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Geographic variation in the skull morphology of *Ellobius lutescens* Thomas, 1897 (Mammalia: Rodentia) by geometric morphometric analyses

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Abstract

In this study, we examined a total of 43 samples belonging to three *Ellobius lutescens* populations from Turkey, Iran and Nakhchivan, which are geographically separated by the Zagros, Tendürek and Alborz mountain ranges. We applied geometric morphometric methods (GMMs) to explore the differences in size and shape of the cranium and mandible. Indeed, we intriguingly found that the populations differed in cranium but not mandible size. Comparison of the Iranian and Turkish populations alone revealed morphological differences in the shape of the cranium and mandible that could be used as a barometer to predict the origin of individual animals. Importantly, our findings indicate that the Zagros and Tendürek mountain ranges may have acted as a barrier between these two populations, resulting in evolutionary divergence in these anatomical features. Consequently, we propose that within *E. lutescens,* subspecies including *E. lutescens woosnami* exists and in time, genetic, besides geographical barriers, may prevent subspecies from interbreeding with each other.

Key words

Ellobius, Cranial Variation, Geometric Morphometrics, Turkey, Iran.

Introduction

The Palearctic mole voles (genus *Ellobius*) are adapted to underground life; five species are currently recognized: *E. fuscocapillus, E. lutescens* (*Afganomys*), *E. talpinus*, *E. tancrei* and *E. alaicus* (*Ellobius*). The voles of this genus occur from Eastern Europe to Central Asia, and from Ukraine, Kazakhstan and Mongolia to Turkey and Iran. *E. lutescens* is distributed in Iran, Armenia, Azerbaijan and East Anatolia (Musser & Carleton 2005).

E. lutescens (Transcaucasian mole vole) was described on the basis of six specimens collected from Van-Ercek (Thomas 1897). *E. lutescens* was considered a valid species, different from *E. fuscocapillus*, and distributed in East Anatolia by Ellerman (1941), Vinogradov & Argiropulo (1941) and Osborn (1962). However, Walker (1964), Lay (1967), Hassinger (1973), Corbet (1978), Morlok (1978), Doğramaci (1989), Harrison & Bates (1991) state that the species occur in East Anatolia was *E. fuscocapillus*. Lay (1967) define *E. fuscocapillus* and *E. lutescens* as distinct, but possible subspecies. Harrison & Bates (1992) announced that *E. lutescens* was synonymous with *E. fuscocapillus*. Coşkun (1997, 2001) and Coşkun & Ulutürk (2003) report that a single species occurs (*E. lutescens* Thomas 1897) of the genus *Ellobius* in Turkey. The first record of *Ellobius* from Iran was *E. lutescens woosnami* (synonym of *E. lutescens*) by Thomas (1905), collected from Isfahan province. Moradi & Kivanç (2003) and Ellerman & Morrison-Scott (1951) stated that three species of the genus *Ellobius* occur (*E. fuscocapillus, E. lutescens* and *E. talpinus*) in Iran. Also, Moradi & Kivanç (2003) clarified the status of *E. woosnami* and *E. fuscocapillus legendrei* (synonym of *E. fuscocapillus*).

