Analecta Praehistorica Leidensia 31 / Hunters of the Golden Age : the mid upper palaeolithic of Eurasia : 30,000-20,000 BP

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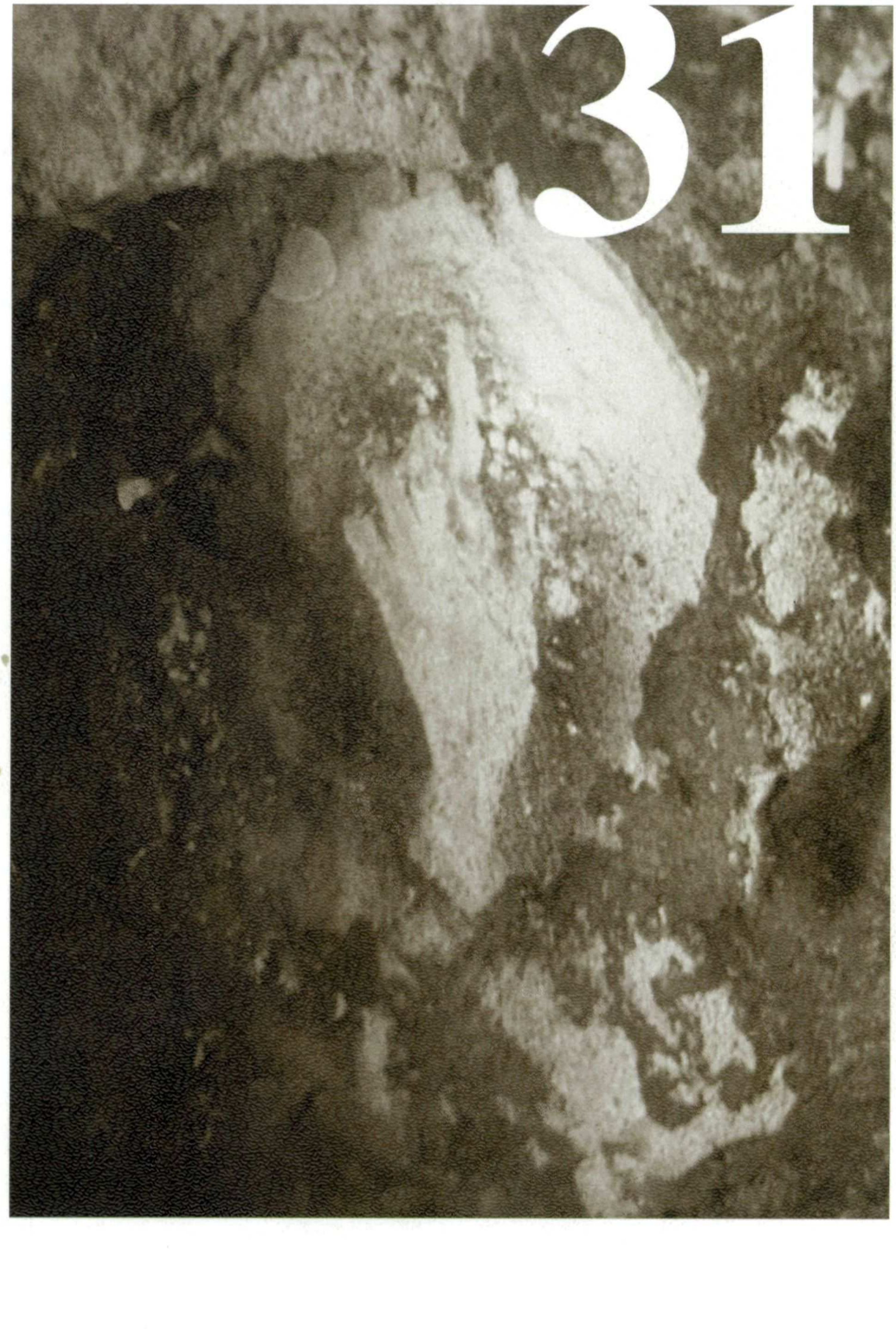

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HUNTERS OF THE GOLDEN AGE

THE MID UPPER PALAEOLITHIC OF EURASIA 30,000 – 20,000 BP

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4 The Upper Palaeolithic population of Europe in an evolutionary perspective

This paper, resulting from the collaboration of five researchers working on different aspects of the skeletal biology of Upper Palaeolithic populations, examines patterns of variation in cranial morphology (B.A.S.), body shape (T.W.H.), stature (V.F.), robusticity and bony architecture of upper (S.E.C.) and lower (B.M.H.) limb bones. Analysis of cranio-facial morphology suggests a relative stability among regions and some restructuring over time of the major dimensions, particularly those reflecting length and breadth of the skull, a process not necessarily indicative of a decrease in cranial robustness. As concerns body shape, principal components analysis of a variable set representing limb proportions, body mass, and trunk breadth suggests that early modern Europeans exhibit a linear physique, like that of sub-Saharan Africans. This finding points to elevated levels of gene flow from more equatorial regions at the time of emergence of modern humans in Europe. A gradual evolution toward a cold adapted morphology, approaching that of modern Europeans, can only be detected during the Late Upper Palaeolithic. Stature shows a marked decrease over time, and an absence of regional differentiation. The magnitude of the trend suggests the synergistic effect of many factors including selective forces, dietary changes, and possibly inbreeding effects. Like other contributions, this section of the paper underscores the major evolutionary importance of the Last Glacial Maximum. Biomechanical analyses of upper and lower limbs produce a somewhat contrasting picture. Cross-sectional geometric properties of lower limb bones indicate decreased activity levels, i.e. mobility, while those of the upper limb reveal increased biomechanical loads in the Late relative to the Mid Upper Palaeolithic. This latter finding clearly does not support models proposing links between developing technology and postcranial gracilisation, and may reflect resource stress during the Late Upper Palaeolithic. Here again it is possible to hypothesize that the ecological changes that followed the Last Glacial Maximum created a complex situation requiring broad ranges of biological and cultural adaptations. Geometric analysis applied to upper limb bones also provides important information on habitual activities. It can be noted that robusticity measures of the humerus tend to be highly bilaterally asymmetrical, particularly in males, likely an effect of regular weapon use, while changes in shaft shape possibly reflect shifts in habitual hunting technology during the Late Upper Palaeolithic.

1. Introductory remarks

More than a decade ago Frayer (1984: 211) pointed out a general lack of interest among human paleontologists in the fossils of early modern humans associated with European Upper Palaeolithic cultures. This indifference stemmed from the common assumption that human evolution had ceased with the emergence of Cro-Magnons. In recent years interest in the biology of Upper Palaeolithic peoples has renewed, in part due to a revival of the debate about the origins of anatomically modern humans and the fate of the Neanderthals, and in part because of a growing appreciation of the wealth of fossil material from this time period and its potential to teach us about population relationships, adaptation and behaviour in the earliest modern humans of Europe. Accordingly, a number of biological anthropologists have in recent years turned their attention to the Upper Palaeolithic period.

Four interrelated issues have emerged as foci for this recent work. The first concerns the larger issue of modern human origins, and whether European Early Upper Palaeolithic populations arose by *in situ* evolution from European archaic populations (the Neanderthals) or by in-migration from other regions (possibly Africa). A second closely related issue concerns the adaptive and evolutionary significance of body form changes, in both stature and body shape, in the European Pleistocene fossil record. Stature, as a genetically determined trait with a large environmental component, is a useful indicator of both life conditions and microevolutionary trends. Body shape, largely genetically determined and highly correlated with climatic variables, can provide clues into both thermoregulatory adaptations and populational affinities of modern humans. Thus examination of body form changes through time serves as a tool both for exploring competing models of origins of anatomically modern populations (Regional Continuity versus Replacement) and for evaluating long-term effects of climatic and environmental changes during the late phases of the Upper Pleistocene.

A third issue concerns the nature of adaptive subsistence and technological shifts during this time, their action as agents of morphological change and their role, if any, in the morphological transition (whether by *in situ* evolution or replacement or a combination of the two) from archaic to modern humans in Europe. Ecological conditions, dimensions and mobility of prey, changes in faunal composition, and improvements both in lithic technology and in weapon efficiency, had important effects on hunting strategies and subsistence patterns. Temporal shifts in adaptive strategies, subsistence organization and technological sophistication can be reflected, indirectly, by changes in skeletal robusticity and structurally important aspects of bone shape. Analyses of upper limb bony architecture (i.e., by geometric analysis of long bone shaft cross-sections) provide insight into subsistence and technological activities of prehistoric populations, while the same techniques applied to the bones of the lower limb provide important information about the degree and patterning of mobility in these peoples. Biomechanical studies of the postcranial skeleton thus serve to illuminate the adaptive characteristics of Upper Palaeolithic hunters and gatherers.

Finally, of interest are patterns of regional differentiation occurring after modern peoples were established in Europe, and the information that these patterns contain about demography, adaptive strategies and the evolution of social complexity in the later stages of the Ice Age. In this regard it is important to know if the spread of apparently small bands of hunter gatherers over vast territories (from western and southern Europe to the Russian Plain and beyond) and attendant genetic isolation of these groups led, via drift phenomena, to a geographic differentiation in biological traits (mostly detectable in cranio-facial morphology). Gamble's (1986) concept of 'open systems' in the Upper Palaeolithic, i.e. a continuous flow of information and of genes (as part of a social adaptive strategy) over a vast depopulated territory, can potentially be tested with available fossil data, since such a system should prevent phenomena of regionalisation. Examination of the patterning of morphological variability among regions during the Upper Palaeolithic is of critical importance for deciding issues of social organization and adaptive complexity in these peoples. Studies of temporal and regional differences in craniofacial morphology play the leading role in addressing these issues. But here again the examination of variations of stature through time provides some critical insights, as such shifts may signal important changes in socio-economic and biodemographic aspects.

