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Review

Shape speaks loud: a geometric morphometric perspective on veterinary osteology

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ABSTRACT

Geometric morphometrics has created a significant field in the study of skeletal variation in veterinary osteology by providing a robust framework for investigating shape variation. This technique allows for the analysis of anatomical structures in a variety of biological contexts. This review examines the extant literature, demonstrating how dietary consistency and biomechanical structure significantly shape and often lead to intergenerational morphological changes. The investigation further explores the function of locomotion strategies, including habitat preference and diversity, in the context of the skeletal system. The merits of geometric morphometric analysis are evident in its capacity to facilitate species identification and close relative discrimination in scenarios where conventional methods encounter constraints. The utilisation of geometric morphometric analysis offers distinct advantages in ontogenetic studies, allometric scaling in morphology, and the consideration of developmental constraints. Additionally, it provides a framework for investigating sexual dimorphism and variations in shape across varied species and anatomical regions. From a clinical and welfare perspective, geometric morphometrics provides a powerful framework for orthopaedic surgical planning, detection of pathological changes, phenotyping in animal models, and translational research. Finally, the integration of artificial intelligence (AI)-powered automation and high-resolution imaging is also being reviewed in studies. These developments position geometric morphometrics as an indispensable method for integrating form, function, and health in veterinary research.

Keywords: Geometric morphometrics, Morphological variation, Shape analysis, Veterinary osteology

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Introduction

The skeletal morphology provides essential insights into taxonomic classification, evolutionary biology, forensic investigations, and clinical applications. Skeletal forms are dynamic structures shaped by the interaction of genetic programs, developmental processes, and functional factors. Bone responds to biomechanical loading and environmental changes; therefore, understanding skeletal shape is essential for interpreting an animal's life history, ecological niche, and health status (16, 23, 25, 33, 41, 55, 60, 75, 82, 84, 85, 96). Thus, shape-based analysis enables a transition from descriptive approaches toward a comprehensive understanding of how biological and environmental factors interact to shape the vertebrate skeleton.

Traditional osteometry based on linear measurements has long been used in biological and anatomical research

(9, 11, 17, 45). Although effective for structures with simple linear geometry, these methods often fail to capture subtle, region-specific shape variations (48, 72). Linear morphometry provides general information about size but may obscure complex geometric relationships and morphological signals associated with functional adaptation and evolutionary processes (59, 72, 98). Measurements such as distances, angles, and ratios represent shape incompletely and result in information loss that limits interpretation and comparison (5, 48). Furthermore, original geometric relationships among anatomical points cannot always be reconstructed from selected distance measurements (59).

In contrast, geometric morphometrics (GM) provides an effective framework for analysing irregular geometric shapes and complex anatomical surfaces (68, 96). This capability enables accurate quantification of intricate bones and structures that are difficult to assess using traditional methods (76). For example, GM is particularly suitable for complex basicranial structures such as the sphenoid bone, which contains numerous foramina, grooves, and irregular components including the dorsum sellae (29, 71). The use of semi-landmarks and 3D modelling further facilitates the representation of biological features in structures lacking discrete homologous points (59, 96). Moreover, traditional linear methods are susceptible to measurement error and observer bias, while specimen positioning and preservation conditions may affect data consistency and reproducibility (5).

GM provides a powerful and integrative framework for the visual and statistical analysis of biological shape. By using landmark-based data or three-dimensional (3D) surface models derived from computed tomography (CT) and micro-CT (μCT), GM enables detailed assessment of shape independent of size-related scaling effects, or allometry (2, 6, 19, 21, 52, 65, 98). This methodology has demonstrated high accuracy in species identification, overcoming limitations of traditional osteology and achieving concordance with molecular approaches (34, 38). Its ability to localize shape changes within specific functional regions makes GM a valuable framework for linking form and function. The integration of advanced imaging modalities further enhances this approach by enabling high-resolution 3D reconstruction of skeletal structures (15, 22, 48).

This review bridges evolutionary biology with practical applications in animal management, welfare, and clinical practice. By quantifying the effects of diet, habitat, and captivity on skeletal morphology, GM provides insights that may support genetic selection programs, welfare improvements, and surgical planning (28, 36, 43, 58, 64, 66, 73, 86). The integration of automation and artificial intelligence (AI) is transforming osteological and taphonomic research by overcoming limitations of traditional methods, standardizing analyses, reducing observer bias, and increasing data production capacity (3, 89). Deep neural networks enable rapid segmentation of skeletal photographs and automated measurement of functional traits, improving both efficiency and reproducibility (89). These approaches can also identify subtle differences, such as those between flint and metal tool marks, which are difficult to distinguish using traditional techniques. Ultimately, AI-assisted workflows facilitate the generation of high-volume and high-resolution datasets required to address major macroecological and macroevolutionary questions (56, 89).

The following review provides a comprehensive overview of the diverse applications of geometric morphometrics in veterinary osteology. GM reveals how shape variation in veterinary bones is structured across biological scales by linking morphological patterns with functional, developmental, and evolutionary processes. The review begins with sexual dimorphism across species and anatomical regions, followed by functional and dietary influences on skeletal morphology and analyses of ecomorphology and behavioural ecology. Subsequent sections examine the role of GM in taxonomy, species identification, developmental mechanisms, and ontogenetic trajectories. Finally, the article discusses genetic and allometric factors shaping the skeleton, alongside clinical perspectives and recent methodological innovations in automation and imaging integration (Figure 1).

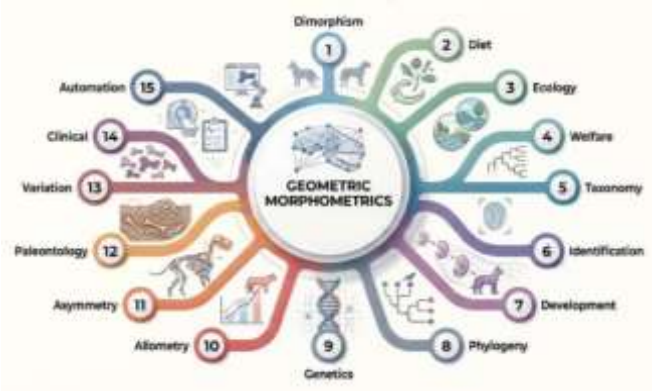

Figure 1. Framework of shape variation in veterinary osteology.