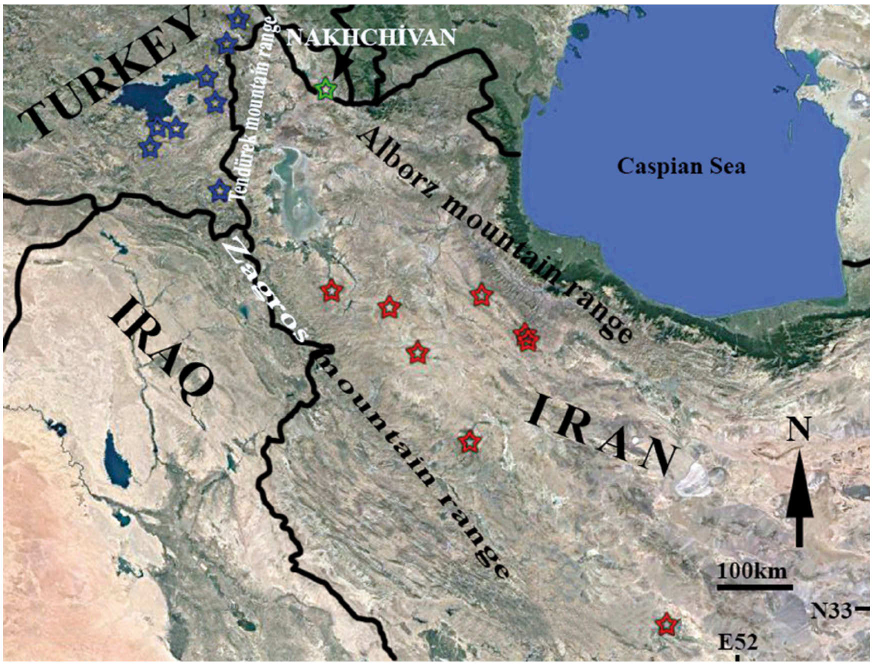

Fig. 1. Sample locations (Blue: Turkish population, Green: Nakhchivan sample, Red: Iranian population).

The habitat range of *E. lutescens* and *E. fuscocapillus* has become clear only very recently due to extensive karyotyping. *E. lutescens* has 2n = 17 (Matthey 1953, 1958, Zima & Kral 1984, Coşkun 1997, 2001, Coşkun & Ulutürk 2003, Romanenko *et al*. 2007), *E. fuscocapillus* 2n = 36 (Moradi & Kivanç 2003, Borisov *et al*. 1991).

Geometric morphometrics methods (GMMs) deal directly with the Cartesian coordinates of anatomical landmarks and are a strong tool in taxonomy and systematic which have a noteworthy statistical power (Rohlf & Bokstein 1990, Bookstein 1991, Klingenberg 2011). Such statistical models may reveal subtle morphological variations in the size and shape of various bone structures, which may be undetectable by traditional morphometric approaches (Klingenberg *et al*. 2002, Baylac *et al*. 2003, Adams *et al*. 2004, Zelditch *et al*. 2004, Mitteroecker & Gunz 2009). Such changes might provide hints of sub-species divergence within what is considered a single species. GMMs have advantages over traditional methods of analyzing biological material. (1) The use of landmarks by this approach anchors the descriptions of shape differences and potential explanations for those shape differences in specific regions of the organism. (2) This approach provides independent measurements based on size and shape. (3) Potential shape differences can be visualized easily by deformation grids (Rohlf 2000, Slice 2001, Macleod & Forey 2002, Janžekovič & Kryštufek 2004, Klingenberg 2013).

GMMs analysis has gone through a revolution during the last twenty five years, with a large number of books (Elewa 2010, Macleod & Forey 2002, Hammer, 2002) and journals devoted to this method (Cooke & Terhune 2015, Meloro *et al*. 2014, Collyer & Adams 2013, Polly *et al*. 2013, O'Higgins & Milne 2013, Monteiro 2013, Mitteroecker *et al*. 2013, Adams *et al*. 2013). The field of GMMs is rapidly developing and recent advances allow for geometric techniques to be applied easily to many zoological problems (Adams *et al*. 2011, Adams 2014, Álvarez *et al*. 2015, Caumul & Polly 2005, Jojić *et al*. 2014, Klenovšek & Kryštufek 2013)

The goal of this study was thus to compare the size and shape differences of the ventral cranium and mandible between three populations of *E. lutescens* that were collected from Iran, Nakhchivan and Turkey and geographically separated by the Zagros, Tendürek and Alborz mountain ranges.

Material and Methods

In this study, 43 *E. lutescens* from 18 sites in Iran (8♀, 10♂), Nakhchivan (1?) and Turkey (12♀, 12♂) (Fig. 1) were investigated by GMMs. Almost all samples were verified by morphologically and karyotypically (as this species possesses an XO chromosome system). However, for reasons that are uncertain, we encountered difficulty performing cytogenetic analyses on the Nakhchivan samples. Yet, gross dissection was used to verify their sex and that they were indeed *E. lutescens*. From all samples, pictures of the cranium (ventral side) and mandible (lingual side) were taken by a Pentax X70 digital camera, and the same view and parameters (high, angle, resolution, etc.) were used across all samples (Figure 2 provides example views for the cranium and mandible).

