

Chapter 16

A Three-Dimensional Look at the Neanderthal Mandible

Katerina Harvati, Nandini Singh, and Elisabeth Nicholson López

Abstract 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. These features have been shown to separate Neanderthals from modern humans in both non-metric and metric, including 3-D geometric morphometric, studies. However the degree to which these differences are related to size and function is still under discussion. The aim of this study is to further assess the effects of allometry and evaluate the influence of masticatory and paramasticatory activities on mandibular shape using a morphological integration approach. Data were collected in the form of three-dimensional coordinates of 27 landmarks, superimposed using generalized Procrustes analysis, and analyzed using canonical variates, regression and partial least squares analyses. Consistent with previous findings, Neanderthals are separated from modern human mandibles in the canonical variates analysis. However, partial least squares analysis indicates a similar pattern of integration for the two human groups, suggesting homology across modern humans and Neanderthals in the mandibular features examined. This finding does not support a paramasticatory hypothesis for Neanderthal mandibular shape, although it also does not refute this hypothesis. Finally, allometry was found to influence the expression of the retromolar gap.

Keywords Mandibular morphology • Variation • Integration • Function • Phylogeny • Neanderthals • Geometric morphometrics

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Introduction

Differences between Neanderthal and modern human mandibular morphology have been extensively documented and include both archaic and presumed derived characters. Primitive features retained in Neanderthal mandibles include overall robusticity and a receding symphysis which results in the absence of a mental eminence or chin. Proposed derived traits include a posteriorly positioned mental foramen; a large retromolar space; a rounder, less angled gonial area; a mandibular notch that meets the condyle in a more medial position, resulting in a laterally expanded condyle; a shallow and asymmetric mandibular notch with a higher coronoid process than condyle; very deep submandibular and pterygoid fossae; and an oval-horizontal shape of the mandibular foramen. These features have been shown to successfully discriminate Neanderthals from modern human in both metric and non-metric analyses (Fig. 16.1; Boule 1911–1913; Coon 1962; Vandermeersch 1981; Stringer et al. 1984; Tillier et al. 1989; Condemi 1991; Rosas 1992, 2001; Franciscus and Trinkaus 1995; Creed-Miles et al. 1996; Arensburg and Belfer-Cohen 1998; Hublin 1998; Rak 1998; Jabbour et al. 2002; Rak et al. 2002; Trinkaus et al. 2003; Nicholson and Harvati 2006). However, the degree to which Neanderthal mandibular morphology is influenced by allometry and by masticatory adaptations is still a matter of discussion (see e.g. Humphrey et al. 1999; Nicholson and Harvati 2006).

Allometry

Recent studies have evaluated the role of size and allometry in producing Neanderthal-like mandibular morphology. Rosas and Bastir (2002) explored the allometric trends in the human craniofacial complex using 2D geometric morphometric techniques. They found that size-related variation in the mandible among modern humans occurs mainly in the vertical dimensions of the ramus. In a more recent study using the same methods, these authors (Rosas and Bastir 2004) evaluated the

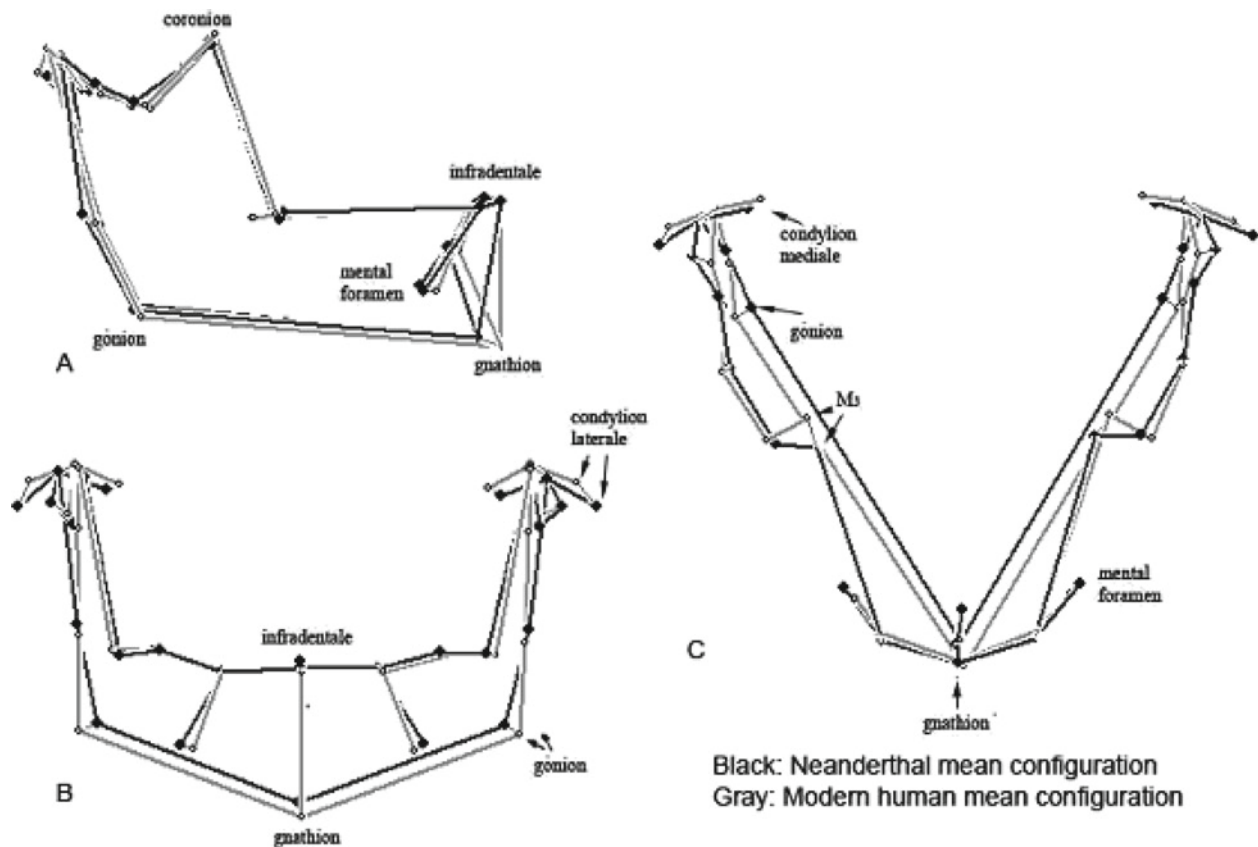


Fig. 16.1 Mean Neanderthal mandibular configuration superimposed with the mean modern human configuration (Adapted from Nicholson and Harvati 2006)

role of size in a large sample of hominoids, including modern and Pleistocene humans. They found a trend for greater retromolar spaces with increased mandibular size in Neanderthals, *H. heidelbergensis*, chimpanzees, gorillas, and modern humans, suggesting that this feature may not necessarily indicate Neanderthal affinities. This result agrees with those of Nicholson and Harvati (2006), who, using 3D geometric morphometric techniques, found that increased mandibular size in modern humans does not produce Neanderthal-like morphology with the exception of the retromolar space. All of these studies used regression of shape on centroid size to evaluate allometric shape differences. Recently, however, the logarithm of centroid size has been shown to be a more appropriate size variable for use in such analyses (see Mitteroecker et al. 2004), thus throwing these results into question.

