

The Relationship of Pleistocene and Modern Mandibles Evaluated by Principal Component Analysis of the Arcade Dimensions

Les rapports des mandibules fossiles pléistocènes et subactuelles évalués par
analyse en composantes principales des dimensions de l' arcade

Helga Roth and Christian Simon *

Abstract

To understand the variation among 64 fossils mandibles usually organized in evolutionary groups such as *Homo erectus*, Neandertal or anatomically modern humans, a multivariate analysis of principal components was performed on twelve representative dimensions of their arcades. Eleven fossils of the Lower Pleistocene were also analyzed. The distribution of each group is characterised by an ellipse. The association of the groups are represented by dendrograms indicating the average distances between them. The principle results show a continuous evolution from the oldest Middle Pleistocene fossils to modern man. There are also some interesting superpositions : the Neandertals and anatomically modern humans, especially those of the early Wurm period in Palestine, greatly resemble each other. The arcades of the Lower Pleistocene hominids are distinguished from other populations by their narrow shape. This study clearly indicates a gradual development of the dimensions which combines different morphological types.

Résumé

La variabilité de 64 mandibules fossiles, réparties en groupes évolutifs (*Homo erectus*, Néandertalien, hominidés d'anatomie moderne...) est étudiée à l'aide d'une analyse en composantes principales qui concerne douze dimensions des arcades. Onze individus du Pléistocène inférieur sont également pris en considération. La disposition de chaque groupe est caractérisée par une ellipse équiprobable. Le classement des populations est représenté par des dendrogrammes qui montrent les distances moyennes entre elles. Les analyses mettent en évidence une évolution continue entre les fossiles les plus anciens du Pléistocène moyen et les hommes actuels, avec cependant une certaine superposition des groupes. Les Néandertaliens et les premiers hommes anatomiquement modernes (surtout les individus de Palestine) sont les plus semblables. Les fossiles du Pléistocène inférieur sont séparés des autres populations par l'étroitesse de leurs arcades. L'étude montre d'une façon évidente le développement graduel des dimensions qui regroupe différents types morphologiques.

Key words : mandibles, arcades, principal component analysis.

Mots clés : mandibules, arcades, analyse en composantes principales.

* Helga Roth, 10 Staaderstrasse, 7750 Konstanz, Germany

Christian Simon, Département d'Anthropologie et d'Ecologie, Université de Genève, Suisse

Introduction

Due to discovery of new human fossils, more exact dating methods and recent results of genetics, numerous articles have appeared which reattempt to define phylogenetic taxons. The relationship among the different fossil groups has also been shown using cladistic methods (ex. as in Andrews and Franzen, 1984, and Stringer, 1987). The concept of anteneandertalians or preneandertalians as members of *Homo erectus* provokes many controversies (Hublin, 1982; Lumley *et al.*, 1982; Stringer *et al.*, 1984; Vandermeersch 1986; Aguirre *et al.*, 1985, 1987, 1989; Rosas, 1987). According to Stringer (1985), European fossils can be divided into 2 groups ("Primitive *Sapiens* - Neandertal Model"), in which signs of continuity can be observed. In his cladistic analysis (1987) using statistic package PAUP he cannot clearly separate the Neandertals from the archaic *Homo sapiens* and the taxon Skhul-Qafzeh from modern man.

New results concerning the low genetic variation between modern human populations (Stringer *et al.*, 1988; Mellars and Stringer, 1989; Stringer, 1991) are presently being discussed postulating at least two models, the multiregional origin or the single recent origin of modern man in Africa or in bordering areas in the Middle East.

In this paper we attempt to describe the relationship among the fossils using variations of the arcade dimensions.

Definition of measurements and analysed material

The mandible is adjusted horizontally according to the alveolar Klaatsch's plan and is checked against the reticle of the measuring system. The method used to determine the measuring points in the form of Cartesian coordinates is described in detail in Roth (1985, 1988). The schema in figure 1 presents the seven lengths and seven widths which make up the coordinates of 14 key points of the arcade. They are defined as intersections of the distal and vestibular tangents to the alveolar border.

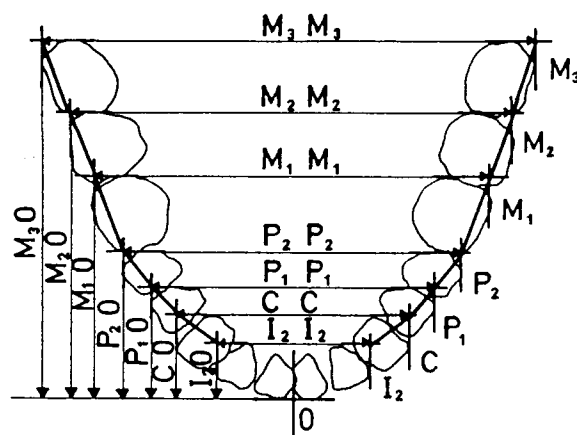


Fig. 1 Definition of lengths and widths.

The analyzed specimens belong to adult or adolescent individuals maintaining intact arcades and a maximum of measuring points. The results of Atapuerca 1 are obtained from the original. They are organized in five groups of different geological ages providing evidence for nearly one million years of human evolution on the continents (Table 1).

The multivariate analysis of principal components examines the following four populations :

- *Homo erectus* (HER) with African and Asian fossils (PAS) and the European representatives (AN);
- *Homo sapiens neanderthalensis* (HSN);
- a population (HSSF) referring to early anatomically modern hominids in the Middle East (HS PAL) and to the Upper Palaeolithic period;
- a population (HSSR) of European mandibles (from 4150 BP to the present).

A second analysis evaluates the position of older hominids which have been added to the fossils of the preceding analysis. This population is composed of eleven individuals of the Lower Pleistocene (LP), belonging to different species including *Homo habilis*, *Australopithecus afarensis*, *affricanus* and *boisei*. Since there are so few of them their arcades were grouped together for the purpose of statistical comparison.

