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Discrimination of the sister hedgehog species *Erinaceus concolor* and *E. roumanicus* (Erinaceomorpha: Mammalia): a geometric morphometric approach

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Abstract: This study investigates skull variation between the two closely related hedgehog species, *Erinaceus concolor* and *E. roumanicus* by using geometric morphometric analyses based on 2-dimensional landmarks. For this purpose, a total of 68 specimens were evaluated: 54 *E. concolor* and 14 *E. roumanicus*. The results of PCA, ANOVA and MANOVA analyses showed significant shape differences between the species, especially for the dorsal cranium. Shape differences were most prominent on the neurocranium and viscerocranium regions of the dorsal surface of the cranium and in mandibular ramus and the premolar regions. DFA tests were statistically significant against the null hypothesis of equal species means and crossvalidation scores were high enough to distinguish the species. Regression analyses also showed highly significant allometric differences between the two species, for both crania and mandibles. Finally, this study indicates that *E. roumanicus* is not only present in the European part of Turkey, but also in northwestern Anatolia.

Keywords: Erinaceus, dorsal cranium, mandible, shape variation, geometric morphometric, Turkey

1. Introduction

Four species of the genus *Erinaceus* (*E. amurensis*, *E. europaeus*, *E. concolor*, and *E. roumanicus*) are distributed across the Palaearctic region. Of these species, *E. concolor* Martin, 1838 (the southern white-breasted hedgehog) and *E. roumanicus* Barrett-Hamilton, 1900 (the northern white-breasted hedgehog) are found in different geographical regions of Turkey. The range of *E. concolor* covers the Asian part of Turkey (Anatolia), northwestern Iran and the Levant. *E. roumanicus* is mainly confined to the European part of Turkey (Thrace) and is also found in much of Central and Eastern Europe (Filippucci and Simson, 1996; Seddon et al., 2001; Hutterer, 2005). Morphological differentiation between *E. concolor* and *E. roumanicus* may be considered insignificant when compared with their genetic divergence, supporting a sister relationship between these two parapatric species. (Kryštufek, 2002; Bolfikova and Hulva, 2012; Bannikova et al., 2014). Although *E. concolor* and *E. roumanicus* share the same diploid chromosome numbers ($2n = 48$), the distribution of large heterochromatic blocks in autosomes (e.g., the autosome no. 15) was found to be different in the two species, suggesting that taxa are distinguished on some species-specific cytogenetic features (Arslan et al., 2008).

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Conventional morphologic studies previously indicated that a single species, *E. concolor*, was present in Turkey (Doğramacı and Gündüz, 1993; Kryštufek, 2002). Doğramacı and Gündüz (1993) showed that the Thracian and Anatolian hedgehogs were highly similar morphologically except for a few characters such as occipital length and condylobasal length in the skull. Subsequently, the *concolor* and *roumanicus* morphotypes were defined, based on the presence-absence or length of the nasomaxillary suture (Kryštufek, 2002). Both *concolor* and *roumanicus* morphotypes were present in much of western Anatolia and the Levant, however morphometric analyses in the same paper indicated that *roumanicus* specimens were confined to northwestern Anatolia (İzmit and Sakarya), leading Kryštufek (2002) to suggest that the nasomaxillary structure was not a reliable taxonomic character.

Using a landmark-based geometric morphometrics approach, the present study aims to investigate size and shape variations on the dorsal surface of the cranium and the mandible of what are nowadays considered distinct species, *E. concolor* and *E. roumanicus*. Specimens were obtained throughout Turkey, including northwestern Anatolia, where the two species come into contact.

2. Materials and methods

2.1. Study specimens

Adult specimens of *E. concolor* (n = 39 for dorsal cranium, n = 54 for mandible) and *E. roumanicus* (n = 10 for dorsal cranium, n = 14 for mandible) from different locations in Turkey were selected and assessed in this study (Figure 1). Molecular markers (Seddon et al., 2001) and the geographic locations (Doğramacı and Gündüz, 1993; Kryštufek, 2002) were used in the identification of the two species.