The study of the biology and behaviour of Upper Palaeolithic peoples is clearly awakening from a period of dormancy. We have collected together the contributions of five researchers who, in recent years, have addressed the above issues through a variety of approaches. These contributions are intended to summarize the current state of research into the European peoples of the latest Pleistocene, and to more clearly define major points of articulation and discordance in the works of the various authors (rather than to present a unified view of Upper Palaeolithic paleoanthropology). As such, we hope that this work will serve as a springboard for future, broad spectrum collaboration (both among physical anthropologists working on these populations and between them and palaeolithic archaeologists) in the human biology of Upper Palaeolithic peoples.

2. Cranial morphology: temporal and spatial patterning (B.A.S.)

Studies of cranial morphology in the European Upper Palaeolithic have focused either on the relationship between the earliest anatomically modern humans in Europe and the preceding Neanderthals (Frayer 1984, 1992a, 1992b; Smith 1984, 1985, 1991) or the nature of biological change throughout the Upper Palaeolithic (Frayer 1978, 1984, 1988; Van Vark 1990; Van Vark *et al.* 1992; Henke 1992; Sarich 1995; Schumann 1995). While most of these studies examine the Upper Palaeolithic for temporal trends by dividing the hominid fossils into either early (pre-20 kyr) and late (post-20 kyr) periods or by geographical regions, rarely is work focused on Upper Palaeolithic hominids associated with the Aurignacian. While this may be due to the limited or smaller sample size or the lack of clear chronological or archaeological provenance, recent studies by Gambier (1989a, 1989b, 1992) have, however, identified cranial features which reflect differences in robusticity and levels of variation within those hominids from Central Europe and those from Southwest France which date prior to 30 kyr.

While little work has focused solely on the morphological patterns of the earliest Upper Palaeolithic hominids, there persists a consensus that the hominids from the Early Upper Palaeolithic are larger and more robust than those from succeeding periods, including the latest Pleistocene and earliest Holocene populations of Europe (Frayer 1978, 1984, 1988; Frayer *et al.* n.d.; Simmons and Smith 1991). This section seeks to establish the exact nature of cranial morphology in the Early and Mid Upper Palaeolithic by testing a total sample of 58 European Upper Palaeolithic fossil hominids, 34 of which date prior to 20 kyr, for temporal and geographical patterns, using 113 metric cranial, dental and mandibular features. These features are standard variables described in Howells (1973), Lahr (1992) and Schumann (1995).

The earliest Upper Palaeolithic hominids are divided into two chronological groups, one including those hominids associated with (either directly or by inference from the literature) an aurignacian industry (i.e. they date prior to 30 kyr, referred to as the EUP) and the other including those hominids which date between 30 and 20 kyr (i.e. those associated with the Gravettian or Perigordian or Proto-Magdalenian, and referred to as MUP). These two groups are analyzed using a Mann-Whitney nonparametric comparison of group means. Further comparisons are then made in order

Table 1. Upper Palaeolithic specimens used in this analysis grouped according to chronological provenance.

EUP >30 kyr	MUP 30-20 kyr	LUP <20 kyr
Cro Magnon 1-4	Arene Candide 1	Arene Candide 2, 4, 5
Mladec 1, 2, 5, 6	Barma Grande 1, 2, 3, 5	Bruniquel 24
Stetten 1, 2	Brno 1, 2	Cap Blanc 1
Svitavka 1	Cioclovina	Chancelade 1
Zlaty Kun 1	Grotte des Enfants 4-6	Gough's Cave
	Dolní Věstonice 1, 2, 3, 14, 16	Laugerie Basse 1, 2
	Kostenki 2	Maritza
	Pavlov 1	Oberkassel 1, 2
	Předmostí 3, 4	Ortucchio 1
		Le Placard 1-7
		Saint Germain 1
		San Teodoro 3, 4

Table 2. Statistical results of the analysis of 113 cranial, dental and mandibular traits for temporal differences.

ANALYSIS	CRANIAL	DENTAL	MANDIBULAR	TOTAL
EUP -MUP	4 (3.5%)	0	2 (1.77%)	6 (5.31%)
EUP+MUP - LUP	10 (8.85%)	3 (2.65%)	0	13 (11.5%)
EUP - LUP	15 (13.27%)	1 (0.88%)	1 (0.88%)	17 (15.04%)
MUP - LUP	7 (6.19%)	5 (4.43%)	0	12 (10.62%)

to identify any morphological differences between the whole Early and Mid Upper Palaeolithic and those hominids which date to after the Last Glacial Maximum (Table 1).

The geographical analysis for differences in cranial morphology in the EUP and MUP was conducted initially by dividing the hominids into four geographical regions based on their original location. These four geographical groups were analyzed using a nonparametric Chi Square test. Due to small sample sizes, and based on these results and those from an earlier study (Schumann 1995), a Mann-Whitney test was conducted in order to compare the EUP and MUP hominid material from Central Europe with that from all other regions of Europe. Any geographical patterns in the EUP and MUP are discussed within the contexts of spatial patterning in the late Pleistocene.

2.1 TEMPORAL ANALYSIS

The comparison between EUP and MUP indicated that there are four cranio-facial features and two mandibular features which are significantly different at the $p<0.05$ level (Table 2). This accounts for 5.31% of all variables examined. Of the 12 mandibular features examined, the height of the corpus and the breadth at the ramus were significantly different. Prior to 30 kyr, the mean height of the mandibular corpus is 7.6 mm higher than it is between 30 and 20 kyr. Accordingly, the mandible is over 12 mm wider across the rami in the EUP. No dental dimensions, however, were identified as significantly different between these two periods.

Four cranial dimensions were identified as significantly different between EUP and MUP. Contrary to the differences in the breadth of the mandible, which is broader prior to 30 kyr than it is between 30 and 20 kyr, the EUP specimens have on average narrower internal palate breadths than those hominids associated with the Gravettian; the breadth at M1/P4 is significantly narrower prior to 30 kyr than it is after. The maximum breadth of the cranial vault (measured across the parietal bones), however, is significantly larger (broader) prior to 30 kyr than it is after. In fact, while not statistically significant, five other measures of cranial vault breadth, including biasterionic breadth, biauricular breadth, bistephanic breadth, minimum frontal breadth and fronto-malar breadth, are greater in the EUP sample.

Other significant differences were identified in the length of the naso-frontal suture (a shortening through time) and in

Table 3. Temporal group means (value in mm), sample size (N) and standard deviation (SD) for the three Upper Palaeolithic periods for the seventeen variables with significant differences between the Aurignacian associated hominids and those from the Late Upper Palaeolithic.

VARIABLE	EUP >30 kyr			MUP 30-20 kyr			LUP <20 kyr		
	value	N	SD	value	N	SD	value	N	SD
asterion-bregma (ASTBR)	142.98	9	4.97	141.62	20	8.28	136.42	15	7.20
basion-prosthion length (BPL)	104.58	2	2.29	104.78	11	7.68	93.51	13	5.30
frontal arch (FARCH)	137.38	8	11.62	132.18	21	7.18	127.66	16	6.71
frontal chord (FRC)	119.96	9	11.06	114.83	22	5.82	110.48	18	5.59
glabella-opistocranium length (GOL)	196.20	9	7.05	192.91	19	7.85	185.11	16	8.12
lambda-opistocranium length (LAMOPIS)	40.47	7	5.89	32.03	19	6.82	31.54	15	8.00
external palate breadth (MAB)	64.55	6	1.57	61.24	14	4.85	62.49	15	3.51
naso-frontal breadth (NFRB)	23.04	4	2.17	18.84	13	2.54	17.54	9	5.00
nasion-opistocranium length (NOL)	194.37	7	4.42	189.04	17	7.43	183.96	15	10.50
orbit breadth (OBB)	44.03	4	3.09	40.92	17	3.66	40.41	14	3.02
bistephanic breadth (STB)	122.28	5	10.34	117.89	17	10.01	111.12	14	6.30
temporal fossa length (TFL)	47.56	2	4.57	43.33	10	3.9	39.36	10	2.98
maximum frontal breadth (XFB)	118.76	8	4.65	118.56	20	5.19	114.12	17	5.43
maximum cranial breadth (XPB)	144.47	7	6.93	136.51	17	5.68	138.19	15	5.11
zygo-orbital breadth (ZOZO)	62.24	4	4.47	59.25	14	9.85	55.74	10	4.63
ramus breadth (RAMB)	109.3	7	4.52	96.68	11	8.39	97.84	6	9.57
distance from maxillary P3 to M3 (MAXP3/M3)	43.86	2	3.05	42.53	12	1.93	39.55	13	1.64

the distance from lambda to opistocranium on the occipital bone. This latter difference indicates that the position of the opistocranium is shifting towards a more superior placement (moving towards lambda) from EUP to MUP.

While there are few metric differences which distinguish EUP from MUP hominids, 13 variables (11.5%) can be used to distinguish the former groups from the Late Upper Palaeolithics (LUP). These differences may indicate temporal trends throughout the entire Upper Palaeolithic, for the greatest differences in morphology are found between the earliest (pre-30 kyr) and the latest (after the Last Glacial Maximum) periods of the Upper Palaeolithic. In other words, greater differences exist between EUP and LUP (15.04%; n=17) than between MUP and LUP (10.62%; n=12). This suggests that there are clearer and more significant temporal trends throughout the whole of the Upper Palaeolithic than there are before the Glacial Maximum, as only six variables were found with significant differences between EUP and MUP. Any morphological change which can be identified is therefore most likely accounted for by differences between those hominids associated with the Aurignacian and those which date after the Last Glacial Maximum, with those hominids dating from 30 to 20 kyr falling in an intermediate position for fourteen of those seventeen variables (Table 3). The reduction in size (lengths and breadths), although not statistically significant, in fourteen of these seventeen variables suggests that there are changes in several major cranial vault dimensions through time, specifically in the length (GOL, NOL, FRC, ASTBR) and breadth (STB, XFB, XPB) of the cranium. Other noticeable trends are found in the position of the face relative to the cranial vault (BPL), and upper facial breadths (NFRB, OBB and ZOZO = breadth from the most superior point of the zygo-orbital suture on the inferior orbital margin to the same point on the other orbit). Compared to recent modern European populations, these metric differences are very small; differences in morphology between two of Howells' (1973) European populations, the Norse and Berg, amount to 56.1% of all cranial variables he examined.

