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# Allometric analysis of the skull in *Pan* and *Gorilla* by geometric morphometrics

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**Summary –** *Classical metric analyses have shown that much of the morphological variation between* Pan *and* Gorilla *is due to size-related shape differences. Geometric morphometrics, which operates a removal of size (as a consequence of GLS superimposition of landmark points), can shed further light on the issue. With these methods and with particular reference to facial and basal regions of the cranium, we examine here a sample including skulls at different ontogenetic stages of* Gorilla gorilla *and* Pan troglodytes. *Landmark co-ordinates were acquired in two dimensions from lateral view. Multivariate analysis of transformed data shows that the first principal component (representing 61.2% of total variance) does not separate the two genera, while sets the whole sample in an ontogenetic scaling perspective which involves mostly muzzle growth and airorhynchy The second principal component (16.8% of total variance) is related to an increasing midface flattening along the two ontogenetic series, with* Gorilla *trajectory displaced toward a larger level of midface projection. The cranial shape variation observed along the first principal component corresponds to the pattern observed when the shape vector is regressed on centroid size, where shape results clearly size-related (r = 0.92).*

**Keywords** – *Allometry, Thin-plate-spline, Ontogenetic scaling, African apes.*

## Introduction

Most part of the inter- and intraspecific morphological diversity among the African apes (Panidae: *Pan* and *Gorilla*) has been explained with the different regulation of a common pattern of growth and development, i.e. as the heterochronic result of evolutionary shifts in the onset, rate, or timing of the same ontogenetic "program" (Leigh & Shea, 1996; Shea, 1983a, 1983b).

The variation (i.e., extension or truncation) of a given ontogenetic trajectory produces shape differences which are size-related. Thus, "allometry" – defined as "size related changes in shape" (Cheverud et al., 1983) or, simply, as the "study of size and its consequences" (Gould, 1966) – plays a major role in this process. The diversity between taxa or individuals may be produced by a simple regulation of the same ontogenetic pattern; the allometric result, in this case, is called *ontogenetic scaling*.

The morphology of the facial and palatal components of the cranium of the African apes appears particularly affected by ontogenetic scaling, and this was clearly pointed out by analyses based on multivariate traditional morphometrics (e.g., Shea, 1983b). The recent development of geometric morphometrics allows to integrate the quantitative analysis

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of shape variation with its qualitative component (Bookstein, 1989, 1991; Marcus et al., 1993, 1996; Rohlf & Marcus, 1993). During the last decade, these techniques began to be applied in primatology, with the aim of both re-evaluating traditional approaches and developing new perspectives (e.g., Lynch & al., 1996; O'Higgins and Dryden, 1993; O'Higgins & Jones, 1998). In this paper, we examine the relative dislocation of landmarks localised in the face and the base of crania of *Pan troglodytes* and *Gorilla gorilla*, using geometric morphometric techniques based on the interpolant function *thin-plate-spline*.

## Materials and methods

Specimens were sampled in Rome from collections of the Museum of Anthropology «G. Sergi», the Museum of Comparative Anatomy «G.B. Grassi» and the Civic Museum of Zoology. The total sample includes 10 crania of *Gorilla gorilla* and 13 crania of *Pan troglodytes*. Specimens were assigned to four age classes, depending upon the stage of molar eruption (from no molars at the masticatory plane, class 1, to the full eruption of the upper third, class 4), and sexed by museum records, when possible, or by the level of sexual dimorphism in the adults.

