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Early View

Original Research Article

Mandibular Shape Variation and Asymmetry in Pramenka, Akkaraman, and Kangal Akkaraman Sheep: A Geometric Morphometric Study

Key words

geometric morphometrics;
mandible;
sheep;
fluctuating asymmetry;
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Abstract: The aim of this study was to characterise mandibular shape variation and asymmetry patterns in three sheep breeds from two geographical regions: Pramenka from Bosnia and Herzegovina, and Akkaraman and Kangal Akkaraman from Türkiye. Thirty-four male mandibles (10 Pramenka, 12 Akkaraman, 12 Kangal Akkaraman) were analysed by landmark-based geometric morphometrics, with eleven homologous landmarks digitised on lateral photographs. Generalised Procrustes Analysis, Principal Component Analysis (PCA), Discriminant Function Analysis (DFA), allometric regression, and Procrustes ANOVA were performed in MorphoJ. The first three principal components explained 63.37% of total shape variation. In the PCA morphospace, Akkaraman and Kangal Akkaraman specimens overlapped almost completely, whereas Pramenka formed a clearly separated cluster. DFA confirmed significant shape differences in all pairwise comparisons, with cross-validated classification accuracy of 79.2% between the two Anatolian breeds and 100% for both Pramenka comparisons. Shape differences were most pronounced in the pars incisiva, pars molaris, corpus mandibulae, and ramus mandibulae. Centroid size explained only 2.51% of shape variation ($P = 0.3467$), indicating no significant allometric effect. Fluctuating asymmetry exceeded directional asymmetry for both size and shape; directional asymmetry in shape nevertheless remained statistically significant, consistent with a degree of masticatory laterality.
Mandibular morphology therefore differs primarily between geographically distant breeds, while the two Anatolian breeds remain morphologically close, and the observed asymmetry patterns point to developmental instability as the principal source. These data provide morphometric reference values for future work on breed differentiation, functional adaptation, and zooarchaeological identification of ovine remains.

Introduction

The Akkaraman sheep breed is extensively reared in Türkiye, particularly in Central Anatolia, where it constitutes nearly half of the national sheep population. Among Türkiye's diverse sheep breeds, the Kangal Akkaraman holds a prominent position due to its high population density; this variety is larger than the standard Akkaraman and is categorized as a medium-sized breed (1). Following domestication, sheep populations expanded from the Middle and Near East into Europe via the Balkan region (2). In the Balkan Peninsula, the majority of local sheep breeds belong to the coarse-wool group known as Pramenka (3).

Morphological studies are frequently employed for species identification, age estimation, and genetic and forensic investigations (4), and analyses of skull morphology have revealed significant differences between Turkish and Balkan sheep populations (5). From a zootechnical perspective, mandibular structure is intrinsically associated with feed intake capacity and masticatory efficiency (6), whereas in a clinical context, the identification of mandibular asymmetry and shape variation may provide a baseline for the early diagnosis of dental anomalies and masticatory dysfunctions (7). Consequently, morphometric data may serve as valuable markers in selective breeding programs and as an anatomical guide for veterinary maxillofacial interventions.

The analysis of mandibular asymmetry and shape variation also serves as a biological indicator of developmental stability and environmental adaptation, potentially reflecting adaptive responses of sheep breeds to specific geographical habitats and dietary conditions. In geometric morphometrics (GM), shape—

defined by its invariance to location, size, and orientation—is quantified through the statistical evaluation of biologically homologous landmark coordinates (8–12), providing a more robust framework for morphological assessment than traditional linear approaches.

In recent years, GM methods have been widely applied to investigate shape variation in the skulls and mandibles of different animal species (13–15). Despite this growing body of literature, no previous research has directly examined the influence of geographical proximity on mandibular morphology among Pramenka, Akkaraman, and Kangal Akkaraman sheep. Therefore, the present study aimed to investigate breed- and geography-related differences in mandibular morphology using GM analysis, comparing two Anatolian breeds raised under similar ecological conditions with Pramenka sheep native to the geographically distinct Balkan region.

