Chewing asymmetry in dogs : exploring the importance of the fossa masseterica and first molar teeth morphology.

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Abstract

Dogs are animals with strong bite force. This strong bite mechanism has led to significant changes in the skeletal system such as fossa masseterica. It can be thought that one side is used more than the other side in chewing and is related to the preference of using the same side's hand, eye, and foot. In the study, directional asymmetry and fluctuating asymmetry, which occurs as a result of chewing asymmetry, were examined on the first molar teeth and the fossa masseterica in 85 dog mandibles including a wide diversity of morphotypes. The association of high PC1 values for directional asymmetry with a pronounced cranial index, as evident in breeds like pekingese, pomeranian, and bulldog, indicates a potential evolutionary or selective breeding trend favouring brachycephaly. On the contrary, guardian breeds like the German shepherd and Bernese mountain dog, which typically require strong jaws for their roles, showcased reduced PC1 values, which might be related to their functional morphology. Similarly, the PCA results for the first molar teeth shape variations also highlighted the influence of cranial shape, with boxer dogs displaying notably higher PC1 values. The fluctuating asymmetrical distributions provided valuable insights into individualistic variations. Interestingly, no specific breed distribution trend was observed for these asymmetries, indicating a more individual-based variation rather than breed-based. It's essential to note that while these results provide valuable insights, further studies are required to understand the underlying causes better. Factors like genetic variations, developmental processes, dietary habits, and external environmental factors could play pivotal roles in these observed morphological differences.

Key words: Fluctuating asymmetry, geometric morphometry, mandible, shape analysis.

Introduction

The domestic dog exhibits the highest variability in skull shape within the Carnivora order, reflecting the last thousand years of artificial selection and inbreeding (Drake and Klingenberg 2010; Selba et al. 2019). With over 400 different breeds (https://www.fci.be/en/), domestic dogs provide a good subject for studying the functional purposes and issues related to the variation in skull and mandible shape. This high morphological variationhas attracted significant scientific interest. However, the role of the mandible and its mastication function, has been comparatively overlooked. The morphology of the mandible is directly related to the development of the abductor and adductor muscles, and in most vertebrates species, variation in the shape of the mandible and cranium is tied to changes in the jaw adductor muscles (Wat and Williams et al., 1951). This endures despite intense artificial selection in the skeletal structure of the dog's head.

Although the mandible is engaged primarily in functions like chewing, the cranium and face have more diverse roles, such as protecting the brain and vital sensory organs. The jaw muscles, including the adductors and abductors, together with the mandible, contribute to a stabilising functional system, providing support and strength to the skull (Frost and Schonau et al., 2000). These parts are moved by forces caused by muscle contractions, and bones are morphologically modified in response to external forces such as joint force and bites (Frost et al., 2001). To achieve effective biting and mastication, the muscular system and bones must be functionally integrated (Olson and Miller et al., 1951). Previous studies have inadequately described the quantitative interaction between jaw muscles and bones in domestic dogs (Liebman and Kussick, 1965) in contrast to other mammals (Crompton et al., 1963).

Geometric morphometric techniques are powerful tools for quantifying morphological differences and have been widely used in the study of skeletal structures (Klingenberg, 2015). Geometric morphometric methods have been used in ecological and evolutionary research in recent years, as they provide a comprehensive measurement of biological shape (Adams and Otárola-Castillo, 2013).

Directional asymmetry (DA) refers to consistent differences between the left and right sides of a structure while fluctuating asymmetry (FA) refers to shape variations that lack a specific (Klingenberg, 2003). These differences can be caused by genetic or environmental factors (Klingenberg, 2015). Assymetry has been shown to result from inbreeding, hybridization or fitness considerations (Palmer and Strobeck, 1986; Palmer and Strobeck, 2003; Parsons, 1990). In chewing mechanics, unilateral chewing has been thought to cause FA in the jawbone (Ginot et al., 2018). Previous studies have tied chewing preferences to consistent handedness and other unilateral preferences in humans (Nissan et al., 2004; Kazazoglu, 1994; Martinez-Gomis et al., 2009). However, this issue has never been explored in domestic carnivorans. Particularly, dogs, characterised by strong chewing power due to their robust masseter muscles, have not been examined in this context.

In this study, we explore both DA and FA in dog mandibles using 3D geometric morphometrics. Our working hypothesis is that there is a significant asymmetry component in the domestic dogs' mandible. More specifically, we suspect that this DA will be most prominent in the fossa masseterica and the first molar teeth, as these two structures are integral parts of the skeletal system that have significant implications in chewing mechanisms.

