Ontogenetic Allometry, Heterochrony, and Interspecific Differences in the Skull of African Apes, Using Tridimensional Procrustes Analysis

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ABSTRACT   Ontogenetic studies of African ape skulls lead to an analysis of morphological differences in terms of allometry, heterochrony, and sexual dimorphism. The use of geometric morphometrics allows us 1) to define size and shape variations as independent factors (an essential but seldom respected condition for heterochrony), and 2) to calculate in percentage of shape changes and to graphically represent the parts of shape variation which are related to various biological phenomena: common allometry, intraspecific allometry, and allometric and nonallometric shape discrimination. Three tridimensional Procrustes analyses and the calculation of multivariate allometries, discriminant functions, and statistical tests are used to compare the skulls of 50 *Pan troglodytes*, and 50 *Gorilla gorilla* of different dental stages. The results both complement and modify classical results obtained from similar material but with different methods (Shea [1983] Am. J. Phys. Anthropol. *62*:275–289; Shea [1983] Folia Primatol. (Basel) *40*:32–68; Shea [1985] Size and Scaling in Primate Morphology, New York: Plenum, p. 175–205). As previously described by Shea, the common growth allometric pattern is very important (64% of total shape variation). It corresponds to a larger increase of facial volume than of neurocranial volume, a more obliquely oriented foramen magnum, and a noticeable reshaping of the nuchal region (higher inion). However, the heterochronic interpretation based on common allometry is rather different from Shea. Gorillas differ from chimpanzees not only with a larger magnitude of allometric change (rate peramorphosis), as is classically said, but also grow more in size than in shape (size acceleration). In other words, for a similar stage of growth, gorillas have the size and shape corresponding to older chimpanzees, and for a similar shape, gorillas have a larger size than chimpanzees. In contrast, sexual dimorphism actually corresponds to allometric changes only, as classically demonstrated (time hypermorphosis). Sexual dimorphism is here significant in adult gorillas alone, and solely in terms of allometry (size-related shape and size, given that sagittal and nuchal crests are not taken into account). The study also permits us to differentiate two different shape variations that are classically confused in ontogenetic studies: a very small part of allometric shape change which is specific to each species (1% of the total shape variation), and nonallometric species-specific traits independent of growth (8% of total shape change). When calculated in terms of intraspecific allometries (including common allometry and noncommon allometry), shape changes are more extensive in gorillas (36% of total shape change) than in chimpanzees (29% of total shape change). The allometric differences mainly concern the inion, which becomes higher; the position of the foramen magnum, more dorsally oriented; and the palate, more tilted in adult gorillas than in adult chimpanzees. In contrast, nonallometric species-specific traits in gorillas are the long and flat vault characterized by a prominent occipital region, the higher and displaced backward glabella, and the protrusive nose. Biomechanical schemes built from shape partition suggest that the increased out-of-plumb position of the head during growth is partially compensated in gorillas by a powerful nuchal musculature due to the peculiar shape of the occipital region. Am J Phys Anthropol 124:124–138, 2004.   © 2004 Wiley-Liss, Inc.

Geometric morphometric methods aim to calculate, to statistically test, and to visualize complex morphological shape changes. Recent studies largely demonstrated that skulls are particularly suitable for studying ontogenetic shape changes using geometric morphometrics (e.g., O'Higgins et al., 1990; Penin, 1997, 1999; Penin and Baylac 1999; O'Higgins, 2000; Penin and Berge, 2001; Ponce de León and Zollikofer, 2001; Hennessy and Stringer, 2002; Penin et al., 2002). This study has several objectives: 1) to identify global shape changes in skulls during ontogeny; 2) to distinguish in two closely related species, common chimpanzees and gorillas, various biological phenomena, such as the common allometry, and interspecific differences which may or may not be related to growth (allometric and nonallometric traits). Such a partition of shape changes allows us to propose 3) heterochronic hypotheses, and 4) a functional interpretation in terms of head equilibrium. The results are compared

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with the classical growth studies and heterochronic hypotheses of Shea (1983a, b, 1985a).

BACKGROUND TO ONTOGENETIC COMPARISON

Growth changes in the cranium and face have been approached from several viewpoints. The first studies which made reference to the growth of African apes used fetal and perinatal data to illustrate the "neotenic theory" proposed by Bolk (1926) and contemporaries. The framework of this theory is clearly expressed by Schultz (1927), who considered monkeys and great apes as primitive stages of a single evolutionary trend leading to modern humans. Years later, Schultz (1949) compared midsagittal sections of juvenile and adult skulls in various primates, including great apes and humans. Schultz (1949, p. 212) concluded that the sections illustrate "the well-known postnatal differentiation between man and most other primates in regard to the degree of oral projection of the face in relation to the brain cases." He noted that great apes have a specially marked ontogenetic change, but he did not indicate within-group differences. Thus the morphology of great apes was not described per se, but as a reference for human studies. The technique of sagittal superimposition had been settled by Krogman (1931a, b) to investigate shape changes in the cranial growth of African apes. Later a similar technique was used by Delattre and Fénart (1956) with a different referential horizontal plane (the lateral semicircular canal; see de Beer, 1947). Although these studies were based on extensive material, they used a small number of selected skulls, or average representatives of dental age groups, representing ontogenetic shape changes within species by means of sagittal superimposition. The quantitative amount of shape changes was calculated in percentages of adult dimensions (Krogman, 1931a, b; see also Randall, 1943), or estimated using movements of landmarks and angular values (Delattre and Fénart, 1956). However, for our purpose, these studies did not allow ontogenetic comparisons between species or precise calculation within species. Heintz (1964, 1966) and Petit-Maire (1972) used cranial dimensions to compare ontogenetic trajectories in a large range of species, including African apes. Heintz (1964, 1966) or Petit-Maire (1972; Heintz and Petit-Maire are same author) demonstrated that apes and modern humans share a common growth pattern in terms of shape changes, differing in terms of magnitude and velocity only. Her study aimed at focusing on ontogenetic similarity within African apes so as to demonstrate human neoteny, and not at discussing species-specific differences.

Statistical studies of growth skull in African apes were later renewed with the notion of heterochrony enlarged to nonhuman species. Sexual dimorphism in size is a good example of the two ways to apprehend the two evolutionary approaches defined and discussed in Alberch et al. (1979) and McKinney and McNamara (1991). In the externalist approach, sexual dimorphism in body size may be viewed as the consequence of selective processes, such as male competition, which lead to increased male body sizes, and to peculiar male traits such as long canines (Leutenegger and Cheverud, 1985; Masterson and Leutenegger, 1992; O'Higgins and Dryden, 1993). In the internalist approach, sexual dimorphism in body size is interpreted in terms of heterochrony as the consequence of differences in growth rhythm and growth duration, males having generally a longer period of growth than females and consequently a larger size (Shea, 1983a, 1985b, 1986; Dean and Wood, 1984; Leigh, 1992). The two approaches are complementary, since selective processes act directly in animals, and indirectly in genotypes that also include genetic aspects of the growth pattern.

One of the main questions arising in ontogenetic studies of African apes by Shea (1981, 1983a–d, 1984, 1985a, b, 1986, 1992) is whether interspecific allometric differences may also be explained by heterochronic processes, as is the case for the intraspecific differences of sexual dimorphism. With the use of classical bivariate and multivariate methods, Shea (1983a, b, d, 1984, 1985a) demonstrated that chimpanzees and gorillas exhibit a common general pattern of cranial growth, with some minor but significant differences. Allometric studies revealed that the body of African apes (skull and postcranium) grows according to a relatively similar bauplan for all the African apes (Shea, 1981, 1985a; Berge, 1995a, b, Berge, 1998). However, as explained by Shea (1983b) for the skull, several departures from the general growth pattern reflect species-specific differences in the growth patterns of chimpanzees and gorillas. Shea (1983b) described allometric differences in the craniofacial complex, such as the proportion of the vault, the relative position of the nasal aperture, the shape of the nuchal region, and the buttressing of the facial region in gorillas just above the nasal aperture.

