

3D Morphometric Study of the Mandibular Fossa and Its Implication for Species Recognition in *Homo erectus*

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Received 4 May 2015; accepted 7 August 2015; published 10 August 2015

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Abstract

The problem of species recognition in paleoanthropology has been the subject of numerous studies. In the current study, we have used the complex topography of the mandibular fossa to assess its potential as a species-specific indicator. Six landmarks were registered using a microscribe 3Dx digitizer on four extant species: *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and two ethnical groups of modern humans. Using principal component analysis (PC), the results statistically separated between the species and within the two *Homo* groups. The same method was applied to a sample of 13 casts of Pleistocene hominids from Asia, Europe and Africa. The first PC separated Asian *Homo erectus* from African *Homo erectus* and *Homo heidelbergensis*. The second PC separated African *Homo erectus* from *Homo heidelbergensis*. Interestingly *Homo floresiensis* groups with *Homo heidelbergensis*. Adding recent human sample to the analysis showed them to fall within the African *Homo erectus* group. Cluster analysis on the superimposed fossil data had turned the same results. These results favor the view that *Homo erectus* is actually made from at least two distinct species. *Homo floresiensis* is not a form of pathologic *sapiens*, and *Homo sapiens* has descendent solely from early African-like species.

Keywords

Homo erectus, *Homo heidelbergensis*, *Homo ergaster*, Morphometrics, Species Recognition

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1. Introduction

Species recognition is one of the most debatable topics in biology. Many studies had tried to define the nature of species and speciation processes (see Groves, 2001; Bruner, 2013). In paleoanthropology, where these issues are worsened by the loss of taxonomic characters (Tattersall, 1986, 2005), the problem is dealt by comparing known & defined species' skeletal elements to an unknown or unassigned fossil hominoids (Argue et al., 2006; Kaifu et al., 2007; Curone & Tobias, 2006; Susman & de Ruiter, 2004). The use of distinct qualitative anatomical traits to distinguish between two closely related taxons may be problematic, as finding unique (autapomorphic) characters that separates the species becomes a difficult task. Some of the traits, like keels, tori and protuberances, may be debatable as these may not appear the same to all eyes. The use of univariate metric methods also holds difficulties. As noted by Godfrey & Marks (1991) "Univariate dimensions are likely to display considerable overlap among closely related species..." (p. 58). Some of the disagreements that had risen between studies about morphological traits and taxonomic affinities (Rak, 1986; Trinkaus, 2003; Ascenzi et al., 2000; Bruner, 2007) are in fact, due to different methods of analysis, as was noticed by Trinkaus (1990). Applying multivariate analysis is more useful in these cases, because it sums the degree of variations, variations that univariately are statistically insignificant. The mandibular fossa of the temporo-mandibular joint is topographically complex structure, and as such it possesses many taxonomic characters. Each of these characters can be quantified and evaluated as unique trait and thus the fossa may be suited for taxonomic analysis. Because of its "hidden" anatomical location within the skull base and its solid build, the fossa is frequently present and complete in fossils (Durband, 2008) making this area easier to analyse without encountering missing data problem (Holt, 2000; Strauss, 2003; Couette & White, 2010).

Most studies of the fossa, like Ashton & Zuckerman (1954) milestone paper, and Durband (2008) are descriptive and not quantitative, while others used univariate-metric measurements such as Hinton & Carlson (1979), Wish-Baratz et al. (1996) and Green (2005). This kind of data may still be problematic when attempting to separate two closely related species. Using 3D morphometric techniques (Richtsmeier et al., 2002; Lawing & Polly, 2010) allows us to define more accurately the shape of an object, and thus bring much more analytical data.