Materials and Methods

Material and Landmarking

A total of 85 modern canine mandibla were examined. Mixed breed samples were included. None of the specimens exhibited any pathological formations. Specimens were sourced from Istanbul University-Cerrahpaşa, Osteoarchaeology Research Center. 3D scans of the mandibles were obtained using the Einscan SP 3D scanner, boasting a scan accuracy of ≤0.05 mm. The mandibular shape was delineated using Stratovan Checkpoint, with 81 anatomical landmarks placed manually on each fossa masseterica using a 9x9 grid. Landmarks were placed from the lower border of the fossa masseterica to the posterior border of the ramus mandible and the upper border of the processus coronoideus (Figure 1). Both the right and left fossa masseterica were landmarked in the same order. An additional 15 anatomical landmarks were identified on the right and left of the first molar teeth (Figure 1). Landmark coordinates for each specimen were captured and saved with the ''morphologica'' the file extension.

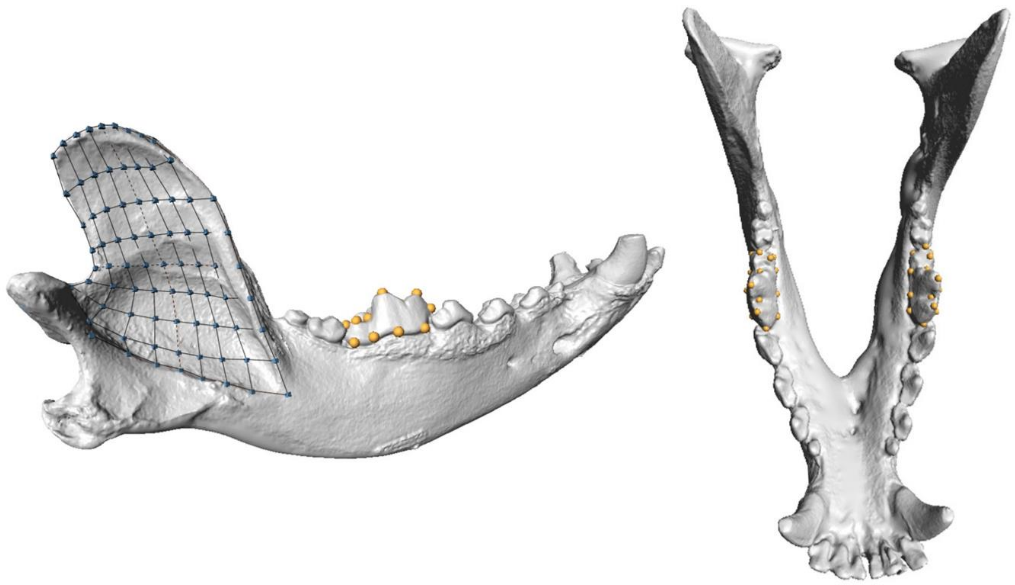

Figure 1. Landmarks for the fossa masseterica (highlighted in blue; 9x9 grid) and the first molar teeth (in yellow, 15 landmarks).

Statistical Analysis:

For the statistical evalutations, MorphoJ software (Klingenberg, 2011) was utilised. Date files in ''morphologica'' format were imported into MorphoJ using the ''symmetry'' option, after which symmetrical landmarks were aligned. The landmark data were first transformed using a standard Procrustes fit to eliminate positional, orientational, and scale differences. A covariance matrix incorporating both DA and FA components was then generated. Subsequently, a Principal component analysis (PCA) was conducted to evaluate mandibular morphological variations.

Procrustes Analysis of Variance

To assess the asymmetry across various dog groups, a Procrustes ANOVA was performed. This evaluated the potential correlation between asymmetry and canines' societal habits.

Classficiation followed the FCI guidelines (https://www.fci.be/en/). Nine distinct categories were considered, including Bully (9 samples), Guard (6 samples), Gundog (11 samples), Herding (2 samples), Hound (1 sample), Mastiff (15 samples), Primitive (3 samples), Shepherd (30 samples), Terrier (8 samples). Procrsutes ANOVA, conducted using MorphoJ software, assessed the influence of these groupings on both DA and FA. Given the significant size variation among the dogs, the centroid size discrepancies between the groups were disregarded.

Allometry

To investigate allometric patterns within dog mandibles, a regression analysis was employed in MorphoJ. This analysis aimed to discern any relationships between mandibular shape and size. The relationships of the DA and FA components were explored with the log of the mandibular centroid size, based on 1000 random permutations.

