

Molecular and morphological assessment of the snake-eyed lizard, *Ophisops elegans* Menetries, 1832 (Sauria, Lacertidae) in Anatolia

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Abstract. *Ophisops elegans* Menetries, 1832 includes six subspecies in Turkey. Here, we investigated the systematic status and distribution range of the subspecies of *O. elegans* in Anatolia concerning molecular and morphological approaches. Two mitochondrial (*cytb* and *16S rRNA*) gene regions were used for the phylogenetic analyses. The phylogenetic trees were constructed with the Bayesian and Maximum Likelihood approaches. For morphological evaluations, ANOVA, Discriminant Function Analyses, and Mann Whitney-U Test were performed via SPSS. The *O. elegans* complex was split into six main clades. Clade A corresponded to nominate subspecies *O. e. elegans*. Clade B included African and Levant *Ophisops* samples. Clade C (*O. e. ehrenbergii*) was separated into two subclades, and the subspecies distribution was much broader than suggested in the literature. Clade D was defined as *O. e. centralanatoliae*. The distribution of *O. e. centralanatoliae* was also much broader than reported in the literature. Clade E can be named as *O. e. basoglui*, and its range was found to be narrower than mentioned in the literature. Clade F refers to the *O. e. macrodactylus*, and phylogenetic analyses did not recover *O. e. budakibarani* as a separate clade. Therefore, *O. e. budakibarani* was assigned as a junior synonym of *O. e. macrodactylus*.

Keywords: Anatolia, *Ophisops elegans*, morphology, phylogenetics, taxonomy.

Introduction

The lacertid genus *Ophisops* Menetries, 1832 is distributed in southeast Europe, North Africa, and Asia, and it was suggested to be originated from a "Saharo-Sindian" lineage and evolved in southwest Asia, including eleven currently recognized species; *Ophisops leschenaultii* (Milne-Edwards, 1829), *O. elegans* Menetries, 1832, *O. jerdoni* Blyth, 1853, *O. beddomei* (Jerdon, 1870), *O. microlepis* Blanford, 1870, *O. occidentalis* (Boulenger, 1887), *O. persicus* (Boulenger, 1918), *O. elbaensis* Schmidt and Marx, 1957, *O. minor* Deraniyagala, 1971, *O. kutchensis* Agarwal et al., 2018 and *O. pushkarensis* Agarwal et al., 2018 (Kyriazi et al. 2008, Venugopal 2010, Agarwal et al. 2018, Montgerald et al. 2020). However, the status of two Mediterranean species (*O. elegans* and *O. occidentalis*) has been questioned and may be regarded as a species complex (Kyriazi et al. 2008).

The species *O. elegans* was first described in Baku, Azerbaijan, and it is distributed in Bulgaria, Greece, the Aegean islands, Cyprus, Turkey, Israel, Syria, Jordan, Lebanon, Armenia, Azerbaijan, Iran, Iraq, Pakistan, Egypt, Libya and Algeria (Tok et al. 2017). In addition, eight further subspecies were proposed within the *O. elegans* species complex. *O. e. blanfordi* Schmidt, 1939 is known to occur in southern Mesopotamia (Iraq, Iran, and Jordan), and *O. e. schlueteri* Boettger, 1880 was reported from Cyprus (Anderson 1999, Göçmen et al. 2008). The distribution ranges of the remaining six subspecies are mostly included within Anatolia. *O. e. elegans* Menetries, 1832 was reported to range from northern Mesopotamia (Iraq) and Hatay province of

the eastern Mediterranean coast of Turkey to east and northeast regions of Turkey; *O. e. ehrenbergii* (Wiegmann, 1835) occurs in southeast Anatolia including Syrian borderline; *O. e. basoglui* Baran and Budak, 1978 was reported from Mediterranean coastal provinces of Alanya, Antalya, and Adana; *O. e. centralanatoliae* Bodenheimer, 1944 occurs mainly in the central Anatolian region; *O. e. macrodactylus* Berthold, 1840 is regarded as western subspecies of Anatolian peninsula with Thracian, west and southwest Anatolian and Aegean Islands distribution and *O. e. budakibarani* Tok, Afsar, Yakın, Ayaz and Çiçek, 2017 is ranged in Mut, Mersin (Bodenheimer 1944, Baran & Budak 1978, Baran 1982, Tok et al. 1997, Kyriazi et al. 2008, Yıldız et al. 2012, Tok et al. 2017). Kyriazi et al. (2008) suggested that the genus *Ophisops* was separated into three major groups in which (1) Clade A from Greece to Lebanon and Azerbaijan, and Iran, (2) Clade B from Tunisia, Libya, and Israel, and (3) Clade C northeast Turkey (Aralık samples), Armenia and northwest Iran. However, the subspecific positions of *O. elegans* in Anatolia were not evaluated in this study and remained controversial. Kyriazi et al. (2008) suggested that the presented phylogenetic hypothesis must be supported by morphology and distribution data.

The aim of our study is to present complete distribution data of the *O. elegans* subspecies and resolve the taxonomic problems of *O. elegans* in Anatolia in the light of the morphologic and genetic data. Here, we used two mitochondrial markers (*16S rRNA* and *cytb*) for genetic analysis and metric and meristic characters for morphological analysis.

Materials and methods

Sampling

Before the study, the ethics committee approval, no B.30.2.ADÜ.0.06.00.00/124-HEK/2007/0039, on 28.12.2007, was obtained from ADÜ-HADYEK. Morphological analyses were conducted on 507 (248 males and 259 females) specimens, and 224

were museum material.

These specimens are deposited in the Zoology Museums of Ege University and Aydın Adnan Menderes University. Specimens collected in the field study were anesthetized with ether, fixed with a 96% ethanol injection, and deposited in 96% ethanol. A total of 261 *O. elegans* tissues were preserved in 99% ethanol for DNA extraction (Figure 1 and Appendix).

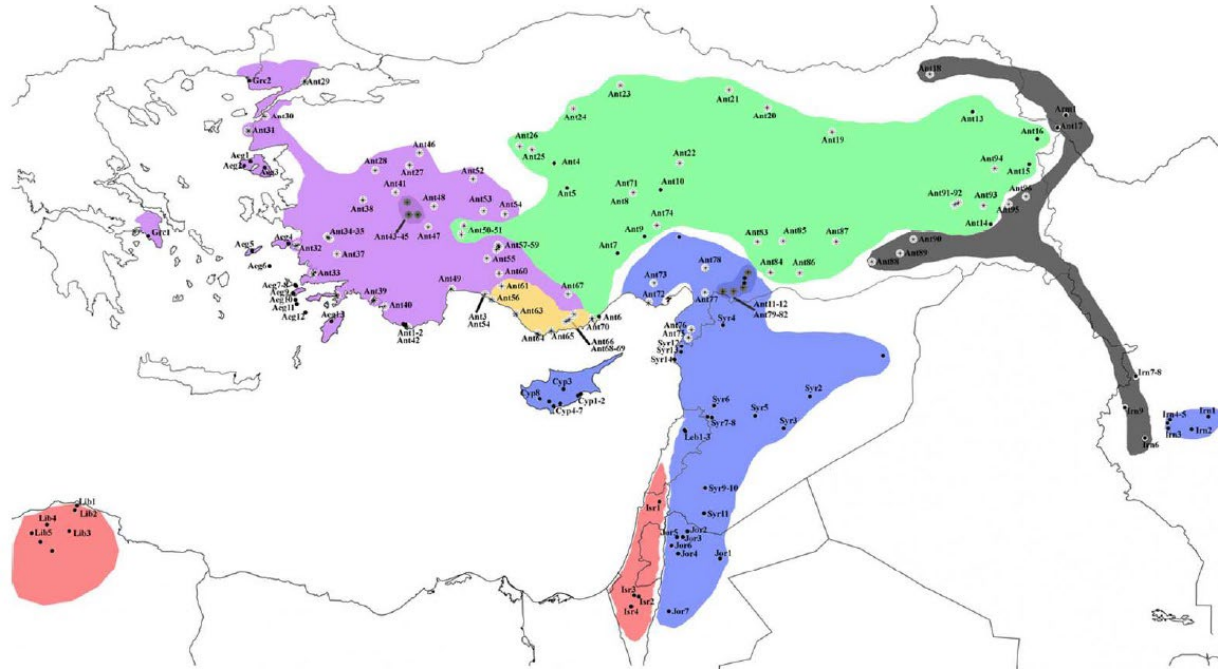


Figure 1. Sampling localities of the *Ophisops elegans* species complex. Collection sites from previous studies indicated by asterisk; sampling localities are grouped into six regions based on clades obtained from phylogenetic analyses and shown with different colors. Detailed information for sampling localities is given in Appendix.