The age of specimens was estimated based on the shape of the teeth and interparietal bone. In adult specimens, shape deformations occur on tooth surfaces due to excessive wear and tartar accumulation, and the interparietal process is evident. In juvenile specimens, however, the tooth deformations are less and the interparietal process is slight (Doğramacı and Gündüz, 1993; Chaprazov et al., 2014). These two main characters are used in age determination. Specimens were also considered adult based on a condylobasal length >57 mm for the cranium and length >40 mm for the mandible, because the deformations on the tooth surface and the appearance of the interparietal process were generally compatible with skulls at these threshold values.

The skulls are preserved in the Department of Biology, Faculty of Sciences and Arts, Ondokuz Mayıs University, Samsun, Turkey.

2.2. Imaging and landmarks

The dorsal cranium and mandible (right side) were studied from 2D images. These parts were photographed using a Nikon D5000 (18–55 mm lens) camera mounted on a large flexible tripod and the middle-line of these materials

was set with a scale bar. Thin-plate spline (TPS) series programs were used to prepare and edit datasets. The software tpsUtil version 1.74 (Rohlf, 2015) was used to download the digital images. Two-dimensional landmarks (LM) were digitised on the images of the cranium and mandible using the software tpsDig version 2.31 (Rohlf, 2015). A total of 17 landmarks were set for the dorsal cranium and 18 landmarks for the mandible (Figure S1). Landmark locations on dorsal cranium: premaxillary-maxillary suture (1), beginning point of maxillary breadth (2), nasolacrimal canal (3), anterior point of zygomatic arch (4), anterior part of the orbit (5), frontal-parietal suture (6), back of the orbit (7–8), posterior point of zygomatic arch (9), tympanic bulla notch (10), exterior tip of the occipital crest (11), back of the lateroccipital protuberances (12), parietal-temporal suture (13), nasal-frontal suture (14), midpoint of nasomaxillary suture (15), most anterior points at nasal-premaxillary (16), tip of the nasal (17). Landmark locations on mandible: midpoint of the embedded portion of tooth roots (1–9), the highest points of coronoid process (10–11), ventral point between coronoid and condylar processes (12), the highest point of the condylar process (13), point of inflection between condylar and angular processes (14), caudal tip of angular process (15), ramus anterior to angular process (16–17), anterior extremity of mandible (18).

2.3. Geometric morphometric analysis

The raw landmark coordinates comprise information about size and shape, but also location and orientation, therefore, they are not directly suitable for geometric morphometric analysis. For this reason, the most common approach to distinguish shape from size and location and rotation is