Biomechanics

Several biomechanical hypotheses have been proposed to explain the combination of features exhibited by Neanderthal cranio-mandibular form (Linderholm and Wennstrom 1970; Smith 1983; Rak 1986; Demes 1987; Trinkaus 1987; Smith

and Paquette 1989; Antón 1990, 1994a, 1996a; Spencer and Demes 1993; Lieberman et al. 2004; O'Connor et al. 2005). A number of these researchers have linked Neanderthal facial and mandibular morphology to paramasticatory adaptations.

Excessive attrition on the anterior dentition, differential occlusal wear patterns, along with the presence of degenerative disease in the temporo-mandibular joint of Neanderthals was attributed to heavy loading on the anterior dentition and commonly referred to as the “anterior dental loading hypothesis” (hereafter ADLH; Smith 1983; Rak 1986). Neanderthal facial morphology was therefore hypothesized to be an adaptive response to heavy paramasticatory activities, such as using “teeth-as-tools” (Brace et al. 1981; Smith 1983). An assumption of the ADLH is that those activities generated high-magnitude forces on the anterior dentition, leading to extensive occlusal loading and wear on the anterior teeth (Rak 1986; Demes 1987; Smith and Paquette 1989).

To test some of the assumptions made by the ADLH, Spencer and Demes (1993) conducted a quantitative study of the Neanderthal masticatory system. Their approach included pair-wise comparisons of Neanderthal facial morphology with that of Inuit and other Native American modern humans. Because the Inuit are known to produce intense incisal bite

force, they served as a good comparative model for Neanderthals (Balicki 1970; Hylander 1977). Spencer and Demes' biomechanical analysis of bite-force production efficiency showed that Neanderthals share a number of morphological similarities with the Inuit that are possibly related to extensive usage of the anterior teeth. Moreover, pair-wise comparisons between Neanderthals and Middle Pleistocene hominins showed that Neanderthal anterior dental architecture was better adapted to repeated and high-level usage than other Pleistocene hominins'. Based on their findings, these authors concluded that the Neanderthal face was well-designed for and capable of high-force production. However, their study was based entirely on the face and did not include elements of the mandible.

Conversely, others have suggested that the facial morphology of Neanderthals lacked the ability to produce high anterior bite forces. According to Trinkaus (1987), large anterior dentition was not related to intensified usage of incisor teeth in Neanderthals. Their overall reduction in facial robusticity, posterior placement of the zygomatico-ramal region and anterior placement of the dentition further implied a lack of ability to produce high-level masticatory loads. According to Trinkaus (1987), this particular combination of posteriorly placed masticatory muscles and mid-facial prognathism reduced the potential of generating heavy bite forces in Neanderthals, thus refuting the assumptions made by the ADLH that Neanderthal cranio-mandibular morphology was mechanically advantageous for anterior tooth use.

This interpretation was supported by the work of Antón (1990, 1994a). She conducted a quantitative study on the amount and capability of bite force generated by Neanderthals to evaluate the extent to which these biomechanical factors contributed to the evolution of the Neanderthal face. Based on low estimates of bite force production and occlusal loading, Antón concluded that Neanderthals were less capable of and efficient at generating high-magnitude bite force than the modern humans in her comparative sample. In other words, she rejected the ADLH hypothesis as an explanation for the evolution of Neanderthal cranio-mandibular structure.

More recently, O'Connor et al. (2005) conducted a more comprehensive study on bite force capability and efficiency in Neanderthals and modern humans. Their overall results indicated that masticatory biomechanical explanations such as "bite force dissipation" do not adequately account for the underlying mechanisms driving Neanderthal facial and mandibular form, concurring with Trinkaus (1987) and Antón (1990, 1994a). However, their results differed from Antón's (1990, 1994a) in that they found less of a difference in force production efficiency between Neanderthals and modern humans than indicated by her study. Their findings further suggested that size did not affect force-production "efficiency" of the cranio-mandibular system, although force production "capability" was significantly correlated with overall size.

The majority of these studies have focused on the effects of biomechanical forces in the evolution of overall facial architecture in Neanderthals. And even though they reached diverging conclusions on the degree of impact of biomechanical factors on Neanderthal cranio-mandibular morphology, a point of agreement among the studies was the excessive and repetitive usage of the anterior dentition by Neanderthals.

This study does not propose to test biomechanical hypotheses contributing to Neanderthal mandibular features. Instead, it aims to examine whether increased dental attrition found in Neanderthals impacts the integration of the anterior and posterior regions of the mandible and, consequently, contributes to the shape variation seen between modern human and Neanderthal mandibles. Studies on mandibular patterns of integration are few and primarily on aspects of the mouse mandible (Cheverud et al. 1991; Leamy 1993; Klingenberg et al. 2003) with the exception of Bastir et al. (2005). Morphological integration is generally defined as the coordinated variation between units of a phenotype (Olson and Miller 1958; Klingenberg et al. 2001a). The pattern and degree of integration among anatomical units or subsets is correlated with the degree of developmental and functional relatedness among those subsets. For example, a subset of traits related due to masticatory activity is characterized as a functional unit.

So far no work has been done exclusively on morphological integration in the mandible of Pleistocene hominins and modern humans. Though exploring integration patterns, Bastir et al. (2005) included aspects of the cranium, with the primary objective of determining the degree of morphological integration between the cranium and mandible.

