Skull morphology of shepherd dogs in Poland

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ABSTRACT

This study aims to assess the skull morphological features of shepherd dog breeds raised in Poland, with an emphasis on native breeds such as the Tatra Sheepdog and Polish Lowland Sheepdog, by utilizing a detailed dataset to analyze and compare the structural traits of their skulls. To achieve this, a total of 32 dog skulls were modeled in 3D, and geometric morphometric analysis was performed to reveal skull shape variations. Among the shepherd samples used, the Polish Lowland Sheepdog exhibited the smallest average skull size. The Tatra Shepherd Dog displayed a skull size similar to that of other sheepdog breeds, although it was larger than that of the Polish Lowland Sheepdog. The results indicate that the Tatra Shepherd Dog possesses a more robust and elongated skull structure compared to the Polish Lowland Sheepdog. Both of these Polish shepherd breeds share similar skull morphology with other shepherd breeds, with the notable exception of collies. Collie breeds exhibit a markedly dolichocephalic skull morphology that sets them apart from the other samples in this study. The analysis revealed that neither Procrustes distance nor shape variation from PC1 had a statistically significant effect on skull size. To enhance our understanding of Poland's shepherd dog diversity, future studies should focus on expanding the dataset to include additional native Polish breeds and exploring a broader range of morphological features beyond the skull.

Introduction

Livestock guardian dogs are specialized breeds used to safeguard livestock from predators and deter potential threats such as thieves (13, 25). In recent years, the protection of livestock grazing in mountainous and foothill regions from predators such as wolves, bears, and lynxes has become increasingly important, not only in Poland but across Europe (13). Unlike herding dogs, which are bred to "manage" and direct herds, livestock guardian dogs have been selectively bred to "protect" herds from external dangers (19). For many years, as a result of these breeding conditions, shepherd dogs have generally been characterized by their large body size and strong musculature; these traits enable them to withstand harsh climatic conditions and sustain prolonged physical activity. This common functional necessity may also indicate shared morphological traits among these breeds. However, significant structural differences can still be found among shepherd dogs, and these differences may provide insight into how they have morphologically adapted to specific environmental conditions and intended uses (6, 9). In this context, skull morphology serves as an anatomical reference for understanding functional differences among dog breeds. The shape and structure of the skull can influence various biological factors, such as chewing mechanics, visual perception, or brain size. Furthermore, it can be suggested that shepherd dogs raised in different geographical regions may have developed distinct morphological adaptations in response to ecological factors such as local climate and predator pressure.

Understanding the morphology of livestock guardian dogs can help uncover how their physical traits contribute to their protective roles and resilience in challenging environments, while also providing insights into their morphological adaptations. Additionally, studies conducted with different livestock guardian dog breeds allow for the identification of anatomical variations in dogs with similar functional characteristics. These studies, which focus on detailed analyses of skull and skeletal morphology, can provide reference data on species-specific adaptations, such as their ability to withstand predators and endure harsh climatic conditions.

The skull, as the most critical structure of the axial skeleton, protects the brain and houses essential sensory organs such as the eyes and inner ears, playing a vital role in animal biology (4, 12, 15). The skull's anatomical design, with distinct regions like the neurocranium and viscerocranium, demonstrates its adaptation to various functions such as housing sensory structures, supporting feeding mechanisms, and providing muscle attachment sites for mastication and head movement. Its structure is a key element in determining breed, age, and sexual dimorphism, as well as being fundamental in veterinary anatomy for taxonomy and species identification (5, 12, 16, 22). Moreover, studying skull morphology provides practical applications in veterinary medicine, including guiding skull nerve anesthesia and supporting forensic investigations (11, 24). In carnivora, skull shapes and sizes show remarkable variation, shaped largely by ecological roles and dietary needs. This study evaluates the skull morphological characteristics of Polish shepherd dog breeds to characterize their breed-specific skull features and enhance understanding of their skull variation.