The 15 landmarks from the cranium and 12 landmarks from the mandible (Fig. 2A, B) were digitized by tpsDig 2.17 (Rohlf 2015). The Principal Component Analysis (PCA), Canonical Variance Analysis (CVA), MANOVA, Discriminant Function Analysis (DFA), Procrustes ANOVA were performed by MorphoJ 1.06d (Klingenberg 2011), after GPA (Generalized Procrustes Analysis) was perfomed.

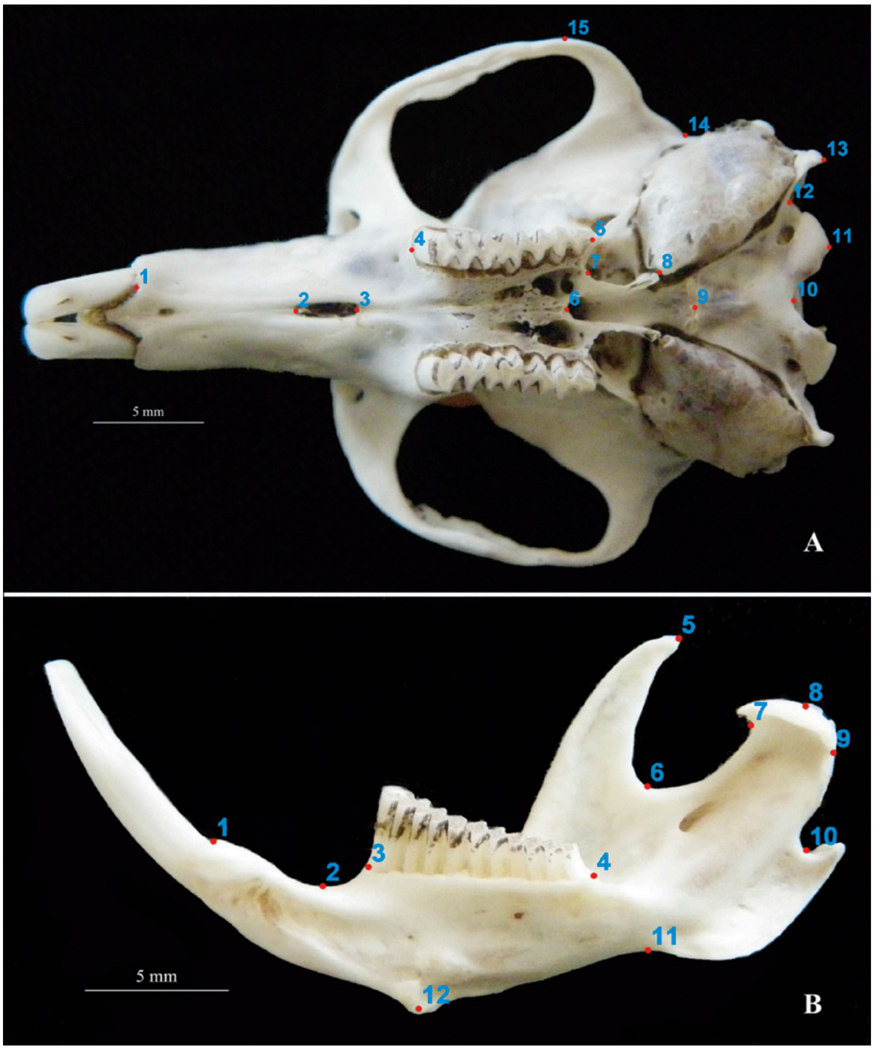

Fig. 2. The landmark locations; **A**: ventral side of cranium, **B**: lingual side of mandible).

