



News and Views

The one-million-year-old *Homo* cranium from Bouri (Ethiopia): a reconsideration of its *H. erectus* affinities

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Introduction

Describing the one-million-year-old *Homo* specimen BOU-VP-2/66 from the Dakanihylo Member at Bouri, Middle Awash (Ethiopia), referred to as “Daka”, [Asfaw et al. \(2002\)](#) recently raised questions about the distinction between *H. ergaster* and *H. erectus*. They concluded that there is a “lack of calvarial evidence for a deep phylogenetic division between the African and Asian fossils” ([Asfaw et al., 2002, p. 319](#)). There is a long-standing controversy (see, e.g., [Wood, 1994](#)) whether it is preferable to group together in a single hypodigm such a fossil record (*H. erectus s.l.*), or to classify the same evidence in two distinct species, respectively representing the African (*H. ergaster*) and the eastern Asian (*H. erectus s.s.*) variants of an archaic morphotype within the genus *Homo*. Our goal is to briefly show here that data provided by [Asfaw et al. \(2002\)](#) indicate continuity of features in Africa up to 1 Ma, and that human cranial morphology in eastern Africa at that time is rather distinct from the far eastern Asian side, where the typical *H. erectus* phenotype is actually observed. A phenetic analysis of the

available calvarial evidence shows that while Daka is close to earlier African samples it is distinct from the Asian *H. erectus s.s.* It is also different from more derived and more recent African (e.g., Bodo, Kabwe) and Eurasian hominids, represented by Ceprano, Atapuerca TD6, and (subsequently) by *H. heidelbergensis*.

Although [Asfaw and colleagues \(2002\)](#) perform a cladistic analysis, they recognise limitations to this approach in identifying phylogenies among fossil representatives of closely related and time transgressive samples, whatever they are considered: extinct species, chrono-subspecies, or (according to [Howell, 1999](#)) paleo-demes. The cladistic approach requires assumptions that have to be tested when dealing with the fossil record ([Lieberman, 1995, 1999](#)). By contrast, a phenetic analysis may offer a more critical perspective, furnishing results that require interpretation, but that are, conversely, less *a priori* conditioned. We may also note that cladistic techniques are not appropriate to infer alpha taxonomy (e.g., [Trinkaus, 1990](#)). In our understanding cladistics is simply not designed to do this. Rather, it is a method of phylogenetic inference which logically takes place after alpha taxonomy has been appropriately established.

Another bias possibly affecting the cladistic analysis performed by [Asfaw et al. \(2002\)](#) originates from their decision to group fossils into

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Table 1
Presence/absence scores for selected (*H. erectus*-like) traits

	Features																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
Sangiran 2	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	–	1	1	–	0	0	0	1	0	1	1	1	1	1	1	0
Sangiran 17	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	0	1	0	
Zhoukoudian III	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	1	0	0	1	1	0	1	1	1	1	1	1	0	
Zhoukoudian X	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	
Zhoukoudian XI	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	0	0	
Zhoukoudian XII	1	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	0	
Ngandong 7	1	1	1	–	0	0	0	1	1	1	1	1	0	1	0	1	0	1	0	1	1	0	0	1	1	1	0	1	0	0	
Dmanisi 2280	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	–	–	1	0	0	0	
Dmanisi 2282	1	1	1	–	1	0	0	1	1	1	1	0	1	1	0	–	0	0	–	1	0	1	1	1	–	–	1	0	0	0	
KNM-ER 3733	1	1	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	
KNM-ER 3883	1	1	1	1	1	0	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	
OH 9	1	1	1	1	1	0	0	–	1	0	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	1	0	0	0		
Daka	1	1	1	0	1	1	0	0	0	–	0	0	1	1	0	1	0	1	0	1	1	0	0	1	0	–	0	0	0	0	
Bodo	1	1	–	1	0	0	1	0	0	–	0	0	–	–	–	1	1	0	1	1	1	–	–	–	–	–	–	–	–	–	
Kabwe	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	1	1	1	1	–	
Saldanha	1	1	–	1	0	0	1	0	0	1	–	0	–	1	1	–	0	0	1	1	1	0	–	–	–	–	–	0	1	0	
Ceprano	0	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	
Arago XXI	1	1	–	0	0	0	0	0	1	0	–	–	–	–	–	1	0	1	1	1	1	1	1	–	–	–	–	–	–	–	
Steinheim	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1	0	0	0	1	0	0	0	
Petralona	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	0	1	1	1	–	–	–	1	1	0	0	
Atapuerca SH Cr.4	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	1	0	1	1	
Atapuerca SH Cr.5	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	1	0	1	0	

Legend: 1 = presence; 0 = absence; – = missing value.

