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Evolution of Cranial and Endocranial Profiles in *Homo* Species: a Study in 2D Geometric Morphometrics

Évolution du profil crânien et endocrânien chez les espèces du genre *Homo*. Une étude par la morphométrie géométrique en deux dimensions

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Abstract Cranial anatomical features play a prominent part in the definition of extinct *Homo* taxa and in species identification in fossils. Thus, knowledge of cranial morphology considered within its geochronological framework is essential to the understanding of the evolution, chronology, and dispersal of the genus *Homo*. The brain is also a valuable object of study for research on human evolution, because of features such as its large size and a high encephalization quotient in some *Homo* species, as well as the complexity of human cognition. However, the joint evolution of endo- and ectocranial anatomies is still little studied, and landmarks representing cerebral anatomy rather than inner cranial bone anatomy are still rarely used. This exploratory piece of research examines endo- and ectocranial profiles in samples representing 3 *Homo* taxa: *Homo sapiens* (fossil and recent specimens), *Homo erectus*, and *Homo neanderthalensis*. We used 2D geometric morphometrics to analyze the shape of the endo- and ectocranial vaults, as well as the relationships between selected anatomical features such as the extension of lobes and bones. The shapes of the vaults were computed using both fixed landmarks and sliding semi-landmarks. The fixed landmarks used for the endocranium were chosen in order to represent cerebral anatomy, in that they are defined by the imprints left by brain structures on the inner bone surface of the skull, and not by bony structures such as the inferior side of cranial sutures. Among other results, we have shown or confirmed specific features in the shape of the endocranium in *Homo sapiens*, as well as a few differences in the patterns of interplay between lobes and bones. These data, and any further results obtained with larger samples, may provide new insights into the development of the endocranial anatomical pattern in *Homo sapiens* and of its variability.

Keywords *Homo* genus · Covariation · Cranial and endocranial evolution · Geometric morphometrics

Résumé Les caractères anatomiques crâniens jouent un rôle important dans la définition des espèces fossiles du genre *Homo* et dans l'identification taxonomique de spécimens fossiles. Ainsi, la connaissance de la morphologie crânienne, considérée dans son cadre géochronologique, est essentielle à la compréhension de l'évolution, de la chronologie et de la dispersion du genre *Homo*. Le cerveau est lui aussi un objet précieux pour la recherche sur l'évolution humaine. Des caractéristiques telles que la taille importante du cerveau et le quotient d'encéphalisation particulièrement élevé chez des espèces du genre *Homo*, ainsi que l'évolution de la cognition complexe humaine, expliquent l'intérêt accordé au cerveau dans les sciences de l'évolution. Cependant, la covariation des morphologies exo- et endocrâniennes et son évolution restent peu étudiées, et l'utilisation pour l'étude de l'endocrâne de points repères liés à l'anatomie cérébrale plutôt qu'à l'anatomie de la table osseuse interne reste rare. La présente étude explore cette problématique au travers de l'examen des profils exo- et endocrâniens dans des échantillons représentant trois espèces du genre *Homo* : *Homo sapiens* (spécimens fossiles et récents), *Homo erectus* et *Homo neanderthalensis*. Nous avons analysé la forme des voûtes exo- et endocrâniennes, ainsi que les relations entre des caractères anatomiques choisis, par la morphométrie géométrique en deux dimensions. La forme des voûtes a été digitalisée à l'aide de *landmarks* et de *semi-landmarks*. Les *landmarks* utilisés pour l'endocrâne ont été choisis de manière à représenter l'anatomie cérébrale et sont définis grâce aux empreintes

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causées par les structures anatomiques du cerveau sur la table interne de l'os crânien, et non grâce à des structures osseuses telles que la face inférieure des sutures crâniennes. Nos résultats montrent notamment des spécificités dans la conformation de l'endocrâne chez *H. sapiens* et de légères différences interspécifiques dans les interactions entre os et lobes. Ces données, ainsi que de futurs résultats sur de plus larges échantillons, pourront offrir de nouvelles perspectives quant au développement des schémas anatomiques de l'endocrâne propres à *H. sapiens* et de leur variabilité.

Mots clés Genre *Homo* · Covariation · Évolution crânienne et endocrânienne · Morphométrie géométrique

Introduction

Because of the large number of diagnostic anatomical structures that are present on the skull and reflect its diverse functions, palaeoanthropologists have long favoured the study of hominin heads in order to differentiate between fossil species and develop hypotheses about phylogeny, cognitive abilities, gait, adaptation to environmental conditions, the respective importance of the olfactory, visual and auditory senses, etc. (for recent studies and discussions see for instance [1–6]). Pragmatically speaking, cranial features are also of particular importance because of the comparatively large number of calvaria and crania available in the fossil record, since they tend to be relatively well-preserved in fossil-bearing sites and because they have always been easier to identify and collect than post-cranial remains. Species-relevant features visible on the mid-sagittal profile of the skull include shape and size of the cranium, projection of the supra-orbital torus, verticality of the frontal and angulation of the occipital bone (for general and more specific descriptions of characters see for instance [1,4,7–10]). Most diagnostic of *Homo sapiens* are its globular neurocranium and short retracted face (see for instance [1]; for a description of bony *Homo sapiens* autapomorphic characters, see [11]). A vertical frontal squama, long, wide and curved parietals and an occipital bone that is not projected to the back, are among the features taken into consideration when deciding whether or not to attribute a fossil calvaria to *Homo sapiens* or when examining the archaic and derived features of a fossil of doubtful attribution. The morphology of the skull is closely linked to the multiple functions that it serves (protective case for the brain; seat of the olfactory, auditory and visual organs; feeding, breathing and speaking apparatus) [12]. Evolution in cranial morphology could be partly dependent on cerebral anatomy, as the two units develop jointly and according to morphogenetic processes that are dependent on genes and on their regulatory programmes [13]. It has also been shown that during ontogeny,

the inner table of the bone is shaped after the dura mater, itself reflecting cerebral development, whereas the shape of the outer table develops according to other factors such as circum-orbital morphology [12], emphasising the fact that the inner and outer tables of the skull belong to different morphological "units".

Given its features and abilities [2,14–16] and its importance from an evolutionary point of view, it is not surprising that the brain is the subject of a great deal of research. The human brain may be considered to represent a decisive evolutionary advantage, having contributed to the success of the species thanks to the adaptive, social and information-processing faculties it allows for [17]. The absolute increase in brain size in *Homo* species up to *Homo neanderthalensis* [18] and a particularly high encephalisation quotient [19,20] go together with reorganisations of cerebral morphology, among which are variations in relative lobe sizes in different species [2,16,21]. In the absence of fossilised brains, the external anatomy of the brain in extinct hominins is studied through the endocranium, a representation in three dimensions of the imprints left by the brain and the meninges on the internal surface of the cranium. Studies of the endocranium often use anatomical structures that do not pertain to cerebral anatomy, such as the internal side of the cranial sutures (e.g.: endobregma, endolambda) due, perhaps, to difficulties in locating *Homo*logous structures on the endocranium. This is due to the highly variable quality of brain imprints on the bone, which can be relatively faint because brain and bone are separated by three layers of meningeal tissues, the cranial nerves and the cerebro-spinal fluid [22], but also to the poor preservation of some fossils. High image quality is crucial to decipher the endocranium.

