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Patellar Shape Diversity as a Functional Indicator of Locomotor Specialization in Selected Ruminant Species

Oya Kahvecioğlu[1], Burak Ünal[1], Barış Can Güzel[2], Ermiş Özkan[1], Barış Batur[3], Gülsün Pazvant[1], Nazan Gezer İnce[1], Caner Bakıcı[3], Zihni Mutlu[4], Sedef Selviler Sizer[5], Tomasz Szara[6], Oleksii O. Melnyk[7], Reşide Merih Hazıroğlu[3], Ozan Gündemir[1,8]

[1] Department of Anatomy, Faculty of Veterinary Medicine, Istanbul University-Cerrahpaşa, 34320 Istanbul, Türkiye

[2] Department of Anatomy, Faculty of Veterinary Medicine, Siirt University, 56100 Siirt, Türkiye

[3] Department of Anatomy, Faculty of Veterinary Medicine, Ankara University, 06110 Ankara, Türkiye

[4] Department of Surgery, Faculty of Veterinary Medicine, Istanbul University-Cerrahpaşa, 34320 Istanbul, Türkiye

[5] Department of Anatomy, Faculty of Veterinary Medicine, Ondokuz Mayıs University, 55270 Samsun, Türkiye

[6] Department of Morphological Sciences, Institute of Veterinary Medicine, Warsaw University of Life Sciences-SGGW, 02-776 Warsaw, Poland

[7] Department of Animal Anatomy, Histology and Pathomorphology, National University of Life and Environmental Sciences of Ukraine, Kyiv, Ukraine

[8] Osteoarchaeology Practice and Research Centre, Istanbul University-Cerrahpaşa, 34320 Istanbul, Türkiye

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Abstract

This study investigates interspecific and intraspecific variation in patellar morphology among the examined species of ruminants and explores whether these differences are consistent with their reported locomotor ecology. While the patella functions as a crucial lever during locomotion, the extent to which this relatively small bone reflects adaptive variation across species remains uncertain. This research aims to characterize patellar shape diversity in five selected ruminant species and to explore its potential functional implications within this limited comparative framework. A total of 352 patellae representing five ruminant species (*Bos taurus, Bison bonasus, Ovis aries, Capra hircus*, and *Capreolus capreolus*) belonging to the families Bovidae and Cervidae were digitized as three-dimensional models and analyzed using geometric morphometrics. Morphospace distributions, shape variation, and allometric relationships were assessed. Distinct patellar morphologies were observed among the examined species. *Bos taurus* formed a distinct cluster, whereas European bison (*Bison bonasus*) largely overlapped with the sheep cluster in shape space. Nevertheless, Bovids tended to exhibit relatively more medio-lateral expansion and more developed cartilaginous processes, consistent with greater weight-bearing demands and joint stability. In contrast, *Capreolus capreolus* and *Capra hircus* displayed slender, elongated patellae with reduced projections, a

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morphology that may be associated with agility and speed-related locomotor demands. *Ovis aries* occupied an intermediate morphospace, overlapping partially with both large and small ruminants. Procrustes ANOVA confirmed significant shape differences among the examined species, excluding sheep and goats. Allometric analyses revealed a strong association between patellar shape and centroid size in this dataset of five species. These findings demonstrate that, in the studied species, patellar morphology reflects an intricate interplay of functional adaptation, phylogenetic relatedness, and allometric scaling. Despite its small size, the patella may serve as an informative morphological marker of ecological and functional differentiation among ruminant species within the comparative framework examined here, and the patterns observed in this study may help generate hypotheses for broader comparative analyses in other ruminant taxa.

Keywords: Allometry, Functional morphology, Locomotor adaptation, Species variation.

The ruminant clade (Ruminantia) within the order Artiodactyla is a highly specialized group of mammals characterized by a multi-chambered stomach that enables efficient digestion of cellulose-rich plant material[1-3]. Ruminants comprise approximately 200 extant species distributed across multiple families (e.g., Tragulidae, Cervidae, Giraffidae, Antilocapridae, Moschidae, and Bovidae). In this study, we focused on a subset of ruminants representing both domestic and wild bovids, including cattle (*Bos taurus*), sheep (*Ovis aries*), goats (*Capra hircus*), European bison (*Bison bonasus*), and roe deer (*Capreolus capreolus*)[4-5]. These taxa occupy a wide range of ecological niches, from open grasslands to forested and mountainous habitats, and display locomotor behaviours ranging from climbing and balancing on steep, rugged terrain to high-speed running and rapid changes of direction in open environments[6-9]. This diversity manifests not only in soft tissues but also throughout the skeleton, including major limb elements involved in support and propulsion (e.g., the calcaneus)[10]. Given its direct role in the knee extensor mechanism and load transmission at the stifle, patellar shape is expected to vary with joint mechanics and habitual loading regimes. This expectation is tested in the present study.

The patella is the largest sesamoid bone in the body, situated within the tendon of the quadriceps femoris muscle and positioned anterior to the articulation between the femur and tibia within the knee joint[11-13]. The proximal base of the patella serves as the insertion site for the quadriceps femoris tendon, including fibers from the rectus femoris, vastus lateralis, vastus medialis, and vastus intermedius. Distally, the apex of the patella anchors to the tibial tuberosity via the patellar ligament[14, 15]. On the medial surface of the patella, between the cartilaginous process and the quadriceps tendon, lies a fibrocartilaginous structure that plays a critical role in load transmission, shock absorption, and ensuring smooth joint motion[16, 17]. This structure, commonly referred to as the fibrocartilago patellae in the literature, also functions to reduce friction within the femoropatellar joint, thereby protecting the articulating surfaces[17, 18].

Geometric morphometrics has become an important approach in veterinary anatomy for the quantitative and comparative assessment of morphological variation among taxa[19, 20]. Unlike traditional linear morphometric methods, this

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technique preserves the spatial relationships between landmarks, allowing for a more holistic and detailed analysis of shape[21]. The integration of three-dimensional models enhances the accuracy and reproducibility of these analyses, enabling the detection of subtle shape differences that may be associated with functional or ecological adaptations[21-23]. Geometric morphometric methods have been applied to various ruminant skeletal specimens, providing valuable insights into morphological variation both among species and within species[24-27].

