THE FIRST HOMININ OF EUROPE: A MULTIVARIATE EXPLORATORY ANALYSIS

Walter Alves Neves[1] e Danilo Vicensotto Bernardo[2]

1_Coordenador do Laboratório de Estudos Evolutivos Humanos, Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, bolsista de produtividade em pesquisa 1A CNPq – CP 11461, São Paulo, SP, CEP 05422-970 – waneves@ib.usp.br
2_Doutorando do Programa de Pós-Graduação em Ciências (Biologia/Genética) do Departamento de Genética e Biologia Evolutiva do Instituto de Biociências da Universidade de São Paulo, bolsista FAPESP – CP 11461, São Paulo, SP, CEP 05422-970 – danvb@ib.usp.br

ABSTRACT

Recently an international team of archae-ologists reported the oldest hominin skeletal remains ever found in Europe. A mandible fragment and an isolated tooth were found in the TE9C level of Sima del Elefante, Atapu-erca, Spain, associated with a typical Old-owan industry. In the study, the authors claim that the TE9-1 hominin can be assigned to *Homo antecessor*, being the result of a local speciation event that occurred during the Early Pleistocene. Here we present a multi-variate analysis applied to four dimensions of the mandible, comparing the TE9-1 hominin with other key hominin fossils. Considering the strong association that we found between ATE9-1, the Sangiran specimens, and the large mandible from Dmanisi, the main con-clusions of Carbonell and associates can be seriously challenged.

KEY WORDS_Early Homo; Atapuerca; Dmanisi

RESUMO

Recentemente uma equipe internacional reportou a descoberta dos remanescentes ósseos humanos mais antigos já encontra-dos na Europa. Um fragmento de mandíbu-la e um dente isolado foram encontrados no nível TE9C de Sima del Elefante, Atapuerca, Espanha, associados à uma típica indústria Olduvaiense. No estudo, os autores afirmam que o homíneo TE9-1 pode ser classifica-do como *Homo antecessor*, sendo resultado de um evento de especiação local ocorrida durante o início do Pleistoceno. Aqui nós apresentamos uma análise multivariada aplicada às quatro dimensões da mandíbu-la, comparando o homíneo TE9-1 com outros homíneos fósseis. Considerando a forte associação que encontramos entre ATE9-1, os espécimes de Sangiran, e a gran-de mandíbula de Dmanisi, as principais afirmações de Carbonell e associados po-dem ser seriamente questionadas.

PALAVRAS-CHAVE_Primeiros-Homo; Atapuerca; Dmanisi

INTRODUCTION

Carbonell et al. (Carbonell et al., 2008) have reported the oldest hominin skeletal remains ever found in Europe. Accordingly, a fragment of mandible and an isolated tooth (LP4) of one same individual were found in TE9C level of Sima del Elefante, Atapuerca, Spain. TE9 is estimated to be dated between 1.2-1.1 Myr. The skeletal remains were found in association with a typical Mode 1 (or, its equivalent, Oldowan) lithic technology. This new material suggests that the first settlement of Western Europe could be related to an early demographic expansion out of Africa.

In accordance with the original study, the TE9-1 hominin is very similar to the one found by the same team in the Grand Dolina TD6 level some years ago. Both can be assigned to *Homo antecessor* and are interpreted as the result of a local speciation event that occurred during the Early Pleistocene. Carbonell and collaborators (Carbonell et al., 2005, 2008) based their diagnosis on metric and non-metric mandibular traits but with no formal quantitative treatment of the former.

Here we present a multivariate analysis applied to data presented in Table I in Carbonell et al. (2008), where four dimensions of the mandibular corpus, including the symphyseal region, are provided (thickness of the corpus at the M1 level and symphisis level and height of the corpus at the P3-P4 level and symphisis level). Our aim is to assess the morphological affinities of the Sima del Elefante specimen compared with other key Early *Homo* fossils using multivariate techniques as quantitative treatment.

MATERIAL & METHODS

To assess the morphological affinities of the specimens included in this study, we performed a Principal Components Analysis (PCA) based on a covariance matrix obtained from the original metric data provided by Carbonell and collaborators (Carbonell et al., 2008). First, all hominins listed in their Table I, with exception of Sangiran 6, were included in the analysis. Sangiran 6 was removed from the data bank because of its extreme values.