Despite the wealth of research focusing on either the cranium or the endocranium throughout hominin evolution, very few researchers have taken on the topic of the joint evolution and covariation of the skull and brain or endocranium. Within the body of work published so far are studies that uncover the enormous informative potential of this field of palaeoanthropology. Such approaches include Bookstein *et al.*'s study of inner and outer frontal vault morphology in *Homo sapiens*, *Homo heidelbergensis* and *Homo neanderthalensis* [10], or Balzeau *et al.'s* debunking of the received wisdom of the "endinion below inion" feature as an autapomorphic trait in *Homo erectus* and its diagnostic implications [23]. Questions relating to phylogenetics as well as to morphology and morpho-functionality are addressed in these studies. It is not yet clear whether and how re-organisations in the brain throughout evolution affect cranial morphology. Several authors have described specific variations in cerebral shape among *Homo* species [24,25], either through visual examination or using metrical analyses. Perhaps surprisingly, Bookstein *et al.* (1999) found, using geometric morphometrics, that

the inner mid-sagittal profile, at least on the frontal, is stable among Middle Pleistocene hominins and *Homo sapiens*, while ectocranial profiles show significant diversity. This is particularly striking as it suggests great stability in earlier brain morphology (at least in its mid-sagittal profile) over a period spanning the emergence of "modern human cognitive capacities" [10]. The frontal bone is often singled out as a marker in the *Homo* genus because of the large number of species-distinctive features that it carries [10], and there are questions regarding the respective influence of brain growth and mechanical factors in the shaping of the bone [26]. The parietal bone [1] and the parietal lobe have been shown to increase substantially in height in *Homo sapiens* compared with other *Homo* species [24], although additional morphometric analyses could perhaps add to current knowledge about this pattern. The occipital area is also known to show diversity among fossil hominin species and *Homo sapiens* [1,24] but the bone and lobe have rarely been studied in conjunction (see however Balzeau *et al*. 2011 as mentioned *supra*).

To our knowledge, there are currently no studies looking at covariation between the skull vault and the endocranium using the whole profile, or using ectocranial and cerebral structures as landmarks in order to explore the relationship between bone and lobe extension throughout human evolution. Digitalising the ecto- and endo-cranial vaults both as a single object and as separate items enabled us to analyse covariation patterns and to observe interspecies differences in bone thickness and in cerebral profile. This is a pilot study on a relatively small sample, using several types of multivariate analyses in order to cross-examine the results.

Our aim is a better understanding of the emergence of the endocranial pattern in *Homo sapiens*. The main hypothesis of this paper is that there might be interspecific differences in the relationships between cranial and endocranial morphologies. In order to test this, we explored the following issues:

- Does the relative extension of the different lobes vary according to species?
- Concerning the issue of covariation and interplay between cranial and endocranial shape, we tested the following hypotheses:
  - Some features (e.g. the posterior extension of the frontal lobe and of the frontal bone) may interact differently among *Homo* species;
  - There is a high degree of covariation between the morphologies of the ecto- and endocranial vaults, and a lower degree of covariation between outer bony landmarks and cerebral features.

Materials

We analysed 65 specimens altogether: 58 recent and fossil *Homo sapiens*, four *Homo erectus*, two *Homo neanderthalensis* and one *Homo heidelbergensis* (Table 1). All analyses were carried out on virtual models. Cranial surfaces were reconstructed from medical CT scan data using Avizo Fire 7.1 (Visualization Sciences Group, FEI, 2012) and the endocasts were segmented for each individual. Acquisition parameters varied according to specimen size and degree of mineralisation, and voxel size was below 0.5mm in the

Table 1 List of specimens used for this study / *Liste des spécimens utilisés pour cette étude.*

Species	Specimen	Country	Date (BP)
Homo erectus	Ngandong 7	Java, Indonesia	31k [25]
Homo erectus	Ngandong 12	Java, Indonesia	31k [25]
Homo erectus	Ngawi	Java, Indonesia	200k [25]
Homo erectus	Sambungmacan 3	Java, Indonesia	400k [25]
Homo neanderthalensis	Spy 1	Belgium	68k [25]
Homo neanderthalensis	Guattari 1	Italy	52k [25]
Homo heidelbergensis	Petralona	Greece	200k [25]
Homo sapiens	Skhul V	Israel	100k [25]
Homo sapiens	Afalou 2,12,13,28,30,34	Algeria	11.2–13.5k [50]
Homo sapiens	Taforalt XIc1, XIIc1, XVc4, XVIIc1	Morocco	10.8–11.9k [50]
Homo sapiens	Cro–Magnon 1,3	France	30k [25]
Homo sapiens	Rochereil 1	France	Magdalenian/Azilian [25]
Homo sapiens	Téviec 8,9,16	France	6.7–5.7k [51]
Homo sapiens	34 individuals (Oloriz collection)	Spain	Recent
Homo sapiens	3 individuals (Wilno)	Lithuania	Recent
Homo sapiens	1 individual (Cap Bon)	Tunisia	Recent
Homo sapiens	1 individual (Qafzeh)	Israel	Recent

great majority of cases (with a maximum size of 1 mm). The bulk of the recent *Homo sapiens* sample is from a collection housed at the National Museum of Natural Sciences in Madrid, and comprises 34 sexed adult individuals (17 males and 17 females) collected in Spain in the 19th century. We also added 3 individuals from a cemetery in Wilno (Vilnius, now in Lithuania), 1 from Cap Bon (Tunisia) and 1 from a recent site in Qafzeh (Israel), all unsexed and curated at the Institut de Paléontologie Humaine in Paris. The fossil *Homo sapiens* sample (17 adult individuals: Afalou 2, 12, 13, 28, 30, 34, Cro-Magnon 1, 3, Rochereil 1, Téviec 8, 9, 16, Skhul V, Taforalt 11c1, 12c1, 17c1, 15c4) was expected to show considerable variability, as it encompasses a wide geographic and chronological range, with fossils from sites in France, Algeria, Morocco and Israel ranging from the Upper Pleistocene to the Mesolithic of Western Europe. The *Homo erectus* sample comprises four later Indonesian specimens from Ngandong, Ngawi and Sambungmacan (Ngandong 7, 12, Ngawi, Sambungmacan 3). The *Homo neanderthalensis* sample is made up of the Spy 1 and Guattari 1 individuals. The Petralona fossil, whose taxonomic status is disputed, was added as a representative of *Homo heidelbergensis* [27–29], which does not affect the outcome of the study as Petralona is the only fossil in our *Homo heidelbergensis* sample. The fossils chosen for analysis do not show any obvious signs of taphonomic distortion and all the areas under study were complete so that no landmarks had to be estimated due to damaged cranial structures. All the specimens except Sambungmacan 3 (Sm 3) are adults. We retained Sm 3 for analysis despite its probable sub-adult status in order to better capture variations in the *Homo erectus* species and to assess whether its unusual cranial features are reflected on its endocranium.

Methods

Data preparation and software

Profile morphology was analysed by means of 2D geometric morphometrics on the skull's mid-sagittal plane (for more information on the uses of geometric morphometrics see for instance [30]). The mid-sagittal plane was defined through a series of 3D cranial landmarks taken on the mid-line (nasion, glabella, supra-glabellar point, bregma, lambda and inion, cf. Fig. 1) and used to create a cross-section of the skull, which was then applied to the endocranium to serve as its mid-sagittal section. Projections of the 3D landmarks onto the 2D profile image created with the cross-section tool were then digitized as 2D landmarks. We used Avizo Fire 7.1 to define the mid-sagittal plane and extract the cross-section, and the TPS suite [31,32] to digitize 2D landmarks and semi-landmarks. All semi-landmarks (ecto- and endocranial) were slided together using the 'bending energy' setting of TpsRelw.

