

# Quantitative Analysis of Human Mandibular Shape Using Three-Dimensional Geometric Morphometrics

Elisabeth Nicholson<sup>1</sup> and Katerina Harvati<sup>2\*</sup>

<sup>1</sup>Department of Cell and Molecular Biology, Northwestern University Feinberg School of Medicine, Chicago, Illinois 60611-3008

<sup>2</sup>Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, D-04103 Leipzig, Germany

**KEY WORDS** modern human variation; Neanderthals; climate; paramasticatory behavior

**ABSTRACT** Human mandibular morphology is often thought to reflect mainly function, and to be of lesser value in studies of population history. Previous descriptions of human mandibles showed variation in ramal height and breadth to be the strongest difference among recent human groups. Several mandibular traits that differentiate Neanderthals from modern humans include greater robusticity, a receding symphysis, a large retromolar space, a rounder gonial area, an asymmetric mandibular notch, and a posteriorly positioned mental foramen in Neanderthals. Nevertheless, the degree to which these differences are part of modern human variation and/or are related to size and function remains unclear. The aim of this study was to document geographic and functional patterning in the mandibular shape of recent humans, to assess the effects of allometry on mandibular form, and to quantitatively evaluate proposed “Neander-

thal” mandibular traits through comparison with samples of geographically diverse recent humans. Data were collected in the form of three-dimensional coordinates of 28 landmarks. Unlike previous studies, this analysis found that modern human mandibular shape exhibits considerable geographic patterning, with some aspects of mandibular morphology reflecting a climatic gradient, and others, a functional specialization. Population history is also reflected in mandibular form, albeit relatively weakly. Proposed “Neanderthal” traits were found to separate Neanderthal from modern human mandibles successfully in the statistical analysis. Of these, the retromolar gap was found to be related to increased mandibular size in modern humans. The status of this trait as a Neanderthal autapomorphy should therefore be treated with caution. *Am J Phys Anthropol* 131:368–383, 2006.

© 2006 Wiley-Liss, Inc.

The usefulness of mandibular anatomy in studies of human regional variation and population history has often been debated. Early on, human mandibular variation was considered to result from ontogenetic or functional processes, and not to accurately reflect population history. It was therefore thought not to be of great value in identifying recent human groups (Harrower, 1928; Cleaver, 1937; Hrdlička, 1940a,b; Humphrey et al., 1999). Later studies of the human mandible focused on describing the morphology of specific recent human groups (Murphy, 1957; Lee and Choi, 1961; Aitchison, 1964, 1965; Chang and Lee, 1990). A comprehensive literature review and quantitative analysis of linear measurements from large samples of multiple human and great ape populations were not undertaken until quite recently (Humphrey et al., 1999). Analyses of human mandibular form addressed the temporal trend toward gracilization observed in modern humans (Moore et al., 1968; Lavelle, 1972; Kaifu, 1997); evaluated the usefulness of the mandible in classifying human groups (Harrower, 1928; Cleaver, 1937; Hrdlička, 1940a,b); assessed patterns of sexual dimorphism (Weidenreich, 1933; Morant et al., 1936; Martin, 1936; Hrdlička, 1940a,b; Aitchison, 1963; Giles, 1964; DeVilliers, 1968a,b; Hunter and Garn, 1972; Wood et al., 1991; Muller, 1998; Rosas and Bastir, 2002) and functional aspects of mandibular morphology (Hrdlička, 1940a,b; Hylander, 1977); and described differences between modern and fossil forms (Boule, 1911–1913; Franciscus and Trinkaus, 1995; Stefan and Trinkaus, 1998; Rosas, 2001; Rosas and Bastir, 2002; Jabbour et al., 2002; Rak et al., 2002). Traits found to differ among recent human populations include ramal height and breadth, ramal obliqueness, corpus robusticity, mandibular

(sigmoid) notch shape, bicondylar breadth, and mental foramen position (Murphy, 1957; Hylander, 1977; Anderson, 1998; Humphrey et al., 1999). However, in some cases, these differences are thought to be related to masticatory behavior and adaptation (Hylander, 1977; Humphrey et al., 1999). In general, mandibular morphology was found to be a poor discriminator of recent human groups (e.g., Humphrey et al., 1999).

Differences between Neanderthal and modern human mandibular morphology have been extensively documented. Primitive features retained in Neanderthal mandibles include overall robusticity and a receding symphysis, which results in the absence of a mental eminence or chin (Tillier et al., 1989; Arensburg and Belfer-Cohen, 1998; Rak, 1998). Proposed derived traits include a posteriorly positioned mental foramen (Stringer et al., 1984; Condemi, 1991; Arensburg and Belfer-Cohen, 1998; Hublin, 1998; Rosas,

Grant sponsor: Centennial Scholars Program, Barnard College; Grant sponsor: New York University; Grant sponsor: Max Planck Institute for Evolutionary Anthropology.

\*Correspondence to: Katerina Harvati, Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany.  
E-mail: harvati@eva.mpg.de

Received 29 September 2005; accepted 21 December 2005.

DOI 10.1002/ajpa.20425

Published online 14 April 2006 in Wiley InterScience (www.interscience.wiley.com).

TABLE 1. Hypotheses presented in text and their predictions

Hypothesis	Prediction
<i>Analysis of recent human samples</i>	
1A. Mandibular shape reflects population history (as inferred from geography)	Geographically neighboring samples show smallest morphological distances to one another; high classification success
1B. Mandibular shape reflects climate	Mandibular shape separates cold- from warm-climate groups
1C. Mandibular shape reflects paramasticatory behavior	Mandibular shape separates North American Arctic sample
<i>Analysis of recent and fossil human samples</i>	
2A. Neanderthal mandibular shape reflects phylogenetic relationships	Mandibular shape separates Neanderthals from recent humans and Upper Paleolithic specimens; morphological distance between Neanderthals and modern humans greater than distances among recent human groups
2B. Neanderthal mandibular shape reflects paramasticatory behavior	Neanderthals, but not early modern humans, are similar to North American Arctic sample in some features that distinguished the latter from other recent human groups
2C. Neanderthal mandibular shape is not product of large size	Increasing size in modern humans does not result in Neanderthal-like morphology

2001); a large retromolar space (Coon, 1962; Stringer et al., 1984; Condemi, 1991; Franciscus and Trinkaus, 1995; Arensburg and Belfer-Cohen, 1998; Hublin, 1998; Rak, 1998; Rosas, 2001); a rounder, less angled gonial area (Rosas, 1992, 2001; Creed-Miles et al., 1996); a mandibular notch that meets the condyle in a more medial position, resulting in a laterally expanded condyle (Boule, 1911–1913; Vandermeersch, 1981; Hublin, 1998; Rak, 1998; Rosas, 2001; Jabbour et al., 2002); a shallow and asymmetric mandibular notch with a higher coronoid process than condyle (Rak, 1998; Rak et al., 2002); very deep submandibular and pterygoid fossae (Rosas, 1992, 2001; Creed-Miles et al., 1996); and an oval-horizontal shape of the mandibular foramen (Hublin, 1998; Trinkaus et al., 2003). Pre-Neanderthal Middle Pleistocene European specimens show an increasing occurrence of these derived traits over time (Hublin, 1998; Rosas, 2001). Upper Paleolithic European specimens tend to have relatively robust mandibles, and some researchers proposed that they exhibit some Neanderthal traits, although their overall morphology is predominantly modern (Frayer, 1992; Thorne and Wolpoff, 1992; Trinkaus et al., 2003). The early modern human specimens from Skhul and Qafzeh are generally thought to resemble modern humans more than Neanderthals, despite their observed robusticity. Skhul 5 was described as having a moderately developed chin, a tall and narrow ramus, and condyles with a modern human morphology (McCown and Keith, 1937). Qafzeh 9 shows an extremely antero-posteriorly long and medio-laterally narrow mandible, a shape probably exaggerated by deformation, with a supero-inferiorly tall symphysis, a chin, and a coronoid process that is slightly taller than the condyle (Vandermeersch, 1981).

Our analysis follows up and expands on previous research by analyzing mandibular three-dimensional (3-D) shape in recent human populations and in Middle and Late Pleistocene fossil human specimens from western Eurasia. This is the first study to use 3-D geometric morphometric methods to assess mandibular shape in a large recent and fossil human sample. These methods enable a better representation of shape than traditional linear and angle measurements, allow visualization of shape differences between specimens and between group means in specimen space, and can quantify traits previously described qualitatively (Dean, 1993; Harvati, 2003a,b; Harvati et al., 2004). Our goal is to document geographic and/or functional patterning among recent human populations, to assess the effect of allometry on

human mandibular shape, and to quantitatively evaluate the expression of proposed “Neanderthal” mandibular features.

## MATERIALS AND METHODS

### Hypotheses

We measured a large sample of modern human mandibles, representing 10 broad geographic areas, and 15 Middle and Late Pleistocene western Eurasian fossil specimens. The analysis was conducted in two parts: the first on a data set consisting exclusively of modern humans, and the second on the combined modern and fossil human sample. In the first set of analyses, we tested the hypothesis that mandibular shape shows geographic patterning among recent human populations, reflecting relatedness among these groups (hypothesis 1A, Table 1). This hypothesis predicts that geographically neighboring samples would show the smallest morphological distances, and that classification success would be high, with misclassified specimens mostly being assigned to populations from the same wider geographic region. We also hypothesized that the mandible will reflect climatic (hypothesis 1B) and functional (hypothesis 1C) adaptations. Based on these hypotheses, we predicted that aspects of mandibular shape, as revealed in the principal components analysis, would separate cold- from warm-climate groups, and other aspects would separate the North American Arctic sample (for which paramasticatory and extreme dietary practices are documented; see below) from the other groups.

In the second (combined recent and fossil sample) set of analyses, we tested the hypothesis that proposed Neanderthal mandibular features do characterize Neanderthals, and to some extent their *H. heidelbergensis* predecessors, but not recent or Upper Paleolithic European modern humans (hypothesis 2A). This hypothesis predicted that the described Neanderthal morphology would separate Neanderthals from modern humans in the principal components analysis, and that the morphological distance between Neanderthals and modern humans would be larger than the distances among recent human groups. As the paramasticatory behaviors of North American Arctic populations have been important in evaluating the biomechanical properties of Neanderthal facial and mandibular morphology (e.g., Spencer and Demes, 1993; Antón 1996a), we also hypothesized that Neanderthal mandibles would share some functional specializations with the North

American Arctic specimens (hypothesis 2B). We predicted that Neanderthals, but not early modern humans, would be similar to the North American Arctic sample in some or all of the features that distinguished the latter from other recent human groups. Finally, we tested the hypothesis that the expression of these traits is not the result of a larger mandibular size (hypothesis 2C). This hypothesis predicted that increasing size would not result in Neanderthal-like morphology in the recent human sample.

