doi:10.20944/preprints202206.0044.v1

Bony orbital form in two groups of Catarrhini primates: how asymmetrical are they?

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Abstract

The aim of this study was to compare left and right osseous orbit forms in two different Catarrhini primate genera using geometric morphometric techniques. The analysis was carried out on 20 well-preserved skulls from gorilla (*Gorilla gorilla*, n=10) and papios (drill [*Mandrillus leucophaeus*, n=3] and mandrill [*M. sphinx*, n=7]) from animals kept in zoo, which were photographed in their frontal norm. A set of 4 sagittal landmarks on the face and 23 semilandmarks on each orbita contour were used. According to results, right and left orbitas were similar in size but not in shape, appearing to be significative for individual-by-side interaction (fluctuating asymmetry). It is supposed this due to a developmental instability due to captivity life. Fluctuating asymmetry was clearly higher among gorillas, seeming logical that hominoidea primates suffering in captivity is higher than among cercopithecids (papios and mandrills). Side directional differences were significative only for papios. We supposed it to be due to a stronger stroke of lateralized mastication as, compared to gorillas, mandibles in papios are longer.

Key words: drill, gorilla, mandrill, nonhuman primates, papio, stress

Introduction

Bilateral asymmetry is defined as a deviation of a whole organism or a part of it in a trait (or character) that is expected to be perfectly symmetrical (Auffray et al., 1999). Two forms of expressions of bilateral asymmetry are commonly described: one is the fluctuating asymmetry (FA), defined as the subtle random developmental variation of a trait on average (Kwiatkowska et al., 2015). The other one is directional asymmetry (DA), which occurs when one of the side shows skewed deviation compared to the other (Carter et al., 2009).

Geometric morphometrics methods (GMM) are based on landmark coordinate data. GMM improve morphometric studies as they have the ability to measure displacements, deformations and rotations (Zelditch et al., 2004), thus enabling more complete evaluations of shape than traditional linear and angle measurements do (Adams et al., 2013). In recent years, there have been a huge number of zoological studies applied to the study of symmetries carried out with the applications of GMM (Mardia et al., 2000) (Klingenberg, 2016).

The osseous orbit in primates is a cone-shaped cavum, formed mainly by the frontal, zygomatic, and maxillary facial bones (Xing et al., 2013). Its function is to protect and accommodate the eye, as well as some relevant muscles and nerves (Barone, 1999). Although both orbitas could seem macroscopically identical, in this research we studied:

1) If orbital (a)symmetries appear among two distantly related primate genera: gorilla (*Gorilla gorilla*) and papio (drill [*Mandrillus leucophaeus*] and mandrill [*M. sphinx*]).
2) The levels of fluctuating asymmetry for both groups.
3) The levels of directional asymmetry for both groups.

Materials and methods

Sample

A sample of adult skulls in good preservation state belonging to gorilla (*Gorilla gorilla* superfamily Hominoidea, n=10) and papios (drill, *Mandrillus leucophaeus* n=3, and mandrill, *M. sphinx*, n=7, superfamily Cercopithecidea) was studied. Bones had no evidence of trauma, malformations, or other pathologies. Specimens were from the collection of the *Museu de Zoologia de Barcelona* (Catalonia, Spain) and belonged to captive animals held in the Zoo of Barcelona (Catalonia). Sex and age were not considered.

Geometric morphometrics

Skulls were fixed in a standard plane so osseous orbitas were observed in coplanarity on the anterior aspect of the face. Pictures were then obtained using a digital camera Canon EOS 1100D DSLR with a Lent Canon EFS 18-55. A scale was included and placed parallel to the face plane. Ulteriorly, the software TpsUtil v. 1.50 (Rohlf, 2015a) was used to prepare and organize the files, which were digitized twice using TpsDig v. 2.16 (Rohlf, 2015a). A set of 4 landmarks along the sagittal skull plane and 23 semi-landmarks for each orbita was located in each picture. Semi-landmarks are points on smooth curves, for which the exact location on the curve cannot be identified (Figure 1). Digitalization was done in two separated sessions. Semi-landmarks were ulteriorly transformed to landmarks with the program TpsUtility v. 1.70 (Rohlf, 2015a). All coordinates were then aligned using a Procrustes superimposition, thus eliminating non-shape information (Adams et al., 2013). Size (expressed as Centroid Size CS) was estimated as “the square root of the sum of squared distances from the centroid of a landmark configuration” (Adams et al., 2013).