In recent years, geometric morphometrics has become increasingly prominent in veterinary anatomical studies, particularly in the field of taxonomy (2, 10, 23). The skull, as one of the most informative skeletal structures, was extensively analyzed using these techniques to identify species-specific traits and classify animals more accurately. Three-dimensional geometric morphometrics, in particular, advanced the precision of such studies, enabling the detailed examination of skull morphology (1). This method proved invaluable for exploring factors such as allometric changes, sexual dimorphism, and phylogenetic relationships (14, 15, 18, 20). By incorporating 3D models, researchers were able to capture subtle morphological differences, making this approach a crucial tool in both taxonomic classification and broader veterinary anatomical research.

The primary objective of this study is to evaluate the skull morphology of shepherd dog breeds raised in Poland, with a particular focus on native breeds (Tatra Sheepdog and Polish Lowland Sheepdog), using a comprehensive dataset to identify and compare the distinct morphological traits of their skulls. Understanding the morphological variations among these Polish breeds is essential for several reasons: it contributes to the preservation and conservation of Poland's rich canine heritage, while also enhancing our knowledge of breed-specific traits that may be associated with their historical adaptations and roles. By conducting a thorough analysis of skull morphology, this study aims to provide a valuable reference for future morphological research on these two breeds, ultimately aiding in their preservation and informing breeding practices. The findings will serve not only to enrich the scientific community's understanding of Polish dog breeds but also to foster greater appreciation for their unique characteristics and contributions to Poland's cultural identity.

Materials and Methods

Animals and Modeling: 26 skulls (2 Tatra Shepherd and 3 Polish Lowland Sheepdogs) from the bone collection at the Archaeozoology Laboratory and Museum of Standards, Department of Biostructure and Animal Physiology were used in this study. Most of the samples were sheepdogs, but there were also examples such as Cane Corso and Husky. Additionally, 6 Illyrian shepherd skull samples were taken from the study of Jashari (12). The breeds of each skull were known, and all samples belonged to adult dogs (Table 1). Skulls with extreme brachycephalic or dolichocephalic features were excluded, except for those of shepherd dogs (such as collies), which were the main focus of the study.

Table 1. Distribution of skull samples by breed

Breeds	Number	Breeds	Number
German Shepherd	5	Bracco Italiano	1
Bucovina Shepherd	1	Cane Corso	1
Shar Pei	1	Collie	6
Illyrian Shepherd	6	Siberian Husky	1
Labrador Retriever	1	Siberian Mastiff	1
Mioritic Shepherd	2	Moloss	1
Polish Lowland Sheepdog	3	Tatra Shepherd Dog	2
			Total: 32

The skulls were modeled in 3D using the Shining 3D EinScan Pro 2X scanner. To minimize errors during scanning, the rotary table, an accessory of the scanner, was used (manual scanning was not conducted). The scanning accuracy was set to 0.04 mm. After scanning, the 3D models were merged using EXScan Pro software (version 4.0.0.4) and saved in "ply" format.

Landmarking: A total of 19 landmarks were used in the study, all classified as type 1 and corresponding to specific

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anatomical regions (Figure 1). The landmarks used in this study were selected from anatomical landmarks employed in previous studies (9). All landmarking procedures were performed manually by the same researcher to ensure consistency. Slicer software (version 5.2.2) was used for the landmarking operations (21).

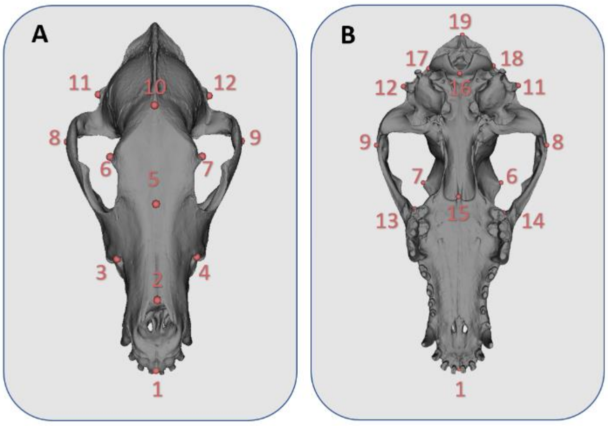

Figure 1. Landmarks

Geometric Morphometrics: The centroid size (CS) for each dog skull was calculated to represent the overall size of each specimen, providing a standardized measure for comparing the target breeds in the study—Tatra Shepherd and Polish Lowland Sheepdog. Additionally, procrustes distances were recorded within each dog to capture within-group variation and evaluate morphological diversity among individuals of the same breed.