Table 1. Procrustes ANOVA results (F: Goodal's F, CS: Centrid Size, Bolded: significant difference).

Individuals	Dataset		F	p-value
Localities	Cranium	CS	11,67	**0,0001**
		Shape	1,61	**0,0047**
	Mandible	CS	0,66	0,5213
		Shape	2,03	**0,0002**

Results

The Procrustes ANOVA indicated that the size (as centroid size) and shape of cranium between localities were significantly different, but just the shape was different for mandible (Table 1). However, there was no difference in the size or shape of the skull between sexes. According to the MANOVA results, only the mandible shape was significantly different between localities (Pillai trace = 1,27, p = 0,0199).

The PC1 and PC2 explain 40.3%, the first five PCs explain 69.3% of the total variation for cranium in the PCA. In the positive and negative directional shape changes affecting PC1 were contraction in rostrum, maxilla, incisive foramen and diastema and expansion in mastoid. Additionally, mesopterygoid fossa came forward and foramen magnum went backward and zygomatic arch became narrow. In the positive and negative directional shape changes affecting PC2 were contraction at lateral and posterior side cranium (Fig. 3A). The PC1 and PC2 explain 46.5%, the first five PCs explain 72.s% of total variation for mandible in PCA. In the positive and negative directional shape changes affecting PC1 were contractions in ascending ramus, incisura mandibula and high of mandible. In the positive and negative directional shape changes affecting PC2 were expansion in condyloid process and contraction in angular process of mandible (Fig. 3B).

In CVA, there were significant difference between all localities according to permutation p values based on Mahalanobis distance and only the samples collected in Iran and Turkey differed significantly according to permutation p values based on Procrustes distance for cranium shape (Table 2). Iran and Turkey samples were also well separated along first canonical axis, and Nakhchivan samples were separated along second axis (Fig. 4A).

Table 2. CVA results for Cranium (Ir: Iran, Nh: Nakhchivan, Tr: Turkey, Mah. Dist.: Mahalanobis distance, Proc. Dist.: Procrustes distance, Perm. p: Permutation p value, Bolded: significant difference).

Groups	Ir		Nh	
	Mah. Dist./Perm. P	Proc. Dist./Perm. p	Mah. Dist./Perm. p	Proc. Dist./Perm. p
Nh	8,3688/**0,0152**	0,0310/0,6279	—	—
Tr	3,6189/**<.0001**	0,0185/**0,0070**	9,0465/**0,0212**	0,0302/0,7794

