

# The skull from Florisbad: a paleoneurological report

Emiliano Bruner<sup>1</sup> & Marlize Lombard<sup>2</sup>

1) Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain  
e-mail: emiliano.bruner@cenieh.es

2) Palaeo-Research Institute, University of Johannesburg, Auckland Park, South Africa

**Summary** - *The Florisbad fossil cranium was found in South Africa in 1932. Different authors proposed a taxonomic affinity with early Homo sapiens, Neandertals or late Homo heidelbergensis. Here, we review its neurocranial morphology, to supply an updated perspective on its paleoneurological features. The curvature of the frontal squama is definitely within modern human variation, although the anterior cranial fossa is very broad, comparable to that of the Neandertals. In contrast, the parietal lobe and the vascular networks are more similar to the morphology observed in more archaic human species, such as Homo heidelbergensis. The endocranial anatomy of the Florisbad skull displays a mosaic of derived and plesiomorphic features, which makes this fossil compatible with distinct phylogenetic scenarios. None of these traits are, however, strictly diagnostic in terms of taxonomy. This specimen is central to the question on the possible anagenetic evolution from Homo heidelbergensis sensu lato to modern humans.*

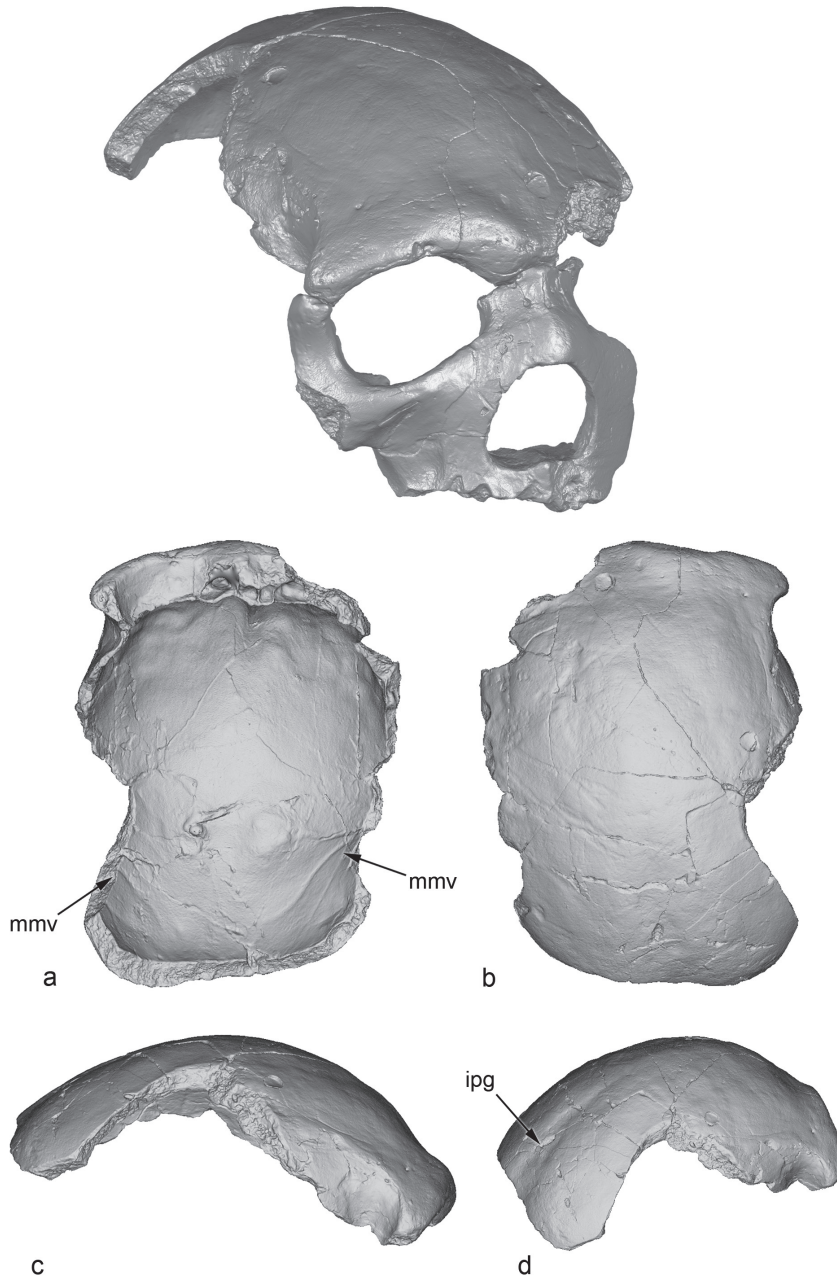
**Keywords** - *Human evolution, Paleoneurology, Middle Pleistocene, Southern Africa.*