To explore the skull shape differences across these breeds, Principal Component Analysis (PCA) was applied (3). PCA is a powerful method for simplifying complex datasets by transforming the original correlated variables (landmark coordinates) into a set of orthogonal, uncorrelated components known as principal components (PCs). The first two principal components, PC1 and PC2, accounted for the largest proportions of total variation in skull shape, and therefore, were the primary focus for identifying and interpreting significant shape differences. Components explaining less than 10% of the variation were excluded from further analysis to streamline results and focus on the most informative shape changes.

To visualize these results, scatter plots were generated to illustrate the distribution of individual specimens along PC1 and PC2 axes, highlighting shape patterns specific to each breed. Additionally, the study examined potential associations between skull size and shape by assessing the effect of size (as captured by centroid size) on Procrustes distance and shape variation along PC1. A multivariate regression analysis was performed to quantitatively assess the relationship between size and shape, aiming to determine whether size influences skull morphology in these breeds.

Results

In evaluating the skull morphology of Tatra Shepherd and Polish Lowland Sheepdog breeds, other herding and shepherd dog breeds in the sample pool, particularly the German Shepherd, Illyrian Shepherd, and Collie, were also included for comparison. This approach allowed for a more comprehensive analysis of breed-specific morphological traits by similarities and differences in skull structure that may relate to each breed's functional roles and environmental adaptations. Among the samples used, the Polish Lowland Sheepdog had the smallest average skull size (Figure 2). Although the other breeds were close in skull size, the Illyrian Shepherd had the largest skull on average, along with the greatest size variation. The Tatra Shepherd, meanwhile, displayed a skull size similar to the other sheepdog breeds, though larger than that of the Polish Lowland Sheepdog.

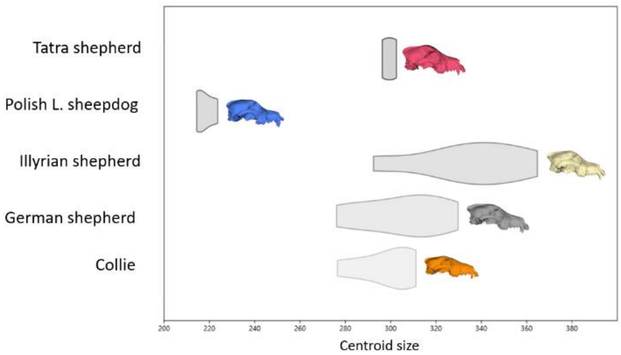

Figure 2. Results of centroid size for dog breeds in the study.

As a result of the shape analysis, it was observed that PC1 explained 37.2% of the total variation in skull morphology, while PC2 accounted for 25.1%. The prominent shape variation along PC1 represented a shift in skull morphology from mesocephalic to dolichocephalic characteristics. Specifically, in specimens with positive PC1 values, the facial structure was thinner and more elongated, creating a distinctly narrow and extended facial profile (Figure 3). In this positive PC1 range, the hard palate exhibited a longer, slender shape, whereas, in specimens with negative PC1 values, the palate was comparatively wider and more robust. The occipital region remained relatively consistent across PC1, with no significant shape differences detected in this area.

In PC2, notable morphological differences were observed, particularly in the nasal-frontal junction and the contour of the orbital region (Figure 3). At negative PC2 values, the junction between the nasal and frontal bones showed a more pronounced curvature, giving this region a rounded appearance. Conversely, in specimens with positive PC2 values, this section appeared straighter and more aligned. Furthermore, the shape of the lacrimal rim within the orbit differed, with a straight configuration in positive PC2 values, while specimens with negative PC2 values displayed a more oval-shaped lacrimal rim, contributing to a distinctive orbital contour.

The distribution of samples along PC1 and PC2 is illustrated in Figure 4, highlighting distinct trends among the different shepherd breeds. Polish Lowland Shepherd samples tended to cluster within the negative range of PC1 values, indicating a broader, more robust skull morphology, while their distribution along PC2 was more centered, suggesting average variation in this dimension. Tatra Shepherd samples, on the other hand, displayed a central position along PC1, reflecting a balanced skull morphology, but were more positively distributed on PC2, implying subtle shape differences that distinguish them from the other shepherd breeds.