Materials and methods

Samples

A total of 34 mandibles from three local male sheep breeds originating from two different countries were examined; geographical origins, sample sizes, and breed characteristics are provided in Table 1. Specimens were obtained from the osteological collections of the Faculty of Veterinary Medicine, University of Sarajevo (Bosnia and Herzegovina) and from slaughterhouses in Türkiye. All animals were non-castrated males with body condition scores of 3.0–3.5 and showed no evidence of pathological abnormalities affecting mandibular morphology.

Imaging, Digitization and Landmark Configuration

Lateral photographs of the left and right mandibles were acquired using a digital camera (Canon EOS 600D, Japan) with an 18–55 mm lens at a fixed distance of 25 cm from the specimens (resolution: 890 × 1065 pixels; JPG format to minimize image distortion and maintain a) consistent focal plane.

Eleven homologous landmarks were digitized on each image using TpsUtil (v1.79) and TpsDig2 (v2.31), and landmark precision was assessed with TpsSmall (v1.34) prior to statistical analyses. Anatomical definitions and locations are provided in Figure 1 and Table 2. The configuration was designed to capture the three major mandibular parts—pars incisiva, corpus mandibulae, and ramus mandibulae—encompassing landmarks related to dental alignment and occlusal length (LM1, LM9–LM11), masticatory muscle attachment and articulatio temporomandibularis function (LM5, LM6, LM8), and neurovascular reference points (LM2: foramen mentale; LM4: incisura vasorum facialium).

Statistical Analysis

All geometric morphometric analyses were performed in MorphoJ. Raw landmark coordinates were subjected to Generalized Procrustes Analysis (GPA) to remove non-shape variation associated with size, position, and orientation, followed by Principal Component Analysis (PCA) on the Procrustes coordinates to characterize overall shape variation. Discriminant Function Analysis (DFA) was used to evaluate morphological differences among breeds, with Procrustes and Mahalanobis distances calculated and significance assessed by both parametric and permutation tests. Regression analysis was performed to examine allometric effects, and Procrustes ANOVA was conducted to partition symmetry and asymmetry components, including individual variation, directional asymmetry, fluctuating asymmetry, and measurement error.

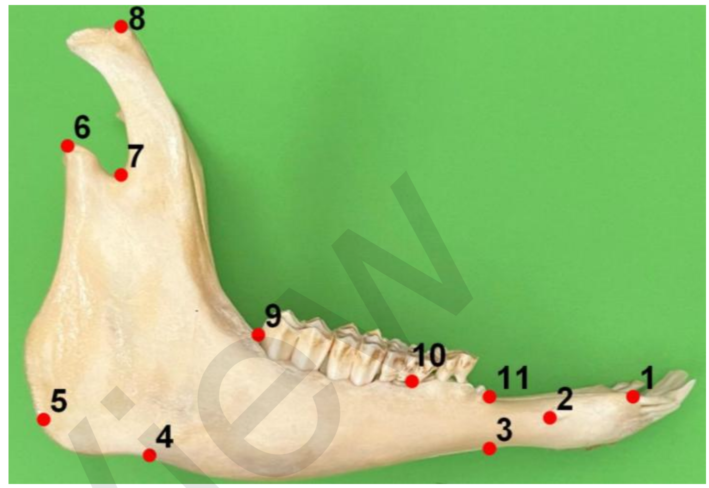

Figure 1: Landmarks on the mandible (I: Incisor; PM: Premolar; M: Molar)

Results

Table 3 presents the results of the Principal Component Analysis (PCA) performed on the landmark coordinates of the sheep mandibles. PC1 accounted for 29.25% of total shape variation, and the cumulative contribution of PC1–PC3 reached 63.37%, with a clear inflection point between PC3 and PC4 (Figure 2). In the resulting morphospace, Akkaraman and Kangal Akkaraman specimens overlapped almost completely, and only Pramenka formed a distinctly separated cluster (Figure 2); as PCA is an exploratory, unsupervised ordination technique, this pattern reflects the dominant axes of overall shape variation rather than constituting evidence of breed discrimination.

Wireframe analysis (Figure 3) showed that shape changes associated with PC1 were mainly expressed around LM1 (caudoventral endpoint of the I1 alveolus dentalis), LM5 (angulus mandibulae), and the pars molaris region (LM8–LM9). Shape changes associated with PC2 were mainly expressed in the pars incisiva (LM1), incisura vasorum facialium (LM4), and the region extending from the incisura mandibulae to the processus coronoideus (LM7–LM8). Shape changes associated with PC3 were mainly expressed around LM4 and LM7.