Shea (1983a, c, 1984, 1985a, 1986) integrated allometric data and growth in time to propose heterochronic hypotheses. The differential extension of the common pattern of cranial growth leads adult gorillas to have the cranial shape expected for chimpanzees enlarged to gorilla size. Thus, gorillas are in many ways "accelerated" chimpanzees. However, Shea (1983a) recalled that gorillas grow faster in body size and shape (and not longer in time) than chimpanzees. He created the term "rate hypermorphosis" to describe a heterochronic process which produces a peramorphic morphology from faster body growth, to be distinguished from "time hypermorphosis," which also produces a peramorphic morphology but from a longer period of growth (this last term being equivalent to "hypermorphosis" in Gould, 1977; Alberch et al., 1979). Thus, Shea (1983a) concluded that differences between species (adult chimpanzees and gorillas) are the result of

"rate hypermorphosis," whereas differences within species (sexual dimorphism) which are related to an increased period of growth in males are rather the result of "time hypermorphosis."

THE SHAPE THEORY AS A FRAMEWORK TO STUDY HETEROCHRONY

Heterochrony is classically defined as a change in developmental timing of an organ or a feature relative to the same structure in ancestors (De Beer, 1930; taken up by Gould, 1977, 2000; Alberch et al., 1979; Alba, 2002; McNamara, 2002). In other words, heterochronic studies refer to morphological features or "form" (form = size + shape) in descendants displaced in relative time in comparison to ancestors. Strictly speaking, heterochrony is the study of shape changes relative to size and developmental timing, and not the study of size changes alone (Klingenberg, 1996; Gould, 2000; Alba, 2002). Thus, we may focus on the problem of what is meant by size and shape. According to Gould (1977) and Alberch et al. (1979), the definition of different heterochronic categories necessitates the strict separation of size and shape as potentially independent vectors. Such a separation in the calculation of size and shape allows the distinction between two very different categories of heterochronies, depending on whether shape changes are related to size (allometries) or independent of size (size-shape dissociation) (Berge, 2002; Shea, 2002). Gould (1977, p. 246) explained that "the standard techniques of allometry do not provide an optimal metric for heterochrony because they subtly reinforce a prejudice directed against the dissociability upon which heterochrony depends." This is the reason why Gould (1977, p. 247) recommended building clock models with a dimensionless ratio or angle as a measure of shape, and with length as a measure of size. For the same reason, the quantitative method presented by Alberch et al. (1979) for describing heterochrony makes reference to ontogenetic trajectories defined as variations in a Euclidean space formed by three independent vectors of size, shape, and ontogenetic age. The Procrustes method is particularly suitable for heterochronic studies, because it allows the calculation of size and shape as independent vectors. The Procrustes method defines size and shape as multivariate concepts (Rohlf and Slice, 1990), which gives the advantage of avoiding statistical bias created by ratios (Atchley et al., 1976). The first and fundamental step of the method is size normalization (i.e., same size for all specimens). Thus, shape is defined as a geometrical feature, which remains unchanged after scaling, translation, and rotation of superimposed specimens (Goodall, 1991; O'Higgins, 2000). Thus, shape is independent of size. Size is calculated as the square root of the sum of squared Euclidean distances from each landmark to the centroid (mean of landmarks coordinates). In such a framework, allometry is defined in the sense of Mosiman (1970) as size/shape covariance (see also Penin, 1997; Penin and Baylac, 1995, 1999; O'Higgins, 2000; Ponce de León and Zollikofer, 2001; Penin et al., 2002). Thus, allometry calculated with independent size and shape vectors may give different results from classical bivariate allometry calculated with dependent size and shape vectors. Heterochronic hypotheses may also differ for the same reason. Here heterochrony becomes the comparison of ontogenetic size and shape changes (as independent vectors) between and within gorillas and chimpanzees at different stages of growth. In other words, it is the real means of visualizing ontogenetic trajectories and to compare them, as recommended by Gould (1977) and Alberch et al. (1979).

Extrapolation to living species is now classical (e.g., Shea, 1983a, c, 1984, 1985a, 1986). A fundamental notion is the notion of size/shape covariation. The comparison of ontogenetic trajectories in living primates provides numerous examples of size-related shape changes (size/shape association) or size-unrelated shape changes (size/shape dissociation) (Shea, 1983a, 1986, 1989, 1992, 1995). In terms of heterochrony, size/shape association corresponds to a simple extension or truncation of the common growth pattern (i.e., rate or time hyper- or hypomorphosis), as is the case, for example, in African apes for Shea (1983a). On the contrary, size/shape dissociation corresponds to size-unrelated shape changes, an instance of which is found in the neotenic skull in humans that is retarded in shape but not in size in comparison to the chimpanzee skull (Gould, 1977; Shea, 1989; Penin et al., 2002).

THE POINT IN QUESTION HERE

The present study aims to reconsider intra- and interspecific ontogenetic changes in male and female gorillas and common chimpanzees during ontogeny, using mathematical definitions of size and shape given by the "shape theory" (Kendall 1984, 1989; Bookstein, 1991). APS software (Penin, 2000) is used to calculate and graphically represent shape variations which correspond to allometric and non-allometric traits in chimpanzees and gorillas, including sexual dimorphism in some stages of growth. Here the objective is to calculate in percentage of shape variation and to graphically represent differences in shape which are related or not related to growth. We add simplified models of shape/size graphs obtained from our results to explain the method. The differences between ontogenetic trajectories in chimpanzees and in gorillas are interpreted in terms of heterochrony in comparison with classical hypotheses (Shea, 1983a, b, 1985a), and in terms of functional adaptation with biomechanical models of head equilibrium.

MATERIALS AND METHODS

Sample

The material comprises 100 adult and juvenile skulls of extant African apes of known sex: 50 *Go-*

TABLE 1. Material studied (100 specimens)[1]

Material	M0	M1	M2	M3	Total
Male *Pan troglodytes*	4	7	7	9	27
Female *Pan troglodytes*	5	5	5	8	23
Male *Gorilla gorilla*	5	7	4	10	26
Female *Gorilla gorilla*	4	6	7	7	24

[1] M0, no permanent molar erupted; M1, first permanent molar erupted; M2, second permanent molar erupted; M3, third permanent molar erupted.

rilla gorilla and 50 *Pan troglodytes* (Table 1). The specimens were classified into four stages of growth, based on the eruption status of permanent molars. In stage 0, there is no permanent molar erupted; in stage 1, the first permanent molar is erupted; in stage 2, the second permanent molar is also erupted; and in stage 3, all the permanent molar are erupted.

All skulls are in the collections of the Powell-Cotton Museum (Birchington, UK).

Landmarks and Procrustes superimposition

Twenty-nine landmarks (Fig. 1, Table 2) were digitized on skulls using a 3 Draw Space Digitizer® (Polhemus, Inc.). As detailed in Penin et al. (2002), homologous landmarks are defined according to the three levels of homology given in Bookstein (1991). Sixteen landmarks are type I, i.e., located at the discrete juxtaposition of two or three bones; 13 landmarks are type II (i.e., located at a characteristic point of a line). The pterion may be regarded as type II, although it may have different shapes. Twelve landmarks are located in the sagittal plane, and 17 on the right side of the skull. For adult gorillas, which possess developed cranial crests, the sagittal landmarks were digitized at the base of the crest. For each specimen, the spatial configuration of the landmarks sets up a "figure" (Goodall, 1995). The 100 "figures" (corresponding to the 100 specimens) are scaled, translated, and rotated to be superimposed (Rohlf and Slice, 1990). The tridimensional superimposition may be viewed in three planes: sagittal, horizontal, and frontal. However, only shape changes in sagittal planes, which correspond to the main differences, are given here. A wire frame is drawn between landmarks for graphical representation. This wire frame delineates several anatomical regions: outline of the vault (landmarks 7, 26, 8, 9, 27, and 10); orbital cavity (landmarks 14–17); palate (landmarks 3, 29, 4, 18, 19, and 20); glenoid fossa (landmarks 21–23); zygomatic arch (landmarks 11–13); and sphenoidal clivus (landmarks 1, 2, and 24). The basicranium includes the foramen magnum (landmarks 1 and 10), the glenoid fossa, and the sphenoidal clivus.