DNA extraction, PCR, and sequencing

Genomic DNA was extracted from the small pieces of the tail using the method described by Sambrook et al. (1989), with some modifications. Two mtDNA fragments were amplified: *cytb* with primers L14841, 5'-AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA-3' and H15149, 5'-AAACTGCAGCCCCCTCAGAATGATATTTGTCCTCA-3' (ca. 380 bp, Kocher et al. 1989) and *16S rRNA* with primers 16SAR-L, 5'-CGCCTGTTTATCAAAAACAT-3' and 16SBR-H, 5'-CCGGTCTGAAGTACAGTACAGT-3' (ca. 530 bp, Palumbi et al. 1991). The 50 µl volume for each PCR reaction contained: 0.5 U of Taq polymerase, 5 µl of 10x reaction buffer (100 mM Tris-HCl, pH 8.8, 500 mM KCl, and 0.8% Nonidet P-40), 10 pmol of forward and reverse primers, 0.2 mM of each of the four dNTPs, 1.5 mM MgCl₂, and 1 µl of DNA template (≈75–100 ng of DNA). Cycling conditions for *cytb* were: 2 min at 94 °C, 35 cycles of denaturing 30 sec at 94 °C, annealing 30 sec at 42 °C, and extending 30 sec at 72 °C, a final extension at 72 °C 5 min. *16S rRNA* parameters were: initial denaturing at 94 °C for 3 min, 35 cycles of denaturing at 94 °C 45 sec, annealing at 47 °C 1 min, and extension of 30 sec at 72 °C, a final extension of 72 °C for 5 min. Amplification products were run at 1.5% agarose gel electrophoresis and cleaned for sequencing using GenElute PCR Clean-Up Kit (Sigma) according to the manufacturer's instructions. Sequencing reactions were carried out in both directions using the same PCR primers. The forward and reverse nucleotide sequences were assembled, edited, and aligned manually by the CodonCode Aligner 3.5.6 (CodonCode Corporation). Eighty-four specimens of *O. elegans*, five specimens of *O. occidentalis*, and a specimen of *Eremias velox* (Pallas, 1771) as the outgroup, retrieved from GenBank and added to the datasets (Kyriazi et al. 2008) (see

Fig. 1 and Appendix for detailed specimen information). The alignment of the concatenated *cytb* and *16S rRNA* sequences (hereafter, *cytb-SrD*) was performed with MEGA v5 (Tamura et al. 2011), and detailed comparisons were made manually. In the *cytb-SrD* fragment, concatenated sequences were trimmed to equal lengths. The sequences obtained from each gene fragment were submitted to GenBank (Appendix).

Phylogenetic analysis

Haplotype datasets of *cytb*, *16S rRNA*, and *cytb-SrD* sequences were generated using DnaSP v.5 (Librado & Rozas 2009) prior to the phylogenetic analyses. The combinability of the *cytb-SrD* dataset was estimated with the partition homogeneity test (PHT; Farris et al. 1995) using 1000 replicates and 10 random addition replicates per replicate in PAUP v.4.0b10 (Swofford 2002). Phylogenetic analyses were only conducted on the haplotype dataset of *cytb-SrD* sequences. Nucleotides were used as discrete and unordered characters. The most appropriate model of nucleotide substitution and the parameter estimates used for tree constructions were assessed using Modeltest v.3.7 (Posada & Crandall 1998) according to the Akaike information criterion (AIC) in PAUP. Phylogenetic trees were constructed by application of maximum likelihood (ML) and Bayesian Inference (BI) methods. For ML trees, the analysis was performed at a high-performance facility using the program PhyML v.3.0 (Guindon & Gascuel 2003, Guindon et al. 2010). The AIC results from Modeltest provided the GTR+I+G model (gamma shape parameter = 1.48, 0.44, 0.81; the proportion of invariable sites = 0.53, 0.41, 0.54 for *cytb*, *16S rRNA*, and *cytb-SrD*, respectively) were identified as the best-fit substitution model. Node robustness of ML trees was evaluated by generating 1000 bootstrap replicates. For BI

trees, the analysis was performed with the software MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003) using a partition dataset according to *cytb* and *16S rRNA* fragments and by implementing the likelihood parameters $nst = 6$, $rates = \text{gamma}$. The analysis was run with four chains for 50 million generations, and trees were sampled every 100 generations. This generated an output of 500,000 trees. To confirm that the chains had achieved a stationary state, we evaluated “burn-in” plots by plotting log-likelihood scores and tree lengths against generation numbers using the software Tracer v.1.5 (Drummond & Rambaut 2007). After assessing for apparent convergence, 50,000 trees were discarded as “burn-in”. A majority rule consensus tree (BI tree) was calculated from the posterior distribution of trees, and the posterior probabilities were calculated as the percentage of samples recovering any particular clade (Huelsenbeck & Ronquist 2001).

Network approaches are often more compatible for interpreting evolutionary relationships within species (Posada & Crandall 2001). Therefore, a median-joining (MJ) network approach (Bandelt et al. 1999) was constructed to visualize haplotype relatedness and geographical haplotype distribution within the *O. elegans* species complex. Analysis was only conducted on the *cytb* data set using the software Network 4.5.1.6 (available at <http://www.fluxus-technology.com>) with the default settings for building networks.

Morphological methods

Mensural, meristic, and qualitative data were recorded following the system of Baran & Budak 1978, Baran 1982, Olgun & Tok 1999, Ilgaz et al. 2005, and Ilgaz 2006. The metric characteristics were measured with a 0.01 mm digital caliper, and meristic characteristics were counted with an Olympus brand binocular microscope.

The following meristic characteristics were counted: supraciliar plates (left-right, SCPa-SCPb), supraciliar granules (left-right, SCGa-SCGb), sublambial plates (left-right, SBLa-SBLb), temporalia (left-right, TEMa-TEMb), collare (C), gularia (G), ventral plates (longitudinal, VP), transversal series of the midtrunk (DS), subdigital lamella in the 4th toe (SDLa, SDLb), femoral pores (left-right, FPa-FPb), preanal plates (PA) and anale (A).

The following metric measurements were taken: SVL (snout-vent length), the tip of snout to anal cleft; FLL (left forelimb length) outstretched limb from shoulder joint to the tip of the toe; HLL (left hind-limb length), outstretched limb from hip joint to tip of toe; FHLL, forelimb to the hind-limb; HW (head width), the longest distance from left to right in the head; HH (head height), largest point to under and below of head; HL (head length), the tip of snout to anterior of the ear opening; TBL (total body length), tip of snout to tip of tail; TL (tail length), the tip of tail to anal cleft; PW (pileus width), at the widest point between parietal plates; PL (pileus length), tip of snout to the posterior margins of parietals. The following indexes are calculated HW/SVL, FLL/SVL, TBL/SVL, TL/SVL, HLL/SVL, PL/SVL, and HH/SVL.

Statistical analyses were performed with SPSS 22.0, and descriptive statistics were used for each taxon. To determine the normal distribution, the Kolmogorov-Smirnov test was performed. The Mann-Whitney U test was used to determine sexual dimorphism. Characters showing sexual dimorphism continued to be analyzed separately for each gender. Characters that did not show sexual dimorphism were used to analyze with combined data. ANOVA and Tukey HSD tests were applied for comparative analyses. Discriminant function analysis was used for multiple comparisons of subspecies of *O. elegans* with normally distributed characteristics.

Results

Genetic analysis

The length of *cytb* sequences was 287 bp, with a total of 100 variable sites, while the length of the *16S rRNA* sequences ranged from 321 to 331 bp, with a total of 88 variable sites,

including ten indel positions. Ninety-seven haplotypes were identified among the 326 *O. elegans* individuals analyzed for the *cytb* fragment, and eighty-seven haplotypes were obtained for the *16S rRNA* gene region from the 327 individuals (Appendix). The concatenated alignment of *cytb-SrD* yielded a total of 618 bp considering indels positions and revealed 161 haplotypes (including two individuals of *O. occidentalis* and the outgroup taxon); 211 positions were variable, of which 182 were parsimony informative (without *O. occidentalis* and outgroup: 159 haplotypes and 188 variable positions, of which 176 were parsimony informative).

The *O. elegans* species complex was characterized by six main clades, with some including subclades (Figure 2). Despite slight differences among the supporting values of clades, posterior probabilities (p.p) of BI were congruent with ML bootstrap values (Figure 2). The clades correspond to geographical regions as follows: Clade A, which was sister to a lineage composed of all other clades with 1.0 p.p and 0.99 bootstraps values as well as forming the most basal clade, was subdivided into three highly supported subclades mainly including the specimens from the east part of Anatolia and northwest Iran (Figure 2). The Subclade A1 consisted of specimens from northwest Iran (Eslam Abade-Gharb, Ghasr-e-shirin) and one specimen from northeastern Anatolia (Aralık Iğdır province). Subclades A2 and A3 were sisters, and A2 included the specimens from the eastern part of Anatolia (Van and Artvin provinces) and Armenia (Chosrov), while A3 represented specimens from southeastern Anatolia (Batman and Mardin provinces). Samples of Clade A were used in morphological analysis as *O. elegans elegans*. Clade B was divided into two well-supported subclades (B1 and B2, Figure 2) with the altered placement of the Cyprus population between ML and BI trees (Figure 2, ML tree not present). Subclade B1 included only the specimens from Israel, while B2 consisted of specimens from Libya (including the specimens of *O. occidentalis*). Clade C (*O. e. ehrenbergii*) appeared as an assemblage mainly from the southern part of the species' distribution range with the presence of two subclades. Subclade C1 represented the specimens from Iran (Kurdistan-Sarvabad, Kermanshah, Kngavar, Harsin) and Cyprus. Subclade C2 comprised all specimens from Syria, Jordan, and Lebanon, as well as those belonging mainly to the southern region of Anatolia (Hatay, Adana, Osmaniye, Gaziantep, Kilis, and Kayseri provinces). The remaining three clades exhibited low support values (Figure 2). The Clade D (*O. e. centralanatolia*) consisted of the specimens from central and eastern Anatolia and was recovered as a sister group to the remaining two monophyletic groups. The Clade E (*O. e. basoglui*) occurred in the southern part of Anatolia, west of Mersin and east of Antalya. In contrast, the locations from the western part of Anatolia, Thrace, Greece, and the Aegean Islands were clustered in clade F (*O. e. macrodactylus*).