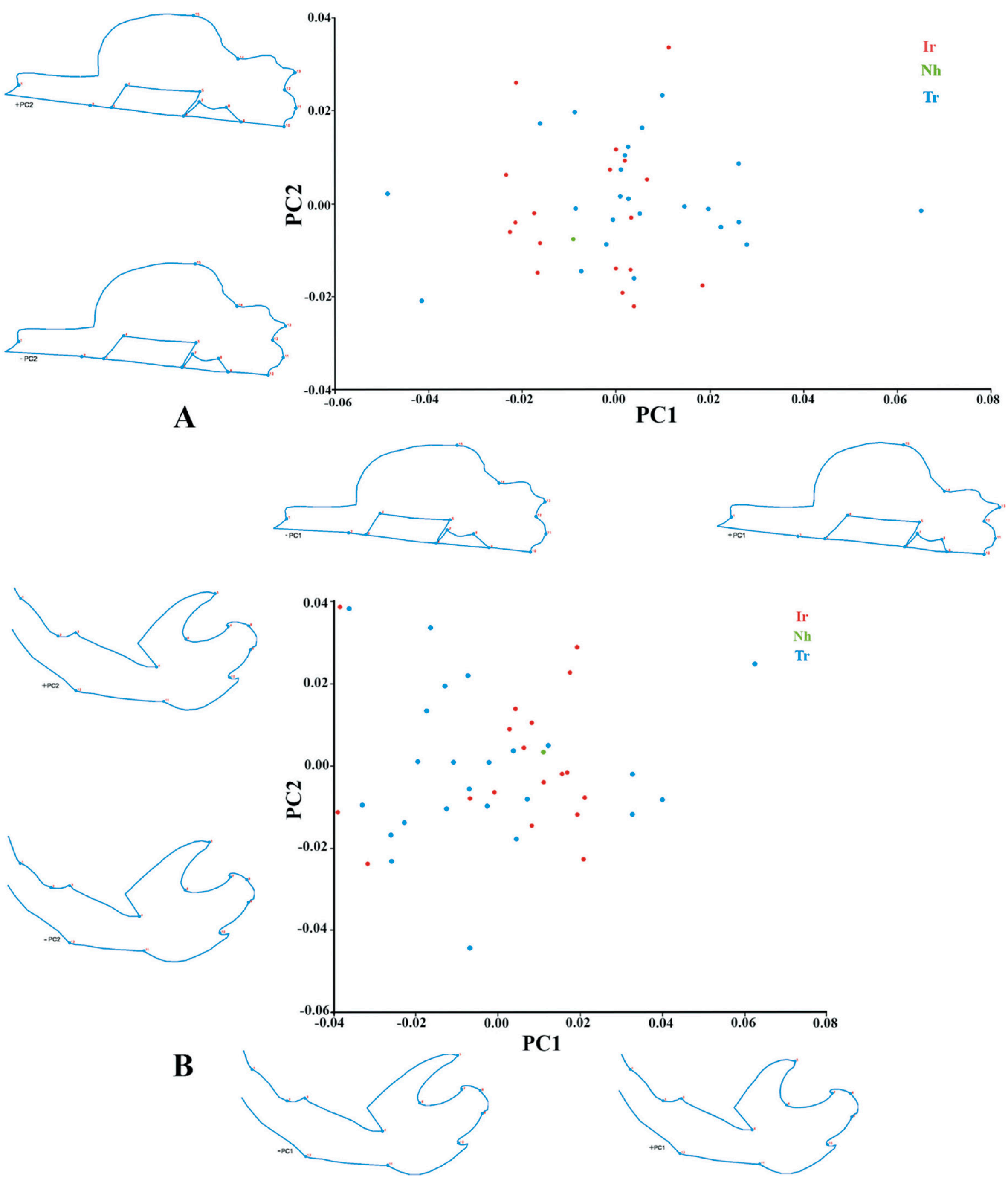

Fig. 3. Scatter plot of PC1 and PC2 of Cranium (**A**) and Mandible (**B**) of *E. lutescens* and shape change associated with negative and positive PC values (Ir: Iran, Red; Nh: Nakhchivan, Green; Tr: Turkey, Blue).

CVA indicate that there were significant differences between three localities according to permutation p values based on Mahalanobis distance and just Iran and Turkey samples were different according to permutation p values based on Procrustes distance for mandible shape (Table 3). According to scatter plot of CVA for mandi-

Table 3. CVA results for the mandibles (Ir: Iran, Nh: Nakhchivan, Tr: Turkey, Mah. Dist.: Mahalanobis distance, Proc. Dist.: Procrustes distance, Perm. p: Permutation p value, Bold: significant difference).

Groups	Ir		Nh	
	Mah. Dist./Perm. P	Proc. Dist./Perm. p	Mah. Dist./Perm. p	Proc. Dist./Perm. P
Nh	5,9480/**0,0435**	0,0338/0,6856	—	—
Tr	4,2279/**<.0001**	0,0246/**0,0003**	6,3002/**0,0164**	0,0352/0,6758

Table 4. DFA results for Cranium (Ir: Iran, Nh: Nakhchivan, Tr: Turkey, T^2: T-square, Param. p: Parametric p values, Perm. p: Permutation p value, Bolded: significant difference).

Groups	Ir			Nh		
	T^2	Param. p	Perm. p (T^2/Proc.)	T^2	Param. p	Perm. p (T^2/Proc.)
Nh	70,5790	0,9410	0,3650/0,6080	—	—	—
Tr	134,7096	0,0905	0,0890/**0,0100**	208,2199	0,8754	0,7110/0,7720

Table 5. DFA results for Mandible (Ir: Iran, Nh: Nakhchivan, Tr: Turkey, T^2: T-square, Param. p: Parametric p values, Perm. p: Permutation p value, Bolded: significant difference).