The quadriceps muscle group transmits its force to the tibia via the patellar ligament, enabling knee extension[14, 15]. Knee extension is a key component of both the swing and stance phases of the locomotor cycle in ruminants, contributing to limb protraction before foot contact and to body-weight support and forward progression during stance[28]. However, locomotor behaviors and the functional use of knee extension vary considerably among ruminant species[29-31]. For instance, *Capra hircus* (domestic goat) is well known for its ability to climb and balance on steep and rugged terrains, whereas *Capreolus capreolus* (roe deer) is characterized by high-speed running and rapid directional changes[10, 32]. Larger-bodied species, such as *Bos taurus* and *Bison bonasus*, exhibit a more robust posture suited for weight-bearing and sustained, stable movements. Previous studies have demonstrated that such functional differences are associated with morphological variation in various parts of the skeletal system. Nevertheless, despite acting as a lever during knee extension in both swing and stance, the extent to which the relatively small patella reflects these functional and ecological differences among ruminant species remains insufficiently understood. The aim of this study is to characterize patellar morphological variation in five selected ruminant species and to explore whether interspecific differences in patellar shape are consistent with their reported body size and locomotor ecology, within the limitations of this restricted taxonomic sample. In addition, we examine intraspecific variation in patellar morphology among selected *Bos taurus* and *Ovis aries* breeds that differ in their primary selection for meat or dairy production.

Results

Centroid Size Variation Across Ruminant Species and Breeds

Analysis of centroid size, as expected given the marked differences in overall body size, revealed pronounced variation among the examined species and within specific taxonomic and breed-level groupings (Fig. 1). Among the large-bodied ruminants in the study sample, *Bos taurus* exhibited significantly greater centroid sizes compared to *Bison bonasus* ($F_{1,171} = 30.37$, $p < 0.001$), indicating a more robust skeletal framework. Within small ruminants, a highly significant disparity was detected among *Ovis aries, Capra hircus*, and *Capreolus capreolus* ($F_{2,176} = 38.59$, $p < 0.001$), with *Ovis aries* showing the largest average centroid size (CS), followed by *Capra hircus*, while *Capreolus capreolus* consistently exhibited the smallest values.

Breed-level analyses further highlighted more subtle intraspecific variability. Within *Bos taurus*, breed-related differences were evident ($F_{3,136} = 5.76$, $p < 0.001$), with Holstein and Simmental generally exhibiting larger CS values compared to Angus and Hereford. Similarly, *Ovis aries* breeds differed significantly ($F_{2,88} = 3.14$, $p = 0.048$), where Akkaraman and Hamdani displayed larger centroid sizes relative to Morkaraman. In contrast, *Capra hircus* breeds (Honamlı, Saanen,

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and Hair Goat) showed no significant differences in centroid size ($F_{3,68} = 0.93$, $p = 0.429$).

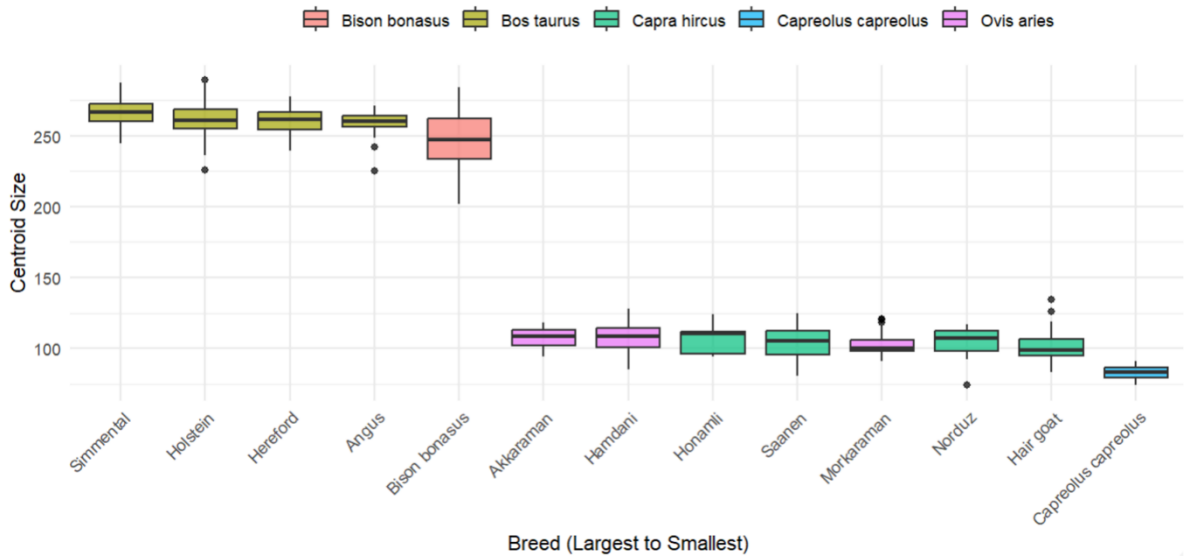


Fig. 1. Centroid Size Variation Across Ruminant Breeds, Ordered by Mean Size (Breeds arranged from largest to smallest; species color-coded)

Morphospace Distribution of Ruminant Species

The primary morphological variation captured by PC1 is associated with the medio-lateral width, dorso-ventral height and overall massiveness of the patella. At negative PC1 scores, patellae are medio-laterally broad, dorsoventrally high and overall more massive, with a medially projecting cartilaginous process that is wider and more strongly developed. At positive PC1 scores, patellae are thinner and more elongated, with a relatively narrow central region and a smaller, less projecting cartilaginous process. Variation along PC2, on the other hand, relates to the overall outline of the bone and specific proximal features. Negative PC2 scores are characterised by a more equilateral triangular shape, a more prominent cranial surface and a more developed base of the patella. In contrast, positive PC2 scores do not show a marked difference in the cartilaginous process, but the lateral margin of the patellar base is shorter and less laterally projecting, giving the bone a more quadrangular rather than triangular outline.

