Neurocranial evolution in modern humans: the case of Jebel Irhoud 1

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Abstract Jebel Irhoud 1 represents an almost complete cranium from the North African late Middle Pleistocene. Despite the good preservation of most of its anatomical regions, its phylogenetic position is still uncertain, particularly its relationship to the emergence of the modern human lineage. The present paper supplies a basic morphometric description and comparison of the endocast of Jebel Irhoud 1. The endocast's maximum width is large when compared with the hemispheric length, with values similar to those of Neandertals. Conversely, the frontal width is less pronounced, showing proportions compatible with modern and non-modern human taxa. The vertical proportions are similar to those displayed by *Homo erectus*, while the lateral proportions are comparable to Neandertals. Furthermore, the upper parietal areas show a certain parasagittal lateral bulging, as in European Neandertals. It remains to be established if this trait evolved independently in both the Neandertal and modern human lineages, or if it was already present in a common ancestor of these two groups. Given that Jebel Irhoud 1 in North Africa and Herto in East Africa have similar geological age, similar facial morphology, but different vault proportions, it seems likely that the origin of the modern human lineage may have predated the origin of many aspects of the modern human brain.

Key words: human evolution, neurocranium, paleoneurology, *Homo sapiens*

Introduction

Since the discovery of Jebel Irhoud 1 by workmen in 1961 and Ennouchi's (1962) description of it as a Neandertal, the phylogenetic position of Jebel Irhoud has been controversial. The site of Jebel Irhoud lies in a barite mine, 60 km southeast of Safi, Morocco (Day, 1986). Subsequently, the site yielded a second adult cranium, Jebel Irhoud 2 (Ennouchi, 1968), and additional human fossils were recovered including Jebel Irhoud 3, a mandible of a 7–8 year old child (Hublin and Tillier, 1981), and Jebel Irhoud 4, a juvenile humerus (Hublin et al., 1987). All were recovered from cave fill of caverns within Pre-Cambrian limestone and are associated with a Levallois-Mousterian Middle Stone Age industry, which precedes the Aterian in North Africa. An early electron spin resonance (ESR) study by Grün and Stringer (1991) placed the Jebel Irhoud specimens within the broad interval of 100–200 ka. More recently, T. Smith et al. (2007) reported a uranium-series and ESR date for the site of 160 ± 16 ka.

Currently, there is no agreement on the phylogenetic position of the skull of Jebel Irhoud 1, and on the interpretation of its neurocranial and endocranial morphology (Figure 1). Since Ennouchi's (1962) initial description of Jebel Irhoud 1

as a Neandertal, analyses of this cranium and other specimens from the site have reached different conclusions, especially with regard to whether any of the fossils from the site have the derived traits common among Neandertals.

Santa Luca (1978) concluded that Jebel Irhoud 1 had no trace of the Neandertal apomorphies of a strongly projecting juxtamastoid process, mastoid tubercle, or suprainiac fossa. Hublin and Tillier (1981) noted that the juvenile mandible (Jebel Irhoud 3) differed substantially from Neandertals, possessing none of their apomorphies and bearing instead a very weakly developed chin, with all of the components of the chin present, albeit without much of an incurvature above it. A number of other researchers have disputed that this non-projecting eminence constitutes a true chin (e.g. Schwartz and Tattersall, 2000, 2003, 2010).

Jebel Irhoud 1 has been investigated with both univariate and multivariate morphometric techniques. Stringer (1974) included a suite of Howells' (1973) measurements of Jebel Irhoud 1 in his multivariate study of Middle and Upper Pleistocene human crania. His analysis showed the Moroccan specimen differed from both western European 'classic' Neandertals and from Upper Paleolithic Europeans. The differences from classic Neandertals lay in Jebel Irhoud 1's cranial vault's greater bregma–lambda chord, bifrontal breadth, nasion–bregma subtense, and its smaller bregma–lambda subtense, glabella–opisthocranium length, and bistephanic breadth. In its face, Jebel Irhoud 1 differed from Neandertals in its larger biorbital breadth and its smaller nasiofrontal subtense, nasal height, zygoorbitale radius, subspinale radius, and orbital breadth. The differences between Jebel Irhoud 1 and Upper Paleolithic humans were equally