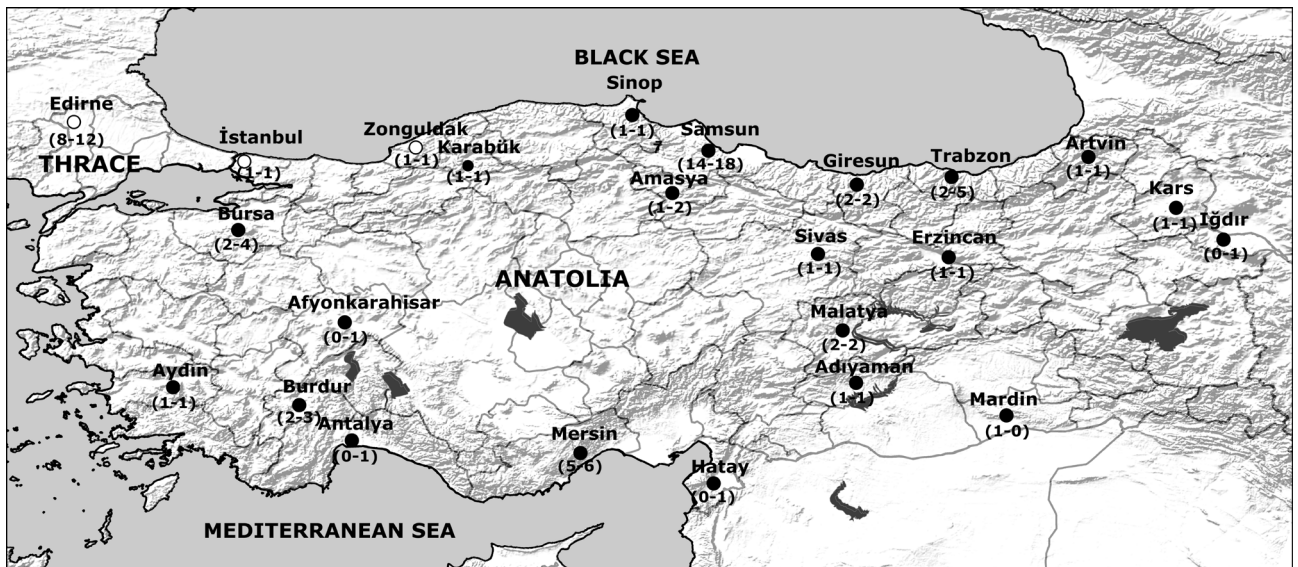


Figure 1. Collection localities for all hedgehog specimens used in this study from Turkey. Closed circle: *E. concolor* and open circle: *E. roumanicus*. Numbers in parenthesis refer to the sample sizes for the dorsal cranium and mandible, respectively.

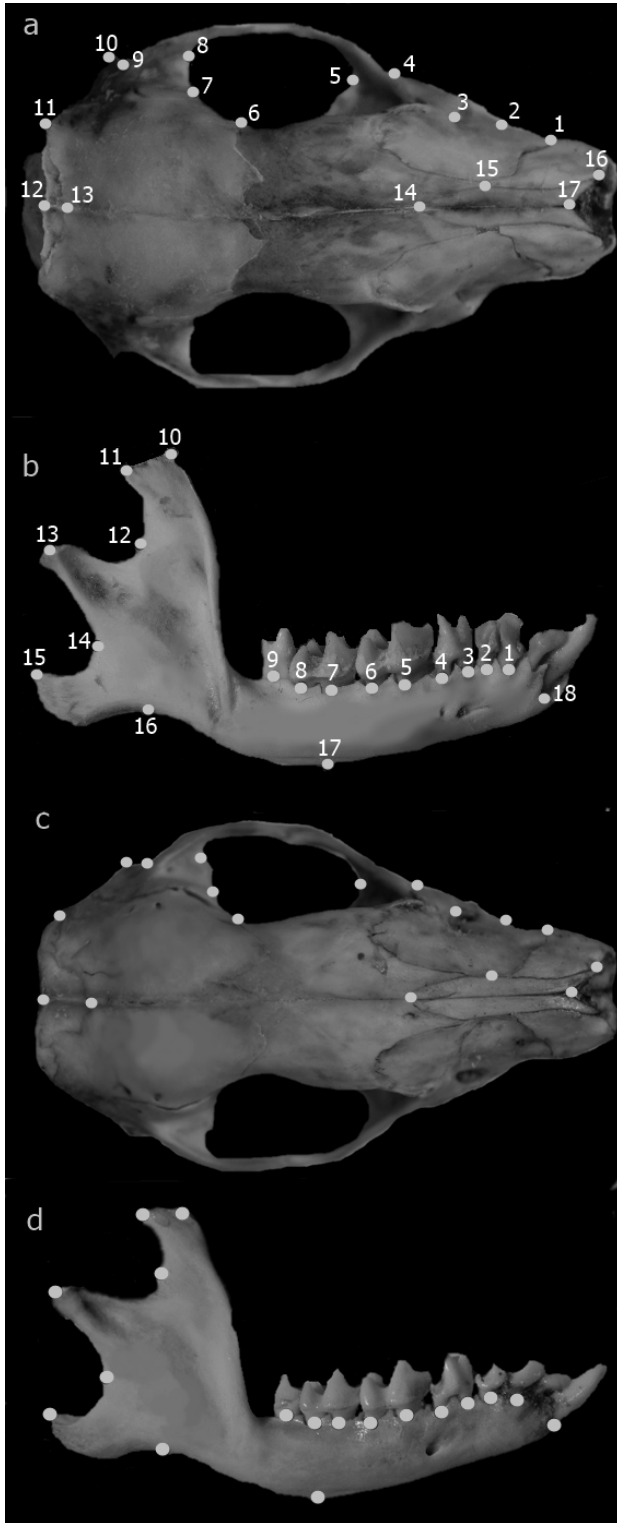


Figure S1. Ba–c) Landmarks recorded on the dorsal surface of cranium in *E. concolor* and *E. roumanicus*, respectively. b–d) Landmarks recorded on the mandible in *E. concolor* and *E. roumanicus*, respectively.