The MJ network included 96 *cytb* haplotypes and was highly congruent with the phylogenetic trees (Figure 3). Many mutational steps were observed among all clades and subclades. In contrast, the number of mutational steps among haplotypes within clades/subclades was relatively small (1-6), except for the Clade E and two haplotypes

within the Clade D (Figure 3). The topology of Clade A was characterized by two very well-structured groups (between subclade A1 and A2 with subclade A3) by many mutational steps (21). On the other hand, the star-like pattern was partly observed in Clade F and consisted of more closely connected haplotypes. The high degree of divergence between Clade A and C provided further evidence about the root of the MJ network. This also allowed us to deduce the possible ancestral haplotype within each clade (Figure 3). The stated

ancestral haplotypes from the *cytb* network were also congruent with haplotypes found in the most basal placement of each clade in the BI tree (Figure 2). The observed haplotype diversity among clades for *cytb* and *16S rRNA* were 0.57-0.90 and 0.67-0.89, and nucleotide diversity was 0.012-0.048 and 0.014-0.056, respectively (Table 1). The greatest observed nucleotide diversity was within Clade A, followed by Clade B and Clade E, whereas Clade F and Clade D showed moderate nucleotide diversity (Table 1).

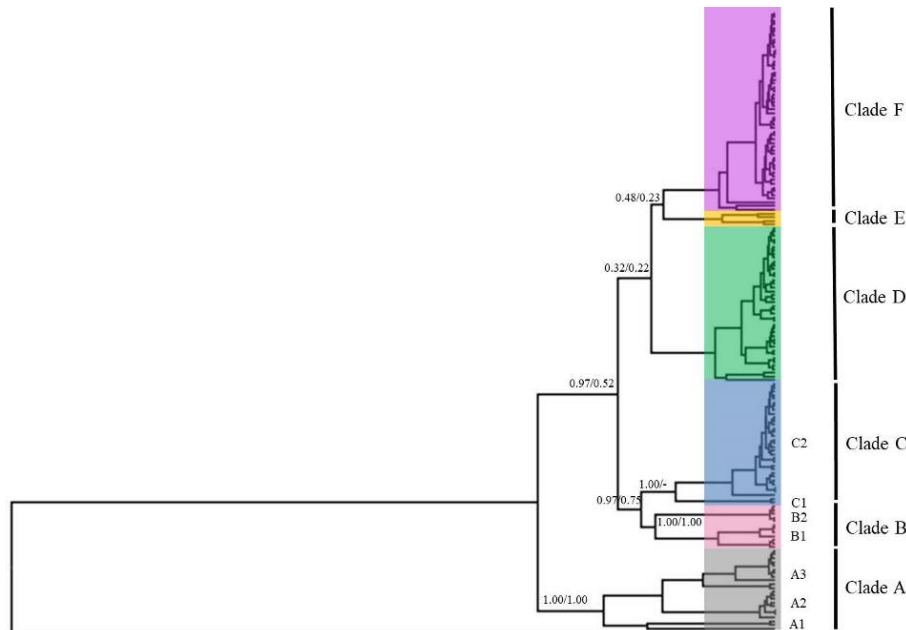


Figure 2. Phylogenetic tree combined from Bayesian Inference (BI) and Maximum Likelihood (ML) analyses of *Ophisops elegans* species complex. Tree reconstructed from the combined mtDNA dataset (*cytb*-*SrD*). *Eremias velox* was used as an outgroup. Numbers on the nodes show posterior probability and bootstrap values for BI and ML, respectively. - indicates that the node is not supported by the ML analysis. Clade/subclade names and colors correspond to that in Figure 1.

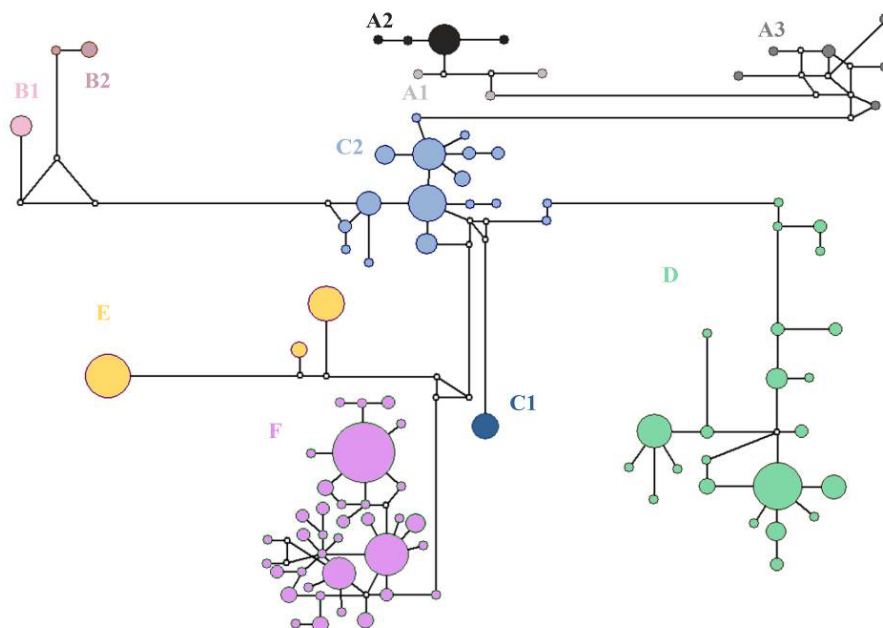


Figure 3. Median-joining network constructed using *cytb* haplotypes of *Ophisops elegans* species complex. Colored circles represent haplotypes of each clade obtained in the phylogenetic tree, and open circles indicate missing haplotypes. The circle area is proportional to the number of individuals. Letters from A to F correspond to clade/subclade names (Figure 2).

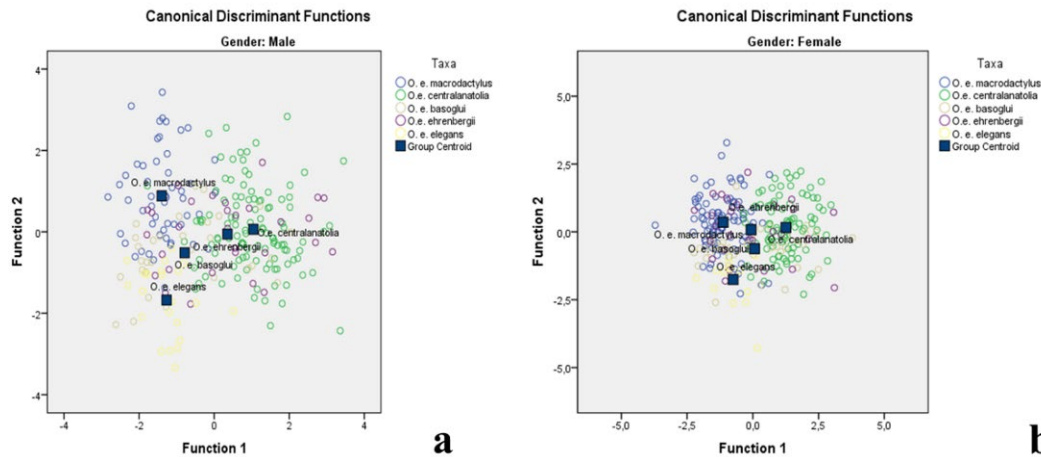


Figure 4. Discriminant function analysis of the meristic characteristics which shows the sexual dimorphism.

Table 3. Predicted group membership determined by discriminant function analysis in meristic characters

		Predicted Group Membership				
		<i>O. e. elegans</i>	<i>O. e. ehrenbergii</i>	<i>O. e. macrodactylus</i>	<i>O. e. centralanatolia</i>	<i>O. e. basoglui</i>
Males						
<i>O. e. elegans</i>		59.1	4.5	0.0	4.5	31.8
<i>O. e. ehrenbergii</i>		10.0	6.7	23.3	56.7	3.3
<i>O. e. macrodactylus</i>		1.9	1.9	83.0	5.7	7.5
<i>O. e. centralanatolia</i>		0.0	4.5	1.8	90.9	2.7
<i>O. e. basoglui</i>		16.7	10.0	23.3	26.7	23.3
Females						
<i>O. e. elegans</i>		40.0	0	46.7	6.7	6.7
<i>O. e. ehrenbergii</i>		3.7	3.7	55.6	37.0	0.0
<i>O. e. macrodactylus</i>		2.2	0.0	92.3	3.3	2.2
<i>O. e. centralanatolia</i>		1.1	1.1	4.4	88.9	4.4
<i>O. e. basoglui</i>		2.8	0.0	44.4	41.7	11.1

As a result of the analysis, 92.3% of *O. e. macrodactylus*, 88.9% of *O. e. centralanatoliae*, 40.0% of *O. e. elegans*, 11.1% of *O. e. basoglui* and 3.7% of *O. e. ehrenbergii* females were correctly classified for the seen as sexual dimorphism characteristics (Figure 4 and Table 3). A total of 67.6% of females were correctly classified within their own taxa.