The variable used for size normalization is the centroid size (CSI), calculated for each specimen as the square root of the sum of the squared deviations of landmarks from the centroid (Gower, 1975). The superimposition algorithm is the generalized least square, which translates and rotates the normalized
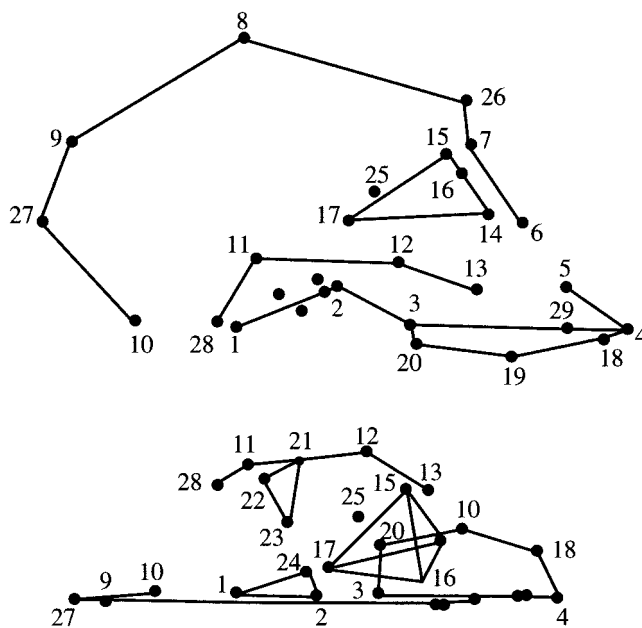

Fig. 1. The 29 landmarks are plotted on consensus (mean shape of 100 specimens). Top: Sagittal view. Bottom: Inferior view. Face of skull is turned to right. For definitions of landmarks, see Table 2. Links are drawn to make anatomical structures clearer. Landmarks 7-26-8-9-27-10: Outline of cranial vault. Landmarks 14-16-15-17: Orbital cavity. Landmarks 3-29-4-18-19-20: Palate. Landmarks 21-22-23: Glenoid fossa. Landmarks 28-11-12-13: Mastoid and zygomatic arch. Landmarks 1-2-24: Sphenoid clivus. Foramen magnum is located between landmarks 1 and 10, and nasal aperture between landmarks 5 and 6.

figures to minimize squared differences between landmarks (Rohlf and Slice, 1990). The superimposition also computes a mean shape of the specimens named "consensus." The shape of each specimen is defined by Procrustes residuals, which are the deviations of landmarks relative to the consensus. Procrustes residuals are the starting point of the statistical analysis. As recommended by Bookstein (1996), for multiple group comparison, a single superimposition of all specimens is realized. Thus, three Procrustes analyses were calculated: one to study chimpanzees, one to study gorillas, and one with both species to compare chimpanzees and gorillas.

Statistical models

The principal components of shape (PCs) are computed from a principal component analysis of the Procrustes residuals (Bacon and Baylac, 1995; Penin and Baylac, 1995, 1999; Penin 1997, 1999; Dryden and Mardia, 1998; Bacon, 1999, 2000; Penin and Berge, 2001; Hennessy and Stringer, 2002; Penin et al., 2002). The principal component analysis defines an orthogonal basis, which captures the variability by decreasing order of magnitude. Projection of Procrustes residuals onto PCs gives PCs scores.

The PCs procedure is particularly suitable for the superimposition method for the two following reasons:

TABLE 2. Landmarks

Anthropological landmarks and definitions	Type
1. Basion[1]	II
2. Hormion[1]	I
3. Staphilion[1]	I
4. Prosthion[1]	I
5. Nasospinale[1]	I
6. Superior border of nasal aperture (sagittal plane)	I
7. Nasion[1]	I
8. Bregma[1]	I
9. Lambda[1]	I
10. Opisthion[1]	I
11. Porion[1]	II
12. Zygion[1]	II
13. Zygomallare[1]	I
14. Orbitale[1]	I
15. Fronto-malar suture (orbit margin)	I
16. Dacryon[1]	I
17. Optic foramen	II
18. Premaxillary suture, between I^2 and C (external edge of alveolar process)	I
19. External edge of alveolar process between P^2 and M^1	II
20. Maxillare tuberosity (dorsal extremity of alveolar process)	II
21. Lateral condylion[1]	II
22. Postglenoid process of mandibular fossa	II
23. Medial condylion[1]	II
24. Foramen lacerum medium (sphenoid body-pterygoid ala)	I
25. Pterion[1]	II
26. Glabella[1]	II
27. Inion[1]	II
28. Extremity of mastoid process	II
29. Anterior palatine canal	I

[1] Classical anatomical landmarks defined in Aiello and Dean (1990, p. 50–53). Type I and II homologies are defined in Bookstein (1991) and in present text. Landmarks are situated either in sagittal plane or in right side of skull.

1) After superimposition, all landmarks are interdependent (they are all used for fitting). Therefore, an isolated landmark movement is hardly interpretable. Because PCs are a composite variable, shape changes are analyzed in PCs as a movement of a set of landmarks.
2) Procrustes residuals are too numerous to be used directly in statistical tests. In other words, too many variables create an excess of degrees of freedom and a decrease in the power of statistical tests (Rao, 1966). PCs are a means to reduce the number of variables by selecting those which have the greatest eigenvalues (Penin, 1997; Penin and Berge, 2001; Penin et al., 2002). The selection of PCs also allows us to eliminate nuisance parameters generated by superimposition (Goodall, 1991, 1995).

One may notice that PCs do not automatically have a biological significance, because they are computed from a purely numerical method (Marcus, 1990). Therefore, to study shape changes, it is better to compute the combination of PCs corresponding to the studied factors, here growth, sex, and taxonomy (Penin, 1997, 1999; Penin and Baylac, 1999; Penin and Berge 2001; Penin et al., 2002). We compute statistical tests with the reduced number of PCs corresponding to the
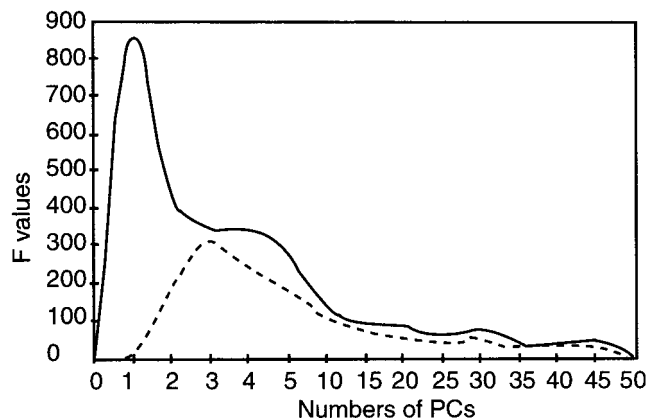

Fig. 2. F values obtained for allometric shape (solid line) and nonallometric discriminant shape (dashed line), according to different numbers of PCs used for calculation (see Materials and Methods).

highest value of the F-test (Fig. 2). To calculate the loss of information which may be caused by a reduced number of PCs, we compared the allometric vectors computed with a reduced number of PCs with the allometric vectors computed with all the PCs.

The next steps of the study are the two following statistical procedures.

Multivariate regression to calculate allometry. Here allometry is used in the sense given by Mosiman (1970) as shape changes which are related to increased size. Isometry is the stumbling block between classical allometry and allometry in Mosiman (1970). In classical bivariate allometry, when covariance between any two variables is studied, invariant proportions (isometry) are included in allometry as a special case. The two variables are correlated, and the slope of the regression line (allometric coefficient) is 1 (Huxley and Teissier, 1936; Gayon, 2000). However, in the sense of Mosiman (1970), when covariance between size and shape variables is studied, as here, invariant proportions (geometric similarity) are excluded from allometry as the "null hypothesis" of allometry (e.g., Jungers, 1985). Isometry corresponds to a zero slope in a size/shape graph (model III in Fig. 7). Thus, in this study, allometric shape is the part of shape which is modified with size, whereas nonallometric shape is the part of shape which is invariant with size and discriminates groups of specimens.

