Quantification of hominoid disparity:
identifying organization plans and
major events in skull transformation

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RRH : ANALYSIS OF HOMINOID SKULL DISPARITY
LRH : JEAN CHALINE ET AL.
Abstract. — Landmark-based morphometric methods are applied to adult hominoid skulls in three planes (sagittal, Francfort and ortho-sagittal), and pairwise disparity patterns are analyzed. Morphological differences between species are estimated with Procrustes methods. Distance trees suggest the existence of three discrete organization plans: "Great Ape", "Australopithecine", and "Homo". Morphological changes quantified by vector fields indicate that these skull plans are characterized by distinctive degrees of cranio-facial transformation. The transition from the "Great Ape" skull plan to the "Australopithecine" skull plan is characterized by occipital rotation, facial contraction and expansion of the upper cranial vault, with the foramen magnum at the skull base moving to a more horizontal position. The transition from the "Australopithecine" skull plan to the "Homo" skull plan is reflected in tilting and forward movement of the foramen magnum, posterior extension of the skull, facial contraction and broadening of the frontal bone definitively separating the bregma and stephanion, a clear characteristic of the genus Homo. This study further confirms that within the Homo lineage, neandertalization introduces a regression in the tilt of the foramen magnum relative to the Francfort plane. Statistical analysis shows that the extent of shape change between skull plans is significantly greater than the extent of shape change within plans.

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Introduction

The study of morphological evolution in great apes and hominids is based on the comparative anatomy of both extant and extinct species, and on the analysis of structural differences as manifested in time and space. It is now widely acknowledged that the evolutionary process in great apes and hominids led to extensive modification of the cephalic and locomotor systems. Indeed, the transition from great apes to hominids is characterized by two general apomorphies, corresponding respectively to the acquisition of bipedalism in australopithecines and Homo, and to a substantially increased cranial capacity in Homo. These two major changes were accompanied by substantial restructuring of cranial morphology, a fact emphasized by many investigators (Schultz 1926, 1936, 1955, 1960; Biegert 1936, 1957; Delattre and Fenart 1954, 1960; Delattre 1958; Dambricourt Malassé 1987, 1988, 1993, 1996; Chaline 1998). New fossil finds, taxonomic revisions, and phylogenetic analyses have also highlighted many foci of variation in the skull (Wood 1992; Lierberman 1999). Accordingly, a number of morphometric studies have approached hominoid cranial evolution in an explicitly multivariate context (e.g., Boyce 1964; Oxnard 1975; Shea 1985; Godfrey and Sutherland 1996; Lynch et al. 1996; Chaline et al. 1998; Eble 2002a; Lierberman et al. 2002).

Nevertheless, many debates on human evolution have been dominated by a focus on traits such as bipedalism or cranial capacity taken individually. Emphasis on a few selected traits appears to be variously motivated by assumptions about their adaptive importance and ecological consequences, by an emphasis on apomorphic over plesiomorphic change, and by the perception that other traits are conditioned on their preexistence. As a result, the application of multivariate morphometrics to biological anthropology and paleoanthropology is still limited.

The hominoid evolutionary tree is a bush, and different lineages may have been subject to different selective pressures, population bottlenecks, and patterns of correlated evolution.
Assessing morphological variation in multivariate fashion allows for better detection of such lineage-specific evolutionary patterns, and broadens the scope of evolutionary analysis by allowing consideration of multiple traits as components of fitness in multivariate selection (Lande and Arnold 1983), as modules of organization (Riedl 1978), or as potentially neutral units of phenotypic redundancy (Rice 1998). In this context, recent analytical and conceptual approaches in evolutionary paleobiology, such as disparity (Gould 1991; Foote 1997) and morphospace (Raup 1966; McGhee 1999), can help refine the documentation and interpretation of multivariate patterns of hominoid evolution (Eble 2002a).

The development of new methods of shape analysis, and especially of methods based on the description of morphology by landmarks (topologically homologous points) (e.g., Sneath 1967; Siegel and Benson 1982; Bookstein 1991) means the question of shape changes can now be tackled with increased rigour. Such methods are often grouped under the general term "geometric morphometrics". They can prove especially relevant for quantifying skull shape, identifying morphological themes, and assessing the magnitude of evolutionary differences between and among species. In this study, we apply such methods to a sample of hominoid skulls, including higher apes (Pongo, Gorilla, Pan), australopithecines (Australopithecus africanus, A. boisei), early humans (Homo ergaster - H. erectus - H. neandertalensis) and modern humans (H. sapiens).

Our main objectives are (1) to visualize and quantify at the adult stage the morphological differences among these species using geometric morphometrics; (2) to estimate disparity for various taxon pairs; and (3) to present a synthesis of the major morphological events that marked evolutionary transitions in hominoid evolution.
Material and Methods

Studied skulls. — In macroevolutionary studies, interspecific variation is the focus of morphological analyses, and the assumption that intraspecific differences are comparatively smaller is often appropriate to address questions related to disparity and morphospace occupation. Accordingly, we are interested primarily in broad patterns of skull transformation, for which each taxon can be represented only once in the analysis. However, we also included additional specimens to address, in exploratory fashion, possible confounding factors associated with intraspecific variation: comparability of measurements on otherwise similar specimens (Pongo), sexual and size dimorphism (Gorilla), controversial taxonomic status (Australopithecus boisei), and wide temporal or geographic distribution (Homo erectus). In total, fifteen skulls were used to characterize morphological changes in higher apes and hominids at the adult stage. Skulls of modern individuals were used for extant species, while high quality casts were used for fossil hominids. They are coded as follows:

CERCO - Cercopithecus sp, female, Present, UMR-CNRS 5561, Dijon, France, used as outgroup.
PONGO 1 - Pongo pygmaeus, female, Present, IPH, UMR-CNRS 9948, Paris, France.
PONGO 2 - Pongo pygmaeus, female, Present, IPH, UMR-CNRS 9948, Paris, France.
GORI 1 - Gorilla gorilla, female, Present, UMR-CNRS 5561, Dijon, France.
GORI 2 - Gorilla gorilla, male, Present, UMR-CNRS 5561, Dijon, France.
GORI 3 - Gorilla gorilla, male, Present, IPH, UMR-CNRS 9948, Paris, France.
BONO - Pan paniscus, female, Present, IPH, UMR-CNRS 9948, Paris, France.
AU PL5 - Australopithecus africanus, Sts 5, 2.4-2.7 Ma, Sterkfontein, South Africa.
AU OH5 - Australopithecus boisei (Zinjanthropus boisei), OH5, 1.75 Ma, Olduvai, Tanzania.
AU 406 - *Australopithecus boisei*, KNMER 406, 1.6 Ma, Koobi Fora, Kenya.

H 3733 - *Homo ergaster*, KNMER 3733, 1.75 Ma, Koobi Fora, Kenya.

EREC 1 - *Homo erectus* (Pithecanthropus VIII), 700 Ka?, Sangiran, Java.

EREC 2 - *Homo erectus*, 400 Ka, Broken Hill, Zambia.

NEANDER - *Homo neandertalensis*, 40 Ka, La Chapelle-aux-Saints, Corrèze, France.

SAPI - *Homo sapiens*, female, Present, UMR CNRS 5561, Dijon, France.

*Landmarks.* — The homologous exocranial points selected are single points in the sagittal plane, and bilaterally symmetrical twin points, but recorded only on the right side (Fig. 1A-F). We endeavoured to select standard anthropological landmarks that are generally located at the junction of bone sutures to ensure they were homologous. The landmarks fall into two main categories (*sensu* Bookstein 1991): (1) juxtaposition points at the junction of bone sutures; (2) extremal points corresponding to less precisely localized landmarks (such as points of tangency).

Single points in the sagittal plane:

1. Prosthion (Pr): the anteriormost point of the alveolar margin of the maxilla between the upper incisor teeth (1).

2. Nasospinale (Ns): the midpoint on the tangent to the lower edges of the nasal aperture at the suture of the two maxillae (1).

3. Nasion (Na): the point of junction of the fronto-nasal and inter-nasal sutures, the root of the nose (1).

4. Glabella (Gl): the most anterior point in the midline at the level of the supra-orbital ridges, when the skull is in the Francfort plane (2).

5. Bregma (Br): the point of junction of the coronal and sagittal sutures (1).

6. Lambda (La): the point of junction of the sagittal and lambdoidal sutures (1).

7. Opisthocranion (On): the most posterior point of the skull oriented in the Francfort plane (2).
8 - Inion (In): the most prominent point of the external occipital protuberance (2).
9 - Opisthion (Op): the midpoint of the posterior margin of the foramen magnum (2).
10 - Basion (Ba): the midpoint of the anterior margin of the foramen magnum (2).
11 - LBoS: basioccipital-basisphenoid suture (1).

Symmetrical twin points (coordinates are taken from the right half of the skull only):
12 - Zygomaxillare (Zm): lower anterior point of the maxillo-malar suture (anterior part of the zygomatic arch) (2).
13 - Zygion (Zy): most salient lateral point of the zygomatic arch measured on the jugal suture (1).
14 - Orbitale (Or): sub-orbital point measured on the suture with the maxilla (1).
15 - Fronto-malar-orbital (Fm): point on the lateral orbital edge, on the anterior part of the fronto-malar suture (1).
16 - Maxillo-frontal or dacryon (Mf): point on the maxillo-frontal suture in line with the lower lacrymal crest (1).
17 - Minimum frontal width (LFm): back from the orbital arch, at the junction of the sphenoid-parietal-frontal bones (1).
18 - Stephanion (St): point at the junction of the fronto-parietal suture and the upper temporal line (1).
19 - Porion (Po): uppermost point on the margin of the external auditory meatus (ear-hole) (1).
20 - Mastoid process (Ma): lowest point of the mastoid (2).
21 - Posterior zygomatic arch point (Azp): posteriormost point of the zygomatic apophysis as viewed from below (2).
22 - Posterior point of M³ [or its alveolus (socket)]: point marking the posterior part of the alveolar arch of the maxilla (1).
Angles. — The description of skull shape based on homologous points was supplemented by two angular measurements, in order to better visualize occipital tilting and facial retreat (Fig. 2): the foraminal angle and the facial angle.

The foraminal angle is the angle formed by the foramen magnum (landmarks 9-10) with the Francfort plane (defined by landmarks 14 and 19) in the sagittal plane (Fig. 2A). Viewing the skull from the right, we used negative values when point 9 was higher than point 10, with the foramen magnum plane cutting the Francfort plane posteriorly, and positive values when point 10 was higher than point 9 with the foramen magnum plane cutting the Francfort plane anteriorly. These angular values correspond to the trigonometric direction of rotation. The angle is similar but not identical to the "angle foraminien" of Perez (in Delattre 1958), which is based on the horizontal vestibular plane determined by the plane of the semi-circular external canals (difficult to locate on fossil skulls).

The facial angle is the angle formed in the sagittal plane by the straight line containing landmarks 1 (prosthion) and 3 (nasion) and the straight line perpendicular to the Francfort plane through landmark 3 (Fig. 2B). This angle provides an estimation of the tilt of the face and consequently of prognathism, which is more marked when the angle is larger. It is always positive in the trigonometric direction of rotation.

Methods. — Measurements were made in 3D with a 3D Digitizer (Hyperspace™). The skulls were positioned on the digitizer table using a directional needle to match the sagittal plane with the digitizer XY plane. The Francfort plane was oriented parallel to the YZ plane of the digitizer. All the measurements were thus made on the right half of the skulls. The morphology of the skull was represented by 22 landmarks, whose X, Y and Z coordinates were digitized.