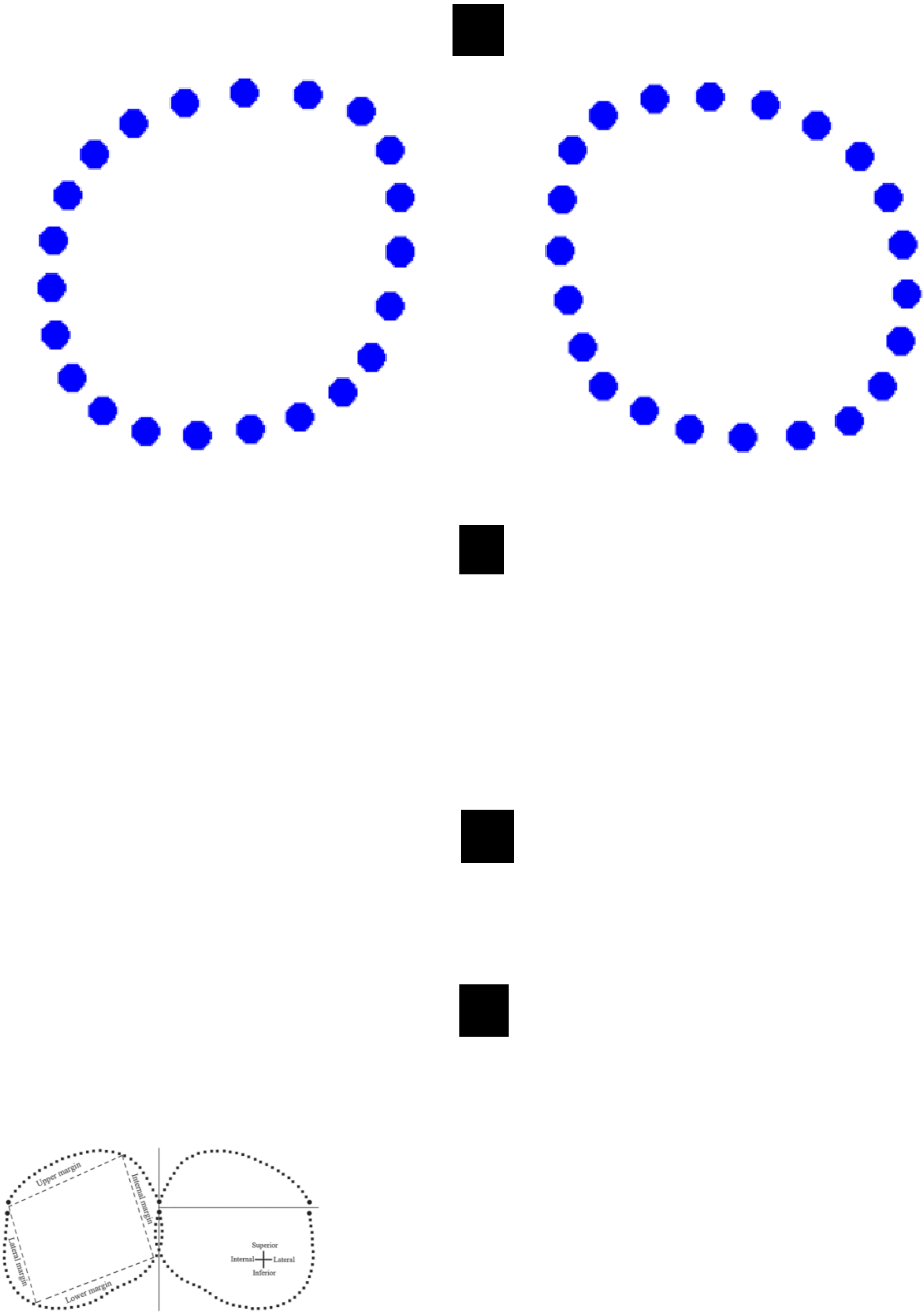

Figure 1. The definition of landmarks, semi-landmarks. The squares and circles indicate the landmarks and semi-landmarks, respectively, the former on the saggital plane. For ease of interpretation, the orbit rim is presented here divided into four margins.

It has been pointed that some problems may derive from working on 2D projections of 3D objects, such as the possible distortion of the original size and shape of the structures To assess this change, a correlation between the tangent distances and the Procrustes distances spaces was computed using the TpsSmall v. 1.33 application (Rohlf, 2015b). The result of this correlation (0.999966) confirmed that both spaces were almost identical, so we proceed with ulterior analysis.

To detect the asymmetries, a Procrustes ANOVA was used, which allowed separation of the symmetric and asymmetric components of total shape variation. In this analysis, the *individuals* effect denoted the individual variations of shape and size of each animal; the *individuals mean square* being a measure of total phenotypic variation and it is random; the main effect of *side* indicated the variation between side and considered as the measure of DA, whereas the *individuals x side* was the mixed effect, this indicating FA in the data (Klingenberg & McIntyre, 1998); *measurement error* represented the variation due to measurement error in taking landmarks (Klingenberg & McIntyre, 1998), allowing to test if individual variation was significantly larger than error.

Data was analysed in MorphoJ v. 1.6.0c (Klingenberg, 2011) and PAST v. 2.17c (Hammer et al., 2001) softwares. The statistical significance level was set at 95%. For ease of interpretation, the orbit rim was divided into four margins, according to Xing *et al*. (Xing et al., 2013).

