



GEOMETRIC MORPHOMETRIC ANALYSIS OF SCAPULAR SHAPE AND MORPHOLOGICAL PHYLOGENY AMONG BARASINGHA, SLOTH BEAR, SMALL INDIAN CIVET, STRIPED HYENA, AND INDIAN PARIAH DOG

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(Received 1 September, 2025; accepted 20 October, 2025)

ABSTRACT

Understanding scapular morphology is essential for interpreting species-specific adaptations related to locomotion, muscle attachment, and ecological strategies. This study used geometric morphometric techniques to analyse scapular shape variation and morphological phylogeny in five mammalian species, barasingha (*Rucervus duvaucelii*), Sloth bear (*Melursus ursinus*), small Indian civet (*Viverricula indica*), striped hyena (*Hyaena hyaena*), and Indian Pariah dog (*Canis lupus familiaris*). The study was aimed to understand how scapular morphology reflects species-specific adaptations. A total of 144 homologous landmarks were digitized from high-resolution images of lateral and medial scapular surfaces. Shape variation was analysed using principal component analysis (PCA) and Procrustes ANOVA. Morphology-based clustering was performed using hierarchical UPGMA dendrograms based on PCA. Results revealed that PC1 accounted for 80.40% of shape variance (species-wise), mainly associated with acromion process orientation and scapular spine morphology. PCA analysis (surface-wise) described the lateral and medial scapular surfaces showed a more balanced variance distribution (PC1: 33.71%, PC2: 20.81%, PC3: 18.83%). Procrustes ANOVA showed a significant effect of scapular surface on shape ($F = 10.34$, $P < 0.0001$) but not on size ($P = 0.0888$). The phylogenetic dendrogram separated the species into two major phenetic groups. The study offers new insights into scapular shape diversity and its ecological and evolutionary significance among studied mammals.

Keywords: Functional adaptation, geometric morphometrics, mammalian morphology, phylogeny, scapula

INTRODUCTION

The scapula is a critical component of mammalian pectoral girdle that links forelimb to the axial skeleton. Its morphology reflects a delicate balance between phylogenetic constraints and functional adaptations driven by ecological demands. As a flat bone that serves as the origin and insertion site for numerous forelimb muscles, the scapula plays a central role in controlling limb orientation, stride length, muscle leverage, and ultimately the locomotor performance (Pu *et al.*, 2016; Talukder and Jo, 2025). Even subtle changes in scapular shape can significantly influence forelimb kinematics, offering valuable insights into the adaptive strategies of different mammalian lineages (Martín-Serra *et al.*, 2015; MacLaren and Nauwelaerts, 2016; Rothier *et al.*, 2024).. The several

anatomically distinct regions on the scapula vary between species to support different movements. In particular, acromion shape affects muscle leverage, helping animals specialize in climbing, digging, or running. (Polly, 2007; Sakoma *et al.*, 2011; Gómez *et al.*, 2022). Scapular spine morphology regulates the balance between supraspinous and infraspinous fossae, which house major shoulder stabilizers like supraspinatus and infraspinatus muscles (Mathewson *et al.*, 2013; Cavanaugh *et al.*, 2024; Krystalli *et al.*, 2024). The glenoid cavity orientation affects the range of humeral motion and contributes to the locomotor specialization, such as cursoriality in runners versus scansoriality in climbers (Polly, 2007; Arias-Martorell, 2019). Thus, scapula acts as a morphological proxy in understanding the functional performance, ecological roles, and evolutionary histories. Mammalian scapulae exhibit adaptations corresponding to distinct locomotor ecologies (Larson, 1995; Young, 2006). Cursorial mammals have elongated, caudally angled scapulae that enhance stride efficiency (Coombs, 1983). Arboreal and scansorial species exhibit broader, more robust scapulae that support versatile climbing motions (Pathak *et al.*, 2022). Scavengers like hyenas show reinforced scapular structures for powerful forelimb use, highlighting the scapula's value in studying functional adaptation (Janis and Figueirido, 2014). Selective pressures on forelimb performance shape these traits, making the scapula a useful indicator of adaptive evolution and functional differences. (Kang *et al.*, 2023).

