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Could there be a relationship between feeding characteristics and the shape of condylus occipitalis and foramen magnum in mammals?

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Abstract: The aim of the study was to investigate the shape of the foramen magnum and condylus occipitalis of mammalian species belonging to different feeding groups. For this, two-dimensional geometric morphometric method analyses were applied. The data from the skulls of the 12 species were used. In principal component analysis, the first three principal components accounted for 70.353%of the total shape variation. According to the first principal component, the dorsal edge of the condylus occipitalis and foramen magnum contributed the most to shape variation. Most of the individuals were correctly separated according to the feeding groups. The most accurate grouping features were herbivorous and omnivorous. The mean shape of the foramen magnum and condylus occipitalis differed according to the feeding groups. As a result, our hypothesis was strengthened that the general shape of the analyzed region is influenced by the feeding factor.

Key words: Geometric morphometrics, skull, semilandmark, taxonomy

1. Introduction

The foramen magnum (FM) is a hole in the occipital bone. The spinal cord, meninges, and some cranial arteries pass through it. Bilateral condylus occipitalis (CO), which is involved in the head-neck connection (articulatio atlantooccipitalis), is located around this hole [1]. Different fields such as comparative anatomy, anthropology, evolutionary biology, and surgery are interested in the anatomical features of FM [2–6]. At the same time, some researchers have asserted that the morphological features of the FM have undergone evolutionary changes and therefore the region has aroused interest in special anthropological [7].

Nutritional preferences considerably affect the morphology and performance of vertebrate species [8]. Therefore, estimating the relationship between form and function helps to link morphology, ecology, and compatibility [9]. Skull shape depends on many factors such as genetics, developmental restriction, size, nutritional ecology, and locomotion [10,11,12]. Researchers have focused on skull morphology according to different nutritional patterns (sucking, tongue, hunting, etc.) [13,14,15]. Metzger and Herrel [16] reported that mechanical restrictions caused by dietary conditions may result in changes in the cranium. The information obtained from this type of research is important as it provides some inferences for vertebrates that cannot be captured and studied [8,17]. Thus, even comparisons in distantly related species may show interesting similarities [18]. In this respect, we aimed to investigate on similarities/differences in the shape of FM and condylus occipitalis with a two-dimensional geometric morphometric method in herbivorous, carnivorous, and omnivorous mammalian species.

2. Materials and methods

2.1. Samples

In the study, 110 mammalian skulls were used. The materials were samples used for educational purposes in the laboratories of the Anatomy Departments of different universities. According to laboratory records and macroscopic examination, there were no pathological conditions in the samples used. All of the specimens were adults according to dental examination and suture

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closure. The numerical and taxonomic information about the included mammalian species are given in Table 1 and Figure 1.

2.2. Photographed and digitization

The standardization of the photographing strategy was important because the samples belonged to different species and the analyzed region varied in anatomical location. Examples were photographed in the following steps.

1. The samples and the camera (18 × 55 lens, Canon 600 D, Japan) were placed on the same plane with the FM and the long axis of the lens parallel to each other.

Table 1. Information on the mammals species included in the study.

Species	Number (N)	Feeding
Bos taurus (BT)	8	**Herbivorous**
Ovis aries (OA)	14	
Equus caballus (EC)	11	
Capra hircus (CH)	13	
Homo sapiens (HS)	9	**Omnivorous**
Pan troglodytes (PT)	1	
Sus srofa (SS)	14	
Canis familiaris (CF)	13	**Carnivorous**
Canis lupus (CL)	7	
Vulpes vulpes (VV)	12	
Meles meles (MM)	5	
Lynx lynx (LL)	3	

