğla provinces) and Thrace (Istanbul) (Figure 1). Specimens were collected on roadsides and forest edges throughout the daytime. We injected sodium pentobarbital intraperitoneally to euthanize the samples as approved by the Animal Experiments Local Ethics Committee of Istanbul University. All samples were preserved in 99% ethanol. In addition to the field surveys, samples were obtained from zoological collections of Çanakkale Onsekiz Mart University, Biology Department and Dokuz Eylül University, Biology Department.

DNA extractions and sequencing. DNA was isolated from the tail and tongue tissues of the samples. Genomic DNA was extracted using Qiagen DNeasy Blood & Tissue Kits following the manufacturer's protocol. We used cytochrome oxidase subunit I (*COI)*, cytochrome b (*cyt-b*) gene regions from mitochondrial for phylogenetic approaches. PCR protocol was performed using the following primers: *COI* (F- 5' TCCTGCTTCTATCCTCTTCT 3', R- 5' TAGTGGAAATGGGCAACTAC 3'), *cyt-b* (F- 5' AGGCCTCTTCTTAGCTATACAC 3', R- 5' TAGGTGAAGTAT TGGTGAGGTA 3'). Amplification reactions were conducted using 20 µL volumes containing 0.5 µl of each primer, 50 ng template DNA, 2 µl buffer, 0.8 µl dNTPs, 0.5 µl $MgCl_2$, and 0.2 µl Taq DNA polymerase (5 U/µL) (Thermo Fisher). PCR reactions were performed by initial denaturation step at 95°C for 3 min, followed by 30 cycles of: 30 s at 95°C, 30 s at 52.3°C for *COI* gene and 52°C for *cyt-b* gene, and 1 min at 72°C, final extension at 72°C for 10 min. 5 µl of each PCR product was examined by 1.5% gel electrophoresis. The purified PCR products were sequenced using Sanger dideoxy method by BGI Shenzhen (Shenzhen, China).

Phylogenetic analysis. 59 samples (707 bases) of the *COI* gene region and 157 samples (414 bases) of the *cyt-b* gene region were used in the phylogenetic analysis. *Lacerta agilis* Linnaeus, 1758, *L. citrovittata* Werner, 1938, *L. viridis* Laurenti, 1768, *L. media,* and *L. pamphylica* Schmidtler, 1975 were used as outgroups. Locations and Genbank accession numbers are given in Table S1 (Supplementary material). We aligned each locus using MAFFT (Katoh et al., 2019),

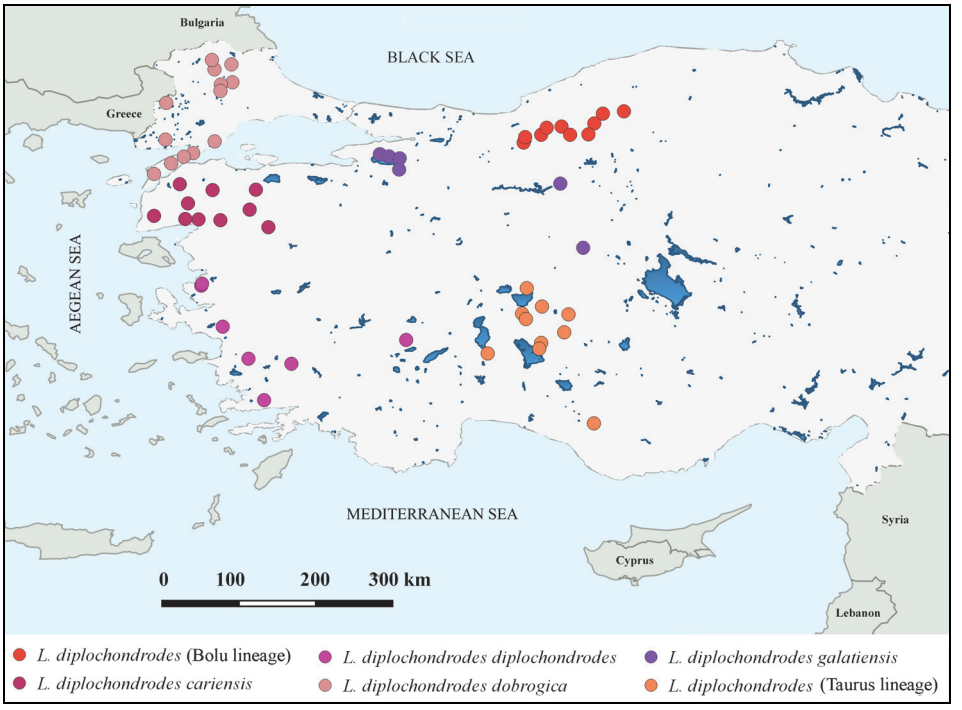

Figure 1. Localities *of L. diplochondrodes* (Bolu lineage), *L. d. cariensis*, *L. d. diplochondrodes*, *L. d. dobrogica*, *L. d. galatiensis*, and *L. diplochondrodes* (Taurus lineage).