PCA based on 81 three-dimensional landmarks revealed distinct morphological differences among the examined species (Fig. 2 and 3). The first two principal components accounted for 38.65% of the total shape variation, with PC1 explaining 27.79% and PC2 accounting for 10.86%. A one-way ANOVA on PC1 scores showed a significant overall effect of species ($p < 0.001$), but not all pairwise contrasts were equally strong. Taken together, these patterns suggest that PC1 describes a shape gradient from broad, massive patellae with enlarged cartilaginous processes, which are consistent with increased load-bearing and joint stabilisation, towards slender, elongated patellae with reduced projections, which fit more closely with agile or cursorial locomotion. Species described as relying more on climbing or rapid escape behaviours, such as *Capra hircus* and *Capreolus capreolus*, occur at the gracile, high-PC1 end of this axis, whereas heavily built

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cattle and European bison, which engage more in weight-bearing and stabilising locomotor patterns, occur at the robust, low-PC1 end. By contrast, PC2 appears to capture a secondary aspect of patellar form related to proximal outline and the development of the patellar base. The higher PC2 scores of *Capreolus capreolus*, associated with a more quadrangular base and a less laterally projecting lateral margin, may reflect an alternative way of distributing loads at the proximal patella in a species that frequently performs rapid directional changes, although this pattern is less clear-cut than the main gradient described by PC1.

PC1 (27.79%) captured a gradient from robust to gracile patellar morphologies. When mean PC1 values were examined, *Bos taurus* had the most negative scores (mean ≈ –0.053) and exhibited the most robust, broad-bodied patellae with a distinctly developed cartilaginous process, consistent with strong weight-bearing in large-bodied ruminants. *Bison bonasus* also occupied the negative side of PC1 (mean ≈ –0.036), showing a similarly sturdy morphology but with a slightly less pronounced cartilaginous process. *Ovis aries* had an intermediate mean PC1 score (≈ +0.012) but exhibited a wide dispersion, with some specimens overlapping the European bison/cattle region (more robust morphology) and others overlapping the goat/roe deer region (more gracile morphology). Thus, sheep did not form a clearly separate cluster; instead, only a subset of individuals aligned with robust versus gracile patellar features. *Capra hircus* and *Capreolus capreolus* had positive PC1 scores (means ≈ +0.049 and +0.061, respectively) and were characterised by slender, elongated patellae with a relatively narrow central region and a less developed cartilaginous process. Along PC2 (10.86%), *Capreolus capreolus* had the highest mean score (≈ +0.067) and displayed a less robust lateral margin of the base of the patella (basis patellae), giving the bone a more quadrangular rather than triangular outline, whereas *Bos taurus* (mean ≈ –0.021) and *Ovis aries* (mean ≈ –0.019) clustered toward the lower end of PC2 and *Capra hircus* (mean ≈ +0.008) occupied a near-intermediate position with considerable dispersion along this axis.

Convex hulls effectively visualized the morphospace distribution of species. Notably, *Bos taurus* and *Bison bonasus* formed more isolated morphological clusters, whereas *Ovis aries* overlapped partially with the small ruminants (*Capra* and *Capreolus*), highlighting its intermediate position in the overall patellar morphospace.

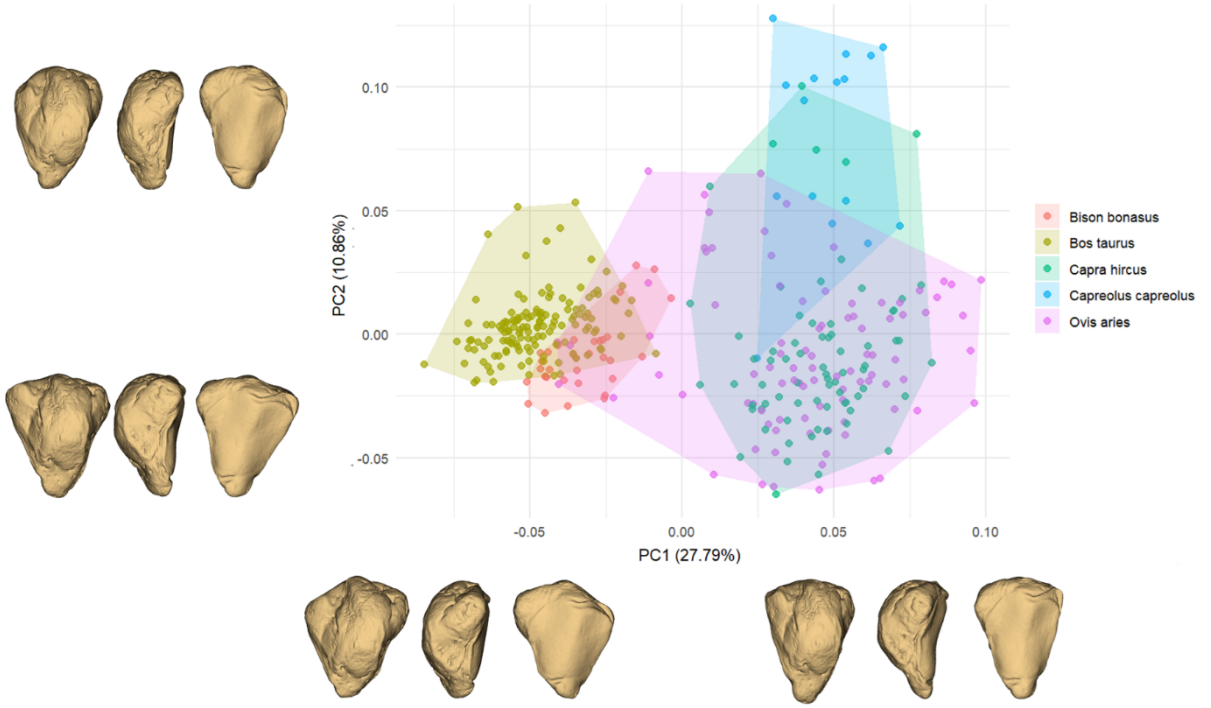
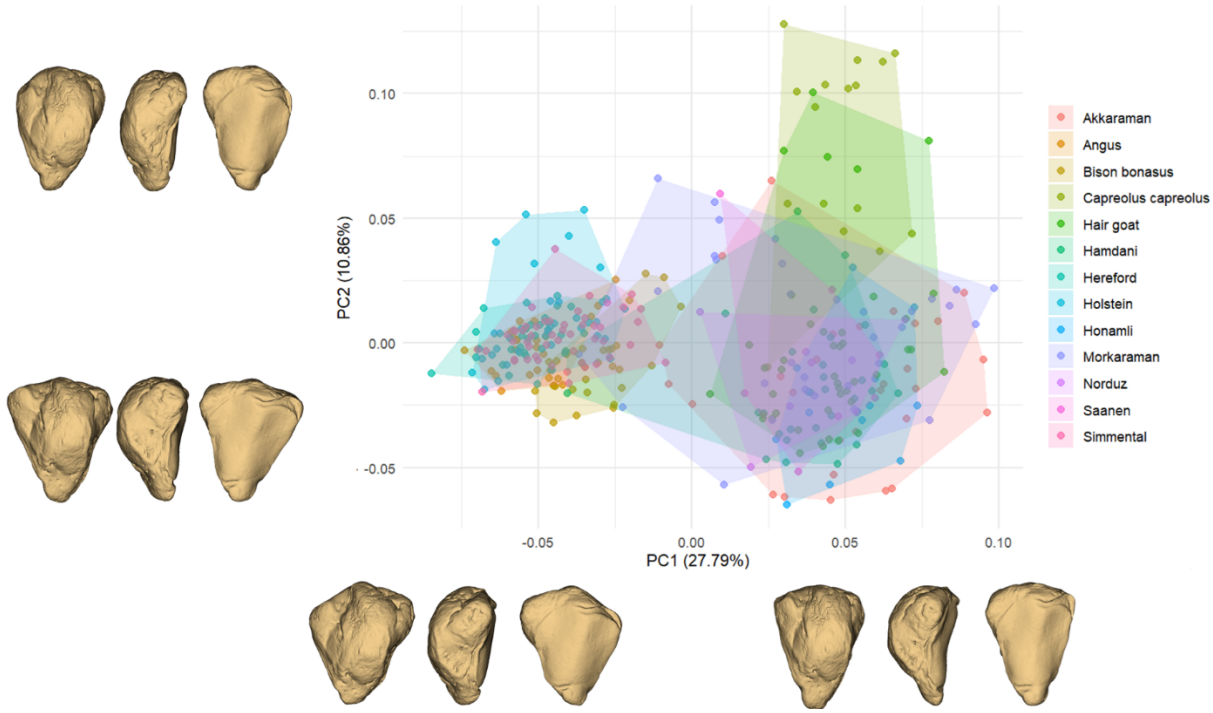