Table 1 List of measured mandibles

GROUPS	CODE	INDIVIDUALS
Population of the Lower Pleistocene (LP) :		
<i>A. afarensis</i>	L 4	Laetoli H 4
	A 40	AL 400-1
	A 26	AL 266-1
	A 28	AL 288-1
<i>A. africanus</i>	M 18	MLD 18
	S 52 (1)	STS 52B
<i>H. habilis</i>	O 7 (2)	Olduvai H 7
	O 13	Olduvai H13
	E 02	KNM-ER 1802
<i>A. boisei</i>	O RO	Omo L7A-125
	NA	Lake Natron
(1) Reconstruction of Schmidt		
(2) Reconstruction of Andrews		
Middle and earlier Pleistocene Hominids (HER) :		
Afro-asiatic		
<i>H. erectus (PAS) :</i>		
	AT 1	Ternifine 1
	AT 3	Ternifine 3
	ZG (1)	Zhoukoudian G1
	ZH	Zhoukoudian H
	RA 1	Rabat 1
	TE 1	Temara 1
European representatives (AN) :		
	M	Mauer
	AR 2	Arago 2
	AR D (2)	Arago 13
	AP 1	Atapuerca 1
	MT	Montmaurin
	E 6	Ehringsdorf 6
	B	Banolas
(1) Reconstruction of Weidenreich		
(2) Reconstruction of de Lumely		
<i>H. s. neanderthalensis (HSN) :</i>		
	AC 1	Arcy 1
	AC 2	Arcy 21
	MA 1	Malarnaud 1
	RE	Regourdou
	K G	Krapina G
	K H	Krapina H/58
	O 1	Ochoz 1
	MC 3	Mte Cicero 3
	A 1	Amud 1
	T 1	Tabun 1
	MO	Moustier
	SU 1	Subalyuk 1
	S 1	Spy 1
	HO 4	Hortus

*H. s. sapiens (HSSF) :**H. s. sapiens*

from Palestine (HS PAL) :

Q 9	Qafzeh 9
T 2	Tabun C2
SK 5	Skhul

H. s. sapiens

of Upper Palaeolithic :

CC	Combe Capelle 1
CM 3	Cro Magnon 3
PI	Pinar
PA	Pavlov 1
PR	Predmosti 3
W 2	Wadjak 2
Z UC	Zhoukoudian UC 1
LM 3	Lake Mungo 3
KS 5	Kow Swamp 5
CH 1	Chancelade 1
K 14	Kostenki 14
G 4	Gambles Cave 4
H 2	Hotu Cave 2

Modern western European sample (HSSR) :

14 Specimens of the Laboratoire
d'Anthropologie of Marseille
and the Institut d'Anthropologie
of Geneva

Results and discussion

1. Results and discussion of dimensions

The measuring results of lengths and widths of 64 individuals and the mean values and standard deviations of eight populations are presented in tables 2a, 2b and table 3. The eight groups are *A. afarensis*, *A. boisei*, *H. erectus* of Africa and Asia (PAS) and the European representatives (AN), Neandertalians (HSN), three modern humans of Palestine (HS PAL), Cro-Magnon group (HSSF) and modern Europeans (HSSR). These values have been used to construct the arcs of the groups and individuals. Some of them are presented in figures 2a, 2b, 2c, 2d in order to support the interpretation of the statistical results.

The results of table 3 immediately display the well-known evolutionary tendency

for all dimensions to become more gracile. Generally the lengths are more affected by this phenomenon. These changes are allometric as can be seen in the extremely wide Neandertalian arcades or in the great length of the Palestine specimens.

In order to evaluate the individuals of sometimes very different dimensions, the results are examined with the help of the principal component analysis, which partially eliminates the effect of size as well as the strong correlation inherent in the totality of the figures.

Twelve of the best preserved dimensions, six lengths and six widths, dealing with the distances of the lateral incisor to the 2nd molars (see diagram fig. 1 and the values tables 2a, 2b) were studied with this multivariate technique.

As is often the case in human paleontology, due to the limited amount of usable

Table 2a Measured results of lengths
of the individuals (mm)

Table 2b Measured results of widths
of the individuals (mm)

