The Period of Transition between *Homo erectus* and *Homo sapiens* in East and Southeast Asia: New Perspectives by the Way of Geometric Morphometrics

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Abstract

Anatomically modern humans origin is one of the most passionately debated questions of the moment. The objective of this work, using a new methodology (3D geometric morphometrics) for studying human cranial shape evolution, is to shed some light on the evolution of the genus *Homo* in East and Southeast Asia, with African fossils for comparisons. This is a region of major palaeoanthropological interest due to the large number of fossil remains discovered beginning at the end of the 19th century. This part of the Old World is a key geographical area as far as the debate on the origin of anatomically modern humans is concerned. We present here our first results of architectural comparisons of human skulls dating from about 2.5-2 Ma to present days (from *H. habilis* to extant *H. sapiens*). We attempt to underline the main architectural differences between *Homo erectus* and *Homo sapiens*, but also to analyse eventual geographical and/or temporal intraspecific architectural variability.

Keywords: Modern humans origin; *Homo erectus; Homo sapiens;* Cranial vault; 3D geometric morphometrics; Procrustes analysis; East Asia; Southeast Asia

1   Introduction

1.1   The Origin of modern humans

Two major conflicting evolutionary models are classically proposed to explain the evolution from *Homo erectus* to *Homo sapiens*.

The replacement - or "Out of Africa" - model [1-3] considers that anatomically modern *Homo sapiens* appeared first in Africa, at the end of the Middle Pleistocene. They subsequently migrated to the Middle East and Asia about 100 ky ago and into Europe and Australia 50 ky later. During these migrations, modern humans totally replaced archaic populations without any interbreeding. This model appears to be strongly supported by the majority of recent molecular studies [4-6].

The multiregional model [7-11], inspired from Weidenreich's work, is essentially based on the observation that, to some extent, Australian Upper Pleistocene *Homo sapiens* cranial morphology is inherited from Javanese *Homo erectus* while the Chinese human fossil record would tend to show an *in situ* evolution from early *Homo erectus* to recent *Homo sapiens* [12-16]. After the dispersal of *Homo erectus* outside Africa, about 1.5 My ago, an uninterrupted gene flow allowed the gradual and continuous evolution of *Homo erectus* into *Homo sapiens* in all the regions, without population replacement. This gene flow was stronger within than between the main regions. Consequently, this heterogeneous gene flow explains the persistence of regional phenotypic differences observed on human fossils during 1.5 My [8].

However, some scholars argue in favour of less extreme models [17-18]. They propose the possibility of replacement in Europe (Neandertals replaced by modern *Homo sapiens*) and at the same time of evolutionary continuity in Asia. This evolutionary continuity could be the result of interbreeding between *in situ* archaic populations in place ("late *Homo erectus*") and the newly evolved *Homo sapiens* migrants from Africa.

1.2   Comparisons of human crania

In palaeontological studies, two main approaches based on fossils studies are traditionally used to deal with evolutionary problems. The first one is phylogenetic (mainly cladistic) and is based on characters state analyses to construct parsimonious evolutionary trees. The second one is morphometric: with a more phenotypic approach, fossil or present skeletal parts are statistically

compared to make groups of morphologically more related specimens in order to demonstrate and interpret morphological and/or morphometrical changes in the course of evolution.

For years, this second approach, mainly based on analyses of linear measurements ("traditional morphometrics"), has been used in palaeoanthropoloy to assess regional or temporal differences from human cranial morphologies. But interpretations of such analyses are often very complex and unable to account for slight variations of the geometry of anatomical parts such as human skulls. Geometrical morphometrics in three dimensions, which considers shape as a whole and uses coordinates of homologous landmarks, appears to be appropriate for the shape analysis of such a complex structure [19-20]. Procrustean landmarks superimpositions allow accurate architectural comparisons [21-22]. Separating shape from size during the study provides the possibility to investigate relationships between size and shape (allometry) and prevents the confusion arising from size and shape differences in the analysis.

We present here our first results of architectural comparisons of human skulls dating from about 2.5-2 Ma to present days (from *H. habilis* to extant *H. sapiens*). We compare the configurations of the skull cap, the best documented portion of fossil skeletons. It is also, without any doubt, the most studied human anatomical part with the other methodologies described above. This is an important point for testing and sometimes guiding some of the methodological choices we made during this study.