We calculate allometries using regressions in which the explicative variable is size and the dependent variables are PCs scores. A regression where many dependent variables are used instead of a single one is a multivariate regression. The basic principles of multivariate regression are given in Kraznowski (1988), and have been widely applied to geometric morphometry (Penin and Baylac, 1995, 1999; Penin, 1997; Penin and Berge, 2001; Penin et al., 2002). The equation of multivariate regression used to calculate the multivariate shape as an "allometric shape vector" is given in Penin et al. (2002).

Three analyses have been done: 1) within chimpanzees, 2) within gorillas, and 3) in both gorillas and chimpanzees. The multivariate regressions corresponding to intraspecific shape vectors are computed from intraspecific variance-covariance matrices, whereas the multivariate regression corresponding to the common shape vector is computed from the mean variance-covariance matrix of the two species. The method is the extension of a procedure widely used in classical multivariate morphometry for a sample corresponding to more than one taxon. (Burnaby, 1966; Humphries et al., 1981; Bookstein et al., 1985; Rohlf and Bookstein, 1987). From a biological viewpoint, such calculation of a chimp-gorilla prototype of growth is only possible because we may assert, as in this study, that chimpanzees and gorillas share very similar growth patterns. To sum up, four allometric shape vectors have been calculated: 1) the allometric vector which is common to chimpanzees and gorillas, 2) the noncommon allometric vector which is the rest of allometry that differentiates species, and 3 and 4) the two intraspecific allometric vectors.

Discrimination. The discriminant function is used to identify "taxonomic" differences between chimpanzees and gorillas. These traits are independent of size and correspond to the null hypothesis of allometry (see above). Computation of the discriminant function is similar to multivariate regression, in which the x variable is a dummy variable which characterizes the group (e.g., 0 for chimpanzees and 1 for gorillas) (Penin, 1997, 1999; Penin and Baylac, 1995, 1999; Penin and Berge, 2001; Hennessy and Stringer, 2002; Penin et al., 2002). We calculated the shape vector which discriminates gorillas from chimpanzees, and shape and size vectors which discriminate females from males within species.

Graphs and sketches

The discriminant function and multivariate regression shape vectors allow us to build graphs where coordinates of specimens indicate shape changes associated with either allometries (Fig. 4) or discriminant differences (Fig. 6). We may visualize shape changes in "sketches" corresponding to the magnitude of shape changes for allometric and discriminant shape vectors (Figs. 3, 5).

Statistical tests

Two sorts of statistical tests were calculated.

1) Multivariate regressions and discriminant functions are tested using the F test, which is the coefficient of multiple determination (R^2) weighted by the degrees of freedom (Sokal and Rohlf, 1981; Tomassone et al., 1992) (Table 3). R^2 is directly computed from each variance-covariance matrix. Three R^2 are calculated: one for the chimpanzees, one for the gorillas, and one from the pooled mean covariance matrix when the two genera are studied together. This last procedure
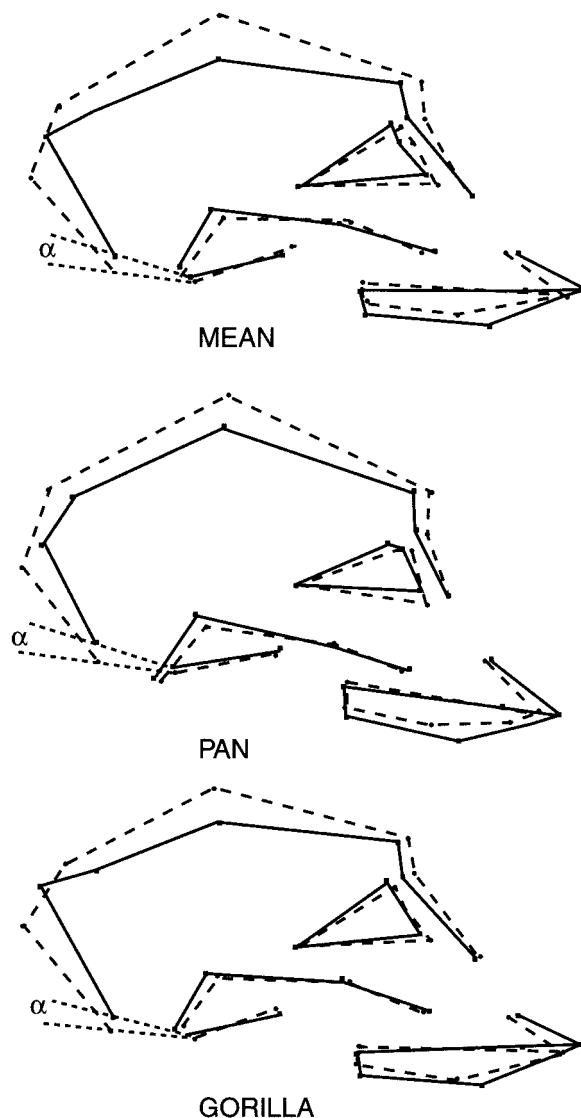

Fig. 3. Common allometry and intraspecific allometries in chimpanzees and gorillas. "Figures" are represented in sagittal view. Faces of skulls are turned to right. Dashed lines, juvenile specimens (no permanent molar); solid lines, adult specimens; dotted lines, plane of foramen magnum (landmarks 1–10). Otherwise, same as Figure 1. Mean: common allometric shape vector. *Pan*, and *Gorilla*: intraspecific allometric shape vector. Most important change in shape during growth is common allometry. It corresponds to a larger increase of facial volume relative to neurocranial volume, a more obliquely oriented foramen magnum, and a noticeable reshaping of nuchal region (higher inion). Allometric differences between *Pan* and *Gorilla* mainly concern inion, which becomes higher; position of foramen magnum, more dorsally oriented; and palate, more tilted in adult gorillas than in adult chimpanzees. There are no species-specific differences in ontogenetic change of plane of foramen magnum (same value for α in three "figures").

avoids mixing the effects of different factors (Burnaby, 1966). The F value enables us to test the significance of the multivariate regression with a single explicative variable (here size). Such an approach is particularly helpful to test allometry (Mosiman, 1970; Bookstein, 1991). As explained in Penin (1997) and Penin and Berge
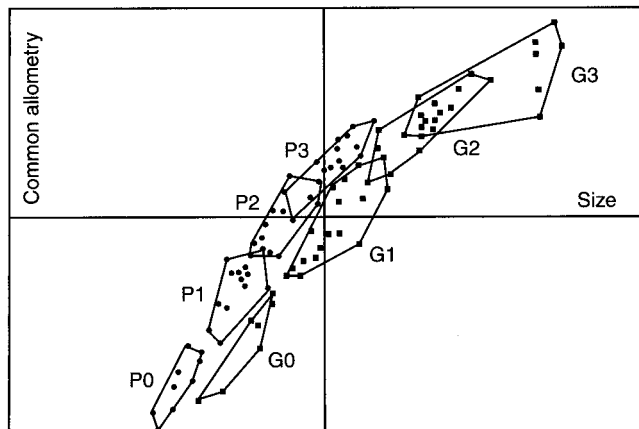
Fig. 4. Allometric changes in chimpanzees and gorillas. Growth stages: 0, no permanent molar; 1, first permanent molar; 2, second permanent molar; 3, third permanent molar. P0–P3, *Pan troglodytes*; G0–G4, *Gorilla gorilla*. Common allometry: common shape allometric vector. Size: centroid size. Comparison of two ontogenetic trajectories indicates that in terms of common allometry, adult gorillas exceed size and shape of adult chimpanzees with increased allometric dimensions (size/shape association within each growth trajectory), and with greater size at any stage of growth (size/shape dissociation as a lateral transposition of gorilla growth trajectory).
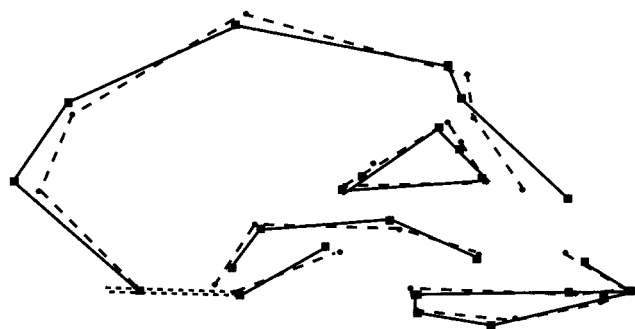

Fig. 6. Allometric vs. discriminant shape changes. Stages of growth: 0, no permanent molar; 1, first permanent molar; 2, second permanent molar; 3, third permanent molar. P0–P3, *Pan troglodytes*; G0–G4, *Gorilla gorilla*. Common allometry: common shape allometric vector. Discrimination: discriminant vector. Ontogenetic trajectories are perpendicular to discriminant vector (y-axis) and parallel to common allometric vector (x-axis), showing independence of two processes.