the generalized least square Procrustes superimposition (GPA; Gower 1975, Rohlf and Slice, 1990), which preserves all information about shape differences among specimens and standardizes each specimen to unit centroid size (CS). CS, the size measure used in geometric morphometrics, is equal to the square root of the summed squared Euclidean distances between the landmarks and their centroid (Bookstein, 2007). Procrustes distance is approximated by the Euclidean distance between two sets of Procrustes shape coordinates as well as a measure of shape difference between two landmark configurations. Procrustes shape coordinates, which contain information about the shape of the configurations, originate from superimposed landmark configurations. Standard multivariate methods, such as principal component analysis (PCA), can thus be applied to Procrustes shape coordinates in order to yield a low-dimensional representation of shape space. PCA arranges data by major axes based on measured variables. For shape analysis, PCA and MANOVA were used in this study. A one-way ANOVA analysis was also performed with centroid size for detecting differences in size between both species. The dorsal surface of cranium and mandible mean shape differences between *E. concolor* and *E. roumanicus* were analysed using discriminant function analysis (DFA) to determine the classification success of the two species. The number of shape variables used in the MANOVA and DFA were reduced to the first few principal components (10 PCs), because the sample size difference between *E. concolor* and *E. roumanicus* was quite high. Additionally, a crossvalidation test was used to assess classification accuracy. Wireframe graphs were used to visualize shape differences. Morphological changes based on size were investigated by multivariate regression of shape variables onto centroid size. Mann–Whitney U test was conducted to compare the centroid size variations in the dorsal cranium and mandible of *E. roumanicus* and *E. concolor* samples. The mean rank and z-score were also calculated using the same test for equal medians. The size difference in cranium and mandible CS values between the two species was analysed using Monte Carlo permutation test. Moreover, a multivariate regression analysis was used to test for significant relationships between centroid size and shape in each species. To estimate any allometric effect, the multivariate regression (permutation test with 10,000 rounds) of shape variable on log centroid size was analysed among species and within each species separately. All of the analyses were carried out using the PAST version 4.03 (Hammer et al., 2001) and MorphoJ version 1.07 (Klingenberg, 2011) packages. The output files were adjusted (font, colour change, etc.) in Inkscape version 1.0.

3. Results

3.1. Size variation

The centroid size of *E. concolor* and *E. roumanicus* was significantly different for both the dorsal surface of the cranium ($df = 1$, $F = 14.59$, $p < 0.0001$) and mandible ($df = 1$, $F = 22.28$, $p < 0.0001$). These differences can also influence shape difference between the two species due to allometric effects (see below). As determined by Mann–Whitney U test, the mean ranks were 8.18 (dorsal surface) and 11.47 (mandible) for *E. roumanicus* and 16.81 (dorsal surface) and 23.03 (mandible) for *E. concolor*. Besides, the Mann–Whitney U test showed the size differences were significant between the two species (z -score = 3.73, $p < 0.0001$ and Monte Carlo permutation $p = 0.0001$ for dorsal surface and z -score = 4.49, $p < 0.0001$ and Monte Carlo permutation $p = 0.0001$ for mandible). Moreover, box and whisker plot graphics showed that *E. roumanicus* was larger in centroid size than *E. concolor* in both the cranium and mandible (Figure 2).