Extensive research on murine mandibles has contributed greatly to our general understanding of mandibular integration patterns and allows for further testing of similar functional hypotheses in a paleoanthropological context. Previous studies have shown that the alveolar (tooth bearing corpus) and ascending ramus are two key regions of variation in the mandible (Atchley and Hall 1991). Examining mandibular patterns of integration in modern humans and Neanderthals is a novel way of investigating the underlying processes that generate morphological variability in modern and fossil human mandibles.

Our Goals

The goals of the present study are: (1) To further explore the effect of size and allometry on modern human and Neanderthal mandibular shape using a size-shape analysis. Only the modern human sample was used in this analysis, as Neanderthals differ from modern humans both in shape and in their greater size. (2) To evaluate the influence of masticatory and paramasticatory behaviours on mandibular shape using a morphological integration approach to understanding the shape differences

between Neanderthals and modern humans. By dividing the mandible into the anterior and posterior regions, we hypothesized that given the repetitive usage of the anterior dentition in Neanderthals, the pattern and degree of integration between the alveolar region and ascending ramus of Neanderthals will be different from other Pleistocene and modern humans.

Materials and Methods

Samples

Our modern human sample is a subset of that used by Nicholson and Harvati (2006) and comprises 141 mandibles (Table 16.1) from 10 relatively broad geographic regions. These samples do not represent biological populations in the sense of demes. The fossil sample comprises two Middle

Table 16.1 Modern human samples from the American Museum of Natural History included in this study

Population	Specimens
Total	141
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, Bantu)	8
Europe	26
South America	11
Central America (Central America and Mexico)	9
North America Arctic (Alaska, Greenland, and Northern Canada)	10

Pleistocene European specimens, seven Neanderthals, seven Upper Paleolithic specimens from Europe and Asia, and two Late Pleistocene early anatomically moderns (Table 16.2). Where original specimens were unavailable for study, casts were measured from the collections of the Departments of Anthropology of the American Museum of Natural History and New York University, and of the Department of Human Evolution of the Max Planck 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 27 landmarks, were included in this study, limiting sample sizes for both recent and fossil groups. Sex was known only for few specimens in each sample, making an assessment of sexual dimorphism in mandibular shape impossible. Although the mandible is sexually dimorphic (see e.g. Morant et al. 1936; Martin 1936; Hrdlička 1940a, b; De Villiers 1968a, b; Hunter and Garn 1972; Humphrey et al. 1999), here we pooled sexes in our analyses due to the lack of secure sex assignments for either recent or fossil specimens.

Data

Twenty-seven landmarks, represented by 81 three-dimensional coordinates and selected to represent the overall shape of the mandible, were collected with a Microscribe 3DX digitizer

Table 16.2 Fossil sample used in this study^a

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

^aAMNH 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

^bIndicate casts from the collections of the AMNH, MPI and NYU

Table 16.3 Definitions of landmarks used. The first 12 landmarks were collected from both right and left sides

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

(Table 16.3). Three of these were located on the midsagittal plane; the others consisted of 12 pairs of homologous points on the left and right sides. All recent human specimens were measured by EN, as were most of the casts of fossil specimens used. Some casts and all the original fossils were measured by KH (for inter- and intra-observer error assessment see Nicholson and Harvati 2006).

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.

Methods

The landmark coordinates were superimposed using generalized Procrustes analysis (GPA) in Morphologika (O'Higgins and Jones 2006). GPA superimposes the specimens landmark configurations by translating them to 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 removes 'size' as a factor (although size-related shape differences may remain). 'Shape' and 'size' can therefore be analyzed separately (Rohlf and Marcus 1993; Slice 1996; O'Higgins and Jones 1998, 2006).

Size-Shape Principal Components Analysis

Here we evaluate the effect of size on mandibular morphology by performing a principal components analysis on the Procrustes aligned coordinates and logarithm of centroid size, a more appropriate proxy variable for size than centroid size (see Mitteroecker et al. 2004), using the software Morphologika (O'Higgins and Jones 2006). Because the Pleistocene fossil humans are differentiated from modern humans by their larger size in addition to their shape differences, we conducted this analysis on the modern human sample alone. In this way we were able to evaluate whether increased size in the modern human mandible results in Neanderthal-like morphology.

Partial-Least Squares Analysis (PLS)

For the purpose of the analysis, the mandibular landmarks were divided into two subsets *a priori*, representing the alveolar (tooth-bearing) and ascending ramus (attached to the skull and muscles of mastication); this sub-division is based on previous work on the development and morphological integration of mouse mandibles (e.g. Atchley and Hall 1991; Klingenberg et al. 2003). Prior to conducting the PLS analysis, a GPA was performed on the subset of landmarks for the anterior and posterior regions separately. This was done in order to reduce possible effects of extra correlations from the original Procrustes fit.

A two-block PLS analysis of shape variables was conducted to examine co-variation patterns between the anterior and posterior parts of the mandible. This method finds pairs of axes, one axis per block of variables, which successively account for the maximum amount of covariance between the two sets of variables examined. Each PLS axis in one block is only correlated to the corresponding axis in the other block, but not to the other PLS axes in that set. Therefore, the patterns of covariance can be analyzed one pair of PLS axes at a time (Bookstein et al. 2003; Klingenberg et al. 2003).

In addition, permutation tests were conducted to assess the statistical significance of the observed correlations between blocks.

Results

Allometry

As expected, the first principal component was very strongly related to variation in size (see Fig. 16.2). Visualization along this axis (Fig. 16.3) allowed for an evaluation of the presence of Neanderthal-like morphology in large modern human mandibles. Larger modern human mandibles are characterized by a medio-laterally wider and antero-posteriorly shorter overall mandibular shape; a supero-inferiorly higher ramus and symphysis; a antero-posteriorly wider ramus; and a lightly more laterally projecting gonion. The features commonly described as “Neanderthal-like” among modern humans refer to a more anterior placement of the

distal margin of the M_3 , which results in a morphology? similar to the Neanderthal retromolar space, and secondly, a coronoid process that is higher than the condyle. The latter trait is exhibited by Neanderthal mandibles, which, however, display several additional differences in this area from modern humans (i.e. a shallow, asymmetric notch, a laterally expanded condyle, a more medial placement of the root of the sigmoid notch; see Rak 1998; Jabbour et al. 2002; Rak et al. 2002; Nicholson and Harvati 2006). Our results very closely match those found previously by Rosas and Bastir (2002, 2004) and Nicholson and Harvati (2006).