The final dataset was composed of 17 specimens, presenting 11.76

Specimen	Taxonomic classification	Thickness		Height	
		M₁	Symphysis	P₃-P₄	Symphysis
ATE9-1	*Homo antecessor* [a]	17.000	15.300	30.000	33.500
ATD6-96	*Homo antecessor* [b]	16.600	**17.962**	28.500	**35.554**
D211	*Homo ergaster* [c]	18.100	16.500	26.000	31.000
D2735	*Homo ergaster* [d]	19.300	16.000	24.600	32.000
D2600	*Homo georgicus* [e]	21.600	21.000	42.400	49.000
Sangiran 9	*Homo erectus* [f]	21.200	18.000	38.200	42.000
Sangiran 22	*Homo erectus* [f]	17.300	16.100	31.100	36.000
Sangiran 1B	*Homo erectus* [f]	16.300	**17.962**	35.700	**35.554**
KNM-ER 1802	*Homo habilis* [g]	23.000	21.300	35.800	36.200
UR 501	*Homo rudolfensis* [h]	21.300	16.800	34.100	34.000
OH 13	*Homo habilis* [i]	18.000	**17.962**	26.000	**35.554**
OH 22	*Homo habilis* [j]	19.400	18.900	29.000	30.700
KNM-ER 730	*Homo ergaster* [k]	19.000	17.600	31.300	31.000
KNM-ER 992	*Homo ergaster* [l]	20.200	**17.962**	31.000	**35.554**
Tighenif 1	*Homo erectus* [m]	19.000	18.800	36.200	36.000
Tighenif 2	*Homo erectus* [m]	16.900	18.000	33.400	33.300
Tighenif 3	*Homo erectus* [m]	19.000	19.200	38.400	37.500

TABLE 1 – *Variables and values used to perform the Principal Components Analysis [Bold values are grand means used to replace missing values; all measurements were made in millimeters; references used for taxonomic classification: a Carbonell et al. (2008); b Carbonell et al. (2005); c Gabunia et al. (2000); d Vekua et al. (2002); e Gabunia et al. (2002); f Mayr (1950); g Schwartz & Tattersall (2003); h Ramírez-Rozzi et al. (1997); i Wood (1992); j Curnoe & Tobias (2006); k Rosas & Bermúdez de Castro (1998); l Groves & Mazak (1975); m Rightmire (1990)].*

Specimen	Thickness		Height	
	M₁	Symphysis	M₁	Symphysis
ATE9-1	0.75183	0.67665	1.32677	1.48156
ATD6-96	0.81715	0.74492	1.17381	1.39955
D211	0.86919	0.72058	1.10788	1.44115
D2735	0.69326	0.67400	1.36084	1.57267
D2600	0.75789	0.64349	1.36563	1.50148
Sangiran 9	0.73209	0.68131	1.31606	1.52342
Sangiran 22	0.81480	0.75458	1.26826	1.28243
Sangiran 1B	0.83926	0.66196	1.34361	1.33967
KNM-ER 1802	0.81162	0.79070	1.21324	1.28436
UR 501	0.79609	0.73743	1.31145	1.29888
OH 13	0.72740	0.71974	1.38589	1.37823
OH 22	0.70073	0.74634	1.38487	1.38072
KNM-ER 730	0.70575	0.71318	1.42635	1.39292
KNM-ER 992	0.75183	0.67665	1.32677	1.48156
Tighenif 1	0.81715	0.74492	1.17381	1.39955
Tighenif 2	0.86919	0.72058	1.10788	1.44115
Tighenif 3	0.69326	0.67400	1.36084	1.57267

TABLE 2 – *Size corrected values used to perform the Principal Components Analysis.*

% of missing values. Taking into account that PCA requires that all variables are present in every individual or series (Gower, 1966), missing values were replaced by the grand mean of all specimens. Since this strategy can potentially artificially decrease the amount of inter-specimen variation, we performed a second run, including only specimens with no missing values (13 specimens).