Fig. 2. Morphospace Distribution and Principal Component-Associated Patellar Shape Variation Among the Examined Ruminant Species. The figure illustrates the distribution of ruminant species within the morphospace based on PC1 and PC2, along with 3D visualizations of patellar shape changes associated with the negative and positive extremes of each principal component. The shape deformations are depicted using the right patella, shown from anterior, medial, and posterior views (left to right) for each PC axis.



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Fig. 3. Morphospace Distribution and Principal Component-Associated Patellar Shape Variation Across Ruminant Species and Domestic Breeds. The figure illustrates the distribution of ruminant species within the morphospace based on PC1 and PC2, along with 3D visualizations of patellar shape changes associated with the negative and positive extremes of each principal component. The shape deformations are depicted using the right patella, shown from anterior, medial, and posterior views (left to right) for each PC axis.

Shape Differentiation Among Ruminant Species and Breeds

Procrustes ANOVA results revealed significant shape variation across multiple taxonomic and hierarchical levels of ruminants (Table 1). A clear morphological differentiation was observed among species ($R^2 = 0.311$, $F = 39.22$, $p = 0.001$), highlighting that patellar shape varies substantially among the examined ruminant species and between large- and small-bodied ruminants in our sample. When grouped by body size, large-bodied taxa (*Bos taurus* and *Bison bonasus*) were significantly distinct from smaller ruminants (*Capra hircus, Ovis aries*, and *Capreolus capreolus*), explaining 23.7% of the total shape variation ($R^2 = 0.237$, $F = 108.58$, $p = 0.001$). This distinction aligns with the previously observed distribution along PC1, where larger ruminants consistently exhibited more robust and mediolaterally broader patellae.

In contrast, the comparison between sheep (*Ovis aries*) and goats (*Capra hircus*) did not reveal a statistically significant shape difference ($R^2 = 0.010$, $F = 1.58$, $p = 0.080$), indicating substantial morphological overlap between these two small ruminant species. However, when breeds within each taxon were analyzed separately, significant within-species (breed-level) shape variation emerged. Cattle breeds displayed detectable but modest shape differentiation ($R^2 = 0.065$, $F = 3.13$, $p = 0.001$), while sheep breeds also exhibited significant, albeit similarly limited, differences ($R^2 = 0.059$, $F = 2.75$, $p = 0.001$).

Table 1. Procrustes ANOVA results testing shape differences among ruminant species and breeds.

Predictor Variable	Question	R^2	F	p	Interpretation
Species	Is there a shape difference among ruminant species?	0.311	39.22	0.001	Yes
Large–Small ruminants	Is there a shape difference between large and small ruminants?	0.237	108.58	0.001	Yes
Sheep–Goat	Is there a shape difference between sheep and goats?	0.010	1.58	0.080	No
Cattle breeds	Is there a shape difference among cattle breeds?	0.065	3.13	0.001	Yes
Sheep breeds	Is there a shape difference among sheep breeds?	0.059	2.75	0.001	Yes
Cattle production type (Meat vs Milk)	Is there a shape difference between meat- and milk-type cattle breeds?	0.025	3.51	0.001	Yes

To test the hypothesis that patella morphology differs between breeds primarily selected for meat versus milk production, we grouped cattle breeds into meat-type (Angus, Hereford, Simmental; n = 102) and milk-type (Holstein; n = 38). Centroid size did not differ between production types (Welch t-test: $t = 0.967$, $df = 54.50$, p

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= 0.338; meat: 263.31 ± 10.00; milk: 261.08 ± 12.90). However, patella shape differed significantly between production types (procD.lm: $R^2 = 0.0248$, $F = 3.51$, $p = 0.001$), and this effect remained significant after accounting for allometry (shape ~ log(CS) + production type; production type: $F = 3.37$, $p = 0.001$; log(CS): $p = 0.044$). For sheep, all studied breeds fell into a single production category in our dataset, preventing a comparable meat–milk contrast.

Hierarchical clustering of the mean patellar shapes revealed two primary morphological groupings among the analyzed ruminant species (Fig. 4). *Bos taurus* and *Bison bonasus* formed a distinct cluster, reflecting their relatively robust patellar morphologies and closer morphological affinity. In contrast, *Capreolus capreolus, Ovis aries*, and *Capra hircus* were grouped within a separate branch, with *Ovis aries* grouped with the slender morphologies of *Capreolus* and *Capra*, rather than the more massive structures of large-bodied bovids.