Co-variation Between the Anterior and Posterior Regions

For the pooled modern human and fossil PLS analysis, the first axis accounts for 64.91% of the total co-variance (Fig. 16.4), with a correlation of $r=0.62$. The P -value of the permutation test is not statistically significant ($P=0.75$),

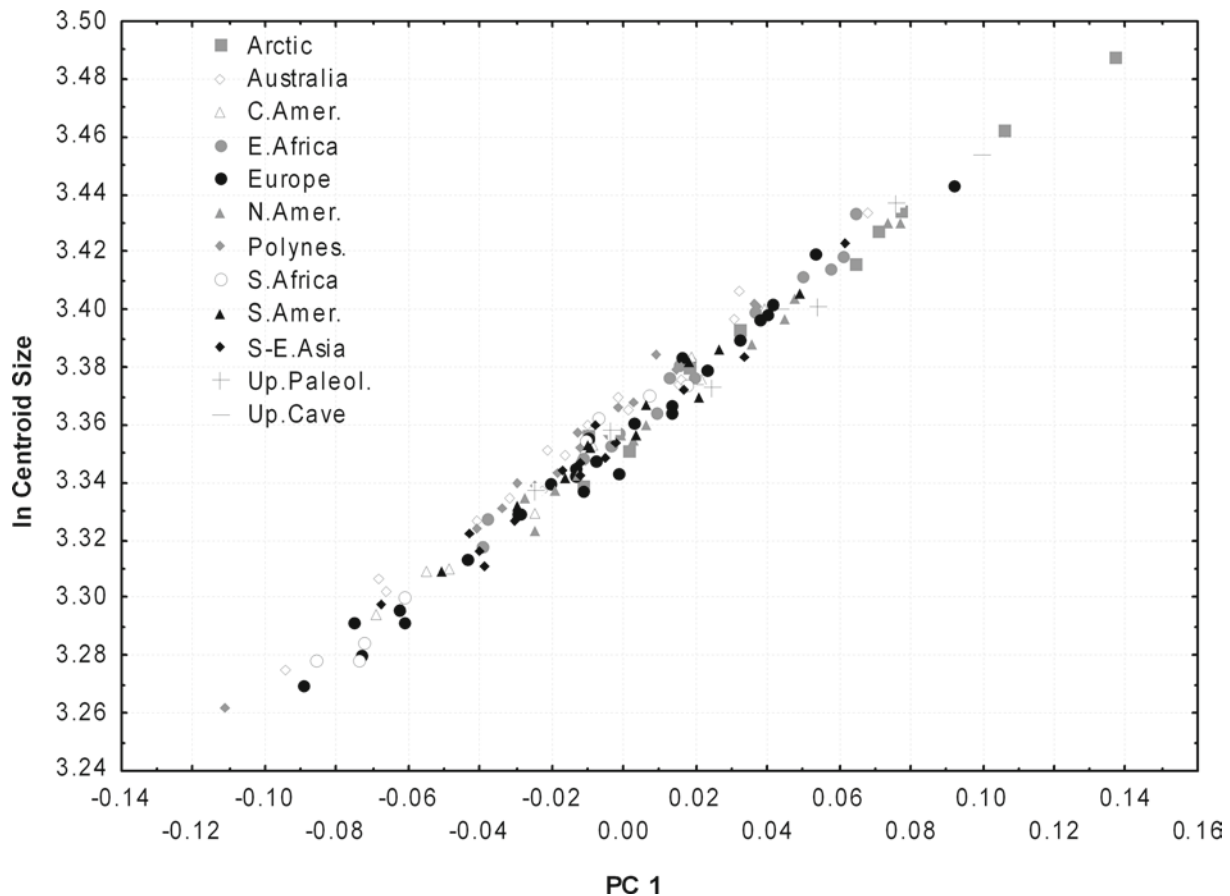


Fig. 16.2 PC 1 plotted against log centroid size in the size-shape analysis of the modern human sample

Fig. 16.3 Shape differences along PC 1, associated with small (*left*) and large (*right*) size among modern humans. Lateral (*top*), frontal (*middle*) and occlusal (*bottom*) views

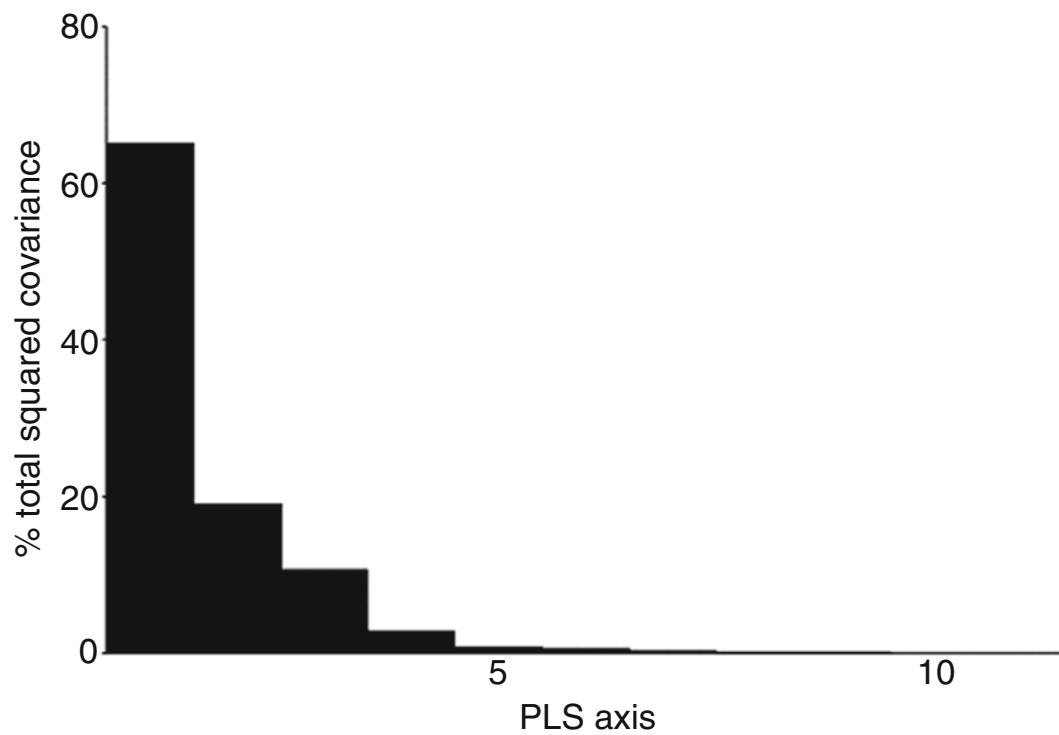
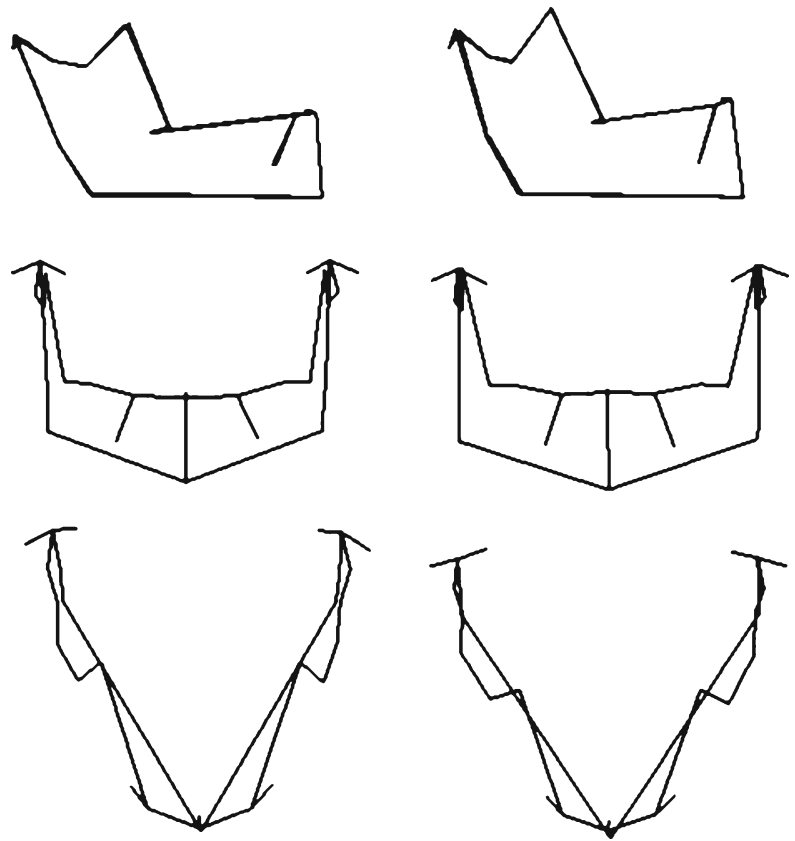