Principal Component	Eigenvalue	% Total	Cumulative	% Cumulative
1	0.012995	54.57071	0.012995	54.5707
2	0.008767	36.81496	0.021762	91.3857
3	0.002047	8.59488	0.023809	99.9805
4	0.000005	0.01945	0.023814	100.0000

TABLE 3 – *Eigenvalues and original variation retained by the four Principal Components extracted from a covariance matrix.*

Variables		PC 1	PC 2
Thickness	M1	**-0.815993**	0.293143
	Symphysis	-0.524624	0.240457
Height	P3-P4	**0.954718**	0.291531
	Symphysis	0.248605	**-0.967453**

TABLE 4 – *Correlations between the first two Principal Components and the original variables. The values in bold represent the highest correlations for each PC (r > 0.75 or r < -0.75).*

In both cases, size effect was removed from the data using the strategy recommended by Darroch & Mosemman (1985). In other words, only shape was considered in the analyses. Table 1 presents the data bank used to perform the analyses and the taxonomic classification classically attributed to each specimen. Table 2 shows the size corrected data.

PCA was our choice due to its operational simplicity. PCA is widely used in Physical Anthropology to assess biological affinities between the specimens or populations (for an example see Spoor et al., 2010). Two different, but complementary strategies were adopted to infer the biological affinities between the specimens investigated in this study: a bidimensional scatter plot based on the scores of the first two PCs, and a Cluster Analysis, based on the scores of the first three PCs. The Cluster Analysis was based on Euclidean Distances. Single Linkage was the algorithm adopted.

RESULTS

Table 3 presents the main characteristics of the principal components extracted when all specimens were used. As can be seen, the first two PCs retained approximately 91% of the original information expressed by the four initial variables. Table 4 presents the correlations between the original variables and the PCs extracted. These correlations allow interpreting the meaning of the first two PCs as follows: high positive values of PC1 are associated with high mandibular corpus at

| Specimen	PC 1	PC 2	PC 3	PC 4
ATE9-1	0.46478	-0.54606	0.78286	-1.21956
ATD6-96	-0.30475	-1.25732	-1.57340	-0.67547
D211	-1.19102	-0.05689	-0.02020	-0.71258
D2735	-1.77248	-0.61790	1.01555	1.81168
D2600	1.10047	-1.44560	0.27138	0.83433
Sangiran 9	0.82620	-0.63444	1.56991	0.21595
Sangiran 22	0.52061	-1.02904	0.47612	-0.97194
Sangiran 1B	1.55293	0.14881	-1.09830	1.90522
KNM-ER 1802	-0.68214	1.42767	-0.17007	-0.03801
UR 501	0.05033	1.06599	2.04143	0.74054
OH 13	-1.31625	-1.52920	-1.01926	0.45314
OH 22	-1.14429	1.25424	-0.96805	0.73284
KNM-ER 730	-0.22858	1.35751	0.00426	-0.62881
KNM-ER 992	-0.61719	-0.05745	0.48769	-1.59137
Tighenif 1	0.75564	0.67548	-0.30974	-0.79447
Tighenif 2	0.80690	0.62477	-1.12723	-0.24985
Tighenif 3	1.17884	0.61944	-0.36295	0.18837

TABLE 5 – *Principal Components scores for each specimen.*
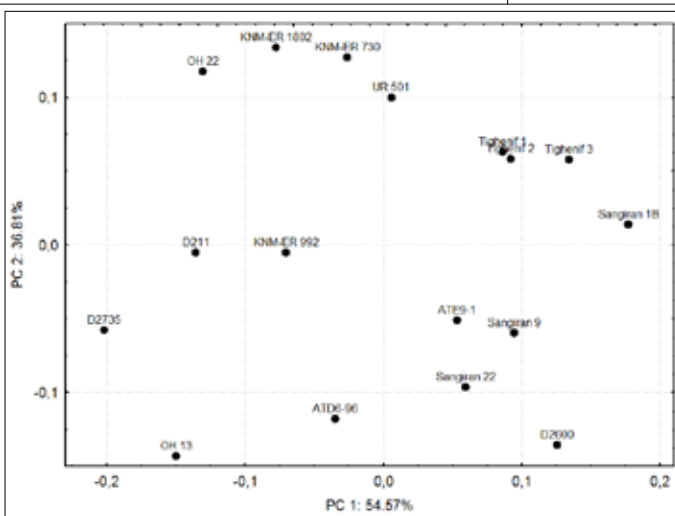
FIGURE 1 – *Morphological affinities between specimens as defined by the first two principal components*