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Figure 1. Jebel Irhoud 1 (cast) and the endocast in upper, lateral left, and posterior views (cast: Museo di Antropologia, University La Sapienza, Rome; endocast: Institut de Paléontologie Humaine, Paris).

striking, with dissimilarities in the cranial vault due to Jebel Irhoud 1's greater bifrontal breadth, maximum cranial breadth, nasion–subtense fraction and its smaller bregma–lambda subtense and lambda–opisthion chord. In the face, Jebel Irhoud 1 differed from Upper Paleolithic specimens in its larger supraorbital projection, nasal breadth, prosthion radius, orbital height, and its smaller zygoorbitale radius. The length of the bregma–lambda chord makes Jebel Irhoud 1 more derived than Neandertals but less than Upper Paleolithic humans.

The midsagittal profile of Jebel Irhoud 1 has been also described in terms of geometry and shape analysis (e.g. Manzi et al., 2000; Hublin, 2002; Bruner et al., 2004; Bräuer, 2006a, b). Figure 2 and Figure 3 show a comparison of Jebel Irhoud 1's midsagittal profile with average forms of other hominid groups as well as with some representative fossil specimens, aligned along the neurocranial baseline (original data from Bruner et al., 2004). Major differences between this specimen and the principal human taxa can be recognised in both face and vault. The vault profile is definitely more bulging than *Homo ergaster/erectus*, but not as much as in *H. sapiens*. The vault profile is similar to the Neanderthal configuration but is slightly flatter at the parietal portion of the outline and more bulging at the frontal squama. The vault profile does not display the parietal enlargement of the

Qafzeh/Skhul specimens and it is quite similar to the Middle Pleistocene profiles. The face is vertically shorter when compared with extinct species, but shows a certain alveolar prognathism when compared with Upper Pleistocene modern humans. The facial profile is also shorter when compared with Middle Pleistocene specimens such as Kabwe or Sima de los Huesos 5, but is very similar to Qafzeh 9.

Hublin (1992) concluded that Jebel Irhoud 1 and the rest of the hominin specimens from the site had a combination of primitive traits as well as some derived traits of modern humans that developed gradually in North Africa (Hublin, 1985) or elsewhere in Africa (Bräuer, 1984; Rightmire, 1984), but no trace of derived Neandertal features. Hublin's conclusions have proven influential, but the argument for special Neandertal affinities of Jebel Irhoud has persisted. Recently, T. Smith et al. (2007) demonstrated that the rate of enamel formation in the molars of Jebel Irhoud 3 indicated it had developed at a slow, modern rate, providing the earliest known instance of a modern life history. In contrast, F. Smith et al. (1995) argued that the long, low, and broad cranial vaults, lambdoidal flattening, and occipital bun-like projections (or "hemi-buns") of the Jebel Irhoud crania did, in fact, link these fossils with European Neandertals. This led F. Smith et al. (1995) to propose that Jebel Irhoud lay at one pole of a circum-Mediterranean ring of interbreeding

Figure 2. Jebel Irhoud 1 midsagittal profile (a) has been largely investigated through traditional and geometric morphometrics. Here the Jebel Irhoud profile is compared through superimposition according to the neurocranial (nasion–inion) baseline with average *Homo ergaster/erectus* (b), Neandertals (c), and modern human (d) profile (br: bregma; gl: glabella; in: inion; la: lambda; na: nasion; ns: nasospinale; pr: prosthion; orthogonally projected points are at 50% of the frontal, parietal, and occipital chords, respectively). Target configuration: Jebel Irhoud (bold links); reference configuration: group means (thin links). Mean reference shapes have been computed averaging KNM-ER3733 and the Zhoukoudien reconstruction by Weidenreich (1943) for *Homo ergaster/erectus*; Chancelade, Cro-Magnon 1, and Fonterossi for modern humans; Saccopastore 1, Tabun 1, la Ferrassie 1, La Chapelle-aux-Saints, Guattari 1, Amud 1, and Shanidar 1, for Neandertals. Original data from Bruner et al. (2004). Spatial differences are also visualized through thin-plate spline deformation grids (Bookstein, 1991).