Regression analysis showed that centroid size explained only 2.51% of shape variation (P = 0.3467); mandibular shape was therefore independent of size, with no significant allometric effect.

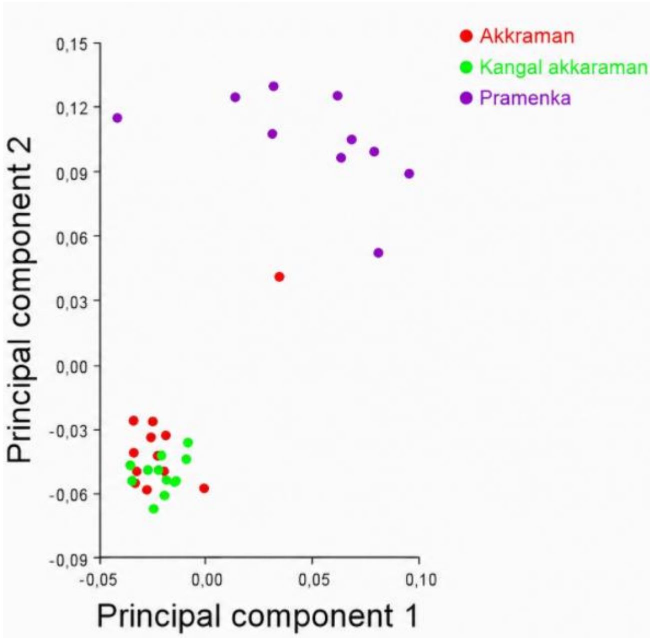

Figure 2: The distribution of individuals on the graph is based on the first and second principal component (Red:Akkaraman, Green:Kangal Akkaraman, Purple:Pramenka)

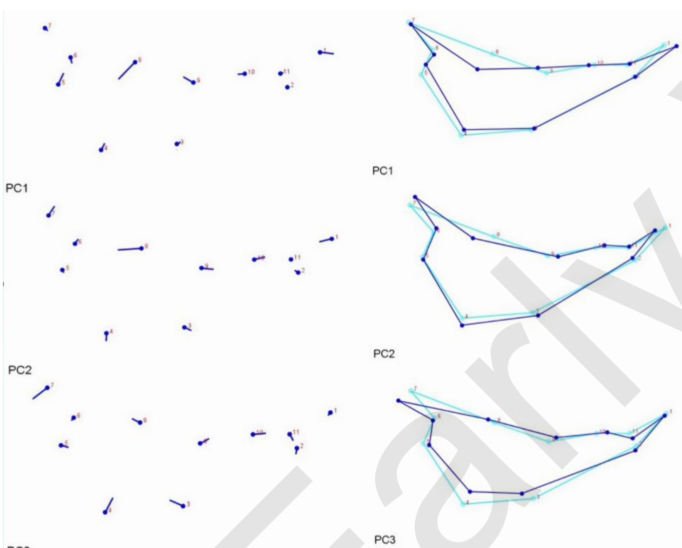

Figure 3: Wireframe and lollipop graphical representation of shape differences concerning PC1, PC2 and PC3. Dark blue represents the positive bounds of principal component scores

Because PCA is an unsupervised exploratory method, breed discrimination was further evaluated using Discriminant Function Analysis (DFA). DFA revealed statistically significant shape differences in all pairwise breed comparisons (Figure 4). For Akkaraman vs. Kangal Akkaraman, the Procrustes distance was 0.036 and the Mahalanobis distance was 13.527 (parametric $p = 0.0043$; permutation $p < 0.001$); classification accuracy was 100% for the original sample and 79.2% after cross-validation (66.7% of Akkaraman and 91.7% of Kangal Akkaraman specimens correctly classified). For Akkaraman vs. Pramenka, the Procrustes distance was 0.603 and the Mahalanobis distance was 471.845 ($p < 0.0001$; cross-validated accuracy: 100%). For Kangal Akkaraman vs. Pramenka, the Procrustes distance was 0.587 and the Mahalanobis distance was 192.868 ($p < 0.0001$; cross-validated accuracy: 100%). Mandibular shape differences were therefore comparatively limited between the two Turkish breeds, while Pramenka differed markedly from both, with the largest differences concentrated in the pars incisiva, pars molaris, corpus mandibulae, and ramus mandibulae.