	I2 O D 1	CO D2	PI O D3	P2 O D4	M1 O D5	M2 O D6	I2 I2 D8	CC D9	PI PI D10	P2 P2 D11	M1 M1 D12	M2 M2 D13
L4	8,90	12,20	19,35	28,65	39,40	53,45	21,68	36,35	44,85	49,95	56,10	61,50
A 40	9,10	13,30	20,25	29,00	40,65	56,60	21,30	35,35	44,05	49,10	53,05	59,80
A 26	7,27	12,35	17,64	27,42	39,85	53,90	18,00	32,45	43,05	49,20	56,60	63,00
A 28	8,20	11,95	17,85	25,35	35,86	49,20	18,00	28,85	36,20	41,90	47,97	54,40
M 18	8,50	11,80	19,15	27,30	38,75	51,93	20,20	35,05	45,60	52,04	62,80	72,00
S 52	9,73	13,10	21,08	30,00	42,26	57,52	20,40	31,70	40,90	46,80	57,90	67,68
O7	10,00	15,00	24,10	35,40	48,10	65,00	23,30	39,95	46,85	51,00	56,60	58,60
O 13	7,75	10,70	18,10	26,80	39,10	52,40	18,20	30,70	40,20	46,70	52,80	57,60
E 02	9,30	12,20	19,15	29,12	42,85	59,65	21,80	33,90	44,90	51,10	59,10	63,30
ORO	7,85	10,60	18,70	30,53	43,05	58,55	18,55	29,85	44,00	54,90	65,00	72,15
NA	8,45	10,55	19,10	31,70	45,50	61,87	19,80	32,75	44,95	53,90	69,15	75,80
AT 1	10,70	15,20	21,80	29,30	41,80	55,60	21,40	36,90	47,80	56,70	67,00	74,20
AT 3	11,00	16,33	25,07	32,85	44,20	56,48	26,05	41,03	49,00	57,80	66,35	73,93
ZG	10,00	14,70	20,40	29,15	40,60	53,30	23,30	36,90	46,50	55,00	64,90	71,10
ZH	8,80	12,10	17,80	24,20	35,00	44,45	18,80	32,03	41,85	49,00	56,70	59,30
RA 1	8,95	11,68	16,95	25,97	37,50	49,85	21,97	35,10	45,05	51,70	60,90	67,00
TE 1	9,35	13,40	20,00	27,80	39,55	53,05	21,85	36,20	45,05	53,95	62,25	67,85
M	7,68	11,15	16,07	22,37	33,70	46,00	21,10	34,03	45,00	53,70	59,80	65,40
AR 2	7,90	12,51	17,30	22,79	32,65	44,53	23,03	37,70	46,25	54,50	64,00	70,00
ARD	9,70	14,00	20,70	29,30	41,50	56,00	25,00	40,05	49,50	59,00	67,95	71,10
AP 1	6,40	9,80	15,20	20,90	30,90	41,00	20,50	35,40	46,10	54,00	63,80	68,60
MT	6,60	10,35	16,05	23,15	34,60	46,00	22,00	34,40	44,05	52,00	58,30	64,30
E 6	9,00	13,80	19,75	27,05	38,55	49,98	24,03	38,63	46,40	51,40	58,00	64,20
B	7,40	11,35	17,60	23,80	35,65	46,45	21,15	32,00	42,00	52,00	61,15	66,60
AC 1	6,80	9,65	12,10	20,60	30,70	42,60	18,20	31,20	42,00	50,00	61,00	66,20
AC 2	10,00	13,40	18,70	27,10	37,50	49,10	27,37	40,00	49,00	58,05	66,10	73,80
MA 1	6,87	8,95	13,61	20,70	32,20	45,20	15,95	31,80	43,10	51,00	62,40	69,00
RE	8,05	11,90	15,20	21,00	29,90	40,30	19,05	33,45	43,15	48,95	59,70	66,00
KG	5,30	8,45	12,00	19,55	28,20	40,60	19,75	33,50	42,77	49,97	61,80	67,90
KH	9,40	13,20	17,35	23,75	34,50	45,60	22,10	35,40	47,10	53,20	60,20	65,80
O 1	9,30	11,80	17,05	23,80	33,50	45,70	32,10	37,70	48,00	54,40	62,80	68,30
MC 3	7,30	11,82	15,22	20,52	30,55	41,85	20,10	34,95	45,10	52,65	61,80	70,10
A 1	7,40	10,70	14,60	19,80	28,45	38,30	18,90	33,25	44,00	52,85	63,10	72,50
T 1	8,80	11,80	16,50	21,50	30,30	41,20	23,80	36,50	45,40	52,60	62,00	66,80
MO	7,30	10,60	17,05	24,50	35,85	48,30	22,50	35,80	46,90	54,40	59,90	64,90
SU 1	8,00	11,87	15,67	21,67	30,97	43,02	22,10	36,00	47,00	56,60	60,20	64,00
S 1	8,60	11,70	14,60	20,60	29,95	39,85	20,80	34,10	44,60	52,70	63,50	68,80
HO 4	7,05	9,50	14,20	20,35	31,30	42,15	23,40	35,60	43,34	50,90	58,25	64,00
Q 9	8,65	11,47	16,10	23,55	34,87	47,15	21,05	37,80	45,90	52,32	61,15	63,80
T 2	8,20	11,00	15,70	23,65	33,60	44,50	23,40	36,50	44,50	51,30	60,30	65,30
SK 5	7,00	10,30	14,80	21,80	34,00	45,50	25,00	37,00	45,40	52,00	60,40	64,80
CC	8,35	10,85	14,10	19,30	30,10	41,25	19,70	34,30	39,90	45,90	53,90	59,20
CM 3	7,30	10,75	13,45	19,60	32,00	44,05	18,00	34,00	41,35	48,85	60,00	65,92
PI	7,95	10,75	14,95	20,05	29,35	40,35	17,60	31,00	39,70	46,40	56,20	62,80
PA	7,30	10,30	14,30	21,00	29,70	40,80	19,00	30,70	39,30	47,80	59,20	64,50
W 2	7,20	9,70	15,00	24,20	34,40	46,40	21,30	34,40	46,50	52,70	64,90	69,00
ZUC	6,90	9,30	13,30	19,20	28,50	38,90	18,20	33,00	41,20	48,00	61,00	68,00
K 14	5,10	8,20	12,00	17,50	27,80	38,00	20,00	32,20	41,30	49,40	58,90	64,00
G 4	7,20	9,00	13,75	19,70	29,82	40,45	19,10	32,05	41,10	47,90	56,20	60,30
H 2	6,40	8,80	13,50	19,55	28,55	38,15	19,80	32,20	39,70	46,90	54,70	61,00
P 1	7,50	9,60	13,70	19,40	28,60	38,55	18,20	31,85	38,30	45,50	54,85	57,90
P 3	6,90	7,70	12,10	17,70	26,40	36,50	16,10	32,20	38,20	44,30	54,00	59,90
P 6	6,00	8,40	11,20	17,90	28,40	38,60	18,90	31,30	39,50	45,10	53,60	60,90
AL	7,90	10,75	13,75	19,85	29,15	39,60	17,45	29,00	37,10	43,10	53,95	61,90
VE	7,55	9,07	13,02	19,80	30,50	41,90	18,45	32,77	39,52	46,40	56,15	62,25
FO	7,80	8,75	13,55	20,50	29,62	39,60	19,00	31,95	38,95	47,40	57,75	63,20
G 1	7,00	7,00	8,35	16,20	24,40	34,10	16,20	27,95	37,05	45,00	58,50	66,70
CN	8,05	8,05	8,82	18,00	27,70	37,93	17,40	31,75	40,50	46,70	56,50	63,95
FR	8,95	8,95	10,00	19,17	29,22	40,08	17,77	31,00	41,10	43,90	53,35	61,85
V 2	7,60	7,60	10,95	19,10	28,35	39,95	17,70	31,05	38,75	46,05	57,10	65,00
HA 1	9,40	9,40	11,60	21,50	31,70	41,20	17,50	28,30	38,50	46,50	55,20	62,00
HA 2	7,90	7,90	9,80	19,70	29,40	41,10	15,90	29,80	38,90	42,00	50,70	56,50
H 15	7,50	7,50	10,45	21,60	30,75	41,15	18,70	30,90	40,00	47,80	57,60	63,20
H 20	6,50	6,50	9,30	20,50	29,95	40,90	20,00	32,00	40,70	49,00	58,40	64,60

specimens, there is no guarantee of a perfectly normal distribution of data. However, since the results found are not extremely aberrant, it seems correct to use them as they are for the biostatistical method.

2. Results and discussion of the multivariant analysis with principal components

The main statistical results, the weight of the first two axes and the correlation of the variables are summarized in table 4. The weight (%) shows the importance of each axis for the explanation of the total variability. The correlation between the principal components and the variables indicates the role of dimensions as a discriminating factor. In analysis 1, which compares the groups of *Homo erectus* and *sapiens* (HER, HSN, HSSF, HSSR), axes 1 and 2 express 74.5 % respectively, 11.3 % of the total variation. In analysis 2, with the fossils of the Lower Pleistocene period (LP) and more recent forms, axes 1 and 2 explain 63.8 % and 18.4 %. The high result of the first two axes, which occurs rather seldom in anthropometry is due to the strong correlation of the output values and indicates the necessity of using the multivariant technique.

According to the correlation of the characteristics and axes generally, the lengths are more important for axis 1 and the widths for axis 2. In analysis 1, the different lengths of the jugal arcade and the canine (D2 to D6) together with the premolar widths (D10 and D11) have meaning for the first axis. For axis 2 the length of the incisors (D1) and the molar widths or maximal width (D12 and D13) make a notable contribution. This discriminating factor of the short distances between segments, compared to the total dimension of the arcade, suggests that the chosen points are coherent and structurally significant. In analysis 2 of the five populations, the variable D11 (the width of the second premolars) is important for axis 2 with the molar widths (D12 and D13).