populations that was interrupted only by the Strait of Gibraltar. Because of the mixture of archaic and derived traits, the question of the cranial affinities of Jebel Irhoud 1 has remained open.

The endocranial surface and endocasts of the Jebel Irhoud specimens have received less attention although they too have the potential to yield phylogenetic insights. The endocasts have been described by Holloway (Holloway, 1981; Holloway et al., 2004) and Grimaud-Hervé (2005). Jebel Irhoud 1 may present some minor distortions in its anterior portions. However, it displays a standard human pattern of asymmetry, with right-frontal left-occipital petalia. Broca's area is definitely larger on the right side. Cranial capacity is estimated in 1305 cm³ for Jebel Irhoud 1, and around 1400 cm³ for Jebel Irhoud 2. In both cases, the meningeal pattern is complex but not extensively reticulated, with dominance of the anterior branch (more patently so in Jebel Irhoud 2). Holloway et al. (2004) suggested that the endocast from Jebel Irhoud 1 retains the classic structure of the European Middle Paleolithic morphs (i.e. Neandertals). On the other hand, Grimaud-Hervé proposed that the same endocast displays some modern human features such as the morphology of the meningeal vessels or the anatomy of the

frontal and parietal areas.

In the present paper we compare the morphology of the endocranium of Jebel Irhoud 1 with representative specimens of the human genus, in order to describe its main geometrical differences and affinities. This information may be relevant to provide inferences about the evolutionary position of Jebel Irhoud 1, but most of all to supply information on the dynamics of human endocranial variations at the transition between Middle and Upper Pleistocene.

Materials and Methods

Morphometrics were taken on an endocranial cast preserved at the Institut de Paleontologie Humaine, Paris (Figure 1; see also Grimaud-Hervé, 2005). Bivariate correlations were computed among the three main endocranial diameters, namely hemispheric length (mean value of both hemispheres) versus maximum endocranial width and versus frontal width at the Broca's area. These diameters are generally regarded as potentially informative within hominid evolution because of the changes in the relative proportions of the frontal lobes and of the parietotemporal areas (Bruner and Holloway, 2010). The frontal width is measured

Figure 3. The Jebel Irhoud 1 midsagittal profile is compared through neurocranial baseline with the profiles from Kabwe (a), Sima de los Huesos 5 (b), Skhul 5 (c), and Qafzeh 9 (d). Original data from Bruner et al. (2004).

at the posterior part of the third frontal gyrus (i.e. the widest section of the anterior cranial fossa). The maximum endocranial width is measured at the temporoparietal boundary. These metrics must be interpreted as geometric references but not necessarily homologous areas. Both diameters were measured orthogonally with respect to the midsagittal plane, regardless of possible asymmetries. Jebel Irhoud 1 was compared with specimens belonging to archaic small-brained human taxa (Salé, Sangiran 2, Trinil 2, Zhoukoudian 10, Zhoukoudian 12, Zhoukoudian 3, Arago, and Sima de los Huesos 5), Neandertals (Feldhofer 1, Guattari, La Chapelle-aux-Saints, La Ferrassie 1, Saccopastore 1, Teshik-Tash), and modern humans (Combe Capelle, Předmostí 3, Předmostí 4, Předmostí 9, Předmostí 10, Skhul 5, Vatte di Zambana).