Sexual Dimorphism in Veterinary Osteology

Core Principles of Geometric Morphometric Analysis: Geometric morphometrics is based on the quantitative analysis of shape using the spatial coordinates of anatomical landmarks. Landmarks represent homologous points that can be consistently identified across specimens, whereas semi-landmarks capture curves and surfaces where exact homology is not defined but geometric correspondence can be approximated (8). The combined use of landmarks and semi-landmarks enables detailed representation of complex skeletal structures (16, 98). Configurations are aligned using Generalized Procrustes Analysis (GPA), which removes the effects of translation, rotation, and scale. This standardizes specimens into a common coordinate system, allowing direct comparison of shape differences while preserving geometric relationships among points (8, 59). Following alignment, multivariate statistical techniques are applied to explore and interpret shape variation. Principal Component Analysis (PCA) summarizes major axes of variation and visualizes morphological patterns, whereas Canonical Variate Analysis (CVA) facilitates discrimination among predefined groups by maximizing between-group differences (1, 12, 41). Since shape can be influenced by size, allometric effects are typically evaluated and, when necessary, removed through regression of shape variables on centroid size. This separates size-dependent and size-independent components of variation, enabling more accurate interpretation of skeletal morphology (42, 59, 93).

Size, Shape, and the Interpretation of Skeletal Variation: Sexual dimorphism constitutes a key component of skeletal morphological variation, reflecting interactions among developmental and functional factors. In veterinary osteology, identifying sex-related differences is important for taxonomy, breeding, clinical evaluation, and forensic investigations. However, their often subtle and region-specific nature requires analytical approaches capable of detecting shape variation with high sensitivity. Accordingly, GM has become an indispensable tool for assessing sexual dimorphism. Cranial structures are among the most extensively studied regions because of their functional and developmental importance. Several studies have demonstrated that GM effectively detects sex-related differences in cranial morphology. Parés-Casanova et al. (72) assessed cranial sexual dimorphism in the Kangal dog using ventral, lateral, and dorsal skull views and reported significant differences in both size and shape, with males exhibiting larger crania. Yalin et al. (96) examined guinea pigs using CT-based 3D GM and found significant sex-related differences, with males displaying larger neurocranium and viscerocranium bones. Conry et al. (15) investigated *Stenella coeruleoalba* and identified significant dorsal and ventral cranial shape differences despite the absence of size differences. Demircioğlu et al. (18) reported significant cranial shape disparities between male and female New Zealand rabbits, particularly in the temporal and facial regions, although overall size did not differ. Similarly, Yunus et al. (98) demonstrated significant size-independent shape differences in the caudal skull region of Wistar albino rats. Beyond the cranium, Özkan et al. (68) analysed pelvic shape variation in different dog classes using CT-based 3D GM and found shape differences in the pelvic canal and crista iliaca, with significant directional asymmetry in males.

The analysis of additional skeletal structures has also contributed to the understanding of sexual dimorphism. Bilgiç et al. (6) analysed the humerus and femur of *Apus apus* using landmark-based GM and found strong directional asymmetry in the humerus and weaker but significant asymmetry in the femur, while sex had no detectable effect on shape or asymmetry. De Felice et al. (17) combined geometric morphometric and conventional biometric analyses of the roe deer mandible, identifying additional mandibular parameters and significant sexual differences that were not detected through traditional measurements alone. Berdnikovs et al. (5) examined pelvic development in rats and showed that males achieved larger pelvic sizes through faster growth, whereas females exhibited greater rates of pelvic shape change during development. Despite these findings, sexual dimorphism is not consistently detectable across all species or anatomical regions. Gordon et al. (29) investigated the caudal cranial fossa of domestic cats using CT-based 3D GM and detected size-independent shape variation, particularly in the exoccipital bones, ventral supraoccipital region, dorsum sellae, and osseous tentorium cerebelli. However, no significant differences were identified between breeds, sexes, or age groups. Overall, the current literature indicates that GM provides a powerful framework for investigating sexual dimorphism in veterinary osteology, although its detectability depends on species-specific biology, anatomical region, ontogenetic stage, and functional adaptation.

Functional, Ecological, and Behavioural Drivers of Skeletal Shape: Skeletal morphology is shaped not only by genetic and developmental factors but also by functional demands and environmental influences, particularly those associated with feeding behaviour and diet. In veterinary osteology, understanding how dietary habits and biomechanical loading influence bone shape is essential for interpreting adaptive variation, optimizing animal welfare, and improving production systems. GM, with its capacity to capture subtle and spatial shape

variation, has proven especially effective in elucidating these relationships.

Experimental studies have demonstrated the direct impact of diet consistency on skeletal development. Pulcini et al. (73) analysed the relationship between growth dynamics, locomotor activity, and bone morphology in broiler chickens reared under organic and commercial farming systems, identifying a close association between tibia shape, body weight, growth rate, and locomotor patterns. Onbaşılar et al. (66) showed that a probiotic supplement containing *Lactobacillus acidophilus* and *Pediococcus acidilactici* improved feed efficiency, eggshell quality, antioxidant capacity, and immune response in Lohmann Brown laying hens, while also influencing wing and leg skeletal development. Salcido and Polly (79) demonstrated that mandibular shape in Carnivoraformes is strongly associated with diet, with distinct morphological patterns differentiating mesocarnivorous, hypercarnivorous, and osteophagous taxa, particularly in the condyle, muscle attachment areas, carnassial length, and horizontal ramus. Similarly, Onbaşılar et al. (67) reported that dietary xylanase and protease supplementation significantly improved growth performance and feed efficiency in broiler chickens, with associated changes in the tibiotarsus and femur, decreased intestinal viscosity, and increased villus height and villus-crypt ratio. Taken together, these studies demonstrate that dietary composition, feeding behaviour, and associated biomechanical forces are key drivers of skeletal shape variation. GM facilitates the detection and interpretation of these changes, enabling a more integrated understanding of form-function relationships beyond simple size assessments. This approach is particularly valuable in veterinary contexts, where linking morphology to function can inform both evolutionary interpretations and practical applications in animal management and health.