## The Florisbad braincase

The Florisbad fossil cranium was found close to Bloemfontein (South Africa) in 1932 (for a review see e.g. Rightmire, 1978; Curnoe & Brink, 2010), and it is currently dated to about  $259 \pm 35$  ka (Grün *et al.*, 1996). It consists of large portions of the frontal and parietal bones, and fragments of the face (Fig. 1). The estimation of the cranial capacity is imprecise, because of incompleteness of the fossil, and could span between 1280 cc. (Kappelman, 1996) and 1450 cc. (Keith, 1938). Despite the calotte being well preserved, the taxonomic and phylogenetic interpretation of this specimen remain controversial. Similarities with the Broken Hill 1 cranium from Kabwe (Zambia) have been frequently recognized, despite the “more advanced” morphology of the Florisbad specimen (Galloway, 1937; Keith, 1938; Rightmire, 1978; Clarke 1985). Grün & colleagues (2020) recently dated the Broken Hill specimen to  $299 \pm 25$  ka, narrowing the gap between the two fossils also in a chronological sense.

The Florisbad remains are often hypothesized to belong to an early *Homo sapiens* population

(e.g., Clarke, 1985). A link with modern southern African San was supposed soon after the discovery, and Dreyer (1935) proposed the specific name of *Homo (Africanthropus) helmei* to characterize this intermediate morphotype. However, later analyses were not able to support the hypothesis of a regional continuity based on local features (Rightmire, 1978; Habgood, 1989). Something that was also noticed from early on, was a similarity with Neandertals, largely because of the fronto-parietal curvature and browridge morphology (Drennan, 1937). The difficulties in the taxonomic interpretation of the Florisbad specimen are due to the admixture of plesiomorphic and derived features and, in fact, it fits with the possible ancestral morphology of distinct subsequent human lineages (Schlebusch *et al.*, 2017; Mounier & Mirazón Lahr, 2019). Its phenotype is compatible with several different human species, such as *Homo heidelbergensis*, *H. sapiens*, and *H. neanderthalensis*. Actually, a mosaic-like scenario has been frequently proposed to explain the human evolutionary radiation, with “transitional” specimens showing distinct patchworks of primitive and derived traits



**Fig. 1** - Virtual reconstruction of the fossil skull of Florisbad, after laser scan of the high-resolution cast (above). The endocranial (a), ectocranial (b), right lateral (c) and posterior skewed (d) view show the features described in this article, including the interparietal groove (ipg) and the traces of the middle meningeal vessels (mmv). Images not at scale.

(Bruner & Pearson, 2013; Athreya & Wu, 2017; Neubauer *et al.*, 2018).

Although the frontal and parietal bones are well represented in this specimen, the braincase is too incomplete to allow a full morphological analysis of its general form (Neubauer *et al.* 2018). In this report, we consider some anatomical traits of the fossil that could open up some paleoneurological considerations dealing with brain form, brain-skull spatial relationships, epigenetic cranial features, and vascular imprints. These considerations are based on the information available from literature, on the inspection of the original specimen, and on a cast commissioned to the National Museum of South Africa in 2013 for research purposes.