The meristic characters except VP, DS, PA, TEMa, and TEMb displayed no significant differences between sexes. Combined data were analyzed in all taxa for those characteristics that did not contribute to sexual dimorphism. The descriptive analyses of these characteristics are summarized in Table 4.

The connection of occipital and interparietal plates was 45.5%, 56.8%, 59.4%, 62.1%, and 73.7% in *O. e. basoglui*, *O. e. elegans*, *O. e. centralanatoliae*, *O. e. macrodactylus* and *O. e. ehrenbergii*, respectively. *O. e. basoglui* was significantly lower than *O. e. centralanatoliae*, *O. e. macrodactylus* and *O. e. ehrenbergii* in terms of the connection of occipital and interparietal plates ($P \leq 0.05$).

According to ANOVA, differences were observed for SBLa ($F = 4.266$, $P \leq 0.005$), SBLb ($F = 8.214$, $P \leq 0.001$), SCPa ($F = 5.558$, $P \leq 0.001$), SCPb ($F = 5.744$, $P \leq 0.001$), SCGa ($F = 18.450$, $P \leq 0.001$), SCGb ($F = 14.561$, $P \leq 0.001$), C ($F = 9.471$, $P \leq 0.001$), G ($F = 8.407$, $P \leq 0.001$), FPa ($F = 7.607$, $P \leq 0.001$),

FPb ($F = 3.586$, $P \leq 0.01$), A ($F = 7.694$, $P \leq 0.001$), SDLa ($F = 6.705$, $P \leq 0.001$) and SDLb ($F = 8.071$, $P \leq 0.001$). According to the discriminant analysis, which was not detected sexual dimorphism, *O. e. macrodactylus*, *O. e. ehrenbergii*, and *O. e. elegans* tend to separate from *O. e. basoglui* and *O. e. centralanatoliae* as shown in Figure 5.

O. e. elegans has a significantly lower mean number of sublabial plates than the remaining. When we compare the taxa in terms of a mean number of supraciliar granules, *O. e. macrodactylus* had a lower number than all taxa except *O. e. elegans*, and *O. e. basoglui* had a higher number of supraciliar granules than all taxa except *O. e. ehrenbergii*. *O. e. ehrenbergii* also had a higher mean number of supraciliar granules than *O. e. elegans*.

The comparison of collare showed that *O. e. macrodactylus* had a significantly lower number than *O. e. centralanatoliae* when *O. e. ehrenbergii* has a lower mean number of collare than all other taxa except *O. e. macrodactylus*. *O. e. centralanatoliae* had a higher mean of gularia than *O. e. macrodactylus*. Meanwhile, *O. e. basoglui* had a lower number of gularia than *O. e. centralanatoliae* and *O. e. ehrenbergii*. While *O. e. centralanatoliae* had a higher number of mean femoral pores than others, *O. e. elegans* had a higher mean number of anal plates than the rest ($P \leq 0.05$).

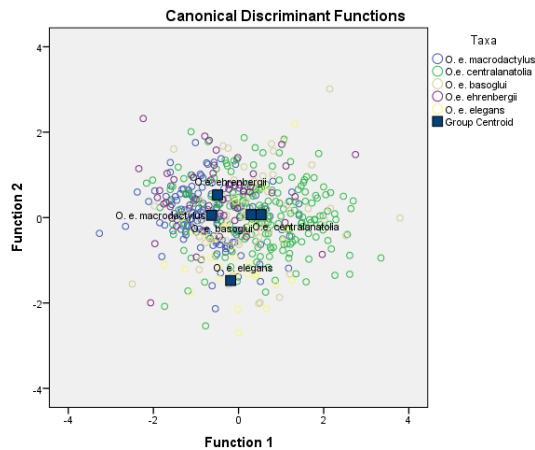


Figure 5. Discriminant function analysis of thirteen meristic characteristics for the *Ophisops elegans* in Anatolia

Metric analysis

The results of the Mann-Whitney U test showed that all

measured characteristics and calculated indexes displayed sexual dimorphism ($P \leq 0.05$). According to ANOVA of the characters with normal distribution performed between males of all taxa, significant differences were found for PL ($F = 6.628, P \leq 0.001$), HL ($F = 6.956, P \leq 0.001$), PW ($F = 13.750, P \leq 0.001$), HW ($F = 5.068, P \leq 0.001$), HH ($F = 4.959, P \leq 0.001$), FLL ($F = 17.732, P \leq 0.001$), HLL ($F = 12.338, P \leq 0.001$), FHLL ($F = 9.630, P \leq 0.001$), SVL ($F = 8.306, P \leq 0.001$), HW/SVL ($F = 3.002, P \leq 0.05$), HH/SVL ($F = 3.032, P \leq 0.05$), PW/SVL ($F = 4.035, P \leq 0.001$), PL/SVL ($F = 3.655, P \leq 0.01$), FLL/SVL ($F = 2.701, P \leq 0.05$), HLL/SVL ($F = 2.750, P \leq 0.05$), FHLL/SVL ($F = 3.863, P \leq 0.01$), TL/SVL ($F = 2.726, P \leq 0.05$) and TBL/SVL ($F = 2.726, P \leq 0.05$).

As a result of discriminant function analysis, 51.2% of males among group variation was explained by the first canonical variate. For males, 82.0% of *O. e. centralanatoliae*, 67.9% of *O. e. macrodactylus*, 72.7% of *O. e. elegans*, 60.0% of *O. e. basoglui* and 58.3% of *O. e. ehrenbergii* were correctly classified for the meristic characteristics. Totally 72.4% of males were correctly classified within the taxa (Figure 6 and Table 5).

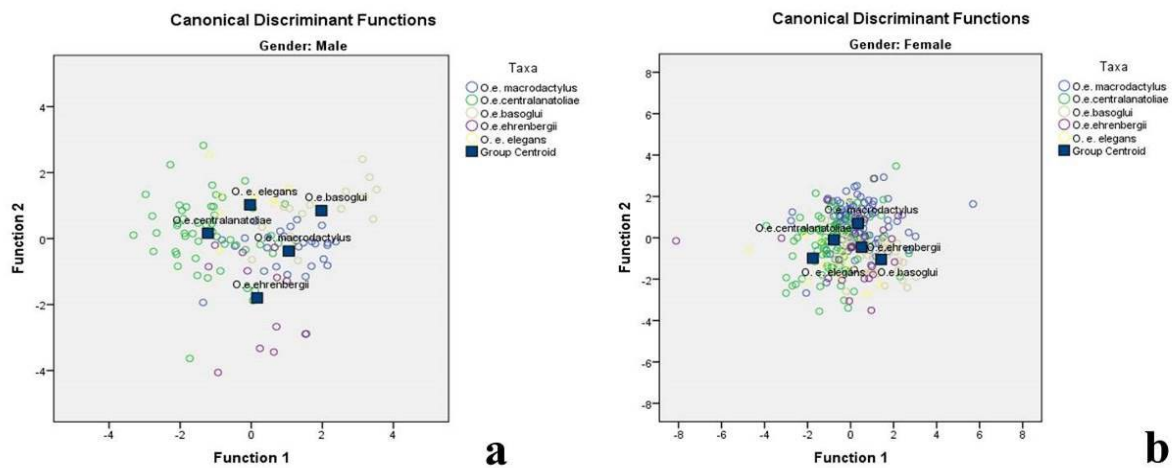


Figure 6. Discriminant function analysis of the metric characteristics which shows the sexual dimorphism.

Table 5. Predicted group membership determined by discriminant function analysis in metric characters

	Predicted Group Membership				
	<i>O. e. elegans</i>	<i>O. e. ehrenbergii</i>	<i>O. e. macrodactylus</i>	<i>O. e. centralanatolia</i>	<i>O. e. basoglui</i>
Males					
<i>O. e. elegans</i>	72.7	0.0	9.1	18.2	0.0
<i>O. e. ehrenbergii</i>	0.0	58.3	16.7	25.0	0.0
<i>O. e. macrodactylus</i>	3.6	7.1	67.9	10.7	10.7
<i>O. e. centralanatolia</i>	4.0	6.0	4.0	82.0	4.0
<i>O. e. basoglui</i>	0.0	0.0	26.7	13.3	60.0
Females					
<i>O. e. elegans</i>	20.0	0.0	26.7	40.0	13.3
<i>O. e. ehrenbergii</i>	3.7	18.5	40.7	22.2	14.8
<i>O. e. macrodactylus</i>	2.2	3.3	74.7	13.2	6.6
<i>O. e. centralanatolia</i>	12.2	1.1	21.1	62.2	3.3
<i>O. e. basoglui</i>	0.0	5.6	11.1	25.0	58.3

According to ANOVA) of the characters with normal distribution performed between females of all taxa, significant differences were found for PW (F = 6.470, P ≤ 0.001), FLL (F = 7.131, P ≤ 0.001), HLL (F = 5.784, P ≤ 0.001), FHLL (F = 4.947, P ≤ 0.001), SVL (F = 3.736, P ≤ 0.01), HL/SVL (F = 3.497, P ≤ 0.01), HW/SVL (F = 2.651, P ≤ 0.05), HH/SVL (F = 5.078, P ≤ 0.001), PW/SVL (F = 5.960, P ≤ 0.001), PL/SVL (F = 3.138, P ≤ 0.05), FLL/SVL (F = 2.593, P ≤ 0.05), HLL/SVL (F = 8.505, P ≤ 0.001), FHLL/SVL (F = 4.414, P ≤ 0.005), TL/SVL (F = 4.575, P ≤ 0.01) and TBL/SVL (F =

4.575, P ≤ 0.01).

