Parietal expansion during later hominin evolution, and the validity of *H. heidelbergensis* – A quantitative approach

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Summary

The evolution of the modern cranial shape and globularity is the result of a variety of morphological changes that occurred during the later Pleistocene, parietal expansion being one of them. However, this trend has also been described in Neandertals, which bears the question, when and where this character appears, and what it implies for middle Pleistocene human phylogeny. This study presents a quantitative comparison of parietal shape in various species of Homo based on 3D geometric morphometrics. The results confirm the existence of a shared trend toward parietal expansion found in both *H. sapiens* and *H. neanderthalensis*, but absent in *H.erectus* and *H. rhodesiensis*. If confirmed by additional samples, this would be consistent with an afro-european last common ancestor of modern humans and Neandertals, though to the exclusion of Petralona and Kabwe.

Key words: Cranial globularity, parietal expansion, middle Pleistocene Homo, geometric morphometrics

Zusammenfassung

Die Evolution der modernen Schädelform und Globularität resultiert au seiner Reihe morphologischer Änderungen im Laufe des späteren Pleistozän, darunter die Expansion der Scheitelbeine. Solch ein Trend zu ausladenderen Parietalia wurde jedoch auch bei Neandertalern beschrieben, was zur Frage des zeitlichen und geographischen Ursprungs dieses Merkmals, sowie dessen phylogenetischen Implikationen für mittelpleistozäne Homininen führt. Die vorliegende Studie unternimmt einen geometrisch morphometrischen Vergleich des Parietale in verschiedenen Homo-Arten. Die Ergebnisse bestätigen quantitativ, dass der Trend zur erweiterten Parietalregion sowohl in Neandertalern als auch in Sapienten zu finden ist, jedoch weder in *H. erectus* noch *H. rhodesiensis*. Dies bedarf zwar weiterer Daten und Untersuchungen, erweist sich jedoch vorläufig als übereinstimmend mit der Idee, dass der gemeinsame Vorfahr von *H. sapiens* und *H. neanderthalensis* im Afro-Europäischen Raum zu finden ist, jedoch nicht von Funden wie Kabwe und Petralona repräsentiert wird.

Schlüsselwörter: Kraniale Kugelform, Parietale Expansion, mittelpleistozäner Homo, geometrische Morphometrie

Introduction

The phylogeny of later Pleistocene hominins still remains a widely discussed issue in paleoanthropology, despite recent advances, particularly in the area of ancient DNA (Endicott *et al.* 2010, Green *et al.* 2010). While a consensus appears to assign Neandertals the role of sister taxon of the lineage leading up to anatomically modern humans, the exact time and mode of this evolutionary process remains open to debate (cf. Havarti *et al.* 2010, Hublin 2009, Rightmire 2009, Tattersall 1992). It is generally assumed that *H. heidelbergensis* gave rise to the Neandertals, but its phylogenetic relation to *H. sapiens* remains unclear. In this debate, two fundamentally different models oppose each other, depending on how this relation is seen: Either *H. heidelbergensis* is the exclusive ancestor to Neandertals, and its distribution is therefore limited to Europe (Bermúdez de Castro *et al.* 1997). Or, according to the alternative view, it is the common ancestor of Neandertals and *H. sapiens*, in which case its definition includes African fossils as well (Rightmire 2009, Tattersall 1992). Because the Kabwe skull is often grouped with European specimens (Sima de los Huesos, Arago, Petralona among others) as representing this common ancestor, Hublin (2009) has suggested to use the term *H. rhodesiensis*, of which Kabwe is the type specimen. In a recent study of calvarial shape in

Fig. 1: 3D surface scan of a modern human skull.