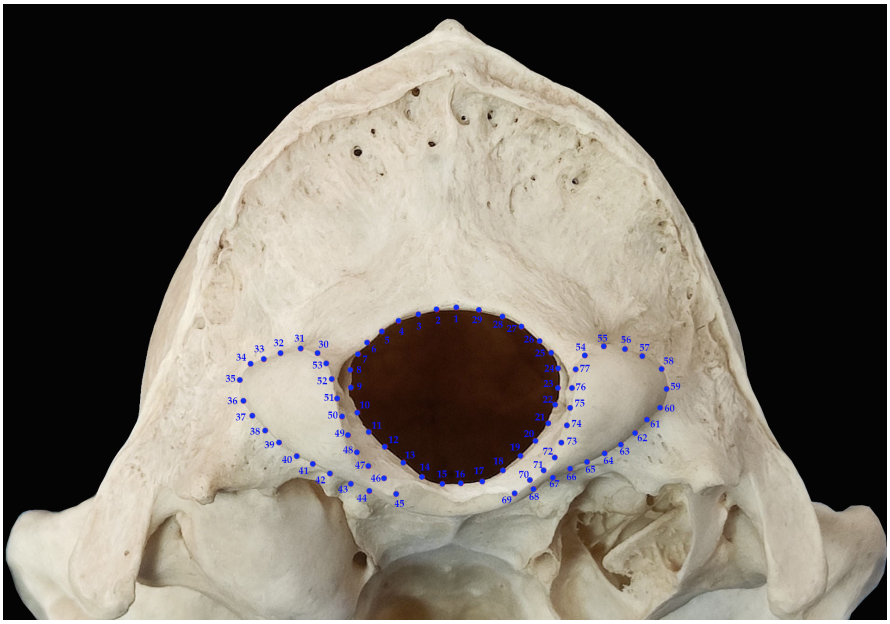

Figure 1. Landmark descriptions in a carnivorous.
LM1. Dorsomedial point of FM, **LM2-15.** Left frame points of FM, **LM16.** Ventromedial point of FM, **LM17-29.** Right frame points of FM, **LM30.** Dorsomedial corner of left CO, **LM1-34.** Dorsal edge of left CO, **LM35.** Most lateral corner of left CO, **LM36-44.** Lateral margin of left CO, **LM45.** Ventromedial corner of left CO, **LM46-53.** Medial edge of left CO, **LM54.** Dorsomedial corner of right CO, **LM55-58.** Dorsomedial corner of right CO, **LM59.** Most lateral corner of right CO, **LM60-68.** Lateral margin of right CO, **LM69.** Ventromedial corner of right CO, **LM70-77.** Medial edge of right CO.

2. The distance between the sample and the front of the lens was determined as 30 cm.
3. The shutter was controlled with a remote control to avoid deviations that may be caused by manipulation.
4. The photos were saved to the computer in JPG format. Seventy-seven landmarks, type I, type II, and type III (semilandmark), were digitized to determine the frame shape of the FM and condylus occipitalis. Information about the landmarks are given in Table 2. TpsUtil (Version 1.79) [19] and TpsDig2 (Version 2.31) [20] programs were used to digitize the landmarks from the photographs, respectively. Thus, the x and y Cartesian coordinates of the landmarks were determined.

MorphoJ [21] program was used to determine shape differences and for a series of analyses. Generalized procrustes analysis (GPA) was carried out to eliminate the differences in the obtained coordinate values such as size, position, and direction, and the Procrustes coordinates were determined [22]. Principal component analysis (PCA) was performed on these new values to reduce the size effect and show the variation in the responsible components [23, 24]. Thus, it was determined at which landmarks the shape differences were concentrated to see whether there was an allometric effect on the shape, which was investigated by multivariate regression analysis on Procrustes coordinates. While conducting the analysis, mostly focused on feeding groups. However, "species" was also applied as a classifier to see shape variation by species, although the number of samples for each species was limited. Canonical Variance Analysis (CVA) and Discriminant Function Analysis (DFA) were performed for grouping features and shape differences according to species [23].

3. Results

The distinction between condylus occipitalis and FM shape is shown in Figure 2 in the principal components analysis made according to the feeding. A total of 109 principal components were determined in this analysis. The first three principal components (PC1: 46.204%, PC2: 15.914%, PC3: 8.235%) explained 70.353% of the total shape variation. In PC1, the dorsal edge of the condylus occipitalis and FM made the greatest contribution to shape variation. In PC2, the general line of the condylus occipitalis was responsible for the shape variation. Although the amount of variation was small in PC3, the responsible anatomical points were the dorsomedial of the left condylus occipitalis, the dorsolateral of the right condylus occipitalis, and the general shape of the FM. The distribution of the samples on the graph was shown in Figure 3. Accordingly, the feeding groups were largely separated. In the scatter plot, the individuals at the intersection of omnivorous and carnivorous were pig (n: 3), dog (n: 1), and wolf (n: 1), while individuals in the intersection of omnivorous and herbivorous were horses and goats (one for each). While one fox remained

Table 2. Landmark descriptions, LM: Landmark, FM: FM, CO: Condylus occipitalis.