In the first set of analyses, recent human samples were analyzed based on geographic origin (hypothesis 1A), climate of the region of origin (temperate/cold vs. tropical/subtropical, hypothesis 1B), and paramasticatory or extreme dietary practices (North American Arctic group, hypothesis 1C). Although food-processing strategies are proposed to have a very strong effect on mandibular morphology (e.g., Moore et al., 1968; Corruccini, 1984, 1990; Corruccini and Beecher, 1982; Lieberman et al., 2004), we did not test this hypothesis in this study, as little information was available regarding the diets of recent human populations included in our sample. All our samples except the Australian and North American Arctic probably came from populations practicing some form of agriculture. Therefore, the effect of even such a gross dietary difference as agricultural vs. non-agricultural cannot be properly assessed. Some detail of dietary practices was known only in the case of the North American Arctic sample, for which ethnographic information suggests extreme dietary and paramasticatory practices. Their facial and mandibular morphology was previously interpreted in terms of the functional demands of these behaviors (Balicki, 1970; Hylander, 1977; So, 1980; Antón, 1996a).

In our second set of analyses, we evaluated the uniqueness of Neanderthal mandibular features by comparing Neanderthal mandibular shape to the shape variation found among recent human samples (hypothesis 2A). We explored similarities and differences in the particular aspects of shape, in addition to the general level of morphological similarity, between Neanderthals and the North American Arctic group (hypothesis 2B). Finally, we assessed the influence of size on the expression of these features by visualizing the shape differences produced in recent human mandibles with increasing or decreasing size (hypothesis 2C).

### Samples

The modern human sample includes 155 mandibles (Table 2) from 10 relatively broad geographic regions, chosen to encompass a wide range of human variation and to span a large part of the recent human geographic range. These samples do not represent biological populations in the sense of demes. The fossil sample comprises two Middle Pleistocene European specimens, several Neanderthal and Upper Paleolithic specimens from Europe and the Near East, and two Late Pleistocene early anatomically moderns (Table 3). The Tabun C2 mandible was excluded from our Neanderthal sample due to its uncertain taxonomic affiliation (Rak, 1998; Quam and Smith, 1998; Stefan and Trinkaus, 1998). The Middle Pleistocene specimens (Mauer and Arago XIII) were previously described as showing a mostly primitive morphology (Hublin, 1998; Rosas, 2001). Where original specimens were unavailable for study, high-quality casts were measured from the collections of the Departments of Anthropology of the American Museum of Natural History and New

TABLE 2. Modern human samples from American Museum of Natural History included in this study

Population	Specimens
Total	155
Oceania (Australia, New Guinea, and Tasmania)	18
Polynesia	18
Southeast Asia (Southeast Asia and China)	14
North Asia (Japan, Korea, Siberia, and Mongolia)	13
East Africa (Masai)	14
South Africa (Khoisan and Bantu)	9
Europe	26
South America	19
Central America (Central America and Mexico)	10
North America Arctic (Alaska, Greenland, and Northern Canada)	14

York University, and of the Department of Human Evolution of the Max Plank Institute for Evolutionary Anthropology.

Specimens were labeled by species and population, with *H. neanderthalensis* and *H. heidelbergensis* assigned to two distinct species, each separate from *H. sapiens*. Upper Paleolithic humans were treated as a population of *H. sapiens*, as were the early anatomically modern humans. Only adult specimens, as determined by a fully erupted permanent dentition, and only mandibles preserving all 28 landmarks were included in this study, limiting sample sizes for both recent and fossil groups. Sex was known only for a few specimens in each sample, making an assessment of sexual dimorphism in mandibular shape impossible. The mandible, however, is sexually dimorphic, and previous studies showed differences in both size and shape between recent human male and female mandibles. Males and females were found to differ most markedly in the height of the symphysis and of the ramus, and differences are more pronounced in the ramus than in the body of the mandible (e.g., Morant et al., 1936; Martin, 1936; Hrdlička, 1940a,b; De Villiers, 1968a,b; Hunter and Garn, 1972; Humphrey et al., 1999). Furthermore, patterns of sexual dimorphism were found to differ between regional samples (Humphrey et al., 1999). Due to the lack of secure sex assignments for both recent and fossil specimens, the two sexes were pooled in the analysis, following the regional analysis in Humphrey et al. (1999).

### Data

Data were collected in the form of 84 3-D coordinates, representing 28 landmarks (Table 4), using a Microscribe 3DX digitizer (Fig. 1). Four of 28 landmarks were located on the midsagittal plane; the others consisted of 12 pairs of homologous points on the left and right sides. Landmarks were selected to represent the overall shape of the symphyseal region, the ramus, and the body of the mandible. All recent human specimens were measured by E.N., as were most of the casts of fossil specimens used. Some casts and all the original fossils were measured by K.H. (Table 4). Measurement error was similar for both observers, and ranged from 0.02–0.11 mm (Table 5). This level of error is within the range reported for similar methods (Singleton, 2002; Harvati, 2003a). After performing a principal components analysis on superimposed coordinates (see below), an analysis of variance (ANOVA) was conducted on the principal component scores to assess the influence of interobserver error in separating specimens. No observer effect was found.

TABLE 3. Descriptions of fossils used in this study<sup>1</sup>

Specimen	Location	Museum	Collected by	Species	Population
Mauer 1 <sup>2</sup>	Germany	AMNH	E.N.	H	H
Arago 13 <sup>2</sup>	France	NYU	K.H.	H	H
Montmaurin	France	MH	K.H.	N	N
La Ferrassie 1	France	MH	K.H.	N	N
Zafarraya <sup>2</sup>	Spain	MPI	K.H.	N	N
Krapina J <sup>2</sup>	Croatia	AMNH	E.N.	N	N
Amud 1 <sup>2</sup>	Israel	AMNH	E.N.	N	N
Tabun 1	Israel	NHML	K.H.	N	N
Shanidar 1 <sup>2</sup>	Iraq	AMNH	E.N.	N	N
Chancelade <sup>2</sup>	France	NYU	K.H.	S	UP
Isturitz 1950-4-1	France	IPH	K.H.	S	UP
Oberkassel 2 <sup>2</sup>	Germany	AMNH	E.N.	S	UP
Grimaldi-Grotte-des-Enfants 6	Italy	AMNH	E.N.	S	UP
Skhul 5	Israel	PEA	K.H.	S	EAM
Qafzeh 9 <sup>2</sup>	Israel	MPI	K.H.	S	EAM

<sup>1</sup> AMNH, American Museum of Natural History; IPH, Institut de Paléontologie Humaine; MH, Musée de l'Homme; MPI, Max Planck Institute, Leipzig; NHML, Natural History Museum, London; NYU, New York University; PEA, Peabody Museum, Harvard; N, Neanderthal; H, *H. heidelbergensis*; S, *H. sapiens*. Fossil *H. sapiens* were divided into two samples: UP, Upper Paleolithic human; EAM, early anatomically modern human.

<sup>2</sup> Casts from collections of AMNH, MPI, and NYU.

TABLE 4. Definitions of landmarks used, with first 12 landmarks collected from both right and left sides

Landmark	Definition
1. Gonion	Point along rounded posteroinferior corner of mandible where line bisecting angle between body and ramus would hit
2. Posterior ramus	Point at posterior margin of ramus at level of M <sub>3</sub>
3. Condyle tip	Most superior point on mandibular condyle
4. Condylion mediale	Most medial point on mandibular condyle
5. Condylion laterale	Most lateral point on mandibular condyle
6. Root of sigmoid process	Point where mandibular notch intersects condyle
7. Mandibular notch	Most inferior point on mandibular notch
8. Coronion	Most superior point on coronoid process
9. Anterior ramus	Point at anterior margin of ramus at level of M <sub>3</sub>
10. M <sub>3</sub>	Point on alveolar bone just posterior to midline of third molar
11. Mental foramen	Point in middle of mental foramen
12. Canine	Point on alveolar margin between canine and first premolar
13. Gnathion	Most inferior midline point on symphysis
14. Infradentale	Midline point at superior tip of septum between mandibular central incisors
15. Mandibular orale	Most superior midline point on lingual side of mandible between two central incisors
16. Superior transverse torus	Most posterior midline point on superior transverse torus

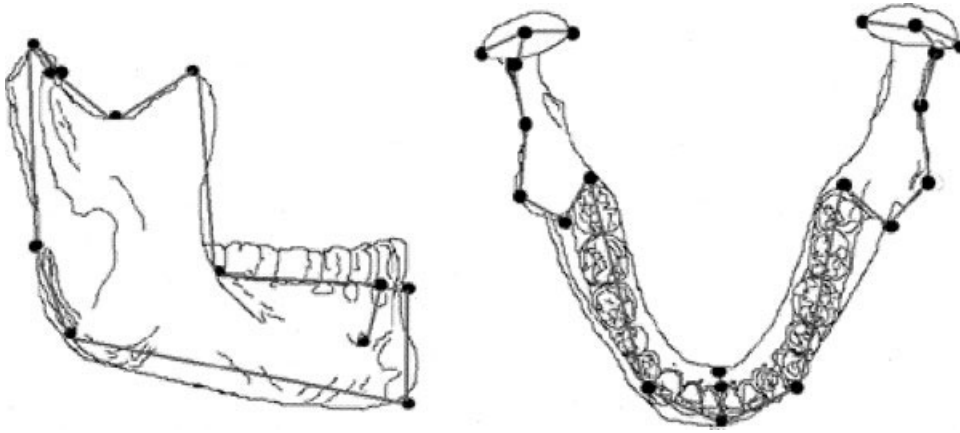
Because morphometric analyses do not accommodate missing data, and because many of the fossil specimens were incomplete, some data reconstruction was allowed. During data collection for specimens with minimal damage, landmarks were reconstructed by estimating the position of the structure of interest, using the morphology of the preserved surrounding areas. Missing landmarks were further reconstructed by reflecting the right and left sides of the specimen. Incomplete specimens were least-squares

superimposed with their reflected equivalents, using Morphueus (Slice, 1994–1999), and missing data were reconstructed from their homologous counterparts on the other side. Further reconstruction by substituting sample means was permitted for a few fossil specimens missing one or two landmarks on both sides (Arago 13, Shanidar 1, Chancelade).

### Analysis

Landmark coordinates were superimposed using generalized Procrustes analysis (GPA) in Morphueus. Multivariate analyses based on Procrustes-aligned specimens were found to have higher statistical power than alternative geometric morphometric approaches (Rohlf, 2000). GPA superimposes specimen landmark configurations by translating them to a common origin, scaling them to unit centroid size (the square root of the sum of squared distances of all landmarks to the centroid of the object; the measure of size used here), and rotating them according to a best-fit criterion. This procedure eliminates “size” as a factor (although size-related shape differences may remain). “Shape” and “size” can therefore be analyzed separately (Rohlf, 1990; Rohlf and Marcus, 1993; Slice, 1996; O’Higgins and Jones, 1998).