allowing missing nucleotides at the flanks of the alignment only if at least 65% of taxa contained data, which is the default option in PHYLUCE. Trimming of alignments was done by eye. NGPhlogeny.fr (Lemoine et al., 2019) portal was used for phylogenetic approaches. Bayesian Inference was conducted using MrBayes V3.2.7_0 (Huelsenbeck & Ronquist, 2001). Maximum Likelihood analysis was conducted using PhyML V 3.3.1 (Guindon et al., 2010) with 1,000 bootstrap replicates.

Morphometric measurements. The populations of the western Black Sea region (Bolu, Karabük) are compared with populations belonging to the Aegean region (Afyon, Aydın, Izmir, Muğla), southern Marmara (Balıkesir, Çanakkale), Thrace (Edirne, Gelibolu, Kırklareli), and western Anatolian (Ankara, Bursa) populations. We used 59 specimens from the populations of *L. diplochondrodes* Bolu lineage (N=20), *L. d. cariensis* (N=8), *L. d. diplochondrodes* (N=9), *L. d. dobrogica* (N=18), and *L. d. galatiensis* (N=4) for morphometric analysis. The Western Taurus population was not used in morphometric analysis since there were not enough samples. A population of *L. media* (Karaman, Mersin) (N=3) was used as outgroup.

We examined the populations in terms of morphometric measurements and pholidosis characters. The following parameters were analysed: F (number of femoral pores), LUFT (number of lamellae under fourth toe), LVR (number of longitudinal ventral scale rows) IL (number of infralabial scales), IP (number of scales contacting with interparietal), SAB (number of scales around midbody), SC (number of supraciliar scales), T (number of temporal scales), ULE (number of scales between the posterior edge of upper labial and anterior of the ear), UL (number of upper labials), and V (number of transversal ventral scale rows). Counts were made with Nikon SMZ 745T stereo zoom microscope. SVL (snout-vent length), HL (head length), HW (head width), HD (head depth), PW (pileus width), PL (pileus length), IW (interorbital width), NOL (distance between the posterior edge of noise and anterior edge of orbit), HOD (horizontal orbit diameter), OTL (distance between the posterior edge of orbit and anterior edge of tympanicum),

FBL (distance between the foreleg and back leg), FL (foreleg length), BL (back leg length), TL (tail length) characters were measured with a 0.01 mm digital calliper. We determined which characters to measure based on the study by Peters (1964), Baran (1969), and Schmidtler (1975).

Statistical analysis. For statistics, 11 different pholidosis characters were used. For body measurements, the PERCRA index (percent of Snout Vent Length; [[each metric character/] SVL] × 100) (Werner, 1971) was used to eliminate errors that may arise from size differences between specimens. In total, 25 different characters were taken as data for morphometric analysis. Minimum (Min), Mean, Maximum (Max), and standard deviation (SD) values of the characters used were calculated according to the defined populations (Table S2, Supplementary material). Hierarchical classification analysis based on morphological characters between populations was performed using Manhattan distance and UPGMA method (Figure S2, Supplementary material). The Shapiro-Wilk test was performed to assess if each character is normally distributed at the population level (Table S3, Supplementary material). ANOVA (One-Way Analysis of Variance) was performed for data comparison among populations. A significance level of 0.05 was used to determine statistical significance (Table S4, Supplementary material). An outlier value in the groups and a critical morphological value distinguishing between populations were detected using boxplots (Figure S3, Supplementary material). We used PCA (Principal Component Analysis) to display the largest axes of variation in morphological characters of the populations (Figure 3). With CDA (Canonical Discriminant Analysis), differences in morphometric characters between populations were analysed (Figure 3). All analyses were made with R version 4.2.1. software (R Core Team, 2022) and were performed using the statistical package MorphoTools2 (Šlenker et al., 2022), a program package that allows users to analyze multivariate data based on morphological characters (Šlenker et al., 2022).