As a result of discriminant function analysis, the first canonical variate explained 54.3% of females among group variation. For females, 74.7% of *O. e. macrodactylus*, 62.2% of *O. e. centralanatoliae*, 58.3% of *O. e. basoglui*, 20.0% of *O. e. elegans* and 18.5% of *O. e. ehrenbergii* were correctly classified for the meristic characteristics. Totally 59.1% of females were correctly classified within their own taxa (Figure 6 and Table 5). All the characteristics show differences between sexes, and taxa determined by ANOVA were given in Table 6.

Table 6. The comparison of taxa with ANOVA in terms of metric characteristics (A: *O. e. elegans*; B: *O. e. ehrenbergii*; C: *O. e. macrodactylus*; D: *O. e. centralanatoliae*; E: *O. e. basoglui*) (* refers to significant differences) (P≤0.05)

Gender	A-B		A-C		A-D		A-E		B-C		B-D		B-E		C-D		C-E		D-E	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
PL	*								*	*	*									
HL	*						*		*	*	*									*
PW	*	*	*	*					*	*	*	*			*	*				*
HW						*				*					*		*			*
HH			*		*				*	*										
FLL	*	*	*	*			*	*	*	*	*				*	*			*	*
HLL	*	*	*	*	*	*	*		*	*	*			*	*			*	*	*
FHLL		*		*	*			*		*			*	*		*	*	*	*	*
SVL	*	*					*	*	*	*			*			*	*	*	*	*
HL/SVL							*						*				*		*	*
HW/SVL	*				*		*	*	*			*	*				*			*
HH/SVL	*		*	*	*		*	*	*	*			*							*
PW/SVL			*				*					*	*	*	*	*	*	*	*	*
PL/SVL		*		*	*		*	*				*	*			*	*	*	*	*
FLL/SVL	*	*					*					*	*	*	*	*	*			
HLL/SVL	*	*		*			*				*	*			*	*	*	*	*	*
FHLL/SVL	*	*	*	*			*				*	*			*	*			*	*
TL/SVL			*	*			*			*		*		*	*			*	*	*
TBL/SVL			*	*			*			*		*		*	*			*	*	*

Discussion

The most basal Clade A comprises specimens from Iran, Armenia, and Eastern Anatolia, corresponding to a likely first colonization area of *O. elegans*, dispersed from an ancestral stock presumed to be in southwest Asia (Mayer & Pavlicev 2007, Kyriazi et al. 2008). This clade was genetically very distant from all other clades, with a sequence divergence of 12.7-18.4% (Table 7). Clade A consists of three well-supported subclades with the greatest observed nucleotide diversity (Table 1, 7). Moravec (1998) and Sindaco et al. (2006) reported that *O. e. elegans* was settled in the northeastern corner of Syria. Our study found that *O. e. elegans* is distributed in northeast Anatolia and southeastern Anatolia between Derik-Mardin and Özalp-Van localities. Clade A appears to largely correspond with the distribution range of the nominate subspecies *O. e. elegans*. These samples were differentiated from the others by the lower number of ventral and sublateral plates.

The second most basal Clade B was divided into two very well-structured subclades, including specimens from Israel (subclade B1) and Libya (subclade B2) corresponding to “the northern African lineage of *Ophisops*” of Kyriazi et al. (2008). The deep-rooted existence of Clade B was supported by both the inter- and intraclade sequence divergence (Table 7) and the observed nucleotide diversity (Table 1).

The next clade branching off was Clade C, with two subclades. The subclade C1 interestingly consisted of specimens from Iran (Sarvabad, Kermanshah, Kngavar, and Harsin) and Cyprus. The subclade C2 included specimens mainly from the southern distribution range of the species (Syria, Jordan, Lebanon, and southeastern Anatolia). The relatively ancient occurrence of the Clade C was mainly supported by the sequence divergence (Table 7) and the observed nucleotide diversity (Table 1). However, the monophyly of clade C was not supported by ML analyses as subclade C1 was placed within clade B and had relatively low support values (Figure 2). Clade C included the

subspecies *O. e. ehrenbergii* previously reported from southeast Anatolia, including the Syrian borderline (Kyriazi et al. 2008). Baran (1982) reported that samples from Hatay were different from *O. e. basoglui*, and these samples showed similarity to *O. e. elegans* in terms of neck coloration, but these samples were not included in any subspecies. Kyriazi et al. (2008) reported that samples from Gaziantep were

identified as *O. e. ehrenbergii* with samples from Lebanon, Jordan, and Syria. Here, we report that the distribution range of the *O. e. ehrenbergii* is wider than mentioned by Baran (1982) and Kyriazi et al. (2008) and was found in Adana, Hatay, Gaziantep, Kilis, Osmaniye, and southeastern Kayseri. *O. e. ehrenbergii* was differentiated from others by a small number of collare except for *O. e. macrodactylus*.

Table 7. Net nucleotide divergence (Da) among cyt b haplotypes of the clades of *Ophisops elegans* species complex

	<i>O. occidentalis</i>	Outgroup (<i>Eremias</i>)				
<i>O. elegans</i>	0.078 ± 0.016	0.262 ± 0.040				
	clade A	clade B	clade C	clade D	clade E	clade F
clade A	0.068 ± 0.013					
clade B	0.127 ± 0.026	0.035 ± 0.009				
clade C	0.169 ± 0.031	0.088 ± 0.019	0.024 ± 0.004			
clade D	0.184 ± 0.033	0.128 ± 0.026	0.099 ± 0.020	0.027 ± 0.005		
clade E	0.162 ± 0.031	0.156 ± 0.032	0.121 ± 0.024	0.132 ± 0.026	0.054 ± 0.012	
clade F	0.159 ± 0.031	0.107 ± 0.022	0.091 ± 0.019	0.111 ± 0.023	0.112 ± 0.023	0.016 ± 0.004

The remaining clades, D, E, and F, consist of a lineage derived from a common ancestor shared with Clade C and include specimens from Anatolia and Aegean Region (Figure 2). Clade D was obtained as a sister group to clades E and F and contained specimens mainly from central and east Anatolia. Clade E interestingly comprised specimens of an isolated pocket of the Mediterranean region in Anatolia, confined by the Göksu River at the east, Manavgat River at the west, and Taşeli Plateau at the north. The last Clade F included specimens from western Anatolia, the Aegean Islands, Thrace, and Greece, and interestingly has been recovered a relatively basal clade in Kyriazi et al. (2008). However, this basal placement may have resulted from a low-density sampling of Anatolia with numerous undiscovered haplotypes (cf. haplotype numbers of both studies). These clades have relatively low support values but a high level of genetic differentiation (Table 7; Figure 2). Except for clade E, the presence of low intraclade sequence divergence, high frequency and star-like pattern of haplotypes, and a moderate level of nucleotide diversity both in clades D and F could suggest a restricted gene flow and recent diversification with sudden expansion (Table 1, 7; Figure 2, 3). The occurrence of all shared haplotypes of 16S rRNA in these clades also may provide further support for the restricted gene flow hypothesis (Table 1). The presence of relatively high nucleotide diversity and intra- and interclade sequence divergence, and a relatively low level of haplotype diversity in Clade E may suggest an establishment of a small and strictly isolated population consequently exposed to the effect of genetic drifts and bottlenecks (Table 1, 7; Figure 2). The Clade E may correspond to the subspecies *O. e. basoglui* with a much more narrow distribution than previously reported (Baran & Budak 1978, Baran 1982). *O. e. basoglui* was defined by the yellow ventral side in the spawning period by Baran & Budak (1978), and it was settled between the Manavgat River and Anamur. Baran (1982) reported that the distribution of *O. e. basoglui* was extended to Adana. *O. e. basoglui* can be distinguished from others except *O. e.*

ehrenbergii in a higher number of supraciliar granules. However, the yellowish ventral coloration of *O. e. basoglui* differentiates it from *O. e. ehrenbergii*, with the whitish ventral coloration of Clade D matches with *O. e. centralanatoliae* with a much wider distribution range and probably in sympatry with both *O. e. macrodactylus* and *O. e. elegans*. Various authors reported that *O. e. centralanatoliae* was distributed in central Anatolia (Bodenheimer 1944, Öktem 1963, Tok 1992, Olgun & Tok 1999). Tok (1993) suggested the sympatric occurrence of *O. e. macrodactylus* and *O. e. centralanatoliae* in Beyşehir. Samples from Azez (north of Syria and borderline of Turkey) were evaluated as *O. e. centralanatoliae* by Moravec (1998). In our study, *O. e. centralanatoliae* was easily differentiated from other subspecies by a higher number of transversal series of the midtrunk, temporalia on both sides, and femoral pores. The most recent Clade F corresponds with *O. e. macrodactylus*, the western subspecies of the Anatolian peninsula, including Thracian, west and southwest Anatolian, and Aegean Islands distribution. The distribution of *O. e. macrodactylus* was known only in Thrace until 1982. Baran (1982) extended the range of *O. e. macrodactylus* from Thrace to western Anatolia and reported that the only difference between *O. e. macrodactylus* and *O. e. basoglui* was ventral coloration. *O. e. macrodactylus* was differentiated from other taxa except for *O. e. elegans* concerning small number of supraciliar granules, but *O. e. elegans* differed from *O. e. macrodactylus* by a small number of ventral plates. In addition, all taxa had some differences in color-pattern characteristics.