To examine the general distribution of taxa in morphospace, we performed a Q-mode principal component analysis of a matrix containing the angle cosines between objects, with the 66 landmark coordinates treated as raw variables. A step in the calculation of cosines
between vectors is row normalization, which standardizes for size differences while retaining
the proportionality of variables (Reyment and Jöreskog 1993). The loadings on the first three
rotated principal components, summarizing 99.5% of the total variance, were used for
plotting.

We employed superimposition methods ("Procrustes methods" -- Chapman 1990a, b) to
model pairwise shape differences. The specimens are represented by a set of landmarks and
the difference between two specimens is expressed by a vector field minimized by an
appropriate criterion (Rohlf and Bookstein 1990). Here, the landmarks were projected onto
three orthogonal reference planes corresponding to the sagittal plane, the Francfort plane, and
the ortho-sagittal (or coronal) plane, and analyzed independently in 2D. Comparisons were
made with the Procrustes 2.0 program (David and Laurin 1992) using the LS option (based
on a least square fit -- Sneath 1967), which reduces all the specimens to a centroid size of 1.
Complementary RF analyses (based on a resistant fit -- Siegel and Benson 1982) were
carried out to check if some parts might be strictly similar. Since the shape changes recorded
between the specimens under comparison are evenly distributed among the landmarks, only
the LS results are presented below. Multiple comparisons (involving all the specimens) were
undertaken using the Procrustes distance (sum of the squared vector lengths, $\sum \Delta^2$) to
characterize the overall shape differences between each pair of specimens. The $\sum \Delta^2$ matrix
was then processed with the FITCH program of the PHYLIP package (Felsenstein 1990) to
compute additive morphological distance trees.

While disparity is usually quantified and conceptualized in terms of total variance or total
range, it can also be approached at the finer scale of pairwise disparity, and allow different
questions to be addressed. A notion of pairwise disparity has been used in studies of nearest
neighbors (Foote 1990), of ancestor-descendant divergence (Wagner 1995), and of
developmental disparity (Eble 2002a,b). For studies of human evolution, where sample sizes
are usually small and specific evolutionary transitions are analyzed in much detail,
quantification of pairwise disparity may be most appropriate, and we will therefore center on it, using the Procrustes distance as a metric.

**Morphospace Projection**

Figure 3 portrays the positions of skulls in principal component space. PCI accounts for 97% of the variance. Loadings are all positive and high, but they do reveal patterns apparently unrelated to size differences. The PCI-PCII projection effectively distinguishes, to different degrees, *Homo neandertalensis* (NEANDER), *Homo sapiens* (SAPI), and EREC 2 (*Homo erectus*) from a cluster that includes australopithecines, EREC 1 (*Homo erectus*) and H 3733 (*Homo ergaster*). This cluster in turn is distinguishable from great apes, which are distributed in smaller clusters. GORI 1 (female) is positioned away from GORI 2 and GORI 3 (males), with an implied distance larger than that separating australopithecines, for example.

The PCII-PCIII projection also appears to separate great apes from hominids, and to place australopithecines, *Homo ergaster* and *Homo erectus* as intermediate. Overall, however, clusters are less clear-cut. Wide separation among australopithecines is present, as well as among gorillas, though here it is GORI 3 that is positioned away.

This global signal is informative, and seemingly robust to analytical method, since correspondence analysis and principal coordinate analysis on the same data produced similar results. However, the arrangement of taxa in ordination space but must be viewed as a summary only. It suggests patterns of clustering that can be tested with cluster analyses, and invites more detailed analysis of the nature of skull differences between taxa.

**Pairwise Disparity**

Based on the computation of Procrustes distances ($\sum \Delta^2$) between all specimens, phenetic trees were built, using *Cercopithecus* as a root (Fig. 4, 5, 6). The following observations can be made for each plane:
Sagittal plane (Fig. 4). — For the sagittal plane, the most substantial differences separate the great apes from australopithecines and australopithecines from early Homo, respectively. Three subsets can be identified within the tree. The first is fairly heterogeneous and groups the great apes together. The large gap between the different gorilla skulls is consistent with the strong sexual dimorphism of the species. The female gorilla is morphologically intermediate between Pongo and the bonobo. Of the three gorillas studied (two of which were males), it is also the closest to the hominids. The second subset encompasses the australopithecines. The third subset includes all of the primitive and modern humans in an arrangement which is consistent with phylogeny. In this plane, modern humans are not strongly separated from primitive humans.

Francfort plane (Fig. 5). — This plane reveals large inter-node distances and generally fairly short terminal branches. The three groups previously identified stand out again. The subset including primitive and modern Homo is noticeably separate from the rest of the tree. The australopithecines are well grouped but not very distant from the great apes. The latter are divided into two subsets: Asian orangutans and African gorillas and bonobos.

Ortho-sagittal plane (Fig. 6). — This plane exhibits markedly different morphological relations from those found for the other two planes. Generally, the distances (inter-nodes and terminal branches alike) are more heterogeneous. While primitive and modern humans are clearly segregated, australopithecines are mixed with the great apes. In this plane modern humans are most clearly distinct from primitive humans as the terminal branch of SAPI is longer than the terminal branches of other Homo.

The preceding disparity analyses based on exocranial homologous points seem to suggest the existence of three relatively discrete sets (see Table 1 and 2): "Great Ape", "Australopithecine", and "Homo":
1. The "Great Ape" set is the least homogeneous and is most distinctive in the sagittal plane. This morphological heterogeneity may be related to the earlier phyletic diversification of the great apes.

2. The "Australopithecine" set is clearly individualized in the sagittal and Francfort planes. It is strictly intermediate between the higher apes and humans in the sagittal plane, whereas in the Francfort plane it is closer to that of the higher apes.