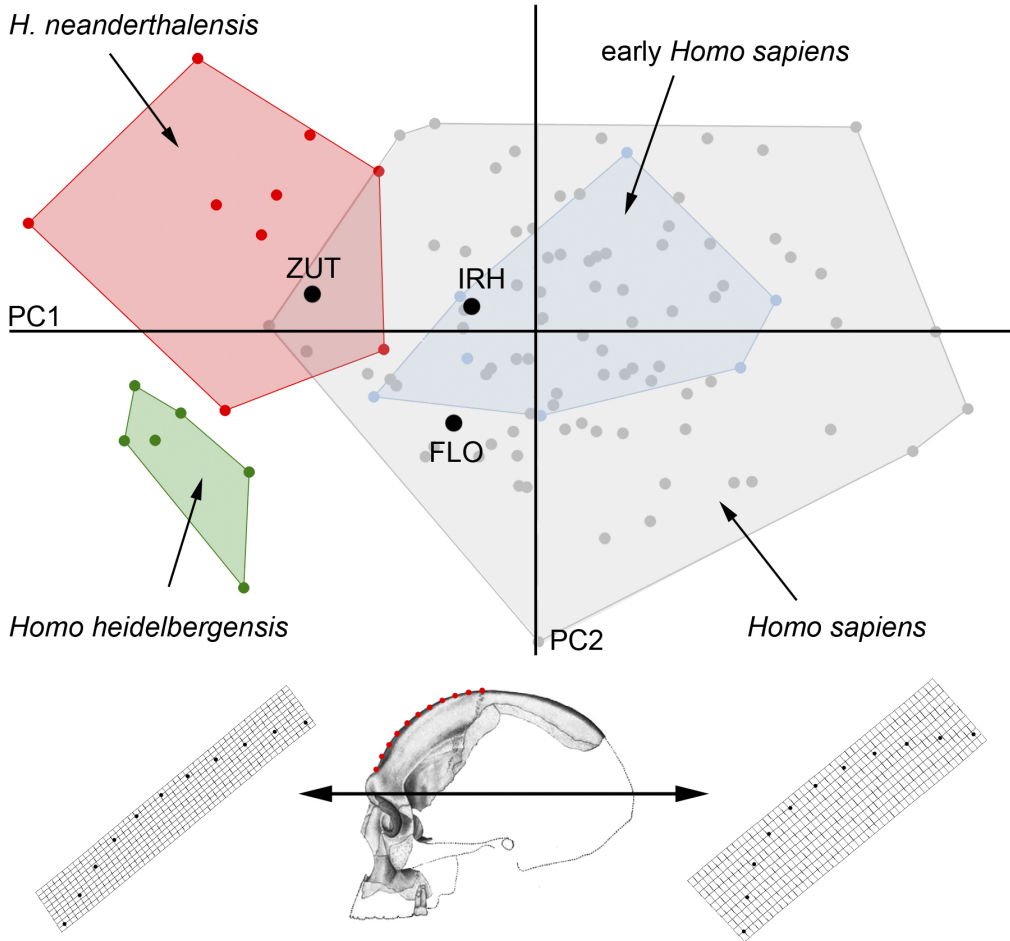
### The frontal bone

Because of the good preservation of the frontal bone, this region of the Florisbad skull has been thoroughly investigated. A shape analysis of the frontal squama midsagittal profile suggested that, at least for this trait, Florisbad clusters with modern humans (Bruner *et al.*, 2013). However, this feature is not taxonomically diagnostic and, in fact, *H. erectus* specimens such as Sambungmacan 3 and Zhoukoudian 3, as well as the Neandertal from La Chapelle-aux-Saints also show profiles that are compatible with modern human variation. In Figure 2 we used the same coordinate dataset of this previous study (11 equally-spaced landmarks to capture the geometry of the frontal squama – see Bruner *et al.*, 2013) to analyse the morphological variation of Afro-European specimens included in the hypodigms of *H. sapiens*, *H. neanderthalensis* and *H. heidelbergensis* through Procrustes Superimposition and Principal Component Analysis. When the midsagittal curvature of the frontal squama is considered, Florisbad shows a morphology that is consistent with the modern human range, while the other two species (*H. neanderthalensis* and *H. heidelbergensis*) are rather separated, in terms of phenotypic variation. According to this analysis, the degree of frontal

bulging displayed by the Florisbad cranium can be regarded as a modern-like trait, at least when only the curvature of the frontal squama is taken into account.