Specimen	Presumed Taxonomy
La Ferrassie I (o)	
Guattari (o)	
La Chapelle-aux-Saints (o)	
La Quina H5 (o)	
Neandertal 1 (o)	
Spy 1 (o)	
Spy 2 (o)	*H. neanderthalensis*
Amud (c)	
Tabun C (o)	
Fontechevade (o)	
Forbes' Quarry (o)	
Saccopastore 1 (c)	
Shanidar 1 (c)	
Reilingen (o)	
SH5 (c)	
Steinheim (o)	*H. heidelbergensis*
Saldanha	
Arago 47 (c)	
Swanscombe (o)	
Petralona (c)	*H. rhodesiensis*
Kabwe (o)	
Dmanisi 2280 (c)	
Sinanthropus pekinensis (c)*	*H. erectus sensu lato*
KNM-ER3733 (c)	
Singa (o)	
Irhoud 1 (c)	*H. sapiens*
Skhul V (c)	
Mladec 1 (o)	

Tab. 1: Sample composition. Scan made from original specimens are marked by (o), all others are casts.
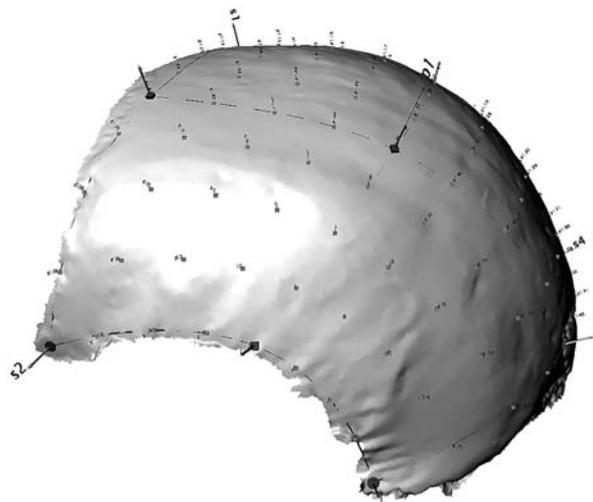* Reconstruction by Tattersall and Sawyer (1996), courtesy of Dept. Anthropology, AMNH.

the Middle Pleistocene, Friess (2010) suggested to reserve this species name (for now) to Kabwe and Petralona, whose strong affinities have been noted in the past (Stringer *et al.* 1979).

In terms of morphology, recognized Neandertal apomorphies, such as the midfacial prognathism, suprainiac fossa, or the occipital bun are often used as demonstrating the phylogenetic link to older European and African material (Dean *et al.* 1998, Righmire 1998). At the same time, the increase in endocranial volume and associated parietal expansion is identified as apomorphic in both Neandertals and *H. sapiens*, in opposition to the elongated and flat vault in *H. erectus* (Day *et al.* 1980, Lieberman *et al.* 2002, Stringer *et al.* 1979, Rightmire 2009). The difficulty in assessing Middle Pleistocene phylogeny and taxonomy is accentuated by the fragmentary state of fossils and issues with quantifying some of the features involved (Hublin 2009, Friess 2010, Harvati *et al.* 2010). The former problem has been addressed by separately comparing the various cranial portions, the latter by the statistical analysis of landmark data (Rohlf and Marcus 1993, Friess 1998, Harvati *et al.* 2010). Of particular interest is the use of 3D scan data, which allow for the analysis of large surfaces without "good" landmarks (type I according to Bookstein 1991). This study represents one such attempt in characterizing the shape of a surface, in this case that of the parietal. Because it is directly subjected to the anatomical consequences of increased endocranial volume, it can be theorized that its shape variation provides further insight into Mid-Pleistocene hominin phylogeny.