A three-dimensional (3D) model was used to compare the raw endocranial geometry (Figure 4). The bilateral configuration includes 17 landmarks: frontal poles, rolandic scissure, parieto-occipital boundary, occipital poles, internal occipital protuberance, temporo-occipito lower boundary, frontoparietal anterior boundary, Broca's area, maximum temporal width, supramarginal gyrus (see Bruner et al., 2003 for further information on landmarks). The coordinates from Jebel Irhoud 1 were compared after Procrustes superimposition with averaged data for *H. erectus* (the mean of Zhoukoudian III, Zhoukoudian XII, and Trinil 2), Neandertals (the average of Feldhofer 1, La Ferrassie 1, La Chapelle-aux-

Saints, Teshik Tash, Guattari, and Saccopastore 1) and Upper Pleistocene through Mesolithic modern humans (the mean of Předmostí 3, 4, 9, and 10, Combe Capelle, Dolní Věstonice 1, and Vatte di Zambana). In Procrustes superimposition the coordinate systems are translated to a common centroid, scaled to unitary size, and rotated so as to minimize the sum of squared differences between corresponding landmarks (Bookstein, 1991; Zelditch et al., 2004). This transformation normalizes size, position, and orientation of the specimens, permitting comparisons of the spatial organization of the anatomical elements after minimization of the differences. Because of the descriptive target of this survey, here we only compare Jebel Irhoud 1 with the group means of the main human taxa, to provide an overall evaluation of the geometrical similarities. By computing reference shapes after superimposition of the available data, group means allows the comparison of the whole endocranial geometry, even though many specimens are incomplete and have missing landmarks. Nonetheless, it is worth noting that this approach can only provide a general description of the raw morphological affinity between groups. The comparisons with averaged shapes were computed on symmetrized models. Superimpositions were computed with Morphue (Slice, 2000) and MorphoJ (Klingenberg, 2011).

Figure 4. Endocranial landmarks used in this study, plotted onto the endocranial cast in left lateral view (bc: Broca's cap; cs: central sulcus; fp: frontal pole; ft: frontotemporal anterior boundary; ip: internal occipital protuberance; mw: maximum endocranial width; op: occipital pole; po: parieto-occipital boundary; sg: supramarginal gyrus; to: temporo-occipital lower boundary). The wireframes show the superimposed configurations in posterior, left lateral, and superior views.

Figure 5. Bivariate plot between hemispheric length (HL) and the main endocranial width, maximum width (MW) and frontal width at the Broca's cap (FW), with least-squares regression fits for archaic humans (ARC), Neandertal (NDR), modern humans (MOD), showing the position of Jebel Irhoud 1 (arrows).

Results

The endocast does not show many cortical details and the lower areas such as the temporal lobes or the cerebellum are generally poorly preserved. Nonetheless, the gross morphology of the endocranial cavity can be easily recognized, as can many basic cortical features.

Relative to hemispheric length, Neandertals and modern humans have wider endocrasts than the archaic group (Figure 5a), and Neandertals have even wider endocrasts than modern humans. Jebel Irhoud 1 fits the Neandertal allometric trajectory, with proportions similar to Guattari 1. Similar differences between the three groups can be recognized in the analysis of frontal width relative to hemispheric length, although in this case the differences are less marked (Figure 5b). In this bivariate comparison Jebel Irhoud 1 falls on the modern human allometric trajectory. However, be-

cause of the limited group-specific differences, its position is not incompatible with the variability of any of the groups. Although we use a limited comparative sample, such results are completely in agreement with wider analyses on the patterns of endocranial widening in the human genus (Bruner and Holloway, 2010). Hence, according to the metrics of the endocast, Jebel Irhoud 1 displays a relatively wide middle endocranial fossa, comparable with the Neandertal proportions. At the same time its anterior fossa shows proportions compatible with any of the extinct human species, but are the most similar to modern human values.