Features considered: 1) long cranial vault; 2) low cranial vault; 3) maximum breadth across the angular torus or supramastoid crest; 4) thick vault bones; 5) pronounced postorbital constriction; 6) frontal keel or ridge; 7) straight junction of torus and frontal squama; 8) coronal ridge; 9) flattened parietal; 10) rectangular parietal; 11) low temporal squama; 12) flat superior border of the temporal squama; 13) small mastoid process; 14) opisthocranium coincident with inion; 15) sharply angulated occipital profile; 16) broad nasal bones; 17) horizontal inferior border of the supraorbital torus; 18) continuous thickness of the supraorbital torus; 19) glabellar inflexion in superior view; 20) mid-orbit torsion of the supraorbital torus; 21) bilateral discontinuity of the supratral sulcus; 22) prominent angular torus at mastoid angle; 23) marked supramastoid crests; 24) marked mastoid crests; 25) occipitomastoid ridge; 26) juxtamastoid ridge absent; 27) marked supraneatal tegmen; 28) occipital torus with supratral sulcus; 29) occipital torus continuous with angular torus and supramastoid crest; 30) mid-sagittal depression of the occipital torus.

Operational Taxonomic Units (or OTUs) created according to chronology and topology. It is clear that this procedure does not appropriately consider the affinities of each single specimen. For instance, looking at the “supplementary information” to Asfaw et al. (2002; <http://www.nature.com>), it can be easily noticed that the character states of Daka are obscured (at least in part) by those of OH9, given that both specimens are included in the same OTU together with the incompletely described fossil cranium from Buia, Eritrea (Abbate et al., 1998). According to such a procedure, OTUs are not adequately supported on the basis of shared morphology, rather than time

and locality. The inclusion in the Daka/Buia unit of a calvaria such as OH9, whose problematic nature is widely recognised (e.g., Clarke, 1990; Rightmire, 1990; Wood, 1991), is not particularly appropriate either on aspects of morphology or time, considering that the Olduvai hominid is between two and five hundred thousand years older than both Daka and Buia (Tamrat et al., 1995).

We prefer to examine separately the morphology of well-preserved single specimens, and rely on the phenetic approach already applied elsewhere (Manzi et al., 2001). Phenetics quantifies overall similarity, and thus is more appropriate for a

Table 2
Matrix of phenetic distances between specimens

	Sng. 2	Sng. 17	Zkd. III	Zkd. X	Zkd. XI	Zkd. XII	Ngd. 7	Dmn. 2280	Dmn. 2282	ER 3733	ER 3883	OH 9	Daka	Bodo	Kabwe	Saldanha	Ceprano	Arago	Steinheim	Petralona	At-SH Cr.4	At-SH Cr.5	
Sangiran 2	0.00																						
Sangiran 17	0.14	0.00																					
Zhoukoudian III	0.14	0.17	0.00																				
Zhoukoudian X	0.21	0.13	0.17	0.00																			
Zhoukoudian XI	0.18	0.17	0.13	0.03	0.00																		
Zhoukoudian XII	0.18	0.17	0.13	0.10	0.07	0.00																	
Ngandong 7	0.44	0.38	0.41	0.38	0.41	0.45	0.00																
Dmanisi 2280	0.38	0.32	0.36	0.25	0.29	0.36	0.41	0.00															
Dmanisi 2282	0.44	0.36	0.36	0.28	0.32	0.36	0.24	0.12	0.00														
KNM-ER 3733	0.39	0.37	0.33	0.37	0.33	0.33	0.38	0.29	0.28	0.00													
KNM-ER 3883	0.32	0.37	0.33	0.43	0.40	0.40	0.34	0.46	0.36	0.33	0.00												
OH 9	0.30	0.31	0.28	0.24	0.21	0.28	0.36	0.37	0.29	0.28	0.34	0.00											
Daka	0.62	0.50	0.43	0.46	0.46	0.43	0.48	0.46	0.35	0.25	0.36	0.30	0.00										
Bodo	0.57	0.69	0.69	0.69	0.69	0.75	0.53	0.56	0.54	0.69	0.63	0.53	0.50	0.00									
Kabwe	0.56	0.55	0.52	0.55	0.59	0.59	0.46	0.48	0.46	0.52	0.59	0.71	0.48	0.25	0.00								
Saldanha	0.50	0.52	0.57	0.67	0.71	0.76	0.45	0.38	0.42	0.52	0.48	0.55	0.50	0.07	0.30	0.00							
Ceprano	0.43	0.50	0.40	0.43	0.40	0.40	0.48	0.50	0.44	0.53	0.53	0.45	0.57	0.19	0.45	0.38	0.00						
Arago XXI	0.57	0.63	0.38	0.56	0.50	0.44	0.27	0.63	0.38	0.44	0.50	0.33	0.33	0.36	0.44	0.40	0.25	0.00					
Steinheim	0.61	0.60	0.57	0.67	0.63	0.57	0.41	0.71	0.56	0.43	0.50	0.48	0.32	0.38	0.52	0.48	0.50	0.13	0.00				
Petralona	0.52	0.59	0.48	0.48	0.52	0.48	0.38	0.52	0.42	0.44	0.44	0.50	0.31	0.25	0.27	0.33	0.33	0.25	0.41	0.00			
Atapuerca SH Cr.4	0.57	0.57	0.47	0.50	0.53	0.60	0.41	0.64	0.52	0.60	0.47	0.59	0.43	0.38	0.34	0.48	0.40	0.38	0.43	0.30	0.00		
Atapuerca SH Cr.5	0.50	0.63	0.47	0.50	0.47	0.53	0.41	0.57	0.52	0.53	0.40	0.52	0.39	0.25	0.34	0.48	0.40	0.31	0.37	0.22	0.13	0.00	