The graphic evaluation of the analysis, i.e. the position of the individuals determined by the value of the principal components, is seen for

analysis 1 in figure 3. The result of analysis 2, which compares the older individuals (LP), is seen in figure 4. The distribution of the different populations is characterized by an equiprobable ellipse which corresponds to an intrapopulation-variability of 80%. The gravity center, the barycentre of each ellipse indicated in the

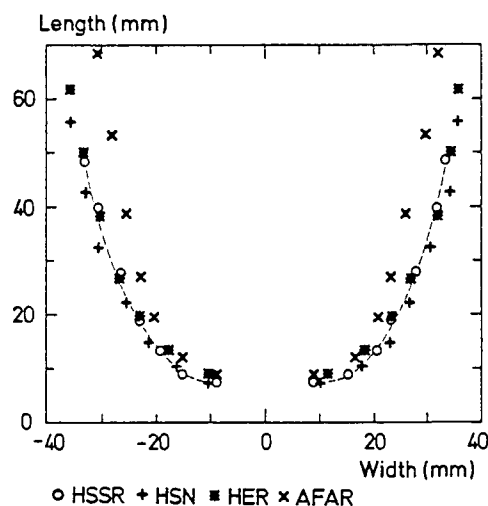


Fig. 2a "Mean arc" constructed by the mean values of table 3 characterizing a population of Afar, of Middle and Upper Pleistocene arcades (HER, HSN) and of modern Europeans (HSSR).

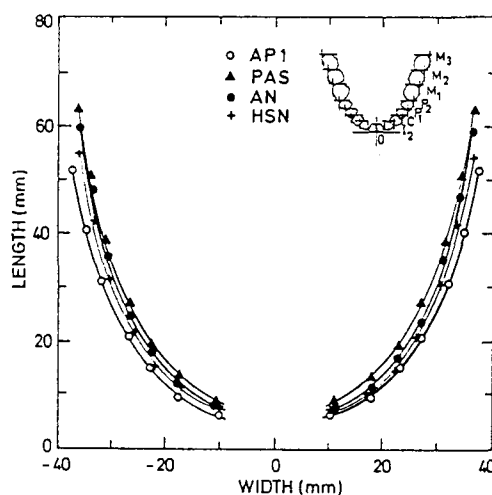


Fig. 2b Arcs of Middle Pleistocene humans (PAS), Anteneandertalians (AN), Neandertalians (HSN) and Atapuerca 1 (AP1).

diagram, is calculated by the mean values of the principal components in relation to the first two axes.

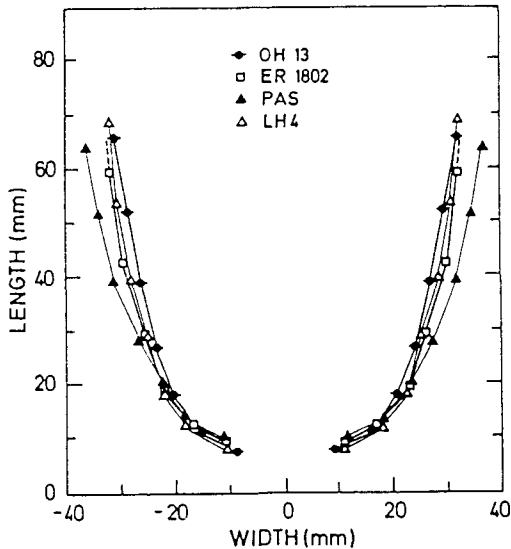


Fig. 2c Comparison of the arcs of Laetoli (L4), East Turkana (KNM-ER 1802), Olduvai (O 13) and PAS.

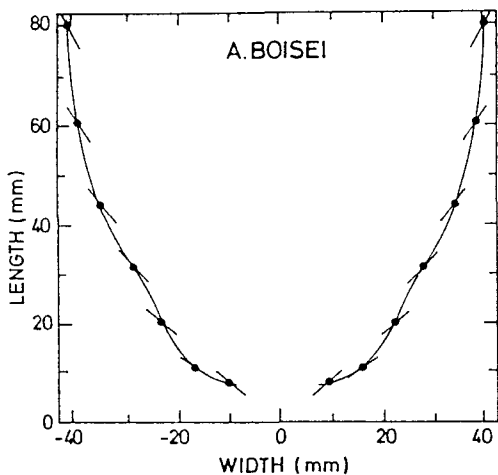


Fig. 2d Arc characterizing of *A. boisei*.

In the graphic of analysis 1 (fig. 3), the evaluation of the distribution for axis 1 shows that the long arcades with large dimensions of individuals of the Middle Pleistocene (HER) are

organized on the left in opposition to modern Europeans (HSSR). The Neandertals (HSN) and the first anatomically modern mandibles (HSSF) are placed between these two groups. The Neandertals are centralized in the lower part of the graph nearer the larger values for the dimensions of axis 2 (the molar widths, D12 and D13). The "Cro-Magnon" are further to the right of the Neandertals on axis 1 and connect modern Europeans with other populations. The population of HER is the most dispersed. The ellipse axis is about a 45° angle to axis 1 and indicates the presence of long-large arcades (Ternifine 1 and 3 -AT 1, AT 3-, Zhoukoudian G1 -Z G-, Arago 13 -AR D-, Ehringsdorf -E 6-) and also wide and small arcades (Arago 2 -AR 2-, Mauer -M-, Montmaurin -MT-, Atapuerca 1 -AP 1-). Both of these distributions constitute groupings corresponding more to differences of sex and less to geographical origins. This would confirm the observations of other authors such as Stringer (1987). The ellipses of HSN and HSSF superimpose each other and this area overlaps with the ellipse of the HER. In contrast to the HSSF the orientation of the HSN in the coordinate system is aligned with those of the HER. Their barycentre, however, is found, displaced to the right extremity of the HER. This indicates that these arcades are wider at the molars (dimensions D12 and D13) and shorter on the whole. Only Arcy 2 (AC 2) is found closer to the large HER.

The statistical analysis clearly shows that it is primarily the short arcades of the Middle Pleistocene (or with the weaker dimensions for axis 1), which align with the HSN. Except for Atapuerca 1, the majority of the HSN are wider (see also the drawings of figure 2b). The arcades of the modern Europeans (HSSR) are located to the right of the distribution according to axis 1 and above the graphic according to axis 2. They only overlap with the HSSF. They differentiate clearly from the HER *grosso modo*, because they are shorter. They are distinctly separate from the HSN, which are wider on the whole (see the population arcs figure 2a). The distribution of the HSSR itself is thus most variable for axis 2 under the influence of the width.