Groups	Ir			Nh		
	T^2	Param. p	Perm. p (T^2/Proc.)	T^2	Param. p	Perm. p (T^2/Proc.)
Nh	65,8178	0,9486	0,4780/0,6520	—	—	—
Tr	183,8594	**0,0004**	**<.0001/<.0001**	97,6391	0,6495	0,5410/0,6720

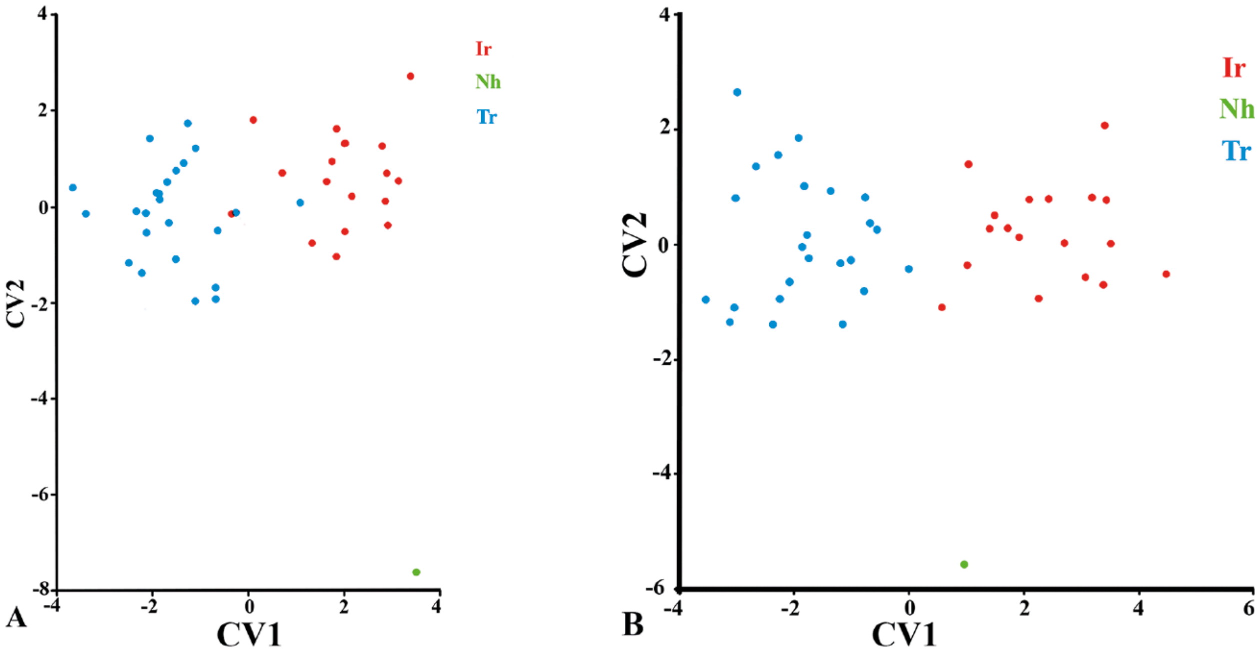

Fig. 4. Result of CVA of Cranium (**A**) and Mandible (**B**) of *E. lutescens* (Ir: Iran, Red; Nh: Nakhchivan, Green; Tr: Turkey, Blue).

ble shape, Iran and Turkey samples separated very well along first axis and Nakhchivan along second (Fig. 4B).

DFA reveal that there were significant differences only between Iran and Turkey samples according to permutation p value based on Procrustes distance for cranium shape (Table 4). According to DFA graphic Iran and Turkey samples were well discriminated. Just one sample from each group was misclassified according to reclassification performed by DFA (Fig. 5A).