As can be seen in Figure 1, ATE9-1 is located near Sangiran 9 and Sangiran 22, in the lower right quadrant of the graph. The same area of the morphospace is also occupied by D2600. The right upper quadrant is primarily occupied by the three specimens from Tighenif, which show very close relationships between themselves. UR501 is located in the transition zone between this quadrant and the left upper one, while Sangiran 1B is located in the transition area of the right lower quadrant. The left upper quadrant is occupied by OH22, KNM-ER 1802, and KNM-ER 730, which seem to form a cluster with UR501, all African specimens. The left lower quadrant is occupied by two specimens from Dmanisi (D211 and D2735), two specimens from Africa (KNM-ER 992 and OH 13) and one specimen from Grand Dolina (ATD6-96). The latter is displaced towards the right lower quadrant, where the other specimen from Atapuerca (ATE9-1) is located. The dendrogram presented in Figure 2 is difficult to interpret. In general it confirms the pattern of association generated by the scatter plot based on the scores of the first two PCs.

Some associations generated by the Principal Components Analysis applied to all specimens provided by Carbonell et al. (Carbonell et al., 2008) deserve special attention: (1) ATE9-1 and to a certain extent ATD6-96 present strong biological affinities with the Sangiran hominins; (2) The Georgian fossil hominins are clearly divided in two very distant groups: one formed by
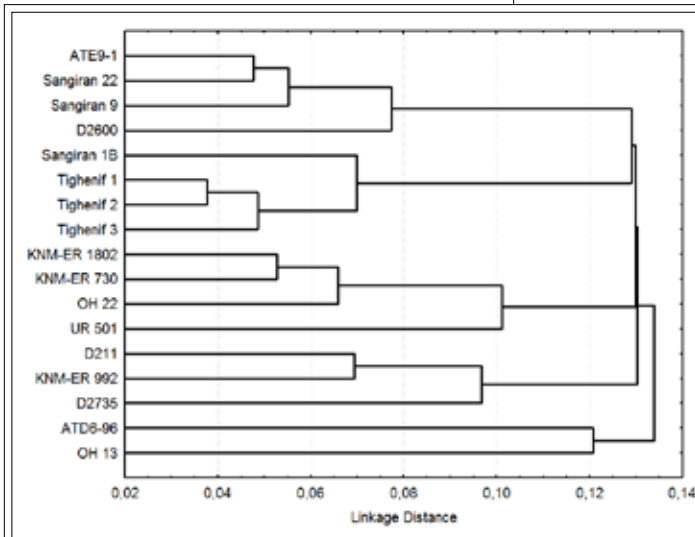
P3-P4 level, and vice-versa. High positive values of the same PC are associated with thin mandibular corpus at M1 level, and vice-versa. On the other hand, high positive values for PC2 are associated with low mandibular symphysis, and vice-versa.

Table 5 presents the principal components score for each specimen. These scores were used to generate the bidimensional scatter plot presented in Figure 1.

FIGURE 2 – *Morphological affinities between specimens derived from Cluster Analysis (Single Linkage) based on Euclidian Distances Matrix calculated over the three first principal components' scores.*

Principal Component	Eigenvalue	% Total	Cumulative	% Cumulative
1	0.013540	60.34366	0.013540	60.3437
2	0.007459	33.24385	0.021000	93.5875
3	0.001436	6.39954	0.022436	99.9871
4	0.000003	0.01295	0.022439	100.0000