Ethics Statement

This study was carried out on skulls from an existing osteological public collection, so no Ethics committee agreement was considered necessary.

Results

Measurement error

Shape error was not a serious concern in this analysis as in ANOVA test, as the mean square value for the error was much less (1.6%) than the rest of factors (Table 1).

Asymmetries

The Procrustes ANOVA for size showed non-significant *p*-values for both genera, but shape analysis showed that FA (the *individuals x side* effect) was significant statistically for both genera, whereas DA (the *side* effect) was only detected among papios (Table 1). DA was expressed towards left. Significant FA made up 14.3 % of total variation among gorillas, while for papios it was 8.8%.

Table 1. ANOVA results for size and shape of orbitas for *Gorilla gorilla* and *Mandrillus* sp. The model allows simultaneous evaluation of the effect of Side (Directional Asymmetry) and the Individual*Side interaction (Fluctuating Asymmetry). SS: sum of squares; MS: mean square; df: degrees of freedom; F: value of the statistics F; SS and MS are expressed in units of distances Procrustes (i.e., dimensionless). The mean square value for the shape individual*side interaction was much larger as the variation between replicates for both size and shape.

A/ *Gorilla gorilla* (n=10)

Size

Effect	SS	MS	df	F	P
Individual	2135.711	237.3012	9	21.33	<.0001
Side	11.20694	11.20694	1	1.01	0.3418
Individual*Side	100.1291	11.12546	9	0.57	0.8051
Error	389.8547	19.49274	20		

Shape

Effect	SS	MS	df	F	P
Individual	0.199245	0.000527	378	4.08	<.0001
Side	0.006513	0.000155	42	1.20	0.1920
Individual*Side	0.048863	0.000129	378	1.37	0.0001
Error	0.079152	9.42E-05	840		

B/ *Mandrillus* sp. (*Mandrillus leucophaeus* n=3 and mandrill. *M. sphinx* n=7)

Size

Effect	SS	MS	df	F	P
Individual	5209.091	578.7879	9	69.47	<.0001
Side	7.634839	7.634839	1	0.92	0.3634
Individual*Side	74.98008	8.331120	9	0.04	1
Error	3718.368	185.9184	20		

Shape

Effect	SS	MS	df	F	P
Individual	0.192591	0.000510	378	4.68	<.0001
Side	0.022754	0.000542	42	4.98	<.0001
Individual*Side	0.041154	0.000109	378	1.38	<.0001
Error	0.066201	7.88E-05	840	840	

Discussion

Both orbitas presented similar sizes, which can be assumed as similar areas, the intra-individual size difference in the orbits ranging from 1% to 4%. So similar eye size must be assumed as the normal anatomic pattern among these primates.

The Procrustes ANOVA for shape showed significant *p*-values for individual-by-side interaction (fluctuating asymmetry, FA) for both genera. FA is often used to estimate the degree of developmental stability, e.g. ability of a population to buffer against developmental noise (Auffray et al., 1999). Its significative presence in our sample may be due to a developmental instability due to captivity of animals. Moreover, as FA is a negative indicator of stress (Auffray et al., 1999), and it appears higher among gorillas, it could be hypothezied this be a consequence to hominoidea primates being much prone to suffer more stress in captivity than cercopithecids.

For directional asymmetry (DA), it seems not to be expressed at orbital level among gorillas, but indeed among papios. As mastication exhibits frequently clear evidence of functional lateralization in mammals (Parés-Casanova & Bravi, 2014) (Ginot et al., 2018) (Parés-Casanova & Cabello, 2020), including primates (Mizumori et al., 2003) (Vinyard et al., 2008) we suppose this significative DA being related to a lateralized masticatory function among papios.

In effect, papios have large mandibles. Masticatory mandible apparatus demands muscular attachments linked to the stroke of mastication. As papios have a longer mandible, it might be predicted that to increase relative maximum gape they have stronger masticatory muscles (superficial masseter and temporal muscles) than gorillas. Larger muscular fibre length (due to longer face and consequently to force-generating capacity) would determine bigger relative size of the muscular attachment areas on bones and thus osseous changes. The superficial masseter arises from the lower border of the zygomatic arch as strong tendinous fibres (Barone, 2000). Some muscle fibres and tendons of the temporal muscle arise from the postorbital septum, which is the bony partition separating the temporal fossa from the orbit so, if these strong muscles are asymmetrically developed due to a masticatory lateralization, their area of their insertion can reflect sided differences. The masseter muscle stretches as a rectangular plate from the zygomatic arch (Barone, 2000).

Acknowledgements

The author thanks Javier Quesada for allowing us access to the mastozoological collection of the *Museu de Zoologia* in Barcelona (Catalonia).

Conflicts of interest

The author declares do not have any conflicts of interest with the results presented in this investigation.

Supplementary material

The contents of all supporting data are the sole responsibility of the author. The datasets generated and analysed during the current study are available from the corresponding author upon reasonable request.

Funding statement

The author received no funding for this work.

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