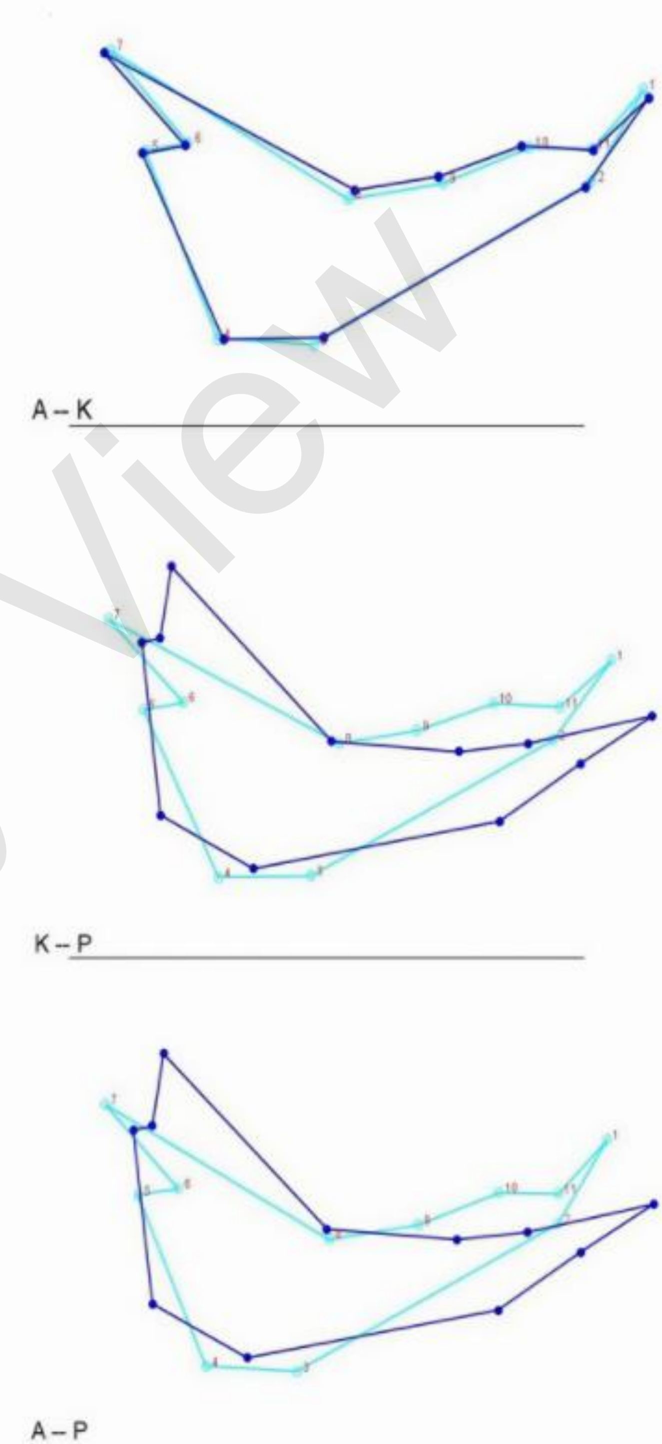

Figure 4: Wireframe graphics of the mandible according to breed in Discriminant Function Analysis (A: Akkaraman sheep, K: Kangal Akkaraman sheep, P: Pramenka sheep)

Table 1: Distribution of sample populations by breed, origin, and sample numbers.