In veterinary osteology, understanding how habitat, locomotor strategy, and body mass influence skeletal form is essential for interpreting adaptive variation, reconstructing paleobiology, and predicting biomechanical performance. GM enables the quantification of shape variation and its relationship with ecological and functional parameters. Habitat and body mass are major determinants of skeletal morphology, influencing both the size and geometry of osseous structures in vertebrates. GM has demonstrated that habitat-specific mechanical demands and ecological constraints are reflected in bone shape variation, while body mass further modulates these patterns through biomechanical loading. As body size increases, bones must withstand greater loads, resulting in shape changes that enhance structural integrity and functional efficiency. Several studies highlight the influence of habitat and body mass on skeletal morphology. Etienne et al. (22) conducted a 3D GM analysis of bovid limb long bones to evaluate the effects of body mass and habitat on skeletal shape. Using landmarks and sliding semi-landmarks on stylopodial and zeugopodial bones from fifty species, the study demonstrated a strong correlation between bone shape, body mass, and habitat, even after accounting for phylogeny. Heavier species exhibited more robust bones with proportionally enlarged articular surfaces, reflecting adaptation to greater mechanical loads. Open-habitat species possessed wider articulations and enhanced insertion areas for propulsion-related muscles, whereas forest and mountain taxa displayed more gracile bones associated with increased manoeuvrability. Anderson et al. (2) investigated functional and ecological signals in the distal humerus of extant and extinct bovids. Distal humerus shape was strongly associated with body mass, habitat preference, and tribal affiliation, with convergent features observed in large-bodied taxa and species inhabiting hard, flat habitats. These relationships supported the placement of the Alcelaphine *Rusingoryx atopocranion* within Alcelaphini and suggested adaptation to open grassland habitats.

Habitat-driven shape variation is also evident in cranial and vertebral structures. Hadley et al. (36) analysed cranial size and shape variation across nine isolated populations of the tammar wallaby. Cranial size increased with body size and latitude, while latitude-related shape changes included palate narrowing, increased cranial flexion and nasal height, lateral expansion of the zygomatic arches, and narrowing of the nares. Most populations exhibited significantly different mean cranial shapes, with greater divergence among island and geographically distant populations. Marchesi et al. (51) investigated allometric patterns and ontogenetic trajectories in the vertebral column of four closely related dolphin species with differing ecologies. Commerson's dolphin exhibited stronger static and ontogenetic allometric effects than *Lagenorhynchus* species, indicating distinct growth-related shape changes, while habitats revealed substantial vertebral shape divergence. Figueirido and Soibelzon (27) demonstrated that cranial and mandibular variation in Tremarctine bears reflects dietary flexibility and adaptive responses to competition, highlighting the influence of habitat and trophic pressures on skeletal morphology. Collectively, these findings indicate that habitat and body mass interact to shape skeletal morphology, with animals of similar size exhibiting distinct morphologies according to their ecological niches. This perspective is particularly valuable in veterinary contexts, where understanding the morphological consequences of environmental conditions and artificial selection can inform animal welfare, management strategies, and breeding practices.

Behavioural ecology constitutes a critical component of skeletal shape variation, as repeated species-specific behaviours impose functional demands directly reflected in osteological morphology. Activities such as foraging, locomotion, aggression, and social interactions generate mechanical loading regimes that influence bone modelling and remodelling. GM has proven effective in capturing these behaviour-linked shape variations. Fabre et al. (24) used 3D GM with surface sliding semi-landmarks to examine forelimb shape evolution and grasping ability in mustelid carnivores. Species with enhanced grasping capabilities possessed distinct forelimb morphologies, particularly in articulations facilitating increased radio-ulnar rotation, supporting the hypothesis that grasping in mustelids originated from arboreal adaptations rather than solely from digging or predatory behaviours. Likewise, Nozaki et al. (65) investigated calcaneal shape variation among extant great apes and identified clear interspecific differences corresponding to degrees of arboreality and terrestriality. Orangutans exhibited features associated with arboreal locomotion, whereas gorillas displayed traits linked to terrestrial support and propulsion. Neaux et al. (64) showed that captivity alters skeletal development in wild boar, with captive individuals exhibiting greater cranial and mandibular shape changes than wild counterparts. Differences in the calcaneus further suggested that reduced mobility and behavioural constraints influence skeletal morphology, highlighting the relationship between form, behaviour, and welfare. Accordingly, integrating behavioural ecology with GM provides a comprehensive framework for understanding the relationships among skeletal form, functional demands, environmental interactions, and animal welfare.

Nutrition shaped by habitat-specific resource availability represents a fundamental driver of skeletal morphology, influencing both the size and shape of osseous structures through functional and developmental pathways. Dietary composition, determined by ecological context, imposes distinct mechanical and metabolic demands that are reflected in skeletal architecture. Animals consuming fibrous, hard, or mechanically resistant food typically develop more robust craniofacial and mandibular structures to withstand increased masticatory loads, whereas softer diets are associated with more gracile morphologies. GM analyses have been particularly effective in investigating these patterns in veterinary osteology. Kassam et al. (40) examined interspecific variation in trophic morphology among Lake Malawi cichlids from distinct feeding guilds using landmark-based GM of the neurocranium, premaxilla, and lower jaw. Significant shape differences between zooplanktivorous and algivorous guilds reflected contrasting cranial and jaw configurations associated with feeding microhabitats. Similarly, Tsolakis et al. (86) reported that prolonged consumption of a soft diet reduced mandibular dimensions compared with a hard diet, with these differences persisting across three generations. Their findings demonstrate that dietary characteristics influence craniofacial morphology and that GM can detect localized developmental responses in nutritionally sensitive regions of the mandible. Pulcini et al. (73) showed that tibia morphology in broiler chickens varies according to growth rate, activity level, and farm classification, with slower-growing and more active breeds exhibiting a more functional bone structure. Collectively, these studies indicate that nutritional and feeding mechanisms interact with ecological and functional requirements to produce measurable variation in skeletal shape. In summary, GM provides a powerful framework for linking skeletal morphology to ecological, behavioural, and functional factors. Body mass, habitat, locomotor strategy, and diet drive significant skeletal variation with important functional and adaptive consequences.