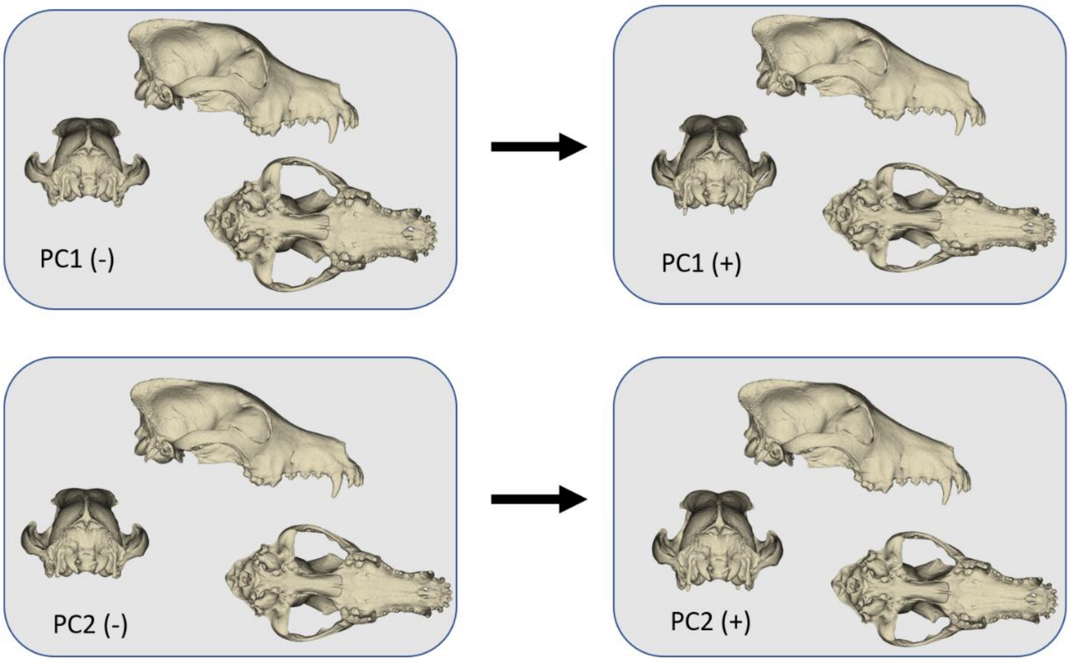

Figure 3. Models describing skull shape changes between the minimum and maximum values of PC1 and PC2.