Results

Phylogenetic Analysis. According to model test, the Hasegawa Kishino-Yano (HKY) with gamma-distributed rate for *COI* gene region, and the general-time-reversible (GTR) with gamma-distributed rate for *cyt-b* gene region were selected as the best substitution model by analysis based on Maximum Likelihood. The phylogenetic analysis showed that *L. diplochondrodes* has six lineages in Türkiye (Figure 2, Figure S1 in Supplementary material) for the phylogenetic tree of the *cyt-b* gene region. In addition to the four previously identified subspecies (*L. d. dobrogica* for the Thrace population, *L. d. cariensis* for the north part of Aegean and the south part of Marmara population, *L. d. diplochondrodes* for the south part of Aegean population, *L. d. galatiensis* for the Western Anatolian population (Kornilios et al., 2020)), a new lineage (Bolu lineage) for the Black Sea population was identified. The phylogenetic tree based on *cyt-b* showed *L. citrovittata* and *L. pamphylica* species were phylogenetically closer to *L. diplochondrodes*.

Morphological analysis. A total of 62 specimens of *L. diplochondrodes* and *L. media* from Türkiye were analysed morphometrically by using 25 different characters (data given in Table S2). In the Hierarchical classification dendrogram based on the Manhattan distance and UPGMA method, the western populations *L. d. dobrogica*, *L. d. cariensis* and *L. d. diplochondrodes* are closely linked to each other (Figure S2). On the other hand, the northeastern populations, i.e. the Bolu lineage and *L. d. galatiensis* were found to be more closely related to each other. The characters of F, IL, SAB, ULE, V, HD*100/SVL, HL*100/SVL, HW*100/SVL, HOD*100/SVL, IW*100/SVL, PL*100/SVL, PW*100/SVL, and OTL*100/SVL that indicate significant differences between the populations of the studied specimens based on ANOVA are shown with boxplots (Figure S3). PCA and CDA analyses showed that populations of the Bolu lineage form a distinct cluster from the other Turkish populations (Figure 3). The western Anatolian population (*L. d. galatiensis*) was closest to the western Black Sea

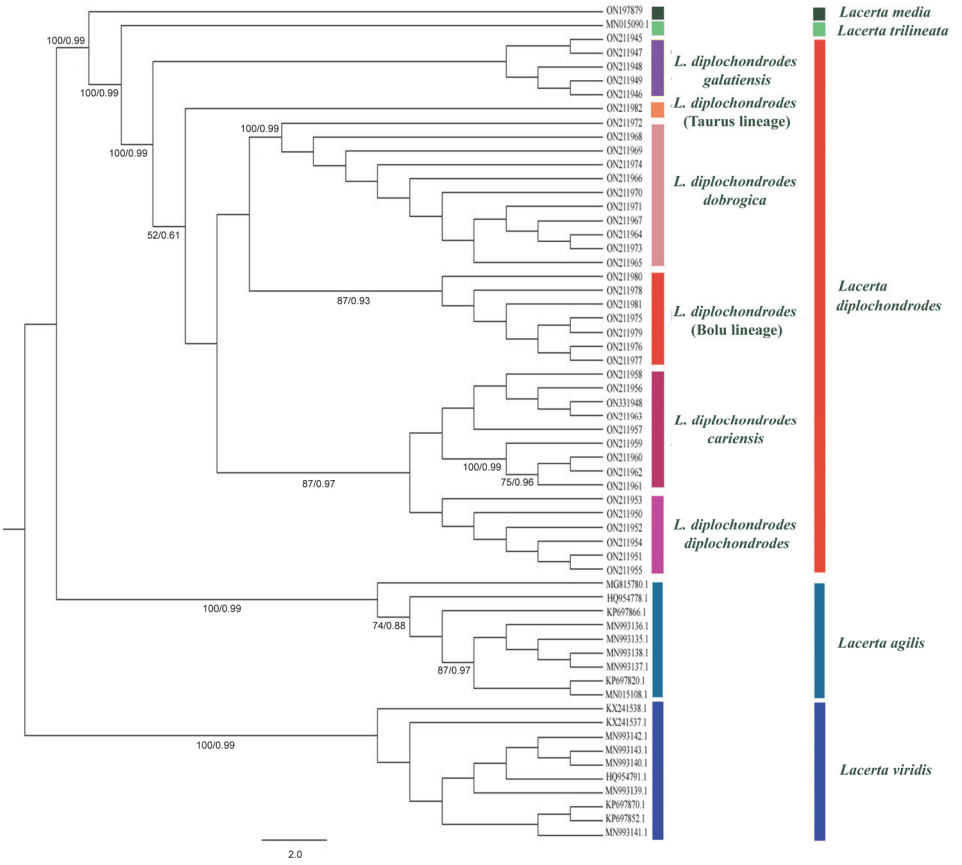

Figure 2. Maximum Likelihood phylogeny of *L. diplochondrodes* (Bolu lineage), *L. d. cariensis*, *L. d. diplochondrodes*, *L. d. dobrogica*, *L. d. galatiensis*, and *L. diplochondrodes* (Taurus lineage) based on mitochondrial COI sequences. Values less than 50 are not shown on the phylogenetic tree.

population (Bolu lineage). The Aegean (*L. d. diplochondrodes*), and the southern Marmara populations (*L. d. cariensis*), cluster quite close to each other.