2 Material and methods

Indonesian *Homo erectus* from Sangiran (casts) and Ngandong (originals) and Chinese *Homo erectus* from Zhoukoudian are compared with fossil *Homo sapiens* from North Vietnam (Lang Cuom: originals), from Indonesia (Wajak, Liang Momer, Gua Nempong: originals) from China (Zhoukoudian Upper Cave) and from Australia (Cohuna). We also include comparative individuals in this sample, in particular African *Homo habilis* and *Homo erectus* / *Homo ergaster* and extant *Homo sapiens*: three extant *Homo sapiens* have been randomly chosen and three have been chosen for their geographical origin (Australia, China & Java).

2.1 Cranial landmarks

As the skull cap is very often the only preserved part of fossil skulls, we focus on this portion for architectural comparisons. As landmarks we selected classical craniometric points that modelise the global architecture as well as possible.

Twenty seven landmarks were digitized on each skull (Figure 1) using the Microscribe® 3DX digitizing arm. Seven landmarks are sagittal points and twenty landmarks are parasagittal points (ten on each side). Following the classification of Bookstein, the majority of the landmarks belongs to the type I (intersection points) and type II (maxima of curvature). They are relatively easy to localise precisely on fossil or extant skulls. Only euryon (n°16) and coronion (n°17) could be considered as constructed points (type III).

2.2 Procrustean superimpositions

For each of both analyses we present below, a Generalized Least Squares fitting [23-24] was computed using the GRF-ND and Morpheus *et al.* software [25]. All the skulls are superimposed on their respective centroïds after what they are scaled down and rotated for the least squares fitting. Then the mean reference configuration for the whole sample is calculated.

Superimposed coordinates were analysed by Principal Component analysis using the SAS software, version 6.11. Along the axis of the principal component analysis, we illustrated architectural variability with the presentation of the extreme configurations (extreme individuals) compared to the mean reference configuration.
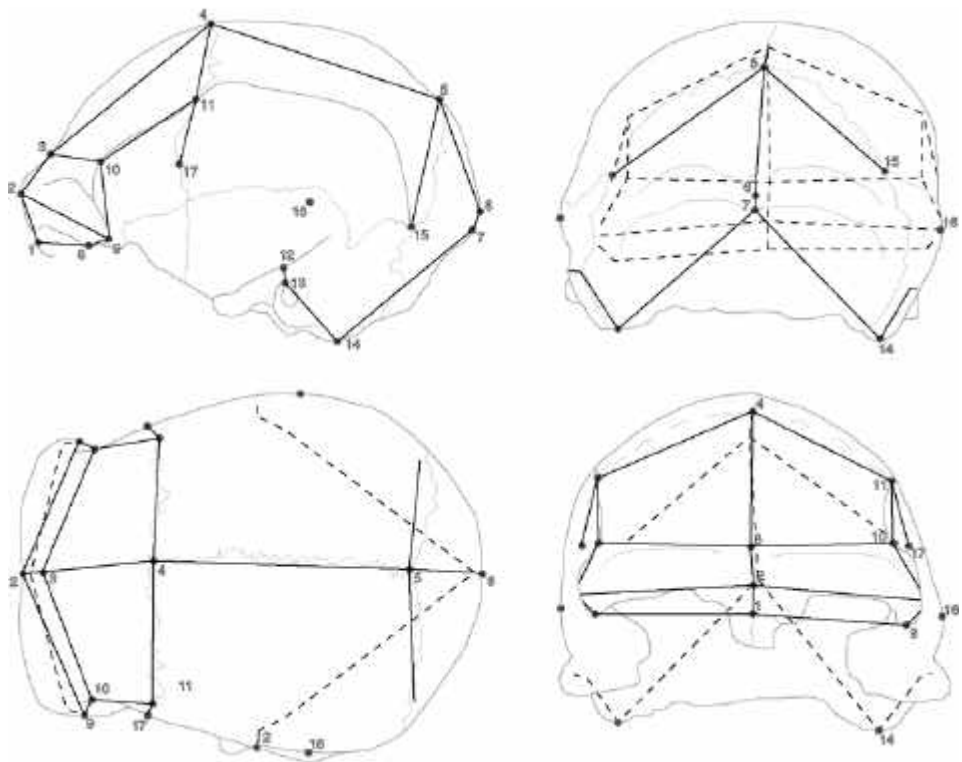
Figure 1   Location of the cranial landmarks and visualisation of the cranial modelisations obtained.
Only the left half skulls are statistically studied (17 landmarks)