Table 3 Mean values (X) and standard deviation (SD) of lengths and widths for 8 groups (mm)

Remarks : for *A. afarensis*, the mean values refer to AL 400-1 and AL 288-1;
for *A. boisei*, they refer to OL7A-125, KNM-ER 729, NA; for HS PAL, they refer
to the Palestinian H.s.s.; for HSSF, they refer to the Upper Palaeolithic modern man.

GROUPS	<i>A. afar.</i> n = 2		<i>A. boisei</i> n = 3		PAS n = 6		AN n = 6	
LENGTHS	X	SD	X	SD	X	SD	X	SD
D1-I2O	8,65	0,64	8,15	0,42	9,40	1,35	7,81	1,20
D2-C O	12,63	0,95	11,08	0,87	13,59	1,86	11,85	1,64
D3-P1O	19,05	1,70	20,17	2,20	19,97	2,83	17,52	2,03
D4-P2O	27,18	2,58	31,75	1,25	27,70	3,05	24,19	2,93
D5-M1O	38,26	3,39	44,83	1,56	39,34	3,18	35,36	3,62
D6-M2O	52,90	5,23	61,41	2,80	51,71	4,17	47,21	4,72
D7-M3O	66,78	6,47	81,51	2,97	64,26	5,89	58,92	5,28

WIDTHS	X	SD	X	SD	X	SD	X	SD
D8-I2I2	19,65	2,33	19,18	0,88	21,73	2,58	22,40	1,68
D9-C C	32,10	4,60	33,00	3,28	35,75	3,12	36,03	2,86
D10-P1P1	40,13	5,55	45,98	2,66	45,33	2,71	45,61	2,32
D11-P2P2	45,50	5,09	56,87	4,30	53,31	3,52	53,80	2,58
D12-M1M1	50,51	3,59	69,65	4,92	62,36	3,95	61,86	3,60
D13-M2M2	57,10	3,82	78,42	7,91	67,85	5,78	67,17	2,77
D14-M3M3	61,93	0,95	81,92	8,90	72,68	6,38	71,54	3,34

GROUPS	HSN n = 14		HS PAL n = 3		HSSF n = 14		HSSR n = 12	
LENGTHS	X	SD	X	SD	X	SD	X	SD
D1-I2O	7,88	1,22	7,95	0,85	7,50	1,09	7,71	0,89
D2-C O	11,10	1,45	10,92	0,59	10,55	1,73	9,48	1,18
D3-P1O	15,34	1,90	15,53	0,67	14,73	1,75	12,83	1,23
D4-P2O	21,89	2,10	23,00	1,04	20,96	2,20	19,07	1,42
D5-M1O	31,79	2,64	34,16	0,65	31,32	2,71	28,62	1,88
D6-M2O	43,24	3,13	45,72	1,34	41,93	3,16	39,09	2,18
D7-M3O	54,72	3,63	58,47	2,03	52,66	3,97	48,44	3,09

WIDTHS	X	SD	X	SD	X	SD	X	SD
D8-I2I2	21,2	2,76	23,15	1,99	19,67	1,58	17,51	1,04
D9-C C	35,02	2,25	37,10	0,66	33,30	1,62	30,73	1,59
D10-P1P1	45,03	2,12	45,27	0,71	41,79	2,60	38,86	1,20
D11-P2P2	52,73	2,55	51,87	0,52	48,70	2,22	45,16	1,60
D12-M1M1	61,63	1,97	60,62	0,46	57,56	2,56	55,14	2,19
D13-M2M2	67,72	2,96	64,63	0,76	63,82	3,25	61,84	2,84
D14-M3M3	72,16	3,13	67,90	0,85	67,46	2,51	65,87	2,61