Note: distances were computed by the single matching coefficient algorithm (Sneath and Sokal, 1973) on the basis of the presence/absence scores reported in Table 1.

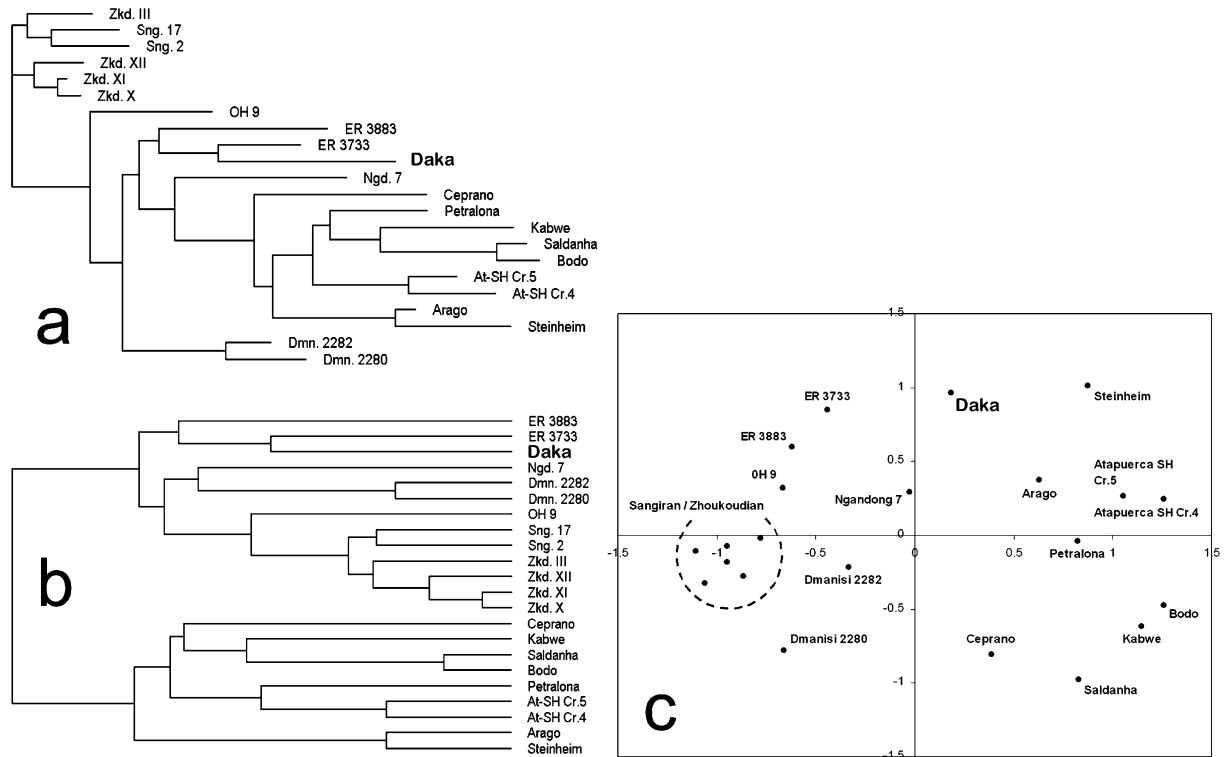


Fig. 1. Comparable outputs are generated by different clustering techniques applied to the same set of data shown in Table 2, namely: a) neighbour joining (NJ); b) unweighted pair group method using arithmetic averages (UPGMA); and (c) multi-dimensional scaling (MDS; stress = 0.17). Acronyms as in Table 2.