Linear and angular scapular measurements capture only limited aspects of shape (Klingenberg, 2010). Geometric morphometrics offers a more comprehensive, landmark-based analysis (Bookstein, 2016) that better links biological and ecological factors. Despite its success in studying other mammalian structures such as cranial, mandibular, and limb structures (Adams *et al.*, 2004, 2013; Araujo *et al.*, 2023), this method has not yet been used to investigate scapular form in India's diverse mammals, leaving a notable gap in regional functional and evolutionary research. This study investigated how scapular morphology in Indian mammals reflects their ecological specializations and evolutionary histories. Five species representing distinct locomotor and functional niches selected were: the barasingha (*Rucervus duvaucelii*) as a cursorial grazer, the sloth bear (*Melursus ursinus*) as a climber and digger, the small Indian civet (*Viverricula indica*) as a scansorial omnivore, the striped hyena (*Hyaena hyaena*) as a scavenging carnivore, and the Indian pariah dog (*Canis lupus familiaris*) as a cursorial endurance predator. Using two-dimensional landmark-based geometric morphometrics, the study quantified and compared scapular shape variation across species. Multivariate analyses, including PCA and a morphology-based phenogram, were used to visualize morphological relationships and assess how well scapular shape corresponds to known phylogeny. Both lateral and medial scapular surfaces were examined to understand the balance between structural constraints and adaptive modifications. Overall, the research aims to clarify the ecological and evolutionary factors driving scapular shape diversity in Indian mammals.

MATERIALS AND METHODS

Sample collection

One scapula from each adult Barasingha (*Rucervus duvaucelii*), Sloth bear (*Melursus ursinus*), small Indian civet (*Viverricula indica*), striped hyena (*Hyaena hyaena*), and Indian Pariah dog (*Canis lupus familiaris*) without visible abnormalities was used in this study. The specimens were utilized from the Section of Veterinary Anatomy, Indian Veterinary Research Institute (IVRI), Izatnagar, Bareilly, Uttar Pradesh, India. All scientific work was conducted in the Department of Veterinary Anatomy, Faculty of Veterinary and Animal Sciences, BHU, Rajiv Gandhi South Campus, Mirzapur, Uttar Pradesh, India during December, 2024 to September 2025. The scapulae studied were included irrespective of age, sex, and side due to unavailability of samples.

Image acquisition and landmark selection

High-resolution photographs of lateral and medial surfaces of each scapula were taken using a digital

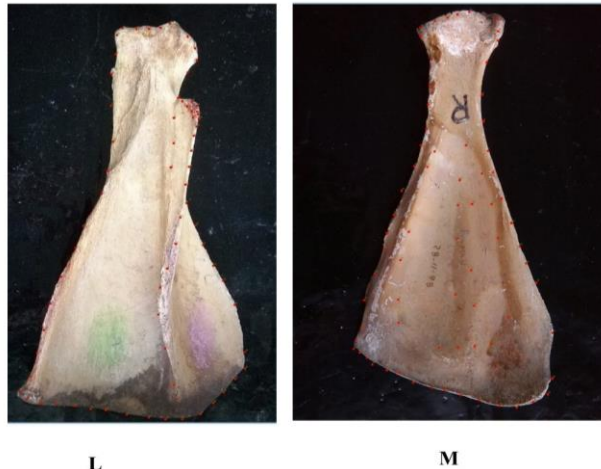


Fig. 1: Anatomical landmarks on the scapula of wild animals, represented here using the barasingha (*Rucervus duvaucelii*). A total of 72 landmarks are indicated by red dots and numbered accordingly. L denotes landmarks located on the lateral surface of the scapula, while M indicates those on medial surface.

camera (Sony ZV-E10L) at a fixed distance of 15 cm under natural day lighting conditions. A total of 72 anatomically homologous landmarks were identified on each surface, yielding 144 landmarks per bone. Landmarks were selected based on repeatable, clearly visible anatomical features (Fig. 1) and broadly categorized as lateral surface and medial surface. In both categories the landmarks were: Cranial border (landmarks 1-15), dorsal border (landmarks 16-30), caudal border (landmarks 31-45), and glenoid cavity (visible from lateral/medial side) (landmarks 46-50). Further, landmark 51-60 and 61-72 represented acromion process and spine, respectively, in lateral surface while landmarks 51-60 and 61-72 represented outlines of cranial and caudal parts of subscapular fossa, respectively, in medial surface.