Fig. 16.4 Plot showing the distribution of total% co-variance on the respective PLS axes

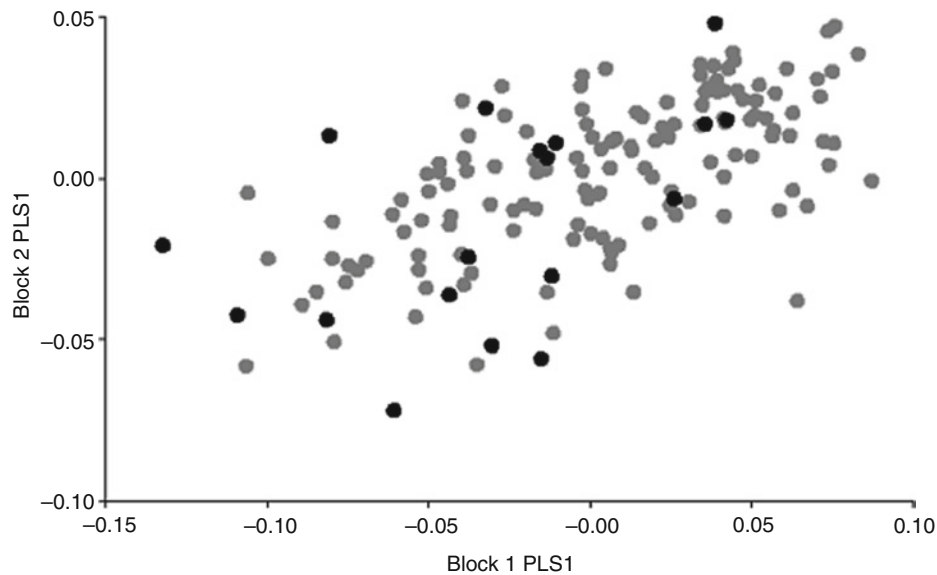


Fig. 16.5 Distribution of groups along PLS 1. Fossils are represented by the *black dots* and modern humans by *gray dots*

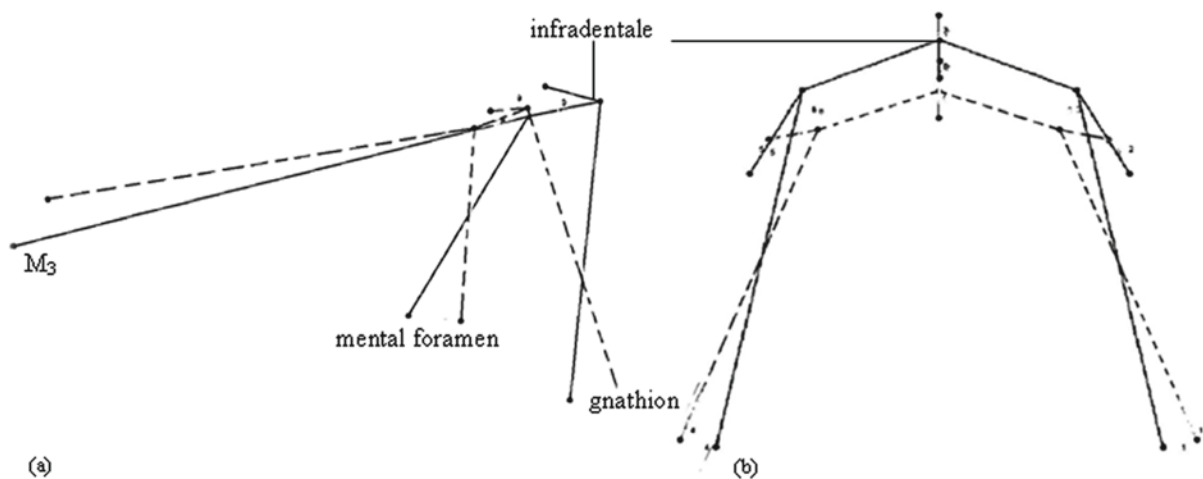


Fig. 16.6 Shape differences in block 1 are shown (a) in lateral view and (b) in superior view along PLS 1: high scores are represented by the *dashed line* and low scores by the *solid line*