2.2 GEOGRAPHICAL ANALYSIS

The analysis for regional patterns in cranial morphology (Table 4) indicated that there are few differences either within the EUP, between MUP or within LUP. When all pre-20 kyr hominids are grouped together and analyzed as two regions (comparing the hominids from Southwest France to those from Central Europe), only two cranial variables were found with significant differences. These variables include the height of the mastoid (MDH) and the height of the parietal subtense (PAS).

Table 4. Statistical results of the analysis of 113 cranial, dental and mandibular traits for geographical differences.

ANALYSIS	CRANIAL	DENTAL	MANDIBULAR	TOTAL
EUP (two regions)	2 (1.77%)	0	0	2 (1.77%)
MUP (four regions)	3 (2.65%)	0	0	3 (2.65%)
LUP (three regions)	1 (0.88%)	2 (1.77%)	0	3 (2.65%)
EUP+MUP (central Europe vs S.W. France)	2 (1.77%)	0	0	2 (1.77%)
EUP+MUP (central Europe vs others)	5 (4.43%)	2 (1.77%)	0	7 (6.19%)

Based on previous analyses (Gambier 1989a, 1989b; Schumann 1995), the pre-Glacial Maximum Upper Palaeolithic hominids from Central Europe are apparently the most 'different', in terms of both cranial size and the level of robusticity. When the Central European material is contrasted with that from Italy, and Southwestern France, 7 (6.19%) cranial and dental variables are identified as significantly different. These variables include the length from pterion to bregma, the maximum breadth across the zygomaxillary suture, the parietal subtense, the internal palate breadth at both M2/M1 and M3/M2 as well as the bucco-lingual length of the maxillary first premolar and the length of the maxillary lateral incisor. In addition to the patterns in EUP and MUP, using the same geographical regions, the sample of LUP specimens displayed few regional differences, with only three variables (one cranial, two dental) significantly different. This suggests that there are no temporal differences in the regional patterning of morphological variation throughout the Upper Palaeolithic and that overall, there are few geographical differences in metric cranial and dental morphology. This need not, however, indicate anything about regional differences in cranial robustness either within the Early and Mid Upper Palaeolithic or between the Early, Mid and Late.

2.3 IN CONCLUSION

Throughout the Upper Palaeolithic, there are more morphological differences between all hominids which date before and after the Last Glacial Maximum. In each case (that is for these 13 variables), the mean value for those hominids living between 30 and 20 kyr falls between the means for the earliest (pre-30 kyr) and the latest (post-20 kyr) groups. These trends, however, reflect the greater differences observed between the aurignacian-associated hominids and those associated with LUP industries (the seventeen variables listed in table 3), rather than differences between either group and the MUP. These results are not unlike those presented by Frayer (1978, 1984, 1988) who found clear, directional trends in the size of the teeth and in the size and morphology of the face and cranial vault. The results of this study suggest that the morphological differences between EUP and MUP specimens are superseded by the number of differences between the whole of the EUP and MUP and the LUP, but this does not necessarily support the notion of significant evolutionary trends in overall cranial morphology throughout this period. Rather than suggesting that strong selective factors were operating on the total cranial and dental morphology of the earliest anatomically modern humans to produce a more gracile hominid by the onset of the Holocene (as suggested by Frayer), it is perhaps better to consider the thirteen (or seventeen when just the aurignacian-associated hominids are compared to the LUP hominids) significantly different variables as indications that there are some skeletal modifications over time which reflect differences between the EUP and LUP.

As the focus of this chapter is morphological patterning throughout the earliest stages of the Upper Palaeolithic, the clearest pattern and most significant changes to emerge prior to 20 kyr are in the breadth of the cranial vault and mandible. Although only maximum cranial breadth across the parietal bones and the breadth of the mandible across the rami are significantly different, there is a reduction throughout this time in overall cranial breadths. There is a consistent decrease, albeit not significant, in the breadth of the upper face (as measured across the fronto-malar suture), in the breadth of the frontal bone (STB and WFB) as well as at the base of the skull (biasterionic and biauricular breadth). In conjunction with the narrowing of the skull, there is also a shortening of the cranium throughout this period. There is not, however, any difference in the height of the cranium, as measured from basion to bregma. This indicates that there is some restructuring of major cranial dimensions, certainly in terms of the length and breadth of the skull, but that these changes are not necessarily indicative of a decrease in overall cranial robustness (Lahr and Wright 1996). The degree of cranial robustness, measured by the presence of cranial superstructures and distinct features such as tori, tubercules and crests, is determined by the size and shape of the cranial vault and the size of the palate and dentition (ibid.). While this analysis did not examine the degree of development of cranial superstructures, the changes in cranial vault breadth (a narrowing) as well as those changes identified in the breadth of the palate (a narrowing) may have lead to the maintenance of high levels of cranial robusticity throughout EUP and MUP.

Contrary to Frayer's find of the loss of robusticity throughout the Upper Palaeolithic, Lahr and Wright (1996) suggest that narrow skulls with large teeth will maintain high levels of robusticity. Previous studies have suggested that the EUP and MUP hominids, and in particular those from Central Europe, display a greater degree of robusticity than those specimens from the LUP (Gambier 1989a, 1989b; Schumann 1995). Interestingly, there is an increase (a broadening) on average of the breadth of the skull at the asterion and across the temporal bones (AUB) by the LUP. These changes combined with the shortening of the cranial vault (as indicated by changes in GOL and NOL) may have led to the decrease in levels of cranial robusticity by the end of the Upper Palaeolithic, but occurring only after the Last Glacial Maximum.

While this analysis did not attempt to document changes in overall cranial and dental robustness throughout the Upper Palaeolithic, it is clear that any trends or significant differences in cranial and dental morphology are most likely the result of differences between those hominids which date earlier than 30 kyr and those which date after the Last Glacial Maximum (20 kyr). Additionally, these differences may also be affected by sexual dimorphism throughout the Upper Palaeolithic, as these analyses were conducted on unsexed material. Frayer (1980, 1981) has found that throughout the Upper Palaeolithic there is a correlation between overall cranial and postcranial changes and the loss of male robusticity. Nevertheless, there are few morphological changes in the first 25 kyr (45 to 20 kyr) of the Upper Palaeolithic and even fewer regional patterns during this time. Based on this analysis, it may be possible to conclude that the EUP and MUP are periods of relative morphological stability, whereby there are few significant differences in the 114 metric variables examined. It is only after the Last Glacial Maximum when differences in morphology can be detected, especially with respect to the length and breadth of the cranium.

3. Body shape: climatic and phylogenetic aspects (T.W.H.)

Body shape can provide clues into climatic adaptation as well as populational affinity of the early modern humans. Body shape variables provide evidence of the former because in the modern world they are known to be highly correlated with climatic variables (Roberts 1953, 1978; Baker 1960; Crognier 1981; Trinkaus 1981; Ruff 1994). They provide evidence of the latter because human body shape appears to be largely genetically determined (Schultz 1923, 1926; Guilbeault and Morazain 1965; Eveleth and Tanner 1976; Y'Edynak 1978; Tanner *et al.* 1982). Both of these factors (climatic adaptation and populational affinity) have implications for understanding modern human origins in Europe, as discussed below.

Multivariate analyses of body shape begin with the computation of 'log size and shape' and 'log shape' variables (Darroch and Mosimann 1985). Log size and shape variables are merely the log-transformed raw measurements. Log shape variables are computed in the following manner – Darroch and Mosimann (1985) argue that the best measure of overall size is the geometric mean of all an individual's measurements. Thus, to create scale-free variables, ratios of each variable and the geometric mean are computed. These logged ratios are called log shape variables, and are scale-free in the sense that an isometric size component (the geometric mean, or 'log size' for that individual) has been removed from each variable. This has not completely removed the effects of size, however. In fact, size and shape may be correlated, and the Darroch and Mosimann technique can be used to determine if this is in fact the case.

This method is ideal for examining the relationship between size and shape for three reasons. First, in this method, unlike residual methods, shape is intrinsic to the individual, and not a function of the comparative sample. Residuals from allometric lines can change with a change in sample constituency. In other words, an individual's residual from an allometric relationship will change with sample size and/or constituency. However, the individual's own shape has, in fact, remained unchanged.

A second advantage of this technique is its ability to detect allometric relationships. The log shape variables are created by removing an isometric size component. This means that size effects due to allometric relationships (i.e., changes in shape associated with a change in size), have not been removed. In order to elucidate allometric effects, one must simply examine the correlation coefficients between the shape variables and log size (i.e., the geometric mean). A significant negative correlation of a shape variable with the geometric mean indicates a subisometric (negatively allometric) relationship, a significant positive correlation indicates a supraisometric (positively allometric) relationship, and a nonsignificant correlation indicates the shape variable is characterized by an isometric relationship with increasing size.

The third advantage of the Darroch and Mosimann technique involves the separate variance/covariance matrices generated when the 'log size and shape' and 'log shape' variables are subjected to principal components analysis

Table 5. Fossils included in this analysis.

MID UPPER PALAEOLITHIC (MUP) (30-20 kyr)	LATE UPPER PALAEOLITHIC (LUP) (20-10 kyr)	MESOLITHIC (MES) (<10 kyr)
Barma Grande 2	Arene Candide 2	Gough's Cave 1
Grotte des Enfants 4	Arene Candide 4	Gramat 1
Dolní Věstonice 14	Arene Candide 5	Hoedic 8
	Bichon 1	Hoedic 9
	Bruniquel 24	Rastel 1
	Cap Blanc 1	Teviec 1
	Le Peyrat 5	Teviec 11
	Romito 4	Teviec 16
	St. Germain la Rivière 4	

Table 6. Recent human samples included in this analysis.

