Comments on the Zambian Kabwe Cranium (BH1) in the Context of Pleistocene Specimens of *Homo* and the Need for Species Definitions

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ABSTRACT

This study is an extension of that which was undertaken by Balzeau et al. and published in this journal (2017), to re-examine the BH1 cranium which was initially described as *Homo rhodesiensis* in 1921, but more recently regarded as *H. heidelbergensis*. It is compared to other Pleistocene specimens of *Homo.* Balzeau et al. (2017) examined various cranial and intracranial characters, including the conformation of the mid-sagittal plane. They discussed the results of a geometric morphometrics analysis of the cranial vault's profile based on two Principal Components (PC1 and PC2). This note includes the third component (PC3). Taken together, the results can be assessed in the context of potential relationships in temporal and geographical dimensions. Recognizing that boundaries between species are not necessarily clear, we appeal for the adoption of a probabilistic definition of a paleontological species (sigma taxonomy, as opposed to conventional alpha taxonomy).

INTRODUCTION

Balzeau et al. (2017) recently published a comprehensive description of the internal cranial characters of the Pleistocene specimen from Kabwe in Zambia (BH1), which was discovered in 1921 in a mining area formerly called Broken Hill (Woodward 1921). This fossil was initially attributed to a new species, *Homo rhodesiensis* (Woodward 1921), but is otherwise often regarded as *H. heidelbergensis*, making it part of a then Afro-European paradigm that may be considered ancestral to *Homo neanderthalensis*, or according to some, to both *Homo neanderthalensis* and *Homo sapiens* (e.g., Rightmire 2013, 2017; Stringer 2012; Wood 2011). BH1 is a key specimen in the hominin fossil record for at least two reasons. First, it is very well preserved and has been µCT scanned at a very high resolution. Second, it is one of the representatives of the Middle Pleistocene era, which remains riddled with question marks as its fossil material tends to be fragmentary, to show varied patterns of morphological characters, and to come from poorly-known contexts. Unfortunately, the BH1 cranium does not contravene this last rule—having been discovered early on by miners, it comes with little contextual record and a date can only be assigned tentatively.

In their article, Balzeau et al. (2017) presented results of multivariate analyses of measurements and landmark data obtained from BH1 and various Pleistocene crania attributed to the genus *Homo*. Balzeau et al. (2017) concluded that for many of its internal cranial features, BH1 does not display the apomorphic conditions of either *Homo neanderthalensis* or *Homo sapiens*. They tentatively pointed out that the general morphology of the skull and brain in this individual might be explained in part by an increase in size of the *Homo erectus* morphology. As part of the ongoing debate about the definition of the *Homo heidelbergensis* paradigm and its relationship to *Homo neanderthalensis* and *Homo sapiens*, an important question is how to assess the BH1 cranium in relation to other Pleistocene specimens representing *Homo*, whether from Africa, Europe, or Asia. With this note, we wish to offer a more detailed interpretation of the mid-sagittal plane analysis (showing PCs 1–3 of the original PCA, and a between-group PCA). We also wish to briefly address the wider question of species definition in paleoanthropology in light of our results, in the hope that this important discussion will be kept alive.

PRINCIPAL COMPONENTS

Two observations can be made from Figure 13 presented by Balzeau et al. (2017). It shows the results obtained for

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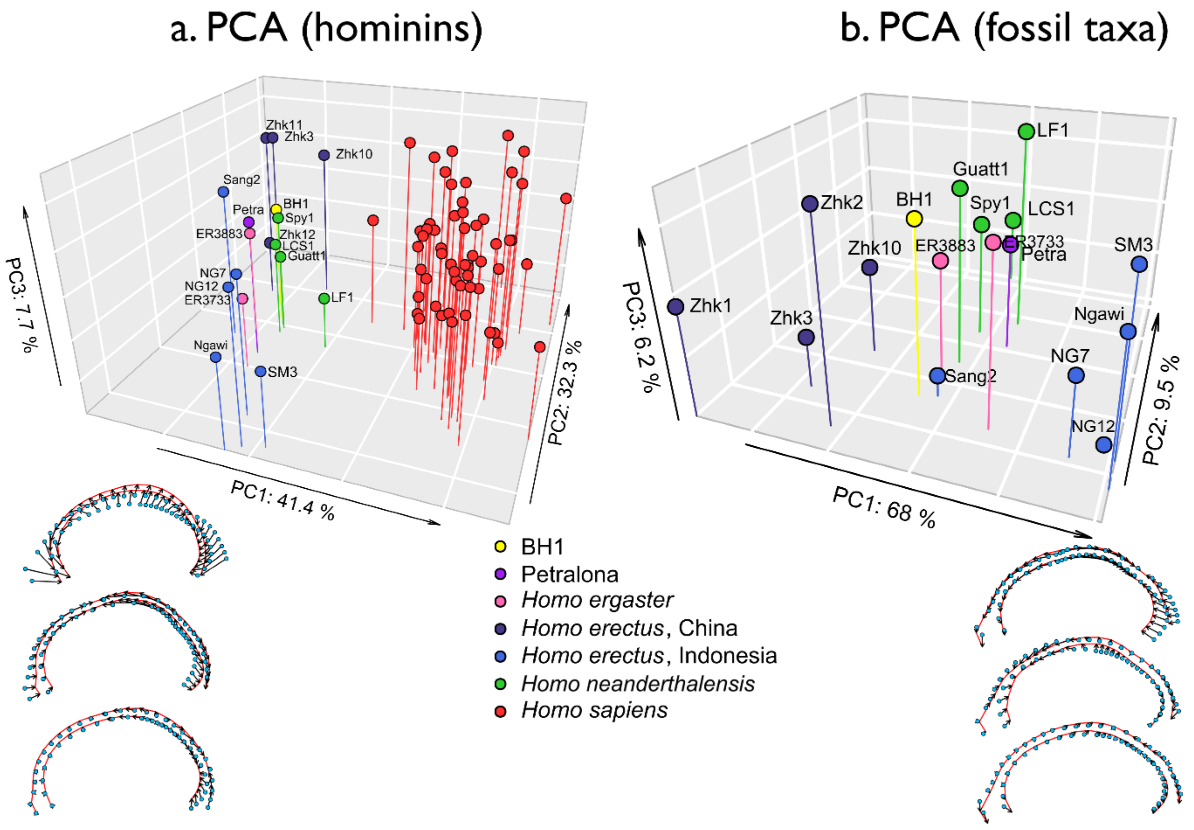

Figure 1. Triplots of the first three components in a PCA analysis based on cranial measurements obtained by Balzeau et al. (2017). Left (Figure 1a): all hominins aligned together, right (Figure 1b): fossil taxa only. Shape change for PCs 1-2-3 (from top to bottom). Blue dots: negative conformations, red outlines: positive conformations, arrows: shape change from negative to positive (all left lateral views).

two Principal Components of a geometric morphometrics analysis of the midsagittal plane in Pleistocene hominins and *Homo sapiens*, reflecting the following:

1. On PC1, the range of variability in extant *Homo sapiens* is comparable to that which is found within the sample of *Homo erectus/ergaster*, but the two sets of data are in distinct groups.
2. On PC2, the range of variability in extant *H. sapiens* is very similar if not identical to that which is found within our small sample of *Homo erectus/ergaster*, but in this case the sets of data are not separated into two distinct groups.

The same conclusion can be drawn from a presentation of a triplot, to include the third component, PC3 (Figure 1a in this study).

In Figure 1b we present results obtained for PC1, PC2, and PC3, focusing on the same features but only in fossil hominins, excluding *Homo sapiens*. It is possible to recognize a cluster of at least 8 specimens of *Homo*, including Early, Middle, and Late Pleistocene crania from Africa, Europe, and Asia. In this figure, Petralona and BH1, which are sometimes both attributed to *H. heidelbergensis*, plot relatively close together, and also to *Homo neanderthalensis* and in the case of Petralona, to *Homo ergaster* KNM-ER 3883.

In the triplot for PC1, PC2, and PC 3 for fossils alone (Figure 1b), PC 1 accounts for most of the variance in the sample (68%) and is driven mostly by variations in the conformation of the occipital area. PC2 and PC3 account for 9.5%, and 6.2%, respectively, with PC2 registering variations in vault thickness and height, and in the conformation of the area including the supra-orbital torus and the anterior part of the frontal lobe. We see specimens teased apart to a greater extent, as compared to results obtained for Figure 1a. BH1 is intermediate between African *H. ergaster* and Asian *H. erectus*, whereas Petralona plots closer to the *Homo neanderthalensis* sample.

In Figure 2, we propose a between-group PCA on the same data to better illustrate the relationships between the fossil groups. BH1 and Petralona were not included in any of the analyzed samples in order to better visualize their potential respective affinities with the other groups. Here, BH1 groups closely with African *H. ergaster* (KNM-ER 3733 and KNM-ER 3883) on PC1, which separates the different groups of *Homo ergaster/erectus*. Overall, BH1 is closest to the mean of the *Homo ergaster* group, that is only composed by two individuals here, but is nevertheless clearly distinct from two populations of Asian *H. erectus*, namely a subsample from Zhoukoudian and a second one with Indone-

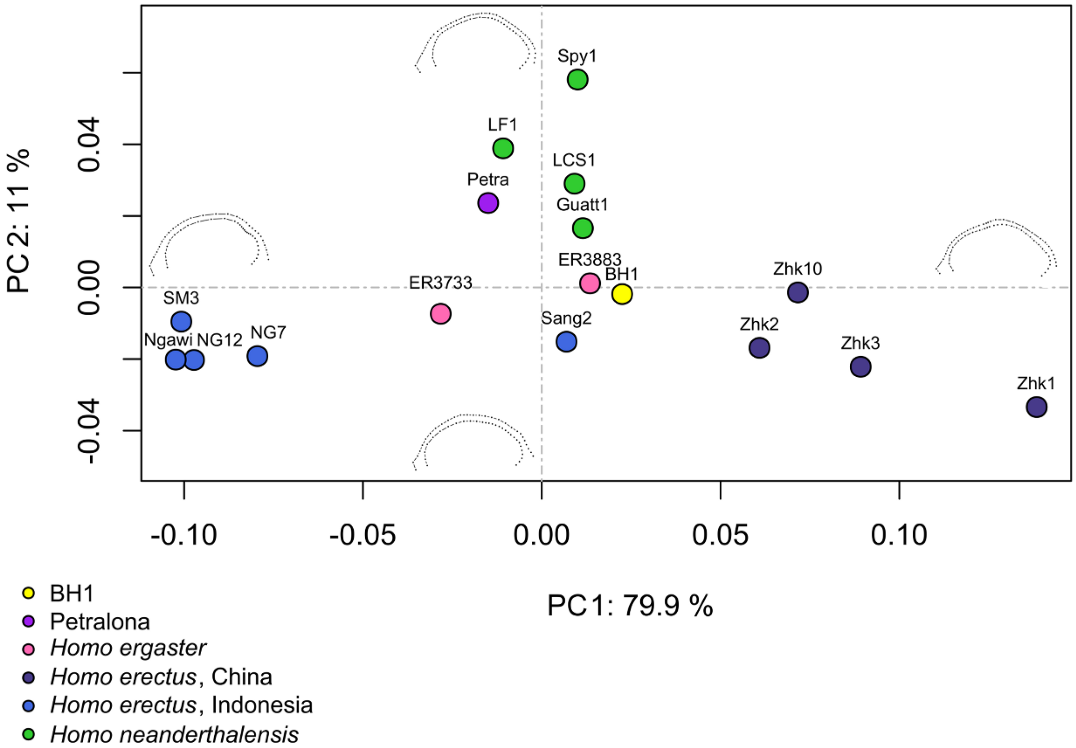

Figure 2. Biplot of between-group PCA on fossil taxa and extreme conformations associated with each axis (left lateral view, +/- 2 sdv).

sian specimens. The position of Petralona is confirmed as being closest to the *Homo neanderthalensis* sample. In particular, Petralona and the *Homo neanderthalensis* sample are separated from the *Homo ergaster/erectus* group as well as from BH1 along the PC2 axis.

DISCUSSION AND CONCLUSIONS

Overall, this study of the mid-sagittal plane satisfyingly teases out specimens attributed to different species or populations, including the different groups of Asian *Homo erectus* and the African *Homo ergaster* specimens. We have no wish to pretend that it would be acceptable to offer a resolution to the many questions surrounding the makeup of different hominin groups and their relationships based on these data only, however, they offer interesting insights into the morphological variations and affinities between these specimens. The mid-sagittal plane captures a measure of a range of characters including the general conformation of the cranial and endocranial profiles, the size and shape of the supra-orbital torus, and vault thickness. Petralona and BH1 show the most morphological affinities when compared against the sample of *Homo sapiens*, which is attributable to the fact that these fossils share some plesiomorphic retentions with the different groups of fossil hominins, such as a low and elongated cranial vault. When compared with fossil hominins only, they differ from each other in a more obvious manner.

Based on these results and others (Balzeau et al. 2017 and other references below), we propose the following working hypotheses:

- BH1 from Kabwe represents a species (initially classified as *H. rhodesiensis* but otherwise regarded as *H. heidelbergensis*) whose vault morphology is closer to the early Pleistocene African *H. ergaster* (represented by KNM-ER 3733 and KNM-ER 3883) than to any other *Homo erectus* group studied here. We suggest that this phenetic relationship could reflect a relationship of ancestry, also supported by the relative geographical closeness of these fossil samples.
- BH1 represents a species whose cranial morphology has been often related not only to *Homo sapiens idaltu* from Ethiopia (White et al. 2003), but also to *Homo sapiens helmei* from Florisbad in South Africa (Thackeray 2010), and furthermore to a variant of *H. sapiens* from Jebel Irhoud in Morocco (Hublin et al. 2017), as part of a Pan-African mosaic that represents a gene pool from which the extant population of *Homo sapiens* is descended.

The results presented in Figure 1b can be assessed in relation to the following comment by Thackeray (1995), in the context of *H. erectus* (*sensu lato*) and Heisenberg's "Uncertainty Principle":

> "All modern humans can trace their origin to descendants of *H. erectus*, but both the ancestral populations of *H. erectus* and descendant populations of *H. sapiens* have expanded and contracted in response to many climatic and habitat changes, with the result that the very concept of "origin" in the context of gene pools can never be precisely determined; continuity occurred in some areas, replacement occurred in other regions, but the net

> effect was a very high degree of morphological variability within the single species which we today refer to as *H. sapiens*".

In terms of the perspective presented here, as a potential scenario, BH1 from Kabwe in Zambia represents a species that was derived from *H. ergaster*, and that was part of a gene pool that led to the spectrum of diversity of *Homo* including *H. sapiens* in Africa within the last 400,000 years. In this scenario we recognize that there are no clear boundaries between populations of species expanding and contracting episodically in response to climate and habitats.

The lack of clear boundaries between human populations is consistent with a view expressed by Scerri et al. (2018) who appeal for a synthesis of paleontological, archaeological, genetic, and paleoenvironmental data with regard to human evolution in the Mid-Late Pleistocene.

At the present time, given the growing number of specimens in the fossil record, there is clearly a need to re-examine species definitions. Both paleogenomics and anatomical studies serve to facilitate the identification of patterns of variation that appear to separate groups in the Late Quaternary *Homo* record, classified (perhaps subjectively) at a species level. Taxonomy becomes the subject of debate when there are no distinct boundaries (either genetic or morphological). Species boundaries become "fuzzy" (Thackeray and Schrein 2017), especially as the number of hominin fossils increases at decadal intervals. This is to be expected, considering the mechanisms leading to speciation and the documented gene flow in and across more recent hominin species (including back-migrations). We appeal to the paleoanthropological community to re-assess species definitions.

Species recognition and the identification of relationships between taxa in the fossil record are now more challenging than ever before. With these points in mind, we question the use of alpha taxonomy based on the traditional biological species definition, especially in the context of Mid-Late Quaternary *Homo*, for which the fossil and paleogenomic record is indicating hybridization between "species." Although the use of species names is a valuable and necessary tool for attempting to make sense of the paleoanthropological record, the biological species concept is, of course, inapplicable in its strict definition in paleontological studies. In this study, we recommend greater use of specimen numbers such as BH1 to designate components of populations which may be morphometrically identified, and (if relevant information is available) genetically recognized, in order to try to provide a framework for the study of diversity and continuity in the paleontological record. A probabilistic definition of a species may be required when boundaries between species are not distinct (e.g., Thackeray and Schrein 2017). The method whereby one may obtain such a probabilistic definition remains a challenge. Thackeray and Dykes (2016) provide just one example as an attempt to address the current problem which Hublin (personal communnication to Thackeray, April 2019) refers to as a "crisis" in paleoanthropology. Instead of applying alpha taxonomy (assuming clear boundaries between "species"), one may explore "sigma taxonomy," where sigma (Σ) refers to S for spectrum (e.g., Thackeray 2018). Each single specimen (e.g., BH1) is part of a spectrum of variation within lineages in ecological space and evolutionary time.

Recently, the model of "braided stream" has been proposed to assess human evolution (e.g., Holliday 2003), instead of the classic image of a "branching tree." Both representations aim to illustrate a complex phenomenon, but we have to be aware that these illustrations are by default partial. Indeed, the available fossil record is too fragmentary to show continuous branching. Moreover, the intersections represent common ancestors that would not be identifiable in the fossil record because of their lack of respective derived features of their descendants. In the "braided stream" model, the largest channel represents the distinct fossil assemblages with their own shared derived anatomical features. The smaller channels that connect the largest ones may be viewed as the exceptional events of hybridization as identified by paleogenetics.

Discussions often focus on the proposed mosaic nature of a whole set of anatomical features to justify new taxa in the hominin record. Because of the lack of sufficient comparative samples for all the anatomical areas, we should remain cautious about such interpretations. This is particularly true for the post-cranial skeleton that is documented (inter alia) for *Homo neanderthalensis* and so-called "anatomically modern" humans. Another pitfall is to consider by default the traits observed in "modern humans" as representing the derived condition and, by extension, any other expression as a primitive condition.

In order to address these issues, we could focus on anatomical features within a sample that allows for the identification of distinct and weighted conditions, and base our interpretation of particular specimens primarily on the expression of its derived traits. Based on analyses reported by Balzeau et al. (2017), regarding the skull and internal features, and based on the scenario proposed here, we consider that BH1 displays at least some anatomical features that distinguish it from *Homo erectus* and *Homo ergaster* and might justify the use of the name *Homo rhodesiensis*.

ENDNOTES

1. In this study we have used conventional species names from a paleontological perspective, in a manner of convenience to refer to groups which are generally considered to be morphologically distinct from each other, but without making further assumptions.

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