Fig. 2: Landmarking along the surface of the parietal using Landmark editor (Wiley *et al.* 2005).
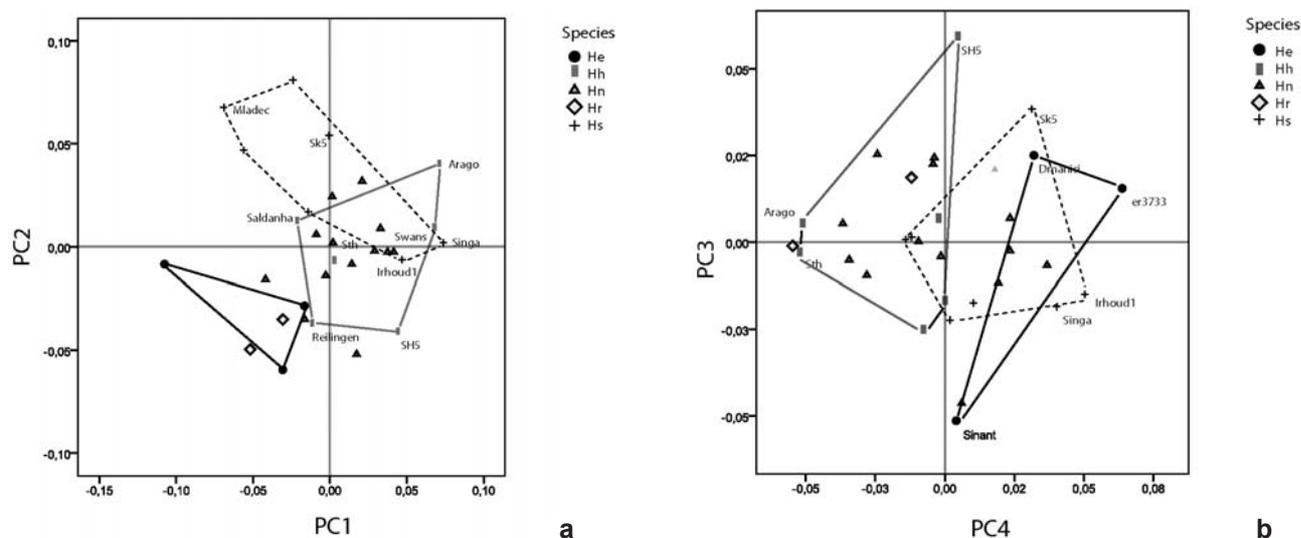
Fig. 3: PCA, components 1–2 (a) and 3–4 (b).

Material and Methods

The present study is based on 3D surface data of fossil hominins and modern human skulls. A total of 28 parietals of fossil specimens were measured, to which 3 anatomically modern humans were added from the collections of the Musée de l'Homme, Paris. Surface scans were obtained with a portable 3D scanner (Breuckmann smartscan stereo), which generates a digital model of the outer surface with a spatial resolution of about 0.26mm (Fig. 1). Surface scanning is a rapid, non-invasive technique for digitally archiving human remains, and making them accessible to 3D analysis. It has become increasingly available in paleoanthropology, mostly due to its relatively low cost and ease of application when compared to CT-scanning (Friess 2006, 2010, Friess *et al.* 2002, Harcourt-Smith *et al.* 2008, Lyons *et al.* 2000, Tocheri *et al.* 2005). Only in one case (Guattari), CT-scan data were used to create a 3D mesh by applying thresholding techniques (Spoor *et al.* 1993). Table 1 lists the specimens included, and also notes whether the original or a cast was used. All specimens were given operational taxonomy based on the most common assignments found in the literature. However, Petralona was grouped together with Kabwe (cf. Friess 2010, and discussion below). Note that group affiliation has no impact on the shape statistics. Once scanned, 3D data were post-processed with standard off-the-shelf software. Post-processing included mesh

decimation and, in several cases, completion through repairing and mirror-imaging. The use of virtually reconstructed specimens in paleoanthropology is a topic beyond the scope of this paper (see Gunz *et al.* 2009). It should be pointed out, however, that for the purposes of the present study, reconstruction was minimal. The process also ensured that major asymmetries, due to plastic deformation or alike, had no significant effect on data analysis.

3D coordinates were recorded for each specimen using "landmark-editor" (Wiley *et al.* 2005). The landmarks (Fig. 2) included standard anthropometric points (bregma, lambda, pterion and the base of the parietal notch) as well as 81 semi-landmarks, evenly spaced across the parietal and bordered by the 4 standard landmarks (Wiley *et al.* 2005, Harcourt-Smith *et al.* 2008).

Landmarks were aligned by a generalized Procrustes Analysis (GPA), in which the semilandmarks were treated as type III landmarks (Maddux and Franciscus 2009, Niewoehner 2001). Procrustes residuals were submitted to a Principal Components Analysis (PCA) to explore major directions of shape variation in the sample. Centroid size (log-transformed) was used as an overall size estimator, and its influence on evolutionary allometry was assessed through scatter plots against the principal components. Landmark configurations along the directions of interest were estimated by multivariate regression, and visualized by NURBS (non-uniform

rational B-splines) surfaces, which were fitted to the semilandmarks to enhance interpretation and readability. GPA and PCA were performed in MorphoJ (Klingenberg 2008), NURBS surfaces were generated in Rhino3D.