Landmark digitization, data preparation and analysis

Each image was digitized using TPSDig2 (version 2.32), and landmark coordinates were saved in TPS format using TPSUtil (version 1.32). The compiled landmark dataset was imported into MorphoJ (version 1.08.01) for statistical analyses (Klingenberg, 2011).

Geometric morphometric analysis and statistical analysis

A Generalized Procrustes Analysis (GPA) was performed to remove variation related to size, position, and orientation, isolating shape variables for further analysis (Wöber *et al.*, 2022). PCA was then applied to identify the main axes of shape variation and visualize interspecific differences (Vida *et al.* 2014). Shape variation patterns were visualized using Wireframe diagrams (showing deformation relative to the consensus shape), PCA scatter plots, all statistical analyses and visualizations were generated in MorphoJ, with supplementary plots and diagrams created in Python for enhanced clarity.

Phylogenetic tree

Morphology-based clustering was performed using the first five principal components (PC1–PC5) derived from the morphometric dataset. These scores were used to calculate Euclidean distances between the species, which were then subjected to hierarchical agglomerative clustering using the unweighted pair group method with arithmetic mean (UPGMA) (Zou *et al.*, 2024). The resulting dendrogram represents phenetic relationships among the species based on overall scapular morphology. The dendrogram was generated in Python using hierarchical clustering algorithms and visualized with the matplotlib and *scipy.cluster.hierarchy* packages.

RESULTS AND DISCUSSION

Principal component analysis (PCA)

The PCA of combined dataset revealed significant interspecific differences in scapular shape (PCA analysis pooled by species). The first three principal components explained approximately 95.4% of

Table 1: Principal component analysis pooled by species (PC1 is the largest contributor)

PC	Eigen value	% Variance	Cumulative%
1	0.11318054	80.396	80.396
2	0.01272188	9.037	89.433
3	0.00839898	5.966	95.399
4	0.00346160	2.459	97.857
5	0.00301620	2.143	100.000

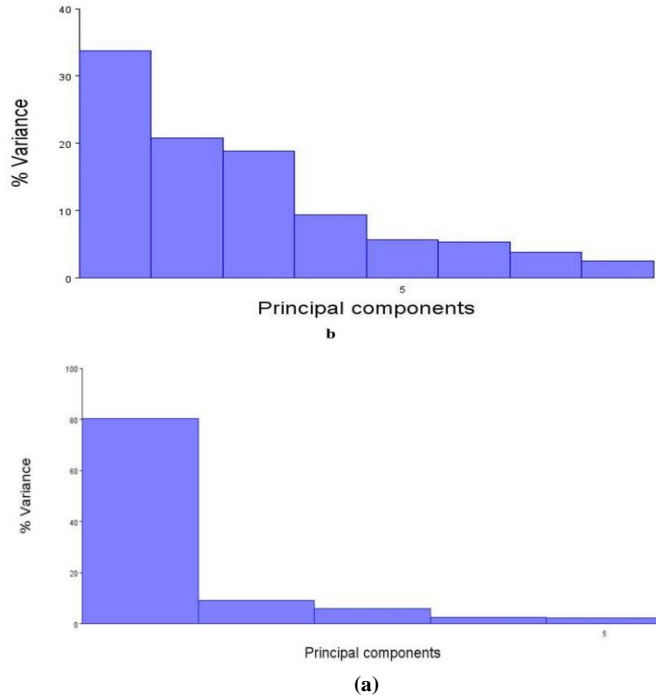


Fig. 2: Principal component analysis (PCA) of wild animal shapes; a) PCA based on species, where the first two principal components (PC1 & PC2) explain about 89% of total shape variation, effectively capturing the main patterns in shape differences among species. b) PCA based on surface characteristics, where the first four principal components (PC1–PC4) together explain approximately 83% of total shape variation. This was dimensionality sufficient to capture and visualize the major trends in shape variation.