No	Description	Type
LM1	Dorsomedial point of FM	I
LM2 - 15	Left frame points of FM	III
LM16	Ventromedial point of FM	I
LM17 -29	Right frame points of FM	III
LM30	Dorsomedial corner of left CO	I
LM31 - 34	Dorsal edge of left CO	III
LM35	Most lateral corner of left CO	II
LM36 - 44	Lateral margin of left CO	III
LM45	Ventromedial corner of left CO	I
LM46 - 53	Medial edge of left CO	III
LM54	Dorsomedial corner of right CO	I
LM55 - 58	Dorsal edge of right CO	III
LM59	Most lateral corner of right CO	II
LM60 - 68	Lateral margin of right CO	III
LM69	Ventromedial corner of right CO	I
LM70 - 77	Medial edge of right CO	III

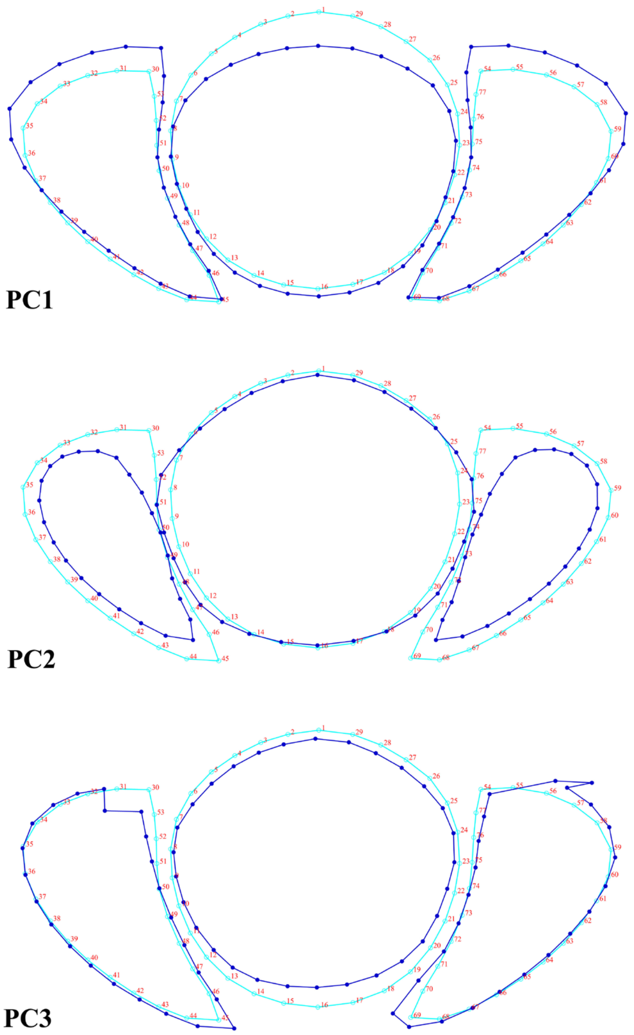

Figure 2. Graph of wireframe shape changes relative to PC1 (46.204%), PC2 (15.914%), and PC3 (8.235%).

omnivorous, one pig remained carnivorous. Based on species, humans (n: 9) and chimpanzees (n: 1) differed markedly from other groups. Cattle (n: 8) were largely separated from other herbivorous. In the carnivorous group, dogs (n: 13) and wolves (n: 7) largely overlapped, while lynx (n: 3) and badgers (n: 5) were completely separated from these species.