Defining the landmarks

The mid-sagittal plane offers robust landmarks on both the skull and the endocranium. The landmarks used to define the extension of cranial bones and cerebral lobes are easily identifiable (type 1 landmarks according to Bookstein's typology [33]). The frontal and occipital poles are type 3 landmarks, which are less robust as inter or intra-observer error is more likely to occur. Because there are few robust landmarks along the frontal and the parietal bones and lobes, we also digitized sliding semi-landmarks to describe the endo- and ecto-cranial profiles (for more on semi-landmarks, see for
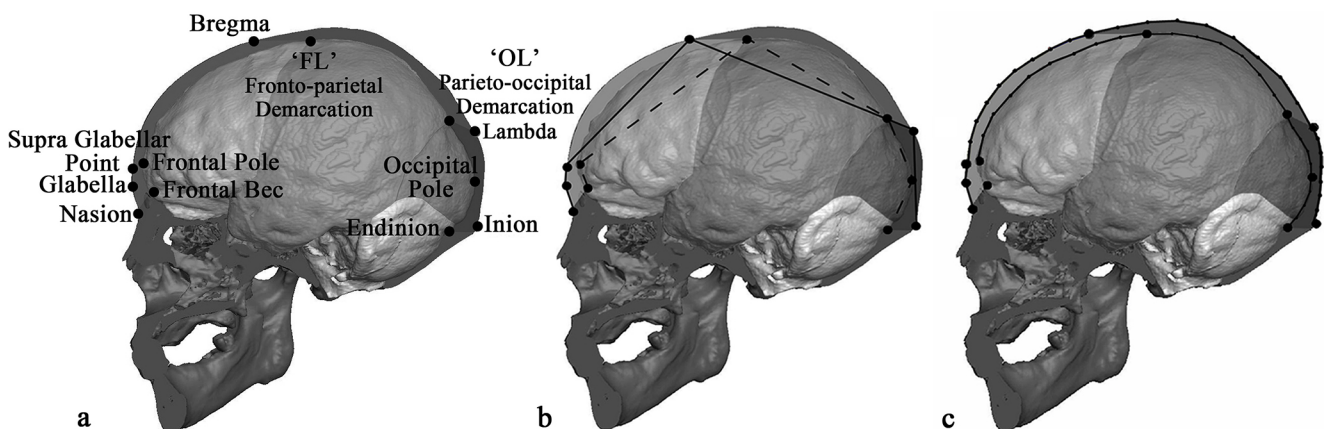
Fig. 1 a: Mid-sagittal plane with fixed landmarks used in this study; b: example of a profile with 6 fixed landmark configurations; c: example of a profile with full-landmark and semi-landmark configurations / *a : plan sagittal médian avec repères fixes utilisés pour cette étude ; b : exemple de profil avec configurations de six* landmarks *fixes ; c : exemple de profil avec configurations complète de* landmarks *et* semi-landmarks

instance [34]). Landmarks were used for *Homo*logous anatomically significant structures, and sliding semi-landmarks to produce optimum descriptions of the curves of the vaults. For the endocranium, cerebral landmarks were chosen while anatomical features pertaining to the inner side of the cranial bone were excluded. Although cerebral landmarks digitized from endocrania are necessarily located on the bone's inner table, they represent cerebral features whose location on the brain may not be linked to bone development. In this regard, the traces showing the extension of a lobe on the bone are independent from the sutures or any other bony landmark. The fixed landmarks and the optimum number of semi-landmarks were determined after trials with test individuals, by discarding unreliable landmarks and upon achieving an accurate description of the vault curves without using an unnecessarily large number of semi-landmarks. Using 3D models allowed us to check, several weeks after first digitizing them, that our landmarks were in the right place and that we had defined them in a coherent way across the entire sample. All fixed landmarks were digitized twice, separately on each individual, and then superimposed in the Avizo interface so as to verify their repeatability. All endocranial landmarks were checked by two different observers (L.A. and A.B.). Finally, we carried out systematic outlier searches after each Procrustes superimposition in order to eliminate any error due to digitizing landmarks in the wrong order or to manual transposition of coordinates from one file to another.

We used 6 landmarks (nasion, glabella, supra-glabellar point, bregma, lambda and inion) and 22 semi-landmarks on the cranium, and 6 landmarks (frontal bec, projection of the frontal pole on the mid-sagittal plane, posterior extension of the frontal lobe (FL= posterior extension of the frontal lobe ; OL= anterior extension of the occipital lobe) and 21 semi-landmarks on the endocranium (Fig. 1, Table 2). Some of the fixed landmarks are of particular interest to us because they provide information about, respectively, the interplay between the extension of the frontal bone and the frontal lobe, the parietal bone and the parietal lobe, and between the occipital bone and lobe (bregma-FL, inion-endinion, lambda-OL).

Points showing maximum extension of the lobes were defined on the mid-sagittal plane, at the intersection between the central sulcus and the longitudinal fissure for the frontal lobe, and at the intersection between the parieto-occipital sulcus and the longitudinal fissure of the occipital lobe. Some landmarks, such as the frontal and occipital poles, are linked to both endo- and ecto-cranial morphologies.

Table 2 List of landmarks used for this study / *Liste des landmarks utilisés pour cette étude.*

Landmark	Definition
Cranial	
Nasion	Intersection of the frontal and the nasal bones
Glabella	Projection of the forwardmost point on the browridge, on the midline
Supra–Glabellar point	Point on the mid–sagittal plane, in the depression above the projecting glabella
	8 semi–landmarks
Bregma	Intersection of the coronal and sagittal sutures (or its projection on the mid–sagittal plane)
	6 semi–landmarks
lambda	Intersection of the lambdoidal and sagittal sutures (or its projection on the mid–sagittal plane)
	6 semi–landmarks
Inion	Intersection of the mid–sagittal plane with the tangent connecting the uppermost points of the superior nuchal line
Endocranial	
Frontal bec	Intersection of the mid–sagittal plane with the imprint of the lower limit of the first frontal convolution on the frontal bec
Frontal pole	Projection of the forwardmost point of the frontal lobe on the mid–sagittal plane
	8 semi–landmarks
Frontal lobe (posterior extension)	Intersection of the central sulcus and the inter–hemispheric sulcus
	6 semi–landmarks
Occipital lobe (anterior extension)	Intersection of the parieto–occipital sulcus and the inter–hemispheric sulcus
	4 semi–landmarks
Occipital pole	Projection of the forwardmost point of the occipital lobe on the mid–sagittal plane
	3 semi–landmarks
Endinion	Crossing point of the four legs of the eminentia cruciata

The focus on cerebral landmarks allowed us to isolate some morphological trends in the brain from changes in the organisation of the bones.