2. African, Asian & European *Homo*

Hominid fossil discovery in the 19th century had led to immense controversies between anthropologists of the time. Neandertals were the first to be discovered in 1829 in Engis, Belgium. It took almost 34 years and the discovery of the Neander valley specimen for a new species to be assigned—*Homo neanderthalensis*—by William King in 1863, and many more years to establish its taxonomic uniqueness. The story of other Pleistocene hominids and their taxonomic relationships is even more complicated. Ever since the discovery of the first *Homo erectus*, its taxonomic status as a species has been controversial. The debate originated with the unearthing of the Trinil skullcap (Dubois, 1894), which was followed by the discovery of a long line of fossils found throughout the old world. It seems that almost every fossil that was dated to the middle Pleistocene and was not assigned as a Neandertal, a new taxon was given. Naming just a few, these include *Sinanthropus pekinensis* (Black, 1927; Weidenreich, 1943) from China, *Homo soloensis* (Oppenoorth, 1932), from Indonesia, *Telanthropus capensis* (Broom & Robinson, 1949) from southern Africa. It was Franz Weidenreich at the 38th meeting of the American Anthropological Association held in Chicago on 1939, which made the first attempt to group all these fossils into one variant species—*Homo erectus* (Weidenreich, 1940). This proposal was accepted by some authors, but the debate continued, and peaked at the 1983 Senckenberg conference where authors like Wood (1984), Stringer (1984) and Andrews (1984) suggested splitting the lineages into African and Asian species, based on proposed autapomorphic features, such as a sagittal keel, angular torus and supraorbital ridges that would separate the Asian from the African species. It was also suggested that the Asian lineage is an evolutionary "dead-end" and that the origin of *Homo sapiens* is solely from the African *Homo* lineage. This view was against those of Kennedy (1991), Rightmire (1984, 1990), and Kramer (1993) that claimed that these features are either present in all lineages or they are the evidence of a polymorphic species. Along with these so-called "classic" *Homo erectus* finds, many other fossils of the same age, on one point or another, classified as *Homo erectus*, *Homo heidelbergensis* or archaic *Homo sapiens*. Examples of such fossils are Petralona from Greece (Kokkoros & Kanellis, 1960), Dali from China (Wu, 1981), Broken Hill (now Kabwe) from Africa (Woodward, 1921) and Steinheim from Germany (Berckhemer, 1933). The ambiguity of these fossils dazzled many authors as can be noted in the work of Howells (1980), Stringer (1979, 1984) and Rightmire (1996, 2004, 2013), and left many of

the Pleistocene hominids in a taxonomic waste basket and an undetermined taxonomic affinity. The discovery of the small bodied hominid from Liang Bua, Indonesia (Brown, 2004) caused similar taxonomic uncertainty (Auge et al., 2006) that ranged from pathologic *Homo sapiens* (Henneberg & Thorne, 2004; Hershkovitz et al., 2007) to new species with erectus like features (Morwood et al., 2005; Baab, 2012) or even habiline like features (Gordon et al., 2008).

The shape of the mandibular fossa and its borders are very variable in all of the above fossils, as noted by authors like Picq (1984, 1990), Rightmire (1990), Martínez & Arsuaga (1997), and Durband (2008). OH-9 for example, displays an impressively deep and narrow fossa (Figure 1(a)), while in KNM-ER 3733, the fossa is shallow and wide with an elevated medial wall (entoglenoid process) (Figure 1(b)). The Dali cranium exhibits a shallow and wide fossa but with a modest entoglenoid process (Figure 1(c)). In spite of these marked changes, the fossa attracted little attention. Delson et al. (2001) and Mowbray (2002) argue with Durband (2002) about the qualitative shape of elements (squamosal fissure and post-glenoid process) within the fossa. Martínez & Arsuaga (1997) published a detailed description of the fossa but with very little quantitative analysis. Terhune et al. (2007) had measured the temporal bone morphology using 18 landmarks, including five landmarks within and around the fossa for species recognition in *Homo erectus*. Baab (2008) used the overall cranial shape with two landmarks within the fossa for the same purpose. Later on the fossa was used to predict feeding behaviour among primates (Terhune, 2011, 2013).