Before the canonical analysis of variance in the study, the effect of size on the shape was determined by regression analysis. The allometric effect of centroid size on shape in the feeding groups was 7.2014% (p = < 0.0001 in 10,000 rounds permutation test). This effect was 1.9674% in species groups (p = 0.0322 in 10,000 rounds permutation test). Therefore, residuals were removed from the multivariate regression and continued for analysis. Canonical variance analysis was performed to determine variation by feeding or species groups (Figure 4). The results and p values obtained by a test with 10,000 permutations based on Mahalanobis distances are given in Tables 3 and 4. Accordingly, the results were significant in the feeding groups (p < 0.0001). In the species groups, except for PT/CT, PT/CL, PT/HS, PT/LL, PT/MM, and PT/OA had significant results. It was taken into account that the results related to PT might be due to the number of samples.

Cross-validation results obtained in DFA on feeding groups are shown in Table 5. The most accurate grouping characteristics were in the herbivorous and omnivorous

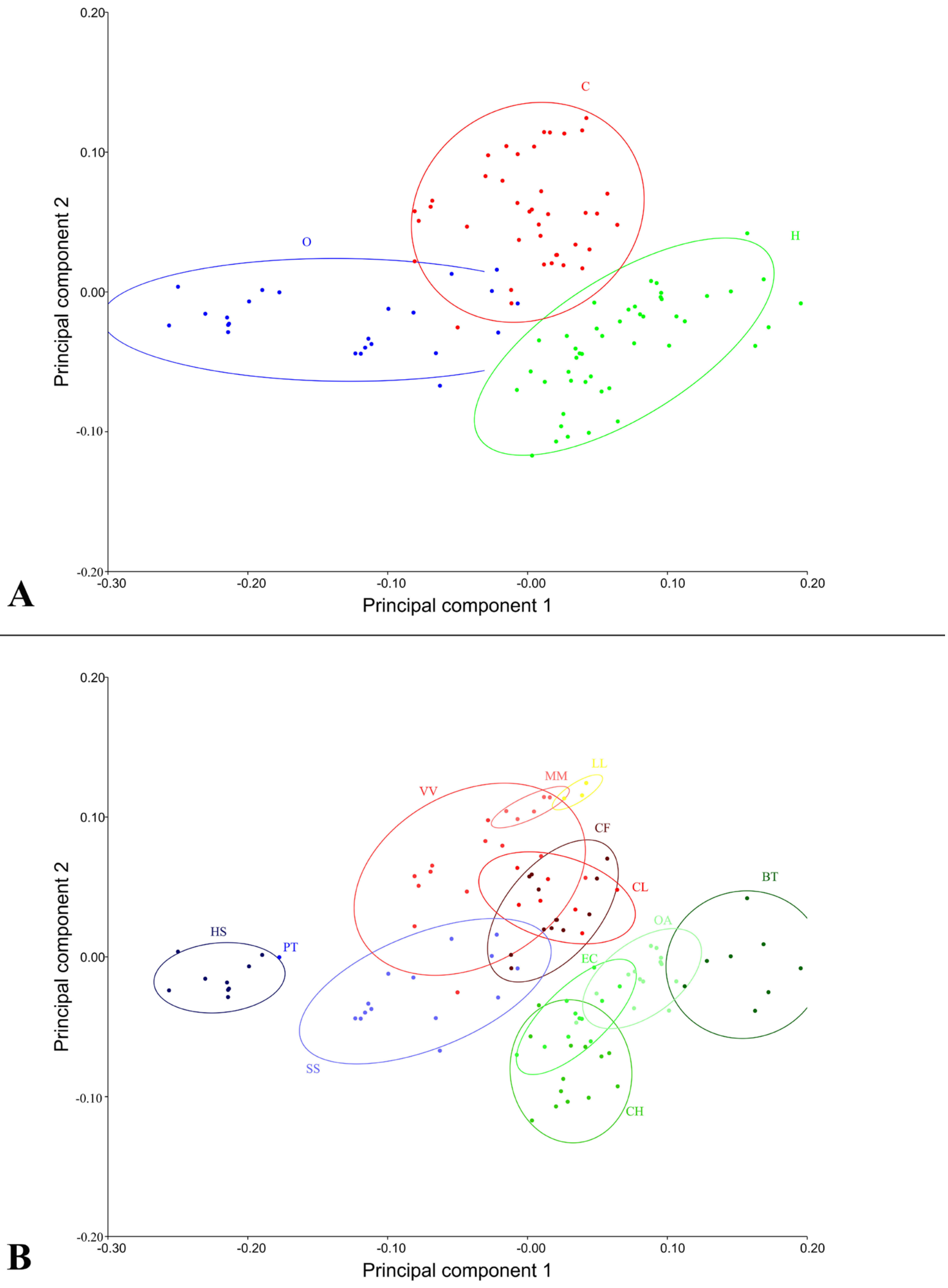

Figure 3. Scatter plot by PCA, A: Feeding groups, (C: Carnivorous/red, H: Herbivorous/green, O: Omnivorous/blue) B: Species groups, (BT: Bos taurus, CF: Canis familiaris, CH: Capra hircus, CL: Canis lupus, EC: Equus caballus, HS: Homo sapiens, LL: Lynx lynx, MM: Meles meles, OA: Ovis aries, PT: Pan troglodytes, SS: Sus scrofa, VV : Vulpes vulpes), 90% confidence ellipse.

comparisons. This was followed by a comparison of carnivorous and omnivorous.

The average shape of the condylus occipitalis and FM of the feeding and species groups is shown in Figure 5. Accordingly, the shape of the FM was dorsoventrally flattened -elliptical in carnivorous, laterolaterally flattened-oval in herbivorous, and laterolaterally flattened-partially conical in omnivorous (egg-shaped). The shape