Sheep Breeds	Origin	Number (n)	Age (month)	Weight (kg)
Pramenka	Sarajevo (Bosnia and Herzegovina)	10	8-12	50-60
Akkaraman	Konya (Turkey)	12	8-12	55-65
Kangal Akkaraman	Sivas (Turkey)	12	8-12	60-70

Table 2: Anatomical description of landmarks on the sheep mandible

Landmark	Anatomical description of landmarks
LM1	Caudoventral end point of alveoli dentales of I1
LM2	Caudal margin of foramen mentale
LM3	The ventral margin of mandible body below the rostral end of PM1
LM4	Incisura vasorum facialium
LM5	Caudoventral corner of angulus mandibulae
LM6	Caudal end point of condylus mandibulae
LM7	Ventral point of incisura mandibulae
LM8	Rostrodorsal point of processus coronoideus
LM9	Most caudal point of the alveolar margin adjacent to M3
LM10	Point on the alveolar margin adjacent to PM3
LM11	Rostroventral edge of PM1

Table 3: Results of the principal component analysis, PC: principal component

PC	Eigenvalues	Variance %	Cumulative %	PC	Eigenvalues	Variance %	Cumulative %
1	0.00064241	29.253	29.253	**10**	0.00003759	1.712	94.652
2	0.00042933	19.550	48.803	**11**	0.00003334	1.518	96.170
3	0.00032005	14.574	63.377	**12**	0.00002173	0.990	97.160
4	0.00021577	9.825	73.202	**13**	0.00002006	0.914	98.074
5	0.00015459	7.040	80.242	**14**	0.00001717	0.782	98.856
6	0.00011447	5.213	85.455	**15**	0.00001017	0.463	99.319
7	0.00005760	2.623	88.078	**16**	0.00000718	0.327	99.646
8	0.00005558	2.531	90.609	**17**	0.00000500	0.227	99.873
9	0.00005119	2.331	92.940	**18**	0.00000282	0.128	100.000

Table 4: Mandibular shape asymmetry calculated by Procrustes ANOVA. SS: sums of squares; MS: mean squares; dF: degrees of freedom, NA: Net asymmetry, F: statistics and parametric p values are provided for each effect

Size	Variance Exp.	SS	MS	dF	F	P
Individual	99.80473541	3566919.512964	84926.655071	34	791.47	<.0001
Side	0.001237897	44.241173	44.241173	1	0.41	0.5243
Ind*Side	0.126100941	4506.719102	107.302836	34	6.81	<.0001
Error 1 (Imaging)	0.037930276	1355.589412	15.762668	86	1.50	<.0001
Error 2 (Digitizing)	0.029995479	1072.007847	12.465208	86	1.02	0.4425
Shape						
Individual	91.36739	1.09032138	0.0014422240	756	20.09	<.0001
Side	0.557998	0.00665880	0.0003699334	18	5.15	<.0001
Ind*Side	4.546941	0.05426035	0.0000717730	756	4.97	<.0001
Error 1 (Imaging)	1.87446	0.02236863	0.0000144500	1548	1.14	0.0019
Error 2 (Digitizing)	1.653207	0.01972834	0.0000127444	1548	0.94	0.9247

Pairwise wireframes showed that the main difference between Akkaraman and Kangal Akkaraman was localized around LM1, with the caudoventral endpoint of the I1 alveolus dentalis positioned more dorsally in Akkaraman. In comparisons involving Pramenka, the corpus mandibulae of Kangal Akkaraman was more horizontal and the ramus mandibulae nearly perpendicular to it, whereas in Pramenka the ramus mandibulae was directed more caudally and formed a wider angle with a dorsally inclined corpus mandibulae. Because Akkaraman and Kangal Akkaraman are morphologically similar to each other, their comparisons with Pramenka produced a similar pattern of shape differences.

Procrustes ANOVA results are summarized in Table 4. Digitizing error was not statistically significant, whereas imaging error, although statistically significant, was small relative to individual variation; both error components were smaller than the fluctuating asymmetry term. Individual variation in size and shape was highly significant ($p < 0.0001$), accounting for 99.80% of total size variation and 91.36% of total shape variation. For size, fluctuating asymmetry was significant ($p < 0.0001$) while directional asymmetry was not ($p = 0.5243$). For shape, both fluctuating and directional asymmetry were statistically significant ($p < 0.0001$), though the contribution of directional asymmetry was lower than that of fluctuating asymmetry; mandibular asymmetry therefore appears to reflect developmental instability more than directional bias. The significant directional asymmetry in shape nonetheless points to masticatory laterality within the examined population..