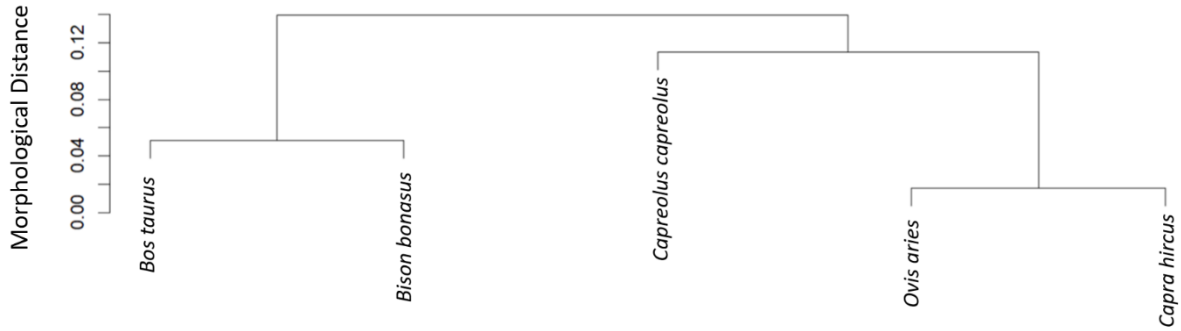


Fig. 4. Hierarchical Clustering of Mean Patellar Morphologies the Examined Ruminant Species.

Allometric Effects and Species-Specific Shape Variation

The general allometry analysis revealed that patellar shape was significantly influenced by body size (centroid size, CS), with size explaining approximately 22.7% of total shape variation (Rsq = 0.227, $F = 102.69$, $p = 0.001$). This indicates that a substantial portion of morphological variability across specimens is driven by size-related changes. When species identity was considered as a grouping factor, both size and species effects were significant (Rsq = 0.227 and 0.113, respectively; $p = 0.001$), and a significant interaction between size and species was also detected (Rsq = 0.014, $p = 0.001$). This interaction suggests that patellar shape does not scale uniformly with size across all ruminant groups; rather, the magnitude and direction of shape changes associated with size differ among species, indicating distinct allometric trajectories for each taxon.

A significant allometric relationship was identified between log-transformed centroid size (logCS) and patellar shape variation along PC1 ($p < 0.001$) (Fig. 5). PC1 describes a shape gradient from broad, medio-laterally wide and overall more massive patellae with a strongly developed, medially projecting cartilaginous process (negative scores) towards thinner, more elongated patellae with a narrower central region and reduced projections (positive scores). The regression analysis revealed a strong negative correlation ($R^2 \approx 0.785$), indicating that as centroid size increased, PC1 scores decreased substantially (slope ≈ –0.090). This suggests that larger ruminants, particularly *Bos taurus* and *Bison bonasus*, tend to

exhibit more robust and wider patellae, associated with negative PC1 scores, whereas smaller ruminants such as *Capreolus capreolus* and *Capra hircus* display more elongated and gracile patellae, represented by positive PC1 values.

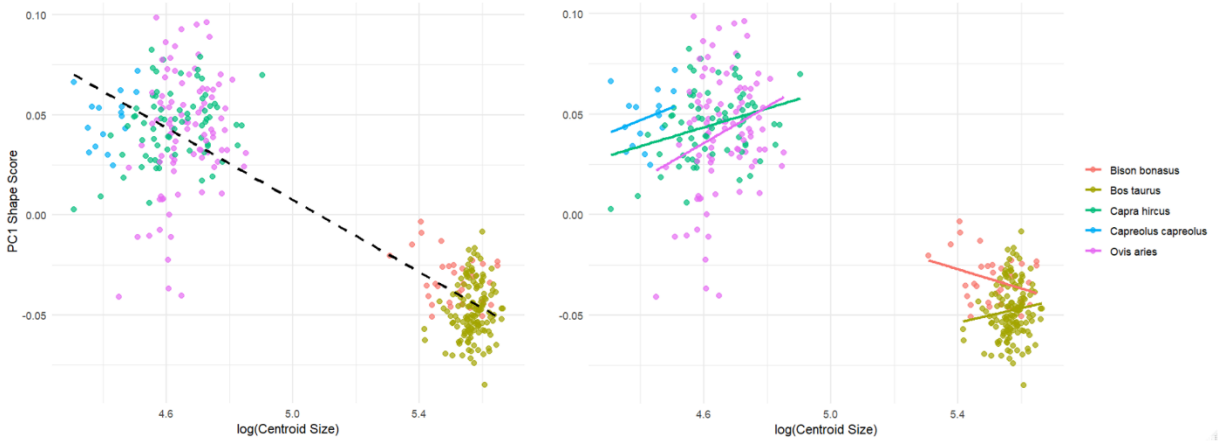


Fig. 5. Allometric Scaling of Patellar Shape (PC1) with Centroid Size Across Ruminant Species. The left panel shows the overall regression of PC1 shape scores against log-transformed centroid size for all ruminant specimens (dashed line). The right panel depicts species-specific regression lines, illustrating differences in allometric trends among *Bison bonasus, Bos taurus, Capra hircus, Capreolus capreolus*, and *Ovis aries*.

Within the five examined ruminant species, allometric trends revealed distinct patterns in the relationship between size and shape along PC1 (Fig. 5). *Ovis aries* showed a significant positive relationship ($\beta = 0.091$, $R^2 = 0.062$, $p = 0.018$), suggesting that larger individuals exhibited relatively more gracile patellae compared to smaller conspecifics. *Capra hircus* also displayed a significant positive trend ($\beta = 0.047$, $R^2 = 0.088$, $p = 0.011$), reflecting a similar, though slightly weaker, size-associated shape change. Conversely, *Bison bonasus* exhibited a weak negative slope ($\beta = -0.048$, $R^2 = 0.106$, $p = 0.065$), suggesting a tendency for larger individuals to have proportionally broader and more robust patellae, although this relationship was not statistically significant. *Bos taurus* ($\beta = 0.036$, $R^2 = 0.012$, $p = 0.198$) and *Capreolus capreolus* ($\beta = 0.064$, $R^2 = 0.074$, $p = 0.309$) did not show significant allometric relationships, although both species demonstrated considerable morphological dispersion along PC1. Collectively, these results suggest that allometric effects on patellar shape are not uniform among the studied species: sheep and goats exhibit stronger size-driven shape variation, whereas European bison (*Bison bonasus*) tend toward an opposite trend.