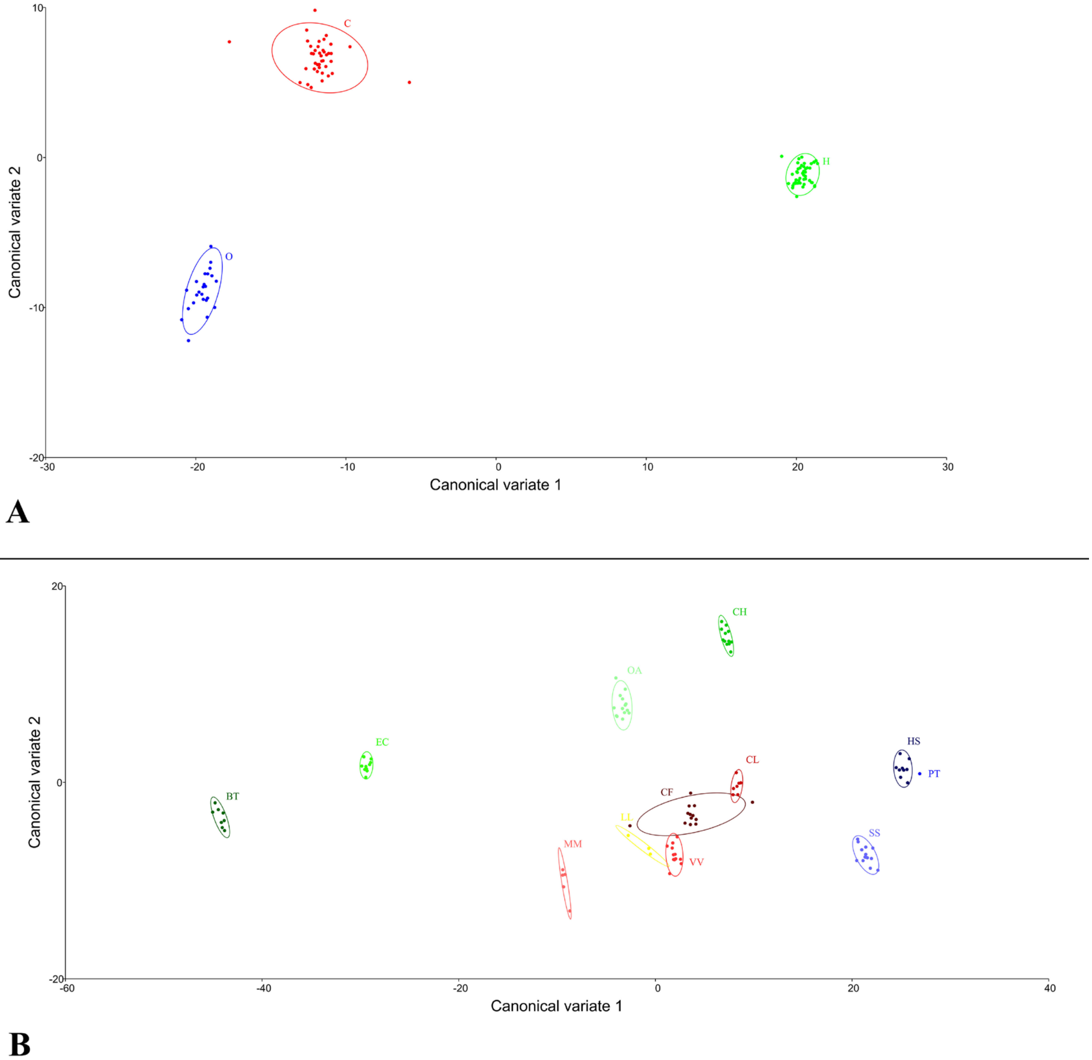

Figure 4. Canonical variance analysis by feeding and species groups, A: Feeding groups, (C: Carnivorous/red, H: Herbivorous/green, O: Omnivorous/blue) B: Species groups, (BT: Bos taurus, CF: Canis familiaris, CH: Capra hircus, CL: Canis lupus, EC: Equus caballus, HS: Homo sapiens, LL: Lynx lynx, MM: Meles meles, OA: Ovis aries, PT: Pan troglodytes, SS: Sus scrofa, VV : Vulpes vulpes), 90% confidence ellipse.

Table 3. Mahalanobis and Procrustes distances among groups.

	Mahalanobis Distance	
	C	**H**
H	33.0732*	
O	17.4106*	40.7207*

*: Significant p values. C: Carnivorous, O: Omnivorous, H: Herbivorous

Table 4. Mahalanobis and Procrustes distances of species groups.

	BT	CF	CH	CL	EC	HS	LL	MM	OA	PT	SS
CF	50.6288*										
CH	55.8557*	21.3855*									
CL	55.8309*	11.6705*	19.1875*								
EC	23.5511*	36.5455*	40.5178*	40.3564*							
HS	70.7319*	28.9491*	26.7874*	27.2148*	56.4846*						
LL	48.3331*	19.3607*	28.5386*	20.8128*	36.1587*	35.8055*					
MM	40.8136*	20.0995*	32.0025*	24.1447*	28.6898*	41.8128*	18.6617*				
OA	45.6308*	18.3464*	17.1838*	17.8676*	30.4643*	37.2580*	24.4761*	24.2400*			
PT	75.7276	39.0109*	36.1933*	35.8906	62.2244*	27.2836	41.5521	48.5902	41.5703		