3. The "Homo" set is very clearly individualized whichever plane is considered. Homo ergaster (H 3733) and Homo erectus (EREC 1) are located at the base of the Homo group. African Homo erectus (EREC 2) is invariably in an intermediate position and Homo sapiens is consistently associated with Neandertal Man. Homo sapiens is morphologically more distinct in the ortho-sagittal plane.

These three sets can be viewed as representing different anatomical patterns of skull organization. We consider them to be three organization plans ("Baupläne") and refer to them below as "skull plans". Because of extensive temporal overlap, and insofar as we assimilate the extant great apes to their Tertiary ancestors (which have a similar architectural design -- Dambricourt Malassé 1988), comparisons among such skull plans are only a working hypothesis about the partitioning of hominoid morphospace, and not an evolutionary model in the strict sense.

**Morphological Changes Between Skull Plans**

From the "Great Ape" Skull Plan to the "Australopithecine" Skull Plan

In this study we used Gorilla as representative of the general "Great Ape" skull plan. Phylogenetically, it is generally accepted that the "Australopithecine" skull plan is derived from that of the great apes. However, different authors give different taxonomic interpretations to the diversification of the australopithecine lineage: as a single species, as a
single genus with several species, or as several genera (Johanson et al. 1978; Coppens 1986; Dean 1986; Kimbel and White 1988; Conroy et al. 1990; Wood 1992; McCollum 1994). In the present study the "Australopithecine" skull plan encompasses the following specimens: Australopithecus africanus (AU PL5 from Sterkfontein), Australopithecus boisei (AU OH5 from Olduvai, formerly known as Zinjanthropus boisei) and Australopithecus boisei (AU 406 from Koobi Fora).

Comparison of GORI 2 (male, with sagittal crest) with AU OH5 (with sagittal crest). — The following characters, in order of importance, accompany the three-dimensional changes (Fig. 7):

1- positive occipital rotation (mostly point 8 and to a lesser extent points 6 and 7) visible in the sagittal and ortho-sagittal planes;
2- very marked recession of the face (points 1, 2) visible in the sagittal and Francfort planes, associated with a strong downward shift of point 1 (ortho-sagittal plane) and with backward shift of point 22;
3- elevation and forward shift of the bregma, stephanion and zygion (points 5, 18 and 13);
4- rise of the clivus (point 11);
5- the rise of the anterior end of the foramen magnum (point 10) associated with the stability of its posterior edge (point 9) leads to its almost horizontal position (the foraminal angle shifts from -47° to -6°);
6- upward extension of the zygomatic arch (point 21).

Comparison of GORI 1 (female, without sagittal crest) with AU PL5 (without sagittal crest). — In the three planes analyzed (Fig. 8), the main changes in skull morphology are:

1- positive occipital rotation corresponding to a downward shift of points 7, 8;
2- very marked combined elevation and forward shift of the bregma and stephanion (points 5, 18);
3- elevation of the post frontal area (point 17);
4- slight recession and marked reduction in height of the face (point 1 and point 2 and 12 to a lesser extent).

In retrospect, the main changes from the “Great Ape” skull plan to the “Australopithecine” skull plan are: (1) a marked cranio-facial contraction, (2) a marked expansion of the skull which is readily visible in the elevation of the bregma and stephanion in all australopithecine forms, (3) a separation of the bregma and stephanion only in those forms with no sagittal crest, and (4) a more horizontal position of the foramen magnum in forms with sagittal crests. The morphological changes give rise to average values of $\Sigma \Delta^2$ that fluctuate around 1 standardized measurement unit in the sagittal and Francfort planes, and which exceed 2 standardized measurement units in the ortho-sagittal plane (Table 1).

From the "Australopithecine" Skull Plan to the "Homo" Skull Plan

The "Homo" skull plan is derived from the "Australopithecine" skull plan and has endured for nearly 2 Myr. The transition from "Australopithecine" to "Homo" skull plan is documented in our analysis by the following skulls: Australopithecus africanus (AU PL5 from Sterkfontein) and Homo ergaster (H 3733 from Koobi Fora, Kenya).

**Comparison of AU PL5 with H 3733.** — In the three planes analyzed (Fig. 9), the main changes in skull morphology are:

1- occipital expansion of the cranial vault (points 5, 7, 8); the relative stability of the stephanion (point 18) leads to new separation with the bregma (point 5);
2- the antagonistic shift of points 9 and 10 leads to tilting of the foramen magnum which is raised anteriorly; the foraminal angle changes from -17° to + 16°;
3- lowering of the anterior part of the maxilla (point 1) and rise of its posterior part (point 22) in a tilting movement; the relative stability of point 3 on the facial-occipital axis, combined with the posterior drift of point 1, produces a facial angle of about 13° in Homo (32° in AU PL5);
4- the anterior part of the zygomatic arch moves downwards (points 12 and 13);
5- the mastoid process shows a slight displacement but in the three directions of space (point 20 and 19 to a lesser extent);
6- slight rise of the clivus (point 11).

Thus, the transition from the “Australopithecine” skull plan to the “Homo” skull plan involves: (1) advancing and tilting of the foramen magnum from negative to positive values (direction of tilt relative to the horizontal plane being reversed between one skull plan and the other), (2) broadening of the frontal bone and marked separation of the bregma from the stephanion. The former can in fact be seen as one of the defining characteristics of the genus Homo and is the result of a new phase of cranio-facial contraction. The morphological changes correspond to average values of $\Sigma \Delta^2$ that are close to those obtained in the comparisons between great apes and australopithecines: they are slightly greater than 1 standardized measurement unit in the sagittal and Francfort planes, and exceed 2 standardized measurement units in the ortho-sagittal plane (Table 1).
Morphological Changes Within Skull Plans

Within the "Great Ape" Skull Plan (Fig. 10)

Two specimens of *Pongo pygmaeus*, one of *Pan paniscus* and three specimens of *Gorilla gorilla* (1 female: GORI 1; 2 males: GORI 2 and 3) here illustrate the "Great Ape" skull plan. We focus on three comparisons: two between genera and one addressing sexual dimorphism.