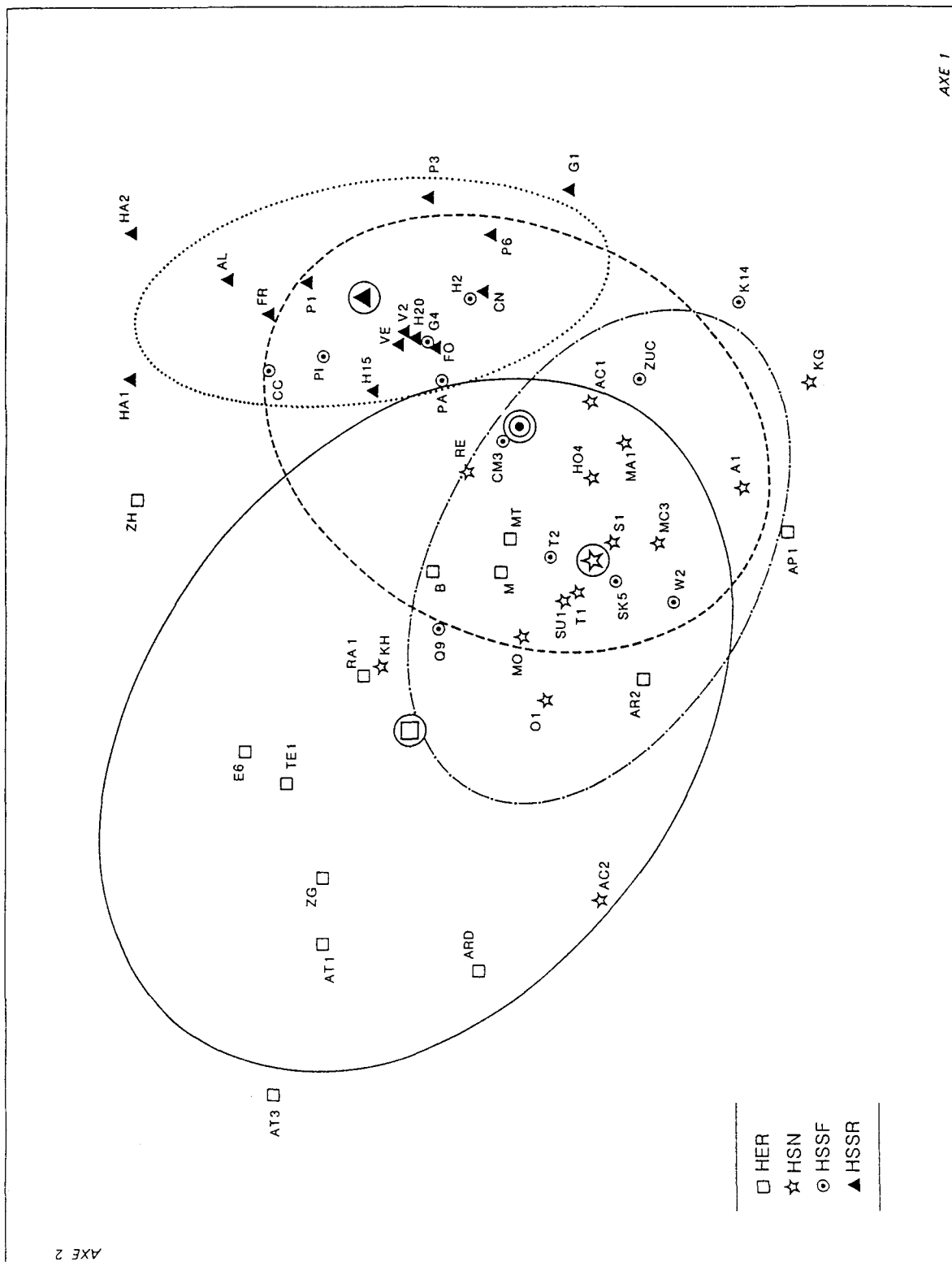


Fig. 3 Analysis 1 : diagram of the principal component analysis of 13 dimension characters and 53 Hominids organized in 4 groups (HER, HSN, HSSF, HSSR).

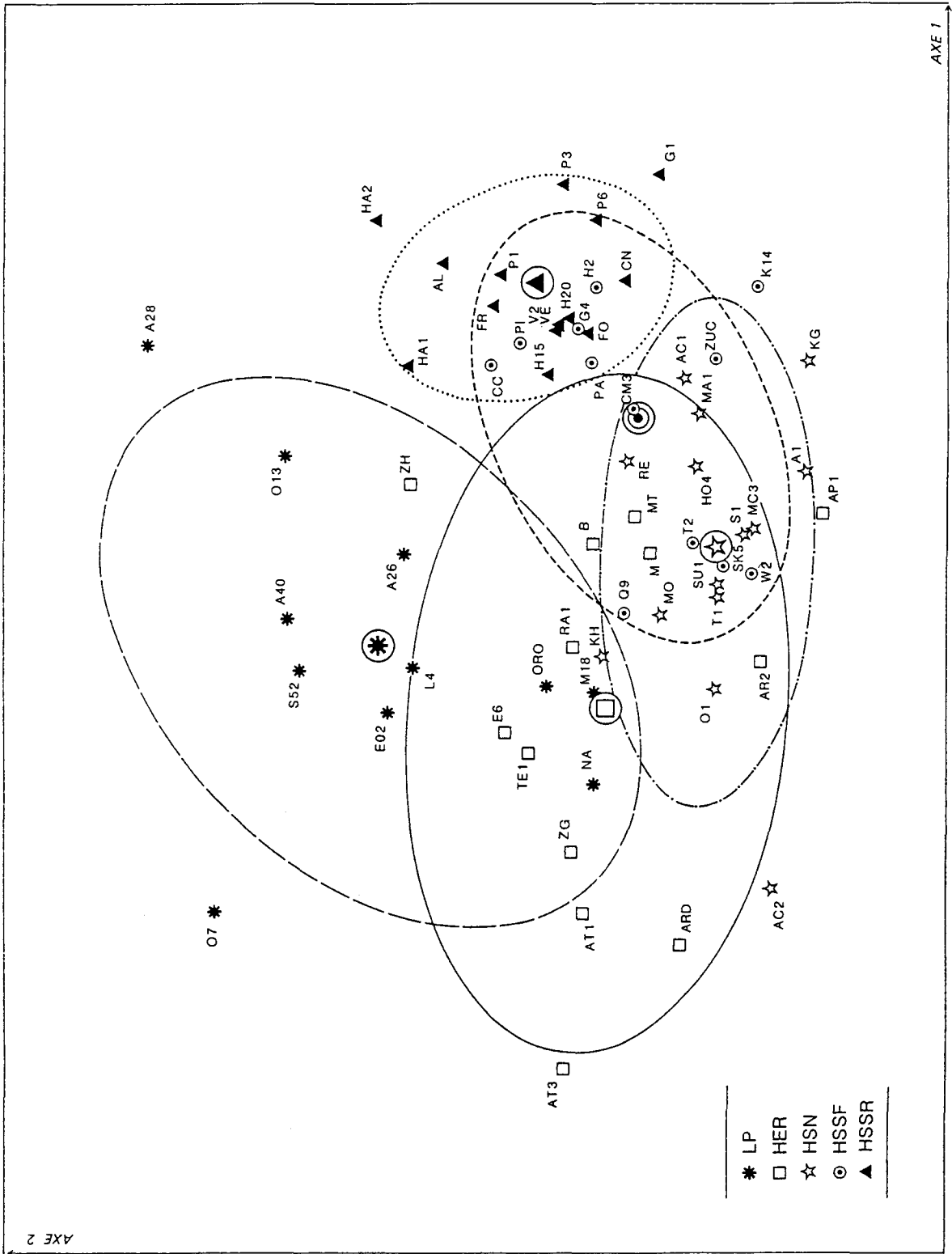


Fig. 4 Analysis 2 : diagram of the principal component analysis comparing 13 dimension characters of 53 individuals (HER, HSN, HSSF, HSSR) and 11 mandibles of the Lower Pleistocene (LP).

Table 4 Statistical results of the correlation and weight of the first two principal components in analysis 1 (HER, HSN, HSSF, HSSR) and in analysis 2 (LP, HER, HSN, HSSF, HSSR).

DIMENSIONS (mm)		ANALYSIS 1 (n = 53) AXES		ANALYSIS 2 (n = 64) AXES	
D 1	I2 O	0,50	0,29	0,52	0,14
D 2	C O	0,78	0,11	0,73	0,09
D 3	P1 O	0,81	0,08	0,77	0,15
D 4	P2 O	0,89	0,06	0,76	0,17
D 5	M1 O	0,85	0,07	0,73	0,18
D 6	M2 O	0,84	0,05	0,68	0,17
D 8	I2 I2	0,69	0,04	0,62	0,06
D 9	C C	0,77	0,04	0,64	0,08
D 10	P1 P1	0,82	0,08	0,74	0,16
D 11	P2 P2	0,82	0,12	0,69	0,24
D 12	M1 M1	0,62	0,21	0,45	0,38
D 13	M2 M2	0,53	0,21	0,34	0,37
WEIGHT	%	74,50	11,30	63,80	18,40

The ellipse of HSSF is similar in its orientation to that of the HSSR. Its barycentre is displaced towards the left on axis 1, with larger dimensions clearly under the influence of three typically long mandibles, Qafzeh 9 (Q 9), Tabun 2 (T 2), Skhul 5 (SK 5) of Palestine and of Wadjak 2 (W 2). In this area of the graph the AN and HSN also overlay each other.