Partition of shape variance according to different biological phenomena

It is possible to calculate the amount of shape variation as the sum of Procrustes residuals associated with each biological phenomenon. Each amount of shape variation is given by the projection of specimens onto the corresponding shape vectors: intraspecific allometry, common and noncommon allometries in *Pan* and *Gorilla*, nonallometric discriminant function, and allometric and nonallometric sexual dimorphism.

Validity of calculation

A resampling procedure (jackknife) was used to assess the validity of shape vectors. It appears that the number of specimens (50 chimpanzees and 50 gorillas) was enough to obtain stable results when calculating shape allometrical and discriminant vectors. However, this is less true within the different stages of growth when calculating discriminant vectors for sexual dimorphism (see Results).

Fig. 5. Discriminant shape changes. Dashed lines, chimpanzees (all ontogenetic stages together); solid lines, gorillas (all ontogenetic stages together). Sagittal view of skull with faces turned to right. Traits which discriminate gorillas from chimpanzees are long and flat vault characterized by a prominent occipital region; glabella, which is higher and displaced backward; and protrusive nose. Plane of foramen magnum (dotted line) is unchanged.

RESULTS
Selection of principal components of shape

As explained in Materials and Methods, it is necessary to reduce the number of principal components of shape (PCs) to calculate statistical tests. Figure 2 gives the variation of F-test values in the calculation of allometry and discrimination, with an increased number of PCs. In the case of allometry, the F-test value is very high for the first PCs, and then rapidly decreases until it reaches zero beyond 50 PCs. In the case of discrimination, the F-test value is very high for the first three PCs, then rapidly decreases until it reaches zero beyond 50 PCs. The choice of the first three PCs was done for all

(2001), the number of PCs to retain is estimated with a forward selection of components. Thus, the F value and the probability are calculated using an increasing number of PCs (Fig. 2).

2) Nonparametric tests (resampling) are computed for allometry using a Pitmann correlation (Good, 1997), and for discrimination using a cross-validation.

Superimposition, graphics, and parametric statistical tests were calculated with APS Software, version 2.21 (Penin, 2000). Nonparametric tests were calculated using specially devised Matlab® 5.3 functions.
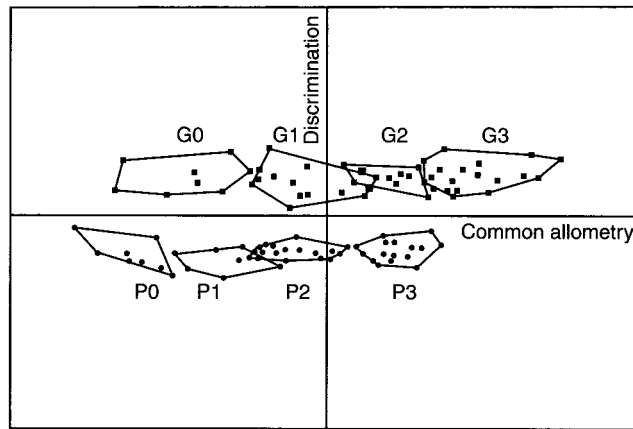
TABLE 3. Statistical tests for allometry and discrimination[1]

Multivariate vectors	R^2 value	F value	DF1	DF2	Probability
Common allometry	0.938	349.437	3	96	$<10^{-6}$
Within *Pan* allometry	0.954	231.549	3	46	$<10^{-6}$
Within *Gorilla* allometry	0.953	227.327	3	46	$<10^{-6}$
Discrimination	0.905	305.396	3	96	$<10^{-6}$

[1] Coefficient of determination (R^2); F degrees of freedom (DF1 and DF2), and probability of null hypothesis are calculated as multivariate vectors in three Procrustes analyses (see Materials and Methods).

calculations. This choice was confirmed by a correlation test calculated between 1) the allometric shape vector computed with all the Procrustes residuals, and 2) the allometric shape vector computed with the first three PCs ($r > 0.999$).

Allometric growth patterns

Allometries are computed with multivariate regressions, using the first three PCs obtained from the principal component analysis of Procrustes residuals and centroid sizes. The main changes in shape are visible in the sagittal plane of the skulls. Figure 3 gives the sketches of shape changes during growth in gorillas and chimpanzees separately (intraspecific allometries), and in both (common allometry). The sketches show that in the three cases, the changes in shape during growth mainly concern the relative proportions of the neurocranium and face. The common allometry indicates that in the common growth pattern, the face becomes proportionally larger with growth (landmarks corresponding to the palate are shifting forward), whereas the neurocranium does the reverse (landmarks corresponding to the vault). In the occipital region, the inion becomes relatively higher. The plane of the foramen magnum (landmarks 1 and 10) is modified with growth, and becomes more obliquely oriented from downward and forward to upward and backward. The main trait visible in the horizontal plane (not given here) is that the skull becomes broader at the level of the zygomatic arch with growth. However, allometries calculated in gorillas and chimpanzees show that the growth patterns are close but not fully similar. The main differences in intraspecific allometries are visible in the sagittal view of the skull (Fig. 3). They concern 1) the inion, which becomes clearly higher in gorillas, and 2) a tilting of the palate in gorillas, the posterior part being shifted downward and the anterior part upward. The parametric F tests are highly significant for the three allometries (Table 3). The null hypothesis of no size/shape differences is rejected, with a probability of less than 10^{-6}. Moreover, the nonparametric Pitmann correlation gives a probability of less than 10^{-3} to reject the same null hypothesis.

Chimpanzees and gorillas are plotted together in Figure 4, with centroid sizes on the x-axis and allometric shape coordinates on the y-axis. The two ontogenetic trajectories (size, shape, and dental stages) are very close and nearly parallel. However, they are clearly separated by a gap resulting from a
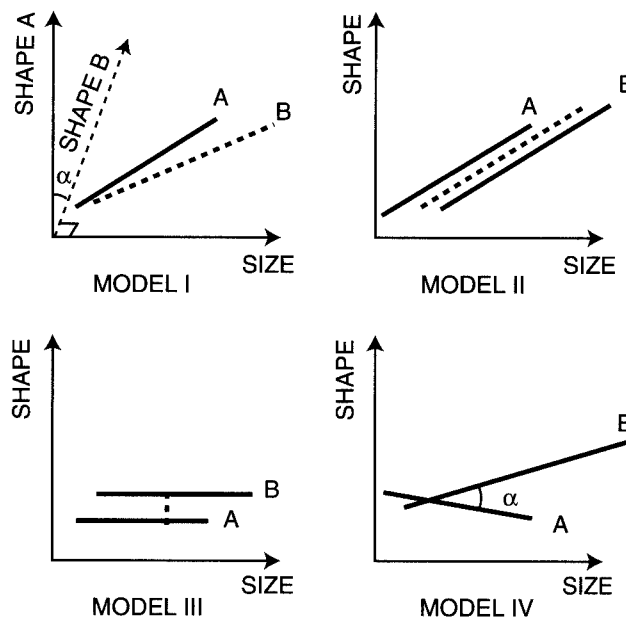

Fig. 7. Schematic representation of ontogenetic size/shape changes from Procrustes results. A, common chimpanzees; B, gorillas. Model I, intraspecific allometries. Two regression lines have quite similar slopes (close to slope of common allometry), but are situated in two different planes (α, 31°). Model II, common allometry (simplified from Fig. 4). Two regression lines are situated in same plane and are parallel to common allometric vector (dotted line), also situated in same plane. As compared with A, B is shifted forward by increased allometric changes (size/shape association) and by increased size in all stages of growth (size/shape dissociation in x-axis). Model III, discrimination. Regression lines are parallel with zero slopes, and are perpendicular to discriminant vector (dotted line), also situated in same plane. Discriminant shape is null hypothesis of allometry within species. A and B present opposite shape discriminant traits, with increased size in B in comparison to A. Model IV, noncommon allometry. Two regression lines are situated in same plane and intersect (α, 29°). Compared with A, B presents opposite and more extensive allometric shape changes and increased size.

lateral transposition. This gap is caused by a size/shape dissociation indicating that, for a given dental stage, gorillas have a greater size than chimpanzees. Ontogenetic stages also differ in shape between *Pan* and *Gorilla*. For a similar stage of growth, gorillas have a shape and size corresponding to older chimpanzees. The size and shape differences between equivalent ontogenetic stages increase with age. The test of Hartley (1950) is used to prove that size variances are different in gorillas and chimpanzees. The magnitude of size variance is significantly greater in gorillas than in chimpanzees ($F = 2.30$, with 49 and 49 degrees of freedom; $P < 0.002$).