**Comparison of PONGO 1 with GORI 1** (inter-genera comparison: Fig. 10A). — In the three planes analyzed, the greatest changes in skull morphology are:

1- retreat and fusion of the bregma (point 5) and stephanion (point 18) are clearly visible in all three planes, especially the Francfort and ortho-sagittal planes;
2- slight recession of the face (point 1) visible in the sagittal and Francfort planes;
3- advance of the supraorbital ridge (points 3, 4) in the sagittal and Francfort planes and elevation in the ortho-sagittal plane;
4- advance of the orbits (points 15, 16) in the sagittal plane only, and very marked elevation of point 16 in the ortho-sagittal plane;
5- lateral extension of the mastoid (point 20) visible in the Francfort and ortho-sagittal planes.

**Comparison of BONO with GORI 1** (inter-genera comparison). — The two skulls are fairly similar, except at the bregma (point 5) and stephanion (point 18), which are fused in the gorilla. The foraminal angle is -17° in both species.

**Comparison of GORI 2 (male, with sagittal crest) with GORI 1 (female, without sagittal crest)** (sexual dimorphism: Fig. 10B). — It is worthwhile to estimate the magnitude of morphological difference associated with sexual dimorphism, as it may mimic disparity.
among species. Some degree of shape dimorphism is expected in the great apes, as males usually have a sagittal crest but it is always absent in females.

In the three planes analyzed, the major changes in skull morphology are:
1- positive occipital rotation (i.e. the skull winds backwards around itself) very conspicuous in the sagittal (point 8) and ortho-sagittal planes (points 6, 7, 8);
2- marked recession of the face (points 1, 2) in the sagittal plane, but only of point 1 and of point 2 in the ortho-sagittal and Francfort planes respectively; slight change in the facial angle from 33° to 29°;
3- marked elevation of the maxillo-frontal suture (point 16);
4- lateral extension and elevation of the mastoid (point 20);
5- very slight elevation and recession of the bregma and stephanion (points 5, 18) visible in all three planes;
6- slight rise of the clivus (point 11) and of the zygion (point 13) in the sagittal plane;
7- antagonistic drift of points 9 and 10 leading to a change of the foraminal angle from -47° to -17°, bringing the foramen magnum to a more horizontal position.

In summary, the differences recorded among genera and species of great apes are relatively small (small $\Sigma \Delta^2$: mean of 0.64 and 0.52 standardized measurement units in the sagittal and Francfort planes, greater than 1 unit (1.24) in the ortho-sagittal plane only: Table 1). Notice that the differences related to sexual dimorphism (gorillas) are of the same order of magnitude as certain differences between genera within the "Great Ape" skull plan.
Within the "Australopithecine" Skull Plan (Fig. 11)

Here we compare *Australopithecus* africanus from Sterkfontein to *Australopithecus* boisei from Olduvai.

**Comparison of AU OH5 (with sagittal crest) with AU PL5 (without sagittal crest).** — In the three planes analyzed, the major changes in skull morphology are:

1- positive occipital rotation related to the downward shift of points 7 and 8 (particularly visible in the ortho-sagittal plane);
2- elevation of the post frontal area (point 17);
3- elevation and slight advance of the base of the face (points 1 and 2) visible in the ortho-sagittal and Francfort planes respectively; this is reflected by a lower facial angle in AU OH5 (approximately 17°) than in AU PL5 (32°), but a less elevated face in the latter;
4- slight lowering of the clivus (point 11) in the ortho-sagittal plane;
5- lowering of the foramen magnum (points 9, 10); correlatively the foraminal angle changes from -7° to -17°;
6- lateral expansion of the skull (point 18) related to a dissociation of the bregma-stephanion (points 5-18);
7- rise of the zygomatic arch (points 12, 13).

Morphological disparity is of the same order of magnitude as in the "Great Ape" skull plan in the sagittal and Francfort planes (on average 0.6 standardized measurement units), and noticeably higher in the ortho-sagittal plane (mean = 1.84).
Within the "Homo" Skull Plan (Fig. 12)

We analysed the changes within the "Homo" skull plan at three levels: (1) *Homo ergaster* [H 3733] versus *Homo erectus* of Broken Hill [EREC 2]), (2) EREC 2 versus NEANDER, to address the phenomenon of neandertalization; and (3) in the transition from *Homo erectus* to *Homo sapiens* (EREC 2 versus SAPI).

*Comparison of H 3733 with EREC 2 (Fig. 12A).* — In the three planes analyzed, the most important changes in skull morphology are:

1. elevation of the bregma (point 5) in conjunction with lowering and lateral extension of the stephanion (point 18);
2. uplift of the posterior part of the foramen magnum (point 9) and small advance of its anterior edge (point 10); consequently, the foraminal angle shifts from $+16^\circ$ to $+3^\circ$;
3. lowering of the prosthion (point 1);
4. lowering of the face (point 16) and of the post-frontal area (point 17);
5. rise of the malar (point 15) and zygion (point 13).

From *H. ergaster* to *H. erectus*, changes are relatively limited and distributed over a large number of vectors. If the comparison is extended to the Asian representative from Java (EREC 1), one can notice the occurrence of two separate trends in *Homo erectus* with respect to changes at the back of the skull. Cranial capacity increases as the skull lengthens posteriorly (recession of the lambda) and anteriorly (advance of the bregma and stephanion) in the Asian form. This is a cranial extension which heralds Neandertals. In the Asian form (EREC 1) the lambda and opisthocranion meet whereas in the African form (EREC 2) they remain separate.
Comparison of EREC 2 (Broken Hill) with NEANDER (Fig. 12B). — In the three planes analyzed, the major changes in skull morphology are:

1- marked forward extension and lowering of the stephanion (point 18) and to a lesser extent of the bregma (point 5);
2- lowering of the clivus (point 11);
3- marked lateral rise of the frontal bone (point 17);
4- uplift of the prosthion (point 1);
5- small anterior extension of the maxilla (point 13);
6- slight recession of the foramen magnum (points 9, 10); the foraminal angle changes from +3° to -6°;
7- slight recession of the mastoid process (point 20).