TABLE 6 – *Eigenvalues and original variation retained by the four Principal Components extracted from a covariance matrix.*
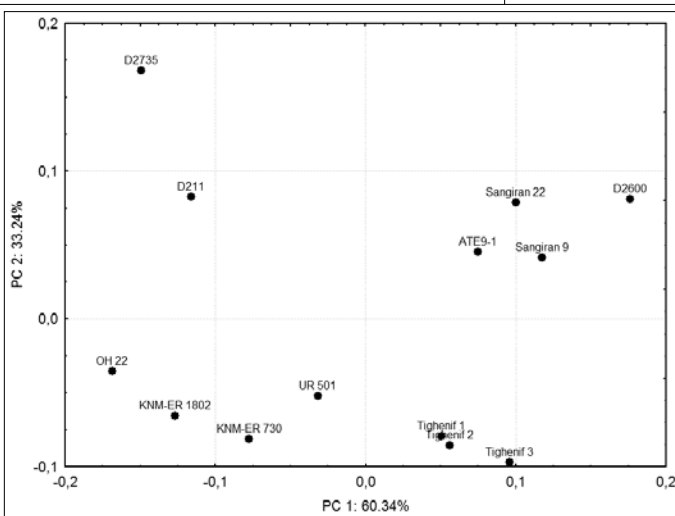

FIGURE 3 – *Morphological affinities between specimens as defined by the first two principal components*

D211 and D2735, and another formed exclusively by D2600; (3) Only part of the African hominins forms a tight cluster, with

KNM-ER 992 but mainly OH-13 placed located very far from this African cluster; and (4) The Tighenif specimens form the tightest cluster in the experiment. It is important to emphasize, however, that these patterns of association have to be evaluated very carefully, because almost 12% of missing values had to be replaced by the grand mean prior to the multivariate treatment.

Table 6 presents the main characteristics of the principal components generated when only complete specimens were used. The first two PCs retained approximately 93% of the information contained in the four initial variables.

Table 7 presents the correlations between the original variables and the PCs extracted. These correlations allow interpreting the meaning of the first PC as follows: high positive values of PC1 are associated with high mandibular corpus at P3-P4 level, and vice-versa, while high positive values are strongly associated with thin mandibular corpus at M1 level, and vice-versa. Table 8 presents the principal components score for each specimen. These scores were used to generate the bidimensional graph presented in Figure 3. The scores of the three first PCs were also submitted to a Cluster Analysis based on Euclidian Distances joined by Single Linkage criteria (Figure 4).
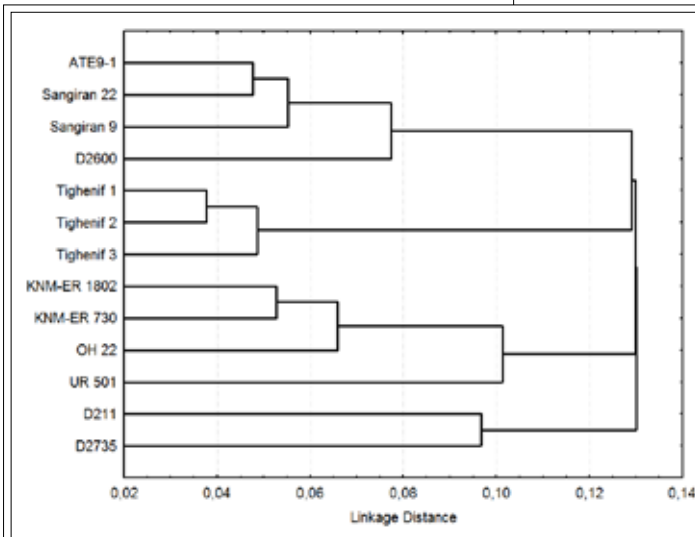
FIGURE 4 – *Morphological affinities between specimens derived from Cluster Analysis (Single Linkage) based on Euclidian Distances Matrix calculated over the three first principal components' scores.*

Variables		PC 1	PC 2
Thickness	M1	**-0.863499**	0.258084
	Symphysis	-0.707298	-0.328216
Height	P3-P4	**0.797749**	-0.594448
	Symphysis	0.734150	0.677825

TABLE 7 – *Correlations between the first two Principal Components and the original variables. The values in bold represent the highest correlations for each PC (r > 0.75 or r < -0.75).*

firms the pattern of association generated by the scatter plot based on the scores of the first two PCs.

Some associations generated by the Principal Components Analysis applied to the complete specimens deserve special comments vis-à-vis the previous analysis: (1) ATE9-1 presents again strong biological affinities with the Sangiran early *Homo* and now also with one of the Dmanisi hominins (D2600); (2) The Georgian fossil hominins are clearly divided in two very distant groups: one formed by D211 and D2735 (the small ones), and another formed exclusively by D2600 (the large one); (4) All African hominins form now a well defined cluster and; (5) The Tighenif specimens continue to form the tightest cluster.