Discussion

This study comparatively evaluated patellar morphology and size variation among five ruminant species using geometric morphometrics, Procrustes ANOVA, and allometric analyses. The findings indicated that, in the studied species, patellar shape differences were associated with both taxonomic identity and body size, with size explaining a substantial proportion of the observed variation. Large-bodied ruminants (*Bos taurus* and *Bison bonasus*) exhibited robust patellae characterized by pronounced medio-lateral expansion and a well-developed cartilaginous

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process, features that are consistent with increased load-bearing capacity. In contrast, small-bodied species (particularly *Capreolus capreolus* and *Capra hircus*) displayed slender, elongated patellae lacking prominent projections, a morphology likely associated with reduced mechanical loading and enhanced mobility. *Ovis aries* occupied an intermediate position within the small-bodied morphospace, showing overlap with the more gracile morphologies of *Capreolus capreolus* and *Capra hircus* rather than clustering with large-bodied bovids. Allometric analyses revealed a strong relationship between patellar shape and centroid size ($R^2 \approx 0.79$). Species-specific regressions indicated that these size-driven shape changes were particularly pronounced in *Capra hircus* and *Ovis aries*, whereas they were weaker or statistically nonsignificant in *Bos taurus* and *Capreolus capreolus*. Centroid size comparisons showed that *Bos taurus* possessed the largest patellae, while *Capreolus capreolus* had the smallest structures. Shape and size differences observed among *Bos taurus* and *Ovis aries* breeds suggest that selective breeding and associated functional demands (for example, meat-oriented breeds with heavier body frames and prolonged weight-bearing in confined housing versus dairy breeds that undertake more frequent locomotion between pasture and milking facilities) may contribute to intraspecific morphological diversification as well. Overall, these findings suggest, for the species analysed here, a complex interplay between phylogenetic relatedness, functional demands, and allometric scaling in shaping patellar morphology. While the robust structures of large ruminants may reflect adaptations to substantial load-bearing demands, the slender and elongated morphologies of smaller taxa appear more compatible with ecological strategies emphasizing speed and agility. Taken together, these results suggest that patellar morphology can provide useful information on adaptive and functional diversity among ruminant species in comparative studies.

The locomotor behaviours, habitat preferences, and morphological traits of different ruminant species are associated with distinct locomotor strategies[33, 34]. Large-bodied species such as *Bos taurus* and European bison (*Bison bonasus*) are characterized by robust patellar and stifle joint structures, which are generally associated with supporting considerable body weight and maintaining joint stability during stance. In European bison, this robust morphology may also be advantageous for locomotion in structurally complex forest environments, where animals must negotiate obstacles such as fallen trees while moving at speed[28]. These adaptations are closely associated with passive locking mechanisms, where the patella and the medial femoral trochlea interact to provide self-stabilization of the stifle joint[35, 36]. This mechanism allows the joint to “lock” during the weight-bearing phase with minimal muscular effort, thereby conserving energy. The presence of such a structure, supported by tendons and ligaments, may explain the pronounced morphological differences in the cartilaginous process observed in our study. In these species, particularly during prolonged standing or steady locomotion, this adaptation is thought to alleviate mechanical stress on the joint while providing functional advantages.

The bilaterally narrow and elongated structure of the calcaneus in goats has been interpreted as a functional adaptation, providing agility and stability on steep, rocky terrains[37, 38]. Similarly, the slenderer and elongated patellar morphology observed in these species may favour faster and more flexible knee extension and is broadly consistent with their described locomotor behaviour. As the patella acts as a lever for force transmission across the stifle joint during knee extension, its

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morphological variation might be expected to align with the structural traits of the lower limb bones. In contrast, sheep, which possess a broader and more robust calcaneus along with a more massive patella, exhibit traits more consistent with sustained weight-bearing and relatively stable, less agile movements compared with goats[10]. This pattern suggests that the ecological and functional adaptations evident in the hindlimb skeleton, particularly the tarsal and distal hindlimb elements involved in load transmission, may also be reflected in smaller yet biomechanically critical structures such as the patella.

In roe deer (*Capreolus capreolus*) specimens, a weaker structure was observed along the lateral proximal edge of the patella. This characteristic is defined by the lateral articular surface of the patella being smaller and less developed compared to the medial surface. Previous linear morphometric studies have also reported that roe deer possess narrower patellae compared to species such as *Ovis aries*[39]. Both in terms of shape and linear dimensions, this relatively slender patella morphology may influence load-bearing and stabilization functions of the patella. It is plausible that roe deer, which rely on rapid running and sudden directional changes, may have evolved a thinner lateral ridge structure to better accommodate these locomotor demands.

Taken together with the Procrustes ANOVA results, these findings indicate that the strongest patellar shape contrasts occur at broader biological scales (e.g., among species and between large- and small-bodied groups), whereas breed-level differences within *Bos taurus* and *Ovis aries* are more subtle but still statistically supported, with comparatively small effect sizes. In cattle, grouping breeds by production type revealed a significant difference in patellar shape between meat- and milk-type breeds, and this effect remained significant after accounting for allometry, whereas centroid size did not differ between production types. These patterns suggest that intraspecific patellar shape variation may reflect not only biological determinants but also the outcomes of artificial selection and breeding strategies. The functional interpretation of these differences (e.g., more robust versus more slender morphologies) remains to be tested explicitly using targeted biomechanical or deformation-based analyses. For sheep, an analogous meat-milk comparison could not be performed with the current sample because all studied breeds belonged to a single production category; thus, future studies with balanced dairy and meat breeds are needed to evaluate this hypothesis.

Additionally, the morphological variation observed among the studied ruminant species, even when overall dimensions were comparable, has potential implications for veterinary surgical practices, particularly in orthopedic procedures involving the stifle joint[40]. Differences in patellar shape, such as the degree of lateral ridge development or cartilaginous process morphology, could influence the fit and stability of implants, pins, or fixation devices. Standardized hardware designs based solely on size may not account for species-specific morphological nuances, potentially impacting surgical outcomes. Therefore, the morphometric data provided here may help to inform refinements in implant and pin designs tailored to ruminant species similar to those examined in this study, thereby potentially improving the precision and effectiveness of such interventions.

