



# A probabilistic approach to the craniometric variability of the genus *Homo* and inferences on the taxonomic affinities of the first human population dispersing out of Africa

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## ABSTRACT

There is probably no paleoanthropological issue with deeper disagreements than the taxonomic status of the Early–Middle Pleistocene members of the genus *Homo*. One reason could be the difficulty of estimating the relationship between morphological and taxonomic diversity. In an attempt to contribute new evidence to this debate, bootstrapping techniques are used for analyzing the cranial variability of *Homo*. The results indicate that: (i) the size of the neurocranium relative to the viscerocranium discriminates better among extant hominoid species than skull size; (ii) no cluster of fossil specimens of *Homo* exceeds the morphological variability of *Gorilla gorilla*, with the only exception of the one that comprises all members of *Homo* except modern humans; and (iii) some clusters are taxonomically more consistent than others, as long as they show a range of morphological variability similar to that found in both *Pan troglodytes* and *Homo sapiens*. According to these results, three taxa are tentatively suggested for *Homo*: (i) anatomically modern humans; (ii) an “erectine” morphotype plus Neanderthals; and (iii) a “habiline” cluster. Finally, the results indicate a greater taxonomic affinity for the human population involved in the first dispersal “Out of Africa” with the “habiline” group, which agrees with the early age reported for Dmanisi (1.77 Ma), a Georgian site placed at the gates of Europe.

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## 1. Introduction

The relationship between morphological and taxonomic diversity has been the focus of a particularly persistent debate in paleoanthropology. Although morphology and taxonomy are obviously interconnected, neither can be explained solely on the basis of the other (Foote, 1993a). Moreover, there are morphological discontinuities such as those arising from sexual dimorphism or geographic subspecies that do not represent valid criteria for defining separate species. And, above all, the low preservational completeness of the hominin fossil record (i.e., scarcity of skeletal remains, with a distribution temporally and geographically biased) even precludes the application of these criteria. As a result, it is commonly assumed

by practical reasons that a cluster of extinct organisms showing a size range that exceeds the variability of that found among modern hominoid species will probably be composed of several taxa.

In this context, the taxonomic diversity of the early members of *Homo* is a central issue of paleoanthropology. Leaving aside the authors who are skeptical of including the “habiline” group within the genus *Homo* (e.g., Wood and Collard, 1999), the literature splits between those who suggest a single species, *Homo habilis* (Howell, 1978; White et al., 1983; Johanson et al., 1987; Tobias, 1987, 1991; Miller, 1991, 2000; Lee and Wolpoff, 2005; Jiménez-Arenas, 2006; Jiménez-Arenas et al., 2007), as opposed to those who advocate for two separate species, *H. habilis* and *Homo rudolfensis* (Walker and Leakey, 1978; Wood, 1978, 1985, 1991, 1992a, 1992b, 1993; Wood and Stack 1980; Alexeev, 1986; Stringer, 1986; Chamberlain, 1987; Lieberman et al., 1988, 1996; Groves, 1989; Kramer et al., 1995; Donnelly, 1996; Grine et al., 1996; Wood and Collard, 1999). The single taxon approach assumes that a marked sexual size dimorphism in early *Homo* accounts for the size and shape variability of all specimens grouped in *H. habilis* and that the level of sexual dimorphism is evenly distributed across modern and extinct hominoid species. In contrast, those who favor two

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separate taxa acknowledge that if it were only one species, it would exhibit a greater degree of sexual dimorphism for most cranial metric traits than any reasonable analogues, and would even show a pattern of sexual dimorphism markedly different from that observed in closely related taxa [e.g., females (KNM-ER 1813, *H. habilis*) having larger browridges than males (KNM-ER 1470, *H. rudolfensis*)].

The debate on the taxonomic diversity of the “habiline” group, traditionally focused on the African specimens of early *Homo*, has recently been fueled by the discovery of a number of well-preserved fossil skulls in the Early Pleistocene Georgian site of Dmanisi, dated at ~1.77 Ma, as these crania show reduced cranial capacities that range from only 600 to 775 cm<sup>3</sup> (Gabunia et al., 2000; Vekua et al., 2002; Lordkipanidze et al., 2005, 2006; Rightmire et al., 2006). In fact, there is strong evidence for integrating this population, named as *Homo georgicus* (Gabunia et al., 2002), within the “habiline” group (e.g., de Lumley et al., 2006; Jiménez-Arenas, 2006). Specifically, Lordkipanidze et al. (2007: p. 309) indicate a number of plesiomorphic features, including a more medial orientation of the foot than in modern humans, the absence of humeral torsion, a small body size and a low encephalization quotient, features which in their opinion suggest that the Dmanisi hominins are cranially and postcranially largely comparable to earliest *Homo* (cf. *H. habilis*). In addition, the recent finding of a human mandible associated with an Oldowan tool assemblage and faunal remains bearing traces of hominin processing in Sima del Elefante (Atapuerca, Spain), dated to the Early Pleistocene (~1.2 Ma) and provisionally assigned to *Homo antecessor*, represents the oldest human remains of Europe (Carbone et al., 2008). It is worth noting that the morphology of the anterior surface of this jaw symphysis and the position of the anterior marginal tubercle suggest similarities with some early *Homo* specimens and, particularly, with the mandibles from Dmanisi. In summary, the “habiline” cluster represents an informal taxonomic group of “transitional hominins” that may encompass up to four different species (Wood and Lonergan, 2008).