Analytical protocol

Principal Component Analyses (PCA) of the shape variables computed through our landmark configurations were performed using the R packages Shapes [35] and Morpho [36]. Generalised Procrustes Analyses (GPA) were performed before each PCA in order to superimpose all specimens, removing size, location, and orientation effects from the sample. For each individual, ectocranial and endocranial vaults were digitized as a single object on which we performed a PCA. Procrustes distances between taxon mean shapes among groups were obtained using the non-parametric f-test of the Integrated Morphometrics Package (IMP) [37]. Although this is a useful tool, these distances require careful consideration as our fossil groups are made up of a very small number of individuals and can only capture a limited amount of species variation. Landmark coordinates for the endocranial and the ectocranial vaults were then computed and Procrustes-aligned separately using the IMP. 2-Block Partial Least Squares (2B-PLS) analyses were performed using the geomorph R package [38] in order to assess the degree of covariation between ecto- and endo-cranial profiles. 2B-PLS analyses allow covariation patterns between two sets of variables to be studied in a symmetrical manner - that is, without using one set to predict variations in the other [39]. PCAs were also performed on the ectocranial and endocranial vaults separately, first using all our landmarks and then only the fixed landmarks. The analyses using all landmarks allowed us to study a more complete representation of the inner and outer cranial vaults, and the analyses using only the fixed landmarks enabled us to observe the interaction between cerebral and ectocranial structures, as well as shape changes in cerebral profiles by discarding the semi-landmarks digitized along the inner curve of the skull. For each PCA, the first 10 to 15 Principal Components (PCs) were examined, so that the cumulative sample variation covered is over 90%, with the remaining PCs accounting for a very small amount of variation each (usually less than 1%). None of the PCs after PC2 showed any interspecies differences.

Results

Interspecies diversity

PCA on the ecto- and endocranial profiles as one object

A PCA was performed on the profile digitized as a single object (Fig. 2). Differences between species are clearly observable along the axis of PC1, which accounts for
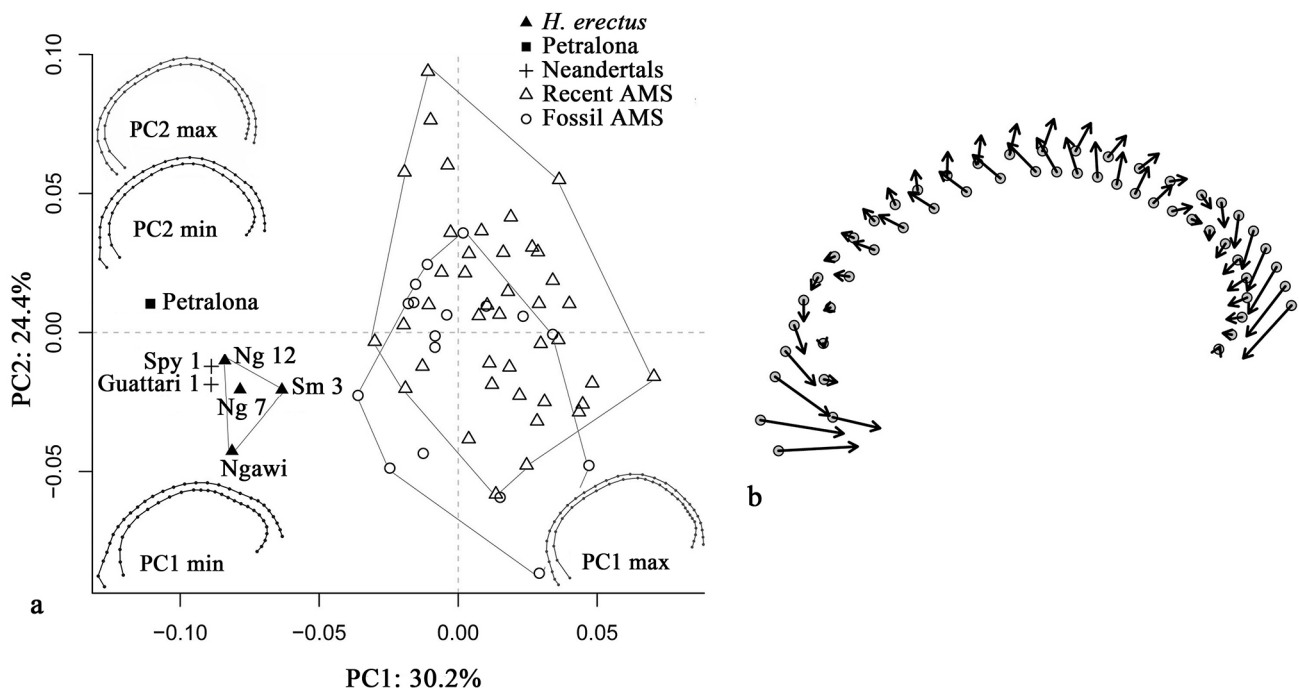
Fig. 2 a: PCA of the profile digitized as a single object, 2.: variations along PC1. Dots: extreme negative conformation (non-*sapiens*), arrow tips: extreme positive conformation (*sapiens*) / *a : ACP sur le profil digitalisé en tant qu'objet unique (voûtes crânienne et endocrânienne) ; b : variations le long de la composante principale 1. Ronds : conformation négative maximale (non-*sapiens*), pointes des flèches : conformation positive maximale (*sapiens*)*

30.2% of the total variance of the sample. Neandertals and *Homo erectus* specimens cluster away from the *Homo sapiens* individuals, all obtaining negative scores whereas the *Homo sapiens* sample is distributed on either side of the zero axis. Individuals obtaining higher values along the PC2 (*Homo sapiens*) have a higher profile and the bone appears to be thinner, in particular in the frontal and occipital areas. PC2 (24.4% of total sample variation) does not allow for any differentiation between the species studied, and both extreme conformations along this axis are represented by *Homo sapiens*, suggesting that variability along this axis is largely accounted for by *Homo sapiens* morphologies. Procrustes distances between mean shapes suggest a greater distance between *Homo sapiens* and the other groups than between *Homo erectus* and Neandertals, but the p-value for this last test is higher than the 0.05 threshold set for this study (0.0927 for *H.sapiens/H.erectus*, p-value <0.05; 0.0983 for *H.sapiens*/Neandertals, p-value<0.05; 0.0532 for *H.erectus*/Neandertals, p-value=0.15).

PCA on the ectocranial vault

We observed clear differentiation between species along the PC1 axis (54.1% of total sample variation for the 6 fixed landmarks, 56.6% of total sample variation for all 28 landmarks) (Fig. 3). There is no separation of groups along the PC2 axis (20.2% and 19.2% of total sample variation for the 6- and 28-landmark configurations respectively), but the non-*sapiens* individuals remain close to or well above the 0 line whereas *H. sapiens* specimens are evenly distributed on either side of the 0 line. The two Neandertal specimens cluster together on the PC1-PC2 plot, while the *Homo erectus* score slightly higher for PC1. Sambungmacan 3 lies closer to the *Homo sapiens* variation but there is no intersection between non-*sapiens* and *sapiens* values. The features associated with higher (*H. sapiens*) scores are: reduced cranial superstructures (supra-orbital torus and occipital thickening), a vertically sloping frontal bone and an elevated parietal vault. A calculation of the bootstrapped full Procrustes distance between the means for each group suggests, again, a higher degree of demarcation in the morphology of *Homo sapiens* relative to the other species (0.1163 for *Homo sapiens*/Neandertals, p-value=0.01; 0.0943 for *Homo sapiens*/ *Homo erectus*, p-value=0.01; distance=0.0451 for *Homo erectus*/Neandertals, p-value=0.17).