Results

The Procrustes ANOVA results for the fossa masseterica structure and the first molar teeth are shown in Table 1. Our results indicate significant variation in symmetric shape ($p < 0.0001$). Directional asymmetry (DA) for fossa masseterica and the first molar teeth was also significant ($p<0.0001$). However, the F value and sums of squares for the first molar teeth surpassed those of the fossa masseterica. It is noteworthy that the interaction between dog breeds and side effects were for both fossa masseterica and the first molar teeth. The main effect (dog groups) explained 29.36% of the total variation observed for the fossa masseterica and 30.93% for the first molar teeth. The digitizing error accounted for 67.36% of the total variance in the fossa masseterica and 66.92% in the first molar teeth.

Table 1. ANOVAs results for fossa masseterica and first molar teeth shape.

	Effect	SS	MS	Df	F	P-value	% Variation
Fossa masseterica	Individual	0,19383954	0,0001013805	1912	10,73	**<.0001**	**%29,36**
	Side	0,00346235	0,0000144265	240	1,53	**<.0001**	**%0,52**
	Ind * Side	0,01814802	0,0000094521	1920	0,78	**NS**	**%2,74**
	Error	0,44476064	0,0000120587	36883			**%67,36**
First molar teeth	Individual	0,14293434	0,0004357754	328	24,39	**<.0001**	**%30,93**
	Side	0,00385670	0,0000918263	42	5,14	**<.0001**	**%0,83**
	Ind * Side	0,00600284	0,0000178656	336	0,36	**NS**	**%1,29**
	Error	0,30917888	0,0000490138	6308			**%66,92**

Sums of squares (SS) and mean squares (MS) are represented in units of Procrustes distances (dimensionless).
Individual refers to the group (dog breeds)
Side is a fixed effect that portrays directional asymmetry
Ind*side signifies the interaction between dog breeds and side effects (denoting fluctuating asymmetry)

Linear regression results are summarized in Table 2. For the fossa masseterica, the relationship between DA and shape relative to centroid size was statistically significant. However, the relationship between fluctuating asymmetry (FA) and shape on centroid size was not significant. For thefirst molar teeth, both DA and Fas regressions related to centroid size were statistically significant.

The regression of shape against centroid size only accounted only for 0.76% (fossa masseterica) and 2.69% (the first molar teeth) for FA.

Table 2. Linear regression results detailing relationships between size (log centroid size) and both directional and fluctuating asymetric components

	Reggression	Predicted SS	Residual SS	% predicted	P-value
Fossa masseterica	Directional asymmetry	0,02570988	0,37926761	6,3485%	**0,0013**
	Fluctuating asymmetry	0,00104509	0,13718999	0,7560%	0,6903
First molar teeth	Directional asymmetry	0,07700449	0,30360147	20,2321%	**<.0001**
	Fluctuating asymmetry	0,00195453	0,07071691	2,6895%	**0,0093**

The Principal Component Analysis (PCA) performed on the DA component of fossa masseterica shape variation revealed that the first two principal components (PCs) accounted for 66.66% of the total variation observed (Figure 2). Increasing PC1 value represents a shorter fossa massaterica in shape. Also, ramus mandible is more extroverted with increasing PC1 value. The PC2 positive limit represents a more inverted ramus mandible. There is a deeper fossa massaterica with increased PC2 value. The distribution scatterplot from the first axis (59.10% of the overall variance) demonstrated a propensity to differentate mandibles based on cranial shape variations. Notably, samples with heightened PC1 values corresponded to those with a high cranial index (brachycephalic). Breeds such as pekingese,pomeranian and bulldog samples had high PC1 values, while breeds typically known as live guardian dogs, like the German shepherd and Bernese mountain dog exhibited the lowest PC1 values. With increasing PC1 value, there was a noticeable reduction in the length of the fossa massaterica accompanied by a shallower depth. The breed with the most pronounced PC2 was the Sharpei. Generally, boxers seemed to have the most elevated PC2 values, with an increase in this value correlating with the lower part of the fossa massateria becoming more lateral.