Tok et al. (2017) defined a subspecies of *O. elegans* from Alahan-Mut/Mersin and named *O. elegans budakibarani*. In our study, genetic data did not support the distinction between *O. e. macrodactylus* and *O. e. budakibarani*. Therefore, *O. e. budakibarani* was assigned as a junior synonym of *O. e. macrodactylus* (Figure 2).

However, additional sampling and data from nuclear genes, as well as integrative species delimitation approaches, are necessary to investigate the taxonomic status of the

species complex comprehensively. The deep divergence and high genetic differentiation, together with the sympatric distribution of populations recovered in separate clades, in some cases here, could be considered as strong additional evidence for the need to raise each clade to species status, as indicated previously.

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Appendix

List of materials used in molecular and morphological analyses. Code refers to the number on the map in Figure1.

Code	No. of samples used in morphological analyses (♂/♀/juveniles)	Taxa	Locality	Cytb	Srd	Reference
Im1		<i>O. elegans</i>	Iran (Kngavar)	EU081671	EU081746	Kyriazi et al. 2008
Im2		<i>O. elegans</i>	Iran (Harsin)	EU081672	EU081747	Kyriazi et al. 2008
Im3		<i>O. elegans</i>	Iran (Kermanshah)	EU081669	EU081744	Kyriazi et al. 2008
Im4		<i>O. elegans</i>	Iran (Kermanshah)	EU081668	EU081743	Kyriazi et al. 2008
Im5		<i>O. elegans</i>	Iran (Kermanshah)	EU081670	EU081745	Kyriazi et al. 2008
Im6		<i>O. e. elegans</i>	Iran (Islam Abade- Charb)	EU081666	n.a	Kyriazi et al. 2008
Im7		<i>O. e. elegans</i>	Iran (Kurdistan-Sarvabad)	EU081665	EU081742	Kyriazi et al. 2008
Im8		<i>O. e. elegans</i>	Iran (Kurdistan-Sarvabad)	EU081664	EU081741	Kyriazi et al. 2008
Im9		<i>O. e. elegans</i>	Iran (Chasr-e-shirin)	EU081667	n.a	Kyriazi et al. 2008
Arm1		<i>O. e. elegans</i>	Armenia (Chosrov)	AF206532	AF206605	Kyriazi et al. 2008
Isr1		<i>O. elegans</i>	Israel (Mezudat Nimrod)	EU081660	EU081731	Kyriazi et al. 2008
Isr2		<i>O. elegans</i>	Israel (Nahal Zin)	EU081662	n.a	Kyriazi et al. 2008
Isr3		<i>O. elegans</i>	Israel (Nahal Zin)	EU081663	EU081732	Kyriazi et al. 2008
Isr4		<i>O. elegans</i>	Israel (Nahal Zin)	EU081661	n.a	Kyriazi et al. 2008
Jor1		<i>O. e. ehrenbergii</i>	Jordan (Azrap)	EU081656	EU081729	Kyriazi et al. 2008
Jor2		<i>O. e. ehrenbergii</i>	Jordan (Al Manshiyya)	EU081654	EU081727	Kyriazi et al. 2008
Jor3		<i>O. e. ehrenbergii</i>	Jordan (Thygratal Jubba)	EU081651	EU081724	Kyriazi et al. 2008
Jor4		<i>O. e. ehrenbergii</i>	Jordan (Dana Natural Reserve)	EU081652	EU081725	Kyriazi et al. 2008
Jor5		<i>O. e. ehrenbergii</i>	Jordan (Jerash)	EU081650	EU081723	Kyriazi et al. 2008
Jor6		<i>O. e. ehrenbergii</i>	Jordan (Zai park)	EU081655	EU081728	Kyriazi et al. 2008
Jor7		<i>O. e. ehrenbergii</i>	Jordan (Al Tafila)	EU081653	EU081726	Kyriazi et al. 2008
Leb1		<i>O. e. ehrenbergii</i>	Lebanon (Bsharri)	EU081659	EU081730	Kyriazi et al. 2008
Leb2		<i>O. e. ehrenbergii</i>	Lebanon (Bsharri)	EU081657	n.a	Kyriazi et al. 2008
Leb3		<i>O. e. ehrenbergii</i>	Lebanon (Bsharri)	EU081658	n.a	Kyriazi et al. 2008
Syr1		<i>O. e. ehrenbergii</i>	Syria (Qal' at Al Rahbeh castle)	EU081646	EU081718	Kyriazi et al. 2008
Syr2		<i>O. e. ehrenbergii</i>	Syria (As Suhlnah)	EU081645	EU081717	Kyriazi et al. 2008
Syr3		<i>O. e. ehrenbergii</i>	Syria (Rocky desert)	EU081644	EU081716	Kyriazi et al. 2008
Syr4		<i>O. e. ehrenbergii</i>	Syria (Kanaten Tafianaz)	EU081647	EU081719	Kyriazi et al. 2008
Syr5		<i>O. e. ehrenbergii</i>	Syria (Al Badiah desert)	EU081643	EU081715	Kyriazi et al. 2008
Syr6		<i>O. e. ehrenbergii</i>	Syria (40 km A.Homs)	EU081648	EU081720	Kyriazi et al. 2008
Syr7		<i>O. e. ehrenbergii</i>	Syria (Preij, 40 km N.Homs)	n.a	EU081721	Kyriazi et al. 2008
Syr8		<i>O. e. ehrenbergii</i>	Syria (Preij, 40 km N.Homs)	EU081649	EU081722	Kyriazi et al. 2008
Syr9		<i>O. e. ehrenbergii</i>	Syria (Buraq)	n.a	EU081709	Kyriazi et al. 2008
Syr10		<i>O. e. ehrenbergii</i>	Syria (Buraq)	n.a	EU081710	Kyriazi et al. 2008
Syr11		<i>O. e. ehrenbergii</i>	Syria (Nizran)	EU081642	EU081711	Kyriazi et al. 2008
Syr12		<i>O. e. ehrenbergii</i>	Syria (Alawit mount. range)	n.a	EU081712	Kyriazi et al. 2008
Syr13		<i>O. e. ehrenbergii</i>	Syria (Maqum Assayedh)	n.a	EU081713	Kyriazi et al. 2008
Syr14		<i>O. e. ehrenbergii</i>	Syria (Lattaakia beach)	n.a	EU081714	Kyriazi et al. 2008
Lib1		<i>O. elegans</i>	Libya (semi-desert Igdeida)	EU081675	n.a	Kyriazi et al. 2008
Lib2		<i>O. elegans</i>	Libya (Conduka-Al Beida)	EU081677	EU081751	Kyriazi et al. 2008
Lib3		<i>O. elegans</i>	Libya (waterfall)	EU081676	EU081750	Kyriazi et al. 2008
Lib4		<i>O. elegans</i>	Libya (canyon after NatPark)	EU081674	EU081749	Kyriazi et al. 2008
Lib5		<i>O. elegans</i>	Libya (Kyrinis-Apolonias)	EU081673	EU081748	Kyriazi et al. 2008