*T*-tests were performed on centroid size to test for significant size differences among populations and taxa. The relationship of principal components (and corresponding shape features that each of them reflected) with centroid size was explored using correlation analysis. The fitted coordinates were analyzed with principal components analysis (PCA), Mahalanobis D<sup>2</sup>, and discriminant analysis, using the SAS statistical software program. PCA is a data-reduction exploratory technique, which summarizes the total variance in a data set by rotating it so that the principal components explain progressively smaller amounts of the total variance (Bennett and Bowers, 1976; Lestrel, 2000). ANOVA was performed on the PCA scores to determine the significance of population, species, and climatic effects along each component. Climate was scored as either warm (tropical and subtropical climate populations, defined by mean maximum and minimum annual temperatures) or cold (temperate and cold climate groups, defined as above). A



**Fig. 1.** Mandibular landmarks used (dots). Grey lines do not represent data, but are used to aid in visualization.

**TABLE 5.** Intraobserver error for each landmark, with landmark numbers as in Table 3

Landmark	Intraobserver error	
	Observer 1, mean deviation (mm)	Observer 2, mean deviation (mm)
1.	0.04	0.02
2.	0.03	0.04
3.	0.05	0.04
4.	0.03	0.04
5.	0.07	0.05
6.	0.06	0.03
7.	0.06	0.05
8.	0.02	0.03
9.	0.04	0.03
10.	0.04	0.02
11.	0.06	0.04
12.	0.05	0.05
13.	0.04	0.03
14.	0.11	0.4
15.	0.07	0.05
16.	0.05	0.04
Mean	0.05	0.06
Maximum	0.11	0.4
Minimum	0.02	0.02

*t*-test was performed on all pairwise comparisons of the population means of the principal component scores, and between cold- and warm-climate samples. Shape differences along principal axes were explored in *Morphologica* (O'Higgins and Jones, 2004) and by examining the eigenvectors for each principal component.

The similarity among groups was measured by the Mahalanobis  $D^2$  statistic, corrected for unequal sample sizes (Marcus, 1993). This statistic measures the morphological difference among groups, scaled by the pooled within-group variation and accounting for covariance between variables (Lestrel, 2000). The larger the values of the  $D^2$  distance, the farther the group centroids are from each other (Lestrel, 2000). A discriminant analysis was conducted in order to test the predictive power of mandibular traits in classifying these groups.

In order to explore the effects of allometry on human mandibular shape more fully, and to more extensively assess the influence of a larger size on the expression of Neanderthal features, an additional analysis of centroid size was undertaken. During Procrustes superimposition, size is removed by scaling all specimens to unit centroid size. However, size-related allometric differences may remain. In order to visualize how recent human mandibular shape changes with increased or decreased

centroid size, we performed a multiple-regression analysis of the superimposed coordinates on centroid size. We then imported the regression coefficients into the GRF-ND software package (Slice, 1992, 1994) as an eigenvector. This software allows visualization of shape differences observed along a particular axis (Slice, 1996). We were thus able to observe the differences in modern human mandibular shape resulting from increasing or decreasing size.

## RESULTS

### Analysis of the recent human sample

Mandibles from the North American Arctic population showed the largest mean centroid size and were significantly larger than every population except East Africans (Table 6). South Africans had the smallest centroid size and were significantly smaller than the Arctic and East African samples. ANOVA revealed a significant climate (cold vs. warm) effect on mandibular centroid size ( $P = 0.026$ ), but this relationship was driven by the large centroid size of the North American Arctic group. When this sample was excluded, the relationship between centroid size and climate was no longer significant.

The first three principal components were statistically significant for population effects ( $P < 0.0001$ ). PC 1 also showed a very strong climatic effect ( $P < 0.0001$ ), even when the North American Arctic sample was removed from the analysis. A discriminant analysis on PC 1 correctly classified 121 of 155 individuals (78.06%) into a cold or warm climate, with Europeans misclassified most frequently. None of these axes were significantly correlated with centroid size ( $r = 0.061, -0.009, \text{ and } -0.108; P = 0.448, 0.915, \text{ and } 0.182$ , respectively).

PC 1, accounting for 25.04% of the total variance, described the overall shape of the mandible. A low score on this component indicated a long and narrow mandible, while a high score indicated a short and wide one (Fig. 2). The Arctic, European, and North Asian populations had significantly higher mean scores along PC 1 (Bonferroni *t*-test,  $\alpha = 0.05$ ) than all but the Southeast Asians and Central and South Americans groups. The former groups were characterized by 1) an antero-posteriorly short and medio-laterally wide mandible with laterally positioned gonias; 2) an anteriorly projecting lower part of the symphysis and a supero-inferiorly taller corpus; and 3) a shorter antero-posterior distance between the canine and the mental foramen (Fig. 2). The Oceanic and Polynesian populations had significantly lower scores than all populations except for East and South Africans.

TABLE 6. T-Test P values (two-tailed), testing centroid size, equal variances assumed, between recent and fossil samples<sup>1</sup>

	AR	OC	CA	EA	EU	NA	PO	SA	SM	SE	N	EAM	UP	H
Mean centroid size	30.78	29.13	28.73	29.74	28.95	29.49	29.16	28.47	29.21	28.82	33.46	30.88	30.18	35.09
AR	1.000	<b>0.001</b>	<b>0.001</b>	0.137	<b>0.000</b>	<b>0.014</b>	<b>0.001</b>	<b>0.001</b>	<b>0.001</b>	<b>0.000</b>	<b>0.001</b>	0.926	0.239	<b>0.001</b>
OC	<b>0.001</b>	1.000	0.379	0.122	0.640	0.380	0.906	0.186	0.823	0.416	<b>0.000</b>	0.062	0.105	<b>0.000</b>
CA	<b>0.001</b>	0.379	1.000	<b>0.033</b>	0.634	0.117	0.278	0.651	0.281	0.831	<b>0.000</b>	<b>0.048</b>	0.138	<b>0.000</b>
EA	0.137	0.122	<b>0.033</b>	1.000	0.054	0.532	0.110	<b>0.016</b>	0.173	<b>0.020</b>	<b>0.000</b>	0.200	0.476	<b>0.000</b>
EU	<b>0.000</b>	0.640	0.634	0.054	1.000	0.204	0.542	0.341	0.481	0.738	<b>0.000</b>	0.055	0.217	<b>0.000</b>
NA	<b>0.014</b>	0.380	0.117	0.532	0.204	1.000	0.387	0.059	0.494	0.097	<b>0.000</b>	0.137	0.280	<b>0.000</b>
PO	<b>0.001</b>	0.906	0.278	0.110	0.542	0.387	1.000	0.120	0.892	0.302	<b>0.000</b>	<b>0.035</b>	0.071	<b>0.000</b>
SA	<b>0.001</b>	0.086	0.651	<b>0.016</b>	0.341	0.059	0.120	1.000	0.132	0.461	<b>0.000</b>	0.051	<b>0.007</b>	<b>0.000</b>
SM	<b>0.001</b>	0.823	0.281	0.173	0.481	0.494	0.892	0.132	1.000	0.272	<b>0.000</b>	<b>0.041</b>	0.078	<b>0.000</b>
SE	<b>0.000</b>	0.416	0.831	<b>0.020</b>	0.738	0.097	0.302	0.461	0.272	1.000	<b>0.000</b>	<b>0.019</b>	<b>0.025</b>	<b>0.000</b>
N	<b>0.001</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	1.000	0.058	<b>0.002</b>	0.145
EAM	0.926	0.062	<b>0.048</b>	0.200	0.055	0.137	<b>0.035</b>	0.051	<b>0.041</b>	<b>0.019</b>	0.058	1.000	0.577	0.094
UP	0.239	0.105	0.138	0.476	0.217	0.280	0.071	<b>0.007</b>	0.078	<b>0.025</b>	<b>0.002</b>	0.577	1.000	<b>0.004</b>
H	<b>0.001</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.145	0.094	<b>0.004</b>	1.000

<sup>1</sup> P < 0.05 in bold. AR, North American Arctic; OC, Oceania; CA, Central America; EA, East African; EU, European; NA, North Asian; PO, Polynesian; SA, South African; SM, South American; SE, Southeast Asian. Fossil group labels as in Table 3.