EUROPE	NORTH AFRICA	SUB-SAHARAN AFRICA
Bohemia (BOH)	Egypt (EGY)	East Africa (EAF)
Bosnia (BOS)	Nubia (NUB)	Pygmy (PYG)
England (ENG)	Sudan (SUD)	San (SAN)
France (FRA)		West Africa (WAF)
Germany (GER)		
Norse (NOR)		

(PCA). Specifically, one can compare the eigenvalues of the two matrices to determine what percentage of the total variance is explained by a combination of size and shape versus shape alone.

The measurements used in the analysis were chosen *a priori* to represent the total morphological pattern of the postcranial skeleton and include all four limb segment lengths (femur, tibia, humerus and radius, or FL, TL, HL and RL, respectively), femoral A-P head diameter (FHAP), bi-iliac breadth (BIB) and clavicular length (CLVL). These variables represent three morphocomplexes known to covary with climate – limb proportions, body mass, and trunk breadth.

The Mid Upper Palaeolithic (MUP), Late Upper Palaeolithic (LUP) and Mesolithic (MES) fossils (Table 5), and 292 recent humans (Table 6) from Africa and Europe (for detailed description of samples see Holliday 1995) were subjected to principal components analysis of the above variable set (FHAP, FL, TL, HL, RL, CLVL, BIB).

Table 7 provides the eigenvalues and eigenvector coefficients for the first two principal components of the log size-and-shape and log shape data. The first principal component (PC1) of the log size-and-shape data explains 70.3% of the variance. It is best interpreted as a size component, since all its eigenvector coefficients are positive, and the PC scores along this axis are highly correlated with log size ($r^2 = 0.998$, $p < 0.0001$). PC2 explains 16.6% of the variance. Scores along this axis are not significantly correlated with log size ($r^2 = 0.004$, $p = 0.7239$), and the component contrasts femoral head diameter and bi-iliac breadth with distal limb segment lengths.

The reduction in variance from the log-size-and-shape to the log shape analysis indicates that 27.8% of the total variance is due to shape. The first shape component accounts for 54.2% of the shape variance, and contrasts femoral head diameter and bi-iliac breadth with limb segment length (particularly distal segments). The scores along this axis are not significantly correlated with log size ($r^2 = 0.005$, $p = 0.2089$). The second component of the log shape data (PC2) explains 20.3% of the variance. It contrasts femoral head diameter with bi-iliac breadth. The scores along this axis are correlated with log size ($r^2 = 0.148$, $p < 0.0001$).

Figure 1 is a plot of the mean PC scores for the log shape data.

PC1 of shape separates recent Europeans and North Africans to the left, who possess relatively cold-adapted bodies (wide trunks, larger femoral heads and shorter distal limbs) from recent Sub-Saharan Africans on the right, who

Table 7. Principal Components of Log Size-and-Shape and Log Shape Variables (seven variables): fossil and recent humans.

	EIGENVECTOR COEFFICIENT			
	Log size-and-shape		Log shape	
	I	II	I	II
FHAP	0.462	0.426	0.385	0.833
CLVL	0.361	-0.030	-0.042	-0.213
BIB	0.278	0.718	0.720	-0.502
FL	0.372	-0.180	-0.193	-0.026
HL	0.377	-0.112	-0.126	-0.021
TL	0.384	-0.333	-0.347	-0.084
RL	0.389	-0.382	-0.398	0.012
Eigenvalue	0.0348	0.0082	0.0082	0.0031
% total variance	70.34	16.58	54.17	20.31

are more tropically-adapted (narrow trunks, small femoral heads and long distal limbs). Interestingly, while European LUP and Mesolithic samples cluster among recent, the MUP sample tends to more closely approximate the Sub-Saharan African condition.

PC2 does not segregate out the groups; rather, it segregates males and females (scores different at $p < 0.0001$), albeit with much individual overlap). This separation is due to the fact that there is a tendency for females to possess smaller femoral heads and wider bi-iliac breadths than males. Thus, the relatively high PC2 scores of the fossil samples merely reflect their male bias. One can see this in figure 2, which is a plot of the individual PC scores for the log shape data for the recent Europeans and Sub-Saharan Africans, and European MUP and LUP samples. This allows one to see where the individual European fossils fall relative to recent Europeans and Sub-Saharan Africans.

Note the positions of the 3 MUP specimens (indicated by dark triangles) relative to the recent groups. Barma Grande 2 and Grotte des Enfants 4 cluster with each other in a region of overlap between the Africans and Europeans. Alternatively, Dolní Věstonice 14 falls squarely among the Sub-Saharan Africans for PC1, although its PC2 score is higher than that of any of the recent Africans. The LUP specimens, on the other hand, cluster squarely among the recent Europeans, although 1 of the 9 specimens, Bichon 1, falls in the region of overlap between the recent regional samples.

While sample size is admittedly small, in this analysis and in other body shape analyses, (most with larger sample sizes; see Holliday 1995, n.d.) the European MUP sample as a whole does not appear to be very 'European-like', but rather

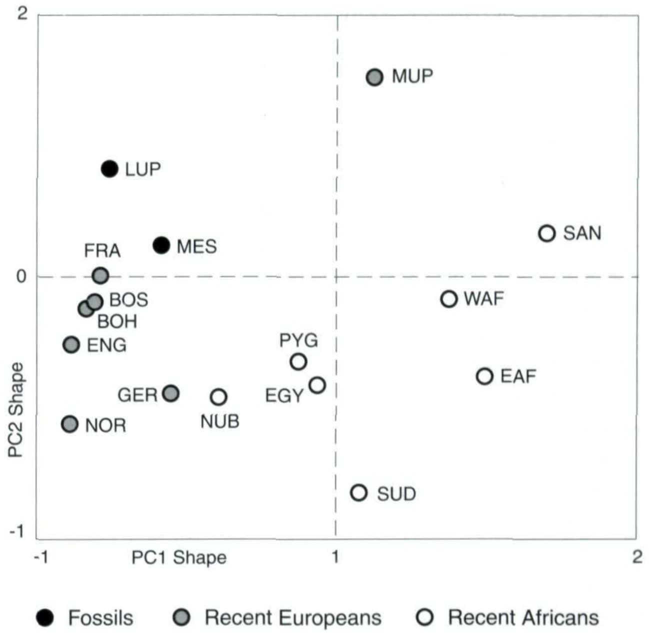

Fig. 1. Scatter plot of PC 2 on PC 1 of the log shape variables. Fossil and recent human mean PC scores are shown.

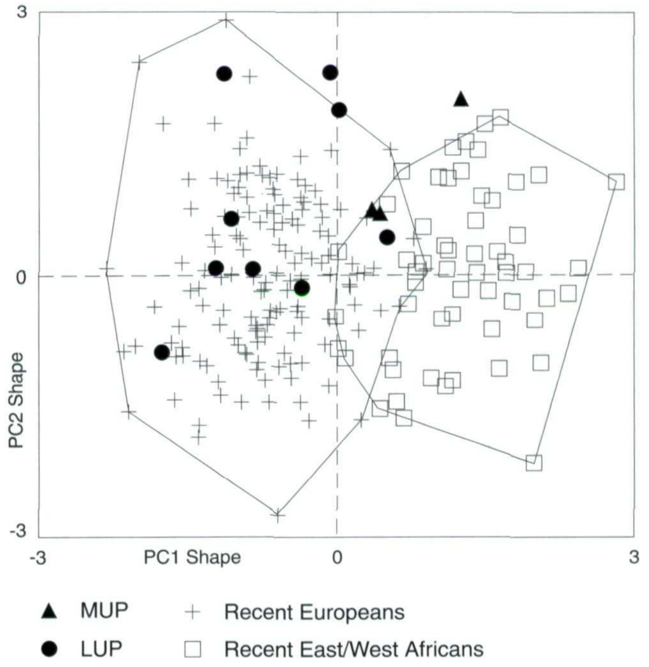

Fig. 2. Scatter plot of PC 2 on PC 1 of the log shape variables. This plot shows the individual PC score data for the MUP and LUP fossils and the recent Europeans and East/West Africans.

tends to possess a longer, more linear physique like that of recent Sub-Saharan Africans. This result fits more easily within a Replacement or Intermediate model framework than within a model of local continuity.

It is important to note, however, that many MUP specimens do not fall outside the range of the recent Europeans. Rather, they tend to fall to the extreme end of the European range, but within the Sub-Saharan African range. In contrast, only one European LUP specimen (Bichon 1) fell within the Sub-Saharan African range in multivariate space. Therefore, if the MUP sample is an unbiased, representative sample, then the early modern humans in Europe were characterized by on average a more tropically-adapted body form than one finds in Europe today.

Size-driven shape differences remain an issue, given that a number of the MUP specimens are large in body size (as reflected in the geometric mean). However, for only two shape features (bi-iliac breadth and trunk height) do the European MUP specimens follow an allometric trend that would tend to make them look more African-like (Holliday 1995). As for the other features in which they look African-like (limb length and relative femoral head size) one cannot easily invoke an allometric explanation, since the pattern exhibited by the MUP sample either violates allometric expectation, or, alternatively, the variable in question is isometric (Holliday 1995).

Additionally, ANOVA's of the fossil samples provide no evidence of a body mass difference between the European MUP and other Pleistocene groups (Holliday 1995). Thus, it is precisely the variables for which the European MUP deviate from the other fossil groups – i.e., limb lengths, and not large body mass *per se* – that are driving their large geometric means. If the European MUP humans are not heavier than other fossil humans, then allometry cannot be easily invoked to explain their different body shape.