PCA on the endocranial vault

Features allowing differentiation between species are less clear on the endocranium than the ectocranium (Fig. 3), and occur along PC2 (20.8% of total sample variation) rather than PC1 (38.47%). Non-*sapiens* species cluster close together and just outside or on the outer margins of the

Homo sapiens range of variation. Features associated with negative scores on PC2 (for the 6 cerebral landmarks configuration) and with positive scores on PC2 (for the full configurations) are a receding, longer frontal bec, vertical development of the frontal and parietal lobes, and a slight shortening of the occipital lobes (Fig. 3).

When comparing the extremes of the 6-landmark configurations for the ectocranial and endocranial vaults along the PC axes showing interspecies differentiation (respectively PC1 and PC2), joint variation appears slightly higher in the parietal and occipital areas of the profile, the reduction of frontal superstructures in *Homo sapiens* being reflected on the endocranium solely by a recession of the frontal bec. There appears to be slightly less vertical expansion of the frontal lobe than of the frontal bone.

Once again, although the Procrustes distances between the means are lower than those observed for the ectocranial vault, *Homo sapiens* emerges as more 'different' from the other two species than *Homo erectus* and Neandertals (0.0772 for *Homo sapiens*/Neandertals, p-value=0.01; 0.0702 for *Homo sapiens*/*Homo erectus*, p-value=0.01; 0.0322 for *Homo erectus*/ Neandertals, p-value=0,49). However, the significance level for the Neandertal/*Homo erectus* pair is very low, so that these results cannot be used as such and need to be tested with larger samples.

## Covariation and morphological co-evolution

2-Block PLS on ecto- and endocranial profiles

A high degree of covariation was detected between the endocranial profile and the outer vault of the skull (Fig. 4). The PLS with the fixed landmark configurations yielded an overall correlation coefficient of 0.76 (p-value <0.01) and the PLS with all landmarks a coefficient of 0.85 (p-value <0.01). Both show a clear distinction between non-*sapiens* species and *Homo sapiens* for PLS 1, with Sambungmacan 3 plotting at the fringe of the *Homo erectus* variance, closer to *Homo sapiens* than the other *non-sapiens* fossils. However, the PLS did not allow us to detect different patterns of covariation between the endo- and ectocranial profiles among the species studied: the different species seem to follow the same slope, suggesting similar integration patterns among species between the ecto- and endocranial profiles.

### Co-evolution of cranial and cerebral features

Our examination of the PCA results suggests the following joint changes in cranial and cerebral features in our sample.

Frontal area: on the *Homo sapiens* brain, the receding frontal bec goes together with a slightly more protruding frontal pole than in non-*sapiens* groups. The skull shows smaller frontal superstructures (supra-orbital torus). Bregma and FL
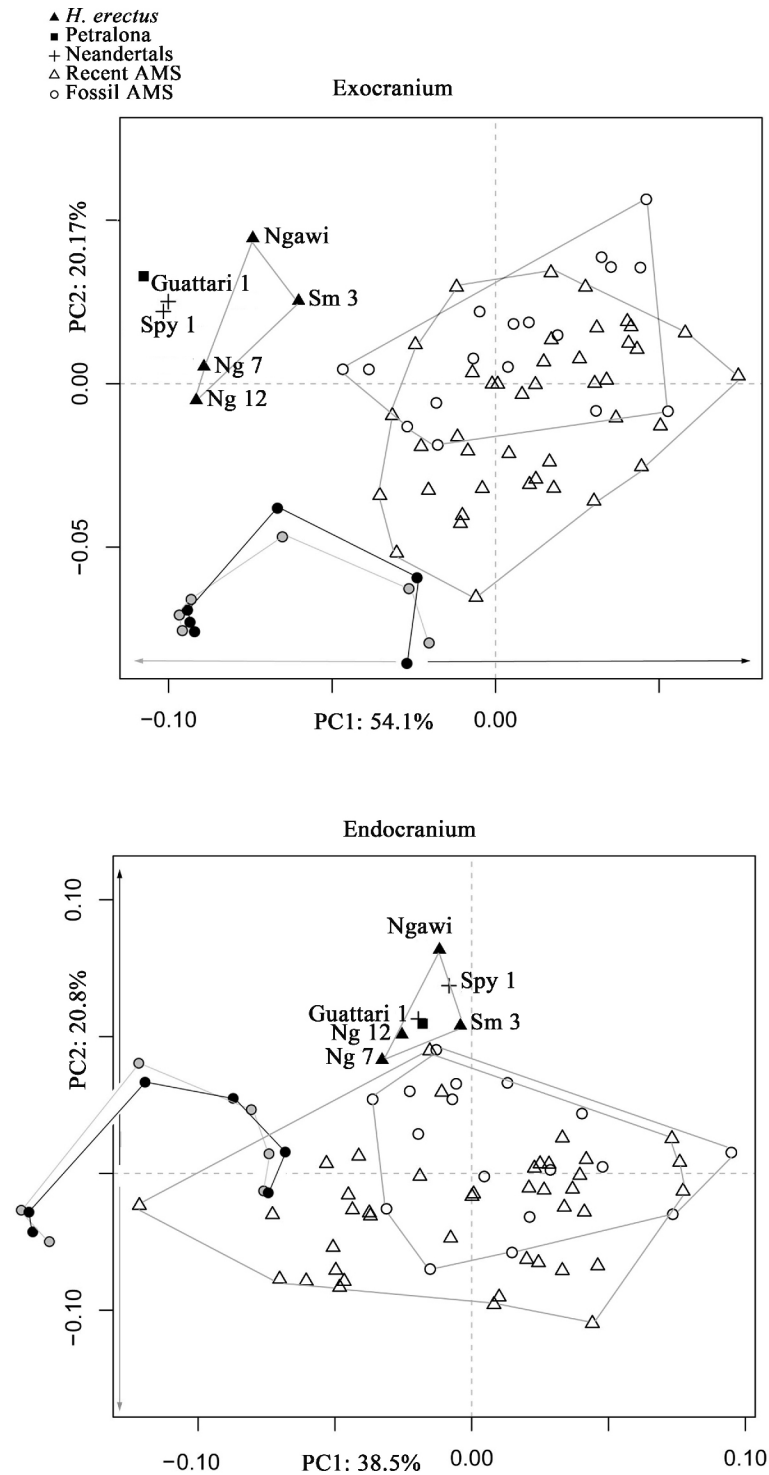
Fig. 3 Top: PCA of the ectocranial vault (6–landmark configurations). Wireframes show the variations along PC1 (grey: low score conformation, black: high score conformation). Bottom: PCA on the endocranial vault (6–landmark configuration). Wireframes show the variations along PC2 (grey: low score conformation, black: high score conformation) / *Haut : ACP sur la voûte exocrânienne (conformation de six* landmarks). *Les illustrations montrent les variations le long de la composante principale 1 (en gris : conformation minimale, en noir : conformation maximale). Bas : ACP sur la voûte endocrânienne (conformation de six* landmarks). *Variations le long de la composante principale 2 (en gris : conformation minimale, en noir : conformation maximale)*
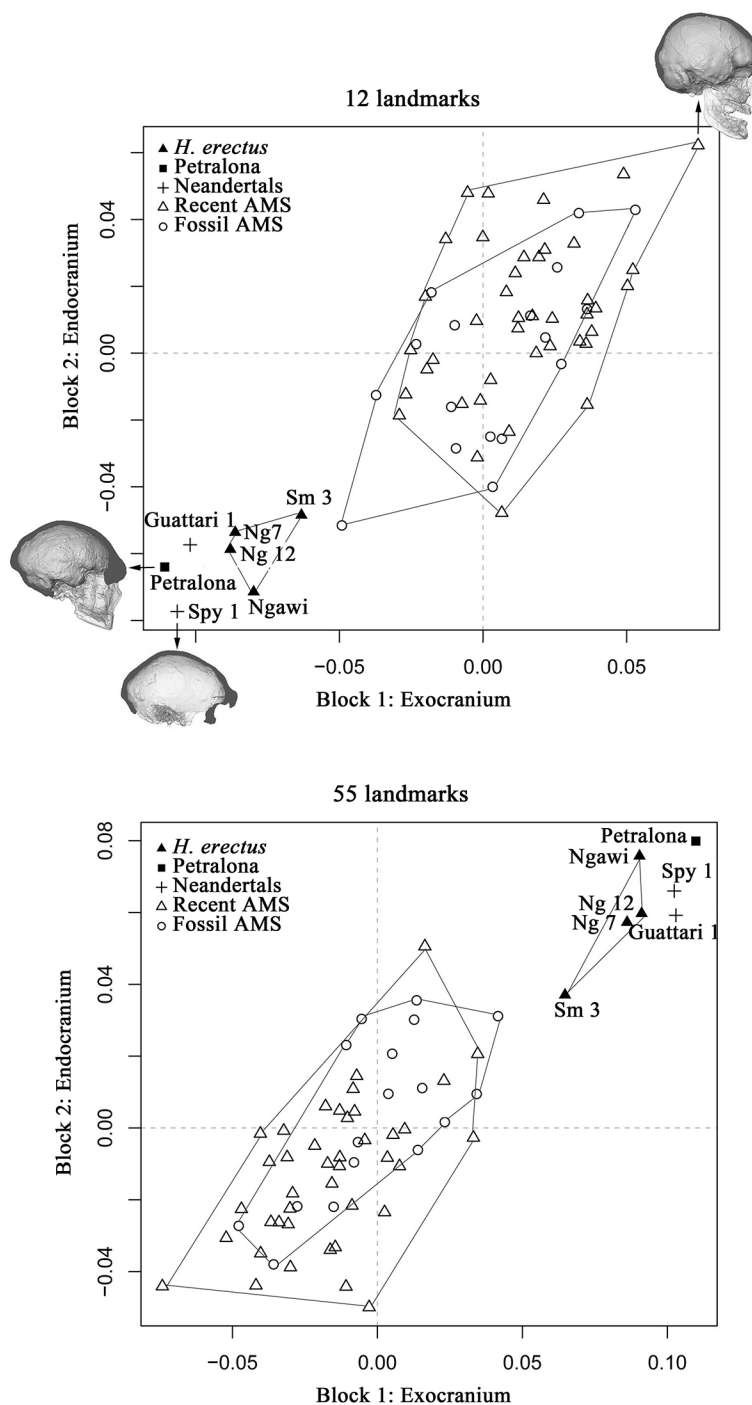
Fig. 4 2B–PLS of the ecto– and endo–cranial vaults / *Analyse en 2B–PLS sur les voûtes exo- et endocrâniennes*