2.3   Damaged or missing anatomical parts

The entire skull cap were digitized but only the left half skulls (seventeen landmarks) were statistically studied. Very often, when studying fossil skulls, points are missing only on one side. So we use here a method to reconstruct a mean half configuration for each fossil. This mean configuration is the mean between the right and the left half skull after the landmarks procrustean superimposition. When one point is missing on the left but is present on the right, it seems to be the more rigorous way to reconstruct this right point on the left side.

3   Results

The first analysis is the principal component analysis of the coordinates of the seventeen superimposed landmarks (Figure 2). The number of individuals in this analysis is very low because some of the points are missing on the left side and on the right side. So, incomplete fossils are automatically excluded from this analysis.

There is some interesting observations to make onto the plane 1-2. The axis 1 which explain 53% of the total variance clearly separate both fossil and present *Homo sapiens* from older African fossils (KNMER 3733, 1813 & Broken Hill). On the left side along axis 1, we found individuals with very low brain cases: in proportion, the bregma and the euryon are very low, the occipital bone is angulated, the supraorbital torus is large, horizontal and straight above the orbite and behind this broad supraorbital torus, the frontal bone is very narrow. On the opposite side, the cranial architecture is more rounded: bregma and euryon are proportionally higher, the glabella is no more projecting; from the frontal view, the supraorbital complex is vertival and rounded above the orbite continuing into a wide and rounded frontal bone. Along this axis Broken Hill is clearly grouped

with the *Homo erectus (Homo ergaster?)* KNMER 3733 and even the *Homo habilis* KNMER 1813 which is surprisingly very close to the African *Homo erectus* morphology when the size parameter is eliminated.
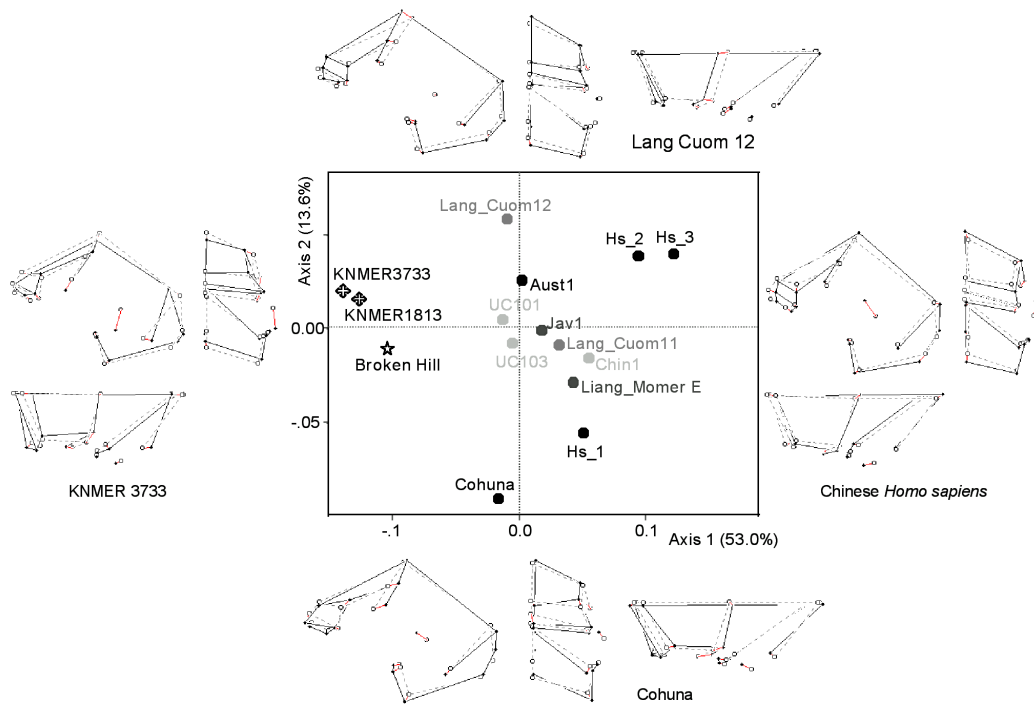