The body shape of subsequent European populations is also important to the question of modern human origins. Regional Continuity predicts all European late Pleistocene/early Holocene humans should have a cold-temperate body shape, although minor fluctuations may be expected, given climatic cycles and improvements in cultural buffering. Replacement, on the other hand, predicts that subsequent to the initial appearance of modern humans in Europe, there should be gradual evolution toward a cold-adapted morphology.

The results with regard to this prediction are interesting. There is evidence for a change toward a more cold-adapted body shape from the MUP to the LUP, but there is no solid evidence for a subsequent change to the Mesolithic. Rather, for most multivariate analyses, these two samples cluster with each other (usually well within the spread of recent Europeans). This lack of evidence for later temporal change could be due to the complicating effects of the warmer temperatures associated with the onset of the Holocene, or perhaps to improved cultural buffering.

To summarize how well the body shape results match predictions derived from the two competing models of modern human origins, the predictions of Regional Continuity are not met. There is very little evidence for continuity in body shape, at least in Europe. Again, under the assumption that the small European MUP sample is representative, they have a different body shape from both the Neanderthals who preceded them in the region (Holliday 1995, n.d.), and from later European populations. Since neither climatic change nor mobility may be invoked to explain this pattern (Holliday and Falsetti 1995), by default it appears some degree of extraneous genetic influence was present.

Unfortunately, the interpretation of these data requires some guesswork. While some amount of extraneous genetic influence has been documented, the question of the relative importance or magnitude of this outside influence is difficult to assess from these data alone.

In other words, these data are compatible with either complete Replacement or an Intermediate model of modern human origins, and it is difficult to argue which model best fits the data.

4. Stature: environmental and genetic factors (V.F.)

Converting bone lengths to stature evaluations provides important information both for qualifying a skeletal population from the physical point of view, and for analyses dealing with body size variations and its links to ecological and biocultural variables.

Historically, the first issue has been largely pre-eminent and height has been a basic feature in building up the typological paradigm. During the first decades of the 20th century, a few Upper Palaeolithic specimens, labelled as 'types', were identified as lineally connected with modern Europeans, like the tall 'protonordic' Cro-Magnons, and the short statured 'protomediterranean' Combe Capelle skeleton. Today, analyzing stature of past populations means investigating life conditions, subsistence patterns, and more generally the relationship between Man and his environment by means of an indicator highly sensitive to ecological and socio-cultural variables. The most recent works dealing with stature variations during the Upper Palaeolithic are more than ten years old (Frayer 1981, 1984). New discoveries and developments in stature evaluation methodologies provide the opportunity to carry out a study based on a substantially increased sample and more reliable techniques.

Long bone lengths of European Upper Palaeolithic remains of adult individuals, not showing pathological

Table 8. The samples.

MID UPPER PALAEOLITHIC

STATE	SITE	M	F
CZECH REP.	Dolní Vĕstonice	3	1
	Pavlov	1	-
	Předmostí	3	2
ENGLAND	Paviland	1	-
FRANCE	Abri Pataud 5	-	1
	Cro Magnon	2	1
	La Rochette	-	1
ITALY	Barma Grande	4	-
	Baousso da Torre	1	-
	Caviglione	1	-
	G. des Enfants 4	-	1
	Ostuni	-	1
	Paglicci 25	-	1
	Parabita	1	1
RUSSIA	Kostenki 2	1	-
	Sungir' 2	1	-

LATE UPPER PALAEOLITHIC

STATE	SITE	M	F
FRANCE	Bruniquel	-	1
	Cap Blanc	-	1
	Chancelade	1	-
	Farincourt	-	1
	Le Peyrat	1	1
	Le Placard	1	-
	St.Germain la Rivière	-	1
	Veyrier 1	1	-
GERMANY	Dobritz	-	1
	Neuessing	1	-
	Oberkassel	1	1
ITALY	Arene Candide	5	2
	G. des Enfants 3	-	1
	Paglicci 11	1	-
	Riparo Continenza	1	-
	Riparo Tagliente	1	-
	Riparo Villabruna	1	-
	Romanelli	1	-
	Romito	1	2
	San Teodoro	-	2
	Vado all'Arancio	1	-
RUSSIA	Kostenki 1	1	-
SWITZERLAND	Le Bichon	1	-

changes affecting growth, represent the basic material for this work. The source of the measurements is the literature up to 1995, and information kindly provided by colleagues.

The material is listed in table 8. Long bone lengths have been transformed into stature estimates by means of new regression equations derived from Early Holocene skeletal samples, using Fully's 'anatomical stature', and the major axis regression technique (Formicola and Franceschi 1996). The sample has been split into two groups: the Mid Upper Palaeolithics (MUP), corresponding to the material dating from approximately 30 kyr to the pre-Glacial Maximum, and the Late Upper Palaeolithics (LUP) chronologically placed between the post-Glacial Maximum and the Pleistocene-Holocene transition.

Data reported in figure 3 clearly show the high stature characterizing MUP males, and the marked difference, statistically highly significant, when compared to the LUP group. The amount of the difference between two groups is apparent in figure 3, showing that the lower limit of the variability of the MUP sample corresponds to the mean value of the later group. Moreover, taking into account the individual data, it can be noted that there is very limited overlap between the two ranges and that in particular very few MUP specimens (Předmostí 9, Cro Magnon 3, and Kostenki 2) are shorter than 170 cm, a stature reached only by two LUP individuals (Paglicci 11, and Romanelli). Significant differences also result from statistical comparisons between females. Differences in distributions are shown in figure 3, and in that case too the samples exhibit very limited overlap of the ranges.

The male-female difference in the MUP group (13.3 cm) is higher than in the later group (12.1 cm) as expected on the basis of the positive correlation between height values and degree of sexual dimorphism (Martin and Saller 1959).

The results of testing for possible regional differences within the two periods are reported in figures 4 and 5. In the first case, the comparison involves gravettian male samples from Moravia and from the Grimaldi caves. In the absence of well-identified regional samples, the comparison between LUP groups has been carried out between Central and South Europe. In both cases, the results indicate absence of significant differences, and suggest that the dramatic decrease in stature after the Last Glacial Maximum is a phenomenon affecting the whole European record.

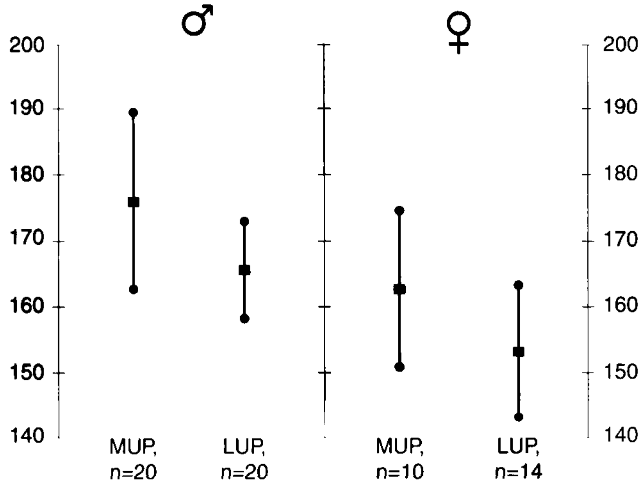

Fig. 3. Comparison (M ± 2σ) between Mid and Late Upper Palaeolithics (significant differences $p<0.01$).

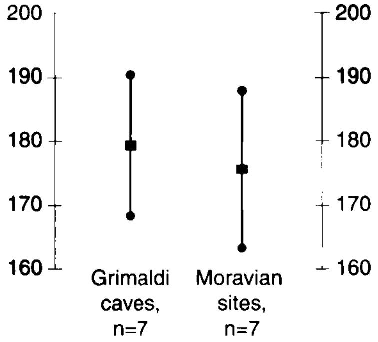

Fig. 4. Comparison (M ± 2σ) between Mid Upper Palaeolithic males from Liguria (Grimaldi caves) and from Moravia (Pavlov, Předmostí). No significant differences.

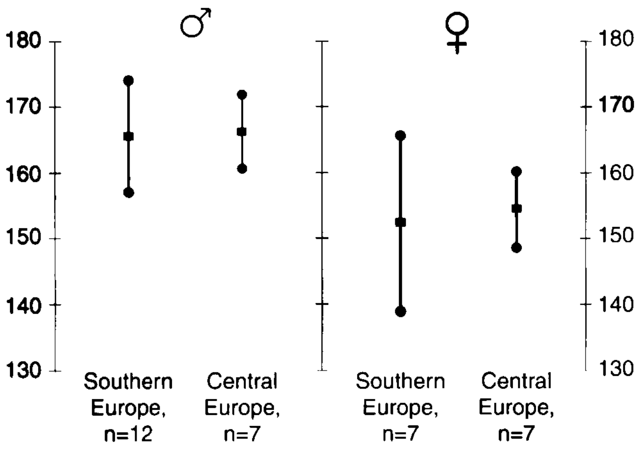

Fig. 5. Comparison (M ± 2σ) between Late Upper Palaeolithics from Southern and Central Europe. No significant differences.

Apparently, the Last Glacial Maximum and not the Upper Palaeolithic-Mesolithic transition, contrary to suggestions of previous works, represents the most critical phase in the negative trend affecting height of Upper Palaeolithic European populations.

Interpretation of the phenomenon of stature decrease has mainly focused on relaxed selective pressures for large body size as a consequence of technological improvements and reduction in dimensions of the prey (Frayer 1981, 1984). Additional factors taken into account include climatic adaptations and nutritional status. Relationships between body size and climate explain a few morphological differences among human populations. The decline in temperature occurring during the Last Glacial Maximum may have brought a shift towards a shorter, cold adapted, body size (Holliday 1997). However, Ruff's (1991) cylindrical model stresses that body breadth rather than height is the critical factor in variations of surface area and body mass ratio. Thus, climatic factors cannot account for the marked negative trend affecting Late Upper Palaeolithic populations. On the contrary, it is well known that nutritional conditions are very important in the growth process (Malina 1987; Eveleth and Tanner 1990), and the mean stature of a population is taken as a parameter indicative of its nutritional status (Prince 1995). High nutritional standards probably played an important role in the attainment and maintenance of the large body dimensions characterizing pre-Glacial Maximum Upper Palaeolithic samples. These populations had wide access to animal proteins, mostly derived from megafauna, and it is likely that tubers, fruits and wild vegetables in general contributed to varying and improving the quality of diet (Mason *et al.* 1994). After the Last Glacial Maximum gregarious megafauna was replaced by smaller more solitary games, and archaeological data indicate a shift toward a broader spectrum of subsistence activities. Moreover, number and size of the sites suggest an increased population density affecting the positive relationship with the available biomass enjoyed by earlier groups.