However, the magnitude of shape variance is not statistically different between gorillas and chimpanzees. This signifies that the magnitude of growth in gorillas is clearly more important in terms of size than in term of shape, as compared with chimpanzees. We must remember that landmarks were digitized at the base of the crest, and therefore sagittal and nuchal crests are not taken into account.

Discriminant traits between *Gorilla* and *Pan*

The discriminant function is highly significant with three PCs ($R^2 = 0.905$, F = 305.39 with 3 and 96 degrees of freedom, $P < 10^{-6}$) and 10^{-3} for cross-validation (Table 3). The discriminant function gives a graphical visualization of shape differences between chimpanzees and gorillas, independently of growth (Fig. 5). Differences are visible in the sagittal plane. The vault of the skull in gorillas is lower and longer than that of the skull in chimpanzees. The region of the nose and of the glabella is more inclined in gorillas. The glabella is slightly higher and displaced backward. The nasal bones and nasal aperture are shifted forward and downward in gorillas, whereas the palate remains unchanged. The mastoid process is situated more upward and forward in gorillas than in chimpanzees.

Allometric shape vs. nonallometric shape

Computation of the angle between the common allometric shape vector and the discriminant shape vector shows that the two vectors are nearly orthogonal (91.39°). This signifies that the ontogenetic shape change and the discriminant one (i.e., specific traits unrelated to size) are fully independent. Figure 6 represents the scatters of *Pan* and *Gorilla* plotted together, where the allometric changes are on the x-axis and the discriminant changes are on the y-axis. The scatters indicate the respective parts of each phenomenon (common allometry and discrimination) in the total shape difference.

Sexual dimorphism

We do not find significant allometrical differences between males and females in both species. This is probably due to the small number of specimens in each stage of growth. The results of multivariate analyses of variance (MANOVA) are significant in terms of size (F = 4.1, DF = 1, DF2 = 48, $P < 0.04$), but not in terms of shape ($P < 0.2$). Calculations also indicate that there is an interaction between age and sex (F = 3.6, DF1 = 3, DF2 = 46, $P < 0.02$). Such an interaction is visible in the first and last ontogenetic stages of growth (G0 and G3 in Fig. 4), but not in intermediary stages (G1 and G2). However, there are opposite differences in G0 and G3. In G0, males have a smaller size and a more juvenile shape than females. In G3, males have a larger size and a more extended shape than females.

For chimpanzees, there are no significant sexual differences in terms of size and shape, and no interaction between age and sex.

TABLE 4. Partition of shape variation according to different biological phenomena[1]

Shape variation	Amount	Percentage
Total	1.254	100%
Common allometry	0.811	64.67%
Noncommon allometry	0.013	1.03%
Discrimination	0.103	8.21%
Unexplained	0.327	26.07%
Within *Pan* allometry	0.396	29.23%
Within *Gorilla* allometry	0.449	35.81%

[1] Amount: amount of shape variation calculated as sum of squared distances between landmarks of specimens and landmarks of consensus. Percentage: amount of shape variation in percentage of total variance.

Sources of variation

The percentages corresponding to the shape variation of each biological phenomenon relative to the total variation are indicated in Table 4. We may observe that shape changes corresponding to the various allometric processes are by far preponderant (Table 4). Within the total shape differences, common allometry is particularly important (64.67%), whereas noncommon allometry is close to zero (1.03%). As regards the nonallometric discriminant shape, the results show that it is relatively important (8.21%). Intraspecific allometries, which include for each species a part of common allometry and noncommon allometry, do not have the same magnitude (29.23% in chimpanzees; 35.81% in gorillas) (Table 4).

DISCUSSION
Ontogenetic shape changes in geometric morphometrics

As previously quoted by Klingenberg (1996), the shape of an organ or of an organism is a multivariate concept. However, the number of variables used to describe such as a multivariate shape is obviously too high for statistical tests (here, 29 landmarks in a tridimensional space; that is to say, 87 variables). There are two main reasons to use the Procrustes methods to solve such a difficulty. Firstly, shape is not regarded here as a set of linear dimensions as in classical multivariate analyses, but as an overall displacement of anatomical landmarks. The Procrustes method allows us to observe shape differences both in a qualitative way (sketches), and in a quantitative one (statistical tests and graphs). The second reason to use the Procrustes method is the possibility of reducing the total variance to the parts that interest us: allometric shape changes, and nonallometric discriminant traits, leaving out perturbations due to individual variability. The PCA provides the principal components of shape (PCs) in decreasing order of importance (Fig. 2). The choice of the first three PCs for calculation of statistical tests gives us the possibility of having significant data in terms of F values and R^2 coefficients (Table 3). Recently, Ponce de León and Zollikofer (2001) com-

pared cranial growth in modern humans and Neanderthals, using geometric morphometrics (TPSplines). They obtained a graph of specimens using a warp analysis, and sketches of shape differences in terms of magnitude and direction of vector fields. In their results, the first PCs extract shape changes corresponding to the common allometry, and the second PCs shape changes corresponding to the discriminant function. Very similar results were obtained in this study, despite the use of a different morphometric method, i.e., Procrustes analysis. Actually, the vector of common allometry is almost superimposed on the first PCs, the vector of discriminant function on the second PCs, and the vector of noncommon allometry on the third PCs. Thus, representing common allometry and discriminant function either with PCs (Ponce de León and Zollikofer, 2001) or with calculated multivariate vectors (this study) gives similar results. This is not the case when further species, such as humans and chimpanzees, are compared (Penin et al., 2002). In this case, calculation of multivariate vectors becomes essential.

We calculated shape changes corresponding to various biological phenomena in percentages of total variance (Table 4). The allometry which is common to chimpanzees and gorillas is by far the most important shape change in ontogeny (64.19% of total shape variation), whereas the rest of allometric shape change which discriminates the two species is very minor but statistically significant (1.04%). When allometry is calculated within species, we obtain more variation, because each intraspecific allometry includes a part of common allometry. It is also the reason why intraspecific allometry is more important in gorillas (35.81%), which have a larger size range than chimpanzees (29.23%).

The common allometry is described by Shea (1983a, b) as positive allometry for the splanchnocranium and negative allometry for the neurocranium. Many authors noted such a similarity in ontogenetic patterns of African apes (Dean and Wood, 1984; Shea, 1983a, b, 1985b; Bromage, 1992; Penin and Berge, 2001). In a larger context of common growth patterns in mammals, the common shape change is generally interpreted as a similarity in developmental constraints due to anatomical interdependence of the neurocranial and facial regions (Maynard Smith et al., 1985; Alberch, 1990). Figure 3 illustrates ontogenetic shape changes which are common to African apes. They confirmed the description by Shea (1983a, b). During ontogeny, the overall face becomes proportionally bigger, whereas the neurocranium does the reverse. Because the overall face scales more than the neurocranium during growth, adult neurocrania seem to be smaller, after size normalization, than juvenile ones. From a biological viewpoint, such a chimp-gorilla prototype of growth (common allometry) is only possible because we may assert, as in this study, that chimpanzees and gorillas share very similar growth patterns. The rest of allometry which is not shared by

chimpanzees and gorillas (noncommon allometry) is too small to be represented by a sketch, and for this reason we compared sketches of intraspecific allometries in Figure 3. We may observe that in comparison with adult chimpanzees, adult gorillas attain a proportionally lower cranial vault. A precise comparison with Shea (1983a, b) is rather difficult due to differences in methods. For example, the gorilla protrusive nose is described by Shea (1983b) as a local shape differentiation related to departures from common growth trajectories; here it is calculated as a nonallometric discriminant trait (Fig. 5), which is basically equivalent from a descriptive viewpoint.