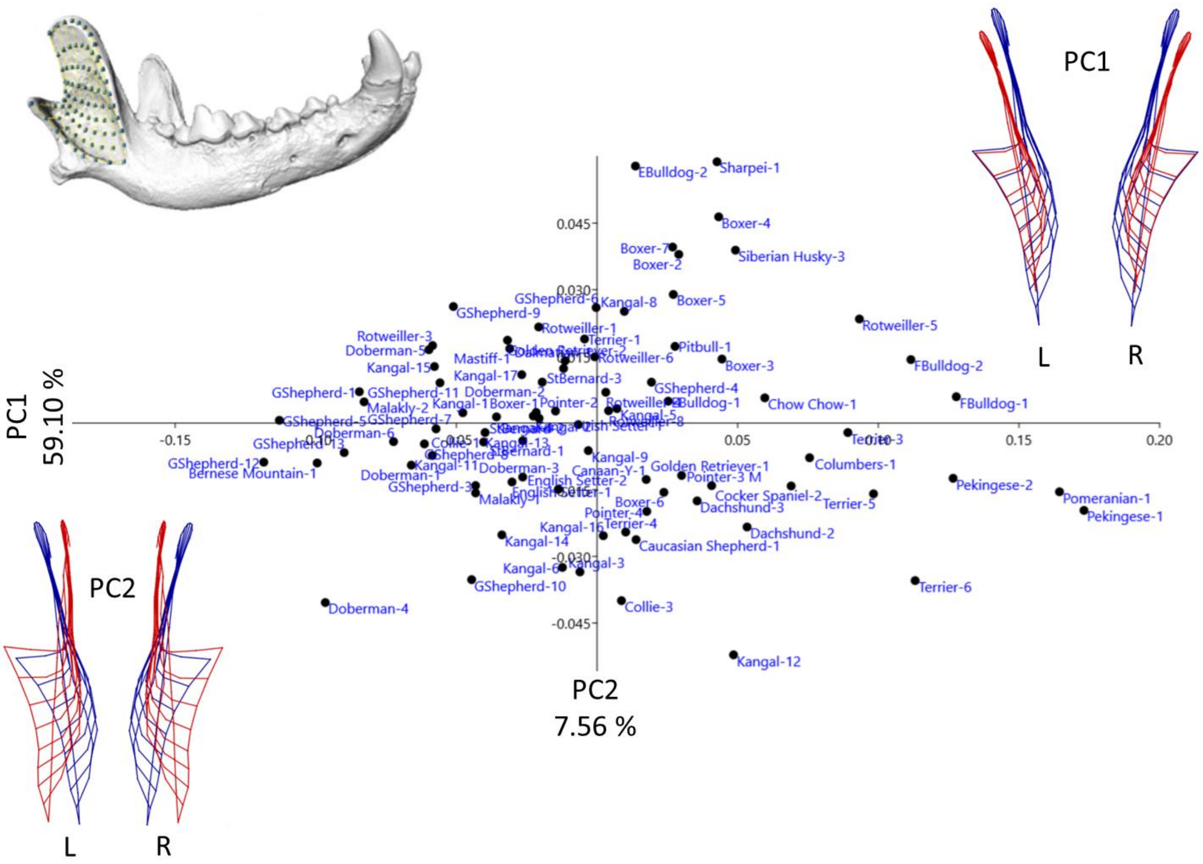

Figure 2. Results of the principal component analyses performed on the directional asymmetrical component of the fossa masseterica. Wire-frame warp plots represent the extremes PC shapes of the fossa masseterica, with blue outlines representing the mean shape configuration and red outlines depicting the positive extremes for each PC axis.

Similarly, the PCA performed on the DA component of the first molar teeth shape indicated that the initial two PCs encapsulated 73.53% of the total variation observed (Figure 3). The distribution defined by the scatterplot of the first axis (65.28% of the overall variance), showed a trend similar to that of the fossa massaterica, distinguishing teeth based on cranial shape variations. Samples with a high PC1 value were those displaying a pronounced cranial index (brachycephalic). In this context, boxers were especially notable, boasting higher PC1 values than other breeds. As the PC1 value increased, the first molar teeth were more lateral in shape. In the PC2 value, the anterior section of the teeth became more lateral, while the posterior part of the teeth was observed to be more medial.