DFA results on mandible shape show that there was significant difference between Iran and Turkey samples according to both parametric and permutation p value based on T^2 and procrustes distance (Table 5). DFA graphic show that Iran and Turkey samples discriminated very well and there was not any misclassified according to reclassification performed by DFA (Fig. 5B)

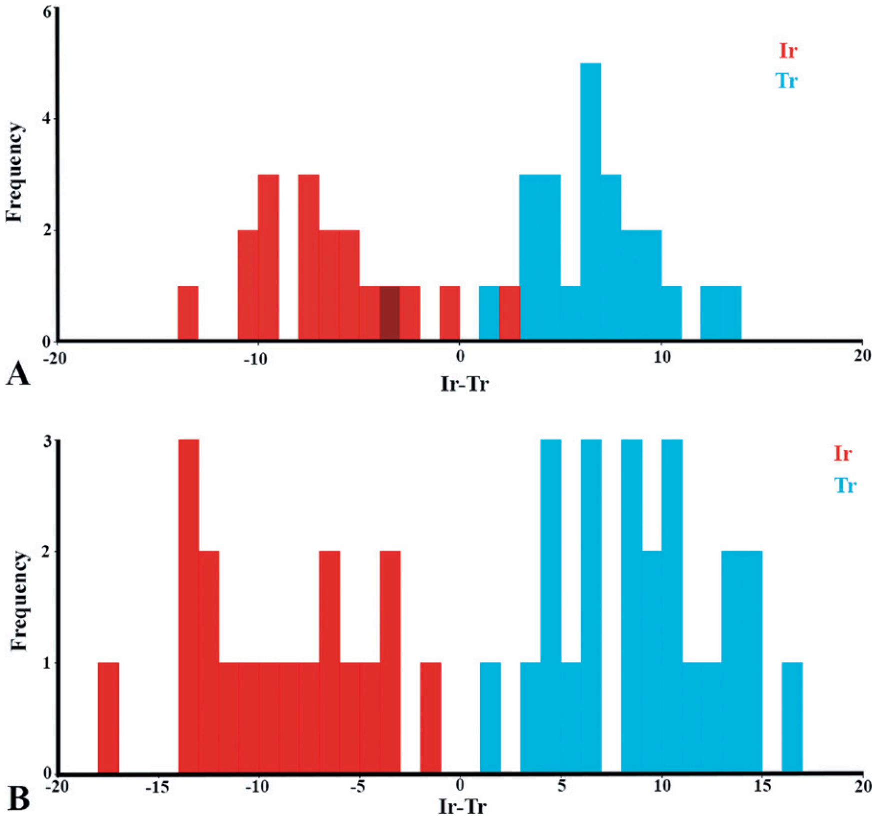

Fig. 5. Result DFA of Cranium (**A**) and Mandible (**B**) of *E. lutescens* (Ir: Iran, Red; Tr: Turkey, Blue)

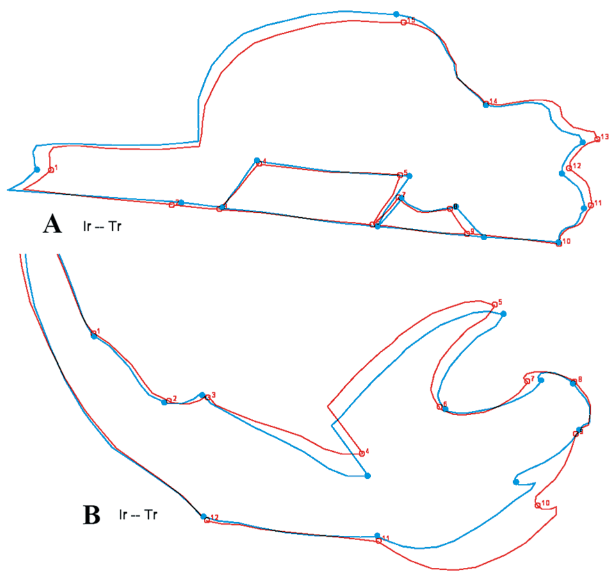

Fig. 6. Mean shape differences based on DFA of Cranium (A) and Mandible (B) of *E. lutescens* (Ir: Iran,Red; Tr: Turkey,Blue).