suggesting a strong association between the two blocks. The trend in the distribution of groups along PLS I (Fig. 16.5) indicates a shared pattern of integration, with no clear separation between Neanderthals and other Pleistocene and modern humans. The distribution along this axis reflects modern human variation, with the fossils not only sharing the slope, but also falling within the range of this variation. Low scores on PLS I relate to shape changes associated with a more forwardly placed alveolar region, posteriorly retracted symphysis area, reduced distance between the M_3 s and posteriorly placed mental foramen (Fig. 16.6). Corresponding changes in the posterior region relate to an antero-posteriorly wider

ascending ramus, shallow mandibular notch and medially drawn in gonion (Fig. 16.7). High scores on this axis show a less anteriorly placed alveolar region, forwardly placed symphysis, wide posterior alveolar region (laterally expanded), and anteriorly placed mental foramen relative to the position of M_3 (Fig. 16.6). Related shape changes in the posterior region are associated with an antero-posteriorly narrow ascending ramus, deep mandibular notch and laterally expanded gonion (Fig. 16.7).

PLS II, which accounts for 19.8% of the total co-variance in the sample, with a moderate correlation coefficient of $r = 0.37$, shows a slight separation between Neanderthals and

Fig. 16.7 Shape differences in block 2 are shown (a) in lateral view and (b) in posterior view along PLS 1; high scores are represented by the *dashed line* and low scores by the *solid line*

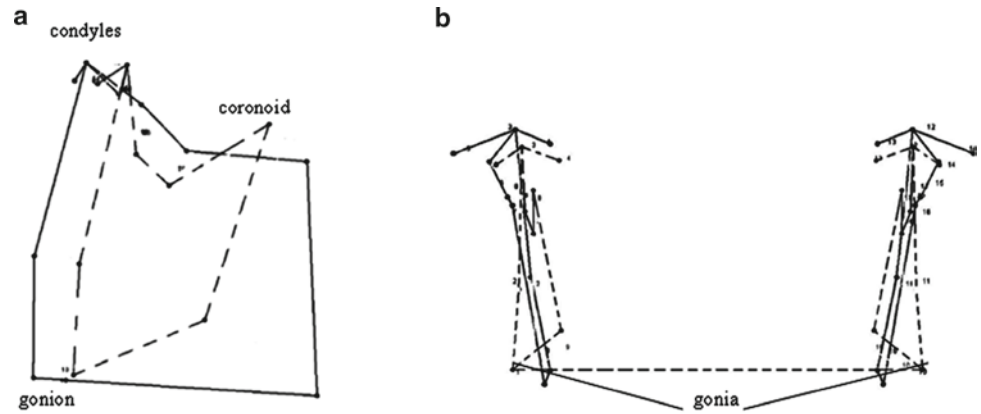
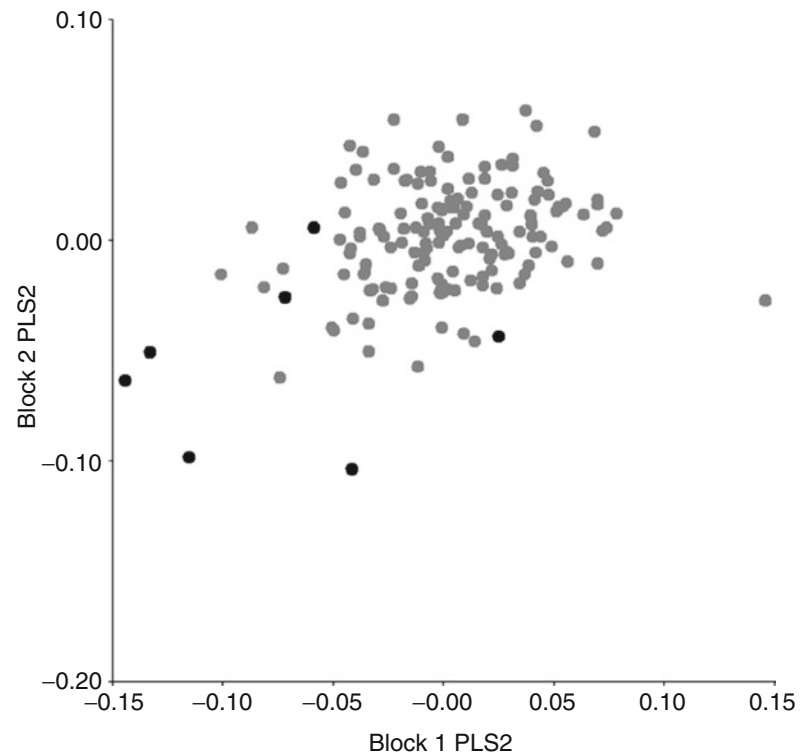


Fig. 16.8 Distribution of groups along PLS II. Neanderthals represented by *black dots* and other Pleistocene and modern humans by *gray dots*



other groups (Fig. 16.8). Neanderthals having lower scores on PLS II than the other taxa suggests a mean difference between the two groups. However, as mentioned earlier, the trend in the distribution of modern human and Neanderthal specimens along the regression line is similar, showing no distinct differences in the respective patterns of integration. Low scores on this axis relate to a posteriorly retracted lower

symphysis and slightly laterally expanded alveolar region (indicated by position of distal M_3 , suggesting a wider mandible (Fig. 16.9). Associated shape changes in the posterior part consist of a shallow and asymmetric mandibular notch with medially (inward) shifted gonion (Fig. 16.10). These shape differences correspond well with those described for Neanderthals and modern humans in the principal