Four models of size/shape graphs are schematized from the Procrustes results (Fig. 7).

The two intraspecific allometries are compared in model I. The two regression lines are situated in two different planes of the multivariate space, and intersect at the level of the size vector with an angular value of 31° (α calculated by Matlab® 5.3). The two regression lines have similar slopes (close to the slope of the common allometry), but the regression line of gorillas (B in Fig. 7) scales more than the regression line of chimpanzees (A in Fig. 7). The two intraspecific shape vectors may be decomposed into three shape vectors projected onto the following orthogonal planes. In model II (simplified from Fig. 4), a great part of intraspecific allometries corresponds to the common allometry shared by species A and B. As compared with species A (chimpanzees), species B (gorillas) is shifted forwards by increased allometric changes (size/shape association), and displaced by increased size in all stages of growth (size/shape dissociation in x-axis). Model III depicts an important part of intraspecific shape which discriminates the two species independently of growth (see discriminant vector in Fig. 6). The regression lines are parallel (zero slopes), indicating that such a difference is unrelated to size. Thus, the discriminant vector is perpendicular to the two regression lines. Finally, model IV depicts the very small part of noncommon allometry which differentiates the species. In the comparison of chimpanzees with gorillas, the noncommon allometry corresponds to opposite regression lines, which intersect at 29° (α calculated by Matlab® 5.3).

Procrustes method as a tool for heterochrony

The Procrustes results lead to heterochronic interpretations which are not identical to the results of Shea (1983a, b, 1985a). Shea (1983b) showed that the three species of African apes share a common growth pattern which is predominant in comparison to intraspecific differences. Shea (1983a, b, 1985a) interpreted differences in adult morphology as the result of a rate hypermorphosis when gorillas are compared with common chimpanzees. In other terms, interspecific differences are strictly allometrical. One may object that a size/shape dissociation in growth allometries is however represented in Shea (1985a, p. 190), in a graph comparing brain

and eye growth in two African apes. For Shea (1983a, 1985a), such a dissociation corresponds to a local allometric difference taking place in early ontogeny, and not, as here, to a general size increase (or decrease) in skull dimensions. In other words, dissociation in Shea (1983a, 1985a) is the consequence of different timings in the growth of various cranial regions (and may also result from early differences in rate), whereas here it is interpreted as a not inconsiderable part of the heterochronic processes. In Figure 3, all the different stages of growth are represented. We may specify that 1) gorillas have the shape and size corresponding to older chimpanzees (common allometry); and 2) gorillas have a larger size at any stage of growth. We interpret differences in size and shape between gorillas and chimpanzees as the result of a composite peramorphic process which includes both a rate hypermorphosis (size-shape association) and a size acceleration (size-shape dissociation). Size/shape dissociation is already visible at the first stage of growth studied here (decidual teeth), and increases until the adult stage. Although there are no neonates in this study, one may assert that such a size difference in gorillas and chimpanzees arises very early. A difference in size is already present at birth. We measured cranial diameters in four neonate heads of common chimpanzees, and in a neonate skull of gorilla (collections of the Laboratoire d'Anatomie Comparée, Muséum Nationale d'Histoire Naturelle, Paris, France). A neonate gorilla skull from the collections of the Anthropologisches Institüt der Universität (Zürich, Switzerland) was also measured by M. Haüsler (personal communication). The material confirms that neonate skulls in gorillas are clearly bigger than neonate skulls in chimpanzees (4 neonate chimpanzees: mean cranial length, 79.2; sd, 2.5; mean biparietal breadth, 67.6; sd, 2.5; 2 neonate gorillas: mean cranial length, 95.9; sd, 6.4; mean biparietal breadth, 80.1; sd, 0.1). The fact that gorillas have larger skulls than chimpanzees at birth does not run counter to the generally admitted opinion that neonate gorillas are particularly small in comparison to adult gorillas (Schultz, 1956; Shea, 1983d).

In Figure 8, we compare the clock built from Procrustes results with the clock given by Shea (1983a) to represent heterochronic changes from common chimpanzees to gorillas. The Procrustes analysis allows us to calibrate size and shape vectors as follows: the quantitative amount of size and shape is measured in Figure 4, by x-axis and y-axis coordinates of mean adult specimens in chimpanzees and gorillas. To calculate the magnitude of size/shape dissociation, we calibrated the size vector with the size that adult gorillas would have if they grew like chimpanzees. The difference between this hypothetical size (35) and the real size of adult gorillas (41) reveals the size/shape dissociation previously neglected in classical allometry (Shea, 1983a). We interpret the clock and the graph of ontogenetic trajectories (Figs. 4, 7, model II) as the result of a
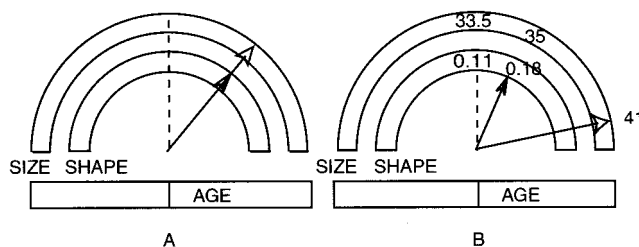

Fig. 8. Clock models for gorilla hypermorphosis. In each clock, "ancestral" condition (adult chimpanzees) corresponds to vertical line. "Descendant" condition (adult gorillas) corresponds to displacement of three independent vectors: size, shape, and age. **A:** Qualitative account of peramorphosis in Shea (1983a). **B:** Quantitative account of peramorphosis from our data (adult coordinates in Fig. 4). "Size" is centroid-size; "shape" is common allometry ("common shape allometric vector"). Calibration of size and shape is given by units on x-axis and y-axis in Figure 4 (numbers not represented in Fig. 4). "Age" is age of maturity. In clock of Shea (1983a, 1985a), peramorphic process from *Pan troglodytes* to *Gorilla* is a rate hypermorphosis, whereas in clock built from Procrustes results, peramorphic process from *Pan troglodytes* to *Gorilla* is a rate hypermorphosis combined with a size acceleration.

composite heterochronic process including two hypermorphoses: a rate hypermorphosis as in Shea (1983a), and a size acceleration. Such a result also shows that Procrustes graphs, with all ontogenetic stages represented, give a more complete interpretation of heterochrony than clock models, with only adult stages schematically compared (see also Penin et al., 2002).

Nonallometric discriminant traits and sexual dimorphism

One could see as a contradiction the fact that the two species share a common growth pattern in terms of shape, although they have significant nonallometric shape differences. Both are statistically validated. Calculation of the nonallometric discriminant shape vector and its orthogonality with the common allometric shape vector proves that a significant part of shape which discriminates gorillas from chimpanzees is independent of size. Nonallometric discriminant traits are relatively important (8.21% of total shape variation) vis à vis allometric species-specific ones (1.04%). Figure 5 shows that there are very few discriminant traits in the face, apart from the morphology of the nose. The shape of the nasal bones contrasting with a smoothed glabella, and a more downward located nasal aperture, characterize the protrusive nose of gorillas. Another nonallometric discriminant trait concerns the cranial vault, which is longer and lower in gorillas than in chimpanzees, independently of growth processes. Surprisingly, the basicranium is not very different in the two species (the foramen magnum has the same situation) apart from the mastoid process, which is bigger in gorillas than in chimpanzees.