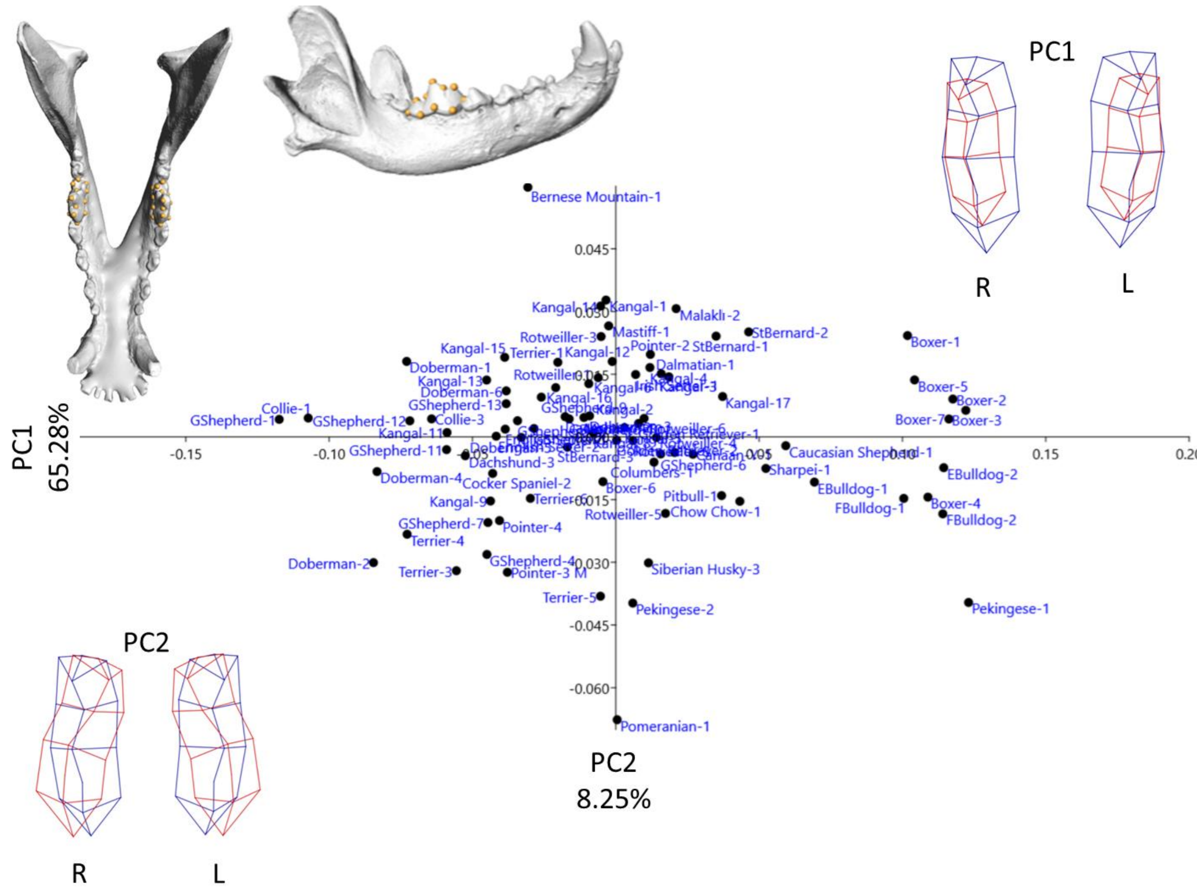

Figure 3. Results of the principal component analyses performed on the directional asymmetrical component of the first molar teeth. Wire-frame warp plots represent extreme PCs shape in the first molar teeth shape, with blue outlines representing the mean shape configuration and red outlines the positive extremes of each PC axis.

Figure 4 illustrated the fluctuating asymmetrical distributions observed for the fossa masseterica are shown in Figure 4 distribution explained 57.26% (PC1+PC2) of the total variation. For the PC1 positive samples, the left fossa masseterica was consistently deeper than its right counterpart. A similar trend was observed in PC2, the fossa massaterica of the left side was closer to the median line.

This pattern of asymmetry was predominantly individual-centric, as no specific breed-based distribution was evident. The Pitbull-1 sample had the highest PC1 value, while the Terrier-4 sample had the lowest PC1 value. A noteworthy observation was the considerable FA variation among the German shepherds, especially those with a significant sample size (n).