Twenty landmarks were co-ordinated in two dimensions with the crania viewed in *norma lateralis*; they are localized mainly in the facial and basicranial regions: 1) prosthion; 2) anterior alveolar border of the upper canine; 3) sagittal inflection premaxilla-maxilla; 4) inferior zygo-maxillar; 5) superior zygo-maxillar; 6) inferior maxillo-nasal; 7) rhinion; 8) anterior fronto-malar; 9) nasion; 10) glabella; 11) maximum depth of the supratoral sulcus; 12) pterion; 13) porion; 14) posterior alveolar border of the upper second premolar; 15) postero-inferior corner of the maxilla (maxilla-pterygoid); 16) opisthion; 17) entoglenoid process (lower point); 18) postglenoid process (lower point); 19) articular eminence (lower point); 20) mastoid apex. The relative position of landmarks was captured using a dioptographer (camera lucida system). Landmarks were then acquired as numerical coordinates by graphic tablets and DS-DIGIT (ver.1.1; Slice, 1989).

Data were analysed by geometric morphometric softwares developed by F. J. Rohlf, based on the *thin-plate-spline* (TPS) interpolant function (Bookstein, 1991). Using this procedure, all the configurations of landmarks (each representing a single specimen) are rotated, translated and scaled to minimize the interindividual distances of homologous landmarks by a generalized least square superimposition method (GLS), and a *consensus* reference form is calculated as the average configuration of landmarks. This passage isolates the shape component from the total "form", eliminating size differences. However, landmarks configurations are scaled in a non-allometric way, and therefore size-related information is expected to remain inside the "residual" shape.

More in detail, the total sample was previously examined with tpsSmall (ver.1.17), to test if the geometrical heterogeneity of the sample is small enough to allow the study. Then, tpsSpline (ver.1.15) and tpsRelw (ver.1.18) have been respectively used for paired comparisons and multivariate statistics on the entire sample. In the multivariate "relative warp" analysis, the parameter a was settled equal to 1 (Bookstein, 1989) in order to give importance to large scale variations, as recommended for allometric analyses (Rohlf, 1993). In addition, TPS-based geometric morphometrics distinguish an affine (or "uniform") component – homogeneously involving the whole configuration of landmarks (e.g., the stretching along a certain axis) – from a non-affine component, which is instead more localised and non-homogeneous. Here, only the non-affine component is reported and discussed, but it has to be pointed out that consistent results were also obtained for $\alpha=0$ and the affine component included. TpsRegr (ver.1.18) and tpsPLS (ver.1.05) were used for the regression of shape on size. *Centroid size* values, calculated for each specimen as the square root of the sum of squared distances of the landmarks from their centroid (Marcus et al., 1996), were used as size index. In all these analytical steps, it was always possible to extrapolate the geometric continuous distortion of the system of landmarks along the axes, and visualise it by deformation of reference grids or by vectorial resolution.

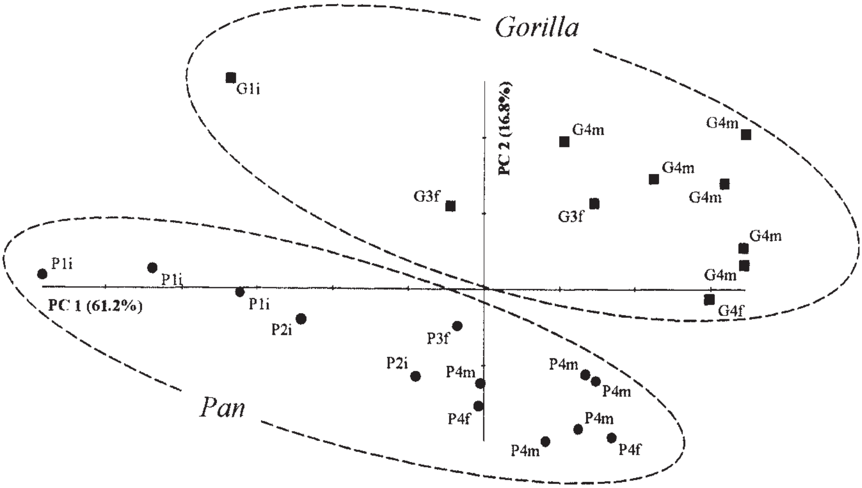


**Figure 1 - Plotting along the first two principal components (or Relative Warps 1 and 2) of samples of African apes at different ontogenetic stages. Specimens have been labelled for species (P = *Pan*; G = *Gorilla*), age class (0-4; see text) and sex (m = male; f = female; i = indeterminate).**