Studies of sexual dimorphism using ontogenetic approaches demonstrated that differences in body size and body weight are consequences of differences

in growth rates or in growth duration (Shea, 1983a, 1985a, 1986; Leigh, 1992; Leigh and Shea, 1996). Different growth trajectories may lead to similar levels of adult dimorphism. In chimpanzees, adult males reach a bigger body size than females (Fénart and Deblock, 1973), more by increased growth rate than by increased growth duration, whereas it is the reverse for gorillas (Leigh and Shea, 1996). On the other hand, Shea (1985a, b, 1986) developed the notion of sexual "bimaturism" (Wiley, 1974) in primates and more specifically in anthropoids and apes. Marked dimorphism in body weight and body size is the consequence of a later onset of maturation in males, and an earlier one in females. For example, gorillas have greater sexual bimaturism than chimpanzees, because female gorillas mature earlier than female chimpanzees, and male gorillas later than male chimpanzees. Gorillas are thus characterized by the greatest sexual difference in terms of body size and weight in reference to chimpanzees.

In this study, sexual dimorphism is only visible in gorillas at the adult stage and maybe also at a very early stage of growth (but the latter result is not totally reliable due to a low number of specimens). Increase in size and shape in adult male gorillas results from an extension of the common growth allometry, from juveniles to adult females, then to adult males. The graphic result corroborates the heterochronic hypothesis by Shea (1983a) of time hypermorphosis for males as compared with females. Allometric traits in male gorillas mainly concern increased prognathism, the change in shape of the nuchal region, and a proportionally lower and longer cranial vault (see also O'Higgins and Dryden, 1993). However, statistical tests indicate that only size differences are significant, and only in gorillas. There are no significant shape differences in terms of allometry or nonallometric discriminant traits. It seems that size dimorphism in gorillas (and to a lesser extent in chimpanzees, even though it is not significant) appears very late in ontogeny, since there are no visible differences in size (males bigger than females) in juvenile periods of growth, or rather the reverse (females bigger than males). This result confirms previous observations and measurements (Randall, 1943; Schmid and Stratil, 1986).

Functional interpretation

Allometric shape changes and discriminant traits in the skull of chimpanzees and gorillas may reflect functional changes, such as in the masticatory system and head equilibrium. There are various diverging opinions in literature concerning relationships between facial shape and diet. For Shea (1983b), there is no dietary shape factor (no significant "reorganization" of the facial complex) which may explain the differences in growth allometry in chimpanzees and gorillas. On the contrary, for Taylor (2002) there is a relationship between the masticatory morphology of the African apes and dietary preference. It is possible to consider the problem

differently with the use of biomechanical models to analyze skull shape in terms of functional adaptation. Preuchoft et al. (1986) and Ravosa (1991) demonstrated that the protrusive nose of gorillas may act as a beam to reduce shearing stresses and bending moments in the chewing process. Indirectly, such a local reinforcement of the masticatory apparatus, which is part of the cranial shape, is linked to diet.

Similarly, we may use the Procrustes results to build biomechanical models to analyze cranial shape in terms of head equilibrium. In Figure 8, partition of shape changes calculated from multivariate vectors allows us to represent cranial outlines which correspond either to ontogenetic shape changes, or to nonallometric shape differences between chimpanzees and gorillas. The two outlines above are obtained from extreme coordinates of the common allometric shape vector (juvenile and adult stages of the mean specimen in Fig. 3). The two outlines below are obtained from the extreme coordinates of the discriminant shape vector (chimpanzees and gorillas in Fig. 5). The comparison is made possible because the sketches come from the same analysis. In each outline, the center of mass was estimated by suspending the cranial shape, as a rigid structure, from three distant extremities (at right angles). The junction of vertical lines gives the placement where the mobile is in equilibrium, i.e., the center of mass (Alexander, 1968). In Figure 9, the skulls are arbitrarily oriented in the Frankfort plane. The nuchal musculature is schematically represented as a fiber which originates from the inion and terminates at the seventh cervical vertebra. The cervical column has a vertical orientation, as is the case in quadrupeds in static conditions (de Beer, 1947; Herbin et al., 2001). As explained in Aiello and Dean (1990, p. 219) with regard to human skulls, the center of gravity of the head falls in front of the foramen magnum, which is the center of movements. Kummer (1959, p. 53) gave a functional model explaining how the nuchal musculature acts to equilibrate the head in quadrupeds. We built our biomechanical models as follows: to maintain the head in equilibrium, the torque produced by skull weight (W) must be counterbalanced by the torque produced by nuchal muscle force (F), according to the formula:

$$F \times d' = W \times d \; ; \; or \; d'/d = W/F \; .$$

The lever arms ratio d'/d is strongly modified during ontogeny (Fig. 9A, B). We observe that the muscle lever arm (d') has approximately the same length as the weight lever arm (d) at the juvenile stage, whereas d' becomes three times shorter than d at the adult stage. Thus, both in chimpanzees and gorillas, skull morphology becomes less advantageous for head bearing with growth. In adults, the muscular nuchal mass may act as a heavy counterweight against skull mass to maintain head equilibrium.
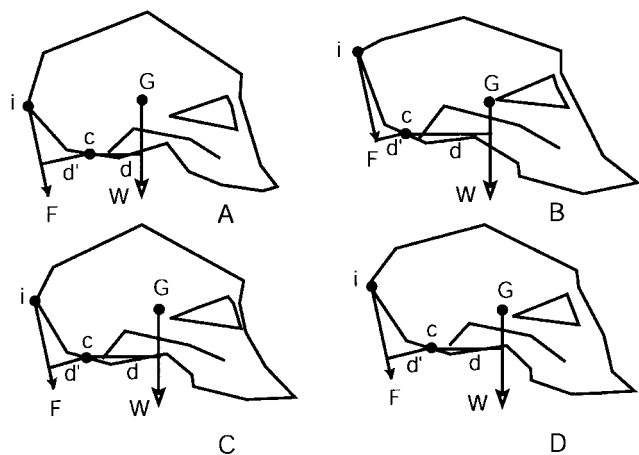
Fig. 9. Biomechanical models for head equilibrium built from shape partition (common allometry and discrimination). A, juvenile shape; B, adult shape in common allometric vector (mean specimen in Fig. 3); C, chimpanzee shape; D, gorilla shape in discriminant vector (Fig. 5); c, center of movements; d, weight lever arm; d′, muscle lever arm; F, nuchal muscle force; G, center of mass; I, inion; W, skull weight. F and W have arbitrary values. See text for biomechanical construction. Ontogenetic shape changes from **A** to **B** (common allometry) lead to an increased out-of-plumb position of head (d′ < d). Nonallometric discriminant traits in skull of gorillas (**D**) compensate for out-of-plumb position of adult head by a more powerful nuchal musculature in comparison to chimpanzees (**C**), with a longer muscle lever arm (d′) and greater muscular mass (not represented here).

This is only possible by considerably increasing the muscular mass.

In Figure 9C, D, the situation is completely the opposite. The discriminant traits in gorillas give a better head equilibrium than in chimpanzees, whatever their stage of growth (the ratio d′/d is higher in gorillas than in chimpanzees). In other words, the long and low skull of gorillas makes it possible to have a powerful nuchal musculature, not only via a greater muscular mass but also via a longer muscle lever arm. This suggests that such a discriminant trait is probably the answer to the problem of the out-of-plumb position of the head arising during growth, a problem which it is particularly difficult to solve for heavy animals such as gorillas.

To conclude, it is interesting to compare heavy primates, such as gorillas and humans, which have solved the problem of head equilibrium with diametrically opposite evolutionary processes. In humans, heterochronic processes (neoteny) lead adults to preserve a juvenile head equilibrium (Gould, 1977; Shea, 1989; Penin et al., 2002). Discriminant traits (reduced prognathism and flexed cranial base) reinforce such an advantageous juvenile-like head equilibrium (Penin et al., 2002). The nuchal region becomes less powerful in adult humans than in adult apes (smaller muscle lever arm and smaller muscular mass). In contrast, heterochronic processes in gorillas (rate hypermorphosis and size acceleration), especially in males who have an extra hypermorphic process in comparison to females (time hypermorphosis), lead adults to have more out-of-plumb

heads. Discriminant traits (long occipital region and high inion) help to counterbalance such a hyper-"adult-like" head equilibrium. The nuchal region becomes very powerful in adult gorillas, especially in adult males by additional species-specific traits, leading to both an increased muscular mass and a longer muscle lever arm.

ACKNOWLEDGMENTS

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