Discussion

In addition to the four previously known genetic lineages of *Lacerta diplochondrodes* (Kornilios et al. 2020) a new lineage was found, which we call Bolu lineage. This lineage is clearly separated from the Western Anatolian lineage described as *L. d. galatiensis*. The North Anatolian Mountains, which run parallel to the Black Sea coast, and the Sakarya River, which has the largest river basin in Northwest Anatolia, seem to act as a barrier between the Bolu lineage and the *L. d. galatiensis* population. Large river basins and river systems with high flow rates such as the Sakarya River tend to form a barrier preventing the transition between populations of terrestrial animals (Kocataş, 2008).

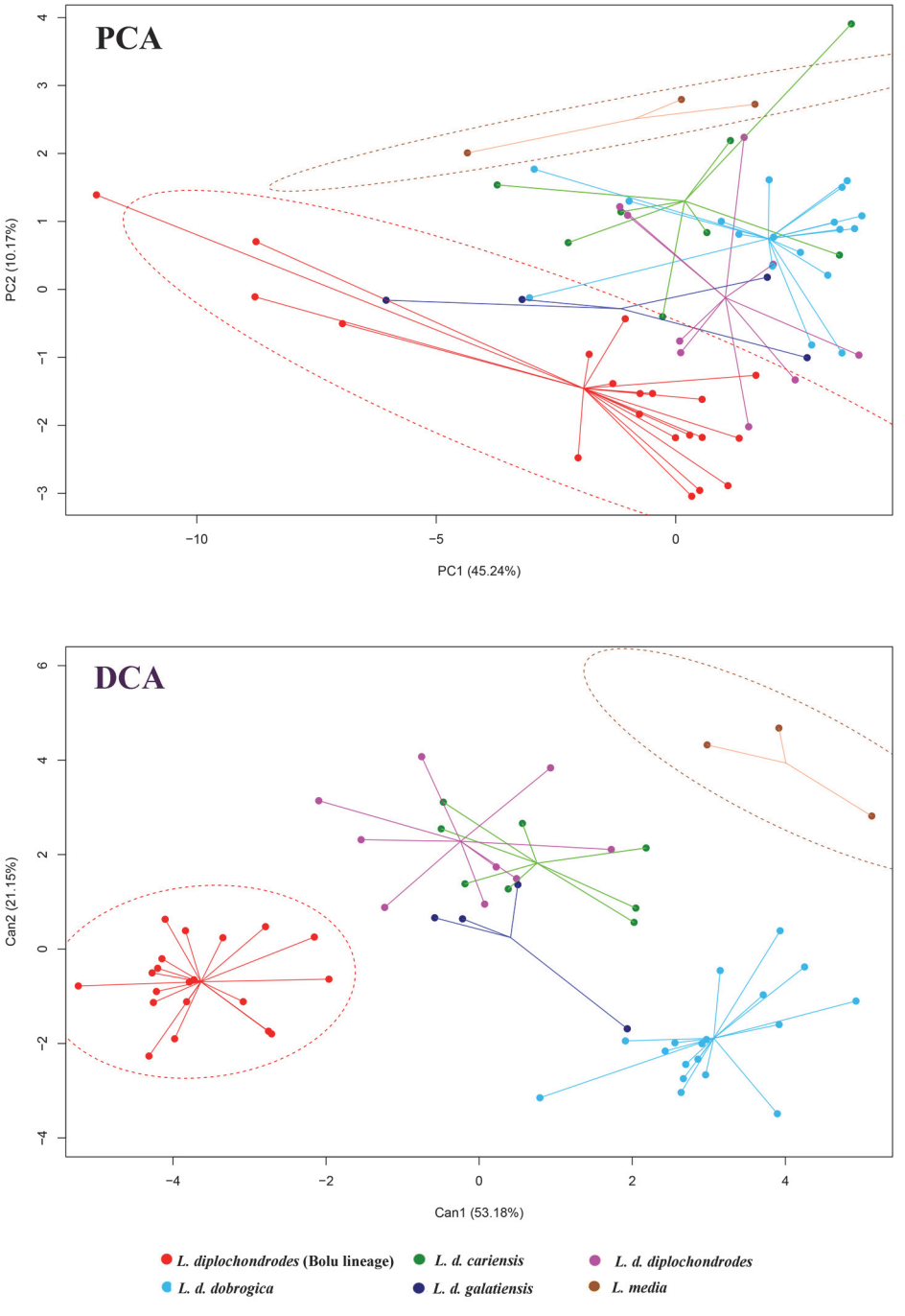

Figure 3. Principal component analysis (PCA) and Canonical Discriminant Analysis (CDA) of populations of *L. diplochondrodes* (Bolu lineage), *L. d. cariensis*, *L. d. diplochondrodes*, *L. d. dobrogica*, and *L. d. galatiensis*, based on morphological characters.

The distribution of *L. d. cariensis* is confined to the North Aegean region, the distribution of *L. d. diplochondrodes* to the South Aegean region (Kornilios et al., 2020). The distribution of *L. d. diplochondrodes* extends as far north as Afyonkarahisar. The population on the Greek island of Lesbos was found to be distinct from *L. d. cariensis*, but is status could not be determined definitively, and is given here as *Lacerta* sp. On the other hand, the population on Chios Island belongs to the *L. d. diplochondrodes* lineage. We also describe *L. d. dobrogica* from the Thrace region, as reported in the literature. The population has been described as *L. d. dobrogica* in Thrace, Greece (Kornilios et al., 2020), but was found to be represented in Türkiye by a different lineage (Figure S1). It is possible that the Meriç River, which forms the border between Greece and Türkiye, constitutes a geographical barrier for the two populations. It may be that *L. diplochondrodes* had a wide distribution extending from Anatolia to the Aegean and Thrace, before the Aegean Sea and the straits were formed. However, the first the collapse of the Aegean plateau, the formation of the sea and the islands and the separation of the island population (1.8 million years ago) and then the opening of the Bosphorus (6,000 years ago) cut off the connection between Thrace and Anatolia (İnan, 2017). As a result, the Thrace population formed a separate lineage (Ahmadzadeh et al., 2013).