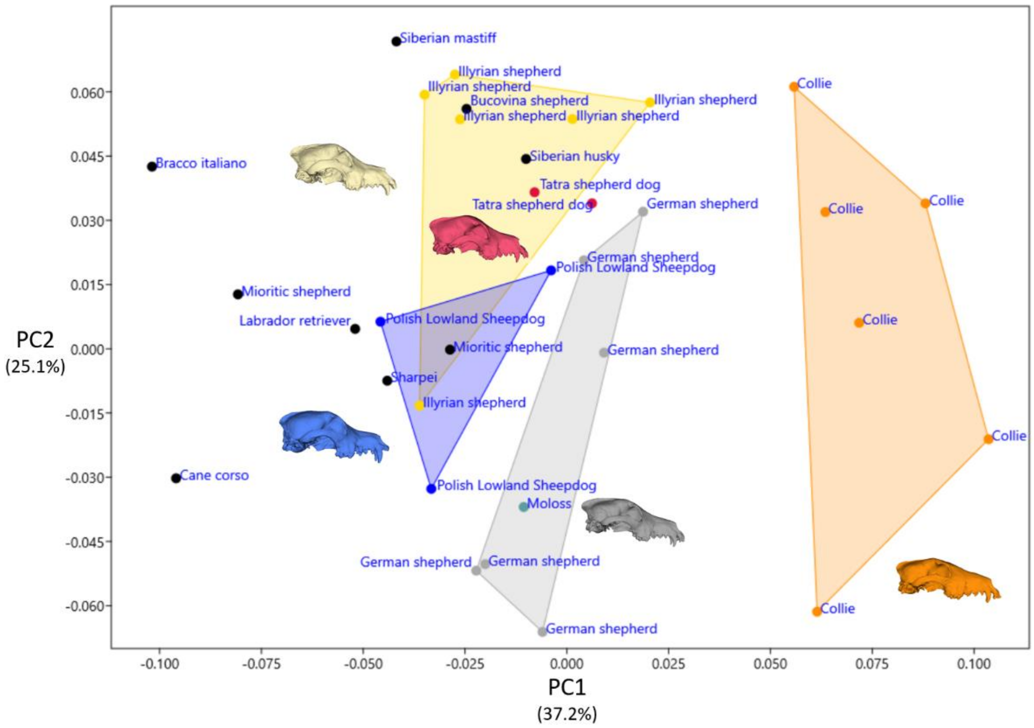

Figure 4. Principal component analysis plot of skull morphology illustrating variation along PC1 and PC2 axes. Convex hulls are shown, delineating the area occupied by each breed of shepherd dog, highlighting breed-specific clustering and overlap in skull form.

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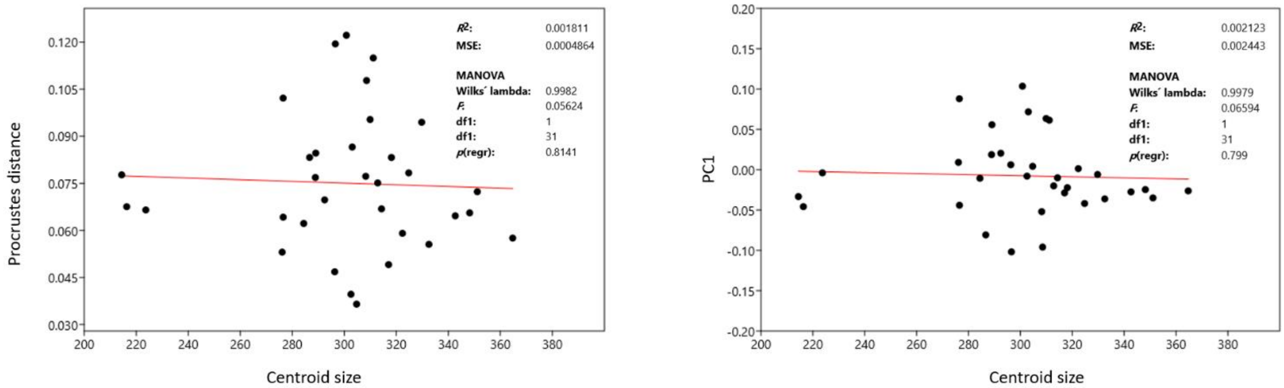

Figure 5. The effect of Procrustes distance and PC1 on skull size.

Collie samples were unique in that they occupied the positive boundary of PC1 exclusively, suggesting that the elongated, narrower skull features associated with positive PC1 values are characteristic of this breed. This distribution suggests that shape variation along PC1 may be largely influenced by the distinct skull morphology of Collies, who consistently exhibit a more dolichocephalic form. In contrast, the remaining shepherd breeds clustered closer together, showing more mesocephalic characteristics, with only slight variation along PC1.

In terms of PC2, no significant differences were observed among most shepherd breeds, reinforcing the notion that skull shape changes along this axis may represent individual variations rather than breed-level morphological trends. However, Tatra Shepherds did display a marginally more positive PC2 value in comparison to Polish Lowland Shepherds, suggesting minor distinctions in the nasal-frontal or orbital regions that set them apart. This finding implies that while shape variations along PC2 are subtle and may be individually based, certain breed-specific trends can still be observed, particularly between Tatra and Polish Lowland Shepherds.

Figure 5 illustrates the relationship between Procrustes distance, PC1, and skull size. Analysis showed that neither Procrustes distance nor PC1 had a statistically significant effect on skull size. This suggests that variations in skull shape captured by PC1, as well as the within-group variation measured by Procrustes distance, do not correlate strongly with changes in overall skull size across the samples.