The synergistic effect of lower protein intake and possibly of relaxed selective forces may account for the observed marked decrease in stature. However, an additional, generally less considered factor, could have played an important role in determining the phenomenon.

One of main difference between Pre- and Post-Glacial Maximum is represented by the gradual disintegration of the cultural homogeneity characterizing the Early and Mid Upper Palaeolithic. This homogeneity, apparent in technological, artistic, and funerary aspects of the archaeological record, probably reflects high mobility, linked to subsistence strategies, and to the need to keep intergroup contacts over vast territories (Gamble 1986). That is a condition resulting in outbreeding and high levels of gene flow. Gene flow is one of the mechanisms of evolution, and outbreeding has been suggested as one of the factors responsible for today's positive secular trend (Malina, 1979). Improved health and nutritional conditions are easily demonstrable environmental factors affecting growth and development, but it is apparent that socio-economic improvements have, as a side effect, increased mobility, breakdown of the isolates, and consequently higher genetic admixture. Thus, because of the concomitance of the changes, the relative importance of genetic versus environmental factors remains an unresolved matter. However, relationships between height and level of inbreeding have been observed in different European countries (Hulse 1957; Schreider 1967; Wolansky *et al.* 1970; Billy 1971), and a negative correlation between levels of inbreeding and stature has been found in Meso-American populations, in the absence of improved health and nutritional conditions (Little and Malina 1986). In that perspective, it is important to note that Late Upper Palaeolithic archaeological information points to the beginning of a process of regional diversification of the cultures, probably an effect of the increased territorialism of groups broadening their ability to exploit natural resources. This phenomenon, coupled with increased population density, prospects of decreased mobility, development of more localised breeding networks, and in particular decreased gene flow, an additional factor to take into account in interpreting the marked negative trend subsequent to the Last Glacial Maximum.

5. Upper limb: a functional interpretation (S.E.C.)

Geometric analysis of long bone cross-sections provides a method of inferring levels and patterns of activity in prehistoric peoples (see Ruff 1992 for a review and justification for this type of research). Application of this method to the bones of the upper limb gives information about habitual subsistence and technological behaviour (Churchill 1994). Humeral mid-distal shaft cross-sections were thus taken on 17 Mid and 23 Late Upper Palaeolithic modern human specimens (Table 9). The Mid Upper Palaeolithic sample is composed primarily of specimens deriving from gravettian or proto-magdalenian contexts, but also includes a small number of specimens from aurignacian levels. These include three individuals most likely derived from late aurignacian levels at Cro-Magnon and probably chronologically best placed at about 30,000 years ago (Movius 1969; Gambier 1989a), and a single individual from Stetten (Vogelherd) associated with a basal Aurignacian, possibly 35,000 years old (Czarnetzki 1980). Thus with one exception, the sample is best seen as comprising fossils falling between 30,000 to 20,000 years bp. Since a sexual division of labour as seen in recent hunter-gatherers may also have characterised Pleistocene groups, males and females were analysed separately. Thus the samples analysed were limited to specimens for which sex could be reasonably determined from associated pelvic and cranial remains. Two specimens, Vogelherd (Stetten) 3 and Le Placard 16, were represented by isolated humeri, and are here considered male based on size, muscularity and robusticity. For comparative purposes, data were also collected on the skeletons of recent foragers, agriculturalists and industrialised peoples. The foragers include Georgia Coast Woodland-period Amerindians (data from Fresia *et al.* 1990), Aleutian Islanders, and Jomon-period Japanese. Agriculturalists were represented by samples of Georgia Coast Mississippian-period (data from Fresia *et al.* 1990) and New Mexican late Pueblo- period Amerindians. Autopsy samples of 20th century European- and African-Americans were used to represent industrialised peoples. Details about the samples can be found in Churchill (1994).

External diaphyseal contour moulds and compact bone diameters taken from anteroposterior and mediolateral radiographs (see Churchill 1994) were used to non-invasively estimate humeral mid-distal diaphyseal cross-sectional anatomy. Cross-sectional properties were estimated from the x-rays alone, using formulae found in Fresia *et al.* (1990), in cases where moulding of the fossils was not possible. Sections were estimated for the mid-distal humeral shaft, at 35% of humeral articular length (HAL) measured from the distal end. Diaphyseal cross-sectional geometric properties are determined by modelling the bone as an irregular, tubular cylinder and using principles of engineering beam theory (see Ruff 1992). These measures reflect the contribution of bone geometry to mechanical strength at the level at which the section was taken (in this case, the mid-distal shaft). The relationship of cross-sectional geometric properties to diaphyseal strength under various biomechanical loads is discussed in more detail elsewhere (Jungers and Minns 1979; Ruff and Hayes 1983a; Ruff 1992). Cortical area (CA) was taken as a measure of the resistance of the bone to pure axial loads (compression and tension), while second moments of inertia and the polar moment of inertia were used as measures of the strength of the bone to bending and torsional loads. I_x, the second moment of inertia about the mediolateral axis crossing through the centroid of the section, measures the strength of the bone to bending in the anteroposterior direction, while the second moment about the anteroposterior axis (I_y) measures strength to bending in the mediolateral plane. The polar moment of inertia (J, calculated as $I_x + I_y$) is a reflection of the strength of the bone to generalised bending and torsional loads. Since the amount of bone tissue in a shaft cross-section is related to the size of the individual, and since size varies in these samples, strength measures were standardised to body size following arguments in Churchill (1994). Specifically, CA

Table 9. The sample composition.

MID UPPER PALAEOLITHIC		LATE UPPER PALAEOLITHIC	
SPECIMEN	SEX	SPECIMEN	SEX
Arene Candide 1	male	Arene Candide 2	male
Barma Grande 2	male	Arene Candide 4	male
Barma Grande 5	male	Arene Candide 5	male
Baousso da Torre 2	male	Arene Candide 10	male
Grotte des Enfants 4	male	Arene Candide 12	male
Grotte des Enfants 5	female	Arene Candide 13	female
Paglicci 25	female	Arene Candide 14	female
Pavlov 1	male	Grotte des Enfants 3	female
Dolní Věstonice 14	male	Romito 3	male
Dolní Věstonice 16	male	Romito 4	female
Cro Magnon 1	male	Romanelli 1	male
Cro Magnon 2	female	Bruniquel 24	female
Cro Magnon 3	male	Cap Blanc 1	female
Abri Pataud 4	male	Chancelade 1	male
Abri Pataud 5	female	St. Germain la Rivière 4	female
Paviland 1	male	Farincourt	female
Stetten 3	male	Le Placard 16	male
		Laugerie Basse 4	male
		Veyrier 1	male
		Veyrier 7	male
		Neuessing 2	male
		Oberkassel 1	male
		Oberkassel 2	female

was standardized by HAL^2, while second and polar moments were standardized by HAL^4. Humeral articular length (M-2: Martin 1928) was estimated for incomplete specimens (Churchill 1994). Mean values of these size-standardised robusticity measures are provided in tables 10 and 11.

Humeral strength measures in both limbs of Mid Upper Palaeolithic (MUP) males are generally below those of recent foragers, and are more consistent with values obtained from agricultural and industrial populations (Table 10). Values for Aleutian Islanders and Jomon-period Japanese (both coastal hunter-gatherers making use of marine resources) are generally higher than those obtained for the Pleistocene fossil groups, undoubtedly a reflection of high biomechanical loads in the upper limb related to frequent paddling of boats and kayaks on the open ocean (see Berget and Churchill 1994).

The Late Upper Palaeolithic (LUP) males have generally greater strength measures, comparable with the values for the Georgia Coast foragers. Although sample sizes are small, analysis of variance followed by Fisher's least significant difference test indicate that the LUP sample is significantly stronger in all measures and in both limbs than males from the MUP ($\alpha = 0.05$).

For females, the fossil sample sizes are inadequate for statistical testing. The two Upper Palaeolithic groups do not appear to differ substantially in size-corrected CA in either limb, or in standardised second moments or polar moments of inertia in the right humerus (Table 11). Late Upper Palaeolithic females are stronger in all measures, but especially in measures of resistance to bending and torsional stresses, in the left humerus than are their MUP counterparts. However, given the high variances associated with humeral strength measures within samples (Table 11) – likely a reflection of interindividual variability in behaviour and resultant upper limb loading intensities – and the small fossil samples, it is impossible to determine whether or not the increase in left humeral strength in LUP females is behaviourally significant. Females in both periods are more robust than the Georgia Coast hunter-gatherers, but comparable to or slightly more gracile than the Aleut and Jomon females.

It is interesting that the Late Upper Palaeolithic, associated with rapidly developing technological innovations such as refined lithic reduction methods (with increased frequencies of backed bladelets and micropoints: see Straus 1993), more

Table 10. Size-standardized[1] humeral mid-distal diaphyseal cross-sectional robusticity measures - males (Mean, SD).