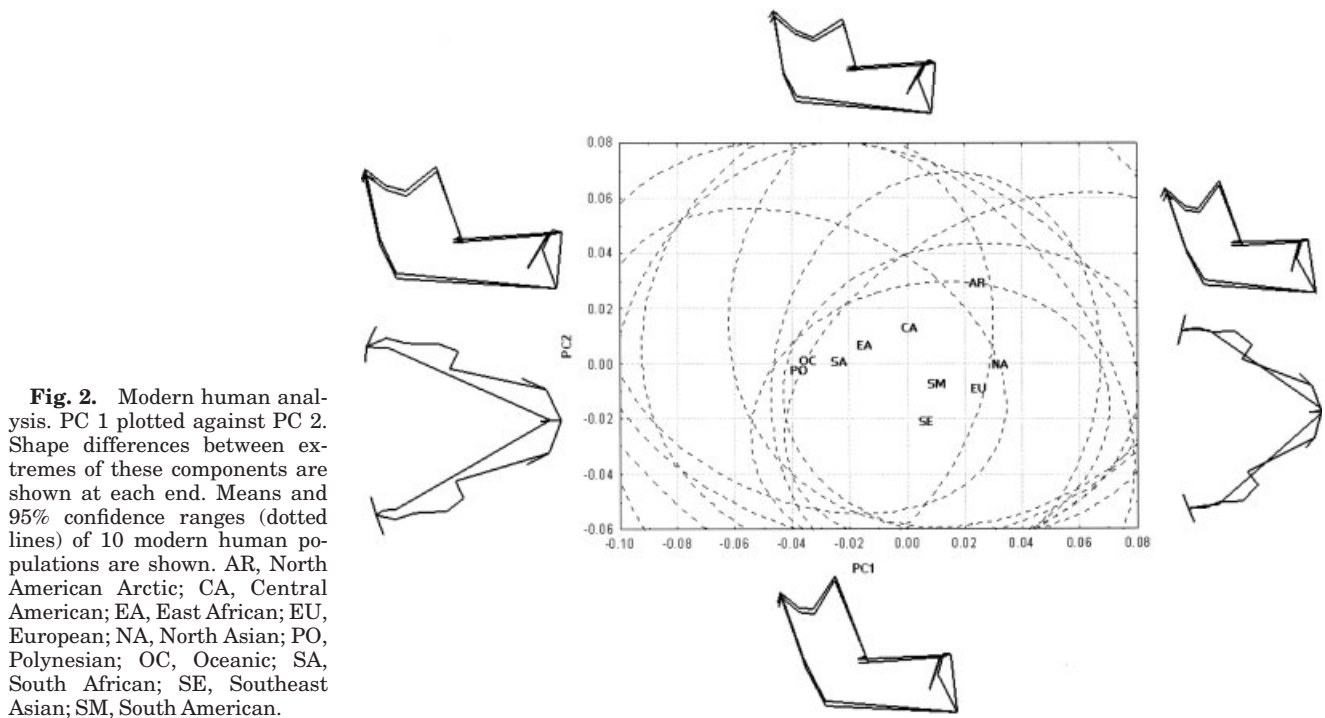


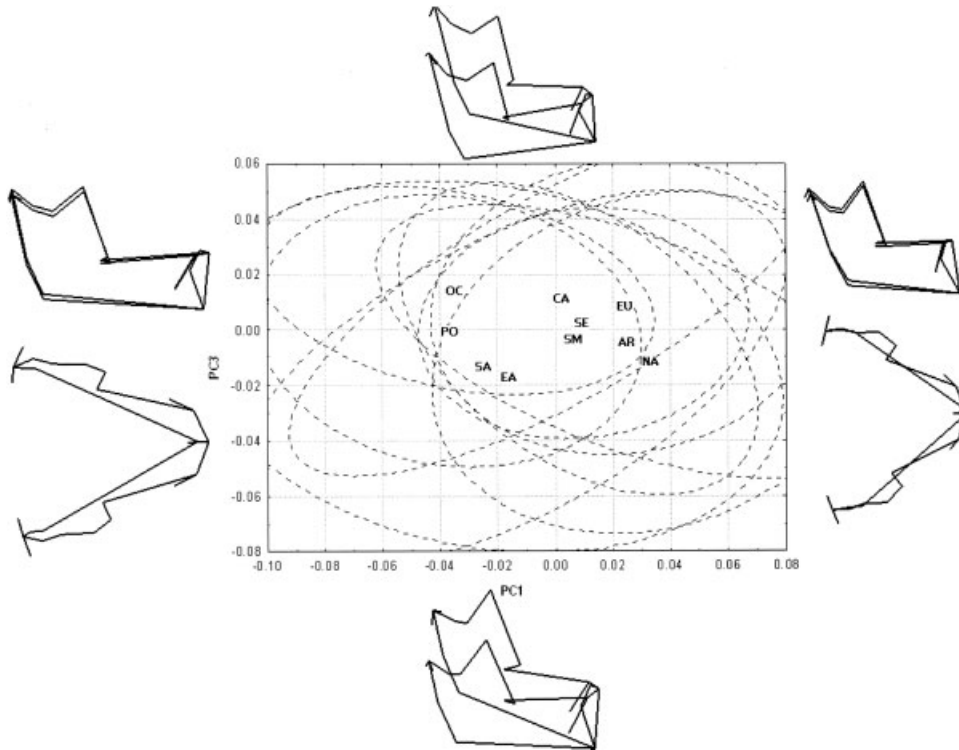
Fig. 2. Modern human analysis. PC 1 plotted against PC 2. Shape differences between extremes of these components are shown at each end. Means and 95% confidence ranges (dotted lines) of 10 modern human populations are shown. AR, North American Arctic; CA, Central American; EA, East African; EU, European; NA, North Asian; PO, Polynesian; OC, Oceanic; SA, South African; SE, Southeast Asian; SM, South American.

They were characterized by 1) a long and narrow mandible with a medially positioned gonion; 2) a more posteriorly receding symphysis; 3) a more superiorly positioned gonion and gnathion, indicating a supero-inferiorly shorter corpus; and 4) a greater antero-posterior distance between the canine and the mental foramen. The most influential landmarks for PC 1 included: gonion (right and left), posterior ramus (right and left), infradentale, mandibular orale, and canine (right and left).

PC 2 (Fig. 2) accounted for 13.89% of the total variance. This axis separated the North American Arctic population from the other groups, although there was much overlap. The Arctic mean PC 2 score was only significantly higher than those of the North Asian, Southeast Asian, South American, and European samples (Bonferroni *t*-test,  $\alpha = 0.05$ ). High values on PC 2 indicated a supero-inferiorly

short and antero-posteriorly wide ramus with a posterior border that meets the corpus nearly at a right angle, as well as posterior thinning of the mandibular corpus. These features tended to distinguish the Arctic population from the other groups in the analysis. Low values indicated a narrow ramus with a high coronoid process relative to the condyle, and a lower gonion. The most influential landmarks for this axis were, by far, coronion (right and left) and gonion (right and left).

PC 3 (Fig. 3) accounted for 8.21% of the total variance. The two African populations tended to have lower scores on this axis than other groups, although their mean scores were not significantly different from those of most of the other samples. The European, Central American, and Oceanic groups had significantly higher mean scores than the East Africans. High scores along this axis indi-



**Fig. 3.** Modern human analysis. PC 1 plotted against PC 3. Shape differences between extremes of these components are shown at each end. Means and 95% confidence ranges (dotted lines) of 10 modern human populations are shown (abbreviations as in Fig. 2).

icated subequal heights of the condyle and coronoid process and a shorter, more vertical symphysis. Low scores indicated a high coronoid process relative to the condyle, and a wider angle at gonion. These features characterize the two African populations to some extent relative to other groups. The most influential landmarks for PC 3 included: the points on the condyle (right and left), posterior ramus (right and left), coronion (right and left), and to a lesser degree, gonion (right and left).

A discriminant analysis was used to determine how well the first 25 principal components (accounting for 91.4% of the total variance) classified the 10 populations. Posterior probabilities correctly classified 83.9% of individuals based on these factors by resubstitution (Table 7). Correct classification for each group ranged from 57.9% (South American sample) to 100% (South African sample). Slightly more than half (52%) of the misclassified specimens were classified into groups from the same major geographical region. These values are generally higher than those reported by Humphrey et al. (1999). Unlike that study, our Oceania sample showed a high degree of correct classification (94.4% compared to 60%). The Mahalanobis  $D^2$  distances between pairs of groups were calculated based on the first 25 principal components (Table 8). Samples from neighboring geographical regions were closer to one another than they were to other groups. The smallest distances were found between Central and South Americans, Oceanics and Polynesians, East and South Africans, Southeast Asians and Europeans, and Southeast Asians and North Asians. The largest distances were between Arctics and Oceanics, Arctics and Polynesians, and North Asians and Oceanics.

#### **Analysis of the combined fossils and recent human samples**

Neanderthals and *H. heidelbergensis* were significantly larger in centroid size than all recent human pop-

ulations and the Upper Paleolithic specimens, but not the Skhul/Qafzeh sample ( $t$ -test;  $P < 0.010$ ; Table 6). Skhul 5 and Qafzeh 9 were significantly larger than 4 of the 10 modern human populations. The Upper Paleolithic humans were only significantly larger than the two smallest human groups: South Africans and Southeast Asians.

The first principal component of the PCA (25.30% of the total variance) described the same overall mandibular shape as it did in recent humans, with low scores corresponding to long and narrow mandibles, and high scores reflecting short and wide mandibles. As in the first analysis, it showed a very strong population and climatic effect (both  $P < 0.0001$ ), but no species effect ( $P = 0.300$ ). The Neanderthal specimens were scattered along this axis, with mostly intermediate scores, and did not group with either the temperate- or cold-climate recent human samples. All Neanderthals except one had more positive scores than those of Mauer and Arago 13, which showed more elongated and narrower mandibles than Neanderthals. Although our sample of *H. heidelbergensis* is very small, this finding is consistent with the trend for a decrease in prognathism documented from *H. heidelbergensis* to *H. neanderthalensis* (e.g., Trinkaus, 2003). Skhul 5 and Qafzeh 9 had strongly negative PC 1 scores, the former being extreme in this regard, and fell with the warm-climate recent human samples. Three of the four Upper Paleolithic specimens showed very positive PC 1 scores, grouping with the temperate and cold-climate samples, although the fourth, Chancelade, showed a strongly negative score on this axis.

As in the recent human analysis, PC 2 (13.57% of the total variance) described the shape of the ramus. Low PC 2 scores corresponded to tall, thin, and antero-inferiorly angled rami, while high scores corresponded to short, wide, and vertically oriented rami, with gonion positioned relatively superiorly and medially. All the fossil specimens fell well within the range of recent human variation along this

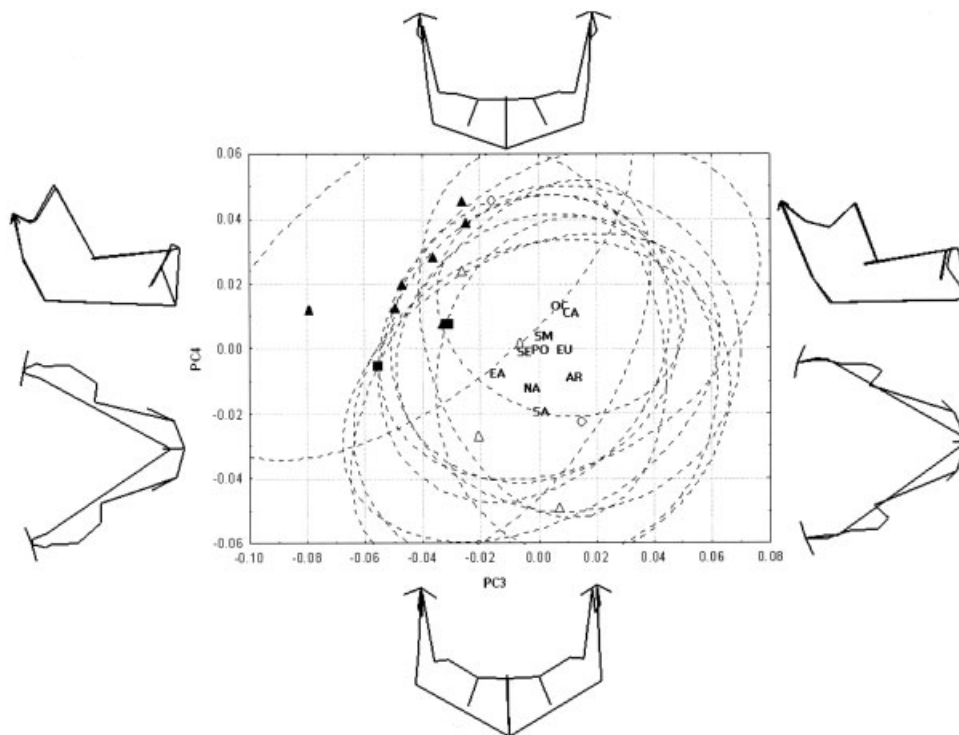




TABLE 8. Mahalanobis  $D^2$  distances between pairs of modern humans corrected for unequal sample sizes (Marcus, 1993)<sup>1</sup>

	AR	OC	CA	EA	EU	NA	PO	SA	SE	SM
AR	0.00									
OC	45.82	0.00								
CA	13.06	18.02	0.00							
EA	24.16	21.92	14.81	0.00						
EU	19.31	24.80	11.93	13.15	0.00					
NA	19.45	42.45	19.21	13.65	12.57	0.00				
PO	41.35	5.73	15.41	15.10	18.32	30.10	0.00			
SA	20.29	23.68	10.85	6.10	10.67	14.43	15.39	0.00		
SE	27.50	21.54	14.75	8.95	6.79	7.45	14.24	8.98	0.00	
SM	11.37	23.79	1.00	13.81	10.02	15.54	18.96	9.80	12.72	0.00

<sup>1</sup> Abbreviations as in Table 4.