Figure 2   PCA of the coordinates of the 17 superimposed landmarks, axes 1 & 2 ; plot of individuals and extreme configurations on each axis, dotted lines correspond to the mean reference configuration

Along the second axis, which explain 13.6% of the total variance, the upper Pleistocene Australian fossil Cohuna appears on an extreme position. When analysing the configurations, the variability in the anteroposterior proportions of the frontal bone is clearly the dominant factor along this axis. On the top, we found the Lang Cuom 12 individual which exhibit a proportionally very short frontal bone. On the bottom, Cohuna exhibit a very particular frontal bone architecture. This frontal is proportionnaly very long and this is particularly true for the frontotemporal, the stephanion and the coronion which are in very posterior positions. In this analysis, we have the confirmation that the cranial morphology of the Cohuna cranium is abnormal certainly due to an artificial deformation as some scholars argued. In this perspective, it should have been very interesting to include in this analysis the Upper Cave 102 specimen that also look artificially deformed. But the cast we have exhibit severe post mortem damages so it was impossible to include it.

For the following analysis, due to its abnormality we decided to exclude the Cohuna cranium from the calculations.

The second analysis is the principal component analysis of the coordinates of only 11 superimposed landmarks (Figure 3). We eliminated some landmarks that are absent on many fossils and we kept landmarks involved in the modelisation of the sagittal outline, the frontal bone and the euryon.
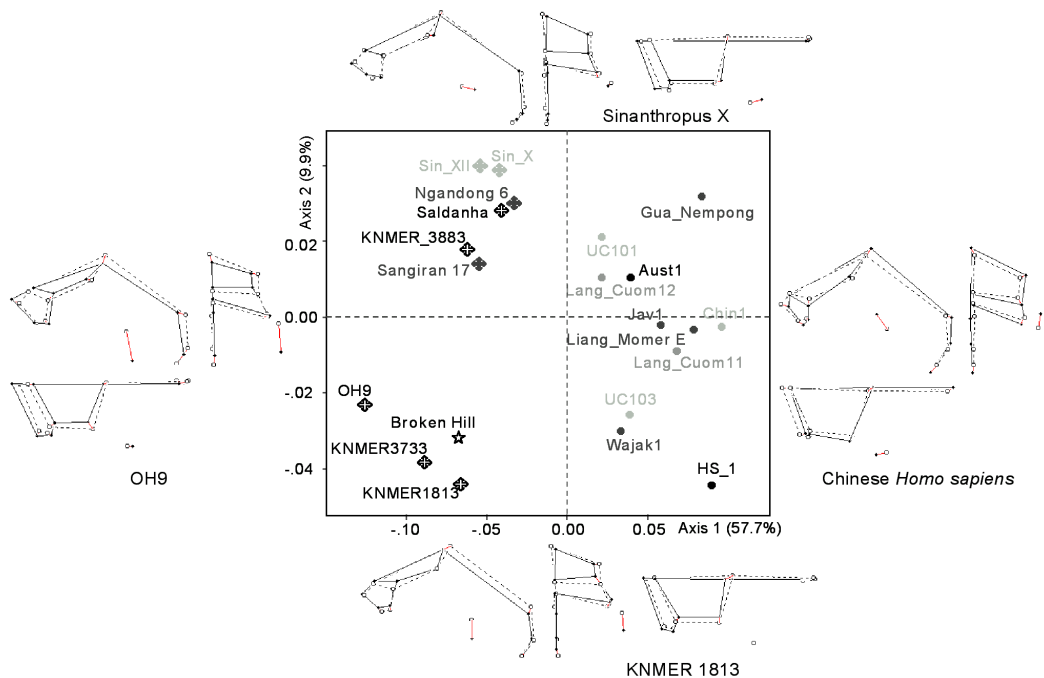
Figure 3   PCA of the coordinates of 11 superimposed landmarks, axes 1 & 2 ; plot of individuals and
extreme configurations on each axis, dotted lines correspond to the mean reference
configuration