are higher in *Homo sapiens*, with a vertical elevation of both the frontal bone and the frontal lobe in *Homo sapiens*, and slightly shorter than the parietal bone in non-*sapiens* configurations (Fig. 3). The frontal lobe in both *Homo sapiens* and non-*sapiens* groups is, proportionally, the longest section of our profile (compared with the upper surface length of the parietal and occipital lobes), whereas the frontal bone is comparatively shorter, with a length roughly similar to that of the parietal bone (Fig. 3). Overall, and apart from the anterior part of the frontal area, there is no noticeable interspecies difference in the interplay between frontal bone and lobe.

Parietal area: The parietal lobe appears slightly longer in *Homo sapiens* as FL and OL are further apart, a similar pattern being observed between bregma and lambda on the skull (Fig. 3, 5). Lambda is located higher in *Homo sapiens* than in other species, but the demarcation between the

parietal and occipital lobes (OL) is not. The full endocranial landmark configurations show that the endocranial vault is higher in *Homo sapiens* than in the other species all along the parietal lobe but less so towards its posterior end where the endocranium of *Homo sapiens* starts sloping downward more abruptly than in the other species (Fig. 6).

Occipital area: The occipital lobe in *Homo sapiens* appears to be more vertical than in the other species, contributing to the globular aspect of the *H. sapiens* endocranium. The occipital pole is more projected in the non-*sapiens* groups but the endinion is not, which gives the occipital lobe an elongated aspect. The globularisation in *Homo sapiens* is in keeping with neurocranial morphology. In the endo-cranial configurations represented by non-*sapiens* individuals, the inion and the endinion appear to move apart, with a lower endinion and thicker bone than is found in *Homo sapiens* (Figs 5, 6). This is slightly more noticeable in the *Homo erectus* individuals.

Discussion

A note on Sambungmacan 3's position in the analyses

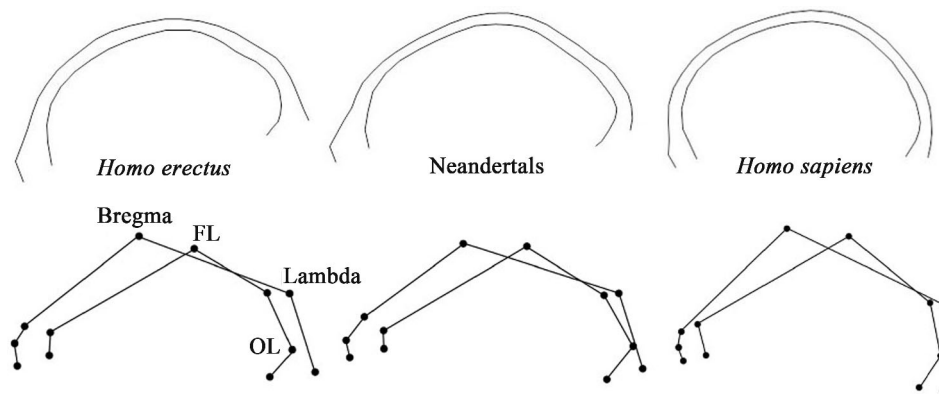In our 2B-PLS and in some of our PCAs, Sambungmacan 3 (Sm 3) is at one extreme of *Homo erectus* variation, closer