**Fig. 4.** Fossil human analysis. PC 3 plotted against PC 4. Shape differences between extremes of these components are shown at each end. Means and 95% confidence ranges (dotted lines) of 10 modern human populations are shown (abbreviations as in Fig. 2). Fossil specimens are plotted individually. Neanderthals, solid triangles; *H. heidelbergensis*, solid squares; early anatomically modern humans, open diamonds; Upper Paleolithic Europeans, open triangles.

derthals than to any of the modern human groups. Interestingly, Skhul 5 and Qafzeh 9 were also very distant from all other samples, including Upper Paleolithic Europeans. However, they were generally closer to modern humans than to Neanderthals or *H. heidelbergensis*. They showed the smallest distance to the Oceanic sample. The Upper Paleolithic humans were very close to recent humans, showing the smallest  $D^2$  (squared distance) values to South Africans and South Americans.

### Allometry

Although the principal components separating Neanderthals from modern humans were not strongly correlated with centroid size, some component of allometry in the differences between Neanderthals and modern humans may be present. In order to evaluate this hypothesis, we explored allometric changes observed in our sample of recent humans. The results are depicted in Figure 5. In recent humans, small centroid size was associated with a relatively supero-inferiorly thin and antero-posteriorly elongate corpus; with a medial and superior position of gonion, a straight posterior margin of the ramus, and

posteriorly placed condyle; and a posterior placement of the distal margin of  $M_3$ . On the other hand, large centroid size was associated with a supero-inferiorly relatively deep and antero-posteriorly relatively short corpus; with a lateral position of gonion, a flexed posterior ramus, and a more anterior and higher placement of the coronoid (resulting in a deep mandibular notch); and an anterior placement of the distal margin of  $M_3$  relative to the anterior border of the ramus (resulting in a retromolar gap).

These results showed that only one feature commonly considered a derived Neanderthal trait, the retromolar gap, is associated with allometric changes in modern human mandibles. This finding is consistent with the previously described trend for greater retromolar spaces with increased mandibular size in Neanderthals, *H. heidelbergensis*, chimpanzees, gorillas, and modern humans in a two-dimensional geometric morphometrics study of mandibular morphology (Rosas and Bastir, 2004). It suggests that the presence of a retromolar gap on mandibular remains does not necessarily indicate Neanderthal affinities. Other traits found to characterize Neanderthals relative to modern humans, such as the medial position of gonion and inward slanting rami, the relatively short supero-inferiorly

TABLE 9. Mahalanobis  $D^2$  distances between pairs of recent and fossil human populations, corrected for unequal sample sizes (Marcus, 1993)<sup>1</sup>

	H	N	EAM	AR	OC	CA	EA	EU	NA	PO	SA	SE	SM	UP
H	0.00													
N	20.42	0.00												
EAM	66.90	66.03	0.00											
AR	71.35	86.36	80.96	0.00										
OC	25.40	42.94	39.69	34.88	0.00									
CA	53.15	61.46	52.94	9.12	14.48	0.00								
EA	41.98	60.48	70.30	19.75	19.04	12.50	0.00							
EU	59.51	67.19	70.41	15.82	21.20	9.15	12.53	0.00						
NA	76.47	80.24	93.26	17.83	35.48	15.01	11.51	10.33	0.00					
PO	30.94	38.65	46.15	31.04	4.81	12.63	13.48	15.77	26.52	0.00				
SA	53.42	69.75	51.22	14.57	20.60	7.61	5.11	9.67	11.84	13.27	0.00			
SE	59.73	69.02	70.64	22.05	19.21	11.67	7.73	5.63	5.30	13.13	8.55	0.00		
SM	61.42	68.47	56.34	8.58	19.57	0.25	12.24	8.15	12.87	15.78	6.99	10.07	0.00	
UP	45.31	60.13	52.19	15.52	20.49	11.76	15.23	14.64	24.96	19.53	10.58	19.55	10.59	0.00

<sup>1</sup> Abbreviations as in Table 6.

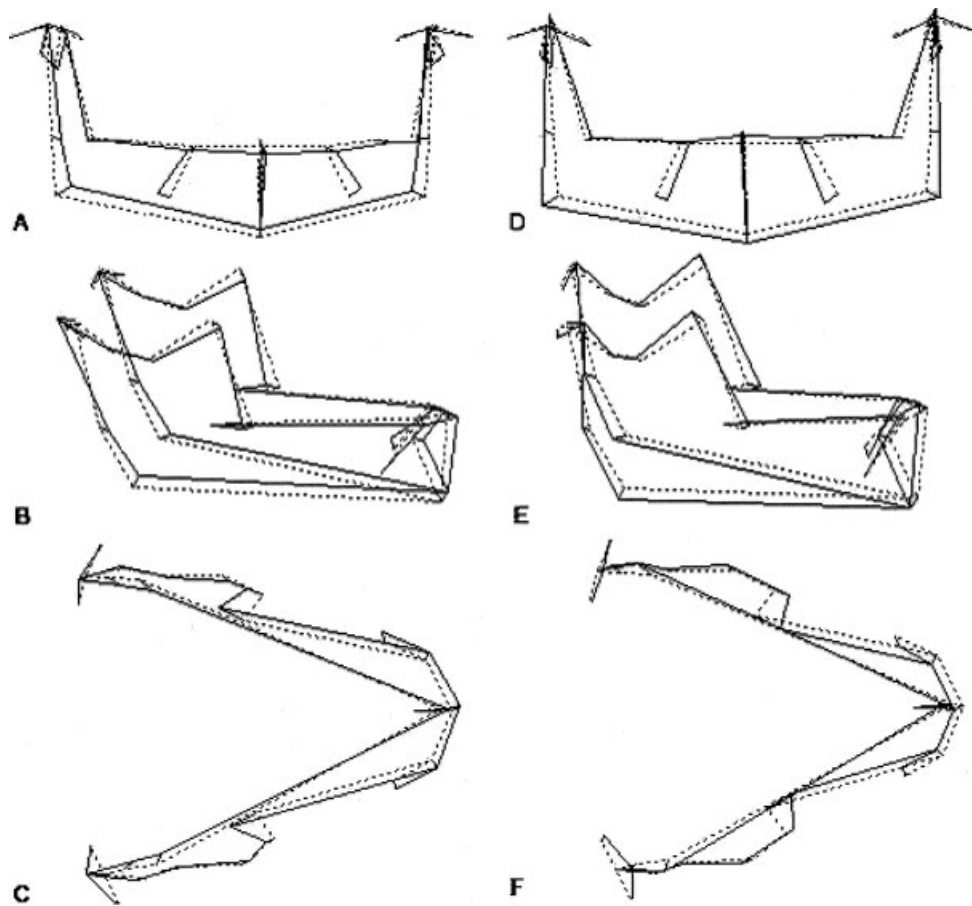


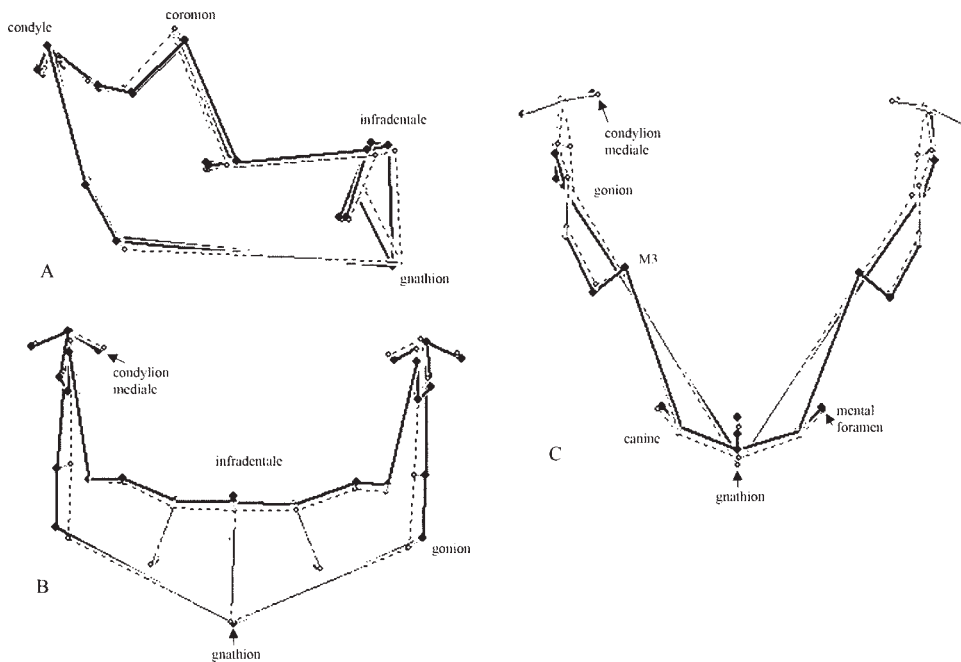
Fig. 5. Size-related shape changes in recent human mandibles. Dotted lines, mean configurations. A–C: Anterior, lateral, and superior views, respectively, of mandibular shape with decreasing centroid size (magnification set to –10). D–F: Anterior, lateral, and superior views, respectively, with increasing centroid size (magnification set to 10).

corpus, and the wide angle at gonion, were associated with smaller centroid sizes in modern humans, and therefore do not appear to be related to the large centroid size of the Neanderthal specimens.

**DISCUSSION**  
**Recent humans**

Consistent with our hypothesis 1A, the present study found geographic patterning in recent human mandibular shape, despite considerable overlap. Classification

success for the 10 geographic samples was higher than that found by Humphrey et al. (1999) (83.9% of the total sample correctly classified by resubstitution, compared to 74.3%), but was still lower than that observed with cranial linear measurements (Howells, 1973). As noted by Humphrey et al. (1999), greater classification success may be related to the larger number of variables: 13 in Humphrey et al. (1999), 70 in Howells (1973), and 28 3-D landmarks in this study. However, our results may not be directly comparable with those of Humphrey et al. (1999), as our samples do not represent biological entities in the sense of demes. The geographic pattern-



**Fig. 6.** Mean North American Arctic configuration (solid) compared to mean configuration of all modern humans (dotted). Lateral (A), frontal (B), and superior (C) views.

ing reported here may become less clear at a more fine-grained geographical scale.