Between Homo erectus and Homo neandertalensis, neandertalization in the "Homo" skull plan is manifested by features such as (1) the "retreat" of the foramen magnum, and (2) the noticeable advance of the stephanion, which correlates with the substantial increase in cranial capacity in all directions.

Comparison of EREC 2 (Broken Hill) with SAPI (present-day) (Fig. 12C). — Homo sapiens appeared about 180 Ka ago (Vigilant et al. 1991; Tishkoff et al. 1996), presumably from late Homo erectus populations in South Africa (Border Cave), East Africa (Omo Kibish 1) and in Asia Minor (Qafzeh, Skhul). Mitochondrial DNA analyses (Cann et al. 1987; Vigilant et al. 1991; Horai et al. 1992; Tishkoff et al. 1996) strongly support an African origin of Homo sapiens (180 to 143 Ka ± 18 Ka B.P.). This interpretation has been corroborated by the absence of polymorphism at the ZFY (zinc-finger exon) locus on the human Y chromosome (Dorit et al. 1995). Because of the probable African origin of Homo sapiens, only comparison with the Broken Hill skull is discussed.
From *Homo erectus* (EREC 2) to *Homo sapiens*, the morphological changes are as follows in the various planes:

1- very marked lateral and vertical expansion of the post-frontal area (point 17);
2- marked reduction of the face particularly visible on the prosthion (point 1);
3- marked lateral and facial expansion of the stephanion (point 18), corresponding to a continuation of the trend towards separation of points 5 and 18;
4- lowering of the inion (point 8) which descends below the Francfort plane;
5- marked descent of the *foramen magnum* (points 9, 10) with almost no change in orientation of the foraminal angle, which shifts from +3° to +8°;
6- slight rise of the lambda (point 6) and the bregma (point 5).

The differences between *Homo sapiens* and *Homo erectus* are close to those seen in the transition from the "Australopithecine" to the "Homo" skull plan and result from the resumption of cranio-facial contraction. Positive occipital rotation is expressed by lowering of the inion, which moves below the Francfort plane. Marked contraction of the face reduces sub-nasal prognathism and is associated with the disappearance of the supraorbital ridge (recession of points 3 and 4: the face becomes vertical). Whereas cranial capacity in *Homo erectus* was distributed more lengthwise because of occipital extensions, in *Homo sapiens* cranial capacity is increased upwards and downwards by the extension of the bregma, stephanion, lambda and inion, and by the widening of the frontal bone and the lowering of the *foramen magnum*.

Morphological disparity is relatively low within the "Homo" skull plan (average $\sum \Delta^2$ less than 0.6 standardized measurement units in the sagittal and Francfort planes, and less than 1 unit in the ortho-sagittal plane: Table 1). This is true in particular of the magnitude of morphological change observed between *Homo erectus* and *H. sapiens*: 0.58, 0.41 and 0.99 units in the three skull plans respectively when comparing EREC 2 and SAPI.
**Discussion**

The rates of shape change between the three skull organization plans identified from the distance trees ("Great Ape", "Australopithecine" and "Homo") are invariably greater than the rates of shape change within these skull plans (Table 1). Single factor ANOVA suggests that the type of comparison (intra-plan or inter-plans) has a highly significant impact on Procrustes distances. Scheffe tests allowed determination of how the 86 possible cross comparisons depart from each other (Table 2). It appears that the three sets of intra-skull plan comparisons have morphological distances of the same order of magnitude; a single significant difference occurs for the ortho-sagittal plane between the intra-Australopithecine and the intra-*Homo* skull plans. These results strongly suggest that the three skull plans identified are actual morphological entities.

There is no basis in our results for recognizing a Neandertal skull plan. Likewise, the distinction of a "sapiens" plan, which was done on the basis of the mandible only by Dambricourt Malassé (1987), is not confirmed for cranial data by this study. This limited differentiation of *Homo sapiens* may stem from the fact that (1) its separation from *Homo erectus* is recent on the geological scale, less than 200 Ka, (2) that it displays few unique features compared with the "*Homo*" ancestral form from which it is derived, and (3) that the allometric variability associated with growth trajectories in *Homo* is either fundamentally limited or had already been extensively deployed by previous species within the genus. The disappearance of the supraorbital ridge, presumably as a result of hypomorphosis, contributes only very slightly to the total morphological change between the two species (Chaline et al. 1998). In contrast, increased cranial capacity, which is a major evolutionary characteristic of the human lineage, is not reflected by the landmark-based methods used here, as they tended to eliminate size effects.

Within the "*Homo*" skull plan, apparent evolutionary trends are observed in both Asian and African forms. From *Homo erectus* to *Homo neandertalensis* in Eurasia (Fig. 12B),
characteristic changes led to a posterior extension of the skull, to a posterior retreat of the foramen magnum to a position nearly similar to that of australopithecines, and to a lowering of the cranial vault accompanied by a shortening of the face. Concomitantly, cranial capacity increased substantially. From Homo erectus to Homo sapiens in Africa (Fig. 12C), there is a resumption of a trend observed during the transition from the "Australopithecine" to the "Homo" skull plan, namely renewed cranio-facial contraction. Positive occipital rotation is amplified. The face contracts to such an extent that it reduces sub-nasal prognathism. Cranial capacity increased both upwards and downwards. Cranial capacity aside, for each of these trends in skull shape the extent of morphological change remained within the intra-plan range of variation.