Concerning analysis 2 (fig. 4; table 4), the eleven individuals of the Lower Pleistocene are ordered on axis 1 with the arcades of the middle-sized *Homo erectus* in spite of a relatively wide distribution (the arcade of A 28, *A. afarensis*, is small). Axis 2, however, differentiates the arcades regarded as *H. habilis* and *A. afarensis* and *A. africanus* from the recent population. These mandibles differentiate from the PAS (African and Asian *Homo erectus*) in the lower overall width as can be clearly seen in figure 2c with the overlapping drawing of its curves. Makapansgat MLD 18 (M 18) and both large-wide arcades of *A. boisei* Omo L 7A- 125 (O RO), Natron (NA) (fig. 2d) are classified in the distribution of HER. Under the influence of the Lower Pleistocene

individuals the other ellipses maintain their relationship. They displace each other by contracting more strongly along axis 2 towards the larger values of the axis.

In order to complete the analysis we have done two dendrograms based on the distance ("average taxonomic distance") computed from the barycentres as the averages of the principal components of each group over five vectors. In analysis 1 and 2 (fig. 5a and 5b) the four populations of the species *Homo* (HER, HSN, HSSF, HSSR) show the same arrangement with an unimportant variation of distances. In terms of statistical similarities of their arcade dimensions, the eleven very old individuals (LP) join the fossils of the Middle Pleistocene (HER). The distances between these and the others is numerically comparable with the distance between the modern European (HSSR) and the cluster of modern man of the Wurm period (HSN and HSSF). Both dendrograms indicate a greater similarity between the populations of the Neandertals and the anatomically modern mandibles of the Wurm period.

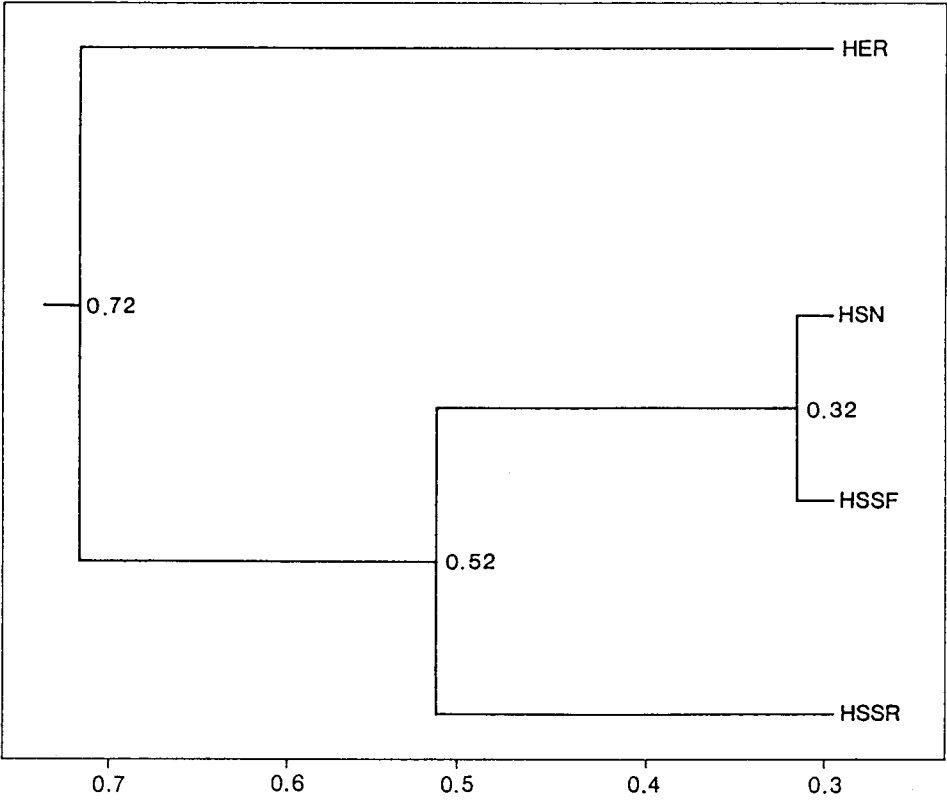


Fig. 5a Dendrogram showing the clusters of the Middle, Upper Pleistocene populations and of the modern period (HER, HSN, HSSF, HSSR).

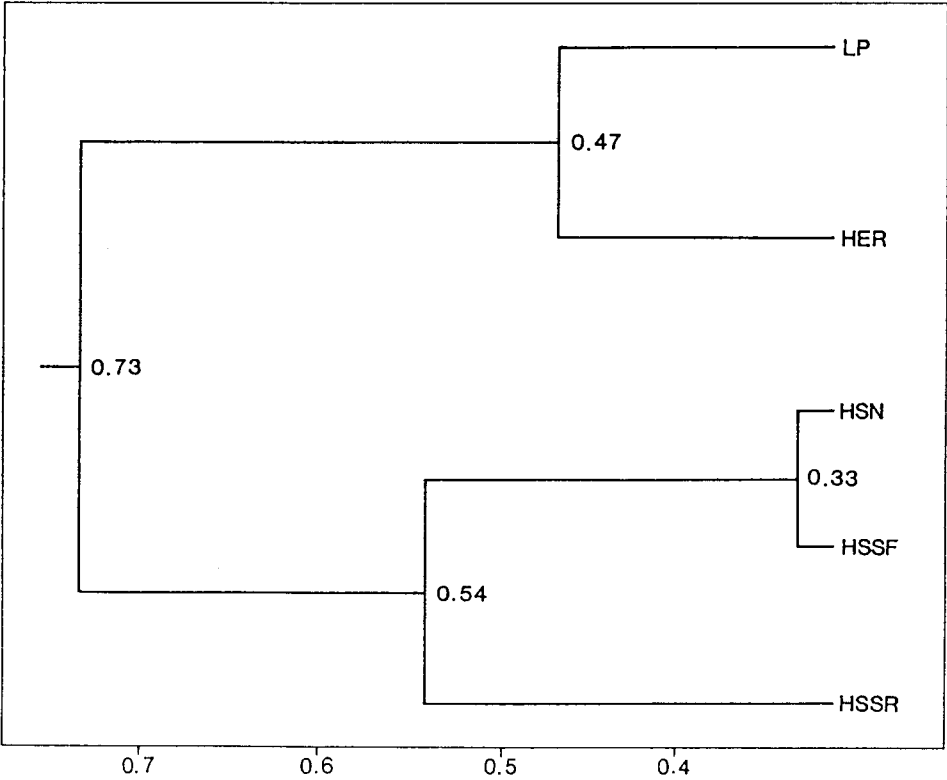


Fig. 5b Dendrogram showing the clusters of 5 populations from the Lower Pleistocene (LP) up to modern man.