The superimposition of the 3D configurations shows that the endocast from Jebel Irhoud 1 is relatively flatter and wider than any other mean shapes (Figure 6). With regard to the vertical diameters, the endocast is more similar to the archaic mean configuration, while the distribution of the endocranial widths is more similar to the Neandertals. In both cases,

Figure 6. Pairwise comparisons of the symmetrized 3D endocranial model after Procrustes superimposition between Jebel Irhoud (bold line) and the average configuration for *Homo erectus* (HE), Neandertal (NDR) and modern (MOD) groups, in left lateral, upper, and posterior view.

it is worth noting that the differences are rather small. The differences from modern mean shape are more marked as a result of the wide lateral morphology of Jebel Irhoud and its lack of the pronounced vertical enlargement associated with modern frontoparietal geometry.

Discussion

General morphology

Although Jebel Irhoud 1 is an almost complete cranium, disagreements persist regarding its phylogenetic role and taxonomic position. Because of its many plesiomorphic traits but large cranial capacity, early authors emphasized its Neandertal affinities (Ennouchi, 1962). Some of these traits (notably the occipital morphology) have been supposed to reflect a genetic admixture between groups from different geographic and taxonomic contexts (Smith et al., 2005). Nonetheless, the derived features suggest a probable link with the morphology associated with the early modern humans, or at least with their ancestors (Lahr and Foley, 1998; Hublin, 2002).

The cranium has a vertically short face with a certain degree of alveolar prognathism, no midfacial projection, a slight amount of frontal bulging, flattened parietals, and occipital bunning (Wolpoff, 1998; Hublin, 2002; Schwartz and Tattersall, 2002). Apart from this general appearance, there is no agreement about the meaning of this architecture. Although the vault is low, the elevation of the frontal squama and the height at bregma suggest a phenotypic similarity

with Skhul 5 and Qafzeh 9 (Hublin, 2002). With respect to the variation in the whole midsagittal profile of Pleistocene *Homo* (including the vault and face), Jebel Irhoud 1 occupies an intermediate position between modern and non-modern samples, but clusters with Skhul 5 and Qafzeh 9 because they share a bulging frontal squama and reduced facial block (Bruner et al., 2004; Bräuer, 2006a, b). If one considers only the vault morphology, the intermediate position of Jebel Irhoud in morphospace is further emphasized. Although constantly midway between modern and non-modern groups, it clusters again with Qafzeh 9 when considering eight basic neurocranial landmarks (Bruner and Manzi, 2007). Nonetheless, when using a more complete anatomical configuration of 18 landmarks, Jebel Irhoud 1 clusters with Shanidar, Sima de los Huesos 4, and Sima de los Huesos 5 (Manzi et al., 2000). Taking into account the whole neurocranial surface it may fall within the Neandertal variation (Weber et al., 2007), or else in a position intermediate between Neandertals and modern humans (Gunz et al., 2009), depending upon the sample. Finally, it completely fits in the Neandertal range when analyzing the frontozygomatic block (Freidline et al., 2012).

Jebel Irhoud 1's intermediate position is determined by its modern-like facial morphology and a non-modern like neurocranial form (Harvati et al., 2010). Its only neurocranial trait that departs from non-modern variation is the curvature of the frontal squama (Bruner et al., 2012). However, its degree of frontal bulging is only moderately higher than most extinct human taxa, and it could be within the normal

range of the variability of the Middle Pleistocene species. Furthermore, taking into account that the anterior part of the frontal bone forms a structural bridge between face and neurocranium (Weidenreich, 1941; Lieberman, 2000), it is likely that such slight bulging of the frontal bone could be a secondary consequence of facial reduction, with subsequent changes of the relationships between facial and neurocranial axes.

Quantitative analyses of the frontal bone have demonstrated that among human species this cranial element displays a remarkable similarity, and differences are often negligible when comparisons include the whole frontal squama (Bruner and Manzi, 2007; Athreya, 2009). Likewise, in an analysis of ectocranial and endocranial profiles of the midsagittal section of the frontal bone, Bookstein et al. (1999) found that most of the differences between human species were determined by disparities in the size and shape of the browridge rather than the frontal squama. Hence, if we interpret the bulging of the frontal squama as a secondary consequence of the structural relationships with the facial block, there are no clearly modern traits that can be recognized in the morphology of Jebel Irhoud 1's cranial vault.