Behaviour represents a central determinant of skeletal morphology, as functionally relevant and welfare-associated activity patterns impose measurable effects on bone shape and structural organization. Behaviourally mediated mechanical loading influences bone modelling and remodelling, while activities such as locomotion, feeding, grooming, and social interactions generate repeatable force regimes that shape anatomical structures. GM captures these biologically meaningful shape variations associated with functional demands. Struthers et al. (83) investigated maxillary beak shape variation in two pure White Leghorn layer lines and demonstrated significant shape differences associated with skeletal, behavioural, and welfare traits. GM has also proven effective for integrating ecological, behavioural, and historical signals in identification and classification. Brassard et al. (11) developed a 3D landmark-based GM approach to distinguish wild and domestic canids among mummified remains from Ancient Egypt using discriminant models based on cranial morphology. The method achieved over 97.5% accuracy in classifying domestic and wild canids and 96.4% accuracy in species identification. Overall, behaviour influences skeletal morphology through developmental processes, with lifelong activity patterns producing lasting effects on bone shape. By separating size-dependent and size-independent variation, GM enables more precise interpretation of behavioural influences on osteology.

Taxonomy, Phylogeny, and Species Discrimination

Skeletal structures serve as enduring biological records, preserving signals of evolutionary history, functional adaptation, and lineage divergence. In this context, bones function as “blueprints” encoding both phylogenetic relationships and ecological specializations. GM has

refined the extraction and interpretation of these signals by enabling high-resolution, quantitative, and visual comparisons of shape across taxa. This approach is particularly valuable in veterinary osteology, where distinguishing closely related species, breeds, or populations often requires detecting subtle differences in skeletal morphology.

Taxonomic classification relies heavily on the identification of morphological traits. GM enhances this process by providing statistically robust methods for distinguishing taxa based on shape variation rather than solely on size or discrete characters. Through multivariate analyses of landmark configurations, GM enables discrimination among species, subspecies, and breed-level differences with high precision, particularly where closely related taxa or selectively bred populations complicate traditional classification. Rankin et al. (75) re-evaluated the traditional classification of "protrogomorph" rodents using geometric morphometric analyses of the *Ischyromys* skeleton, demonstrating that *Ischyromys douglassi* exhibits anatomical sciuromorphy rather than protrogomorphy, thereby challenging long-standing assumptions based on masseter muscle arrangement. Similarly, Evin et al. (23) investigated whether the size and configuration of the inner ear semi-circular canals could serve as markers of pig domestication using 3D GM. Domestic pigs exhibited significantly larger and distinctly shaped semi-circular canals than wild boar, with classification accuracies exceeding 95%. Population-specific variation among wild boar and sexual size dimorphism were also identified. At a broader scale, Ferreira-Cardoso et al. (25) analysed skull shape variation in extant pangolins and revealed clear genus- and species-level cranial differentiation, with Asian pangolins forming a distinct cluster and African taxa differing between small- and large-bodied genera. Beyond species identification, GM also facilitates the assessment of intraspecific variation and population structure by distinguishing variation associated with genetic lineage from that influenced by environmental or developmental factors.

Functional morphology links skeletal form with taxonomic differentiation, as shape variation frequently reflects adaptive responses to ecological and biomechanical demands. Taxa occupying similar environments or performing comparable functions may exhibit convergent morphological traits, whereas closely related groups may diverge because of differences in behaviour or habitat use. GM enables precise quantification of these shape patterns, supporting taxonomic classifications that integrate both form and function. Muñoz et al. (62) used 3D GM of the proximal ulnar articular surface to assess its potential for palaeoecological inference, particularly forelimb function in small mammals. Although whole-surface variation was limited, subdivision of the articular surface revealed functionally meaningful shape variation, with the proximal trochlear notch clearly distinguishing digging rodents from climbing taxa. Likewise, Morgan and Álvarez (61) applied GM within a phylogenetic comparative framework to analyse humeral shape variation in South American caviomorph rodents. Fossorial and digging taxa occupied distinct regions, indicating locomotion-related shape variation shaped by both evolutionary history and ecomorphological differentiation. Durão et al. (20) investigated mandibular variation in the closely related water voles *Arvicola sapidus* and *Arvicola scherman*. Despite their close phylogenetic relationship, the species differed in mandibular morphology, allometric patterns, and estimated bite force, reflecting divergence associated with contrasting ecological specializations. Similarly, Lewton et al. (46) demonstrated significant pelvic shape variation in carnivores associated with phylogeny, body size, and locomotor behaviour through detailed analyses of the ilium and ischium. In the context of aquatic systems, Marchesi et al. (52) examined vertebral centrum shape variation in four closely related dolphin species from the southwestern South Atlantic. Their analyses identified clear interspecific and regional patterns in centrum morphology, distinguishing stable and flexible regions of the vertebral column.

Comparable ecological differentiation was reported by MacLaren and Nauwelaerts (49), who used 3D GM to investigate interspecific variation in the tetradactyl manus of four extant tapir species. The results demonstrated that *Tapirus indicus* is morphologically distinct from Neotropical tapirs and confirmed the manus as a functionally and morphologically variable locomotor unit with species-specific configurations. Goswami et al. (30) investigated cranial disparity in living and fossil carnivorous mammals, revealing substantial variation, particularly along axes associated with facial length and feeding ecology.

Accurate species identification is fundamental in osteology, and GM has improved its precision by overcoming the limitations of qualitative assessments and linear measurements. Through landmark-based analyses that preserve spatial relationships, GM enables high-resolution comparisons of shape and detects subtle morphological differences that are often overlooked using conventional methods. Robinson (76) analysed mandibular corpus shape variation between *Pan paniscus* and *Pan troglodytes*, identifying the mandibular symphysis as a diagnostic region associated with size-related shape variation. Likewise, Lloveras et al. (48) demonstrated the effectiveness of GM for distinguishing ovine and caprine specimens based on calcaneal morphology. Parés-Casanova and Domènech-Domènech

(71) reported significant differences in palatine bone size and shape between sheep and goats, identifying the palatine bone as a useful marker for interspecific discrimination and comparative veterinary anatomy. Figueirido et al. (26) analysed cranial landmarks in the red panda and giant panda relative to other Arctoidea, revealing a strong association between skull shape, feeding behaviour, and convergent cranial morphology among bamboo specialists. Üstündağ et al. (87) further demonstrated clear taxonomic differentiation among bovine, ovine, and caprine species based on astragalus shape, whereas Gürbüz et al. (35) identified significant cranial and mandibular differences between adult male wolves and German Shepherd dogs. Collectively, these studies demonstrate that GM provides a sensitive, quantitative, and reproducible framework for osteological species identification, improving taxonomic resolution while accommodating the complexity of morphological variation across diverse animal groups.