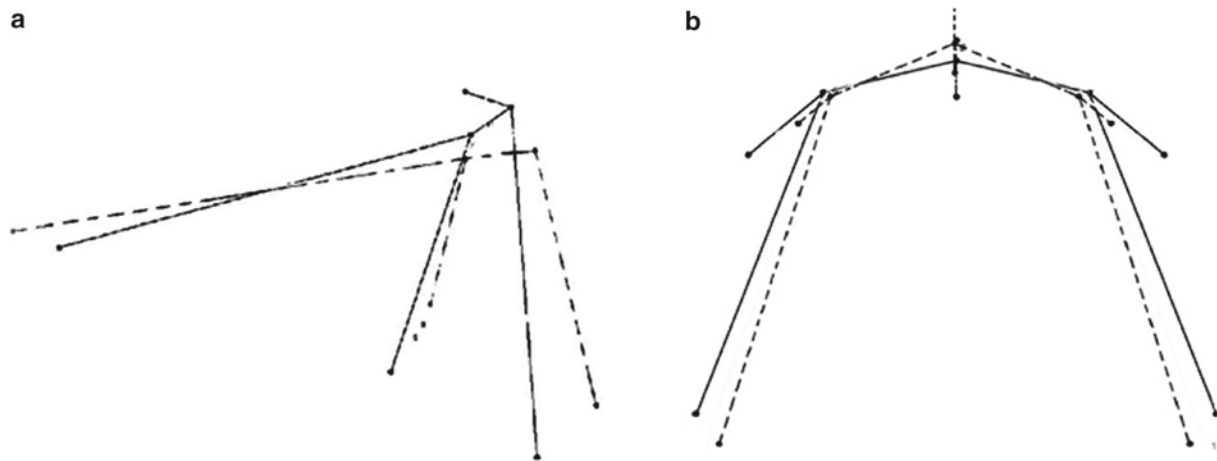


Fig. 16.9 Shape differences in block 1 are shown (a) in lateral view and (b) in superior view along PLS II: high scores are represented by the *dashed line* and low scores by the *solid line*

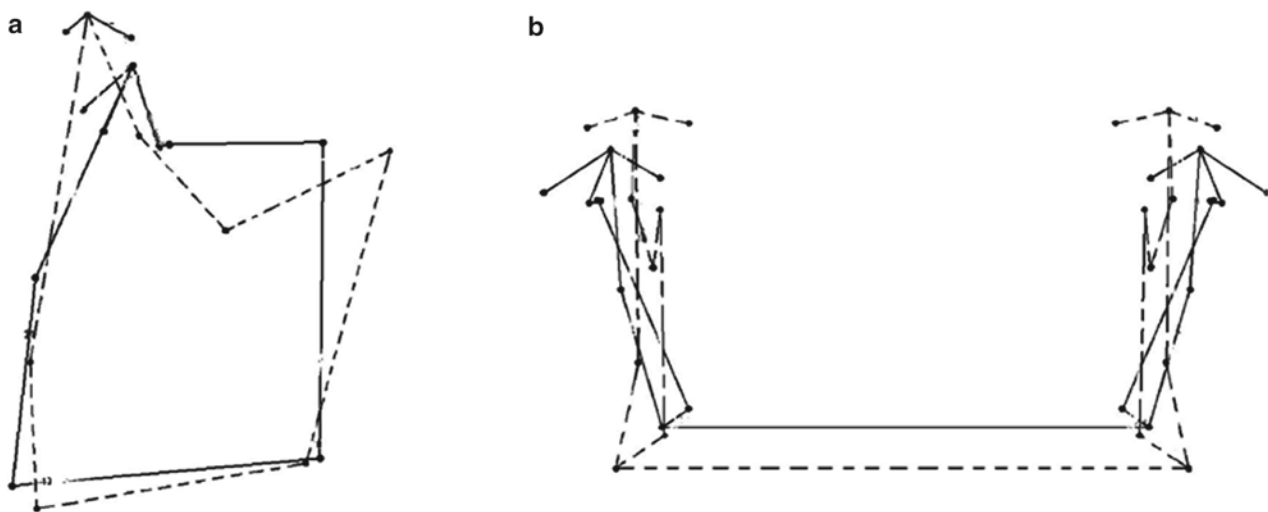


Fig. 16.10 Shape differences in block 2 are shown (a) in lateral view and (b) in posterior view along PLS II: high scores are represented by the *dashed line* and low scores by the *solid line*

components analysis of Nicholson and Harvati (2006). The modern humans and other Pleistocene fossils have higher values than the Neanderthals along PLS II. Majority of the shape changes in the anterior region consist of a forwardly placed lower symphysis, less projecting anterior alveolar region and anteriorly placed mental foramen (Fig. 16.9). Corresponding changes in the posterior region relate to a deep mandibular notch and postero-laterally expanded gonia (Fig. 16.10).

A second analysis was conducted on the fossil taxa alone. This was done in order to clarify subtle differences between the Pleistocene hominins that may have been obscured in the previous pooled-groups PLS analysis. The first PLS axis accounts for 44% of the total co-variation, with a correlation coefficient of $r=0.58$ (Fig. 16.11). A low P -value ($P=0.43$) of the anterior-posterior block permutation test indicates a high level of co-variation between the two parts. This analysis does not separate Neanderthals from other middle-late

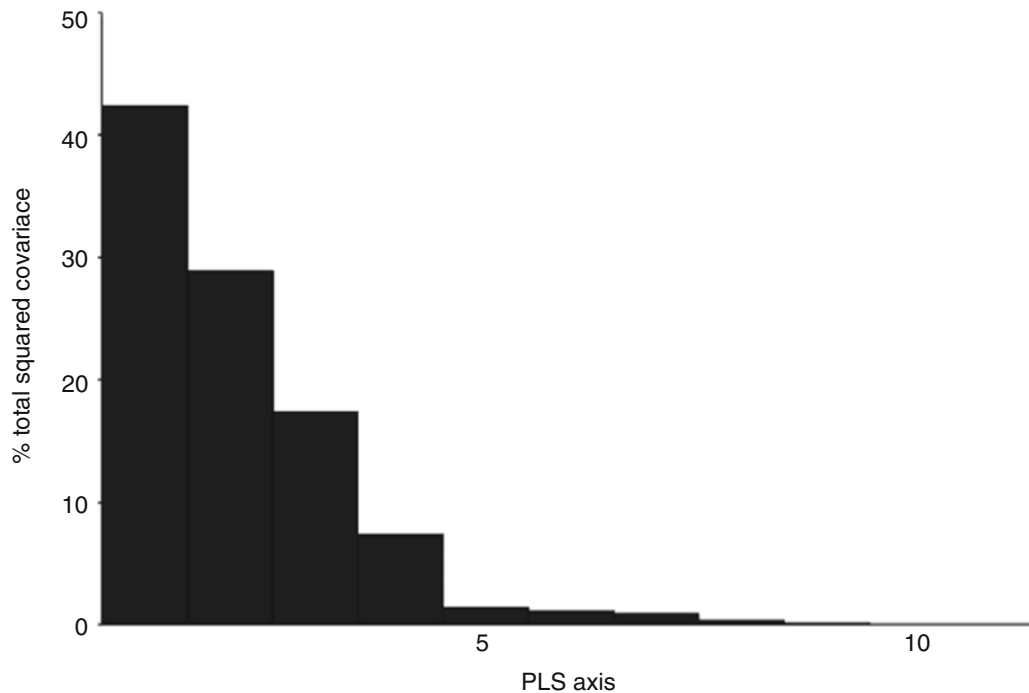


Fig. 16.11 Plot showing the distribution of total% co-variance on the respective PLS axes

Pleistocene hominins (Fig. 16.12). Given the small number of fossil specimens, these results do not reflect the variation within the group and little can be concluded about the pattern and degree of integration between the two mandibular parts. The higher PLS axes do not show any separation between the groups either and are, therefore, not discussed here.