## Results

Figure 1 shows the distribution of the sample along the first two principal components, or Relative Warps (78.0% of the total variation). The first principal component (61.2% of the total variance) does not separate the two *genera*, but distributes specimens in an ontogenetic/size-related series that increases from left (younger/smaller) to right (older/larger). The two ontogenetic patterns result almost totally overlapped and with a comparable range, slightly displaced by a size factor which displaces the *Gorilla* trajectory on the right. Vectorial resolution along this axis (Fig 2a) shows that this principal component is related to the following morphological changes: 1) enlargement of the maxillar (alveolar) area and airorynchy (muzzle protrusion and elevation); 2) shortening and vertical stretching of the cranial base; 3) relative decrease of upper and middle face; 4) development of the supraorbital torus. Distorsion grid at the lower value of the same principal component (Fig 2b) shows the "opposite" condition (infantile/small-sized individuals) and emphasizes two principal planes of growth: 1) a longitudinal one, opisthion-zygomaxillar inferior, that produces a vertical stretching in the adult/large-sized individuals, and (2) a diagonal one which apparently divides the rostrum from the rest of the cranium (zygomaxillar inferior-rhinion).

The second principal components (16.8% of the total variance), operates a further ontogenetic separation at the intraspecific level; at the same time, it displaces the *Gorilla* ontogenetic trajectory at higher values with respect to the *Pan* series. The vectorial resolution along this axis (Fig 2c) involves most of the facial transformations, mainly related (and probably consequent) to prorhinism, or protrusion of the landmark points of the midface (commonly viewed as a transverse section between the orbits and the alveolar arcade). Looking at the plot in Figure 1, it is also apparent that for this 2$^{nd}$ pricipal component the *Gorilla* sub-sample presents a larger intraspecific variability in the adult age class.