SS	66.7977*	23.8227*	28.5055*	21.3730*	52.9211*	20.1872*	32.0054*	35.5335*	30.4997*	27.8995*	
VV	49.5238*	15.4525*	24.3940*	15.4376*	35.0630*	32.1386*	20.6176*	18.8655*	20.0121*	38.2241*	23.6255*

*Significant p-values. BT: Bos taurus, CF: Canis familiaris, CH: Capra hircus, CL: Canis lupus, EC: Equus caballus, HS: Homo sapiens, LL: Lynx lynx, MM: Meles meles, OA: Ovis aries, PT: Pan troglodytes, SS: Sus scrofa, VV: Vulpes vulpes

Table 5. Cross-validation scores for feeding group.

		C--H		**Total**	**Correct grouping (%)**
		C	**H**		
C--H	**C**	31	9	40	77.5
	H	12	34	46	73.9
		C--O		**Total**	**Correct grouping (%)**
		C	**O**		
C--O	**C**	37	3	40	92.5
	O	4	20	24	83.3
		H--O		**Total**	**Correct grouping (%)**
		H	**O**		
H--O	**H**	46	0	46	100
	O	0	24	24	100

*Significant p values. C: Carnivorous, O: Omnivorous, H: Herbivorous

of condylus occipitalis was elliptical in carnivorous and omnivorous, and like a boomerang in herbivorous. The dorsal part was wider in all feeding groups. In terms of species groups, the shape of condylus occipitalis in the wolf and dog was almost exactly the same. In the bovine, it was quite different from other herbivorous.