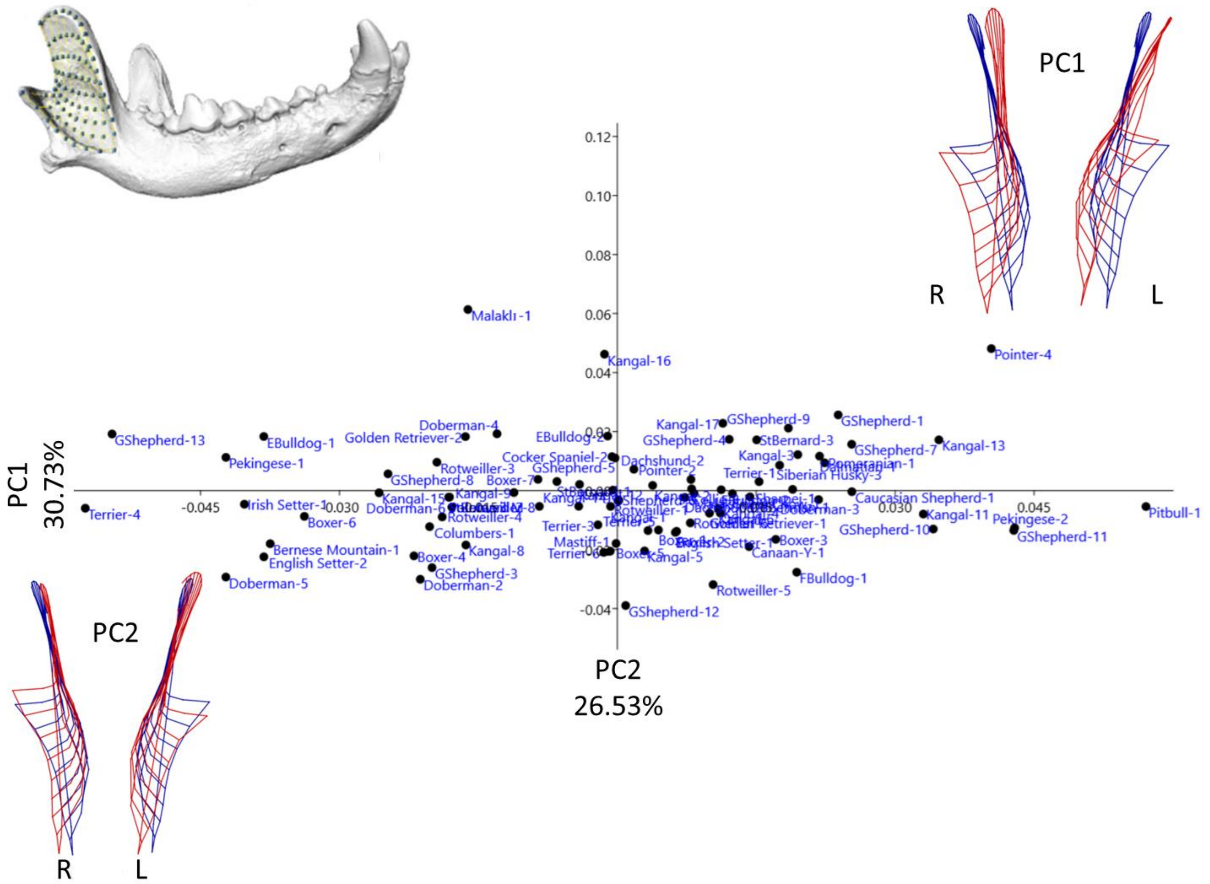

Figure 4. Results of the principal component analyses performed on the fluctuating asymmetrical component of the fossa masseterica. Wire-frame warp plots represent extremes PCs shape in the fossa masseterica shape, with blue outlines representing the mean shape configuration and red outlines the positive extremes of each PC axes.

Figure 5 delinates the fluctuating asymmetrical distributions observed in the first molar teeth, accounting for 32.46% of the total variation. Distinctive patterns emerge from these results: in PC1 positive samples, tips of the right molar oriented medially, contrasteing with the lateral direction of the left molar. For PC2, a similar orientation was noted with right side leaning medially and the left side skewing laterally.