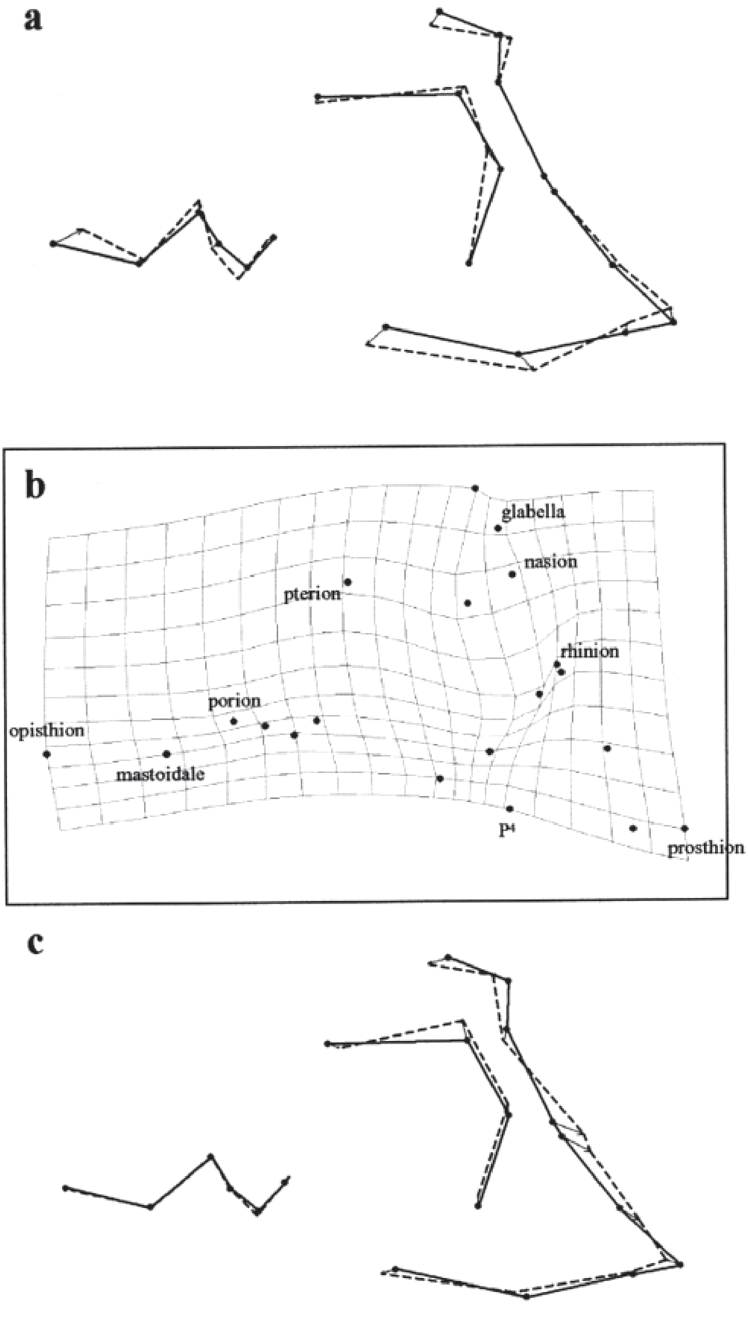


**Fig. 2 - a) Vectorial resolution of the shape deformation along the 1st PC axis of Figure 1, from the consensus to the maximum positive value; b) same transformation, but at the minimum negative value, showed by deformation of reference grid with reference landmarks labelled; c) vectorial resolution along the 2st PC axis of Figure 1, from consensus to maximum positive.**

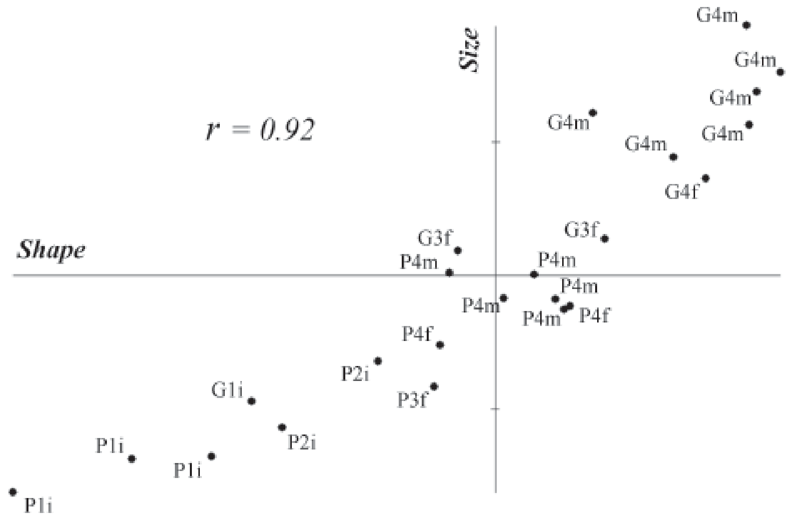


**Fig. 3 - Regression of the shape vector scores (least square regression on partial warp scores) on size (centroid size values); see Fig.1 for labels.**

Vectorial resolution along the size axis computed by regression of centroid size values against each single shape component (partial warps, see Bookstein, 1991; Rohlf 1993) shows the same geometrical pattern previously described for the first principal component (Fig. 2a-b). A correlation analysis (Fig. 3) between the "shape vector" (least square regression of all shape components) and centroid size shows a r value equal to 0.92 ($p = 0.01$). Including small scale variations and the affine component it rises to 0.97. Eventually also including the affine components of the variation, the Uni-x value shows the higher correlation coefficient ($r = -0.91$) of all the single shape parameters (Partial Warps). It is represented by a sella-alveolar stretching of the whole cranium, related to muzzle growth.