Shaping the Skeleton: Developmental Mechanisms and Morphological Outcomes

The vertebrate skeleton is shaped by complex developmental processes integrating genetic programs, biomechanical forces, and environmental influences. Understanding these mechanisms is essential for interpreting morphological variation. GM provides a powerful approach to investigate how developmental pathways shape skeletal form by quantifying growth patterns and ontogenetic trajectories.

Postnatal Growth and Ontogenetic Trajectories: Postnatal growth is a critical period during which skeletal shape is established and refined, reflecting the interaction between genetic, environmental, and functional influences. During development, bones undergo coordinated growth and remodelling in response to mechanical loading, nutrition, and activity patterns. GM approaches enable detailed mapping of ontogenetic trajectories, revealing how shape changes occur over time. Gray et al. (31) examined postnatal cranial growth patterns in eighteen species of Australian agamid lizards. Juveniles exhibited similar cranial morphology, whereas substantial species divergence emerged during ontogeny through differences in the direction and magnitude of shape modification. Similarly, Cardini and Thorington (13) investigated postnatal cranial ontogeny in marmots and demonstrated that cranial shape changes during growth are driven by allometry. Early interspecific differences contributed to cranial diversity among extant marmot species.

Liuti and Dixon (47) investigated age-related shape variation in equine skulls using 3D models derived from CT scans. Their analyses showed that differences between age groups were primarily driven by size-related shape changes, highlighting the dominant role of growth-related scaling in equine cranial morphology. Salamanca-Carreño et al. (78) investigated basicranial variation in the Araucanian horse and demonstrated distinct neurocranium and splanchnocranium forms, with greater morphological stability in the neurocranium. These findings support a modular pattern of cranial development in horses. Mennecart and Costeur (57) examined shape variation and ontogenetic development of the ruminant bony labyrinth in extant *Tragulidae*, revealing distinct variations among the three genera despite similar ecological adaptations. Durão et al. (20) demonstrated that post-weaning mandibular development follows species-specific ontogenetic trajectories, with the most pronounced shape modifications occurring in the angular and condylar processes during early growth. Their findings showed that developmental trajectories differ in both magnitude and direction, indicating that functional demands associated with contrasting lifestyles progressively influence craniofacial morphology throughout ontogeny. This study illustrates how GM can characterize developmental pathways underlying adult skeletal morphology.

Early Functional Influences and Developmental Constraints: The morphology of the skeleton is shaped by early functional demands and inherent developmental constraints, which play a pivotal role in determining bone form. During early life stages, bones respond to mechanical forces that can produce lasting effects on shape and structural integrity. Locomotion, feeding, and maternal interactions generate biomechanical stimuli influencing modelling and remodelling processes, resulting in region-specific reinforcement or modification of skeletal elements. GM enables the quantification of these shape adaptations and helps distinguish changes driven by functional loading. Miller et al. (58) investigated how the transition from suckling to mastication influences craniofacial development in osteogenesis imperfecta (OI) mice using GM analyses of micro-CT data. Although no craniofacial differences were observed at birth, divergence in size and morphology emerged during early postnatal development, indicating that altered biomechanical loading associated with oral motor development contributes to the OI craniofacial phenotype. These findings highlight the role of developmental timing and functional demands in craniofacial morphogenesis. Bennett and Goswami (4) demonstrated that heterochronic shifts in cranial ossification associated with early suckling constrain cranial shape diversity in marsupials compared with placentals. Analyses of extant and fossil taxa revealed a significantly narrower range of cranial variation in marsupials, particularly within the viscerocranium and

oral regions. Lanzetti et al. (45) identified divergent developmental trajectories in cetacean auditory structures, where differences in ossification timing and growth patterns contribute to functional divergence between baleen and toothed whales.

The relationship between skeletal morphology and locomotor behaviour is well documented. Naidoo and Iqbal (63) investigated the correlation between locomotion and hindlimb morphology in leopards and revealed significant interspecific differences in femoral shape. Leopards exhibited a more gracile and elongated femur, associated with smaller body size, greater locomotor flexibility, and arboreal capability. In the vertebral column, Randau et al. (74) applied 3D GM analysis to presacral vertebrae and demonstrated regional variation in felid vertebral evolution. The anterior presacral vertebra exhibited reduced variation, whereas posterior regions showed significant shape differentiation among felid ecomorphs. These differences were primarily expressed through variation in shape trajectories rather than their magnitude.

Forelimb morphology also reflects complex interactions between phylogeny, size, and function. Martín-Serra et al. (54) used 3D GM to assess the effects of allometry and locomotor performance on forelimb bone shape in extant and extinct carnivores. Their findings showed that forelimb morphology is strongly influenced by size variation, whereas shape exhibited limited correlation with locomotor performance proxies such as running speed or daily movement distance. Walmsley et al. (88) further demonstrated that humeral epiphyseal morphology in felids is shaped by both phylogenetic history and adaptive factors, indicating multifactorial influences on skeletal design. Jones (39) investigated the relationship between vertebral morphology and joint mobility in the equine thoracolumbar region by combining linear measurements and GM analysis with experimentally derived ex vivo range-of-motion data. The study demonstrated clear links between osseous anatomy and spinal mobility, providing a methodological framework for integrating vertebral form and function. Overall, early functional influences and developmental constraints reveal the dynamic interaction between mechanical stimuli and intrinsic growth limitations, providing a comprehensive perspective on how skeletal morphology is shaped during critical developmental periods and how these processes contribute to adaptive and constrained variation across species.