3.2. Shape variation

MANOVA showed significant shape differences between the two species ($df_1 = 22$, $df_2 = 26$, Wilk's $\lambda = 0.1244$, $F = 8.321$, $p < 0.0001$) for the dorsal cranium. Moreover, PCA of shape variables strongly supported the shape differences observed on the dorsal cranium. The first 10 principal components used for the shape and size analyses explained 83.7% of total shape variation of dorsal surface of crania between the two species. This is an acceptably high percentage for this analysis. Based on the scatter plot graphic of the first (PC1), second (PC2) and third (PC3) principal components, there was evidence for the presence of dorsal cranium shape differences between *E. roumanicus* and *E. concolor* (Figure 3). There is a clear indication that variation along the PC3 axis is disposed to separate specimens of *E. concolor* and *E. roumanicus*. However, *E. concolor* has distribution from max. PC+ to max. PC– while *E. roumanicus* from zero to PC+ along PC1 axis. Besides, both *E. concolor* and *E. roumanicus* have

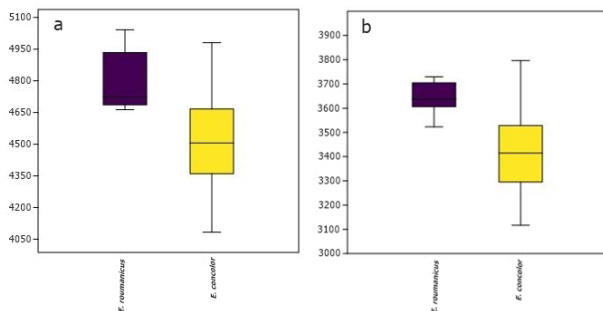


Figure 2. Box and whisker plot graphics showing variation of centroid size for dorsal cranium (a) and mandible (b) between the two species.

distribution from PC+ to PC– along PC2 axis. In other words, there was some overlapping along PC1 and PC2 axis and shape difference between the species is not clear. Moreover, *E. concolor* has distribution from max. PC+ to PC– while *E. roumanicus* from zero to max. PC– along PC3 axis. As shown in Figure 3, *E. concolor* has distribution only to PC3 = –0.02 (0.03 to –0.02) while *E. roumanicus* from PC3 = 0.00 to –0.04 on the PC3 axis, suggesting that the wireframe graphs created using PC3 can be used to display the shape changes between the two species. Visualized shape changes along the PC3 axis showed that the dorsal cranium of *E. concolor* is clearly narrower in the neurocranium and viscerocranium regions than that of *E. roumanicus*, with a shorter distance between the exterior extremity of the occipital crest and the back of the lateroccipital protuberances. In addition, the nasal region is somewhat shorter and narrower in *E. concolor* than in *E. roumanicus* while the maxilla and premaxilla are narrower. Moreover, the parietal bone of *E. roumanicus* is wider and shorter than that of *E. concolor*.

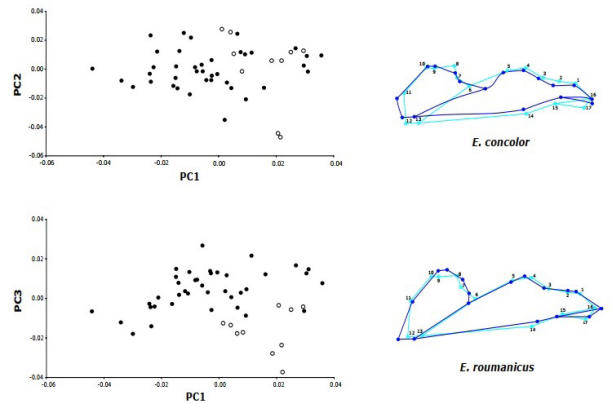


Figure 3. Box and whisker plot graphics showing variation of centroid size for dorsal cranium (a) and mandible (b) between the two species.

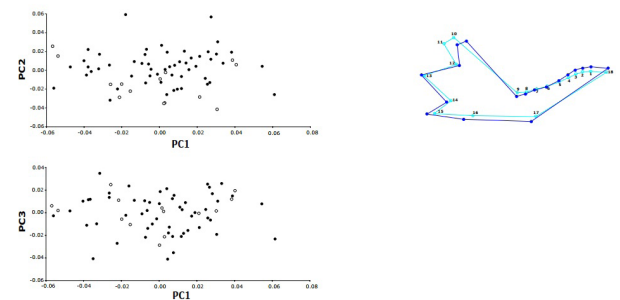


Figure 4. PCA scatter plot graphics showing the variations in the mandible (closed circle: *E. concolor*, $n = 54$; open circle: *E. roumanicus*, $n = 14$) with warped outline drawings describing shape changes along the PC1 axis for each species.