4. Discussion

Broca [25] reported that the condylus occipitalis and FM are in balance at the top of the vertebral column in bipeds since they are located in the middle of the skull base. In our study, an elliptical/nonfeatured condylus occipitalis shape was seen in humans and chimpanzees. Condylus occipitalis was elliptical in pigs and carnivorous, while its upper part was in the form of a wide triangle in herbivorous species. The shape of the condylus occipitalis, which was not expected to be strong for the bipedal species, supported Broca's hypothesis. However, the resemblance of the shape of pigs and carnivorous to bipedal species precluded the conclusion that "condylus occpitalis is elliptical in bipedal species". Therefore, it can be argued that this difference may be due to feeding or other factors. Topinard's statement that the FM and its circumference in quadrupeds require well-developed neck muscles and ligaments to carry the weight of the head [26] may explain the difference in the developed condylus occipitalis in large-bodied animals

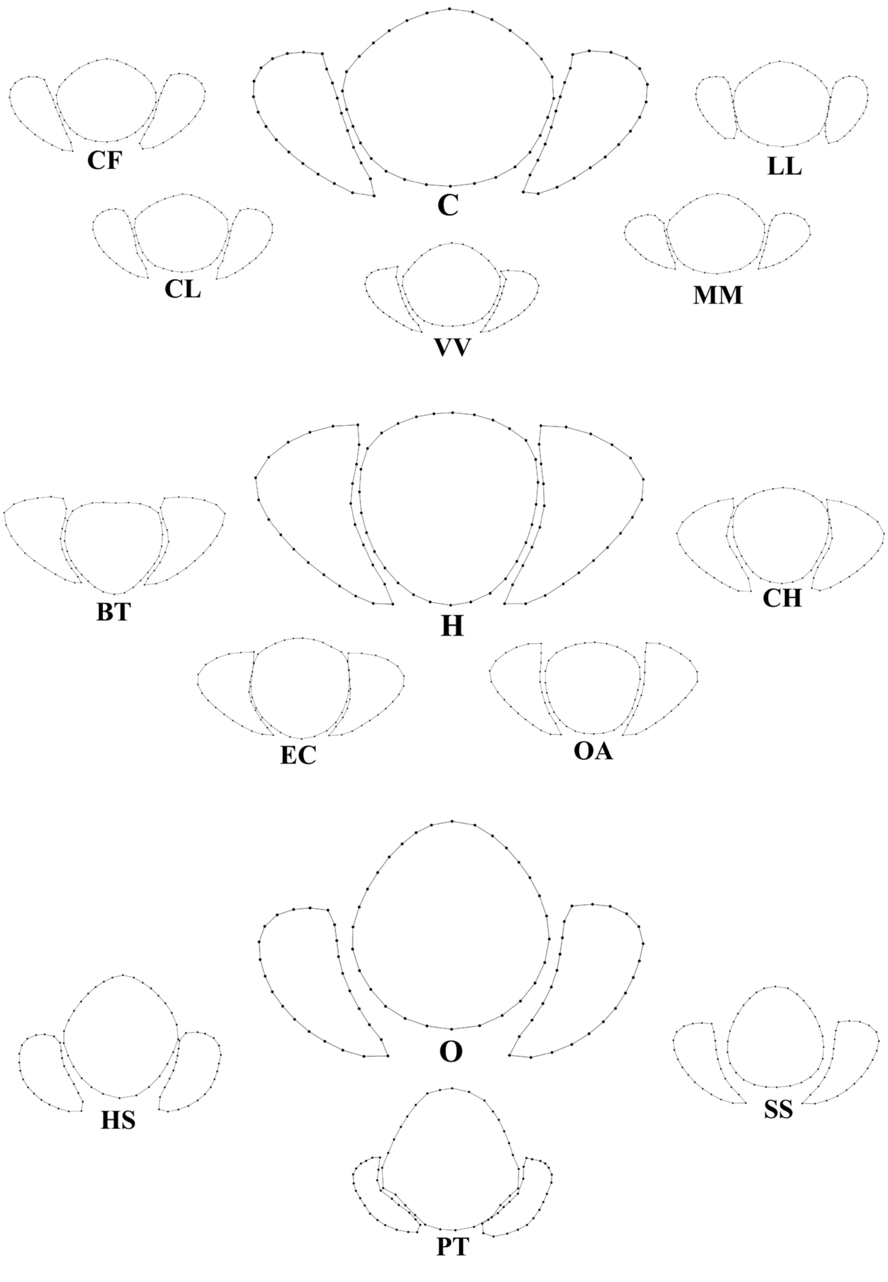

Figure 5. The average shape of the feeding and species groups, C: Carnivorous, H: Herbivorous, O: Omnivorous, BT: Bos taurus, CF: Canis familiaris, CH: Capra hircus, CL: Canis lupus, EC: Equus caballus, HS: Homo sapiens, LL: Lynx lynx, MM: Meles meles, OA: Ovis aries, PT: Pan troglodytes, SS: Sus scrofa, VV: Vulpes vulpes, 90% confidence ellipse.

(such as cattle and horses) compared to other species in our study. However, the resemblance of the shape of the sheep and goat condylus occipitalis to large herbivorous may indicate that head weight alone cannot be a factor that can cause the shape of the condylus occipitalis.

Orientation movements resulting from the resting position of the head-neck complex in the sagittal plane involve two functional regions in quadrupedal mammals. One of them is the atlantooccipital joint and the other is the cervicothoracic vertebral joint. Range of motion in the atlantooccipital joint is significantly limited in monkeys and adult humans compared to quadrupeds. Therefore, head-neck movements in the sagittal plane in monkeys and humans are largely limited to the cervicothoracic junction [27]. This information appears to be consistent with our study results because we detected a smaller condylus occipitalis than the FM in two of the omnivorous species (human, chimpanzee). Strong neck muscles and short cervical vertebrae can explain the situation in the pig. We detected a strongly growing condylus occipitalis with the FM in carnivorous and herbivorous, although its shape differs according to the species. This may be due to the heavy head in herbivorous and the need for biting power in carnivorous.