The frontal bulging of the modern human brain is often interpreted in terms of frontal lobe evolution, although there seems to be little evidence to support this hypothesis. Actually, the gross volume of the frontal lobe has the same proportions in humans and living apes (Semendeferi *et al.*, 1997). The frontal bulging in the human genus is therefore likely to be a secondary consequence of the general cranial architecture, instead of a mark of brain changes. In fact, in *H. heidelbergensis*, the orbits are positioned in a more forward position relatively to the frontal lobes and to the anterior cranial fossa, while in Neandertals and especially in modern humans, they are located right below the anterior cranial fossa, housing the frontal cortex. (Bruner & Manzi, 2008; Pereira-Pero *et al.*, 2017; Beaudet & Bruner, 2017). In this sense, the increase of the frontal curvature is probably a consequence of having a small face positioned below the frontal lobes, namely a spatial arrangement of the facial and neural blocks. The frontal squama and the anterior cranial fossa are in reality a major spatial bridge between splanchnocranial and neurocranial regions, acting like a structural hinge between these two morphological blocks (Moss & Young, 1960; Lieberman *et al.* 2002; Esteve-Altava *et al.*, 2013; Bruner *et al.* 2019).

Accordingly, the frontal bulging in modern humans should not be interpreted as an intrinsic brain change, but instead in terms of changes in the brain-to-face spatial relationship. Probably, the vertical constraint exerted by the upper face (eyes and orbits) on the frontal lobes, is also responsible of the lateral reallocation of the neural mass, leading to relatively wider frontal lobes in modern humans and Neandertals (Bruner & Holloway, 2010). In sum, we can state that the midsagittal shape of the frontal squama of Florisbad is largely compatible with modern humans, which suggests a modern-like spatial relationship between face and braincase.



**Fig. 2 - Principal Component Analysis of the midsagittal shape of the frontal squama in early and modern *Homo sapiens*, *Homo heidelbergensis*, and *Homo neanderthalensis*. The positions of Florisbad (FLO), Jebel Irhoud 1 (IRH) and Zuttiyeh (ZUT) are indicated. PC1 (82% of the variance) is associated with overall bulging/flattening (deformation grids below), while PC2 (9% of the variance) is associated with antero/posterior curvature. The following components explain less than 5% of the variance and are hence intended as not significant. Neandertals: Amud, La Ferrassie, Feldofer, Krapina C, La Chapelle-aux-Saints, La Quina 5, Shanidar 1, Shanidar 5, Spy 1; *Homo heidelbergensis*: Bodo, Ceprano, Elandsfontein, Kabwe, Laetoli 18, Petralona. Early *Homo sapiens*: Abri Pataud, Cro-Magnon 3, Mladech 1, Oase 2, Predmost 3, Qafzeh 6, Skhul 5. Original data from Bruner et al., 2013. Drawing of the skull after Dreyer, 1935. The colour version of this figure is available at the JASS website.**

When we consider the rest of the frontal bone, additional information provides a more complex scenario. For example, the frontal bone and the anterior cranial fossa of Florisbad are very wide, with dimensions similar to the

Neandertal average (Rightmire, 1978; Bruner & Holloway, 2010). The coronal profile and width of the frontal lobes of Florisbad are also reminiscent of some Neandertals (Drennan, 1937), and when the frontal bone is considered in three

dimensions, the Florisbad skull clusters with this taxon (Freidline *et al.*, 2012). The wide frontal lobes once more suggest that its face was probably smaller than *H. erectus* and *H. heidelbergensis*, and largely positioned below the anterior cranial fossa. That is, the pronounced breadth of the frontal lobes suggests a derived condition in the face-to-braincase spatial arrangement, comparable with the phenotype observed in Neandertal or modern human lineages.