Grc1	<i>O. e. macrodactylus</i>	Greece (Simenia)	EU081619	EU081690	Kyriazi et al. 2008
Grc2	<i>O. e. macrodactylus</i>	Greece (Thrace)	EU081623	EU081694	Kyriazi et al. 2008
Aeg1	<i>O. e. macrodactylus</i>	Greece (Lesvos)	n.a	EU081686	Kyriazi et al. 2008
Aeg2	<i>O. e. macrodactylus</i>	Greece (Lesvos)	n.a	EU081685	Kyriazi et al. 2008
Aeg3	<i>O. e. macrodactylus</i>	Greece (Lesvos)	EU081616	EU081687	Kyriazi et al. 2008
Aeg4	<i>O. e. macrodactylus</i>	Greece (Samos)	EU081613	n.a	Kyriazi et al. 2008
Aeg5	<i>O. e. macrodactylus</i>	Greece (Ikaria)	EU081611	n.a	Kyriazi et al. 2008
Aeg6	<i>O. e. macrodactylus</i>	Greece (Patmos)	EU081614	EU081683	Kyriazi et al. 2008
Aeg7	<i>O. e. macrodactylus</i>	Greece (Pserimos)	EU081618	EU081689	Kyriazi et al. 2008
Aeg8	<i>O. e. macrodactylus</i>	Greece (Pserimos)	EU081617	EU081688	Kyriazi et al. 2008
Aeg9	<i>O. e. macrodactylus</i>	Greece (Nisyros - Lies)	EU081621	EU081692	Kyriazi et al. 2008
Aeg10	<i>O. e. macrodactylus</i>	Greece (Nisyros - Giali)	EU081620	EU081691	Kyriazi et al. 2008
Aeg11	<i>O. e. macrodactylus</i>	Greece (Nisyros)	EU081622	EU081693	Kyriazi et al. 2008
Aeg12	<i>O. e. macrodactylus</i>	Greece (Tilos)	EU081615	EU081684	Kyriazi et al. 2008
Aeg13	<i>O. e. macrodactylus</i>	Greece (Rodos-Salakos)	EU081612	EU081682	Kyriazi et al. 2008
Cyp1	<i>O. elegans</i>	Cyprus (Larnaka)	n.a	EU081734	Kyriazi et al. 2008
Cyp2	<i>O. elegans</i>	Cyprus (Larnaka Kamares)	n.a	EU081733	Kyriazi et al. 2008
Cyp3	<i>O. elegans</i>	Cyprus	n.a	EU081739	Kyriazi et al. 2008
Cyp4	<i>O. elegans</i>	Cyprus (Pareklisia)	n.a	EU081738	Kyriazi et al. 2008
Cyp5	<i>O. elegans</i>	Cyprus Roudia	n.a	EU081740	Kyriazi et al. 2008
Cyp6	<i>O. elegans</i>	Cyprus (Lemosos)	n.a	EU081735	Kyriazi et al. 2008
Cyp7	<i>O. elegans</i>	Cyprus (Arkouda)	n.a	EU081737	Kyriazi et al. 2008
Cyp8	<i>O. elegans</i>	Cyprus	n.a	EU081736	Kyriazi et al. 2008
Ant1	<i>O. e. macrodactylus</i>	Turkey (Kas)	EU081626	EU081696	Kyriazi et al. 2008
Ant2	<i>O. e. macrodactylus</i>	Turkey (15 km E of Kas)	EU081625	EU081695	Kyriazi et al. 2008
Ant3	<i>O. e. macrodactylus</i>	Turkey (Manavgat)	EU081627	EU081697	Kyriazi et al. 2008
Ant4	<i>O. e. centralannatoline</i>	Turkey (Karahamzeli)	EU081630	EU081699	Kyriazi et al. 2008
Ant5	<i>O. e. centralannatoline</i>	Turkey (Iuz Golt)	EU081631	EU081700	Kyriazi et al. 2008
Ant6	<i>O. e. centralannatoline</i>	Turkey (Göksül Deltaşı, İçel)	EU081628	n.a	Kyriazi et al. 2008
Ant7	<i>O. e. centralannatoline</i>	Turkey (Ulukışla)	EU081634	EU081703	Kyriazi et al. 2008
Ant8	<i>O. e. centralannatoline</i>	Turkey (Göreme)	EU081633	EU081702	Kyriazi et al. 2008
Ant9	<i>O. e. centralannatoline</i>	Turkey (Demirkazık)	EU081632	EU081701	Kyriazi et al. 2008
Ant10	<i>O. e. centralannatoline</i>	Turkey (Kayseri)	EU081629	EU081698	Kyriazi et al. 2008
Ant11	<i>O. e. ehrenbergii</i>	Turkey (Gaziantep)	EU081641	EU081708	Kyriazi et al. 2008
Ant12	<i>O. e. ehrenbergii</i>	Turkey (Zaziantep)	EU081640	EU081707	Kyriazi et al. 2008
Ant13	<i>O. e. centralannatoline</i>	Turkey (Karakurt)	EU081635	EU081704	Kyriazi et al. 2008
Ant14	<i>O. e. elegans</i>	Turkey (Iac Van)	EU081636	n.a	Kyriazi et al. 2008
Ant15	<i>O. e. centralannatoline</i>	Turkey (Kuskukiran Gecidi)	EU081638	EU081706	Kyriazi et al. 2008
Ant16	<i>O. e. centralannatoline</i>	Turkey (Saz Gölü)	EU081637	EU081705	Kyriazi et al. 2008
Ant17	<i>O. e. elegans</i>	Turkey (Aralık)	EU081639	n.a	Kyriazi et al. 2008
Ant18	<i>O. e. elegans</i>	Turkey (Mutlugün Village-Yusufoğlu/Artvin)	KM011514/ KM011515/ KM011516/ KM011517	KM011341/n.a/ KM011342/ KM011343	Present Study
Ant19	<i>O. e. centralannatoline</i>	Turkey (Between Erzincan and Rehahiye/Erzincan)	KM011518	KM011344	Present Study
Ant20	<i>O. e. centralannatoline</i>	Turkey (Between Koyulhisar and Susehir/Sivas)	KM011519	KM011345	Present Study
Ant21	<i>O. e. centralannatoline</i>	Turkey (Between Nisak and Başçiftlik/Tokat)	KM011520/ KM011521	KM011346/ KM011347	Present Study
Ant22	<i>O. e. centralannatoline</i>	Turkey (Ebulhayr Village-Sarısoğan/Kayseri)	KM011522/ KM011523	KM011348/ KM011349	Present Study
Ant23	<i>O. e. centralannatoline</i>	Turkey (Between İsklip and Osmançık/Çorum)	KM011524/ KM011525/n.a	KM011350/ KM011351/ KM011352	Present Study
Ant24	<i>O. e. centralannatoline</i>	Turkey (Between Kalecik and Çankırı/Çankırı)	KM011526/ KM011527/ KM011528/n.a	KM011353/ KM011354/ KM011355/ KM011356	Present Study
Ant25	<i>O. e. centralannatoline</i>	Turkey (Between Haymana and Gölbaşı/Ankara)	KM011529/n.a/n.a	KM011357/ KM011358/ KM011359	Present Study
Ant26	<i>O. e. centralannatoline</i>	Turkey (Between Polatlı and Haymana/Ankara)	KM011530/ KM011531/n.a/n.a	KM011360/ KM011361/ KM011362/ KM011363	Present Study

Ant27	<i>O. e. macrodactylus</i>	Turkey (Between Aslanapa and Çavdarhisar/ Kütahya)	KM011532	KM011364	Present Study
Ant28	<i>O. e. macrodactylus</i>	Turkey (Between Simav and Demirci/Kütahya)	KM011532	KM011364	Present Study
Ant29	<i>O. e. macrodactylus</i>	Turkey (Between Şarköy and Mürefte/Tekirdağ)	KM011533	KM011365	Present Study
Ant30	<i>O. e. macrodactylus</i>	Turkey (Canakkale)	KM011534/ KM011535/n.a/n.a	KM011366/ n.a/ KM011367/ KM011368	Present Study
Ant31	<i>O. e. macrodactylus</i>	Turkey (Bozcaada/Canakkale)	KM011537	KM011370	Present Study
Ant32	<i>O. e. macrodactylus</i>	Turkey (Kuşadası/ Aydın)	KM011539	KM011372	Present Study
Ant33	<i>O. e. macrodactylus</i>	Turkey (Salih Adası-Bodrum/Muğla)	KM011540/n.a	KM011373/ KM011374	Present Study
Ant34	<i>O. e. macrodactylus</i>	Turkey (Kepez/ Aydın)	KM011541/n.a/n.a	KM011375/ KM011376/ KM011377	Present Study
Ant35	<i>O. e. macrodactylus</i>	Turkey (Tralles/ Aydın)	KM011542	KM011378	Present Study
Ant36	<i>O. e. macrodactylus</i>	Turkey (Tavşan Adası/Muğla)	KM011543/n.a	KM011379/ KM011380	Present Study
Ant37	<i>O. e. macrodactylus</i>	Turkey (Çime/ Aydın)	KM011544	KM011381	Present Study
Ant38	<i>O. e. macrodactylus</i>	Turkey (Kula/Manisa)	KM011545/n.a	KM011382/ KM011383	Present Study
Ant39	<i>O. e. macrodactylus</i>	Turkey (Tersane Adası-Göcek/Muğla)	KM011546/ KM011547	n.a/ KM011384	Present Study
Ant40	<i>O. e. macrodactylus</i>	Turkey (Babadag-Fethiye/Muğla)	KM011548/ KM011549/ KM011550	KM011385/ KM011386/ KM011387	Present Study
Ant41	<i>O. e. macrodactylus</i>	Turkey (Uşak)	KM011551/ KM011552/ KM011553	KM011388/ KM011389/ KM011390	Present Study
Ant42	<i>O. e. macrodactylus</i>	Turkey (Uşak)	KM011554/ KM011555/ KM011556	KM011391/ KM011392/ KM011393	Present Study
Ant43	<i>O. e. macrodactylus</i>	Turkey (Sivashi/ Uşak)	KM011557/ KM011558	KM011394/ KM011395	Present Study
Ant44	<i>O. e. macrodactylus</i>	Turkey (Civril/ Denizli)	KM011559/ KM011560/ KM011561/ KM011562	KM011396/ KM011397/ KM011398/ KM011399	Present Study
Ant45	<i>O. e. macrodactylus</i>	Turkey (Beydilli-Çivril/Denizli)	KM011563/ KM011564	KM011400/ KM011401	Present Study
Ant46	<i>O. e. macrodactylus</i>	Turkey (Simav/Kütahya)	KM011565	KM011402	Present Study
Ant47	<i>O. e. macrodactylus</i>	Turkey (Dinar/ Afyonkarahisar)	KM011566/ KM011567/n.a	KM011403/ KM011404/ KM011405	Present Study
Ant48	<i>O. e. macrodactylus</i>	Turkey (Sandikli/ Afyonkarahisar)	n.a	KM011406	Present Study
Ant49	<i>O. e. macrodactylus</i>	Turkey (Kale/Antalya)	KM011568	KM011407	Present Study
Ant50-Ant51	<i>O. e. centralmatoline</i>	Turkey (Between Eğirdir and Gelendost/Isparta)	KM011569/ KM011570/ KM011571/ KM011572/ KM011573	KM011408/ KM011409/ KM011410/ KM011411/ KM011412	Present Study
Ant52	<i>O. e. macrodactylus</i>	Turkey (Eber-Akşehir/ Konya)	KM011574/ KM011575/n.a	KM011413/ KM011414/ KM011415	Present Study
Ant53	<i>O. e. macrodactylus</i>	Turkey (Akşehir/ Konya)	KM011576	KM011416	Present Study
Ant54	<i>O. e. macrodactylus</i>	Turkey (Manavgat/ Antalya)	KM011577	KM011417	Present Study
Ant55	<i>O. e. macrodactylus</i>	Turkey (20 km to Derebucak-Beyşehir/ Konya)	KM011578/ KM011579/ KM011580/n.a	KM011418/ KM011419/ KM011420/ KM011421	Present Study
Ant56	<i>O. e. basoglutı</i>	Turkey (Kızılot Beach-Manavgat/ Antalya)	KM011581/n.a	KM011422/ KM011423	Present Study
Ant57	<i>O. e. macrodactylus</i>	Turkey (Beyşehir/ Konya)	KM011582/ KM011583/ KM011584	KM011424/ KM011425/ KM011426	Present Study
Ant58	<i>O. e. macrodactylus</i>	Turkey (Çiftlikköy-Beyşehir/ Konya)	KM011585/ KM011586/ n.a	KM011427/ KM011428/ KM011429	Present Study
Ant59	<i>O. e. macrodactylus</i>	Turkey (27 km to Akseki/ Antalya)	n.a	KM011430	Present Study
Ant60	<i>O. e. macrodactylus</i>	Turkey (30 km to Gündoğmuş/Antalya)	KM011587/ KM011588/ KM011589/ n.a	KM011431/ KM011432/ KM011433/ KM011434	Present Study
Ant61	<i>O. e. basoglutı</i>	Turkey (Ilgın/ Konya)	KM011590/ n.a	KM011435/ KM011436	Present Study
Ant62	<i>O. e. basoglutı</i>	Turkey (Melleç-Anamur/ Mersin)	KM011591/ KM011592/ n.a/ n.a	KM011437/ KM011438/ KM011439/ KM011440	Present Study
Ant63	<i>O. e. basoglutı</i>	Turkey (Bozyazı-Anamur/ Mersin)	KM011594/ n.a	KM011443/ KM011444	Present Study
Ant64	<i>O. e. basoglutı</i>	Turkey (Between Aydnak and Gülnar/ Mersin)	KM011595/ KM011596/ n.a	KM011445/ KM011446/ KM011447	Present Study
Ant65	<i>O. e. basoglutı</i>	Turkey (Between Aydnak and Gülnar/ Mersin)	KM011597/ n.a	KM011448/ KM011449	Present Study
Ant66	<i>O. e. macrodactylus</i>	Turkey (Alahan-Mut/ Mersin)	KM011598	KM011450	Present Study
Ant67	<i>O. e. basoglutı</i>	Turkey (Between Bozağaç and Gülnar/ Mersin)	KM011599	KM011451	Present Study
Ant68	<i>O. e. basoglutı</i>	Turkey (Between Mut and Gülnar/ Mersin)	KM011600/ KM011601/ n.a	KM011452/ KM011453/ KM011454	Present Study
Ant69	<i>O. e. basoglutı</i>	Turkey (Between Bozağaç and Gülnar/ Mersin)	KM011602/ n.a	KM011455/ KM011456	Present Study
Ant70	<i>O. e. basoglutı</i>	Turkey (Silifke/ Mersin)	KM011603/ KM011604/ n.a	KM011457/ KM011458/ KM011459	Present Study
Ant71	<i>O. e. centralmatoline</i>	Turkey (Between Avanos and Göreme/ Nevşehir)	KM011605	KM011460	Present Study
Ant72	<i>O. e. ehrenbergii</i>	Turkey (Akyatan/ Adana)	n.a	KM011461	Present Study
Ant73	<i>O. e. ehrenbergii</i>	Turkey (Adana)	KM011606	KM011462	Present Study
Ant74	<i>O. e. centralmatoline</i>	Turkey (Yahyalı/ Kayseri)	KM011607/ KM011608/ n.a/ n.a/ n.a	KM011463/ KM011464/ KM011465/ KM011466/ KM011467	Present Study
Ant75	<i>O. e. ehrenbergii</i>	Turkey (Şakşak-Harbiye/ Hatay)			Present Study