preliminary recognition of alpha taxonomy. On the basis of the presence/absence of 30 features considered typical of *H. erectus* from Java and China (Table 1), adapted from Wood (1991, tab. 2.11), a matrix of phenetic distances can be obtained, based on the single matching coefficient (Sneath and Sokal, 1973; Table 2). Cluster analyses were performed by neighbour-joining (NJ) and unweighted pair group method using arithmetic averages (UPGMA), and the sample was ordered in a multi-dimensional scaling projection (MDS). Phenograms have been computed using PHYLIP 3.57c (Felsenstein, 1989) and visualised with TREEVIEW (Page, 1996). As shown in Fig. 1, the various procedures express in different ways the same result.

Recurrent grouping of specimens in the various analyses, supported by the fact that crania with

obvious affinities, like those coming from the same site/area/chronology (*e.g.*, Dmanisi, Zhoukoudian), cluster together, may help to evaluate the evolutionary significance of some crucial and/or new evidence. In particular, we find that Daka shares the greatest affinities with crania such as KNM-ER 3733 and 3883 from Koobi Fora, Turkana (dated to about 1.6 Ma), and it is farther from the far eastern Asia hypodigm. Moreover, two of the Dmanisi hominids, Georgia (1.7–1.8 Ma), the OH9 partial braincase from Olduvai (approximately 1.2 Ma), and an example of the late *H. erectus* calvaria from Ngandong (less than 100 ka) have somewhat intermediate phenotypes, consistent with the fact that, in different ways, these fossils are detached chronologically and/or geographically from typical *H. erectus* specimens from Java and China. Similarly, Daka is not close

to what is generally described as *H. erectus s.s.*, whereas it appears, among *H. erectus s.l.*, as an expression of the most distant morphology from this phenetic configuration (see for instance the MDS projection; Fig. 1c). At the same time, it shows affinities with *H. ergaster* samples and tends to cluster with them (see Fig. 1a,b). Daka should therefore best be seen as part of a local (African) evolutionary lineage spanning from approximately 1.8 Ma up to about 1 Ma.

Even more distant from *H. erectus s.s.* are Middle Pleistocene hominines from Africa and Europe, for which Ceprano appears to be the best available phenetic link, as far as the adult morphology of the braincase is concerned. This conclusion for Ceprano is also in accordance with the phylogenetic position hypothesised for the penecontemporaneous Atapuerca TD6 fossil assemblage, that is based on completely independent sources of data (see Arsuaga et al., 1999; Manzi et al., 2001). In comparison with Daka, Ceprano shows dissimilarity from *H. erectus s.s.* (see the dimension 1 of MDS in Fig. 1c), but also from *H. ergaster* (dimension 2 in the MDS). On the other side, the Italian fossil is closer than Daka to the subsequent radiation of more derived hominines—those that, in turn, are probably ancestral to the emergence of both Neandertals and modern humans, in Europe and Africa respectively.

There is a extensive literature devoted to the concept of species and how it applies to the fossil record (e.g., Tattersall, 1986; Turner and Chamberlain, 1989; Kimbel and Martin, 1993), but we do not intend to address these issues here. In our opinion, what is more important is the identification of the process itself (compare Lahr and Foley, 1998). The evidence provided here indicates a local phenetic continuity pattern, hence the occurrence in Africa of an anagenetic *continuum* from the emergence of the genus *Homo* up to about 1 Ma. Actually, Asfaw et al. (2002, p.318) do state that the “chronological and morphological seriation of the African fossils from KNM-ER 3733/3883 (Koobi Fora) to OH 9, to Daka/Buia to Bodo [...] comprise a morphocline consistent with the hypothesis that they sample a single evolving lineage”. However, according to our data, we are

not convinced that this *continuum* might have included African Middle Pleistocene specimens such as Bodo and Kabwe, which may be better viewed as representatives of a distinct species (*H. rhodesiensis*).

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