## The parietal bone

### *Parietal gross morphology*

The parietal morphology of Florisbad is not clear, because of the incompleteness of the braincase. Reliable metrics on the traditional chords and arcs are, hence, not available. However, the flat parietal profile of the Florisbad cranium was recognized soon after the discovery, and interpreted as a plesiomorphic feature (Drennan, 1937). Actually, the parietal region does not display a pronounced bulging of its midsagittal profile, as commonly observed in late *H. sapiens*. When compared with more archaic and less encephalized human species, both *H. neanderthalensis* and early *H. sapiens* display a coronal swelling of the dorsal parietal regions (Bruner & Pearson, 2016; Neubauer *et al.*, 2018). In Florisbad, neither this feature is obvious, suggesting a modest expression or even the absence of the trait. In this sense, the overall parietal morphology is probably more similar to *H. heidelbergensis*, or at least not as much derived as in modern humans and Neandertals.

### *The interparietal groove*

Among possible idiosyncratic traits of Florisbad it is interesting to mention the interparietal groove. This feature refers to a depression between the parietal bones, in their posterior region, sometimes associated with some ridges and, in some pronounced cases, extending along the occipital borders (see Shore, 1938 for a detailed analysis). This trait has been often described in modern African examples (from

South Africa to Egypt), without any apparent association with skull proportions, size, or sex. Apparently, this ectocranial feature has no consequence on the endocranial counterpart. Because the presence of this trait in some African modern populations, it has been sometimes interpreted as remnant of an ancient condition (Galloway, 1937; Habgood, 1989). In Florisbad, the braincase is rather thick, because of a pronounced development of the diploe (Curnoe & Brink, 2010). Therefore, the interparietal depression could be due to a parasagittal thickening of the bone. However, an early study on the interparietal groove suggested that the depression is due to a reduction of the diploe at the midsagittal region, more than to thickening or bulging of the lateral surface (Shore, 1938). Any functional or structural meaning of such midsagittal diploic thinning is, at present, not known.

Curnoe & Brink (2010) interpreted distinct osteological features of the Florisbad specimen as possible pathological traits, including diploic reabsorption, bone thinning and alveolar destruction, eventually due to hematological or metabolic disorders. At present, we can therefore only speculate that this skull displays several hypostotic traits commonly expressed through diploic reduction, and that the interparietal groove is a secondary consequence of this condition.

A further terminological comment on this interesting and understudied epigenetic feature is that whilst it is referred to as the interparietal “groove”, it is generally associated with a shallow and smooth curvature of the bone surface. Therefore, in terms of anatomy, it should be probably defined as an interparietal *depression* rather than a *groove* (which is a long narrow channel, according to the Merriam-Webster dictionary), as was done for example by Galloway & Wells (1934) in their anatomical description of some archaeological samples.

### *Vascular traces*

In fossil human species, the vascular traces that can be observed on the endocranial surface principally deal with the middle meningeal artery, the venous sinuses, and the emissary

foramina (Pířová *et al.*, 2017). In Florisbad, the traces of the middle meningeal arteries are visible only for some very minor tracts. Nonetheless, the vascular network is apparently very simple and not ramified, and the posterior branches seem more developed than the anterior ones. This vascular pattern is generally observed in archaic human species, such as *H. erectus* and *H. heidelbergensis* (Grimaud-Hervé, 1997; Bruner *et al.*, 2005; Bruner & Sherkat, 2008).