Several limitations should be considered when interpreting the findings of this study. First, only right patellae were examined, as left specimens were not systematically collected. Although asymmetry in ruminant limb elements is

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generally minimal, this approach limits the ability to assess potential fluctuating or directional asymmetry. Second, most specimens in this study were derived from male individuals, as males are more commonly processed in slaughterhouses. This unbalanced sex distribution restricted direct evaluation of sexual dimorphism. Therefore, we cannot exclude sex-related contributions to the allometric patterns observed in our results, particularly because males tend to be larger in body size. Consequently, the allometric influence on patellar shape may reflect not only functional and species-related factors but also this sex imbalance in the sample. Third, taxonomic coverage was restricted to five ruminant species (four domestic bovids and one wild cervid), including two large-bodied species from the tribe Bovini; as a result, size- and lineage-related patterns observed here should not be generalized to Ruminantia as a whole, and body-size effects cannot be fully separated from phylogenetic relatedness. Fourth, most of the material used in this study originated from domestic animals kept under husbandry conditions rather than from free-ranging populations, so functional and locomotor interpretations should be regarded as tentative and hypothesis-generating rather than definitive.

Conclusion

This study suggests that even a relatively small and seemingly simple bone like the patella can exhibit notable morphological differences among ruminant species. Although the patella is often regarded as a secondary skeletal element, it plays a crucial role during knee extension in both swing and stance phases of the locomotor cycle. In the species analysed here, patellar shape and proportions vary systematically among species in ways that are broadly consistent with reported ecological niches, locomotor behaviour, and functional demands.

These results indicate that informative morphological variation is not confined to large or complex skeletal structures but can also carry meaningful biological signals in relatively small bones such as the patella. Taken together, these observations identify the patella as a potentially valuable marker for understanding biomechanical functions and for generating hypotheses about interspecific ecological differences and locomotor strategies in ruminant species.

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Material method

Sample Collection

A total of 352 patellae representing 13 ruminant breeds across five taxa were analyzed in this study. The dataset comprised specimens from *Bos taurus* (Angus, Hereford, Holstein, Simmental; n = 140), *Bison bonasus* (n = 33), *Ovis aries* (Akkaraman, Hamdani, Morkaraman, Norduz; n = 98), *Capra hircus* (Hair goat, Honamli, Saanen; n = 65), and *Capreolus capreolus* (n = 16). Individual breed counts were as follows: Akkaraman (29), Angus (23), European bison *(Bison bonasus)* (33), *Capreolus capreolus* (16), Hair goat (43), Hamdani (30), Hereford (28), Holstein (38), Honamli (14), Morkaraman (32), Norduz (7), Saanen (8), and Simmental (51).

Only the right patellae of each specimen were included in the present study to standardize the dataset and eliminate potential bias arising from bilateral asymmetry. Left patellae were not collected, and any possible directional or fluctuating asymmetry between sides was intentionally disregarded to focus exclusively on interspecific and intraspecific morphological variation. This

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approach ensured consistency across all specimens and reduced variability unrelated to the primary research objectives.

Specimens of European bison *(Bison bonasus)* and roe deer *(Capreolus capreolus)* were sourced as archived osteological material from the Osteological Museum of the Department of Morphological Sciences, Institute of Veterinary Medicine, Warsaw University of Life Sciences (SGGW, Poland). All remaining specimens were obtained from abattoirs located in Istanbul, Ankara, Samsun, and Siirt (Türkiye). After dissection, patellae were macerated by boiling, treated with 50% hydrogen peroxide to remove residual soft tissues, and air-dried for one month.

All specimens were digitized using a Shining 3D EinScan Pro 2× 3D scanner (Shining 3D, Hangzhou, China) in high-definition mode. The 3D meshes were reconstructed using EXScan Pro software (version 4.0.0.4) provided by the scanner manufacturer and exported in ".PLY" format for subsequent geometric morphometric analyses.

All procedures involving animal-derived materials were conducted in accordance with ethical standards and approved by the Istanbul University-Cerrahpaşa Animal Experiments Local Ethics Committee (Approval No: 2024/77). The collection and processing of specimens adhered to institutional guidelines, ensuring compliance with national and international regulations for the use of animal materials in scientific research. This study is reported in accordance with the ARRIVE guidelines.

Landmarking and Geometric Morphometric Analyses

In this study, 81 three-dimensional landmarks were utilized for each patella. Initially, a draft landmark set was generated using the PseudoLMGenerator module in 3D Slicer (version 5.2.2) (Fig. 6). This draft set was subsequently transferred to all sample models via the ALPACA (Automated Landmarking through Point Cloud Alignment and Correspondence Analysis) module. ALPACA enabled the efficient transfer of landmarks from the reference 3D model to each target specimen by employing point cloud alignment and shape-deformable mesh registration. As a result, a standardized dataset comprising 81 landmarks per specimen was obtained (Supplementary Table 1). Landmark coordinate data are provided in Supplementary File 1 to ensure transparency and facilitate potential reanalysis.

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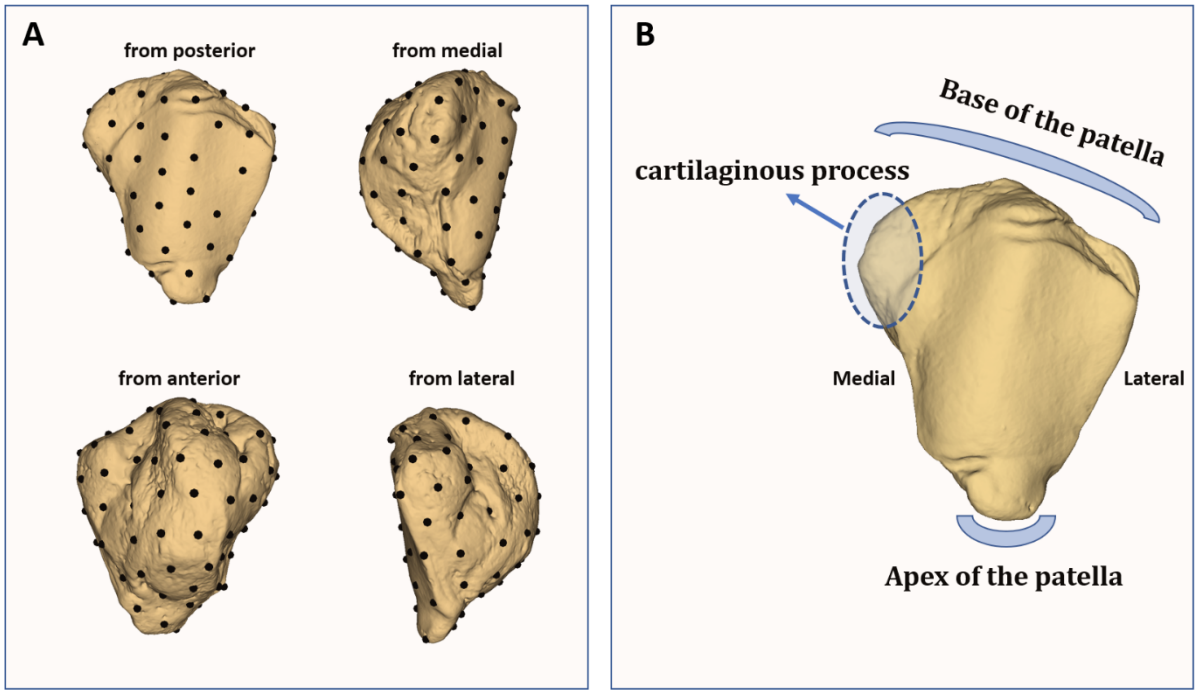