The Phylogenetic Imprint on Osteology

The skeletal system is shaped not only by functional and environmental factors but also by inherited developmental programs reflecting evolutionary relationships. GM enables the quantification of shape variation across anatomical landmarks, providing a statistical and visual framework for assessing phylogenetic similarity and divergence. This approach has been effective in distinguishing closely related taxa, identifying lineage-specific traits, and exploring evolutionary patterns. Catalano et al. (14) evaluated mustelid phylogenetics by combining multiple skeletal configurations in a landmark-based GM analysis. Their results demonstrated that landmarks from significant anatomical structures improved congruence with molecular phylogenies and successfully recovered multiple well-supported monophyletic groups, highlighting the phylogenetic value of GM-based landmark data. Walmsley et al. (88) investigated proximal and distal humeral epiphyseal shape variation in felids to examine the relationship between phylogeny and locomotion. Their analyses revealed that epiphyseal shape is strongly influenced by phylogenetic relationships, with distinct variations among felid lineages. Weisbecker et al. (90) assessed the phylogenetic utility of GM data by comparing basicranial shape with other cranial regions in fifty-seven marsupial species. The basicranium consistently exhibited a lower phylogenetic signal than other cranial regions, a pattern also observed in discrete morphological characters. The application of GM in evolutionary studies is further demonstrated by reconstructing primate evolutionary history through internal dental structures and clarifying taxonomic diversity and phylogenetic relationships in extinct and extant orangutans (44). Advanced GM approaches also enable the analysis of complex cranial developmental trajectories across cercopithecine species, providing insights into evolutionary patterns such as homoplasy and lineage diversification (81). Overall, the phylogenetic imprint on osteology revealed through GM highlights the interaction between functional adaptation, morphological diversity, and evolutionary history, providing a framework for interpreting skeletal form in comparative and applied veterinary contexts.

Genetic Architecture of Bone: Genetically Related Morphological Variation

The genetic architecture of bone contributes substantially to skeletal shape variation, with heritable factors regulating the development, organization, and diversification of osteological traits across individuals and populations. Skeletal morphology is influenced by complex genetic networks controlling processes such as ossification, growth plate activity, and tissue differentiation. Since these processes involve multiple genes, variation in a single genetic pathway may affect multiple aspects of bone shape simultaneously. GM provides a robust framework for investigating genetically driven variation by capturing coordinated shape changes across anatomical structures. Furthermore, interactions

between genetic architecture and environmental inputs contribute to phenotypic plasticity, allowing similar genotypes to produce different morphological outcomes under varying conditions. Böhmer (7) investigated the relationship between Hox gene expression and cervical vertebral morphology in mice. The results demonstrated a correlation between Hox codes and differentiation along the cervical vertebral column, supporting the contribution of genetic factors to morphological variation. Diamond et al. (19) applied three-dimensional computational anatomy and GM analyses to examine craniofacial variation in zebrafish with *bmp1a* mutations. Mutant fish exhibited distinct craniofacial phenotypes, including altered cranial shape, increased centroid size, enlarged otoliths, and greater asymmetry compared with wild-type individuals. These findings demonstrate how genetic alterations affecting skeletal development can be quantitatively associated with craniofacial morphological outcomes. Wilson (92) investigated geographic variation in skull morphology of the greater Japanese shrew-mole and found that the most pronounced differences occurred in the ventral and dorsal cranial regions, whereas dentary outlines showed relatively limited variation. Distinct shapes among island populations further supported the use of morphological data in assessing species boundaries. Overall, investigating the genetic architecture of bone through GM provides an integrative understanding of how heritable factors structure skeletal variation and how genetic regulation, developmental processes, and environmental influences interact to shape osteological diversity.

Allometric Effects on Skeletal Shape

Allometry, the study of size-related changes in shape, represents a fundamental component of skeletal variation, influencing how bones scale and adapt across individuals, populations, and species. Skeletal structures do not increase uniformly in size; instead, growth involves coordinated and often non-linear shape changes reflecting functional, developmental, and biomechanical constraints. GM enables the visualization of allometric patterns and provides statistical data by separating size from shape variables. Esteves-Ponte et al. (21) demonstrated that size-dependent scaling accounts for a substantial proportion of skull shape variation in dolphins and can mask other biological signals. They applied GM analyses to investigate cranial shape differences between offshore and inshore ecotypes of the common bottlenose dolphin, identifying shape differences concentrated in the frontal, zygomatic, squamosal, and occipital regions. Diamond et al. (19) incorporated centroid size normalization within a computational anatomy framework to distinguish shape variation from size-related effects, allowing craniofacial phenotypes to be evaluated independently of overall skull size and emphasizing the importance of accounting for scaling in genetically driven skeletal variation. Lewton et al. (46) demonstrated that pelvic morphology in carnivores is strongly influenced by size, while Robinson (76) showed that mandibular differences among primate species are partially driven by allometric effects. However, not all morphological variation is size-dependent. Contreras and Salinas (16) reported limited allometric influence on mandibular variation in dogs, highlighting the role of modularity and localized shape changes. Similarly, Weisbecker et al. (91) found weak allometric effects in wombat cranial morphology, suggesting that functional loading may override size-related constraints. Overall, the study of allometric effects through GM provides a framework for understanding the relationship between size and shape, revealing scaling patterns that influence skeletal morphology across developmental, functional, and evolutionary contexts.

Asymmetry in Skeletal Structures

Skeletal asymmetry represents an important aspect of morphological variation, reflecting the combined effects of developmental processes, functional demands, and environmental influences on bilateral structures. GM provides a powerful framework for visualizing asymmetrical patterns and obtaining statistical data on shape differences between corresponding anatomical structures. By incorporating landmark configurations from both sides of the skeleton, GM allows the separation of symmetric and asymmetric components of shape variation, enabling detailed assessment of morphological deviations. Salamanca-Carreño et al. (77) revealed directional asymmetry in calf hindlimbs, while Parés-Casanova et al. (70) used GM to quantify craniofacial asymmetry in the sphenoid and palatine bones of adult sheep and goats. Their analyses demonstrated significant fluctuating and directional asymmetry in both bones, with greater asymmetry observed in the sphenoid than in the palatine. The asymmetric component also differentiated sheep from goats, indicating taxon-specific patterns of basicranial asymmetry.

Applications in Palaeontology, Taphonomy, and Archaeology

Geometric morphometrics has become an important method in palaeontology, taphonomy, and archaeology, enabling detailed analysis of skeletal remains to reconstruct past biological and environmental conditions. In palaeontology, GM facilitates the visualization of morphological variation and the obtaining of statistical data from fossil remains, allowing refined interpretations of species differentiation and functional adaptation. Molnar et al. (60) proposed a landmark-based GM method for reconstructing 3D models of fossil bones. Validation

using an early tetrapod vertebra demonstrated high accuracy and repeatability, supporting its utility in palaeontological reconstruction and shape analyses.