Fig. 5 Average profile for each species studied / *Profil moyen pour chaque espèce étudiée*
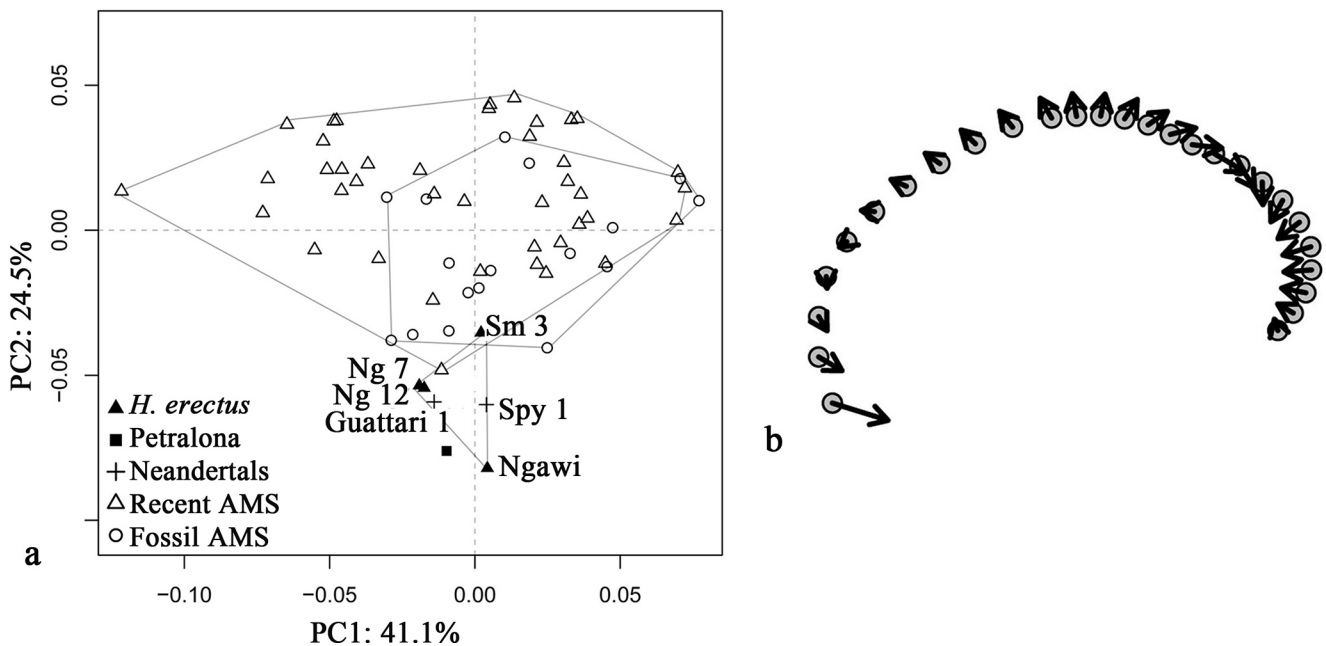

Fig. 6 a: PCA of the endocranium (27 landmarks configuration), b: variations along PC2. Dots: extreme negative conformation (non-*sapiens*), arrow tips: extreme positive conformation (*sapiens*) / *a : ACP sur l'endocrâne (configuration de 27* landmarks*) ; b : variations le long de la composante principale 2. Ronds : conformation négative maximale (non-*sapiens*)*, pointes des flèches : conformation posi-tive maximale (*sapiens*)*

than the other non-*sapiens* fossils to the *Homo sapiens* group (Figs 2, 4, 6). However, even though Sm 3 regularly lies close to the *Homo sapiens* variation - or even within it, as in the PCA on the 27-landmark endocranial configuration (Fig. 6), its position is not unexpectedly distant from that of the other *Homo erectus* specimens and is a reflection of the variation of this species. A similar pattern was detected in Delson *et al*.'s geometric morphometric study of the exo-cranial mid-sagittal plane in *Homo erectus*, "archaic *Homo sapiens*" (including Petralona) and modern humans [40]. This is perhaps unsurprising as Sm 3 is known to have cra-nial features that differ slightly to what would be expected for a *Homo erectus sensu stricto*, such as more globular cra-nial and endocranial vaults or a vertically rising frontal bone [41,42]. Sambungmacan 3's unusual features and position in the PCA plot could be due to an early developmental stage (it has been identified as an individual going through the subadult-adult transition at the time of death [43]) and/or to sexual dimorphism (it is thought to be a female individual [40,42]).

Frontal and parietal lobes and bones

Our results show an elevation of the frontal lobe in *Homo sapiens* (Figs 3, 5), which is consistent with the well-documented, characteristic vertical inclination of the frontal bone in *Homo sapiens* [10,44]. This might seem to be an intuitive finding. Holloway and colleagues mention that the vertical frontal bone of *Homo sapiens* led researchers to expect a larger frontal lobe in this species relative to the rest of the brain and that, when carrying out a visual exami-nation of hominin endocasts ranging from mid-Pliocene individuals up to extant *Homo sapiens*, the frontal lobe seems wider, rounder and higher in *Homo sapiens* [25]. The authors cite a plethora of literature showing the involve-ment of the frontal lobes in the complex cognition that makes humans human. However, they point out that the idea of an enlarged frontal lobe in *Homo sapiens* compared with other extant primates has been disproved - for instance, Semendeferi and colleagues have shown that although the frontal lobe is larger in humans than in extant apes and mon-keys, this is an allometric effect of general brain enlargement and that *Homo sapiens* does not deviate from the pattern observed in the other primates studied in this respect [45]. Moreover, the results obtained by Bookstein *et al*. on the mid-sagittal plane suggest wide differences in the joint evo-lution of the frontal bone and the frontal lobe between mid-Pleistocene *Homo* and *Homo sapiens* [10]. For this study, the inner and outer vaults of the frontal were analysed using 2D geometric morphometrics on a sample of 16 recent *Homo sapiens* and 5 mid-Pleistocene fossils, described by Bookstein *et al*. as 3 *Homo heidelbergensis*, one proto-Neandertal and one Neandertal. Bookstein *et al*. found the

endocranial profile to be stable in the sample, unlike the ecto-cranial profile which shows significant diversity among the taxa studied. Although our respective samples differ in number and in nature (Bookstein *et al*. having stud-ied more *H. heidelbergensis* specimens and no *H. erectus*), it might seem surprising that in this study, *Homo sapiens* shows clear differences in endocranial profiles when Book-stein and colleagues showed that there are no major differ-ences in inner frontal morphology between *Homo sapiens* and the mid-Pleistocene fossils. However, the elevation of the frontal lobe observed in our *Homo sapiens* sample mainly affects the posterior part of the lobe, which lies under the parietal bones, outside the area examined by Book-stein and colleagues. Moreover, their paper focuses on the inner and outer frontal bone and not on the frontal lobe itself (the inner frontal bone being defined here between the fora-men caecum and the endobregma).

Our results suggest that the endocranial profile of *Homo sapiens* may be differentiated from that of the other *Homo* species, and that there are more similarities between the cra-nial and cerebral morphologies and covariation patterns of *Homo erectus* and Neandertal than between either of these and *Homo sapiens*.

The enlargement of the parietal lobe in *Homo sapiens* has been noted previously: its greater height [24] and width [46] and larger surface area relative to that of the frontal lobe [21] are considered autapomorphic. Grimaud-Hervé also showed that reliefs such as Gratiolet's marginal lobule or the angular gyrus increase dramatically in surface area and, in the case of Gratiolet's marginal lobule, in the degree of projection in anatomically modern humans relative to Neandertals and *Homo erectus* endocasts [24]. Our results show the greater height of the parietal lobe but suggest that it is compara-tively shorter relative to other lobes in *Homo sapiens* than in the other species studied, so that its enlargement contri-butes to the general globularisation of the endocranium by increasing its height and width but not its vault length. The patterns of frontal and parietal bone and lobe extension seem to differ in *Homo sapiens* relatively to the other studied species.

Occipital lobe and bone

The globularisation of the endocranium in *Homo sapiens* is no doubt partially caused by the forward shift of the occipital lobes from behind the parieto-temporal complex in *Homo erectus* to under the parietal and temporal lobes in Neander-tals and *Homo sapiens*, as demonstrated by Grimaud-Hervé [24]. The globularisation is not visible in Neandertals, whose occipital poles appear to project much more than in *Homo sapiens*. Both the bone and lobe are more vertical in *Homo sapiens* than in the other species, with a different interplay between inion and endinion (see also [23]).