DISCUSSION & CONCLUSIONS

To the extent that a phenetic approach applied to a mandible fragment can reveal

As can be seen in Figure 3, four clearly separate groups were formed in the bidimensional morphospace. With few exceptions, they present a strong geographical logic. ATE9-1 is located near Sangiran 9, Sangiran 22, and D2600 in the upper right quadrant of the graph. The right lower quadrant is primarily occupied by the three specimens from Tighenif, which, again, show very close relationships between themselves. The left lower quadrant is occupied only by African fossil hominins, while the left upper quadrant is occupied by the two small hominins from Georgia. The dendrogram presented in Figure 4 fully con-

Specimen	PC 1	PC 2	PC 3	PC 4
ATE9-1	0.64324	0.52475	0.28302	1.54969
D211	-0.99766	0.95481	-0.63506	1.35198
D2735	-1.28212	1.94349	0.18718	-1.29210
D2600	1.51228	0.93732	-0.69732	-1.37625
Sangiran 9	1.00757	0.48254	1.20624	-0.20341
Sangiran 22	0.85965	0.91156	-0.32327	1.16768
KNM-ER 1802	-1.09112	-0.75957	0.05743	0.15269
UR 501	-0.27376	-0.60446	2.54772	-0.53939
OH 22	-1.44956	-0.41237	-1.03186	-0.82373
KNM-ER 730	-0.66558	-0.94261	0.28957	0.76145
Tighenif 1	0.43410	-0.91912	-0.29458	0.53060
Tighenif 2	0.47989	-0.99354	-1.26554	-0.38476
Tighenif 3	0.82308	-1.12279	-0.32350	-0.89443

TABLE 8 – *Principal Components scores for each specimen.*

something about phylogeny, the results generated by our comparative multivariate analyses applied to the mandible shape of the ATE9-1 are not consistent with the main conclusions of Carbonell et al. (Carbonell et al., 2008). Considering the close (and stable) associations between ATE9-1, the Sangiran specimens, and the large mandible from Dmanisi, the assignation of the early hominins from Atapuerca to a new species (*Homo antecessor*) can be seriously challenged. If they were the result of a local speciation event as advocated by Carbonell and associates, we would expect to find ATE9-1 and ATD6-96 forming their own cluster clearly separated from the other clusters. Notably, this is not seen in Figures 3 and 4 where only the complete specimens are included.

Our conclusion is only partially supported by the descriptive anatomy of ATD9-1. In accordance with Carbonell et al. (Carbonell et al., 2008), the specimen shows the primitive condition for the genus *Homo* regarding the presence and position of the anterior marginal tubercle. On the other hand, the fossil presents a derived condition regarding the posterior surface of the symphyseal region.

Although the primary aim of this study was to assess the mandibular shape of ATE9-1 in a comparative perspective, some results obtained by us may also be of significance for other current discussions about the origins and diversification of our genus. One of the most striking results obtained by us is that the three specimens from Dmanisi resolved in two well defined and distant positions in the morphospace. While the small specimens (D211 and D2735) occupy one extreme of the graphic, the large specimen (D2600) occupies the opposite position. In fact, the three Georgian specimens constitute the most variable regional sample of Early *Homo* included in this study. Accordingly, we suggest that the small and the large mandibles found in Dmanisi represent different species, if not different genus. Sexual dimorphism can hardly explain such a high degree of variation.

As to the origins of the first Western Europeans, our results point to Asia or to The Caucasus region as possible points of departure, and not Africa, as proposed by Carbonell et al. (Carbonell et al., 2008). This conclusion rests on the fact that in both, Figures 3 and 4, ATE9-1 is clearly associated with Sangiran, from Java, and to the large mandible from Dmanisi.