In taphonomy, GM contributes to understanding post-mortem processes affecting skeletal remains, including deformation, fragmentation, and preservation biases. Maté-González et al. (55) applied 2D and 3D GM analyses to experimentally generated cut marks on bones from different elements and animal sizes. Their findings showed that neither carcass size nor skeletal element type produced significant differences in cut mark morphology, demonstrating the reliability of cut mark shape analysis through GM in taphonomic and archaeological studies. GM is also widely used in fossil morphology reconstruction and interpretation. Gunz et al. (34) employed 3D GM and µCT data to reconstruct the cranium of *Rudapithecus hungaricus*, revealing a combination of characteristics similar to both African apes and hylobatids. This approach highlights the importance of quantitative morphology in understanding evolutionary relationships among taxa.

Intraspecific Variation, Breed Differences, and Population Structure

Intraspecific variation represents a fundamental component of skeletal diversity. Within a species, skeletal morphology may vary among individuals, breeds, and populations due to hereditary factors and local adaptations. GM enables the visualization of these variations and the obtaining of statistical data on shape differences by capturing complex morphological patterns beyond traditional linear measurements. This is particularly relevant in veterinary osteology, where subtle shape differences can distinguish populations influenced by ecological conditions, management systems, or breeding strategies.

Özkan et al. (69) compared mandibular shape variation among four sheep breeds from Turkey, Kosovo, Poland, and Romania. Their analyses revealed differences particularly in the mandibular ramus, mandibular angle, and incisal regions, demonstrating the advantages of geometric methods over traditional morphometric approaches. Toryan et al. (85) investigated interbreed variation in canine calcaneus using linear and GM analyses based on radiographic images of dog breeds. Significant variations were identified among breeds, including differences between large breeds such as Golden Retrievers and small breeds such as Pomeranians. Contreras and Salinas (16) examined mandibular shape variation in adult mesocephalic dog breeds and found that most variation was associated with the coronoid process, mandibular ramus, and mandibular body curvature. In feline studies, Gündemir et al. (33) investigated skull shape variation in British Shorthair, Scottish Fold, and Van cats. Although substantial breed differences were absent, statistically significant variations were detected in dorsal and lateral views, particularly in the orbital region. Yalcin et al. (94) analysed mandibular bones of Anatolian wild and Akkaraman sheep using GM and demonstrated that lateral landmarks enabled clear species distinction despite overall mandibular similarity.

GM has also been effective in identifying population-level differences. Yu et al. (97) investigated morphological variation in Norwegian reindeer using combined linear and GM analyses of teeth and postcranial elements. Their results distinguished continental and insular subspecies based on differences in body proportions, metapodial size, and molar shape relative to body size. Haruda et al. (37) applied 3D GM to the cranium to distinguish *Ovis aries* morphotypes and assess mobility and connectivity among prehistoric Central Asian pastoralists. Using astragali samples from three geographically distant Final Bronze Age sites, the study demonstrated significant morphological variation among sheep populations within the same cultural and chronological framework.

Furthermore, GM has revealed substantial individual-level variability. Weisbecker et al. (91) identified considerable individual variation in wombat cranial and mandibular morphology, particularly in regions exposed to high masticatory stress. Günay et al. (32) assessed pelvic shape variation in domestic rabbits and found no significant effects of sex, reproductive status, age, or breed, with observed differences primarily reflecting individual variation. Overall, the integration of GM into studies of intraspecific variation, breed differences, and population structure provides a comprehensive perspective on how genetic, environmental, and selective forces interact to shape skeletal morphology.

Clinical Perspectives on Skeletal Variation

The application of GM in clinical settings has expanded veterinary osteology by enabling detailed visualization and the obtaining of statistical data on skeletal variation relevant to diagnosis, treatment, and prevention. GM allows clinicians and researchers to detect morphological deviations, assess functional implications, and monitor changes over time. This positions GM as a valuable link between anatomical research and applied veterinary practice, particularly where shape variation influences health, performance, and welfare.

The clinical utility of GM is demonstrated by its ability to statistically quantify pathological deformities, such as bone alterations in newborn calves with septic arthritis, using standard radiometric images (43). As advanced imaging modalities, including CT and high-resolution micro-CT, become increasingly common in

veterinary practice, GM provides a framework for establishing a "normal range" of morphological variation, enabling discrimination between anatomical variation and pathological changes (29). Furthermore, understanding sex-specific and breed-specific cranial conformations through GM can assist veterinarians in interpreting radiographic variation and managing conditions influenced by skeletal architecture, such as dental malocclusions and respiratory disorders (96). Future integration of GM with automated and AI-assisted workflows may facilitate the development of comparative anatomical databases to improve clinical veterinary applications.

In veterinary orthopaedics, skeletal shape variation is closely associated with biomechanical function, and GM provides an approach for identifying clinically relevant morphological differences. Yalin et al. (95) analysed patellar shape and size variation in domestic cats and dogs, demonstrating clear interspecific differences. Canines exhibited larger patellae and greater shape variability, partly influenced by size-related effects. The study highlighted the clinical importance of morphometric variation and supported individualised, imaging-based planning in small animal orthopaedic surgery. Koçak et al. (43) applied GM to investigate carpal bone shape alterations in newborn calves with septic arthritis. Their analyses revealed significant separation between control and arthritis groups based on carpal bone shape in dorsopalmar radiographs of healthy and diseased Simmental calves. These findings demonstrate the utility of GM for quantitatively detecting and interpreting pathological skeletal changes, thereby improving diagnostic accuracy and therapeutic evaluation in veterinary orthopaedics.