Conclusions

The landmark-based morphometric approach here applied to adult hominoid skulls enables us to visualize and quantify the magnitude and amplitude of morphological changes leading from Great Apes to modern humans. From the common ancestor (represented by the modern "Great Ape" skull plan) to modern humans, there are two major steps of cranio-facial contraction separating a succession of three statistically distinct organization plans. The segregation of these three skull plans in hominoid evolution implies that shape change between plans is significantly greater than between species within each plan (Table 1 and 2).

Figure 13 recapitulates the morphological changes observed between the three skull plans in the sagittal plane. It emphasizes the overall cranio-facial contraction that occurred in several transitions and that entailed reshaping of the skull outline and the tilting of the foramen magnum.

The transition from the "Great Ape" to the "Australopithecine" skull plan is reflected in a positive occipital rotation, which winds the skull on itself at the rear (Fig. 7 and 8), confirming the observations of Delattre (1952, 1958), Delattre and Fenart (1954, 1960), and
Occipital rotation, in turn, is combined with a recession of the face. This cranio-facial contraction is accompanied by upward expansion of the cranial vault. The supraorbital ridge falls slightly forward. The bregma and stephanion, which are closely associated in *Gorilla*, are maintained in robust australopithecines (AU OH5 and AU 406), but are clearly separated in the *africanus* form (AU PL5). For this character, robust australopithecines are more *Gorilla*-like than *africanus*. All these changes are associated with an increase in brain size.

A major change separating the "Australopithecine" skull plan from the "*Homo*" skull plan is the new phase of cranio-facial contraction (Fig. 9) with occipital flexion, which moves forward and tilts the *foramen magnum*. This tilt is arguably the most prominent feature of the genus *Homo* (Delattre, 1958), and is necessary for bipedalism. It is accompanied by a posterior extension of the skull and by a broadening of the frontal bone, which separates the bregma and stephanion, a further characteristic of the genus *Homo*. Concurrently, cranial capacity continued to increase. While bipedalism and cranial capacity are cornerstones of hominoid evolution, the skull shapes that lie in between are not causally inert. The quantifiable organizational and transformational regularities they exhibit make them relevant components of macroevolutionary sorting.

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Figure captions

FIGURE 1. Cranial landmarks. A-B): Sagittal plane landmarks; A) single cranial landmarks in the sagittal plane; B) cranial landmarks in parasagittal planes (planes parallel to the sagittal plane), seen from the right half of the skull only. C-D): Landmarks in the Francfort plane; C) skull viewed from above; D) skull viewed from below. E-F): Landmarks in the ortho-sagittal plane; E) front view; F) rear view.

FIGURE 2. Cranial angles measured. A) foraminal angle; B) facial angle.

FIGURE 3. Morphospace occupation of hominoid sample, as inferred from a Q-mode principal components analysis of a matrix of angle cosines between object vectors. PC I is plotted against PC II (top) and PC II is plotted against PC III (bottom).

FIGURE 4. Distance tree for the sagittal plane, depicting morphological relationships among 14 adult specimens representing great apes and hominids. SAPI = Homo sapiens, NEANDER = Homo neandertalensis, EREC = Homo erectus, H 3733 = Homo ergaster, AU OH5 = Australopithecus boisei, AU PL5 = Australopithecus africanus, AU 406 = Australopithecus boisei, BONO = Pan paniscus, GORI = Gorilla gorilla, PONGO = Pongo pygmaeus. Cercopithecus sp. (CERCO) is used as outgroup to root the tree. The tree is computed with the Fitch program of the PHYLIP package using Procrustes distances ($\Sigma A^2$). See text for additional explanation.

FIGURE 5. Distance tree for the Francfort plane, depicting morphological relationships among 14 adult specimens representing great apes and hominids. Labels and procedure as in Figure 4.
FIGURE 6. Distance tree for the ortho-sagittal plane, depicting morphological relationships among 14 adult specimens representing great apes and hominids. Labels and procedure as in Figure 4.

FIGURE 7. Comparison of "Great Ape" and "Australopithecine" skull plans. Least square analyses of morphological differences between Gorilla gorilla (GORI 2, male) and Australopithecus boisei (AU OH5). A) Sagittal plane of the skull; B) Francfort plane; C) Ortho-sagittal plane. Points with no vector indicate zero or negligible morphological difference. Vectors indicate significant changes; vector direction and length specify the orientation and intensity of the morphological differences. The ringed cross marks the center of gravity. Boxed numbers refer to landmarks of the face and ringed numbers refer to landmarks of other parts of the skull.

FIGURE 8. Comparison of "Great Ape" and "Australopithecine" skull plans. Least square analyses of morphological differences between Gorilla gorilla (GORI 1, female) and Australopithecus africanus (AU PL5). Labels and conventions as in Figure 7.

FIGURE 9. Comparison of "Australopithecine" and "Homo" skull plans. Least square analyses of morphological differences between Australopithecus africanus (AU PL5) and Homo ergaster (H 3733). Labels and conventions as in Figure 7.

FIGURE 10. Least square morphological differences within the "Great Ape" skull plan. A): between the species Pongo pygmaeus (PONGO 1, female) and Gorilla gorilla (GORI 1, female; B): variations related to sexual dimorphism (comparison of Gorilla gorilla (GORI 2, male) and Gorilla gorilla (GORI 1, female). Labels and conventions as in Figure 7.
FIGURE 11. Least square morphological differences within the "Australopithecine" skull plan, between the species Australopithecus boisei (AU OH5) and Australopithecus africanus (AU PL5). Labels and conventions as in Figure 7.

FIGURE 12. Least square morphological differences within the "Homo" skull plan. A): between the species Homo ergaster (H 3733) and Homo erectus (EREC 2); B): between the species Homo erectus (EREC 2) and Homo neandertalensis (NEANDER); C): between the species Homo erectus (EREC 2) and Homo sapiens (SAPI). Labels and conventions as in Figure 7.