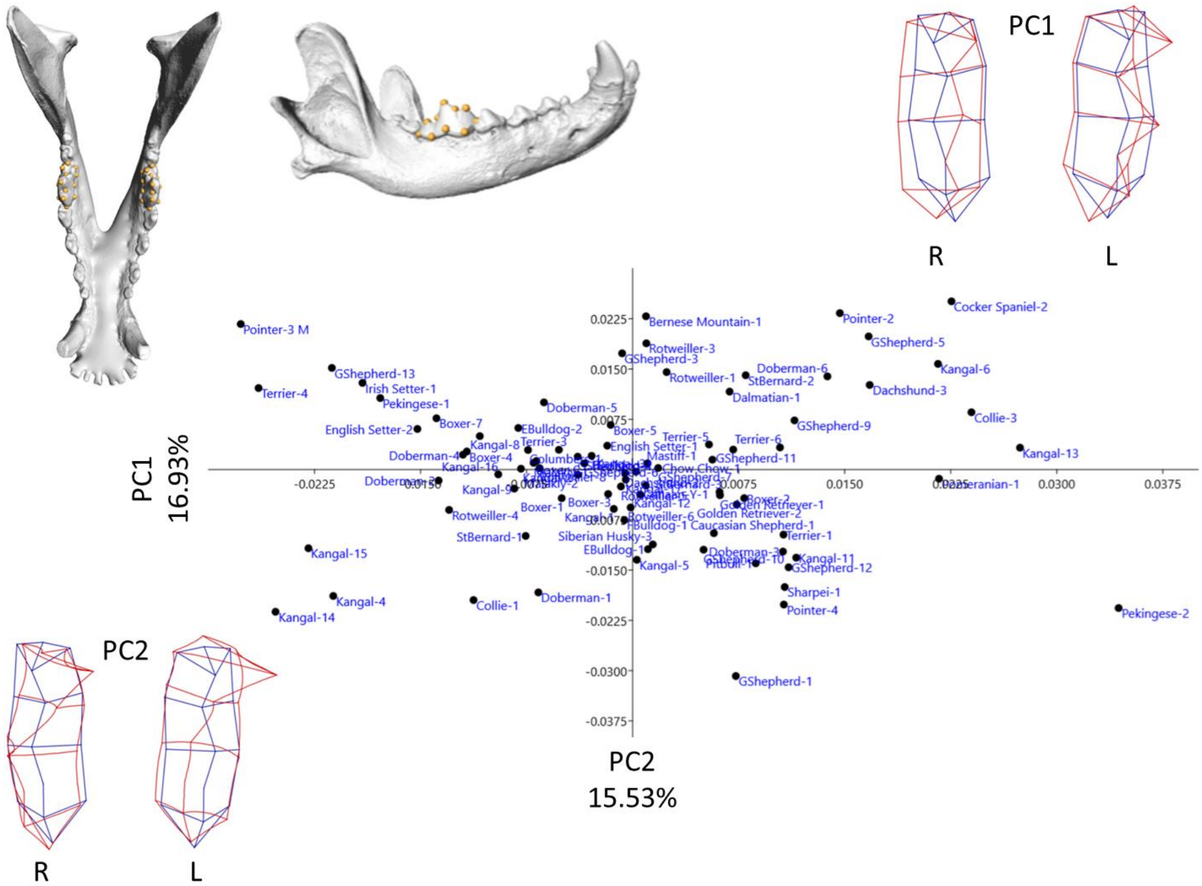

Figure 5. Results of the principal component analyses performed on the fluctuating asymmetrical component of the first molar teeth. Wire-frame warp plots represent the extremes PC shapes of the fossa masseterica, with blue outlines representing the mean shape configuration and red outlines depicting the positive extremes for each PC axis.

Discussion

The Principal Component Analysis (PCA) results on both the fossa masseterica and the first molar teeth shape variations offer profound insights into the morphological variances observed in canine breeds. Notably, the two first components of the PCA accounted for significant portions of the total variations in both structures, hinting at the primary pattern behind their morphological differences.

In this study, the effects of unilateral chewing on the skeletal system in dogs were examined morphologically. We thought that the development of unilateral masticatory muscles might have an effect on the ipsilateral fossa massaterica. PC1 results for FA of fossa massaterica also supported this hypothesis. In the shape variation of 31.73% of the total variation, the fossa massaterica of one side was deeper. This shows that the chewing muscle of that side works more than the other side. And this can create an asymmetry towards the median line of the fossa massaterica, to which this overworked unilateral muscle attaches. In the asymmetry of the first molar tooth, the most deformation was observed at the tip of the tooth. In both PC1 and PC2 results, the tips of the right and left teeth showed distortion in the same direction. However, it would not be correct to say that the animal can chew right or left depending on where this extreme point is directed. Contrary to Fossa massaterica, the deformity of the teeth may be due to reasons such as eating habits and chewing mechanics. The regression between the FA component values of the fossa massaterica and the first molar tooth was examined in the study, but the result was statistically insignificant. In addition, it was seen that the directional deformations of the teeth did not comply with these results when the animals were divided into right or left chewing based on the fossa massaterica.