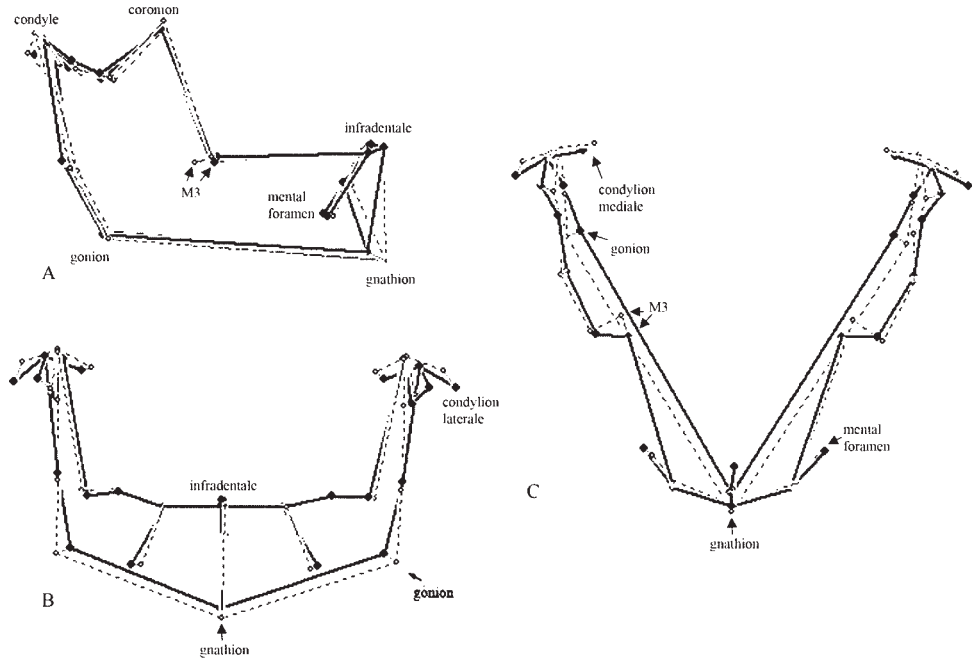
The first principal component in the analysis of the recent human sample showed strong population and climate effects. It separated groups along a climatic axis superimposed on a geographic pattern, consistent with both hypotheses 1A and 1B (that human mandibular morphology would show geographic and climatic patterning). Temperate or cold-climate groups were separated from warm-climate populations, while geographic neighbors grouped close to one another on this component. Southeast Asians, whose closest geographic neighbors among our samples are the North Asian group, were found in an intermediate position, as were South and Central Americans, whose closest geographic neighbors are the North American Arctic specimens. These findings indicate a combination of climate and geography (the latter probably reflecting population history) affecting this axis. Figure 2 shows a relatively short (antero-posteriorly) and wide (medio-laterally) mandible for the temperate and cold-climate groups, and a long (antero-posteriorly) and narrow (medio-laterally) mandible in the tropical and subtropical populations. That facial characteristics may reflect climate adaptation is an old idea. In particular, the flat face and expanded zygomatics of Asian populations were thought to be related to cold-climate adaptation by Coon et al. (1950). This claim, however, was not supported by later studies (Stegmann, 1965, 1967, 1970) and remains controversial. Further analysis of facial and expanded mandibular data sets will help clarify this issue.

The distinctly flat facial morphology of the North American Arctic populations has also been interpreted as related to the functional demands of a tough diet (including chewing frozen sealskins and bones) and of paramasticatory uses (such as using the teeth as a vice during tool manufacture; Balicki, 1970; Hylander, 1977; So, 1980; Antón, 1996a). The mandibles of Arctic populations were described as large and robust, with a short, broad, and oblique vertical ramus; a low and robust coronoid, resulting in a shallow mandibular notch; gonial eversion; a symphyseal height larger than the corpus height at  $M_2$ , resulting in a large gonial angle; and an

extremely wide bicondylar breadth (Hrdlička, 1940a; Hylander, 1977; Anderson, 1998). This morphology is often considered optimal for creating large vertical bite forces in response to dietary and paramasticatory demands (Hylander, 1977; Antón, 1996a; Anderson, 1998). Alaskan Eskimos were shown to have a greater ability to create large bite forces (Waugh, 1937) than either Scandinavians (Linderholm and Wennstrom, 1970) or Americans (Klatsky, 1942). Antón (1996a) found evidence that the anterior temporalis muscle, used in molar biting, is better developed in an Alaskan group compared to other human groups. Antón (1996b) also suggested that short faces with anteriorly positioned masseter muscles and medio-laterally broad rami could be responses to tough diets and high masticatory loads in macaques.

Our sample for the North American Arctic population is quite small. However, it had the largest centroid size among recent human groups. Furthermore, the Arctic mean configuration showed a low coronoid process, an antero-posteriorly broad ascending ramus, a laterally positioned gonion, and a supero-inferiorly tall symphysis. These features match previous descriptions (Anderson, 1998; Humphrey et al., 1999; see Fig. 6). Additionally, Arctic mandibles were found to be relatively short antero-posteriorly, a feature consistent with their flat faces. Among these shape differences, the short antero-posterior length, the great medio-lateral breadth of the mandible, and the lateral position of gonion separated the Arctic group along PC 1, which showed differences predominantly relating to climate and, to some extent, population history (as inferred from geography). This result is consistent with the hypothesis that facial flatness is related to cold-climate adaptation. It is less consistent with biomechanical interpretations (which see the large bicondylar breadth of these groups as increasing mechanical efficiency in unilateral biting; Hylander, 1977), as this morphology appears to be shared with other temperate/cold-climate populations that do not exhibit extreme masticatory and paramasticatory behaviors (North Asians and Europeans).

The North American sample was also found to be distinctive from other populations, albeit weakly, along PC



**Fig. 7.** Mean Neanderthal configuration (solid) compared to mean configuration of modern human sample (dotted). Lateral (A), frontal (B), and superior (C) views.

2. The breadth of the ramus and low position of the coronoid process relative to the condyle separated the North American Arctic sample along this component. These traits have been interpreted as relating to the functional idiosyncrasies of the Arctic mandible. A wide ramus is thought to increase the moment arm of the temporalis and masseter muscles, while the low position of the coronoid process results in a more vertical orientation of the temporalis. The anterior repositioning of both jaw adductors (and perhaps the medial pterygoid) will increase their mechanical advantage during biting and chewing (Hylander, 1977; Anderson, 1998; Humphrey et al., 1999). Again, this result is consistent with our hypothesis that the distinctive masticatory behavior of this group would be reflected in its mandibular morphology (hypothesis 1C). However, a greater sample size, both overall and for this population, will be necessary to fully evaluate these ideas.

In addition to the North American Arctic sample, the Oceanic and Polynesian groups were the most distinct from other human populations, as indicated by PCA and the Mahalanobis squared-distance analysis. Polynesian mandibles were described as being distinctive in their “rocker jaw” morphology, characterized by a convex inferior border of the mandibular body (Schendel et al., 1980). This aspect of mandibular morphology is not captured by our data. However, the mean configurations of the Oceanic and Polynesian groups were very similar to each other, as were their mean scores on the first three principal components. Both samples showed long, narrow mandibles, with relatively high and antero-posteriorly narrow rami. The two African samples were found to be somewhat distinct from other recent human groups on PC 3, although this separation was not strong.

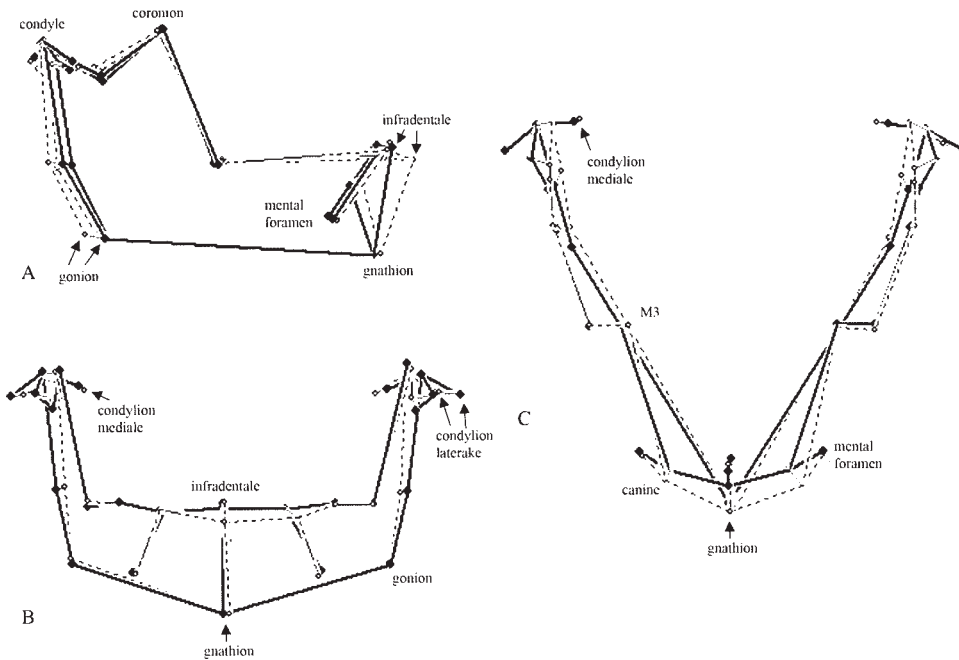
**Fossil humans**

As predicted (hypothesis 2A), mandibular shape was successful in separating modern humans from fossil hominids. All three taxa examined were classified correctly by substitution, with no misclassification between modern humans and Neanderthals. Neanderthals had a signifi-

cantly larger centroid size than all recent humans and the Upper Paleolithic sample (but not Skhul 5 and Qafzeh 9). After scaling for size, the mean Neanderthal configuration (Fig. 7) differed from the mean modern human configuration in traits consistent with previous descriptions: receding symphysis; posteriorly positioned mental foramen; lower placement of the condyle relative to the coronoid process; shallow mandibular notch; retromolar gap; more lateral placement of the condyles; and more medial position of the gonion (Boule, 1911–1913; Coon, 1962; Howells, 1973; Vandermeersch, 1981; Stringer et al., 1984; Tillier et al., 1989; Condemi, 1991; Franciscus and Trinkaus, 1995; Creed-Miles et al., 1996; Arensburg and Belfer-Cohen, 1998; Hublin, 1998; Rak, 1998; Rosas, 2001; Rak et al., 2002). Most of these features separated Neanderthals from modern humans in the PCA (PCs 3 and 4), with the exception of the position of the mental foramina. Williams and Krovitz (2004) also found this feature to be of lesser taxonomic value than previously proposed, in their study of Neanderthal and modern human mandibular ontogeny.

Although our analysis indicated that an asymmetric mandibular notch, a condition previously proposed as a Neanderthal autapomorphy (Rak, 1998; Rak et al., 2002), strongly separates Neanderthals from modern humans, we did not find any evidence that the mandibular notch joins the condyle more medially in Neanderthals than in modern humans, as found by Jabbour et al. (2002). However, we found that Neanderthal condyles were more laterally positioned relative to those of modern humans, both in the mean configuration comparisons and in the PCA (PC 4; Figs. 4, 7). We suggest that a combination of a “lateral expansion” of the condyle and a lateral rotation of the entire condyle process resulted in the various descriptions of this area.