Onto the plane 1-2, we have three groups. Along the first axis, which explain 57.7% of the total variance, we find again two groups really distinct from each other. As in the first analysis, individuals on the left side of the first axis, exhibit low brain cases (low bregma and low euryon in proportion) with broad and straight supraorbital torus whereas on the opposite side the cranial morphology is more rounded with a very weak supraorbital complex continuing into a wide and rounded frontal bone. Along this axis fossil and present *Homo sapiens* form a group clearly opposed to the *Homo erectus* (*sensu lato*) – *Homo habilis* group (including also Broken Hill) without any overlap. It is impossible to distinguish along the axis 1 any geographical or temporal trends inside one of both groups. On the other hand, the second axis which explain 9.9% of the total variance cut the so-called *Homo erectus – Homo habilis* group in two parts. The main architectural differences along the axis 2 appear to be localised in the frontal bone morphology. On the bottom of the axis, we find an exclusively African group (KNMER 1813, 3733, OH9 and Broken Hill) exhibiting strong and wide supraorbital torus associated with relatively narrow frontal bone. Whereas on the top of the axis individuals exhibit moderately developed supraorbital torus associated with relatively broad frontal bone: the postorbital constriction is reduced. In this second *Homo erectus* group there are Indonesian, Chinese as well as African specimens. It seems not possible to evoke a temporal evolutionary trend nor a sexual dimorphism because of the great diversity exhibited by both subgroups. Adding new specimens in the sample may help us to explain this dichotomy if confirmed.

Observation of individuals plots onto plane 1-3 emphasis once again the clear architectural distinction between *Homo sapiens* and *Homo erectus*. The axis 3 which explain 8.5% of the total variance shows the variability of the anteroposterior proportion of the frontal bone. On the top of the axis, individuals such as Ngandong 6 exhibit very long and flat frontal bone in proportion with the overall skull whereas on the bottom, specimens like Lang Cuom 12 exhibit very short frontal bones. There is no particular trend along this axis in the *Homo erectus* group nor in the *Homo sapiens* one.

4   Discussion

The methodology adopted - procrustean landmarks superposition (i.e. GLS) - seems to be very well suited for accurate cranial architectures comparisons. Interpretations of morphological variability during the course of evolution are easier and more understandable in terms of cranial geometry and separating size parameters from the shape information allows new observations. For example we have seen that KNMER 1813 which is a very small skull is architecturally very close to African and other *Homo erectus / Homo ergaster*. A global increase in size could be a sufficient phenomenon to evolve from an *Homo habilis* to an *Homo erectus* cranial vault architecture.

Concerning the Australian Upper Pleistocene *Homo sapiens* cranial morphology that could be inherited from javanese *Homo erectus*, we pointed out without any doubt the abnormal cranial architecture of the Cohuna cranium. It is a very unusual *Homo sapiens* morphology but it is clearly not an *Homo erectus* nor an intermediate shape.

Finally, we always have a very clear distinction between *Homo erectus* and *Homo sapiens* architectures. We never observed any overlap between these two groups even for specimens like Broken Hill. Broken Hill exhibit clearly an *Homo erectus*-like cranial architecture. We never observed any trend concerning geographical groups: Sinanthropus are never more closely to Chinese *Homo sapiens* than to any other fossil or extant *Homo sapiens*, nor are Ngandong specimens with Wajak 1 or other Indonesian or Australian *Homo sapiens*. Other analyses of different sets of landmarks always confirm this clear distinction: nothing seems to indicate any interbreeding between *Homo* erectus and *Homo* sapiens in East and Southeast Asia. Related with this clear separation between the *erectus* - shape and the *sapiens* - shape, we pointed here the fact that the Ngandong specimens, although sometimes considered as archaic *Homo sapiens*, exhibit a typical *Homo erectus* architecture.

However our sampling is not exhaustive and we could not test in this work the position of the so-called transitional Chinese fossils. But we have a very interesting frame for future work and we intend now to include in our sample Chinese specimens like Dali, Jinniushan and Maba; new discovered *Homo sapiens* fossils from Indonesia and Thailand and Upper Pleistocene Australian fossils to go more precisely in the study of cranial shape evolution in East and Southeast Asia since the Middle Pleistocene.

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