Moving from the neurocranial to the endocranial anatomy and diameters, the endocast displays a generally non-modern appearance. The specific endocranial traits of Jebel Irhoud 1 are not well suited to provide detailed paleoneurological information. The pattern of asymmetries, the morphology of the Broca's area, and the organization of the dural sinuses all show common characters that are shared among all species of Pleistocene *Homo* (Holloway, 1981; Holloway et al., 2004). The general shape of the endocranial vault is closest to non-modern specimens of *Homo* (Bruner et al., 2003). The proportions between frontal and maximum endocranial width relative to the hemispheric length have been proved to be related to species-specific allometric trajectories in the human genus (Bruner and Holloway, 2010). In this case, the frontal width of Jebel Irhoud 1 is not informative, showing proportions comparable with modern humans as well as any other taxon of later *Homo*. On the other hand, the relative maximum endocranial width shows a very large value, as frequently described for Neandertals. When brain shape is normalized through Procrustes superimposition, the endocast from Jebel Irhoud 1 is flatter and wider than any of the three mean shapes considered in this study. The vertical dimensions are the closest to the *H. erectus* mean shape. On the other hand the lateral proportions are more similar to the Neandertal average. Therefore, it is tempting to hypothesize that most of these features are shared plesiomorphic traits integrating the overall endocranial form at the individual level: the more the endocranium flattens, the more it widens. As a matter of fact, Jebel Irhoud 1 can be described as having a very flat and wide archaic endocranial form. Several authors note that the neurocranium of Jebel Irhoud 1 is regarded as very broad (Wolpoff, 1998; Cartmill and Smith, 2009). These differences are very subtle, however, and sufficiently small to hamper any robust statistical approach. We must also admit that the degree of idiosyncratic (individual-specific) differences may largely overlap with possible phylogenetic (species-specific) variations. Of course, taking into account the conspicuous maxi-

mum neurocranial width and the noticeable endocranial flattening, one may ask whether these exceptions could be compensatory (idiosyncratic) traits or the result of some hitherto undetected (and presumably unlikely) taphonomic deformation. In either case, the endocast of Jebel Irhoud 1 does not show general endocranial proportion comparable with the modern human form.

Some endocranial traits have been previously used to exclude the Jebel Irhoud 1 cranium from the Neandertal range of variation, suggesting instead a relationship with the modern lineage. In particular, the traces of the middle meningeal vessels show a good level of reticulation and the frontoparietal ascendant circumvolution display similar diameters (Grimaud-Hervé, 2005). However, although *H. sapiens* displays a definite increase in the degree of reticulation when compared with non-modern humans (Grimaud-Hervé, 1997; Bruner et al., 2005), these ranges overlap, and there are exceptions such as the parietal from Arago (Grimaud-Hervé, 1998; Bruner, 2010b) as well as some evidence from Krapina (Bruner et al., 2006).

Phylogeny and evolution

The geographic and climatic changes in the Middle Pleistocene, together with the scarce fossil record and the large morphological variation described for the human groups, make it difficult to delineate a simple scheme to interpret taxonomy and phylogeny of our own genus. Culture may have been a further confounding factor in terms of species boundaries and genetic networks, influencing the social and mating systems (Turner, 1986). In this framework Jebel Irhoud 1 represents an important fossil specimen because of its chronological and geographical position.

The degree of vertical facial reduction suggests a modern rather than Neandertal affinity, and the midsagittal profile fits morphologically and chronologically with a 'modernisation' trend (Bruner et al., 2004). The dental remains from Jebel Irhoud also suggest a delayed and modern-like tempo of development (Smith et al., 2007). The characters linking Jebel Irhoud 1 to non-modern human species are entirely associated with neurocranial/endocranial anatomy. Most of them can be interpreted as symplesiomorphies, providing no information on possible phylogenetic relationships. Its frontal morphology is generally comparable with the Middle Pleistocene variation, and a modern bulging of the frontal squama is likely to be partially related to the orientation of the bone as constrained by facial structures more than to the morphology of the bone per se. In fact, although modern humans are characterized by increased curvature of the frontal squama, this trait alone cannot provide a precise phylogenetic indication for individual specimens (Bruner et al., 2012).