For the fossa masseterica, the findings emphasize the influence of cranial shape variations on mandible characteristics. The association of high PC1 values with a pronounced cranial index, as evident in breeds like pekingese, pomeranian, and bulldog, indicates a potential evolutionary or selective breeding trend favouring brachycephaly. On the contrary, guardian breeds like the German shepherd and Bernese mountain dog, which typically require strong jaws for their roles, showcased reduced PC1 values, which might be related to their functional morphology. Similarly, the PCA results for the first molar teeth shape variations also highlighted the influence of cranial shape, with Boxer dogs displaying notably high PC1 values. The orientation shifts observed in molar teeth with varying PC values might suggest functional implications in mastication or possibly other genetic and developmental factors. Moreover, the fluctuating asymmetrical distributions provided valuable insights into individualistic variations. For the fossa masseterica, the deeper left fossa in PC1 positive samples compared to the right suggests potential functional or developmental causes. Interestingly, no specific breed distribution trend was observed for these asymmetries, indicating a more individual-based variation rather than breed-based. The notable FA variation in German shepherds, despite their vast sample size, may imply inherent genetic diversity or varying external factors affecting the breed. The first molar teeth's fluctuating asymmetrical distributions also presented intriguing observations, such as the medially oriented right molars and laterally oriented left molars. The consistent lateral shift of the left side across both PC1 and PC2 is curious and warrants further exploration.

Increased FA in cranial elements associated with the jaw muscles may be associated with bite-side preference or FA in muscle development (Urošević et al., 2015). The jaw muscles were not directly examined in the study, but the asymmetry in the jaw muscles will directly affect the FA level in the fossa massaterica. The first molar teeth, on the other hand, can be thought to have a FA that can be associated with eating habits more than the jaw muscles. In FA results, no correlation was observed between individuals with high FA values for the fossa masseterica and individuals with high FA values for the first molar teeth.

FA indices are likely to be especially prone to measurement error (Merila and Biorklund, 1995). Measurement errors published in FA estimation range from 10% to 76% (Palmer and Strobeck, 1986). While some authors emphasized the importance of measurement error, others ignored it. Merila (1995) revealed that only 43% of studies on FA estimation consider measurement error, and said FA estimates can be high even when the measurement error of the original characters is very low. It is also known that personal effects can cause errors during measurement (LAjust et al., 2003). In this study, which was performed on the dog's mandible, the measurement error was high. All measurements were made by only one person and repeated twice to reduce errors and avoid inconsistencies. The high measurement error in the study is thought to be due to the sample sizes of different breed groups. Small sample sizes in certain breed groups may produce variability and inconsistency in results. These small samples may be more susceptible to outliers or individual variations, potentially increasing errors. A more homogeneous set could be used to reduce these errors. However, examining the results of studies in a large population can answer many morphological questions, especially among dog breeds. For this reason, many dog breeds with morphological and morphometric differences were used in the study.

It was stated that there is no size difference in molar teeth in horses, but there is FA (Casanova and Morros, 2014). We also detected the presence of FA and DA in the first molar teeth in dogs. In addition, the effect of size on FA and DA was also examined in this study. Size had a statistically significant effect on DA. However, while the effect of size on FA was not effective in fossa massaterica, it was also found to be effective in the first molar teeth. It was observed that as the size of the tooth increased, the asymmetric values also increased. It occurs when asymmetry increases with size (Graham et al., 2010). Growth may be considered developmentally more unstable in larger dogs than in smaller dogs. This may explain why asymmetrical development can be seen more in large dogs.

Potential issues with study

- Sample Size: Some breed groups had notably smaller sample sizes than others. Smaller samples may not accurately represent the entire population of that breed, leading to potential biases in the results. Small sample sizes in certain breed groups can introduce variability and inconsistency in the results. Smaller samples can be more sensitive to outliers or individual variations, potentially amplifying errors. Moreover, it's more challenging to generalize the findings of small sample groups to the broader population of that breed, leading to lower confidence in those specific results.
- Breed Overlap: Breeds with close genetic ties or recent divergences might share morphological similarities, potentially complicating the analyses.
- Developmental Stages: If dogs from different developmental stages (like puppies versus adults) were included, the morphological differences due to growth might impact the results.

In conclusion, it was seen that FA can occur individually, with no particular preference for a dog breed or morphological group. It's essential to note that while these results provide valuable insights, further studies are required to understand the underlying causes better. Factors like genetic variations, developmental processes, dietary habits, and external environmental factors could play pivotal roles in these observed morphological differences. Additionally, a broader sample size across various breeds might offer more comprehensive insights into the interplay of genetics and environment in determining these morphological variations.

Acknowledgments

This work was supported by the Scientific and Technological Research Council of Türkiye (TUBITAK) under Grant number 123O145.

Conflict Of Interest Statement

The authors have no conflict of interest to declare.

Data Availability Statement

The data that support the findings of this study are available from the first author upon reasonable request.

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