Discussion and Conclusion

The findings of this study revealed the skull characteristics of the Tatra Shepherd Dog and the Polish Lowland Sheepdog by analyzing their skull morphology alongside other breeds from the same region, revealing species-specific skull features. The results indicate that the Tatra Shepherd Dog exhibits a longer skull structure compared to the Polish Lowland Sheepdog. Despite these differences, both Polish Shepherd Dog breeds share similar skull morphology with other shepherd breeds, excluding Collies. The most distinctive feature of Collies, which sets them apart from the other samples in this study, is their pronounced dolichocephalic skull morphology.

The dolichocephalic structure of the Collie contributed significantly to the primary axis of shape variation, highlighting its distinctive skull morphology compared to other breeds. In contrast, the remaining breeds displayed more mesocephalic characteristics, aligning with the general morphology observed in many shepherd dogs. Despite these differences, the results of the principal component analysis revealed different shape variations between the breeds, suggesting that skull morphology is influenced by factors beyond basic cephalic indices. Interestingly, even within the shepherd dog group, which shares close functional roles, notable morphological differences were observed. This variation could be attributed to breed-specific adaptations shaped by historical roles, environmental conditions, or selective breeding practices. For instance, shepherd dogs used in different terrains or climatic conditions may have developed subtle structural differences to better suit their environments. Additionally, the morphological distinctions observed might reflect genetic diversity within the group, further emphasizing the complex interplay between functionality, adaptation, and skull structure. These findings underscore the importance of detailed morphological analyses to uncover nuances that may not be immediately apparent from functional similarities alone. They also suggest that while shepherd dogs may share common tasks, their skull morphology is shaped by a combination of ecological, genetic, and selective pressures, resulting in a diversity of forms even within this functional group. Future studies could expand on these results by incorporating additional breeds and investigating the relationship between skull morphology, environmental adaptation, and genetic lineage.

In studies conducted on dogs, the primary skull variations generally showed similar results. The findings that revealed the most significant shape variation (PC1)

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demonstrated that skulls are divided into brachycephalic, mesocephalic, and dolichocephalic types (6, 9, 17). However, the variations following the primary shape variation presented more specific shape differences depending on the sample groups used by the researchers. For instance, in a study on livestock guardian dogs, the main shape component described a gradient between brachycephalic and dolichocephalic skulls, while the second shape component was characterized by braincase shape features (9). In another study, the primary component variation showed a range from short, wide, and round skulls to those with a more elongated shape. However, the second shape variation was associated with flat muzzles in the dogs' skulls (6). In this study on Polish Shepherd Dogs, the primary shape variation was consistent with similar variations reported in previous studies. However, unlike other studies, the second shape variation captured morphological differences, particularly in the nasal-frontal junction and the contour of the orbital region. The classification of carnivora skulls into brachycephalic, mesocephalic, and dolichocephalic types as the primary shape variation is now well-supported by numerous studies in the literature. However, secondary shape variations in these studies often capture subtle but significant nuances. These features may provide detailed and essential information about skull morphological characteristics. For instance, in this study, while the primary shape component did not capture the morphological distinction between Tatra and Polish Lowland Shepherds, the secondary shape variation revealed that these two breeds exhibit distinct morphological patterns. This underscores the importance of examining secondary components to uncover fine-scale morphological differences within and between breeds.