Conclusion

The six lengths and six widths, which the dental arcade describes in detail, are measured on 64 mandibles of the Pleistocene and Holocene age and evaluated by analysis of the principal components. The observation of the metrical data displays dimension variation in the sense of a general reduction. This trend is found again in the organization of fossils which is revealed by the multivariant analysis. The distribution of arcades according to axis 1 (with the jugal lengths as an important contribution) indicates a continuous development between two opposed populations, humans of the Middle Pleistocene and contemporary Europeans, which are clearly separated from each other. The Neandertals and other populations of the Wurm period are inserted and partially overlap. The distribution of the Middle Pleistocene humans (analysis 1) displays groupings of large and small arcades, but does not show a clear differentiation between the European specimens and the Asiatic and African arcades. The orientation of the ellipse of the Neandertals according to the co-ordinates of axis 1 and axis 2 is similar to that of the *H. erectus* and overlaps with the short and wide arcades of the HER. However, they are differentiated by greater overall width dimensions, displayed on axis 2. In

the groups with modern anatomy, the three very old arcades of Palestine (see Stringer, 1988) are classified in the same area near the Neandertalian arcades. The other mandibles of the Upper Palaeolithic period rejoin modern Europeans. The intra-population variability of the two groups is mainly demonstrated along axis 2 and shows the effect of the molar or maximal width of the arcade. The introduction of some much older arcades from Afar, Sterkfontein, Makapansgat, Omo, Est-Turkana and from Olduvai into the statistical analysis do not clearly modify these results (analysis 2). The totality of more modern ellipses displaces itself along axis 2 towards the higher values thereby leaving the area to the very narrow arcades of *A. afarensis*, *africanus* and *H. habilis*. Makapansgat, however, and the mandibles of *A. boisei* are classified with the large arcades of HER.

Both analyses of dendrograms, which exploit the average of five barycentres of a population distribution, confirm the evolution gradient of dimension reduction (based mainly on the lengths) and display two clusters created by the *H. erectus* with the individuals of Lower Pleistocene and the anatomically modern humans of the Wurm period with the Neandertals; modern Europeans are surprisingly distant from this cluster.

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References

- AGUIRRE, E. and ROSAS, A., 1985, Fossil Man of Cueva Mayor, Ibeas, Spain: New Findings and Taxonomic Discussion, in P.V. TOBIAS (ed.), *Hominid Evolution: Past, Present and Future*, Liss, New York, pp. 319-328.
- AGUIRRE, E., CARBONELL, E. and BERMUDEZ DE CASTRO, J.-M. (eds), 1987, El Hombre Fossil de Ibeas y el Pleistoceno de la Sierra de Atapuerca, 1. *Monografías. Investigaciones arqueológicas en Castilla y León*, whole volume.

- AGUIRRE, E., ARSUAGA, J.-L., BERMUDEZ DE CASTRO, J.-M., GARCIA, A., MARTINEZ, I. and ROSAS, A., 1989, Human Remains from Atapuerca. Hominidae, in G. GIACOBINI (ed.), *Proceedings of the 2nd International Congress of Human Paleontology*, Turin 1987, Milan, Jaca Book, pp. 251-255.
- ANDREWS, P., FRANZEN, J.L. (eds), 1984, *The Early Evolution of Man*, Courier Forschungsinstitut Senckenberg 69, Frankfurt, whole volume.
- HUBLIN, J. J., 1982, Les Anténéandertaliens : Présapiens ou Prénéandertaliens, *Géobios*, mémoire spécial 6, pp. 345-357.
- LUMLEY, H. de, LUMLEY, M.-A. de et FOURNIER, A., 1982, La Mandibule de l'Homme de Tautavel, *L' Homo Erectus et la Place de l'Homme de Tautavel parmi les Hominidés Fossiles. Ier Congrès International de Paléontologie Humaine*, Nice, 1, pp. 178-221.
- MELLARS, P., STRINGER, C.B. (eds), 1989, *The Human Revolution, Behavioural and Biological Perspectives on the Origins of Modern Humans*, Edinburgh University Press, whole volume.
- ROSAS, A., 1987, Two New Mandibular Fragments from Atapuerca, Ibeas (SH Site). A Reassessment of the Affinities of the Ibeas Mandibles Sample, *J. Hum. Evol.*, 16, pp. 417-427.
- ROTH, H., 1985, Morphometric Study of the Evolution of Mandibular Arcades, *J. Hum. Evol.*, 14, p. 563-571.
- ROTH, H., 1988, Morphometric Study of Fossil Mandibles, Numerical Representation of Dental Arcades by a Biometric Method. *L'Homme de Néandertal. Actes du Colloque International de Liège 1986, L'Anatomie*, vol. 3, Liège, ERAULT 30, pp. 111-123.
- STRINGER, C. B., 1985, Middle Pleistocene Hominid Variability and the Origin of Late Pleistocene Humans, in E. DELSON (ed.), *Ancestors : The Hard Evidence*, Liss, New-York, pp. 289-295.
- STRINGER, C. B., 1987, A Numerical Cladistic Analysis for the Genus Homo. *J. Hum. Evol.*, 16, pp. 135-146.
- STRINGER, C. B., 1988, The Dates of Eden. *Nature*, 331, pp. 565-566.
- STRINGER, C. B., 1991, Die Herkunft des Anatomisch Modernen Menschen, *Spektrum der Wissenschaften*, 2, 1991, pp. 112-120.
- STRINGER, C. B., HUBLIN, J.J. and VANDERMEERSCH, B., 1984, The Origin of Anatomically Modern Humans in Western Europe, in F.H. SMITH and F. SPENCER (eds), *The Origin of Modern Humans : A World Survey of the Fossil Evidence*, Liss, New-York, pp. 51-135.
- STRINGER, C. B. and ANDREWS, P., 1988, Genetic and Fossil Evidence for the Origin of Modern Humans, *Science*, 239, pp. 1263-1268.
- VANDERMEERSCH, B., 1986, Présapiens et Anténéandertaliens, *Bull. Soc. Belge Préhist.*, 97, pp. 45-57.