FIGURE 13. Simplified outline (in the sagittal plane) of the three skull plans identified. The arrows summarize the main directions of morphological change: the black arrows show cranio-facial contraction and upper vault reshaping, while the grey arrows show tilting of the foramen magnum, the direction of tilt relative to the horizontal plane being reversed between the "Australopithecine" and the "Homo" skull plans.
TABLE 1. Average morphological distances (Procrustes distances $[\sum \Delta^2]$ computed by a least square procedure) for the three cranial planes within and between the three identified skull plans (intra-plan comparisons are in bold print).

<table>
<thead>
<tr>
<th>Organization Plan</th>
<th>Cranial Plane</th>
<th>Great Ape $\sum \Delta^2$</th>
<th>Australopith. $\sum \Delta^2$</th>
<th>Homo $\sum \Delta^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sagittal</td>
<td></td>
<td>.635</td>
<td>1.24</td>
<td>1.743</td>
</tr>
<tr>
<td>Great Ape</td>
<td>Francfort</td>
<td>.517</td>
<td>.90</td>
<td>1.725</td>
</tr>
<tr>
<td>Ortho-sagittal</td>
<td></td>
<td>1.238</td>
<td>2.075</td>
<td>2.466</td>
</tr>
<tr>
<td>Sagittal</td>
<td></td>
<td></td>
<td>.577</td>
<td>1.072</td>
</tr>
<tr>
<td>Australopithecine</td>
<td>Francfort</td>
<td>.567</td>
<td>1.357</td>
<td></td>
</tr>
<tr>
<td>Ortho-sagittal</td>
<td></td>
<td>1.843</td>
<td>2.325</td>
<td></td>
</tr>
<tr>
<td>Sagittal</td>
<td></td>
<td></td>
<td></td>
<td>.59</td>
</tr>
<tr>
<td>Homo</td>
<td>Francfort</td>
<td></td>
<td></td>
<td>.416</td>
</tr>
<tr>
<td>Ortho-sagittal</td>
<td></td>
<td></td>
<td></td>
<td>.938</td>
</tr>
</tbody>
</table>
TABLE 2. Scheffé test results of comparisons of morphological distances ($\sum \Delta^2$) recorded within each skull plan and between skull plans (great apes versus Homo comparisons are not taken into account because they are phylogenetically not founded). The three "intra-" columns give results of the test for comparisons of Procrustes distances computed within a given skull plan with distances computed within another skull plan. The three "inter-" columns give results of the test for comparisons of Procrustes distances computed within a given skull plan with values obtained from crossed comparisons. "ns" stands for nonsignificant ($p > 0.05$); "S" for significant ($0.05 \geq p > 0.01$); "HS" for highly significant ($p \leq 0.01$).

<table>
<thead>
<tr>
<th>Intra-</th>
<th>Cranial Plane</th>
<th>Intra-</th>
<th>Inter-</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Great Ape</td>
<td>Australopith.</td>
</tr>
<tr>
<td></td>
<td>Sagittal</td>
<td>-</td>
<td>ns</td>
</tr>
<tr>
<td>Great Ape</td>
<td>Francfort</td>
<td>-</td>
<td>ns</td>
</tr>
<tr>
<td>Ortho-sagittal</td>
<td>-</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>Sagittal</td>
<td>-</td>
<td>ns</td>
</tr>
<tr>
<td>Australopith.</td>
<td>Francfort</td>
<td>-</td>
<td>ns</td>
</tr>
<tr>
<td>Ortho-sagittal</td>
<td>-</td>
<td>S</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>Sagittal</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Homo</td>
<td>Francfort</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ortho-sagittal</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Australopithecine

Francfort plane

Homo

FORAMINAL ANGLE
(negative or positive)

FACIAL ANGLE

CHALINE et al. : Figure 2
CHALINE et al. : Figure 4
Francfort plane

Homo

SAPI
NEANDER
EREC 2

EREC 1

H 3733

AU PL5

AU OH5

AU 406

PONGO 2

PONGO 1

GORI 2

GORI 3

GORI 1

BONO

CERCO

Australo-pithecan

Great Ape

1 standard deviation unit

CHALINE et al. : Figure 5
Ortho-sagittal plane

SAPI

NEANDER

EREC 2

H 3733

EREC 1

AU PL5

PONGO 2

PONGO 1

AU OH5

AU 406

GORI 3

GORI 2

GORI 1

BONO

CERCO

1 standard deviation unit

CHALINE et al. : Figure 6
Sagittal plane
\[ \Sigma \Delta^2 = 1.94 \]

Francfort plane
\[ \Sigma \Delta^2 = 1.18 \]

Ortho-sagittal plane
\[ \Sigma \Delta^2 = 2.38 \]

CHALINE et al. : Figure 7
CHALINE et al. : Figure 9
"GREAT APE" SKULL PLAN

A Inter-genera comparison
\[ \Sigma \Delta^2 = 0.62 \]

B Sexual dimorphism
\[ \Sigma \Delta^2 = 0.73 \]

CHALINE et al. : Figure 10
"AUSTRALOPITHECINE" SKULL PLAN

\[ \Sigma \Delta^2 = 0.74 \]

upper

Sagittal plane

facial

occipital

lower

1 standard deviation unit

CHALINE et al. : Figure 11
"HOMO" SKULL PLAN

A. From Homo ergaster to Homo erectus
\[ \Sigma \Delta^2 = 0.37 \]

B. From Homo erectus to Homo neandertalensis
\[ \Sigma \Delta^2 = 0.58 \]

C. From Homo erectus to Homo sapiens
\[ \Sigma \Delta^2 = 0.58 \]
Sagittal plane

- upper
- occipital
- facial
- lower

"HOMO" plan (H. sapiens)
"AUSTRALOPITHECINE" plan
"GREAT APE" plan