The lack of a clear parietal bulging is the most patent difference between Jebel Irhoud 1 and specimens belonging to the *H. sapiens* hypodigm. The superimposition of the 3D landmarks on the endocast confirms the absence of this upper parietal enlargement. At the same time, Jebel Irhoud lacks the parasagittal lateral flattening of the upper parietal lobules described in early humans and in archaic species such as *H. erectus* and *H. heidelbergensis* (Bruner et al., 2003). Descriptive approaches characterize the posterior view as "not quite en bombe" for Jebel Irhoud 1 and "almost

Figure 7. The less encephalized human species show a depression of the upper parietal surface in posterior view (1), while Neandertals display an enlargement of the lateral upper outline (2), and modern humans an enlargement of the whole parietal volumes (3). Taking into account the possible phylogenetic relationships between *H. heidelbergensis* (HH), Neandertals (NDR), *H. sapiens* (HS), and Jebel Irhoud (JI), two hypotheses can be considered: (a) the evolution of the ‘domed’ morphology from an ‘en bombe’ morphology; or (b) the evolution of both from a ‘tent-like’ shape, by parallelism.

en bombe” for Jebel Irhoud 2 (Schwartz and Tattersall, 2003). Elsewhere, the posterior view of Jebel Irhoud 1 has been described as showing a pentagonal profile (Hublin, 2002). Unfortunately, the posterior view has no reliable standardized planes and the perspective one adopts depends upon cranial orientation. Nonetheless, the available descriptive and metric approaches suggest that, because of the parietal shape, the Jebel Irhoud 1 neurocranium and endocranial morphology are comparable with the Neandertal morphology.

If we exclude Jebel Irhoud from the Neandertal lineage because of its facial features, we must take into account two possible hypotheses to interpret the evolution of the upper parietal widening: either this trait could have been shared by the common ancestor of modern humans and Neandertals, or else both lineages could have evolved this character independently, after which it was elaborated further in *H. sapiens* (Figure 7). In the first case we lack evidence of a species or population preceding the separation of the modern and Neandertal lineages showing archaic general morphology but lateral expansion of the upper parietal lobules. In the second case we must rely upon a case of parallelism, assuming that modern human brain shape passed through a step of upper parietal lateral enlargement comparable with the Neandertal lineage, and then went through a second step associated with overall parietal bulging. This is not unlikely given the high level of homoplasy in human evolution (Wood and Harrison, 2011). Accordingly, the ‘Neandertal appearance’ of the Jebel Irhoud endocranial morphology is best viewed as either a plesiomorphy or a parallelism with the Neandertal lineage. It is worth noting that the European fossils contemporary with Jebel Irhoud are early Neandertals such as Saccopastore, which have a comparable cranial capacity and similar endocranial morphology but very different cranial architecture (Bruner and Manzi, 2008). Admixture and assimilation of these two lineages has been also proposed to explain such intermediate

phenotype (e.g. Smith et al., 2005). However, there is no reason to assume that interbreeding must necessarily produce intermediate and ‘chimerical’ individuals (e.g. a modern human face coupled with a Neandertal vault). Furthermore, the probability of such admixture is not easy to evaluate in a single individual; a more complete and larger fossil record would be more informative. Taking into account the lack of Neandertal fossils in North Africa, this hypothesis cannot be properly evaluated at present. Finally, it must be also noticed that another trait in Jebel Irhoud that possibly shows Neandertal affinity, occipital bulging, is directly related to the parietal morphology. These two characters are in fact morphologically integrated (Gunz and Harvati, 2007).