In the present study we have used multivariate analysis to examine the shape of the mandibular fossa of the temporo-mandibular joint in living human and nonhuman primates as species specific indicator, and its applicability to species recognition in pleistocene hominids.

3. Materials & Methods

Three non-human primates species, *Gorilla gorilla*, *Pan paniscus*, and *Pan troglodytes*, were used, comprising of 34 specimens, 17 males & 17 females for each species. Primates were studied at the Royal Museum for Central Africa, Tervuren, Belgium. This museum houses one of the largest African zoological collections, was acquired in the early 20th century from central Africa. Two groups of modern humans, native Israeli and Indian were also used consisting of 34 specimens, 17 males & 17 females in each group. Human skulls are housed in the archeological collection of the Sackler Faculty of Medicine in Tel Aviv University. Some of the skulls are designated for the medical school, while others are from archaeological excavations throughout Israel. The total number of specimens used in the analysis was 170 specimens (Table 1). All specimens used in this study are adults, as was determined by presence of the 3rd molar teeth. For fossil material we used 13 *Homo erectus* high quality casts (Table 2), made available from the cast collection of Prof. Yoel Rak in Tel Aviv University.

Six landmarks were digitized (Figure 2, Table 3) using a Microscribe 3D digitizer (Immersion Corporation). This device is an articulated digital arm used to capture 3D landmarks from a physical models. It is widely used in anthropological field & laboratory research (Sládek et al., 2012; Gunz & Bulygina, 2012). The Landmarks captured the complex topography of the fossa. They were chosen as either type I or II, according to Bookstein (1991). These type of landmarks, such as junction of suture or highest/deepest points on the skull are easy to

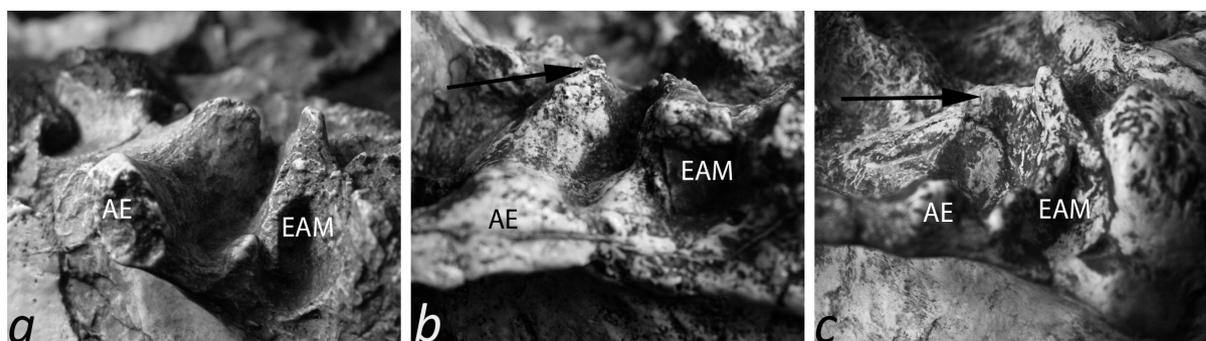


Figure 1. Mandibular fossa of three *Homo erectus* specimens in an oblique basal view: (a) OH 9 from Africa (note the deep fossa); (b) KNM-ER 3733 from Africa (note the shallow fossa and the elevated entoglenoid process, indicated by the arrow); (c) Dali from Asia (note the shallow fossa and the lack of entoglenoid process, indicated by the arrow). EAM, external acoustic meatus; AE, articular eminence.

Table 1. Recent species list.

Species/Group	Source
<i>Pan paniscus</i>	Royal Museum for Central Africa, Belgium
<i>Pan troglodytes</i>	Royal Museum for Central Africa, Belgium
<i>Gorilla gorilla</i>	Royal Museum for Central Africa, Belgium
<i>Homo sapiens</i> , Local Middle Eastern	Tel Aviv University Osteological Collection
<i>Homo sapiens</i> , Indian	Tel Aviv University Medical School Osteological Collection

Table 2. Fossil specimens used in this study.