On the left side, the skull also shows two long traces on the ectocranial surface that strongly resemble the morphology, position, inclination and branching pattern of the superficial temporal artery (Pinar & Govsa 2006). In modern humans, this artery can leave some imprints in 70% of the temporal and parietal bones (Schunk & Maruyama, 1959), with two branches supplying the anterior and central regions of the scalp, respectively (Whetzel & Mathes, 1992). However, the cranium from Florisbad displays many taphonomic alterations, most of them probably due to marks left by the teeth of carnivores such as hyenas (Clarke, 1985). Further histological surveys would be needed to evaluate this issue in detail. At present, we consider the possibility that the vessel-like imprints may be due to taphonomic changes, mimicking vascular morphology and position.

There is no relevant information on the venous sinuses or on the endocranial foramina. A venous lacuna on the right side and some arachnoid granulations on the left side of the Florisbad specimen are at present not of importance, because of the limited knowledge we still have on these vascular features.

### Florisbad and human evolution

In paleoanthropology, the paucity of the fossil record (both in terms of biological representativity and statistical power) generally hampers a traditional approach based on working hypothesis and hypothesis-testing, and scholars must hence rely on descriptive studies and heuristic quantitative analyses. Because of the many

difficulties and debates associated with the species concept (Plavcan & Cope, 2001; Tattersall, 1986; Bruner, 2013), such limitation is even more stringent when dealing with taxonomic inferences (Tarver *et al.*, 2011; Bokma *et al.*, 2012). Due to these limitations, and despite the important advances experienced by paleoanthropology in the last decades, there is still much uncertainty about the origin of our own species (Stringer, 2016). In the past, *H. heidelbergensis* has been considered a likely ancestral species of *H. sapiens*, although alternatives should be carefully considered, including African as well as Euroasiatic taxa (Bermúdez de Castro & Martínón-Torres, 2019). Between 200 ka and 300 ka, Africa could have been occupied by distinct human species with a pronounced variability and different degrees and combination of plesiomorph and derived features (Mounier & Lahr, 2019). Therefore, we ignore whether our species originated from one of those taxa, or else from a more complex pan-African admixture of distinct morphotypes (Hublin *et al.*, 2017; Grün *et al.*, 2020). Because of the combination of traits and chronology, the Florisbad skull has been always central to the debate on the modern human origin, as representative of an ancestral species, more derived than *H. heidelbergensis*, sometimes labelled as *H. helmei* (Lahr & Foley, 1998).

However, the difficulties when interpreting the phylogenetic position of the cranium from Florisbad are due, precisely, to its mosaic pattern of derived and plesiomorphic traits. The same limitation can be found when taking into consideration the endocranial anatomy. The curvature of the frontal squama is completely within the modern human variation. Frontal lobes are very wide, similar to what is often observed in Neandertals. However, the parietal gross morphology does not display derived traits, and the vascular pattern is similar to what is generally described for more archaic species such as *H. heidelbergensis*. Distinct mosaic situations in which the anterior regions are more derived than the posterior ones have been observed in North Africa (Bruner & Pearson, 2016), Asia (Wu & Bruner, 2016) and Europe (Arsuaga *et al.*, 2014),

contradicting a linear interpretation of the human evolutionary radiation. A second complicating factor is that most of these traits (like frontal curvature, frontal width or vascular imprints) are not firmly diagnostic, in terms of taxonomy. There is large individual variability, and species-specific morphological ranges often overlap. That is, most of these traits are useful to recognize the general features of the species, but cannot be used to assign a specimen with certainty to any given taxon.

A key question concerning the cranium from Florisbad is whether it belongs to the *H. heidelbergensis* – *H. sapiens* lineage, and to what extent it approaches the former or the latter taxon, taking into account a possible anagenetic perspective. This deals with the unresolved problem of chrono-species and paleo-species, and with the aim of identifying boundaries or possible discontinuities within a single evolutionary lineage (Tattersall, 1986; Kimbel, 1991; Wood, 1992; Davidson, 2020). Otherwise, it should be considered whether Florisbad may belong to another lineage (like the Neandertal one), to some derived local taxon with no descendants, or to an isolated biogeographical remnant. In all these cases, its position would be even more puzzling.

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