Ani76	9/8/-	<i>O. e. ehrenbergii</i>	Turkey (Sofular-Harbiye/Hatay)	KM011609/ KM011610/ KM011611/ KM011612	KM011468/ KM011469/ KM011470/ KM011471	Present Study
Ani77	3/-/-	<i>O. e. ehrenbergii</i>	Turkey (Cardak Yaylasi-Hassa/Hatay)	KM011613/ KM011614/ KM011615	KM011472/ KM011473/ KM011474	Present Study
Ani78	4/2/-	<i>O. e. ehrenbergii</i>	Turkey (Dumanlı Yaylasi-Düzci/Osmaniye)	KM011616/ KM011617/ n.a	KM011475/ KM011476/ KM011477	Present Study
Ani79	1/-/-	<i>O. e. ehrenbergii</i>	Turkey (Between Kilis and Hassa/Kilis)	KM011618	KM011478	Present Study
Ani80	5/3/-	<i>O. e. ehrenbergii</i>	Turkey (Polateli/Kilis)	KM011619	KM011479	Present Study
Ani81	3/1/-	<i>O. e. ehrenbergii</i>	Turkey (Dokurcum Village/Gaziantep)	KM011620/ KM011621	KM011480/ KM011481	Present Study
Ani82	3/5/-	<i>O. e. ehrenbergii</i>	Turkey (17 km to Yavuzeli/Gaziantep)	KM011622/ KM011623/ n.a	KM011482/ KM011483/ KM011484	Present Study
Ani84	2/-/-	<i>O. e. centralanatoliae</i>	Turkey (Between Halfeti and Birecik/Sanlıurfa)	KM011626	KM011488	Present Study
Ani85		<i>O. e. centralanatoliae</i>	Turkey (Adıyaman)	KM011627/ KM011628	KM011489/ KM011490	Present Study
Ani86	3/2/-	<i>O. e. centralanatoliae</i>	Turkey (Küçükakamlı/Sanlıurfa)	KM011629/ KM011630/ KM011631	KM011491/ KM011492/ KM011493	Present Study
Ani87		<i>O. e. centralanatoliae</i>	Turkey (Between Diyarbakır and Siverek/Diyarbakır)	KM011632/ KM011632/ n.a	KM011494/ KM011495/ KM011496	Present Study
Ani88	7/1/-	<i>O. e. elegans</i>	Turkey (Derik/Mardin)	KM011634/ KM011635/ KM011636	KM011497/ KM011498/ KM011499	Present Study
Ani89	1/2/-	<i>O. e. elegans</i>	Turkey (Savur-Midyat/Mardin)	KM011637/ KM011638	KM011500/ KM011501	Present Study
Ani90	2/2/-	<i>O. e. elegans</i>	Turkey (Between Batman and Hasanköy/Batman)	KM011639/ KM011640/ KM011641	KM011502/ KM011503/ KM011504	Present Study
Ani91		<i>O. e. centralanatoliae</i>	Turkey (Yalmazçamlar Village-Tatvan/Bitlis)	KM011642	KM011505	Present Study
Ani92	6/2/-	<i>O. e. centralanatoliae</i>	Turkey (Tatvan/Bitlis)	KM011643/ KM011644	KM011506/ KM011507	Present Study
Ani93	6/3/-	<i>O. e. centralanatoliae</i>	Turkey (Between Tatvan and Van/Bitlis)	KM011645/ KM011646	KM011508/ KM011509	Present Study
Ani94		<i>O. e. centralanatoliae</i>	Turkey (Between Erciş and Patnos/Ağrı)	KM011647	KM011510	Present Study
Ani95	8/6/-	<i>O. e. elegans</i>	Turkey (Between Van and Gürpınar/Van)	KM011648/ KM011649/ KM011650/ KM011651	n.a/ KM011511/ n.a/ KM011512	Present Study
Ani96		<i>O. e. elegans</i>	Turkey (Between Van and Özalp/Van)	KM011652	KM011513	Present Study
	2/-/-	<i>O. e. elegans</i>	Turkey (Çevreli Village-Yusufeli/Artvin)			Present Study
	-/1/-	<i>O. e. ehrenbergii</i>	Turkey (Yukarı Burhaniye-Mansurlu/Adana)			Present Study
	1/3/-	<i>O. e. centralanatoliae</i>	Turkey (Boğaköy/Amsaya)			Present Study
	1/1/-	<i>O. e. basoglutii</i>	Turkey (Akseki/Antalya)			Present Study
	9/6/-	<i>O. e. basoglutii</i>	Turkey (Between Alanya and Silifke/Antalya)			Present Study
	3/-/2	<i>O. e. macrodactylus</i>	Turkey (Taşanbükü Adası/Muğla)			Present Study
	5/5/-	<i>O. e. macrodactylus</i>	Turkey (Fener Adası-Foça/Izmir)			Present Study
	5/12/-	<i>O. e. macrodactylus</i>	Turkey (Garip Adası-Dikili/Izmir)			Present Study
	4/5/-	<i>O. e. macrodactylus</i>	Turkey (Çatal Adası-Bodrum/Muğla)			Present Study
	8/10/-	<i>O. e. macrodactylus</i>	Turkey (İmralı Adası/Marmara Sea)			Present Study
	4/8/-	<i>O. e. macrodactylus</i>	Turkey (Paşalimanı Adası/Marmara Sea)			Present Study