Specimen name	Name used in study	Locality	Age (Ma)
Petalona 1	Petalona	Katsika Hill, Petralona, Greece	0.4 - 0.2 Grün (1996)
Steinheim	Steinheim	Sigrist gravel pit, Steinheim, Germany	0.25 Adam (1985)
Dmanisi 2280	D2280	Dmanisi, Georgia	1.7 Gabunia et al. (2000)
Broken Hill 1	Broken Hill	Kabwe, Zambia	0.4 - 0.7 Klein (1994)
KNM-ER 3733	3733	Koobi Fora, East Turkana, Kenya	1.78 Feibel (1989)
KNM-ER 3883	3883	Koobi Fora, East Turkana, Kenya	1.5 - 1.65 Antón (2003)
KNM-WT 15000	Nariokotome	Nariokotome, West Turkana, Kenya	1.5 - 1.65 Antón (2003)
OH 9	OH 9	Olduvai Gorge, Tanzania	1.47 Manega (1993)
Sangiran 17	Sangiran 17	Sangiran, Java, Indonesia	1.3 Antón & Swisher (2001)
Sangiran 2	Sangiran 2	Sangiran, Java, Indonesia	1.5 Antón & Swisher (2001)
Zhoukoudian 11	CKN 11	Zhoukoudian Cave, China	0.42 Antón & Swisher (2001)
Dali	Dali	Dali, Shaanxi Province, China	0.2 Rightmire (1998)

identify and repeat. In order to evaluate shape differences, the size, location and orientation of the fossa were removed from the data by superimposing equivalent landmarks using Generalised Least-Square (GLS) method (Rohlf & Slice, 1990), thus leaving only procrustes residuals. Shape analysis was conducted using principal component (PCA), an extremely popular and widely used technique for statistical shape analysis (Bookstein, 1991;

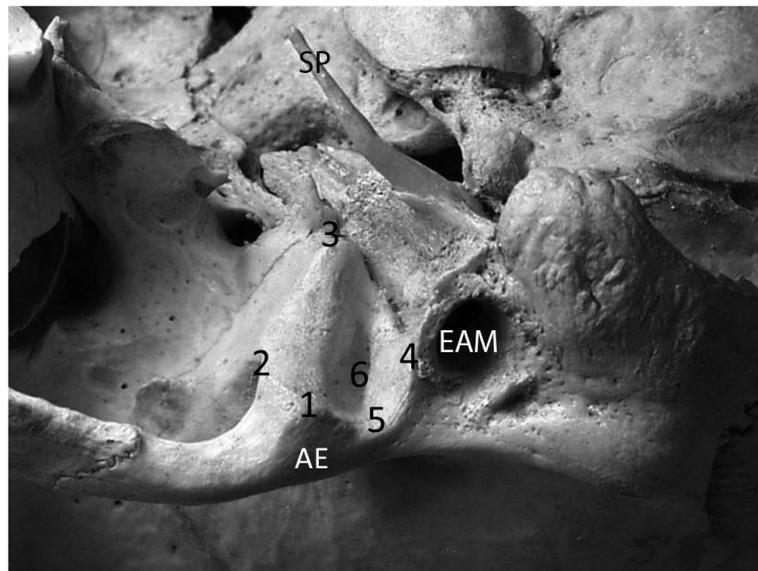


Figure 2. Landmarks used in this study numbered on a human skull, shown here in an oblique basal view. For a full description of the landmarks, see **Table 3**. EAM, external acoustic meatus; AE, articular eminence; SP, styloid process.

Table 3. Landmark definition. Skull is oriented in the anatomical position.