The primary axis of variation (PC1) distinguished breeds with a longer and narrower facial profile from those with a broader and more robust skull morphology. This shape gradient aligns with the functional differences observed among various working and herding breeds. Dogs with higher PC1 values, such as Collies, exhibited a more dolichocephalic skull, a characteristic often associated with enhanced visual perception and agility—traits beneficial for fast-paced herding tasks. Conversely, breeds with lower PC1 values, such as Polish Lowland Sheepdogs, displayed a more compact and mesocephalic skull, which may contribute to stronger bite force and greater resistance to physical strain, advantageous for livestock protection and endurance in harsh environments. PC2 primarily captured shape differences in the nasal-frontal junction and orbital contour, indicating potential variations in olfactory capability and visual field adaptation. Breeds positioned at the negative end of PC2, such as the Illyrian Shepherd and Tatra Shepherd Dog, which are found in higher altitudes, exhibited a more pronounced nasal-frontal curve, which may suggest an adaptation for enhanced olfactory sensitivity—a crucial trait for detecting predators in mountainous terrains. Additionally, the variation in orbital shape may reflect differences in peripheral vision and depth perception, further influencing their ability to navigate and respond to environmental cues. The potential morphological differences observed in dogs living at higher altitudes highlight the need for studies with larger and more homogenous sample sizes to validate these findings. Expanding the dataset would allow for a more robust statistical analysis, helping to determine whether these traits represent adaptive modifications to environmental pressures or merely individual variation. Given the functional significance of skull morphology in sensory perception and survival strategies, such studies could serve as an important reference for future research. Further investigations integrating biomechanical modeling and ecological factors may provide deeper insights into the environmental adaptations of shepherd dog breeds.

Linear skull studies, which measure the distance between two points, provide valuable but limited information about skull dimensions. However, these measurements can be influenced by the curvature between the points or the shape of intervening anatomical structures, potentially affecting the accuracy of the results. In contrast, geometric morphometrics methods allow for a more detailed and holistic analysis of size and shape by incorporating multiple reference points and capturing the spatial relationships between them. In veterinary anatomy, this approach has proven especially useful for analyzing complex structures. For example, horn dimensions in ruminants and even the size of turtle carapaces have been calculated using geometric morphometrics (7, 8). These methods surpass traditional linear measurements by providing a comprehensive representation of the shape and size, enabling researchers to account for curvature, asymmetry, and other morphological nuances. In this study, 19 reference points were used to compare skull sizes. Additionally, these points were selected to ensure repeatability, making them suitable for use in future studies as well.

One limitation of this study was the small sample size for native Polish dog breeds, which included only 2 Tatra Shepherd Dogs and 3 Polish Lowland Sheepdogs. Due to the limited number of samples within groups, the study focused primarily on examining variation and allometric characteristics rather than conducting a detailed analysis of shape differences between groups. To perform more robust statistical analyses and achieve a deeper understanding of intergroup morphological differences, larger sample sizes would be necessary. Increasing the number of specimens in future research would enable the application of advanced statistical tools, allowing for a

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more comprehensive evaluation of skull morphology and a better assessment of the factors contributing to shape variation. Expanding sample sizes across all groups would also help capture the full spectrum of morphological diversity, providing a stronger basis for comparing native Polish breeds with other shepherd dogs.

In veterinary practice, understanding breed-specific skull morphology can assist in procedures such as anesthesia administration, surgical planning, and diagnosing cranial deformities that may be more common in certain breeds. For instance, the differences in orbital and nasal structure observed in Polish Lowland Sheepdogs and Tatra Shepherd Dogs could influence approaches to ophthalmic and respiratory treatments in these breeds. Additionally, skull morphology plays a crucial role in forensic and archaeological applications, where geometric morphometric techniques can aid in identifying breed origins from skeletal remains. Given that many shepherd dogs are working breeds with historical significance, their skeletal characteristics could provide valuable insights into past breeding practices and population genetics.

To further enhance our understanding of Poland's canine diversity, future studies should aim to expand the dataset to include additional local Polish breeds and investigate a broader range of morphological traits. Exploring the functional implications of skull morphology on behavior, health, and performance could provide a more comprehensive perspective on how these traits influence breed abilities and their interactions with the environment. Moreover, conducting longitudinal studies to examine how these morphological traits adapt over time in response to changing environmental pressures and breeding practices will be essential.

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Ethical Statement

This study does not present any ethical concerns.

Conflict of Interest

The authors declared that there is no conflict of interest.

Author Contributions

E.P conceived and planned the experiments. O.G. carried out the experiments. M.J. contributed to the interpretation of the results. E.P. and O.G. took the lead in writing the manuscript. All authors provided critical feedback and helped shape the research, analysis and manuscript.

Data Availability Statement

The data supporting this study's findings are available from the corresponding author upon reasonable request.

Animal Welfare

The authors confirm that they have adhered to ARRIVE Guidelines to protect animals used for scientific purposes.

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