We predicted that Neanderthals and the North Arctic sample would be similar in those aspects of their mandibular morphology that are related to similar masticatory or paramasticatory behavior (hypothesis 2B). Indeed, most Neanderthal specimens fall close to the North American Arctic population on PC 2, which we interpret as reflecting traits relating to masticatory and paramasticatory stress



**Fig. 8.** Mean Neanderthal configuration (solid) compared to mean configuration of *H. heidelbergensis* sample (dotted). Lateral (A), frontal (B), and superior (C) views.

in the latter sample (see above). This suggests that at least some features related to paramasticatory functional demands are shared between these two groups, even though the Mahalanobis squared distance between them was the greatest reported. However, the Upper Paleolithic and *H. heidelbergensis* specimens also fall close to the Arctic sample on this component, a finding that is inconsistent with hypothesis 2B, since these groups are not thought to have practiced such paramasticatory behaviors. A comparison of the Neanderthal and North American Arctic mean landmark configurations shows that the main similarity between these two samples concerns the low position of the coronoid process and hence the small supero-inferior height of the ramus, even though in Neanderthals the condyle is even more inferior, resulting in an asymmetric mandibular notch (not present in the Arctic configuration), and the ramus is narrower antero-posteriorly. The two samples also share a relatively elevated gonion compared to other recent humans, although in Neanderthals, the gonion is also much more medially placed. These shape characteristics are shared by the *H. heidelbergensis* and Upper Paleolithic specimens (but not by the earlier modern human specimens from the Near East), though these fossils also show relatively wide rami. It is therefore difficult to assess the functional implications of these features for Neanderthals.

Although only a weak relationship between centroid size and the principal components separating Neanderthals from recent humans was found, some influence of allometry on Neanderthal morphology could not be completely ruled out (hypothesis 2C). In order to assess the effect of allometry in producing the morphological differences between Neanderthal and modern human mandibular form, the size-related shape differences in recent humans were explored (Fig. 5). Our analysis suggests that the only proposed Neanderthal mandibular derived trait that occurs in modern humans with increased centroid size is the retromolar gap. This finding agrees with a previous study of two-dimensional landmarks (Rosas and Bastir, 2004), and indicates that the Neanderthal derived status of the retromolar gap should be treated with caution.

Our *H. heidelbergensis* sample is too small to statistically evaluate hypotheses about the evolutionary emergence of Neanderthal traits and about possible allometric effects in this process. The two *H. heidelbergensis* mandibles included here, Mauer and Arago 13, were significantly larger than those of all recent humans and Upper Paleolithic Europeans, but not significantly larger than the Skhul/Qafzeh sample. Comparisons of the scaled mean configurations of Neanderthals and *H. heidelbergensis* show that the two differ mostly in the antero-posterior length of the superior part of the corpus, resulting in a more posterior placement of infradentale and a more vertical orientation of the symphysis in Neanderthals; in the reduction of the width of the ramus, with the posterior ramus in a more forward position in Neanderthals; and in the lateral position of the condyle process in Neanderthals (Fig. 8). The two configurations also differ in the position of  $M_3$  relative to the anterior border of the ramus, with Neanderthals showing more of a retromolar gap. In the PCA, these specimens showed an intermediate position between Neanderthals and modern humans on PCs 3 and 4, and clustered with the warm-climate recent human groups along PC 1, reflecting the large antero-posterior length of their corpora.

These results are consistent with previous studies that found a reduction in the ramus width and in the anterior length of the mandible and the face from *H. heidelbergensis* to Neanderthals (Franciscus and Trinkaus, 1995; Trinkaus, 2003). Neither of the two *H. heidelbergensis* specimens included here show a retromolar gap, but it is unclear whether this was due to a wider ramus or a more posterior position of the distal end of the molar row (Rak, 1986; Franciscus and Trinkaus, 1995). The retromolar gap was found to be related to increasing size in taxa as diverse as modern humans, chimpanzees, gorillas, and the Atapuerca sample of *H. heidelbergensis* by Rosas and Bastir (2004) using two-dimensional landmarks, and in modern humans in the present study.

Both Skhul 5 and Qafzeh 9 fall among the warm-climate populations along PC 1, reflecting mandibles that are long relative to their breadth. Qafzeh 9, however, is outside the

95% confidence ellipse of any modern human sample along this axis, probably due to deformation (Vandermeersch, 1981). Both specimens fall among modern humans and outside the Neanderthal range on PC 3. Skhul 5, however, falls in the area of overlap between modern humans and Neanderthals along PC 4, reflecting the more medial position of its gonion and its somewhat receding symphysis. In the Mahalanobis  $D^2$  analysis, the two specimens were treated as a group. They showed very large distances from all samples, but were closest to the Oceanic and Polynesian recent humans. This result is similar to those obtained from other analyses of these specimens (e.g., Harvati, 2003b), and may be due both to the very small number of this sample and to the assumed deformed shape of Qafzeh 9.

Of the four Upper Paleolithic specimens included, two probably date to the Early Upper Paleolithic (Isturitz 1950-4-1, Aurignacian, and Grotte-des Enfants 6, Gravettian). The other two specimens date to the Late Upper Paleolithic (Chancelade and Oberkassel, both Magdalenian). All of these specimens overlap with recent humans along principal components 1–4. All but Chancelade group with the cold-climate specimens along PC 1. Although the Upper Paleolithic sample is very small, this result does not agree with findings, based on postcranial proportions and robusticity, that Early Paleolithic modern Europeans show warm-adapted morphology, with a reversal of this trend in Late Paleolithic specimens (e.g., Holliday 1997a,b; Pearson, 2000).

### CONCLUSIONS

This study found that human mandibular 3-D shape reflects considerable population history (as inferred from geography) as well as phylogenetic information, supporting our hypotheses 1A and 2A. Recent human populations from neighboring geographical regions group together in both the PCA and Mahalanobis  $D^2$  distance analysis, and discriminant analysis correctly classified the 10 recent human geographic groups at a somewhat higher rate than reported previously. Additionally, mandibular shape is found to reflect climate and, to some extent, functional adaptations (supporting our hypotheses 1B and 1C). These findings indicate a more complex combination of population history, climate, and function affecting mandibular form than was suggested by earlier research (Humphrey et al. 1999). Mandibular shape also successfully separates modern humans from fossil hominids. The traits that characterize Neanderthals and separate them from modern humans are consistent with previous descriptions of Neanderthal mandibles. Contrary to predictions (hypothesis 2B), no overall or specific similarities are found between Neanderthals and the North American Arctic sample that can be related to functional demands of paramasticatory practices. Finally, visualization of size-related shape differences in the recent human sample suggests that only one proposed Neanderthal mandibular trait, the retromolar gap, occurs in modern humans with increased centroid size (partially supporting hypothesis 2C), a finding consistent with previous studies (Rosas and Bastir, 2004). We therefore suggest caution in evaluating the derived status of this feature.

### ACKNOWLEDGMENTS

We thank Chris Stringer, Rob Kruszynski, Henry and Marie-Antoinette de Lumley, Philippe Menecier, Dominique Grimaud-Hervé, Ian Tattersall, Ken Mowbray, and

Jean-Jacques Hublin for allowing access to fossil specimens and casts. We also thank Matt Ravosa, Ralph Holloway, Shara Bailey, and two anonymous reviewers for helpful comments and suggestions.

### LITERATURE CITED

- Aitchison J. 1963. Sex differences in the teeth, jaws, and skulls. *Dent Pract* 14:52–57.
- Aitchison J. 1964. Some racial differences in human skulls and jaws. *Br Dent J* 116:25–33.
- Aitchison J. 1965. Some racial contrasts in teeth and dental arches. *Dent Mag Oral Top* 82:201–205.
- Anderson JY. 1998. Mandibular morphology in human populations: an examination of primary muscle attachments and architectonic models for the development of the ramus. *Am J Phys Anthropol [Suppl]* 26:64.
- Antón SC. 1996a. Tendon associated bone features of the masticatory system in Neandertals. *J Hum Evol* 31:391–408.
- Antón SC. 1996b. Cranial adaptation to a high attrition diet in Japanese macaques. *Int J Primatol* 17:401–428.
- Arensburg B, Belfer-Cohen A. 1998. *Sapiens* and Neandertals: rethinking the Levantine Middle Paleolithic hominids. In: Akazawa T, Aoki K, Bar-Yosef O, editors. *Neandertals and modern humans in western Asia*. New York: Plenum Press. p 311–322.
- Balicki A. 1970. *The Netsilik Eskimo*. Garden City, NJ: Natural History Press.
- Bennett S, Bowers D. 1976. *An introduction to multivariate techniques for social and behavioral sciences*. New York: Halstead Press.
- Boule M. 1911–1913. *L'homme fossile de la Chapelle-aux-Saints*. *Ann Paleontol* 6:11–172,7:21–56,8:1–70.
- Chang HH, Lee KL. 1990. A study on the linear ratio of condylar and coronoid processes in Korean adult normal faces. *Korean Acad Oral Maxillofac Surg* 16:55–62.
- Cleaver FH. 1937. A contribution to the biometric study of the mandible. *Biometrika* 29:80–112.
- Condemi S. 1991. Circeo I and variability among classic Neandertals. In: Piperno M, Scichilone G, editors. *The Circeo 1 Neanderthal skull: studies and documentation*. Rome: Istituto Poligrafico e Zecca dello Stato. p 339–353.
- Coon CS. 1962. *The origin of the races*. New York: Knopf.
- Coon CS, Garn SM, Birdsell JB. 1950. *Races: a study of the problems of race formation in man*. Springfield, IL: Charles C. Thomas.
- Corruccini, RS. 1984. An epidemiologic transition in dental occlusion in world populations. *Am J Orthod* 86:419–426.
- Corruccini RS. 1990. Australian Aboriginal tooth succession, interproximal attrition, and Begg's theory. *Am J Orthod Dentofacial Orthop* 97:349–357.
- Corruccini RS, Beecher R. 1982. Occlusal variation related to soft diet in a nonhuman primate. *Science* 218:74–76.
- Creed-Miles M, Rosas A, Kruszynski R. 1996. Issues in the identification of Neanderthal derivative traits at early post-natal stages. *J Hum Evol* 30:147–153.
- Dean D. 1993. The Middle Pleistocene *Homo erectus/Homo sapiens* transition: new evidence from space curve statistics. Ph.D. dissertation, City University of New York.
- De Villiers H. 1968a. The skull of the South African Negro. A biometrical and morphometrical study. Johannesburg: Witwatersrand University Press.
- De Villiers H. 1968b. Sexual dimorphism of the skull of the South African Bantu-speaking Negro. *S Afr J Sci* 64:118–124.
- Franciscus RG, Trinkaus E. 1995. Determinants of retromolar space presence in Pleistocene *Homo* mandibles. *J Hum Evol* 28:577–595.
- Frayser DW. 1992. The persistence of Neanderthal features in post-Neanderthal Europeans. In: Bräuer G, Smith FH, editors. *Continuity or replacement: controversies in Homo sapiens evolution*. Brookfield, VT: A.A. Balkema Publishers. p 179–188.
- Giles E. 1964. Sex determination of discriminant function analysis of the mandible. *Am J Phys Anthropol* 22:129–135.