Landmark No.	Definition
1	Most inferior point on the lateral border of the articular eminence
2	Most posterior point within the temporal fossa
3	Junction of the squamotympanic fissure & sphenosquamous suture
4	Most inferior point of post-glenoid process
5	Most superior point on the lateral border of the glenoid fossa
6	Most superior point within the glenoid fossa

Dryden, 1998; Depecker, 2006 to name a few). This technique however requires a large sample size compared to the number of variables. The exact ratio between variables and sample size is a debatable subject (Osborne & Costello, 2004), but a ratio of 4:1 has been quoted by several authors (Hatcher, 1994; Gorsuch 1983). It is therefore eminent to use as few landmarks as possible in order to be able to get valid statistical analysis, without losing the autapomorphic nature of the studied area. Superimposition process and the PCA were done using Morphologika 2.2 by O'Higgins and Jones (1998). ANOVA test was conducted on each PC in order to evaluate the statistical significance of the difference between studied groups. Two stages of analysis were conducted. The first step was to determine whether the fossa is a good indicator for species recognition. This was done by performing three analyses in order to evaluate the intra vs. inter specific variation. The first analysis was between the two *Pan* species, the second between the three ape species and the third added the two human groups to the apes. After demonstrating that species can be sorted based on the fossa, two analyses were conducted on the *Homo erectus* specimens. The first included the 13 casts of the fossils hominids. In order to assess the nature of taxonomic relationship between *Homo sapiens* and fossil specimens, the second analysis included the 13 casts and 4 recent humans. We further applied a cluster analysis of the superimposed data of the fossil specimens in order to determine the relationships between and within the different fossil groups. Cluster analysis was done using Ward's Linkage method (Ward, 1963). This method is extremely efficient when creating small clusters (Blackwood et al., 2003). The statistical analysis and cluster analysis was done by SPSS, Microsoft excel and PAST software by Hammer et al. (2001).

4. Results

In all of the analyses, the first two components are related to inter-specific variation, while the third is related to intra-specific variation within modern human group only. Generally, the first component explains about 30% of the observed variation; the second component about 20% and the third about 11%. Overall, ten components explained more than 95% of the variation. No size, or sexual dimorphism correlation effect was observed while using more than one species in the analysis. In the following results we will only describe those components that were meaningful for our analysis.

The first analysis compares the two *Pan* species (**Figure 3(a)**). The first PC separates the two species explaining 30.2% of the variance in the data. The significance of separation is $P < 0.005$. The second analysis adds the *Gorilla* to the two *Pan* species (**Figure 3(b)**). The first PC separates the three species and explains 29.5% of the observed variation. The separation between the gorilla and bonobo is $P < 0.001$ while the separation between the two *Pan* species is $P < 0.005$, as same as in the previous analysis. Interesting to notice, the Bonobo group falls between the Gorilla and chimpanzee. Next, the two human groups were added (**Figure 3(c)**). The first PC now separates between the apes and human and contributes 34% of the observed variation. The level of separation between the human and apes is $P < 0.0001$. The second PC, separates between the three ape groups explains 18.8% of the observed variation, while the third PC (not shown here) separated between the two human groups explaining 11.7% of the observed variation. The level of significance of the separation between the apes remained the same as in the previous analysis with $P < 0.001$ between gorilla and bonobo and $P < 0.005$ between bonobo and chimp.

After establishing that the morphology of the mandibular fossa is useful for species recognition, we studied the fossil specimens. The first analysis included the 13 casts (**Figure 4(a)**). The first PC separated the Asian specimens including OH-9 from the European and African groups including Dali and LB1, and contributed 35.2% of the observed variance. Asian specimens were separated from the two other groups with significance level of $P < 0.001$. The second PC separated the European specimens, including Broken Hill, from the African specimens, including Dmanisi, and explained 24.1% of the observed variation with a significance level of $P < 0.01$. Some fossils do not group geographically or spatially: The Dmanisi skull falls deep within the African specimens al-