	CA		I_x		I_y	
	Right	Left	Right	Left	Right	Left
Mid Up. Pal. (n = 9 r, 11 l)	222.9	174.5	827.8	510.6	638.3	411.4
	34.9	28.4	191.5	161.3	148.7	137.6
Late Up. Pal. (n =13 r, 10 l)	275.6	227.9	978.8	697.6	832.8	613.5
	40.5	52.0	279.5	229.5	239.5	280.9
FORAGERS						
Georgia Coast[2] (n = 6 r, 6 l)	260.9	222.6	804.7	811.3	751.6	756.2
Aleuts (n = 25 r, 24 l)	266.0	253.6	983.8	915.6	1101.9	980.6
	40.5	33.0	178.8	174.2	251.0	218.1
Jomon (n = 10 r, 10 l)	244.5	248.8	999.9	959.1	1108.5	1087.9
	45.8	47.6	306.9	250.1	282.1	279.9
AGRICULTURAL						
Georgia Coast[2] (n = 11 r, 11 l)	231.6	213.8	677.1	652.5	601.7	621.9
Pueblo AmerInd(n= 18 r, 16 l)	171.4	156.3	568.6	455.2	520.5	481.4
	26.3	14.4	128.5	83.5	113.9	52.6
INDUSTRIAL						
EuroAmerican (n = 23 r, 19 l)	204.8	197.1	680.9	626.3	593.8	554.5
	38.3	39.4	222.2	187.6	214.8	213.8
AfroAmerican (n = 12 r, 12 l)	210.5	200.4	864.6	719.1	800.3	689.5
	30.3	32.2	181.2	139.9	242.0	223.3

[1] CA standardized to HAL^2 (* 10^5), I_x, I_y and J standardized to HAL^4 (*10^9)

[2] Mean cross-sectional values standardized by mean humeral length (as above); data from Fresia *et al.* (1990)

diverse and efficient foraging technology (including nets, weirs, harpoons, spearthrowers, weapon armatures and possibly bows and arrows: Julien 1982; Tyldesley and Bahn 1983; Straus 1990, 1993; Bergman 1993), is associated with generally stronger humeri in the affiliated fossil hominids. Models that propose a link between developing technology and postcranial gracilization in human evolution (see review in Churchill *et al.* 1996) clearly do not apply here. Both enhanced skeletal robusticity and acceleration of technological development are likely related responses to resource stress – either due to population packing or climatic deterioration, or both – during the later Pleistocene (Churchill *et al.* 1996). From this perspective, foragers of the Mid Upper Palaeolithic likely enjoyed a greater ecological stability, in terms of the balance between resource demand and availability, than did later populations.

Robusticity measures tend to be highly bilaterally asymmetrical in the upper limbs of Upper Palaeolithic males (Table 12), even relative to that seen in recent marine-based foraging groups (data for the more terrestrial foragers from the Georgia Coast were not available). Asymmetry in these measures is pronounced in Upper Palaeolithic females as well, but not to the extent seen in the males (Table 14). In both sexes, the asymmetry reflects a pattern of right hand dominance (greater activity and hence bone tissue deposition in the right side limb relative to the left: Churchill *et al.* 1996). The greater asymmetry in males than females has been attributed to the regular use of hand launched weapons – either hand thrust, hand thrown, or spear-thrower (*propulseur*) projected – in hunting by males (Churchill *et al.* 1996). Examination of ratios of second moments of area in the anteroposterior (I_x) and mediolateral (I_y) planes (Table 13) reveals humeral sections that are, on average, less rounded in the Mid than the Late Upper Palaeolithic males (an I_x/I_y of one denotes a roughly circular section equally resistant to bending in both planes, a value greater than one denotes an anteroposteriorly strong section, while a value less than one denotes a relatively mediolaterally strengthened section). This pattern is slightly more marked for the right than for the left limb. The Mid Upper Palaeolithic males are,

Table 11. Size-standardized[1] humeral mid-distal diaphyseal cross-sectional robusticity measures - females (Mean, SD, n).

	CA		I_x		I_y		J	
	Right	Left	Right	Left	Right	Left	Right	Left
	213.2	183.2	616.4	528.4	511.7	424.7	1128.1	953.2
Mid Up. Pal. (n = 2 r, 4 l)	19.1	28.3	58.8	91.3	36.3	126.2	95.1	213.3
	214.2	196.3	670.1	677.5	504.8	502.7	1171.9	1178.6
Late Up. Pal. (n = 6 r, 7 l)	43.8	29.7	214.8	110.8	172.4	91.0	388.1	196.2
FORAGERS								
Georgia Coast[2] (n = 6 r, 6 l)	204.7	154.3	447.9	377.3	481.0	425.3	928.9	802.6
	205.0	203.9	713.4	708.9	690.8	700.0	1404.2	1408.9
Aleuts (n = 19 r, 16 l)	38.0	34.9	188.4	159.3	171.9	158.6	350.1	313.6
	204.8	199.6	764.6	728.3	851.0	794.0	1615.6	1522.3
Jomon (n = 13 r, 14 l)	33.8	32.9	165.1	129.4	133.2	152.3	287.1	258.1
AGRICULTURAL								
Georgia Coast[2] (n = 11 r, 11 l)	210.5	181.1	494.4	495.7	531.4	564.8	1025.8	1060.4
	164.4	203.9	475.4	479.0	541.0	552.0	1016.4	1031.0
Pueblo AmerInd[2](n = 16 r, 19 l)	26.9	34.9	96.9	115.2	86.9	115.0	161.6	219.9
INDUSTRIAL								
	142.2	136.4	443.5	411.3	370.6	354.7	814.1	766.0
EuroAmerican (n = 18 r, 19 l)	25.2	25.5	110.6	113.4	98.6	115.4	206.1	223.0
	160.8	157.6	567.9	507.6	502.0	446.7	1069.8	954.3
AfroAmerican (n = 14 r, 11 l)	41.9	30.6	182.3	122.9	177.4	125.1	350.7	238.8

[1] CA standardized to HAL^2 (* 10^5), I_x, I_y and J standardized to HAL^4 (*10^9)

[2] Mean cross-sectional values standardized by mean humeral length (as above); data from Fresia *et al.* (1990)

in fact, extreme among the comparative samples in the degree of anteroposterior elongation of the cross-sections (relative to the mediolateral strength). This difference in humeral shaft shape has been interpreted (Churchill *et al.* 1996) as reflecting a shift in habitual hunting technology, from a greater dependence on hand-held thrusting spears (producing anteroposterior bending stresses on the humerus) in the Mid Upper Palaeolithic to a greater reliance on thrown spears (producing torsional stress in the humerus) in the later period. In females, the asymmetry in humeral cross-sectional cortical area is only slightly above (MUP) or within (LUP) the range of recent peoples (Table 13). For the polar moment of inertia (J), again a reflection of resistance to bending and torsional loads, both MUP and LUP females show asymmetry levels well above those of more recent females. This suggests that palaeolithic females, like their male counterparts, were also regularly engaging in activities (such as throwing) that engendered higher bending or twisting stresses in one limb than the other. While the nature of the activities that produced these loads is presently unclear, it does raise the possibility that the sexual division of labour that is a near-universal among modern hunter-gatherers had not fully emerged by the later Pleistocene, and that females were engaging (albeit to a lesser degree based on the magnitude of asymmetry) in regular weapon-use behaviours.

6. Lower limb: biomechanical analysis (B.M.H.)

Archaeological and palaeoecological evidence suggests that major changes took place during the Later Pleistocene of Europe, with important effects on human subsistence. Upper Palaeolithic human postcranial remains provide a unique opportunity to understand the major trends and shifts that characterised this time period.

It has been hypothesized that subsistence changes that followed the Last Glacial Maximum in Europe resulted in decreased stature, skeletal robusticity, and sexual dimorphism (Frayer 1980; 1981). According to this hypothesis, the 'gracilization' process was a consequence of a reduction in the level of musculoskeletal stress as a result of better hunting technology and reduction of prey size.

Table 12. Median percent asymmetry[1] in cortical area (CA) and polar moment of inertia (J) in males (Median, Quartile Range, Range).

	% ASYMM - CA	% ASYMM -J
Mid Up. Palaeo. (n = 7)	29.0	58.7
	13.1 - 40.8	39.9 - 96.4
	11.4 - 68.4	21.7 -170.5
Late Up. Palaeo. (n = 9)	33.8	51.2
	28.9 - 48.0	45.7 - 97.4
	20.1 - 56.8	34.3 -132.2
Aleut (n = 24)	9.5	16.4
	2.6 - 15.3	6.3 - 21.8
	0.2 - 23.9	1.1 - 40.1
Jomon (n = 10)	6.7	6.4
	5.1 - 7.6	3.2 - 10.7
	0.4 - 15.0	1.6 - 16.7
Pueblo AmerIndian (n = 14)	6.8	16.8
	4.0 - 9.1	8.8 - 23.6
	0.4 - 33.4	5.5 - 37.8
EuroAmerican (n = 19)	5.9	7.5
	3.2 - 11.6	3.1 - 21.8
	0.7 - 26.5	1.6 - 41.6

[1] Percent asymmetry calculated as [(max-min)/min]*100

Table 13. Mean I_x/I_y ratios (*100) for male samples - (Mean, SD, n).

	RIGHT	LEFT
Mid Up. Palaeo.	130.8	126.4
	16.5 (9)	16.5 (11)
Late Up. Palaeo.	118.6	121.1
	15.6 (13)	25.0 (10)
Georgia Coast H&G[1]	100.1 (6)	100.3 (6)
Aleut	103.7	101.6
	13.5 (19)	7.8 (16)
Jomon	89.7	89.1
	12.7 (10)	13.2 (10)
Georgia Coast Agricult.[1]	112.5 (11)	104.9 (11)
Pueblo AmerIndian	88.5	87.1
	15.2 (16)	13.5 (19)
EuroAmerican	120.9	118.9
	10.5 (19)	17.1 (20)
AfroAmerican	115.6	115.1
	15.0 (14)	15.7 (11)

[1] ratio calculated using mean I_x and I_y values: data from Fresia *et al.* 1990

However, contrary to the 'technological efficiency' model, biomechanical analysis of upper limb bones (Churchill 1994; this chapter) point to a marked increase in activity levels during the Late Upper Palaeolithic. These contrasting lines of evidence suggest that both postcranial variability in Upper Palaeolithic Europeans and factors underlying that variability are poorly understood. Size alone, whether of the whole body or of long bones, is an imprecise indicator of biological adaptation (Ruff 1987). Changes in bone geometry, or shape, provide more precise information about adaptation to mechanical forces that are indicative of functional use and, thus, behavioural differences (Lovejoy *et al.* 1976; Ruff and Hayes 1983a, b; Ruff 1987). Distribution of bone viewed in cross-section reflects loads placed upon that bone because, during life, bones respond to changes in forces by adding or redistributing osseous material (Wolff 1870; Ruff and Hayes 1983a; Bridges 1991). Therefore, cross-sectional properties of lower limb bones directly reflect activity levels.