Discussion and Conclusions

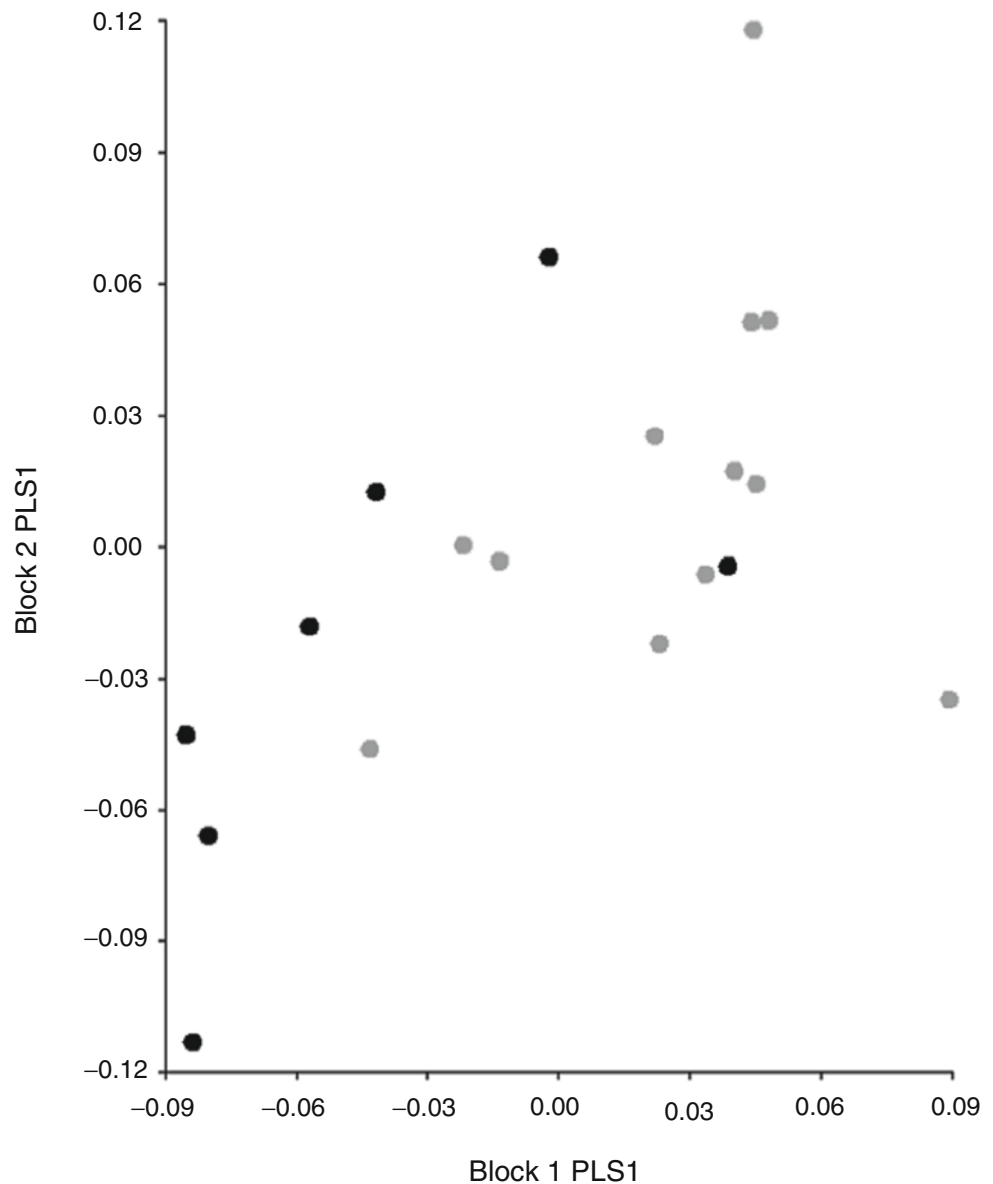
The results of the present study concur with previous findings (Rosas and Bastir 2004; Nicholson and Harvati 2006) suggesting that Neanderthal mandibular morphology is, for the most part, not the result of large size and therefore cannot be accounted for solely through allometric differences. The only Neanderthal-like features found to be related to increased centroid size in modern humans were the retromolar gap – also found in higher frequencies among the larger pre-Neanderthal specimens from Sima de los Huesos, Atapuerca (Rosas and Bastir 2004) – and the higher position of the coronoid process relative to the condyle. Other features commonly described as Neanderthal-like, including a less anteriorly projecting symphysis, an inwardly sloping

ramus and a shallow mandibular notch, are in fact related to smaller centroid size among our sample of recent humans.

Given the extensive use of the anterior dentition in Neanderthals, we had hypothesized that the degree and patterns of integration in the alveolar region and ascending ramus of Neanderthals would be different from other Pleistocene and modern human groups. Our findings suggest that the activities involved in causing intense wear on the incisors and canines of Neanderthals did not influence the pattern of integration between the mandibular regions. Even though our objective was not to test biomechanical hypotheses, our findings concur with results from previous research (Antón 1990, 1994a; O'Connor et al. 2005) that show that evolution of Neanderthal cranio-mandibular morphology cannot be attributed to mechanical demands. Those findings further suggest that Neanderthals were similar to modern humans in their potential to produce high-magnitude bite forces.

Additional fossil specimens are needed to conduct a more thorough comparative analysis of mandibular integration patterns. Nonetheless, our results indicate that modern humans serve as a good model taxon for exploring mandibular integration in Pleistocene hominins. Such an approach could be expanded to include other anatomical subdivisions, which would further refine our interpretations.

Fig. 16.12 Distribution of groups along PLS 1. Neanderthals are represented by the *black dots* and other fossils by *gray dots*



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