Results

The overall shape variation of the parietals across the sample can be summarized quite efficiently with the first few components, seeing that PC 1 through 4 account for 66% of the total variance (31.2%, 14.2%, 11.7% and 9.1% respectively). Hence, by far the largest amount of variance describes the shape difference between *H. erectus* and *H. rhodesiensis* on the one hand and modern humans on the other, with both Neandertals and *H. heidelbergensis* interspersed and partially overlapping. Kabwe and Petralona are always in close proximity (Fig. 3).

The shape changes associated with this component (Fig. 4) combine antero-posterior shortening with moderate vertical expansion, most notably along the temporal suture and, when seen from above, around the parietal eminence. In frontal view, the lateral portions are vertically oriented, and the vault appears more wide than high. The second component, accounting for a rather small portion of the total variance, mostly reflects changes in the width/height proportions, as the vault increases vertically along with pc scores, while the relative width decreases. The lateral walls are also less vertical, more convex, the temporal margin becoming narrower. PC 3 also yields a scatter that appears pertinent with respect to hominin phylogeny. It mainly contrasts between *H. heidelbergensis* and *H. erectus*, whereas both Neandertals and *H. sapiens* overlap, and *H. rhodesiensis* falls within the *H. heidelbergensis* scatter.

Significant size differences exist at the species level, albeit only between *H. erectus* and all other groups, which display comparable ranges for log centroid size (Fig. 5). The smallest value is found for Dmanisi, ER 3733 and *Sinanthropus*, the largest value is shown by Shanidar 1, followed by Singa and several other modern humans and classic Neandertals.

The first PC is significantly correlated with log centroid size (r = 0.5, p<0.005), thus reflecting mostly the small size and distant shape of *H. erectus*, when compared to all other hominins in this analysis.
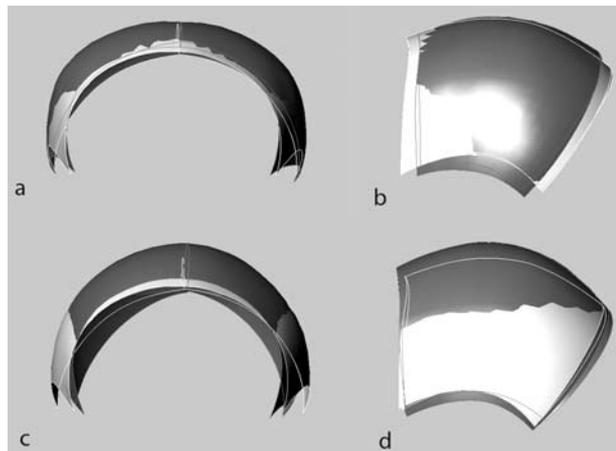

Fig. 4: Shape differences along PC. Shape change from consensus associated with positive scores along pc 1 (a – frontal view, b – lateral view) and 2 (c,d).