total variance (PC1 = 80.4%, PC2 = 9.04%, PC3 = 5.97%). PC1 captured the most variation and was influenced primarily by the landmarks associated with the acromion process and scapular spine. Barasingha occupied positive PC1 axis, characterized by elongated and narrow scapulae suited for cursorial locomotion. In contrast, Sloth bear plotted on negative PC1 side, showed broad scapulae with well-developed spines, adaptations for climbing and digging. PC2

represented differences in glenoid orientation, dorsal border curvature, and cranial margin shaping. The small Indian civet clustered along the positive PC2 axis, indicating moderate scapular curvature that supports scansorial and terrestrial behaviours. The striped hyena occupied negative PC2 region, marked by laterally expanded scapular blades and a reoriented glenoid cavity. PC3 highlighted subtle species-specific refinements, including variation in supraspinous fossa depth and caudal border curvature, contributing to functional distinctions among species (Table 1; Fig. 2a, 3a).

When the dataset was analysed separately for lateral and medial scapular surfaces, variance was more evenly distributed (PC1 = 33.71%, PC2 = 20.81%, PC3 = 18.83%). This indicated that both surfaces contribute independently to overall scapular morphology (Table 2). PCA scatter plots revealed distinct clustering patterns. Barasingha grouped separately along positive PC1, small Indian civet lay closer to positive PC2, showing moderate scapular curvature suitable for mixed locomotion. Striped

hyena extended along negative PC2, characterized by laterally expanded blades adapted for strong forelimb musculature. Indian Pariah dogs clustered opposite to the Sloth bear along PC1 (Fig. 2b). PCA-derived wireframe deformation grids revealed distinct shape variations between the lateral and medial scapular surfaces. PC1 captured the most significant differences, showing that lateral surfaces have a more prominent spine and larger supraspinous fossae, while medial surfaces maintain more conservative curvature. PC2 highlighted differences in the orientation of scapular neck and glenoid cavity between the two surfaces. PC3 and PC4 illustrated subtle asymmetries, likely due to differing muscle attachment functions. The wire- frame grids visually emphasized these variations, aiding in the interpretation of surface-specific morphometrics (Fig. 3b).

Table 2: Principal component analysis pooled by surface (PC1, PC2, PC3 and PC4 are the major contributors)

PC	Eigen value	Variance (%)	Cumulative (%)
1	0.01828631	33.710	33.710
2	0.01128839	20.810	54.520
3	0.01021622	18.833	73.353
4	0.00510003	9.402	82.755
5	0.00306512	5.650	88.406
6	0.00288109	5.311	93.717
7	0.00206526	3.807	97.524
8	0.00134313	2.476	100.000