## Discussion

In this analysis the allometric patterns and ontogenetic scaling of *Panidae*, previously characterized by traditional morphometrics (Leigh & Shea 1996; Shea 1983a, 1983b) have been approached with geometric morphometric techniques based on thin-plate-spline after GLS superimposition.

The main shape differences among and between *Pan* and *Gorilla* rostral crania (1$^{st}$ principal component, 61.2% of the total variance) result to be strongly size related ($r = 0.92$), with both taxa clearly lying on a common allometric trajectory which displace *Gorilla* ontogenetic series slightly at higher values by their larger size. This allometric pattern involves relative shortening of cranial base, muzzle growth and airorhynchy, formation of *torus supraorbitalis* and relative decrease of upper and middle face, as described for many taxa of primates (Corner & Reichtsmeier, 1991; Leigh & Cheverud, 1991; May & Sheffer, 1999; O'Higgins & Dryden, 1993; O'Higgins & Jones, 1998).

This component cannot be considered a typical "size axis", being size removed by GLS superimposition, but a "size-related shape axis", which shows directly allometric shape variability. The pattern observed represents the result of heterochronic processes which lead to a hypermorphotic development of *Gorilla* with respect to the *Pan* morphotype (sensu Shea, 1983a), increasing size, and consequently adjusting spatial shape relationships. In addition, even the second component (16.8% of the total variance) could be size related, but at the intraspecific level: both *Pan* and *Gorilla* shows a decrease in midface downward protrusion (prorhinism), thus midface flattening, with consequent changes in all the areas involved, but the *Gorilla* ontogenetic series is displaced at "younger values" compared to the *Pan* developmental trajectory. More analyses are needed to explained this second source of variability but, if the two trajectories are comparable, then we must assume a possible secondary heterochronic pattern acting in the midface of the hypermorphotic taxon (*Gorilla gorilla*).

Heterochrony and allometry are complex amd multifactorial processes which rarely can be approached by a linear and reductive analyses (Cheverud et al., 1983; Leigh & Shea, 1996; Klingenberg, 1998; Richtsmeier, 1989; Shea 1983a; Shea, 1992). Anyway, geometric morphometrics seems to offer a useful tool to better understand how these processes work and characterize the morphological spatial relationship in an evolutionary context. However, size and shape are components of a system which includes ecological, ethological, physiological, and anatomical operators, as well as non-biological ones. Often we can only confirm relation, not causality, in such a complex network.

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## ABSTRACT

**Analisi dei pattern allometrici nel cranio in *Pan* e *Gorilla* in base a tecniche di morfometria geometrica**

**Riassunto –** Molte delle differenze morfologiche tra i generi *Pan* e *Gorilla* sono il risultato di variazioni allometriche di un comune pattern ontogenetico. La morfometria geometrica, operando tramite una superimposizione di coordinate che elimina le differenze di taglia nel campione e un'analisi multivariata delle componenti della forma residua, viene utilizzata per quantificare e qualificare la componente allometrica nel cranio delle due specie. Sono state acquisite le coordinate in due dimensioni di landmarks localizzati nello splancno- e nel basicranio, in campioni di individui delle due specie a differenti stadi ontogenetici. L'analisi multivariata della forma rivela una prima componente principale (61.2% della varianza totale) che non separa i due taxa ma li ripartisce indistintamente in funzione della taglia, risultando fortemente correlata alla centroid size (r =0.92) e riguardando soprattutto crescita del rostro e airorinchia. Il pattern di trasformazione geometrica lungo l'asse della taglia è inoltre identico a quello descritto per la prima componente principale. Una seconda componente principale (16.8% della varianza totale) induce in entrambe le traiettorie ontogenetiche una compressione dei landmark medio-facciali, separando però la serie di *Gorilla* verso livelli più pronunciati di protrusione.

**Parole chiave –** Allometria, Thin-plate-spline, Scaling ontogenetico, Antropomorfe africane.

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