Discussion

Reconstructing Middle Pleistocene hominin phylogeny has long been a main research focus in paleoanthropology, and has been accentuated by Mayr's recognition of only 2 species, *H. erectus* and *H. sapiens* (Mayr 1950). The ensuing uncertainty regarding the phylogenetic status of fossils of presumably more ambiguous/intermediate morphology led to what some have referred to as the "muddle" in the middle (Butzer and Isaac 1976), and to the unsatisfactory, for obviously preliminary creation of the grab bag called "archaic *H. sapiens*". Following Stringer *et al.* (1979), current research has predominantly replaced this term, in a back-to-the-roots-like effort, by the species *H. heidelbergensis* (Schoetensack 1908), whose recognition predates Mayr's revision, without achieving a consensus on which fossils should be part of it and which should not. While it is true, as Hublin (2009) points out, that the argument is further hampered by the incompleteness of fossil specimens, this issue can hardly be regarded specific to the Middle Pleistocene. Regardless of which characters are used to define the various species involved, researchers recognize unanimously that the evolutionary trend toward increased encephalization was accommodated, in part, by parietal expansion, making this feature in theory a good measure of evolutionary state (Day *et al.* 1982, Liebermann *et al.* 2002). In Neandertals, horizontally expanded parietals contribute to the characteristic oval shape in posterior view, while modern humans undergo
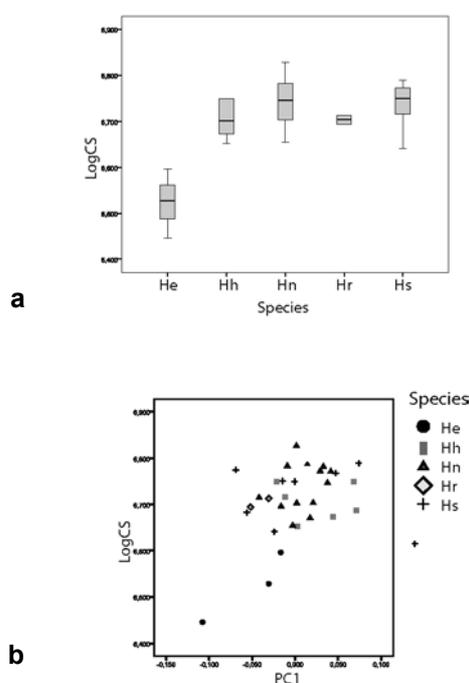
Fig. 5: Size variation (a) and Allometry (b – log size against pc 1).

an additional vertical expansion. However, in the absence of significant size differences, the existence of allometric differences (Bruner *et al.* 2003; Bruner 2010) as driving the shape differences is not corroborated. Therefore, an improved means of quantifying parietal shape should yield a better understanding of the pattern of expansion throughout the Later Pleistocene and across various species. However, when considered isolated, the parietal shape appears much more similar in all later Pleistocene groups including anatomically modern humans. The ancestral condition, low parietal expansion, is found in *H. erectus* and *H. rhodesiensis*, whereas most Neandertals and *H. heidelbergensis* share the trend toward the shortened, and more convex shape of modern humans. Still, antero-posterior lengthening is also seen in some modern humans, most notably Mladec 1, but in these cases the vertical expansion and increased convexity fall into the modern pattern. Several representatives of *H. heidelbergensis* show more affinities to modern humans with respect to parietal shape, while others are much more ancestral, and therefore closer to *H. erectus*. Thus, Arago 47 and Swanscombe, appear surprisingly modern, though at least Swanscombe shows otherwise clear Neandertal apomorphies in the occipital (Hublin 1978). Reilingen,

on the other hand, is marginal to most Neandertals and falls in the vicinity of *H. erectus/rhodesiensis*, despite it being considered a "pre-Neandertal" (Dean *et al.* 1998). SH5, often associated with *H. heidelbergensis*, exhibits antero-posterior shortening akin to modern humans, but is rather ancestral in its vertical height and low convexity. Fossil *H. sapiens* are widespread across the first two components, and it could be argued that this is due mostly to the position of Singa and Irhoud 1. The former might be affected in its parietal shape by pathology (Stringer 1979), the latter may be far from other modern humans because of plastic deformation, or it may be less modern than previously suggested. As was previously noted (Stringer *et al.* 1979, Friess 2010), Petralona and Kabwe are overall quite similar craniofacially, and the present study corroborates these similarities with respect to parietal shape.

Conclusion

The aim of this study was to quantify hominin parietal shape variation by means of 3D morphometrics, in order to reassess the evolution of modern humans and their immediate ancestors. The results, while still preliminary and to be confirmed by extended samples, do provide an additional argument to link Petralona and Kabwe and support their affinities with *H. erectus*, while removing them a little further from the Neandertal lineage and its presumed ancestor *H. heidelbergensis*. The latter, in return, appears to have more modern-like parietals than previously described. However, additional samples may provide a better resolution of this particular aspect of the issue, which therefore remains open until further investigation.

Acknowledgments

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