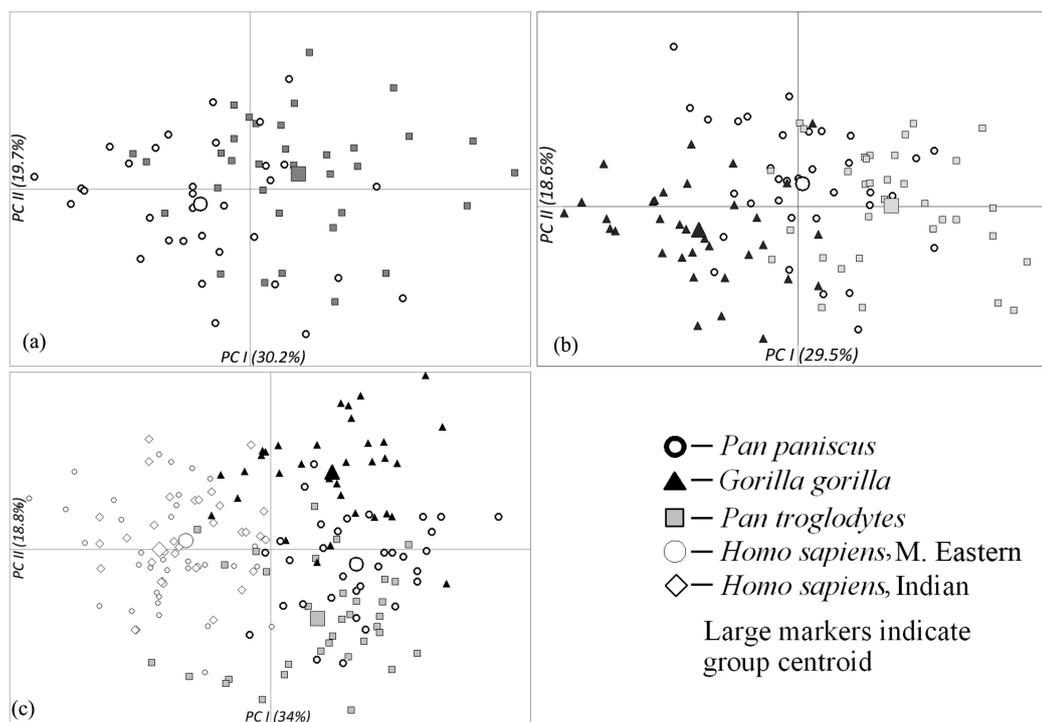


Figure 3. Principal component analysis of living species: (a) Analysis of the two *Pan* species; (b) Analysis of the three ape species; (c) Analysis of the two human groups with the ape species. Note that the relative position of each species is identical in all the graphs.

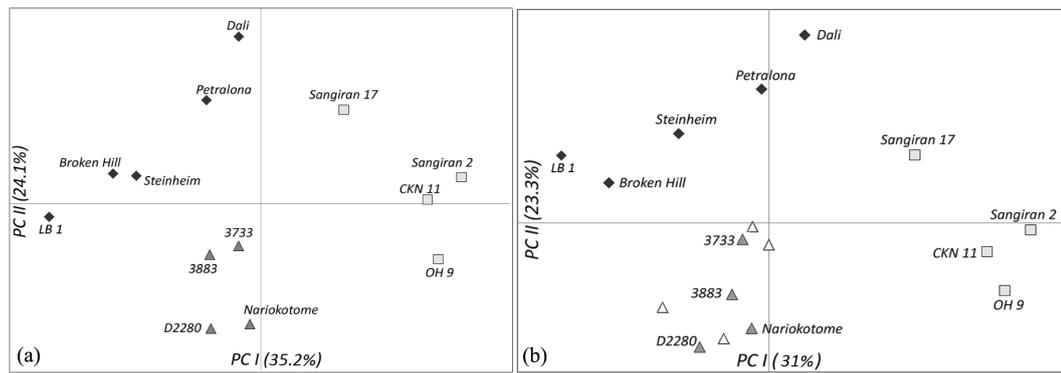


Figure 4. Principal component analysis of the fossil specimens: (a) Analysis of fossil specimens only; (b) Analysis of the fossil specimens with the added human group. Note the stable location of each specimen in both analyses.