According to DFA, the mean shape of the cranium of Iranian samples had a shorter rostrum, palatal, upper molar alveolar length and basisphenoid. The incisive foramen elongated anteriorly and the mastoid elongated posteriorly. Zygomatic arch of Iranian samples was narrower than Turkish ones (Fig. 6A). The mean shape of mandible of Iranian samples had a wider incisura mandibula, coronid and angular process. The ascending ramus of the mandible of Iranian samples were broader than in Turkish samples. The height of the mandible of Iranian samples was larger than in Turkish ones. The lower molar alveolar length of Iranian samples was shorter and the diastema length longer than in Turkish samples (Fig. 6B).

Discussions

Procrustes ANOVA reveal that there was a significant difference between populations only for cranium size (CS), however, there were shape differences for both cranium and mandible based on geographic region (Table 1). Kaya & Coşkun (2015) found that females in this species are larger than males for overall size. On the contrary, in the current work, no sexually dimorphic differences were identified for size (CS) and shape of the cranium and mandible. The previously detected sex differences in body size may thus be due to body weight gain rather than skeleton frame differences. Indeed, females tend to gain weight more rapidly than males.

The first two principal components of the mandible explain more of the total variation than the cranium. Shape change that effect the PC1 of the cranium was contraction on facial and expansion on braincase region posteriorly and effect on PC2 was laterally contraction. Shape change that effect PC1and PC2 of mandible was found mostly on ramus part (Fig. 3A and B).

The three localities had significant difference based on Mahalanobis distance, but just Iranian and Turkish populations had significant difference based on Procrustes distance for cranium and mandible (Table 2, 3). The three localities separated well on scatter plot of CVA for both cranium and mandible, but the best separation could be seen on scatter plot of CVA for mandible. Iranian and Turkish populations separated along the first and Nakhchivan population separated along the second axis (Fig 4A and B).

Discriminant function analysis on cranium shape show that Iranian and Turkish populations had significant difference based on Procrustes distance (Table 4) and only one samples from each group was misclassified (Fig. 5A). However, Iranian and Turkish populations had significant difference based on T^2 (Mahalanobis distance) and Procrustes distance for their mandible shape (Table 5) and all samples were reclassified correctly (Fig. 5B). There were no difference between Iranian-Nakhchivan and Turkey-Nahkchivan populations for cranium and mandible.

According to the difference of mean shape of cranium, Iranian populations had shorter and narrower facial region, upper molar alveolar length and basisphenoid and narrower zygomatic arch, however longer incisive foramen and mastoid part than Turkish populations. Mandible shape of Iranian populations had wider incisura mandibula and coronoid process, broader ascending ramus and higher mandible and coronoid process height (Fig. 6A and B). According to the Moradi & Kivanç (2003) and Coşkun (2001), Turkish populations longer than Iranian populations in terms of lower molar alveolar length, incisive foramen, broader zygomatic arch, higher mandible and coronoid height. Our findings are compatible with these prior results. Notwithstanding, Turkish populations are generally shorter than Iranian populations in terms of nasal, upper molar alveolar, upper diastema length and narrower rostrum breadth. Our data differ from that of similar studies performed by Moradi & Kivanç (2003) and Coşkun (2001).

Herein, we found that Iran and Turkey populations were significantly different in size for the cranium but not for the mandible. Populations from Iran and Turkey were significantly different in terms of shape for cranium and mandible with these parameters allowing for definitive predictions to be made as to site where individual samples were collected. This could indicate that the Zagros and Tendürek mountain ranges may have acted as a barrier between these two populations. Our findings provide strong evidence that there subspecies are developing within name *E. lutescens*, including the previously proposed *E. lutescens woosnami* (Thomas 1905). Future studies are needed to perform comprehensive analyses of the skull and external morphology, along with using molecular biological analyses to confirm the existence of these potential subspecies within *E. lutescens*, which may eventually possess both genetic and geographic barriers to interbreeding with each other.

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