ACKNOWLEDGMENTS

REFERENCES

CARBONELL, E., BERMÚDEZ DE CASTRO, J. M., PARES, J. M., PÉREZ-GONZÁLEZ, A., CUENCA-BESCÓS, G., OLLÉ, A., MOSQUERA, M., HUGUET, R., VAN DER MADE, J., ROSAS, A., SALA, R., VALLVERDÚ, J., GARCÍA, N., GRANGER, D. E., MARTINÓN-TORRES, M., RODRÍGUEZ, X. P., STOCK, G. M., VERGÈS, J. M., ALLUÉ, E., BURJACHS, F., CÁCERES, I., CANALS, A., BENITO, A., DÍEZ, C., LOZANO, M., MATEOS, A., NAVAZO, M., RODRÍGUEZ, J., ROSELL, J. & ARSUAGA, J. L. 2008 The first hominin of Europe. Nature, London, 452:465-469.

CARBONELL, E., BERMÚDEZ DE CASTRO, J. M., ARSUAGA, J. L., ALLUÉ, E., BASTIR, M., BENITO, A., CÁCERES, I., CANALS, A., DÍEZ, C., VAN DER MADE, J., MOSQUERA, M., OLLÉ, A., PÉREZ-GONZÁLEZ, A., RODRÍGUEZ, X. P., ROSAS, A., ROSELL, J., SALA, R., VALLVERDÚ, J. & VERGÈS, J. M. 2005 An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. Proceedings of the National Academy of Sciences, Washington, 102(16):5674-5678.

CURNOE, D. & TOBIAS, P. V. 2006 Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of the other southern African early *Homo* remains. Journal of Human Evolution, Maryland Heights, 50:36-77.

DARROCH, J. N. & MOSIMANN, J. E. 1985 Canonical and principal components of shape. Biometrika, Oxford, 72:241-252.

GABUNIA, L. K., VEKUA ABESALOM, K., LORDKIPANIDZE, D., SWISHER III, C. C., FERRING, R., JUSTUS, A., NIORADZE, M., TVALCRELIDZE, M., ANTON, S., BOSINSKI, G. C., JÖRIS, O., DE LUMLEY, M. A., MAJUSURADZE, G. & MOUSKHELISHVILI, A. 2000 Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting and age. Science, Washington, 288:1019-1025.

GABUNIA, L., DE LUMLEY, M. A., VEKUA, A., LORDKIPANIDZE, D. & DE LUMLEY, H. 2002 Découvert d'un nouvel hominidé à Dmanisi (Transcaucasie, Géorgie). C. R. Palevol., Issy-les-Moulineaux, 1:243-253.

GOWER, J. C. 1966 Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika. Oxford, 53:325-338.

GROVES, C. & MAZAK, V. 1975 An approach to the taxonomy of the Hominidae: Gracile Villafranchian hominids of Africa. Cas. Miner. Geol., Prague, 20:225-247.

MAYR, E. 1950. Taxonomic categories in fossil hominids. Cold Spring Harbor Symp. Quant. Biol., Cold Spring Harbor, 15:109-118.

RAMIREZ-ROZZI, F. V., BROMAGE, T. & SCHRENK, F. 1997 UR 501, the Plio-Pleistocene hominid from Malawi. Analysis of the microanatomy of the enamel. C. R. Acad. Sci. Paris., Paris, 325:231-234.

RIGHTMIRE, P. 1990 The Evolution of *Homo erectus*. Cambridge, Cambridge University Press.

ROSAS, A. & BERMÚDEZ-DE-CASTRO, J. N. 1998. On the taxonomic affinities of the Dmanisi Mandible (Georgia). American Journal of Physical Anthropology, Lawrence, 107:145-162.

SCHWARTZ, J. H. & TATTERSALL, I. 2003 The human fossil record. Hoboken, Willey-Liss.

SPOOR, F., LEAKEY, M.G. & LEAKEY, L. N. 2010 Hominin diversity in the Middle Pliocene of eastern Africa: The maxilla of KNM-WT 40000. Philosophical Transactions of the Royal Society, London, 365:3377-3388.

VEKUA, A., LORDKIPANIDZE, D., RIGHTMIRE, G. P., AGUSTI, J., FERRING, R., MAISURADZE, G., MOUSKHELISHVILI, A., NIORADZE, M., DE LEON, M. P., TAPPEN, M., TVALCHRELIDZE, M. & ZOLLIKOFER, C. 2002 A new skull of early *Homo* from Dmanisi, Georgia. Science, Washington, 297:85-89.

WOOD, B. 1992 Origin and evolution of the genus *Homo*. Nature, London, 355:783-790.