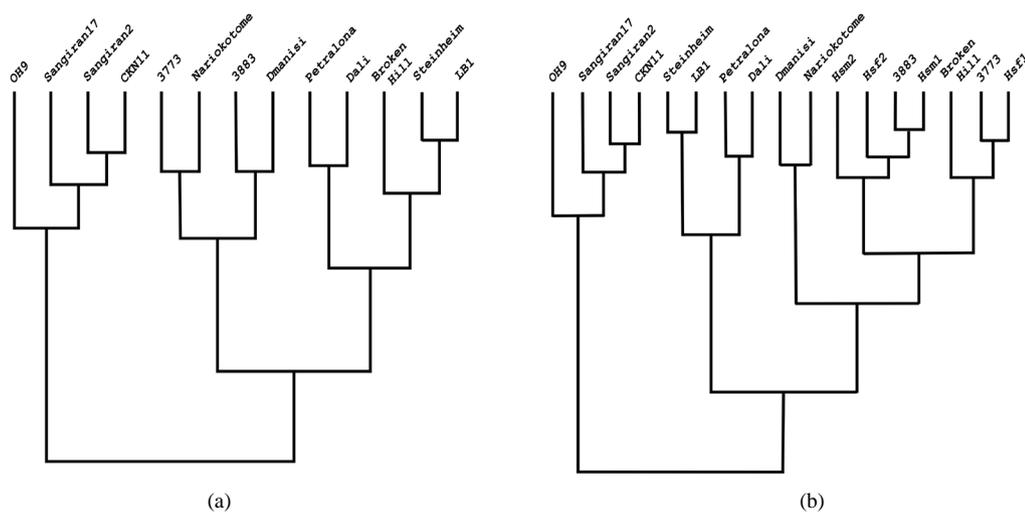


Figure 5. Cluster analysis using Ward's method: (a) Analysis of fossil specimens only; (b) Analysis of the fossil specimens with the added human group. Note the constant location of each specimen in both analyses.

though geographically very remote; The Dali skull from China falls close to Petralona from Greece; OH-9 falls in proximity with the Asian fossils although separated both geographically and temporally. *Homo floresiensis* seems to fall on the border between European specimens and African specimens completely opposite to other Asian material, and its closest neighboring fossil is Broken Hill, which is at least several hundred thousand years older and one of the most robust *Homo* skulls. In the second part of the analysis, four recent human specimens were added (Figure 4(b)). They consisted of two males and two females from the two human groups (randomly chosen). In this analysis all the modern humans fall well, and only, within the African specimens, while the fossils, with the exception of LB 1, retain their original position and their statistical significance, adding to the overall validity of the fossil analysis. The same procedure was repeated and returned the same results while using other recent human sample.

A cluster analysis of the fossils (Figure 5) was done on the superimposed data. The Asian group with OH-9 is the most divergent cluster of the three, while African group with Dmanisi and European group with Dali exhibit greater similarity and a common ancestry. *Homo floresiensis* clusters with the Steinheim skull. The cluster analysis results are very similar to the ones obtained by the PCA, and thus further emphasise and increase the validity and the consistency of the results.

5. Discussion

This study used the morphometric attributes of the mandibular fossa as a method of differentiating between ex-

tant & extinct species. The use of small, confined and highly derived area is important to paleoanthropological studies, as these areas may increase our taxonomic understanding of the fossil record even when dealing with small, fragmentary pieces. In the first part of the analysis, it is clear through the extant species, that the fossa is indeed a good indicator for species recognition. The placement of the human group is opposite to the apes group; the bearing of the ape species is constant throughout the analysis whether humans are included or not. The level of significance of the separation between the different species is also constant throughout the analysis. These results generally coincide with previous works such as Lockwood et al. (2002), Terhune et al. (2007) and Harvati (2003), while using fewer landmarks over smaller area.