The subspecies *L. d. galatiensis* corresponds to the lineage of Western Anatolian (Ankara, Bursa, Eskişehir, Asiatic side of Istanbul, Sakarya). Kornilios et al (2020) assigned the population on the Asiatic side of Istanbul to *L. d. dobrogica*. However, taking into account our results obtained from the central Western Anatolian lineage (north of Bursa) and the Bosphorus, we attribute the population in this region to *L. d. galatiensis*, because it is geographically close to the Western Anatolian population and there is no barrier between these two regions. Additionally, the southern population of *L. d. galatiensis* has a limited distribution in Central Anatolia. Also *Lacerta media* is widely distributed in Central and Eastern Anatolia (Akman et al., 2020; Yaşar et al., 2021).

Morphological studies have been carried out for many years on the *L. diplochondrodes* species in Türkiye, and many subspecies were defined using different morphological characters (Mertens & Müller, 1940; Bodenheimer, 1944; Mertens, 1952; Peters, 1964; Baran, 1969; Schmidtler, 1975). Our morphometric analysis performed on *L. diplochondrodes* populations and samples belonging to the *L. media* revealed distinctions between the populations. The results show that the population in the Western Black Sea region is distinct from the nominate form, and the other populations clustered very close to each other in the PCA analysis. In PCA and CDA analyses, there were no conclusive differences between the *L. d. cariensis* population in the southern Marmara region and *L. d. diplochondrodes* population in the Aegean region. It is concluded that these two populations phylogenetically formed a sister lineage, originating from the same ancestor. In this study, these two populations did not show a clear morphological distinction. There is no strong evidence that these two populations are distinct based on phylogenetic and morphometric data. Thus, both populations can be defined as *L. d. diplochondrodes*. At the same time, the *L. d. dobrogica* population in the Thrace region has a clear distinction in CDA analysis. In phylogenetic analysis, it was seen that it branched as a different lineage from other populations.

In conclusion, with our comparative genetic and morphological studies on *Lacerta diplochondrodes* populations, four different lineages (Bolu lineage, *L. d. diplochondrodes*, *L. d. dobrogica*, *L. d. galatiensis*) can be distinguished in Türkiye. Out of which, the lineage of the Western Black Sea region (Bolu lineage) is described for the first time.

Supplementary Material

Supplementary Material is given as a Supplementary Annex, which is available via the "Supplementary" tab on the article's online page.

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Disclosure Statement

No potential conflict of interest was reported by the authors.

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