Fig. 6. Landmark Configuration (A) and Key Anatomical Features from caudal view (B) of the Ruminant Patella.

This procedure aligned all specimens within a shared shape space centered on the mean shape, enabling subsequent analyses, including Principal Component Analysis (PCA), Procrustes ANOVA, allometric assessments, and size-based comparisons, to focus solely on shape variation.

Statistical Analyses

All statistical analyses were performed in RStudio (version 2024.09.1) using the geomorph package (v.4.0.9). The analytical workflow aimed to evaluate shape variation, group-level differences, and the influence of size across ruminant taxa.

Initially, a dataset comprising 81 three-dimensional landmarks per specimen was subjected to a Generalized Procrustes Analysis (GPA). This procedure standardized the landmark configurations by eliminating variation attributable to position, orientation, and isometric size. During GPA, centroid size (CS) was calculated for each specimen and used as a metric representing overall patellar size in subsequent analyses. The GPA-aligned coordinates formed the basis for generating the covariance matrix of shape variables and served as the foundation for all multivariate analyses.

To visualize the primary patterns of shape variation, a Principal Component Analysis was conducted on the Procrustes-aligned coordinates. The first two principal components (PC1 and PC2) were plotted to illustrate the major axes of morphological variation, with convex hulls outlining the morphospace occupation of each species (*Bos taurus, Bison bonasus, Ovis aries, Capra hircus*, and *Capreolus capreolus*). Mean PC1–PC2 scores were calculated for each taxon to represent central morphological tendencies. Shape changes along the positive and negative extremes of PC1 and PC2 were visualized using 3D deformation grids and models.

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Group-level differences in shape were assessed using Procrustes ANOVA with 1,000 permutations, following a hierarchical modeling framework:

- Among all five species (*Bos taurus, Bison bonasus, Ovis aries, Capra hircus*, and *Capreolus capreolus*).
- Between large-bodied ruminants (*Bos taurus* and *Bison bonasus*) and small-bodied taxa (*Ovis aries, Capra hircus*, and *Capreolus capreolus*).
- Between domestic sheep (*Ovis aries*) and domestic goats (*Capra hircus*).
- Among *Bos taurus* breeds.
- Among *Ovis aries* breeds.

The relationship between shape and size was evaluated through allometric analyses, performed both across the full dataset and within individual species. Procrustes-aligned coordinates were regressed against log-transformed centroid size (log [CS]) as the predictor. Models incorporating the interaction term (log [CS] × species) tested for differences in allometric trajectories among species. Additionally, linear relationships between PC1 scores and log (CS) were quantified, with regression lines visualized for the entire dataset and separately for each species.

To examine size variation, mean and standard deviation of centroid size were calculated at both the species and breed levels. One-way ANOVA and Tukey post hoc tests were applied to:

- Compare large-bodied (*Bos taurus, Bison bonasus*) and small-bodied (*Ovis aries, Capra hircus, Capreolus capreolus*) ruminants separately.
- Assess size differences within breeds of *Bos taurus, Ovis aries*, and *Capra hircus*.

To visualize morphological similarities and divergences among species, a hierarchical clustering analysis (UPGMA method) was performed using Procrustes distances of mean shape coordinates for each species. The resulting dendrogram illustrated the degree of morphological resemblance among the patellar shapes of the studied ruminant species.

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Author information

Authors and Affiliations

Department of Anatomy, Faculty of Veterinary Medicine, Istanbul University-Cerrahpasa, 34320 Istanbul, Türkiye

Oya Kahvecioğlu, Burak Ünal, Ermiş Özkan, Gülsün Pazvant, Nazan Gezer İnce, Ozan Gündemir

Department of Anatomy, Faculty of Veterinary Medicine, Siirt University, 56100 Siirt, Türkiye

Barış Can Güzel

Department of Anatomy, Faculty of Veterinary Medicine, Ankara University, 06110 Ankara, Türkiye

Barış Batur, Caner Bakıcı, Reşide Merih Hazıroğlu

Department of Surgery, Faculty of Veterinary Medicine, Istanbul University-Cerrahpasa, 34320 Istanbul, Türkiye

Zihni Mutlu

Department of Anatomy, Faculty of Veterinary Medicine, Ondokuz Mayıs University, 55270 Samsun, Türkiye

Sedef Selviler Sizer

Department of Morphological Sciences, Institute of Veterinary Medicine, Warsaw University of Life Sciences-SGGW, 02-776 Warsaw, Poland

Tomasz Szara

Department of Animal Anatomy, Histology and Pathomorphology, National University of Life and Environmental Sciences of Ukraine, Kyiv, Ukraine

Oleksii O. Melnyk

Osteoarchaeology Practice and Research Centre, Istanbul University-Cerrahpasa, 34320 Istanbul, Türkiye

Ozan Gündemir

Contributions

All authors conceived and designed the study. B.Ü. and E.Ö. performed the landmark digitization. O.G., C.B. and T.S. conducted the statistical analyses. O.K., R.M.H. and O.G. served as project supervisors. B.C.G., B.B., C.B., Z.M., S.S.S., T.S., O.O.M. and R.M.H. contributed to 3D scanning and specimen collection. All authors contributed significantly to interpreting the data and results, and to writing and revising the manuscript.

Additional information

Supplementary Information

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Supplementary Table 1. Specimen information and three-dimensional patellar landmark coordinates.

Corresponding author

Correspondence to Oleksii O. Melnyk.

Data availability

For academic access to the data, please reach out to the last author (Ozan Gündemir).

Ethics declarations

Competing interests

The authors declare no competing interests.

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