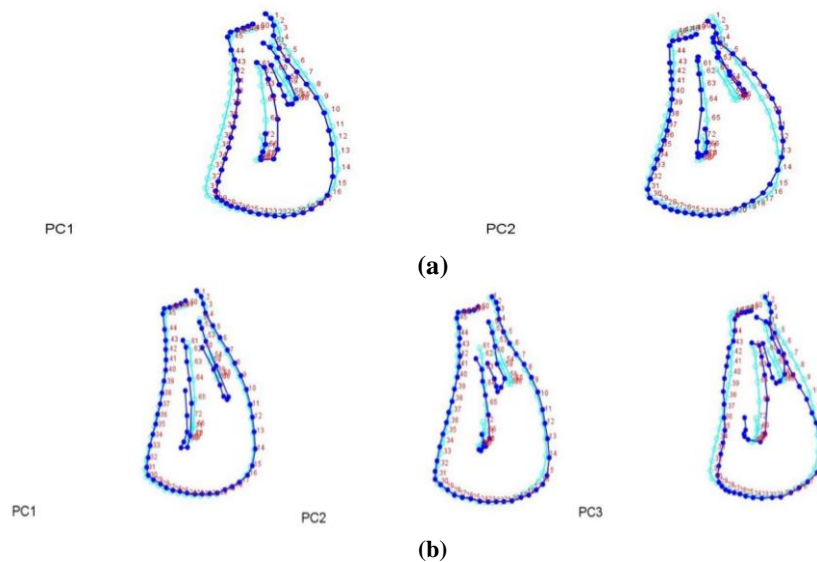


Fig. 3: Wireframe graphs derived from PCA, illustrating mean scapula shape variation; a) Mean scapula shape variation across different wild animal species (PC1 and PC2), b) Mean scapula shape variations across the lateral and medial surfaces of wild animal species (PC1, PC2 and PC3). The green wireframe represents the mean scapula shape, while blue lines indicate shape deviations along the principal components derived from PCA.

Table 3: Shape (Procrustes ANOVA) analysis showing significant shape variation

Effect	SS	MS	df	F value	P value (param.)
Surface	0.56062931	0.0040044951	140	10.34	<0.0001
Species	0.43396440	0.0003874682	1120	-	-

Table 4: Centroid size ANOVA analysis showed no significant size difference between lateral and medial surfaces

Effect	SS	MS	df	F	P (param.)
Surface	1,330,439.93	1,330,439.93	1	3.75	0.0888
Species	2,838,153.72	354,769.21	8	-	-

Procrustes ANOVA

Centroid size analysis showed no significant size difference between lateral and medial surfaces ($F = 3.75$, $p = 0.0888$). Shape, however, varied significantly ($F = 10.34$, $p < 0.0001$) [Table 3 and 4] indicating the functional relevance of surface-specific morphological adaptations. Interspecific shape variation was statistically significant, confirming that scapular morphology is strongly influenced by species-specific locomotor and ecological adaptations. Scapular morphology emerged as a reliable marker of locomotor ecology. Cursorial species such as

barasingha and Indian Pariah dog possess elongated, lightweight scapulae with streamlined fossae, enhancing stride length and running efficiency (Matsuo *et al.*, 2019). Climbing and digging specialists like the Sloth bear display robust scapulae with expanded fossae and prominent spines, supporting powerful forelimb musculature for arboreal activity and excavation (Luziga and Wada, 2018). Scansorial intermediates such as the small Indian civet combine moderate scapular curvature with balanced fossae, allowing for both terrestrial movement and climbing adaptability. Striped hyenas

represent a specialized scavenging adaptation, exhibiting laterally expanded scapulae and unique glenoid orientation to optimize tearing efficiency and forelimb strength (Suedmeyer, 2015). These

findings are consistent with the results obtained from our principal component analysis.

Phylogenetic tree analysis

Hierarchical clustering based on the first five principal components (PC1 - PC5)

revealed distinct morphological groupings among the five species. The dendrogram distinctly separated the species into two major phenetic groups, broadly corresponding to differences in the lateral and medial scapular surfaces (Fig. 4). The morphology-based dendrogram reflects both phylogenetic divergence and functional convergence. Medial scapular traits are more phylogenetically conserved, particularly among the small Indian civet and Sloth bear, which share structural similarities despite ecological differences (Chakravarthy and Ratnam, 2015; Laurie and Seidensticker, 1977; Shameer *et al.*, 2023). Lateral scapular traits demonstrate functional divergence, aligning more closely with locomotor ecology than with evolutionary lineage. The barasingha remains morphologically distinct in both surfaces, suggesting that cervid scapular evolution is highly specialized for grazing and cursorial adaptation.