Although MANOVA showed significant shape difference between the two species ($df_1 = 18$, $df_2 = 49$, Wilk's $\lambda = 0.3879$, $F = 4.295$, $p < 0.0001$) for the mandible, based on the scatter plot graphics (Figure 4) of the first (PC1), second (PC2) and third (PC3) principal component axes, there were no clear evidence for the presence of mandibular shape differences between *E. roumanicus* and *E. concolor* along the three PCs. The first 10 principal components explained 85.1% of the total variance. The plot of PC1 against PC2 axis revealed a weak separation in the shape of mandibles from the two species, but no separation could be seen in the plot of PC1 against PC3. Namely, *E. concolor* and *E. roumanicus* have distribution from PC+ to PC- along PC1, PC2 and PC3 axis. Therefore, a single wireframe graph was created using the total dataset to display shape variations across PC1 axis in both species. The wireframe revealed that the most noticeable shape variations were in the mandibular ramus and the premolar regions (Figure 4).

The number of shape variables used in DFA has been reduced to the first 10 principal components so that the number of degrees of freedom of within-group is greater than the number of covariance matrix variables. The shape comparison of dorsal surface of crania demonstrates a significant difference between the mean shapes of *E. concolor* and *E. roumanicus* ($p < 0.0001$). Also, the permutation tests were statistically significant ($p < 0.0001$). Classification success from the crossvalidation score amounted to 100% for both *E. concolor* and *E. roumanicus*. The crossvalidation test showed that geometric morphometric methods could distinguish between the two species with a reliability rate of 100%. The test scores are shown proportional to their frequency (Figure 5a). The wireframe graphic indicated that *E. concolor* shows an anterior direction especially at the 2nd and 15th landmarks while it shows a posterior direction at the 16th and 17th landmarks on the premolar bone, compared with *E. roumanicus*. Besides, *E. concolor* shows an anterior direction at the 6th landmark on frontal-parietal suture. However, while *E. concolor* shows an anterior direction at the 11th landmark, it shows a posterior direction at the 8th, 12th and 13th landmarks on neurocranium region. On the other hand, there was almost no change in the remaining landmarks.

In the DFA analysis of mandibles, the shape comparison demonstrates a significant difference between the mean shapes of *E. concolor* and *E. roumanicus* ($p < 0.0001$). However, the PCA graphs (Figure 4), test scores (Figure 5b) and permutation test ($p < 0.02$) do not support this. Classification success from the crossvalidation score amounted to 90.74% for *E. concolor* and 100% for *E. roumanicus*. The crossvalidation test showed that the two species could be distinguished with a 92.65% confidence rate. The test scores are shown proportional to their

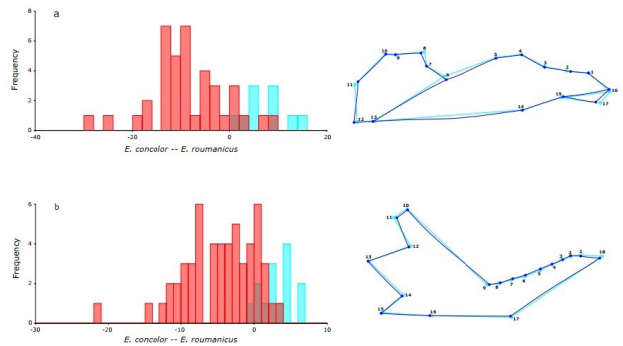


Figure 5. Histograms of the crossvalidation results. a. Dorsal surface of crania, b. Right side of mandible. Red bars: *E. concolor*; blue bars: *E. roumanicus*.

frequency (Figure 5b). The wireframe graphic indicated that *E. concolor* shows an anterior direction especially at the 7th, 8th and 9th landmarks on the molar region while it shows a posterior direction at the 18th landmark at the anterior extremity of the mandible, compared with *E. roumanicus*. However, while *E. concolor* shows an anterior direction at the 11th landmark, it shows a posterior direction at the 12th, 14th, 15th and 16th landmarks on the mandibular ramus. On the other hand, there was almost no change in the remaining landmarks.