The second part of the analysis deals with the extinct species. Here, as expected the image is more complex. This is due to two main facts: first, the nature of fossils with their extensive timeframe and broad geographical distribution, which makes them more variable than extant species; Second, the relative small number of specimens, which lowers the statistical significance of the results. In spite of these shortcomings, few important and interesting aspects are visible. The first PC in the analysis separates Asian specimens including OH-9 from the African specimens including Dmanisi and European group including Broken Hill and Liang Bua. This might imply for an early separation of the two Pleistocene groups and suggests an African ancestry for the European group. The second PC separates European specimens including Dali from African specimens. *Homo floresiensis* seems to fall on the border between these two groups. Same results were evident from the cluster analysis.

These findings when compared to the extant species further corroborate and manifest that our analysis supports the proposition that at least three major different species existed in the Pleistocene: *Homo heidelbergensis* which expanded throughout the old world, *Homo erectus* from the Far East, a probable evolutionary dead-end and an African species that should be named *Homo ergaster* (after Groves & Mazák, 1975), a species that was found throughout Africa and central Euro-Asia, and that is probably the sole ancestor to *Homo sapiens*. The results are further validated by analyzing the geographical and temporal dispersal of the different fossils: Dali from China and Petralona from Greece fall close together, although they come from very distant geographic areas. This result agrees with previous studies that affiliate Dali to *Homo heidelbergensis* (Rightmire, 1998). The Dmanisi skull falls deep within *Homo ergaster* group, especially close to Nariokotome, although separated by more than 4000 kilometres. Allocation of the early Dmanisi skull to *Homo ergaster* has been suggested by other (Gabunia, 2000; Baab, 2008; Lordkipanidze et al., 2013) although Terhune et al. (2007) found this specimen to have Asian origins. In our analysis OH 9 falls close to the Asian *Homo erectus*, although it is an early African fossil (Leakey, 1961; Anton, 2003). An Asian affinity to this specimen was previously suggested by other authors (Clarke 2000; Anton & Swisher, 2001; Terhune et al., 2007), although Baab (2008) assign it to the African lineage. *Homo floresiensis*, despite its recent age, and isolated geographical Javanese location (Brown, 2004) group with *Homo heidelbergensis*, especially close to the massive skull from Broken Hill, suggesting ancient taxonomic origin to this enigmatic specimen.

Our results does not suggest direct taxonomic ancestry between *Homo heidelbergensis* and *Homo sapiens* and contradict the notion of an “archaic” *Homo sapiens*.

Finally, we must bear in mind that our analysis does not necessarily limit the number of species to three. Considering the fact that the *Homo ergaster* specimens clusters with the human sample; the spacious clustering of the “classic” Asian specimens and *Homo heidelbergensis*; and the use of one area within the skull, the number of species may actually be greater than what appears from our analysis. It might turn, for example, that each of the following skulls OH-9, Sangiran 17 and LB1 represents an unknown or yet unassigned species.

6. Conclusion

In the present study, we have tried to use the morphology of the mandibular fossa as a species specific indicator for species recognition. Although we suspect our analysis will not be the final word, it does add to the growing evidence that supports the view that *Homo erectus* is not a single species, but represents a cluster of separate species in space and time, extending throughout the old world and across the Pleistocene. It seems that *Homo sapiens* have evolved solely from *Homo ergaster* or alike species probably in Africa. A closer examination of anatomical features of other skeletal elements, cranial as well as post-cranial, along with more hominids such as *Homo habilis*, *Homo antecessor* and *Homo neanderthalensis*, is needed to shed more light on this interesting stage of human evolution.

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