- Harrower G. 1928. A biometric study of one hundred and ten Asiatic mandibles. *Biometrika* 20:279–293.
- Harvati K. 2003a. The Neanderthal taxonomic position: models of intra- and inter-specific craniofacial variation. *J Hum Evol* 44:107–132.
- Harvati K. 2003b. Quantitative analysis of Neanderthal temporal bone morphology using three-dimensional geometric morphometrics. *Am J Phys Anthropol* 120:323–328.
- Harvati K, Frost SR, McNulty KP. 2004. Neanderthal taxonomy reconsidered: implications of 3D primate models of intra- and interspecific differences. *Proc Natl Acad Sci USA* 101:1147–1152.
- Holliday TW. 1997a. Body proportions in Late Pleistocene Europe and modern human origins. *J Hum Evol* 32:423–447.
- Holliday TW. 1997b. Postcranial evidence of cold adaptation in European Neandertals. *Am J Phys Anthropol* 104:245–258.
- Howells WW. 1973. Cranial variation in man: a study by multivariate analysis of patterns of difference among recent human populations. Papers of the Peabody Museum of Archaeology and Ethnology, volume 67. Cambridge, MA: Harvard University.
- Hrdlička A. 1940a. Lower jaw. The gonial angle, I. The bigonial breadth, II. *Am J Phys Anthropol* 27:281–308.
- Hrdlička A. 1940b. Lower jaw further studies. *Am J Phys Anthropol* 27:383–467.
- Hublin JJ. 1998. Climatic changes, paleogeography and the evolution of Neanderthals. In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neanderthals and modern humans in western Asia. New York: Plenum Press. p 295–310.
- Humphrey LT, Dean MC, Stringer CB. 1999. Morphological variation in great ape and modern human mandibles. *J Anat* 195:491–513.
- Hunter WS, Garn SM. 1972. Disproportionate sexual dimorphism in the human face. *Am J Phys Anthropol* 36:133–138.
- Hylander WL. 1977. The adaptive significance of Eskimo craniofacial morphology. In: Dahlberg AA, Graber TM, editors. Orofacial growth and development. Paris: Mouton Publishers. p 129–170.
- Jabbour RS, Richards GD, Anderson JY. 2002. Mandibular condyle traits in Neanderthals and other *Homo*: a comparative, correlative, and ontogenetic study. *Am J Phys Anthropol* 119:144–155.
- Kaifu Y. 1997. Changes in mandibular morphology from the Jomon to modern periods in eastern Japan. *Am J Phys Anthropol* 104:227–243.
- Klatsky M. 1942. Masticatory stresses and their relation to dental caries. *J Dent Res* 21:387–390.
- Lavelle CLB. 1972. A comparison between the mandibles of Romano-British and nineteenth century periods. *Am J Phys Anthropol* 36:213–219.
- Lee DS, Choi KD. 1961. A study on mandible of Korean. *Korea J Med Digest* 8:971–1005.
- Lestrel PE. 2000. Morphometrics for the life sciences. River Edge, NJ: World Scientific Publishing Co. Pte. Ltd.
- Lieberman DE, Krovitz GE, Yates FW, Devlin M, St. Claire M. 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *J Hum Evol* 46:655–677.
- Linderholm H, Wennstrom A. 1970. Isometric bite force and its relation to general muscle force and body build. *Acta Odontol Scand* 28:679–689.
- Marcus LF. 1993. Some aspects of multivariate statistics for morphometrics. In: Marcus LF, Bello E, García-Valdecasas A, editors. Contributions to morphometrics. Madrid: Monografias Museo Nacional de Ciencias Naturales. p 99–130.
- Martin ES. 1936. A study of an Egyptian series of mandibles with special reference to mathematical models of sexing. *Biometrika* 28:149–178.
- McCown TD, Keith A. 1937. The Stone Age of Mount Carmel volume II: fossil human remains from the Levallois-Mousterian. Oxford: Clarendon Press.
- Moore WJ, Lavelle CLB, Spence TF. 1968. Changes in the size and shape of the human mandible in Britain. *Br Dent J* 125:163–169.
- Morant GM, Collett M, Adyanthaya NK. 1936. A biometric study of the human mandible. *Biometrika* 28:84–122.
- Muller EK. 1998. A test of the accuracy of techniques used to determine sex in the mandible. *Am J Phys Anthropol [Suppl]* 26:168–169.
- Murphy T. 1957. The chin region of the Australian Aboriginal mandible. *Am J Phys Anthropol* 15:517–535.
- O'Higgins P, Jones N. 1998. Facial growth in *Cercocebus torquatus*: an application of three-dimensional geometric morphometric techniques to the study of morphological variation. *J Anat* 193:251–272.
- O'Higgins P, Jones N. 2004. Morphologica. York: University of York.
- Pearson OM. 2000. Activity, climate, and postcranial robusticity: implications for modern human origins and scenarios of adaptive change. *Curr Anthropol* 41:569–607.
- Quam RM, Smith FH. 1998. A reassessment of the Tabun C2 mandible. In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neanderthals and modern humans in western Asia. New York: Plenum Press. p 405–421.
- Rak Y. 1986. The Neanderthal: A new look at an old face. *J Hum Evol* 15:151–164.
- Rak Y. 1998. Does any Mousterian cave present evidence of two hominid species? In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neanderthals and modern humans in western Asia. New York: Plenum Press. p 353–366.
- Rak Y, Ginzberg A, Geffen E. 2002. Does *Homo neanderthalensis* play a role in modern human ancestry? The mandibular evidence. *Am J Phys Anthropol* 119:199–204.
- Rohlf FJ. 1990. Rotational fit (Procrustes) methods. In: Rohlf FJ, Bookstein FL, editors. Proceedings of the Michigan Morphometrics Workshop. Ann Arbor: University of Michigan Museum of Zoology. p 227–236.
- Rohlf FJ. 2000. Statistical power comparisons among alternative morphometric methods. *Am J Phys Anthropol* 111:463–478.
- Rohlf FJ, Marcus LF. 1993. A revolution in morphometrics. *Trends Ecol Evol* 8:129–132.
- Rosas A. 1992. Ontogenia y filogenia de la mandíbula en la evolución de los homínidos. Aplicación de un modelo de morfogénesis a las mandíbulas fósiles de Atapuerca. Ph.D. thesis. Madrid: Complutense University.
- Rosas A. 2001. Occurrence of Neanderthal features in mandibles from the Atapuerca-SH site. *Am J Phys Anthropol* 114:74–91.
- Rosas A, Bastir M. 2002. Thin-plate spline analysis of allometry and sexual dimorphism in the human craniofacial complex. *Am J Phys Anthropol* 117:236–245.
- Rosas A, Bastir M. 2004. Geometric morphometric analysis of allometric variation in the mandibular morphology of the hominids of Atapuerca, Sima de los Huesos site. *Anat Rec* 278:551–560.
- Schendel SA, Walker G, Kamisugi A. 1980. Hawaiian craniofacial morphometrics: average Mokapuuan skull, artificial cranial deformation, and the “rocker” mandible. *Am J Phys Anthropol* 52:491–500.
- Singleton M. 2002. Patterns of cranial shape variation in the Papionini (Primates: Cercopithecoidea). *J Hum Evol* 42:547–578.
- Slice DE. 1992, 1994. © GRF-ND: generalized rotational fitting of n-dimensional landmark data. Stony Brook: Department of Ecology and Evolution, State University of New York.
- Slice DE. 1994–1999. © Morpheus et al., software for morphometric research. Stony Brook: Department of Ecology and Evolution, State University of New York.
- Slice DE. 1996. Three-dimensional generalised resistant fitting and the comparison of least-squares and resistant fit residuals. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice D, editors. Advances in morphometrics. New York: Plenum Press. p 179–199.
- So JK. 1980. Human biological adaptation to arctic and subarctic zones. *Annu Rev Anthropol* 9:63–82.
- Spencer MA, Demes B. 1993. Biomechanical analysis of masticatory system configuration in Neandertals and Inuits. *Am J Phys Anthropol* 91:1–20.
- Steggmann AT. 1965. A study of relationships between facial cold response and some variables of facial morphology. *Am J Phys Anthropol* 23:355–362.

- Steggmann AT. 1967. Frostbite of the human face as a selective force. *Hum Biol* 39:131–144.
- Steggmann AT. 1970. Cold adaptation and the human face. *Am J Phys Anthropol* 32:243–250.
- Stefan VH, Trinkaus E. 1998. Discrete trait and dental morphometric affinities of the Tabun 2 mandible. *J Hum Evol* 34:443–468.
- Stringer CB, Hublin JJ, Vandermeersch B. 1984. The origin of anatomically modern humans in Western Europe. In: Smith FH, Spencer F, editors. *The origins of modern humans: a world survey of the fossil evidence*. New York: Liss. p 51–135.
- Thorne AG, Wolpoff MH. 1992. The multiregional evolution of humans. *Sci Am* 266:76–83.
- Tillier AM, Arensburg B, Duda H. 1989. La mandibule et les dents. In: Bar-Yosef O, Vandermeersch B, editors. *Le squelette Mousterien de Kebara 2*. Paris: CNRS Éditions. p 97–111.
- Trinkaus E. 2003. Neanderthal faces were not long; modern human faces are short. *Proc Natl Acad Sci USA* 100:8142–8145.
- Trinkaus E, Moldovan O, Milota S, Bilgăr A, Sarcina L, Athreya S, Bailey S, Rodrigo R, Mircea G, Migham T, Ramsey CB, van der Plicht J. 2003. An early modern human from the Peștera cu Oase, Romania. *Proc Natl Acad Sci USA* 100:11231–11236.
- Vandermeersch B. 1981. *Les hommes fossiles de Qafzeh (Israel)*. Cahiers de paléontologie. Paris: CNRS Éditions.
- Waugh LM. 1937. Dental observations among Eskimos. *J Dent Res* 16:355–356.
- Weidenreich F. 1933. The mandibles of *Sinanthropus pekinensis*: a comparative study. *Palaeontol Sin [D]* 7:1–162.
- Williams FL, Krovitz GE. 2004. Ontogenetic migration of the mental foramen in Neanderthals and modern humans. *J Hum Evol* 47:199–219.
- Wood BA, Yu L, Willoughby C. 1991. Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record. *J Anat* 174:185–205.