Preclinical and translational research increasingly uses animal models to investigate skeletal biology, and GM provides a framework for analysing morphology in these contexts. Tavitian et al. (84) investigated craniofacial morphology in schizophrenia-related GFAP.HMOX, transgenic mice (10-12 months) transgenic mice using computer vision methods, GM, and linear skull measurements. Compared with wild-type controls, transgenic males exhibited nasal bone elongation, altered head shape anisotropy, and reduced directional facial asymmetry. These craniofacial abnormalities resemble those reported in patients with schizophrenia, supporting the involvement of craniofacial development in disease aetiology and providing a preclinical model for dysmorphology research. Singh et al. (82) performed a quantitative interspecific comparison of craniofacial morphology in TcMAC21 mouse and TcHSA21 rat models of Down syndrome using GM. Both models showed similar features, including increased neurocranial globularity and anteroposterior facial retraction, supporting their translational relevance. Sholts et al. (80) investigated the effects of chronic TCDD exposure on cranial size and shape in Long-Evans and Han/Wistar rats using 3D GM. High-dose exposure resulted in substantial reductions in centroid size across cranial modules, with the facial region showing the greatest size reduction, indicating increased sensitivity of facial growth to toxic exposure. Miller et al. (58) demonstrated that GM can detect progressive craniofacial abnormalities associated with osteogenesis imperfecta before the phenotype becomes fully established. By documenting changes in cranial architecture during postnatal development, the study provided a quantitative framework for monitoring disease progression and evaluating therapeutic timing, supporting the translational relevance of GM in craniofacial disorders.

Skeletal morphology is also associated with behaviour and welfare, and GM provides a valuable approach for assessing how management practices and activity patterns influence bone structure. Fureix et al. (28) applied GM for quantitative analysis of animal postures, overcoming the subjectivity of behavioural descriptions. By capturing whole-body posture through landmarks, this approach enables comparisons among individuals, groups, and contexts. In horses, GM successfully distinguished behavioural states associated with different arousal levels and detected posture changes in response to environmental factors, including human interactions.

From Models to Methods: Comparative Approaches and Automation in Geometric Morphometrics for Veterinary Osteology

The rapid advancement of GM methodologies has substantially influenced the analytical framework of veterinary osteology by enabling more precise, reproducible, and scalable investigations of skeletal morphology. Concurrently, methodological comparisons and automated approaches have gained importance to overcome limitations of traditional techniques and improve analytical efficiency.

Boyer et al. (9) developed polynomial-time algorithms to quantify geometric similarity between anatomical surfaces without predefined landmarks, reducing observer dependency and enabling scalable comparisons of complex biological forms. Extending this framework, Boyer et al. (10) introduced a fully automated three-dimensional correspondence algorithm that generated anatomically meaningful surface alignments and showed strong agreement with landmark-based GM analyses in primate calcanei. Together, these studies demonstrate that automated surface-based approaches provide efficient and reproducible alternatives to traditional landmark-dependent methods, facilitating

large-scale morphological analyses while minimizing observer bias. More recently, automated landmarking techniques have further expanded GM applications in veterinary osteology. Manuta et al. (50) analysed three-dimensional shape and size variation of distal phalanges in Holstein cattle using automated landmarked GM. Principal component analyses revealed significant variation between forelimbs and hindlimbs, as well as medial and lateral phalanges.

Automated approaches have been developed to address limitations associated with manual landmark placement, which, although accurate, is time-consuming and susceptible to observer bias. Bakici et al. (3) compared manual landmarking with an AI-based method (ALPACA) for assessing cranial sexual dimorphism in Romanov sheep using high-resolution CT-derived 3D models. Both approaches successfully identified significant sex-related shape differences, highlighting the potential of AI-assisted workflows as efficient and standardized tools in GM analyses across veterinary and related disciplines.

Landmark-based GM remains essential, particularly for investigating functional and biological relationships. Martin et al. (53) compared conventional linear bone indices with landmark-based GM analyses to quantify covariation between forelimb musculature and skeletal morphology across an ontogenetic series of *Isoodon fusciventer*. Using two-block partial least squares analysis, they demonstrated that landmark configurations captured muscle-bone covariation patterns largely undetected by traditional measurements, illustrating the sensitivity of GM in studying complex developmental and functional relationships. Lanzetti et al. (45) investigated the ontogeny of the tympanoperiotic complex in baleen and toothed whales using traditional measurements and 3D shape analyses. Although both groups shared similar developmental patterns, including periotic growth trajectories, differences in ossification timing, particularly of the periotic, distinguished baleen from toothed whales.

The reliability of GM is further strengthened through integration with complementary methods. JeanJean et al. (38) evaluated GM reliability in archaeological material by comparing morphometric classifications of isolated caprine molars with molecular identifications obtained using ZooMS. The high agreement between approaches validated the landmark-based protocol while revealing morphological differences between modern reference specimens and archaeological populations. These findings emphasize the importance of integrating morphometric and molecular methods for establishing robust reference frameworks in species identification. Overall, GM provides a comprehensive framework for analysing skeletal morphology, from distinguishing closely related species to revealing developmental processes and functional adaptations.

Conclusion

Geometric morphometrics has emerged as a powerful analytical framework in veterinary osteology, enabling visual and statistical assessment of shape variation and its biological significance. GM preserves geometric relationships among anatomical landmarks, allowing comprehensive evaluation of morphological structures in relation to functional, developmental, and evolutionary processes. In veterinary sciences, this approach has been increasingly applied to investigate skeletal variation influenced by factors such as diet, domestication, sexual dimorphism, and welfare conditions. The application of GM in veterinary osteology has significantly advanced the analysis and interpretation of skeletal morphology. By integrating advanced imaging techniques with robust statistical models, GM provides deeper insights into shape variation driven by functional demands, ecological factors, ontogenetic trajectories, sexual dimorphism, habitat effects, nutritional influences, and behavioural patterns. Its versatility enables integration with emerging technologies, including 3D imaging and automated landmarking, enhancing reproducibility and analytical depth. Importantly, GM has demonstrated value not only in evolutionary and comparative studies but also in applied veterinary fields, including pathology, welfare assessment, and production sciences. Despite these advances, challenges remain regarding protocol standardization and sample size limitations. Future research should focus on integrating GM with genomic and biomechanical data to establish a more comprehensive understanding of skeletal form and function.

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This study does not present any ethical concerns.

Conflict of Interest

The authors declare that there is no conflict of interest. Two authors are members of the Editorial Board of the journal; however, they were not involved in the review process or editorial decision regarding this manuscript.

Author Contributions

All authors equally contributed to the conception, design, and manuscript preparation. All authors reviewed and approved the final version of the manuscript.

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No datasets were generated or analysed during the current study.

Declaration of Generative Artificial Intelligence

The authors declare that this manuscript and all figures were prepared entirely without the use of generative artificial intelligence (AI) or AI-assisted tools.

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