The issue of the phylogenetic position of Jebel Irhoud is relevant to the debate on the role of North Africa within the context of the modern human origins, as a possible geographic source of diversity or else as peripheral dead-end (Balter, 2011). Jebel Irhoud is part of a heterogeneous human population (or group of populations) that inhabited Africa in the transition between Middle and Upper Pleistocene. The variation in African hominins from this period may be attributed to multiple dispersals and probably replacements, endemism, mosaic evolution, and genetic drift as a result of small population sizes in heterogeneous and large geographic areas (Stringer, 2006). Some aspects of Jebel Irhoud 1’s morphology are very similar to the Ethiopian skull from Herto (BOU-VP-16/1), dated around 150 ka, which has a cranial capacity of 1450 cm³ (White et al., 2003). Apart from a general resemblance, the facial metrics of these two specimens are definitely comparable (Stringer, 2006). Interestingly, while Jebel Irhoud shows Neandertal-like parietal morphology, Herto displays a visible enlargement of the parietal areas, and at the same time lambdatic ossicles. These supernumerary centres of ossification are frequent in Neandertals, and have been hypothesized to represent hypostotic

responses because of unbalanced growth and development changes during neurocranial morphogenesis (Manzi et al., 1996; Bruner, 2004). Taking into account the degree of isolation of the North African populations between the Middle and Upper Pleistocene (Hublin, 2002), and the penecontemporary evidence of change in the modern human lineage in Sub-Saharan Africa (Bräuer, 2008; Rightmire, 2008), it is plausible to consider Jebel Irhoud as a genetic relic of a earlier human dispersal in Africa. In this case, we can hypothesize an early modern human dispersal around 200 ka that reached Morocco and then become isolated. This population may have belonged to the modern human lineage, but retained an early morphology characterized by non-modern neurocranial/endocranial morphology. While the Sub-Saharan African/Near Eastern groups underwent a further change associated with brain organization and neurocranial adjustments, the Northwest African group may have become extinct. This scenario fits with the Middle Pleistocene fragmentation of the modern human lineage described as *H. helmei* (Lahr and Foley, 1998), although many researchers question or reject the validity of this species-level designation. On the other hand, if this specimen was determined to be older, North Africa could be interpreted as a geographical source of evolutionary variation, directly related with the early modern human lineage.

Independent of the taxonomic interpretation of these specimens, the more interesting hypothesis concerns the possible existence of groups in the modern clade but without a modern human brain. The enlargement of the parietal areas is a discrete and well-expressed trait of the endocranium of *H. sapiens* (Bruner et al., 2003, 2011; Bruner, 2004; Neubauer et al., 2009, 2010; Gunz et al., 2010). Considering the role of the parietal areas in the perception and management of the relationships between inner and outer world (Bruner, 2010a), a two-part model of the evolution of modern humans might also explain some of the differences between early (Middle Stone Age/Middle Paleolithic) and late (Later Stone Age/Upper Paleolithic) modern human cultures (Klein, 2000, 2008; Foley and Lahr, 2003; Wynn and Coolidge, 2003; Coolidge and Wynn, 2005). It has been long suggested that morphological and behavioral modernity could have been decoupled along the evolution of *H. sapiens* and that 'modernity' evolved not as a single package but as a combination of characters evolved in different times and places (Stringer, 2006, 2007; Tattersall, 2009). If physical and cognitive attributes have evolved separately in modern humans, it is not surprising to find geographically isolated populations, such as Jebel Irhoud, that display a subset of modern cranial traits while retaining non-modern brain morphology. While populations with modern cranial traits and enlarged parietal areas such as the Herto specimen lived in East Africa, Northwest Africa was inhabited by a population with almost modern cranial structure but with a non-modern brain geometry. This may be interpreted as geographical diversity, or with an evolutionary sequence in which modern brain evolved after the initial appearance of other modern cranial apomorphies. These scenarios are necessarily speculative, but this interpretation offers a starting point for testing a more detailed model of the origin of *H. sapiens* and the evolution of modern cognition.

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