Biomechanics deals with the systematic reasons for the relationship between structure and movement in animals. Biomechanical properties are also expected to be affected when environmental changes occur [17]. To increase bite force, which is a biomechanical system, species can differentiate to increase the size of the holding points of the jaw adductor muscle. These differentiations may be increases in zygomatic-mastoid width, sagittal crest height, and surface area of the cranial cavity [28]. In addition, mechanical requests caused by differences in food properties are expected to occur with functional changes (anatomical) in the feeding system. In the studies on ungulate [29], primate [30], bear [31], frogs [32], and bats [33] significant correlations were found between nutritional type (diet) and cranial morphology. Van Cakenberghe et al. [33] found a highly significant relationship between morphometric variables and diet groups using phylogenetic simulation analysis. Perez-Barberia and Gordon [29] emphasized that species that eat 'harder' food in ungulates have higher processus coronoideus. All these studies support Biegert's [34,35] hypothesis that "development of the brain (especially the neocortex) and mastication apparatus affects the morphology of the skull base (hence the cranium)". The data show that feeding and its biomechanics have the potential to influence cranial morphology. In this study, we reached results that support this information. Condylus occipitalis was more anterior than the FM in omnivorous. The FM was partially surrounded by condylus occipitalis in carnivorous and completely in herbivorous.

The shape of FM in humans has been described in the literature with many definitions such as asymmetrical, biconvex, two-sided oval, two-round oval, circular, pentagonal, and symmetrical [36]. No description has been found in animals as in humans or otherwise. In our study, the average shape of the FM was determined for each feeding group and type. In terms of average shape, the FM (the posterior end is more pointed) was like an "egg" in omnivorous species. In humans, both ends of the average shape of the FM were oval (see the result).

Faunal-type identification is important for forensic definitions [37]. Defining the differences in morphological structure among species will enable forensic anthropologists to distinguish the human skeleton from other animal species [38]. In this study, it is thought that the shape differences determined will provide information about species identification in forensic definitions.

As a result, in this study, the general shape of the FM and condylus occipitalis was investigated for the first time according to feeding groups and species. The general shape of these two structures seemed likely to be affected by the nutritional factor. It is thought that results will be among the most revealing evidence of this situation. In addition, researchers are suggested to repeat this study with more species.

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