General morphology of the profile

After a neonatal phase of growing together as a function of brain shape, the inner and outer tables of the skull have been shown to be shaped separately under the influence of different factors (the outer shape of the frontal bone, for instance, being influenced by orbital morphology whereas the inner frontal bone is shaped around the frontal lobe [12]). We therefore expected relatively low levels of covariation between the skull and the cerebral landmarks. The results of our 2B-PLS analysis contradict this expectation, suggesting that, where no other stresses influence outer cranial morphology, it is the shape of the brain that is responsible for it. Further investigation, comparing covariation between ecto-and endo-cranial morphologies in different areas of the mid-sagittal profile, would be valuable in order to confirm that this is the case for the parietal and the posterior frontal areas. It is worth keeping in mind that the shapes of the endocranium and of the skull are both influenced by the timing of the closure of the cranial sutures [47], so that they can mutually affect each other's morphology. Our results concerning morphological differences between *Homo sapiens* and other species, and in particular the globularisation of the endocranium and the neurocranium, are consistent with tendencies previously highlighted by other researchers for the cranium [3,10,48,49]. Thus, Athreya's Fourier analyses on the frontal bone of *Homo erectus*, *Homo sapiens* and Neandertals shows differences between the following features in *Homo sapiens* and the other species studied: curvature of the frontal bone, projection of the supra-orbital torus and general shape of the cranium in the mid-sagittal plane and in two para-sagittal planes [37]. Moreover, Bookstein *et al*. show a reduction of facial structures and a globularisation of the neurocranium in *Homo sapiens* in their study of the skull's mid-sagittal plane [48]. Lieberman *et al*. also highlight these morphological changes, and interpret them as *Homo sapiens* autapomorphies linked to ontogenetic particularities that influence basicranial angle, cranial fossae length and width, and facial length [4]. These features could in turn be influenced by changes in brain organisation such as a relative increase in size in the temporal and potentially in the frontal lobes. Our results for the mid-sagittal plane also showed vertical expansion of the parietal lobe in *Homo sapiens* compared to other species. Lestrel *et al*., using Fourier analysis, found significant differences between the shape of the neurocranium in *Homo sapiens* and a group comprising Neandertals and *Homo erectus* [3]. *Homo heidelbergensis* was in an intermediate position between *Homo erectus* and Neandertals, similar to the position of the Petralona fossil in the current study. Lestrel *et al*. propose that these differences in morphological proximity in the taxa studied are due to continuous evolution from *Homo erectus* to Neandertals and to a separate development of *Homo sapiens*. While we do not wish to enter into phylogenic or cognitive considera-

tions in this paper, we can suggest that the specific characteristics of *Homo sapiens* and their differences compared to other taxa are due to its evolutionary history and, potentially, partly to the development of brain functions. The globularisation of the endocranium in *Homo sapiens* has been shown to occur in infants during the first year of life, after a neonatal phase of growth in which *Homo sapiens* and Neandertals share the same elongated endocranial shape pattern [47]. Gunz *et al*. conclude that Neandertals and *Homo sapiens*, from similar-looking elongated newborn endocrania, grow brains of comparable volume through different growth patterns, and that this difference in the rate and timing of the development of brain organisation so early in life may have implications in terms of cognition and behaviour. Investigations of cerebral and cranial co-variation during ontogeny would perhaps be of interest in order to better understand the interplay between cranial bone and lobe extension in different species and to confirm and explain whether or not this interplay remains apparently stable among *Homo* species, as our study suggests.

Our study suggests that the ecto- and endocranial profiles of *Homo sapiens* differ particularly widely from those of *Homo erectus*, Neandertals and *Homo heidelbergensis*. There are a few differences in ecto-endocranial relationships in *Homo sapiens* compared with other taxa, which could be related to a lesser development of sinuses and muscle attachments, but this calls for further investigation. Cranial and endocranial size do not seem to account for the shape differences observed in the sample, as shown by the differentiation of Neandertals relative to *Homo sapiens* despite their similar cranial capacities and by the position of the specimen with the smallest endocranial capacity, SM3, closer to *Homo sapiens* than the other non-*sapiens* fossils. Although closer to *Homo erectus* in overall profile morphology, Neandertals are in an intermediate position for some criteria (orientation of the frontal bec, distance between lambda and the posterior limit of the parietal lobe, distance between inion and endinion). Renewed analyses with a larger fossil sample would help to determine whether the degree of demarcation shown for *Homo sapiens* is unique amongst *Homo* species and to assess *Homo erectus* and Neandertal variability. For instance, although they are informative, the Procrustes distances we computed between mean shapes should be considered with care because of the small number of specimens representing each species in our fossil sample and, consequently, the small amount of variability that can be represented for each fossil species.

Conclusion

We were able to validate our main hypothesis: there does appear to be interspecific differences in the joint variation

of cranial and endocranial morphologies among *Homo* species. This is particularly striking in *Homo sapiens* relative to *Homo erectus*, Neandertals and our *Homo heidelbergensis* specimen. We found variations in the relative extension of lobes according to species, and it seems that some cranial and cerebral features may interact differently in *Homo sapiens* and in the non-*sapiens* groups. The shape of the mid-sagittal profile of *Homo sapiens* was found to differ more from the others than any of the other species studied. Finally, we did find the high degree of covariation that we expected between the morphologies of the ecto-and endocranial vaults, but we also found a high degree of covariation between the outer bony landmarks and the cerebral landmarks. However, although our results support those of other research on various parts of the cranium and endocranium, they only pertain to the mid-sagittal plane, and it is possible that studies of other planes or larger areas might contradict or nuance them. Another nuance should be introduced, as the *Homo sapiens* sample, while differing from the other samples in many respects, fits in with the wider *Homo* evolutionary tendency, as shown by the PLS results for endo-ectocranial vault covariation. A closer look at separate regions of the skull and endocranium would be needed in order to better understand the causes and mechanisms of this covariation. Multiple complex parameters to do with the functions of the skull influence the respective morphologies of the inner and the outer cranial regions [4], and therefore their degree of closeness. Brain growth and evolution, the robustness of muscle attachment and circumorbital morphology are some of these factors. Our study suggests that there are variations in the relationships between skull and endocranium among different species of the *Homo* genus, but that these differences are limited to areas where factors external to brain growth influence outer cranial morphology (like the supra-orbital or the occipital tori). Some of the features highlighted here could be derived in *Homo sapiens* (elevated posterior part of the frontal lobe, globularisation of the endocranium, elevated parietal lobe and cranial vault) while other changes seem to be shared with Neandertals, such as a receding frontal bec, which is accentuated in *Homo sapiens* [24]. The pattern of interplay between lobes and bones appears to differ between species, but this result needs to be tested by analysing the profiles of a larger number of species and individuals. *Homo sapiens* profiles appear to be highly variable, and further work using larger non-*sapiens* samples will allow us to assess diversity in the proximity of cranial-endocranial relations in other species. Renewing these analyses with a larger sample would also help to determine whether the degree of demarcation shown in *Homo sapiens* is unique among *Homo* species and to assess its variability in *Homo erectus* and Neandertals. It is certain that this field would benefit from further work using new methodologies, analysing larger samples and incorporating additional fossil species as well as extant non-human primates. Wider distribution of fossil CT data in the near future would be immensely beneficial to this and to any other studies dealing with morphological variability.

Conflict of interest: None

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