3.3. Allometric effect

For the dorsal cranium, multivariate regression of the Procrustes coordinates on log centroid size for the two species showed a highly significant result ($p < 0.0017$), with allometry explaining 6.85% of total shape variation (Figure 6). Allometry accounted for 2.81% and 16.65% of the overall shape variation in *E. concolor* and *E. roumanicus*, respectively. However, based on a permutation test with 10,000 rounds, the multivariate regression of shape variables on log centroid size was statistically nonsignificant (*E. concolor*: $p < 0.3451$ and *E. roumanicus*: $p < 0.20$) for both species.

In the case of the mandible, regression of the Procrustes coordinates on log centroid size for the two species was highly significant ($p < 0.0001$), and allometry explained 8.82% of total shape variation (Figure 7). Allometry accounted for 8.30% and 16.70% of the overall shape variation in *E. concolor* and *E. roumanicus*, respectively. Based on a permutation test with 10,000 rounds, the multivariate regression of shape variables on log centroid size was, presumably due to larger sample size, more significant for *E. concolor* ($p < 0.0006$) than for *E. roumanicus* ($p < 0.0461$).

4. Discussion

This study attempted to determine shape differences and the relationship between shape and size of the two currently recognized hedgehog species, *E. concolor* and

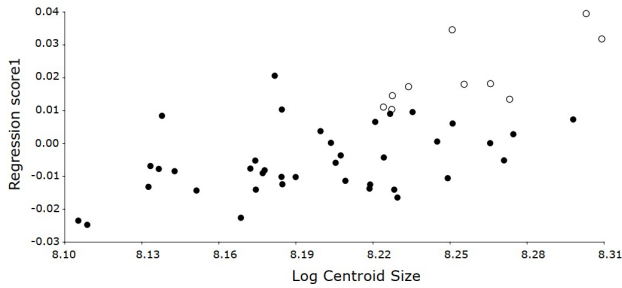


Figure 6. Multivariate regression analysis of shape variables vs centroid size of the dorsal cranium (closed circle: *E. concolor*, n = 39; open circle: *E. roumanicus*, n = 10).

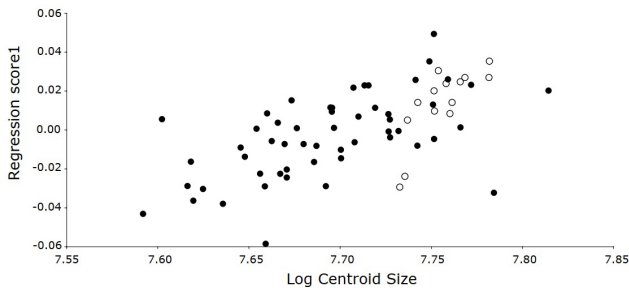


Figure 7. Multivariate regression analysis of shape variables vs centroid size of the mandible (closed circle: *E. concolor*, n = 54; open circle: *E. roumanicus*, n = 14).

E. roumanicus, that are found in Turkey, using geometric morphometric data from the cranium and mandible. In contrast to previous findings, this study revealed a distinct difference, in the shape of the dorsal cranium and mandible between the two species, using a multivariate morphometric approach. The results suggested that geometric morphometry is a more effective method than more traditional metric methods, in terms of discriminatory power, because geometric morphometry can more precisely measure the shape and size of the skull. Moreover, this technique has the advantage of visualizing shape changes in comparative graphics. The analysis here provided more detailed information, on the shape and size differences between the two species, compared to previous studies.

Doğramacı and Gündüz (1993) found a generally close morphometric relationship between Thracian and Anatolian hedgehogs, although there were differences in several features of the skull, such as occipitonasal and condylobasal lengths, interorbital breadth and paroccipital processes. Nevertheless, the measurements used in Doğramacı and Gündüz (1993) showed partial overlap for these. The present study showed that shape differences between *E. roumanicus* and *E. concolor* were present, particularly on the neurocranium and viscerocranium regions of the dorsal surface of crania. The results were therefore compatible with the conclusions of Doğramacı and Gündüz (1993), because shape differences were