Discussion

Mandibular morphology is shaped by breed characteristics, feeding habits, mechanical loading, and developmental processes (16,17). In the present study, mandibular variation between Akkaraman and Kangal Akkaraman sheep—raised under similar geographical and ecological conditions—was relatively limited, as reflected by the lower cross-validated DFA classification accuracy (79.2%). In contrast, Pramenka sheep exhibited distinct morphological characteristics, with complete separation from both Turkish breeds, suggesting that geographical and environmental factors contribute substantially to mandibular morphological differentiation.

These findings are consistent with previous geometric morphometric studies. Demiraslan et al. (18) reported that the first three principal components explained 63.82% of total shape variation in Hamdani and Awassi sheep, with prominent differences in the arcus dentalis, ramus mandibulae, processus coronoideus, and angulus mandibulae. Pares-Casanova (19) similarly found that the first three principal components accounted for 77.5% of total variation in sheep mandibles. In the present study, PC1–PC3 explained 63.37% of total shape variation, with morphological changes concentrated in the pars incisiva, pars molaris, corpus mandibulae, and ramus mandibulae. Collectively with studies on Anatolian Wild and Akkaraman sheep (20) and Honamlı and Hair goats (15), these findings indicate that breed-related mandibular variation consistently involves the arcus dentalis, processus coronoideus, and angulus mandibulae, while the present study additionally identifies the pars incisiva and corpus mandibulae as regions of notable differentiation. No significant allometric effect was detected (P = 0.3467), indicating that the observed shape differences were largely independent of size—a pattern consistent with previous geometric morphometric investigations of small ruminants (15,20,21).

These breed-level distinctions are echoed in broader comparative work on the ovine mandible. Özkan et al. (22) analysed 70 mandibles from four breeds maintained in different countries—İvesi, Bardhoka, Polish Mountain, and Turcana—and recovered significant shape differences among them, and Boz et al. (23) reported the same for Bardhoka, Turcana, and İvesi sheep, with the İvesi breed occupying the widest region of mandibular shape space. For the Balkan Peninsula specifically, Jashari et al. (24) documented the skull and mandibular morphometry of the Sharri sheep (a Balkan Pramenka-type breed) and drew attention to the clinical value of such reference data for anaesthesia and surgery in the head region. Our findings add to this literature: the Pramenka mandible remains readily separable from the two Anatolian breeds, which in turn are difficult to distinguish from one another.

Variations in forage type and feeding behaviour may influence mandibular biomechanics and masticatory patterns in ruminants (21). In the present study, directional asymmetry was detected for mandibular shape, suggesting the existence of masticatory laterality. However, fluctuating asymmetry contributed more substantially to overall variation than directional asymmetry for both size and shape, indicating that mandibular asymmetry primarily reflects developmental instability rather than functional lateralization. A comparable asymmetry structure has been reported for the sheep skull by Manuta et al. (25), in which the first principal component of fluctuating asymmetry (39.62%) exceeded that of directional asymmetry (32.98%) and the İvesi breed showed the greatest fluctuating asymmetry. Those authors attributed interbreed differences primarily to selective breeding rather than to geographical distribution; because the breeds compared here also differ in breeding history, the pronounced separation of Pramenka most plausibly reflects a combination of geographical and lineage-related influences rather than geography alone.

Several limitations warrant consideration. The study comprised 34 mandibles; however, post hoc power analyses demonstrated statistical power exceeding 0.99 for all pairwise comparisons, confirming the adequacy of the sample size. Additionally, analyses were performed on two-dimensional lateral images, and future studies employing larger samples and three-dimensional imaging may provide a more comprehensive morphological assessment.

In conclusion, geometric morphometric analyses revealed clear breed-related differences in mandibular morphology, with limited variation between the two Anatolian breeds and distinct characteristics in Pramenka sheep. Fluctuating asymmetry represented the principal source of asymmetrical variation. These findings provide morphometric reference data for studies on breed differentiation, functional adaptation, and zooarchaeological identification of ovine remains.

Acknowledgements

Ethics approval

This study was conducted with the approval of the Local Animal Ethics Committee of Sivas Cumhuriyet University (Approval No: 6522830-050.04.04-23).

Use of generative artificial intelligence

The authors used artificial intelligence solely for language editing and proofreading purposes.

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Izvleček:

Ključne besede: