Morphological affinities of *Homo naledi* with other Plio-Pleistocene hominins: a phenetic approach

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ABSTRACT

Recent fossil material found in Dinaledi Chamber, South Africa, was initially described as a new species of genus *Homo*, namely *Homo naledi*. The original study of this new material has pointed to a close proximity with *Homo erectus*. More recent investigations have, to some extent, confirmed this assignment. Here we present a phenetic analysis based on dentocranial metric variables through Principal Components Analysis and Cluster Analysis based on these fossils and other Plio-Pleistocene hominins. Our results concur that the Dinaledi fossil hominins pertain to genus *Homo*. However, in our case, their nearest neighbors are *Homo habilis* and *Australopithecus sediba*. We suggest that *Homo naledi* is in fact a South African version of *Homo habilis*, and not a new species. This can also be applied to *Australopithecus sediba*.

Key words: cranio-dental traits, human evolution, human origins, multivariate analysis.

INTRODUCTION

Lee Berger and other 46 co-authors (Berger et al. 2015) presented new important findings of fossil hominins in South Africa. Differently from other discoveries in East and South Africa, skeletal remains of approximately 15 individuals were found at the same locus of a cave chamber denominated by the authors as Dinaledi. Valuable information about the cranial and dental morphology of these Plio-Pleistocene specimens was obtained from approximately five skulls. The original metric data

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obtained for these individuals were presented by Lee Berger and his associates in Table 1 of their publication (Berger et al. 2015). The same table presents craniometric data of several other Plio-Pleistocene hominins. However important, this new material presents a great limitation: no reliable chronology was obtained for the remains found in Dinaledi.

In spite of this limitation Berger et al. (2015) suggested several phylogenetic scenarios to accommodate the new findings. The most important information used by the authors to compare the Dinaledi findings with other "contemporary" hominins is summarized in Table 1. A rapid

TABLE 1
Anatomical traits of *H. naledi* as compared to other Plio-Pleistocene hominins as expressed by Berger et al. (2015).

Homo naledi	*Australopithecus*	Early *Homo*	*Homo erectus*	Unique
Overall morphology		X	X	
Morphology of the skull as a whole		X	X	
Supra-orbital torus		X	X	
Occipital torus			X	
Clivus morphology		X		
Lower limbs			X	
Ankle structure			X	
Foot morphology			X	
Hand and wrist articulation			X	
Thumb morphology			X	
Phalanx morphology	X	X		
Hand structure			X	
Metacarpus				X
Posterior dentition		?	X	
Overall dental morphology	X			
Higher limbs		?	X	
Shoulder articulation	X			
Thorax	X			
Overall body size		X	X	
Brain size	X			
Pelvis morphology	X			

X – Morphological similarity.
? – Possible morphological similarity.

inspection of this table reveals a greater similarity between the Dinadeli findings with *Homo erectus* than with Australopitecines and early *Homo* (*habilis* and *rudolfensis*).

Taking into account the information summarized in Table I, Berger et al. (2015) suggested that the Dinadeli specimens could be classified as a new species: *Homo naledi*. Another suggestion presented by the original authors was that the best way to accommodate this new species in the early human phylogenetic history is to allocate it as the ancestor or a sister group of *H. erectus*, assuming that the material is dated around 2.0 mya (Berger et al. 2015). Ever since the original publication by Berger and associates, the phylogenetic position and the age of *Homo naledi* has been largely debated.

Thackeray (2015), for instance, suggested that the Dinaledi fossil hominins appear to be mostly similar to early *Homo*, especially to *Homo habilis*. Using a least squares linear regression encompassing the 12 hominin species presented by Berger et al. (2015), the author estimated that the age of the Dinaledi material would be around 2.0 mya.

Laird et al. (2016) expanded the studied material included in the original publication (restricted to complete and semi-complete skulls D1 to D5) adding to their study the fragmented bones. They used 100 linear measurements and ratios

encompassing cranial form, facial morphology, and mandibular anatomy. Their main conclusions can be summarized as follows: 1. It is feasible to place the new specimens from South Africa within the genus *Homo*; 2. The skulls from Dinaledi chamber may be excluded from any existing taxa; 3. There are sufficient differences to warrant separation of *Homo naledi* and *Homo erectus*. Another important finding of Laird et al. (2016) was that the whole material from Dinaledi chamber is very homogenous, pointing to a single taxon.

Dembo et al. (2016) used a large supermatrix of cranial traits followed by quantitative analyses based on Bayesian techniques. The analyses performed by them supported the hypothesis that *Homo naledi* forms a clade with other *Homo* species and with *Australopithecus sediba*. The assignment of *Homo naledi* to genus *Homo* was confirmed, but not as a variant of *Homo erectus*. They also proposed a late date for the Dinaledi material, namely 900 thousand years.

Schroeder et al. (2016) performed a geometric morphometric analysis based on skulls D1-D5. In their analysis *Homo naledi* aligned with members of genus *Homo*, with closest affinities to *Homo erectus*. In fact, the analysis revealed a unique combination of features in the Dinaledi material: *Homo erectus*-like cranium and less derived mandible morphology.

Here we present a phenetic analysis of the craniodental metric data of *H. naledi* through a multivariate analysis.

MATERIALS AND METHODS

The cranial and dental metric information was obtained from Tables 1 and 2 of Berger et al. (2015). As can be seen in these tables, the craniometric variables took by Berger and associates covered all main regions of the neurocranium and face, not to mention the mandible. In other words, we believe that the cranial morphology of the fossil hominids

included in their analysis were appropriately characterized. Two variables listed in Table I of the original publication were not used in our study, namely "closest approach of temporal lines", and "root of zygomatic process origin".

In the case of the dental traits, mesio-distal diameters were multiplied by the buco-lingual diameters to generate a proxy for dental crown area. Principal Components Analyses (Somers 1986, 1989, Bryant and Yarnold 1995, Everitt and Dunn 2001) were carried out considering size and shape of two distinct matrices: one more inclusive formed exclusively by craniometric measures (24 variables) and 12 taxa; and one less inclusive formed by craniometric plus dental metrics (40 variables), but only 8 taxa. This strategy had to be adopted because, for unknown reasons, Berger et al. (2015) presented no dental information for the robust Australopithecines. In both cases a covariance matrix was used to generate the PCs (Gower 1966).

RESULTS

Figure 1a presents the position of each taxon in the morpho-space formed by PCs 1 and 2 when only cranial morphology is considered. Both PCs summarize 99% of the original information contained in the dataset. Principal Component 1 is mainly influenced by the following variables: cranial capacity, bi-parietal breadth, and minimum post-orbital breadth. PC 2 is mostly influenced by superior facial breadth, palate depth at M1, and symphysis height. As can be seen in the figure, there is a strong association between *Homo naledi*, *Homo habilis,* and *Australopithecus sediba* which occupy the central upper part of the graph.

Figure 1b presents a graphic representation of a Cluster Analysis, using an Euclidian Distances Matrix based on the scores of the first three principal components (accounting for 99.69% of the original information) under a Single Linkage algorithm as
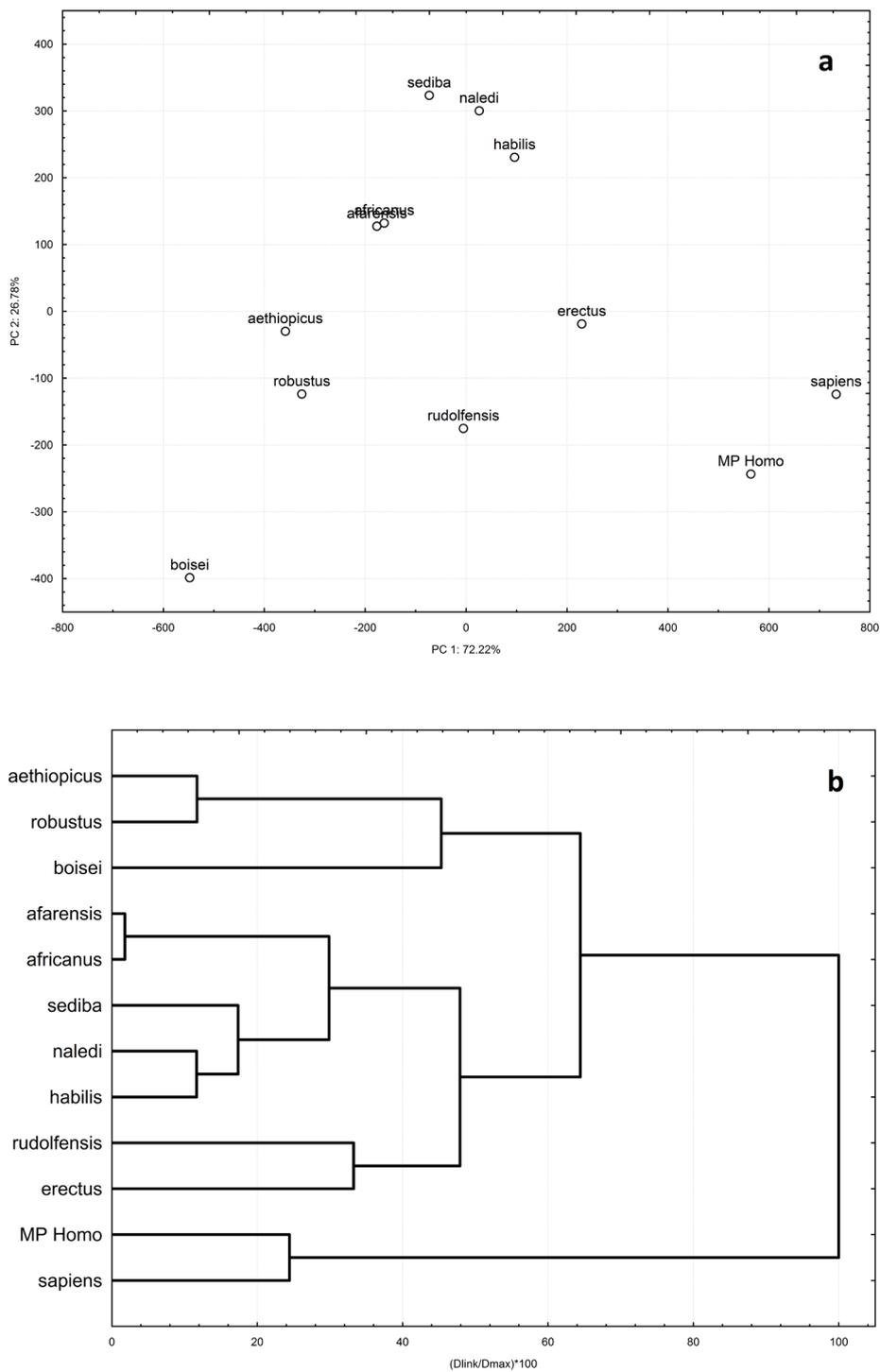
Figure 1 - More inclusive analysis, performed over 24 craniometric variables and 12 hominin taxa. 1**a** (above) Bidimensional graph formed by the first two Principal Components, showing the morphological affinities among *H. naledi* with its contemporary fossil hominins. 1**b** (below) Dendrogram obtained by means of the Cluster Analysis, following Single Linkage criteria over Euclidian Distance matrix obtained from the first three Principal Components, showing the close relationship among *Homo naledi*, *Homo habilis* and *Australopithecus sediba*.

linkage criteria (Gower and Ross 1969). Again, *Homo naledi, Australopithecus sediba, and Homo habilis* have clustered together.

Figure 2a presents the position of each taxon in the morpho-space also formed by PCs 1 and 2 when craniodental information is considered. Both PCs summarize 96.84% of the original information. Principal Component 1 is mainly influenced by the following variables: cranial capacity, bi-parietal breadth, and bi-temporal breadth. PC2 is mostly influenced by symphysis area at M1 (as an ellipse), and crown area of the upper canine. As can be seen in the figure, there is again a strong association between *Homo naledi*, *Homo habilis*, and *Australopithecus sediba*. The three taxa occupy the upper left quadrant of the graphic.

Figure 2b presents a graphic representation of the results of a Cluster Analysis based on the scores of the first four principal components (accounting for 99.47% of the original information) departing from Euclidian distances using the Single Linkage criteria. Again, *Homo naledi, Australopithecus sediba and Homo habilis* cluster together.

DISCUSSION AND CONCLUSIONS

Differently from what Berger et al. (2015) have proposed as the most possible scenario to interpret their new findings, our results strongly suggest that *Homo naledi* has a marked dentocranial similarity with *Homo habilis*, and with *Australopithecus sediba*. There is no clear association between *Homo naledi* and *Homo erectus* in any of the morpho-spaces and topologies generated by our analyses (contra Berger et al. 2015).

Based on our results, *Homo naledi* can be interpreted as a South African variety of *Homo habilis*, and the same can be said of *Australopitecus sediba*. From the point of view of phenetics, there is no reason to propose that the Dinaledi findings pertain to a new species of *Homo* (contra Berger et al. 2015).

The presence of *Homo habilis* in South Africa has been for a long time a much-debated subject in Paleoanthropology (Grine et al. 1993, Kuman and Clarke 2000, Curnoe and Tobias 2006, Smith and Grine 2008, for a few examples), and the idea that the *Homo*-like South African specimens can be classified in this taxon is far from consensus (Grine 2005, Curnoe 2010).

A deep discussion about the origins of genus *Homo* is out of the scope of this study. However, a few words can be said about the subject to better contextualize our findings. Until recently, the earliest specimens of *Homo habilis* (supposed to be the first species of our genus) were firmly dated up to 2.0 mya in East Africa (Olduwai and East Turkana) (Leakey et al. 1964, Johanson et al. 1987). In the last decades, older fossils are claimed to belong to the genus *Homo*, such as the dentition from Shungura Formation (Suwa 1988, Suwa et al. 1996) and Nachukui Formation (Prat et al. 2005), the maxilla from Hadar (Kimbel et al. 1996, 1997), the partial temporal bone from Chemeron Formation (Martyn 1967, Day 1986, Tobias 1991, Sherwood et al. 2002), and the mandible from the Chiwondo Bed (Bromage et al. 1995). They suggest a possible chronology as deep as 2.3 million years to this species. Very recent findings in Ledi-Geraru, Afar State, in Ethiopia, suggest that this date could be extended back to 2.8 million years (Villmoare et al. 2015). Here, we will assume a conservative point of view, namely that the earliest date for *Homo habilis* is 2.3 mya in East Africa (Prat et al. 2005).

Several candidates are suggested as possible ancestors of *Homo*. The most cited are *Australopithecus afarensis*, *Australopithecus garhi*, and *Australopithecus sediba* (Kimbel et al. 1994, White et al. 1994, Asfaw et al. 1999, Strait et al. 1999, McHenry and Coffing 2000, Reno et al. 2003, Berger et al. 2010, Pickering et al. 2011). In the first case, chronology is a problematic matter. The latest remains of *Australopithecus*
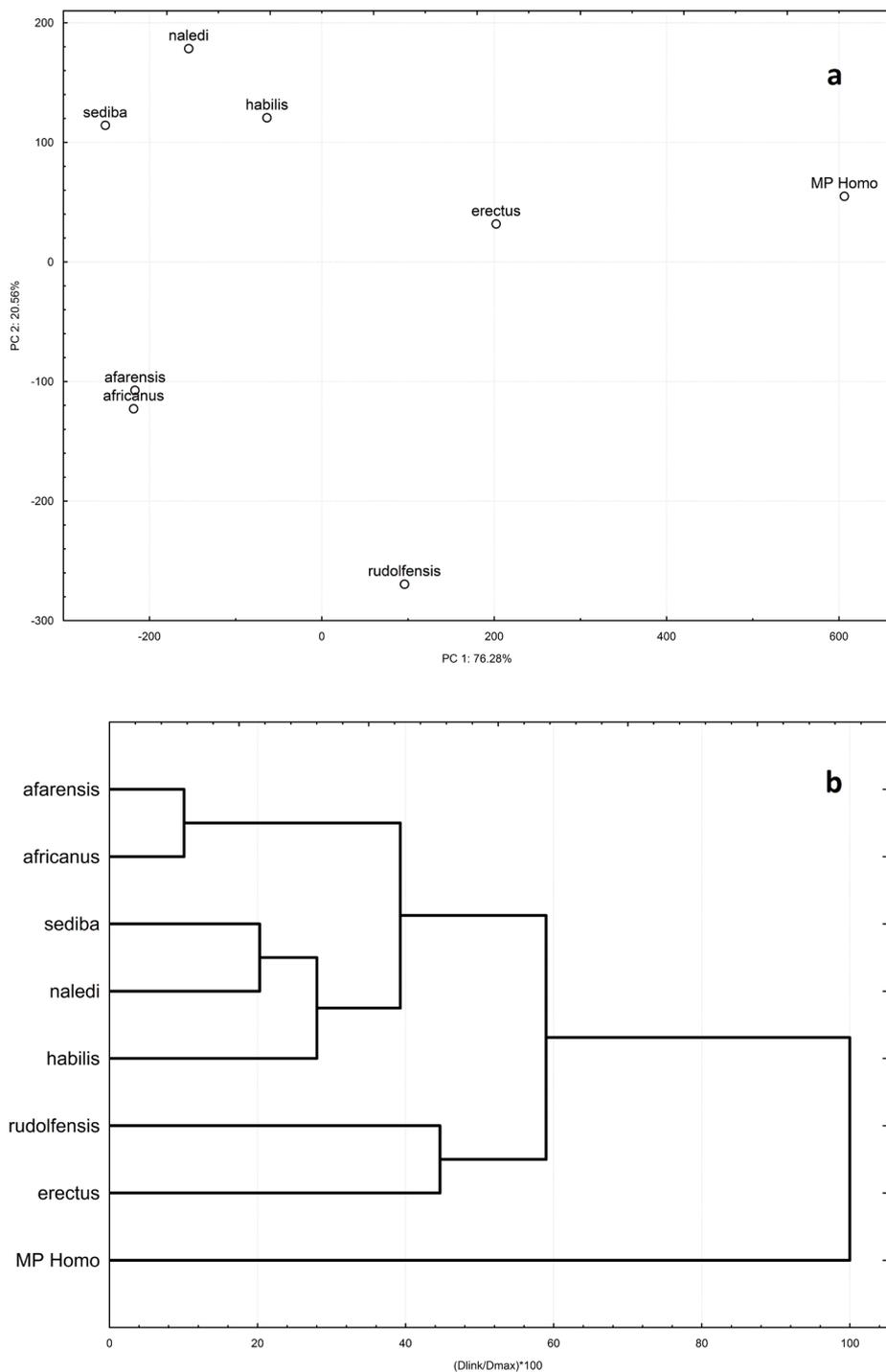
Figure 2 - Less inclusive analysis, counting only 8 taxa, performed over 40 craniodental metric variables. 2**a** (above) Bidimensional graph formed by the first two Principal Components, showing the strong morphological association between *Homo naledi*, *Homo habilis*, and *Australopithecus sediba* in comparison with their contemporary fossil hominins. 2**b** (below) Dendrogram obtained as result of the Cluster Analysis based on the Euclidian Distance matrix calculated from the first four Principal Components, showing the morphological similarity among *Homo naledi*, *Homo habilis* and *Australopithecus sediba*.

afarensis are dated to around 3.0 mya. If *Homo habilis* appeared around 2.3 mya, there is a gap of 700 thousand years between these two species. *Australopithecus garhi*, which is chronologically appropriate to be the ancestor of *Homo habilis*, presents a morphological preclusion to play this role: it has large dental dimensions, mainly in the post canine teeth, while *Homo habilis* presents a small dentition. *Australopithecus sediba* has also a chronological impediment to be ancestral of early *Homo*: it has been dated to 1.9 mya (Dirks et al. 2010), younger than the first *Homo habilis* in East Africa.

A parsimonious scenario to support our results is that *Homo habilis* first appeared in East Africa around 2.3 mya (if not around 2.8 myr) and expanded southward, eventually arriving in South Africa around 2.0 mya. However, this long journey was not enough to modify its basic cranial bauplan. If this scenario is correct, the skeletal remains found in Dinadeli are probably dated around 2.0 mya, as old as *Australopithecus sediba*. Future chronological information about the Dinadeli findings will be necessary to test our proposal.

Do our results fit into what other studies have proposed about the phylogenetic ties of the Dinaledi? This is a very difficult question to answer. As presented in the introductory section of this paper, different analyses have reached different scenarios to accommodate *Homo nadeli* in the phylogenetic tree of our Plio-Pleistocene ancestors. However, they all reached one same conclusion: this material pertains to genus *Homo* (Berger et al. 2015, Thakeray 2015, Dembo et al. 2016, Laird et al. 2016, Schroeder et al. 2016). Dembo et al. (2016) detected some ties with *Australopithecus sediba*, an association clearly found in our analyses. A strong association of *Homo naledi* with *Homo habilis* was suggested by the results achieved by Thakeray (2015), what also converges with our results.

In summary, our analyses generated a much clearer picture about the new findings in South Africa when compared to previous investigations. *Homo habilis*, *Homo naledi*, and *Australopithecus sediba* seem to pertain to a single taxon, namely *Homo habilis*. Future work based on more fossil material from East and South Africa, better chronological contextualization of *Homo naledi*, and the use of more sophisticated statistical tools will be of paramount importance to a better comprehension of the taxonomical and phylogenetic status of the Dinadeli chamber remains, if not of the diversity of early *Homo* in Africa as a whole.

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