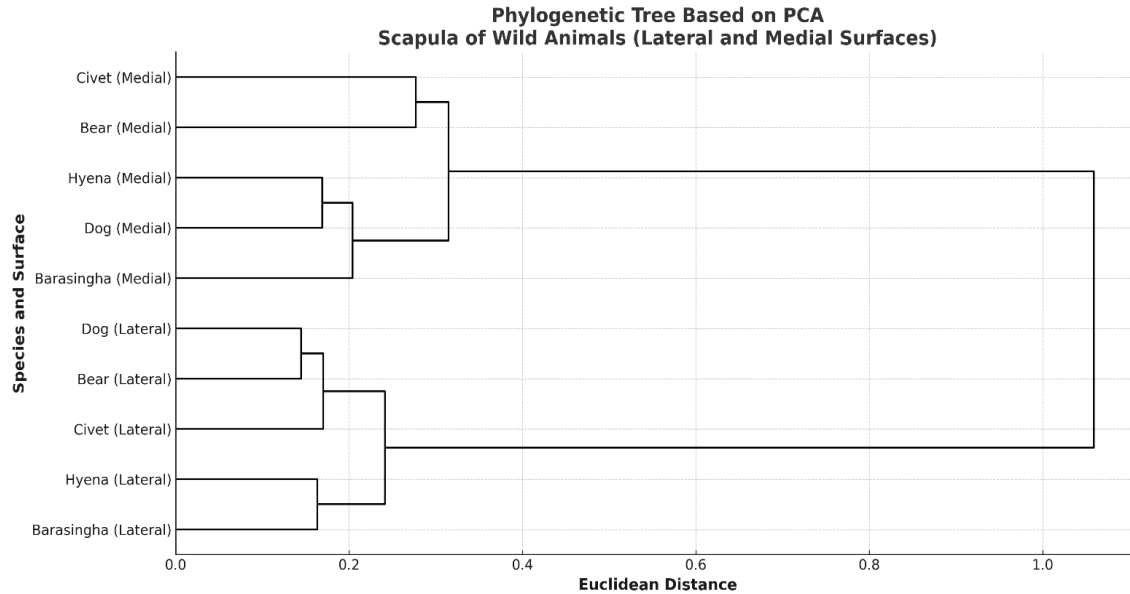


Fig. 4: Hierarchical clustering dendrogram based on scapular shape variation (PC1–PC5). Species are grouped according to their morphological similarity on lateral and medial surface

Medial surface morphology

The medial scapular surface displayed greater interspecies similarity, forming a tightly clustered group. The small Indian civet and Sloth bear grouped together early, sharing traits like broad subscapular fossa and comparable cranial border curvature. The striped hyena and Indian Pariah dog formed another subcluster, suggesting similar fossa depth and muscle attachment areas. The barasingha diverged later, reflecting cervid-specific adaptations like an elongated cranial border and distinct scapular fossa outlines.

Lateral surface morphology

The lateral scapular surface demonstrated greater morphological divergence. The Indian Pariah dog clustered with the Sloth bear, reflecting similarities in acromion orientation and spinal robustness and glenoid cavity positioning. The small Indian civet joined this cluster, representing an intermediate scapular form combining scansorial and cursorial adaptations. The striped hyena and barasingha formed distant branches, each displaying highly specialized scapular traits—the hyena for scavenging and powerful forelimb leverage, and the barasingha for cursorial grazing and stride optimization. The significant shape differences between lateral and medial scapular surfaces, despite similar sizes, highlight their functional specialization: The lateral surface shows adaptations for muscle leverage—species with powerful forelimbs (e.g., Sloth bear, hyena) exhibit deeper fossae and pronounced spines. The medial surface, by contrast, retains more conserved morphology, primarily constrained by subscapular muscle attachment requirements.

Conclusion: This study revealed that geometric morphometrics is effective in analysing the complex shape differences and tracing evolutionary relationships. The scapula proved to be highly responsive to locomotor functions, reflecting clear morphological adaptations. Overall, scapular shape serves as a strong indicator of both functional roles and evolutionary history in wild mammals.

Acknowledgment: Authors thank Dr. Amarpal, Principal Scientist, In-charge, Veterinary Anatomy Section, Indian Veterinary Research Institute, Izatnagar, Bareilly, India, for providing access to wild animal bones for photography.

Conflict of interest: The authors declare that there is no conflict of interest regarding the publication of this manuscript.

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