apparent on the part containing the occipital bone of the neurocranium. Although no change in the shape of the mandible was observed between the two species, premolar tooth and ramus regions of the mandible showed shape variation for each species. Moreover, a difference was observed in the apparent size of the dorsal cranium and mandible, with *E. roumanicus* being generally larger than *E. concolor*. Based on traditional morphometry, occipital and condylobasal lengths were found to be larger in hedgehogs from Thrace, when compared to those in Anatolia (Doğramacı and Gündüz, 1993). The present study was therefore also compatible with the results of that previous study in terms of size. Skull morphology can be affected by genetic factors, environmental factors, or both. Two protein ligands (sonic hedgehog and indian hedgehog) are expressed in the craniofacial complex and are essential to embryonic development (Pan et al., 2013). Meanwhile, interspecific and intraspecific morphological variations due to environmental factors have been clearly demonstrated in various mammalian species (Renaud and Millien, 2001; Grossnickle, 2020).

Kryštufek (2002) mentioned the importance of the contact zone of the nasal and maxillary bones in the separation of hedgehog morphotypes (*roumanicus* and *concolor*) in the region. The warped outline drawings here indicate that the shape variation in the two species is marked in the neurocranium and the anterior part of the nasal region of viscerocranium. Therefore, these regions are more distinctive compared to the contact zone of the nasal and maxillary bones. Moreover, in the current study, Thracian morphotypes (*roumanicus*) were also observed among Anatolian hedgehogs, while Anatolian morphotypes (*concolor*) were also observed among hedgehogs from Thrace. In addition, Chaprazov et al. (2014) demonstrated the importance of diet in the development of zygomatic bones and maxillary premolars. These findings also suggest that differences in the nasomaxillary region of the skull should not be used to distinguish individuals of these two species, as also indicated by Kryštufek (2002).

Two specimens from Zonguldak and İstanbul (Anatolian part) in northern Turkey were identified as *E. roumanicus* based on morphology and this was confirmed using the abovementioned molecular markers (Demirtaş, 2012). Furthermore, *E. concolor* was not found in this region. Previously, three specimens of the European *roumanicus* morphotype were found in northwest Anatolia (Kryštufek, 2002). Therefore, this study revealed that *E. roumanicus* occurs in northwestern Anatolia as well as in the European continent. It is therefore likely that the presence of *E. roumanicus* was not detected there due to the absence of specimens from the area among those used in other studies (Doğramacı and Gündüz, 1993; Santucci et al., 1998; Seddon et al., 2001; Berggren et al., 2005; Arslan et al., 2008).

The existing phenotypic similarity of *E. concolor* and *E. roumanicus* is most likely the consequence of long-lasting evolution under similar ecological pressures in the Mediterranean zone (Gauquelin et al., 2018). They display strong similarity in their external morphological appearance and previous studies based on traditional morphology could not reveal a clear phenotypic distinction. However, the present study has successfully discriminated the two hedgehog species in Turkey using the geometric morphometric approach on a set of dorsal crania and mandibles from previously genotyped specimens. PCA, ANOVA and MANOVA analyses showed significant shape and size differences between these species based on both crania and mandibles. Moreover, DFA indicated significant variation between the two species. The parametric and permutation tests of DFA were statistically significant against the null hypothesis of equal species mean. The classification success obtained from the crossvalidation score was also high enough to show that the species could be distinguished. By analysing relationships between shape and size of both the dorsal cranium and mandible, our results demonstrated that *E. concolor* and *E. roumanicus* show different allometric

growth patterns. In other words, these two sister species show different ontogenic development.

Our results indicated that an allometric effect is not observed in the dorsal cranium while there is an allometric effect in the mandible within the species. The most likely reason for this is the ontogenic development as well as the geographical or seasonal variation in diets of populations in different geographical areas. Changes in mandible morphology depending on nutrition and geography are known in different species and it has been shown that there are significant differences in mandibular performance due to nutrition strategy and ecological environment (Marcé-Nogué et al., 2017; Morales-García et al., 2021). Due to the small number of specimens for *E. roumanicus* available for the present study, further studies including more specimens of both species are recommended to increase the reliability of shape analyses for species discrimination.

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