Concerning the morphological variability of *Homo erectus sensu lato*, the current status of the debate is even more puzzling. Initially, the controversy was confined to Asia. The finding of the Zhoukoudian fossils translated into the establishment of a new genus, *Sinanthropus* (Black, 1927; Weidenreich, 1943), which encompassed also the specimens of *Pithecanthropus* already known from Java (Dubois, 1894). Subsequently, all the Asian fossils were grouped under the name of *H. erectus* (Mayr, 1950, 1963). However, this proposal did not put an end to the splitting taxonomic tradition of paleoanthropology, renewed by the mid-fifties by Von Koenigswald (1954), who divided the Indonesian fossils into two genera, *Pithecanthropus* and *Meganthropus*. In fact, the followers of this tradition suggest that there are several taxa in Asia (e.g., Zeitoun, 2003) and even talk about specific geographic areas (e.g., Indonesia) where multiple taxa would have coexisted (Jacob, 1981; Schwartz and Tattersall, 1999; Tyler, 2001). The Early and Middle Pleistocene African human fossils were also initially split into two taxa, *Telanthropus* (Broom and Robinson, 1949) and *Atlanthropus* (Arambourg, 1955). The description of *Homo ergaster*, based on the fossils found in the Rift valley (Groves and Mazak, 1975), prompted again the one vs. multiple taxa dilemma. On the one hand, a number of researchers that favored the multiple taxa tradition acknowledged a clear distinction between *H. erectus sensu stricto* and *H. ergaster* (Groves and Mazak, 1975; Tattersall, 1986; Andrews, 1989; Groves, 1989; Stringer, 1989; Clarke, 1990, 2000; Wood, 1991, 1994; Wood and Richmond, 2000; Manzi et al., 2003; Bermúdez de Castro et al., 2004; Terhune et al., 2007; Lague et al., 2008) and some of them even suggested that *H. ergaster* should be split into several taxa (e.g., Schwartz and Tattersall, 1999; Tattersall, 2007). On the other hand, the advocates of the single taxon solution suggested that both *H. erectus s.s.* and *H. ergaster* should be grouped within *H. erectus* (Rightmire, 1986, 1998, 2008; Turner and

Chamberlain, 1989; Bräuer and Mbuja, 1992; Kramer, 1993; Bilsborough, 2000; Asfaw et al., 2002; Antón, 2003; Kidder and Durband, 2004; Baab, 2008), a taxon which could even encompass the paleodeme from Dmanisi given the combination of primitive and advanced craniodental traits in this population (Bräuer and Schultz, 1996; Rosas and Bermúdez de Castro, 1998a; Kaifu et al., 2005; Rightmire et al., 2006; Suwa et al., 2007; Martín-Torres et al., 2008; Rightmire and Lordkipanidze, 2010).

In the case of the Middle Pleistocene specimens of Africa and Europe, some researchers suggest that they are better accommodated in a single taxon, *Homo heidelbergensis* (Stringer, 1983; Rightmire, 1988, 1990, 1996; Mounier et al., 2009), while others think that this species was exclusively confined to Europe (Arsuaga et al., 1997; Rosas and Bermúdez de Castro, 1998b) and the African specimens should be placed in a separate species, *Homo rhodesiensis*. It has even been proposed that the two paleospecies that inhabited Europe during middle Pleistocene times, *H. heidelbergensis* and *Homo neanderthalensis*, may represent an anagenetic lineage (Dennell et al., 2010) or be part of the same chronospecies (Hublin, 1982, 2009), which agrees with recent estimates on the early divergence between Neanderthals and anatomically modern humans (Green et al., 2009; Briggs et al., 2009; Endicott et al., 2010). Finally, a minority of researchers suggest that *H. erectus* could represent a distinctive evolutionary stage of *H. sapiens* (Jelinek, 1981; Thorne and Wolpoff, 1981; Frayer et al., 1993; Wolpoff et al., 1994; Wolpoff, 1999).

In summary, there is probably no area of paleoanthropology with deeper disagreements than the taxonomy of the Early-to-Middle Pleistocene fossils of *Homo* (Tattersall, 2007). However, it's worth noting that this study does not deal with the persistent debate on the validity of the species proposed. Instead, it focuses on the morphological variability of *Homo* and on the reliability of the criteria used for species recognition in the human fossil record. For this reason, in an attempt to shedding some light on this topic, the goals of this study are the following: (i) to identify in a set of morphological variables measured in the cranium those metric traits that show less overlap among three living species of hominoids, humans (*H. sapiens*), common chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*); (ii) on the basis of the metric variables selected, to assess with bootstrapping methods the probabilities that the ranges of morphological variability for different clusters of fossil crania are in agreement with the ones exhibited by the three extant hominoids; (iii) to evaluate from these probabilities the taxonomic coherence of the extinct taxa proposed for *Homo* (i.e., morphological species based on phenetic data); and (iv) on the basis of the results obtained, to estimate which taxon was involved in the first human dispersal “out of Africa”.

## 2. Materials and methods

Table 1 shows the samples of crania from the three living species studied (*H. sapiens*, *P. troglodytes* and *G. gorilla*). These samples are composed exclusively of adult individuals, represented by similar numbers of males and females. The specimens of *H. sapiens* are the most heterogeneously distributed both spatially and temporally. The sample of *G. gorilla* shows the highest level of sexual dimorphism. Finally, the cranial set of *P. troglodytes* has the highest taxonomic variability, as it includes specimens from three subspecies (*Pan troglodytes schweinfurthii*, *Pan troglodytes troglodytes* and *Pan troglodytes verus*). All metric data from fossil crania were obtained from the literature (Table 2).

The craniometric measurements include cranial length (GOL, measured as the distance between glabella and opistocranium), biparietal width (XCB, measured as the maximum breadth of neurocranium), basionbregmatic height (BBH, measured as the distance between basion and bregma), facial length (BPL, measured as the distance between basion and prosthion), bizygomatic width

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