Interpreting differences in long bone structure in terms of mechanical forces results in a better understanding of biobehavioural changes that accompany a change in subsistence strategy (Benfer 1990; Ruff and Larsen 1990).

Cross-sectional geometric dimensions reflect the ability of the bone to resist internal loads and bending stresses. Several indicators of femoral and tibial diaphyseal strength are used in this study to assess variability and/or changes throughout the Upper Palaeolithic. The principal axes, I_{max} and I_{min}, indicate the directions of greatest and least bending rigidity at a particular section; I_x and I_y measure the strength of the bone in an antero-posterior (A-P) and medio-lateral (M-L) direction, respectively; J, the polar moment of inertia, measures the ability of the bone to resist torsional loads. In addition, ratios of bending moments are used (I_{max}/I_{min} and I_x/I_y) as a direct way of comparing relative bone area distribution within cross sections (cross-sectional shape).

Table 14. Median percent asymmetry[1] in cortical area (CA) and polar moment of inertia (J) in females (Median, Quartile Range, Range).

	% ASYMM - CA	% ASYMM -J
Mid Up. Palaeo. (n = 2)	14.0	27.3
	0.8 - 14.0	2.4 - 27.3
	8.2	22.3
Late Up. Palaeo. (n = 5)	1.5 - 10.5	14.5 - 23.6
	0.8 - 28.7	10.7 - 58.8
	7.6	16.7
Aleut (n = 14)	1.8 - 17.0	5.3 - 26.1
	0.2 - 49.4	0.7 - 52.9
	4.3	9.8
Jomon (n = 13)	3.7 - 7.0	2.0 - 14.0
	0.6 - 27.3	0.3 - 22.5
	10.2	6.9
Pueblo AmerIndian (n = 15)	2.0 - 16.4	4.2 - 17.3
	0.0 - 20.1	0.1 - 32.8
	11.1	11.7
EuroAmerican (n = 19)	2.3 - 13.6	3.0 - 19.4
	0.1 - 27.2	0.3 - 30.4

[1] Percent asymmetry calculated as [(max-min)/min]*100

Table 15. The samples.

SPECIMENS USED FOR FEMORAL ANALYSIS	SPECIMENS USED FOR TIBIAL ANALYSIS
MUP	MUP
Parabita 1	Parabita 1
Cro-Magnon 1	Barma Grande 5
Grotte des Enfants 4	Arene Candide 1
Barma Grande 2	Paviland 1
Paviland 1	Cro-Magnon 5
Cro-Magnon 2	Parabita 2
Paglicci 25	
Arene Candide 1	
La Rochette	
LUP	LUP
Veyrier 1	Romanelli 1
Chancelade	Romito 3
Neuessing	Oberkassel 1
Riparo Tagliente	Arene Candide 10
Romanelli 1	Arene Candide 5
Arene Candide 4	Arene Candide 4
Arene Candide10	Riparo Continenza
Arene Candide 5	Riparo Tagliente
Arene Candide 12	Romito 4
Riparo Continenza	Neuessing
San Teodoro 4	Veyrier 1
St. Germain	Romito 5
Bruniquel	Cap Blanc
Grotte des Enfants 3	St. Germain

These ratios have been shown to be very useful in documenting changes in shape, reflecting changes in activity levels and patterns (Ruff 1987). Numerous studies demonstrate the sensitivity of cross-sectional geometric properties to changes in specific activity levels that are related to subsistence (see for example Ruff *et al.* 1984; Brock and Ruff 1988; Benfer 1990; Ruff and Larsen 1990; Churchill 1994). Specifically, walking, climbing, and running generate bending loads in the knee region, resulting in A-P elongation of the cross-section at the distal femur and proximal tibia. Thus, the shape of the femur and tibia in the knee region reflects patterns imposed on the bone during locomotion.

The femora and tibia of 12 Mid (MUP) and 19 Late (LUP) Upper Palaeolithic humans (Table 15) were examined to evaluate the variability and changes in lower limb biomechanical strength between these two time periods. With the exception of a few specimens (Cro-Magnon, La Rochette) that could be older, the bulk of the material is dated between 30 and 20 kyr bp.

Expectations of the 'gracilization' model imply that measures of biomechanical strength should decrease by the LUP. Two sections were chosen for this study: midshaft (50%) femur and proximal (80%) tibia. The method used to reconstruct the cross-sections is identical to that described by Churchill (this chapter). Following Ruff *et al.* (1993), second and polar moments were scaled by estimates of femoral and tibial biomechanical lengths raised to a power of 5.33, and areas by length raised to a power of 3 (see Ruff and Hayes 1983a for definitions of the length measurements, and table 16 for list of abbreviations). Although there is little significant bilateral asymmetry in the lower limbs (Ruff and Jones 1981), when possible, the right femur and tibia were used. Because of small sample sizes, females and males were pooled.

Results of the analysis are given in table 16, and illustrated in figures 6 and 7. All measures of midshaft femoral robusticity increase between the MUP and LUP, although the increase in A-P bending strength (I_{max}) is not significant. Increases in TA and CA, as well as the fact that

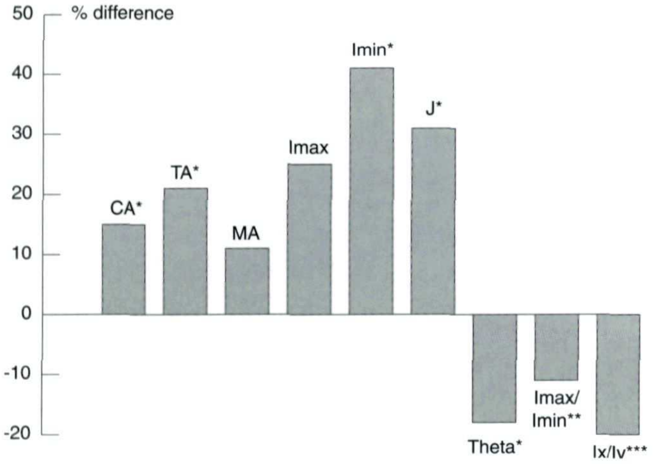

Fig. 6. Percent difference in femoral geometric properties between Mid and Late Upper Palaeolithic.

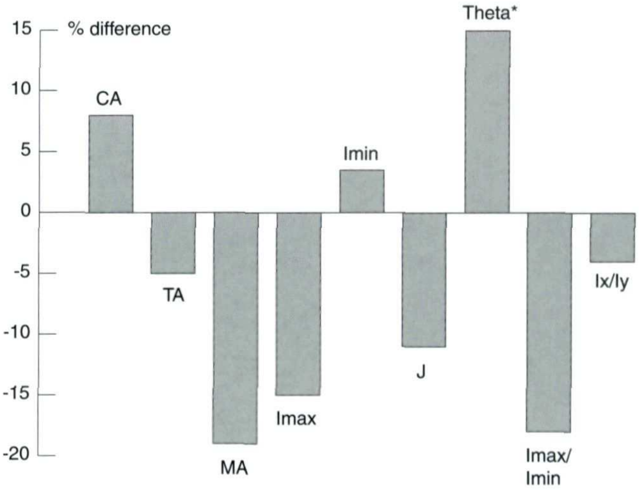

Fig. 7. Percent difference in tibial geometric properties between Mid and Late Upper Palaeolithic.

MA only increases slightly, result in a stronger and larger cross-section, with relatively more bone. The consequent larger J value points to an increase in torsional strength in the LUP group. Lower shape indices (I_{max}/I_{min} and I_x/I_y) show that LUP femora also became rounder in cross-section. This shape change is often associated with a reduction in A-P bending strength (I_{max}), relative to M-L bending strength, reflecting a reduction in activity levels (Ruff and Hayes 1983a, b; Ruff *et al.* 1984; Brock 1985). Here, however, the slight increase in I_{max} is offset by a significant increase in I_{min}, resulting in a decrease in I_{max}/I_{min}. The same is true of I_x/I_y. Thus, while rounder femoral and tibial cross-sections are usually interpreted as reflecting a reduction in levels of activities that involve A-P bending strength, here the change is primarily due to an increase in M-L bending strength. This reorientation of maximum bending strength is reflected in the decrease in theta. Thus, it appears that, while the distribution of bone within an area became more even, the size of the area increased, resulting in femora with larger, but more circular cross-sections. While it is clear that the magnitude of the bending loads increased, the unexpected strong increase in midshaft M-L bending strength also suggests a change in types of mechanical loadings.

In the proximal tibia, all measures of robusticity but two decrease, although none significantly. CA and I_{min} show a slight increase (not significant). Thus, while the femur got stronger and more circular over time, the tibia changed very little, although slight decreases in both shape indices indicate more circular cross-sections as well. Lastly, a significant increase in theta suggests a more A-P oriented-greatest bending rigidity.

The diachronic increase in lower limb robusticity requires a few words of comment. It is important to note that the results are influenced by the method used to standardise cross-sectional dimensions for body size. This apparent increase in robusticity disappears when a more sophisticated approach is used (see Holt 1999). It should be stressed, however, that the method used does not affect dimensions reflecting cross-sectional shape (I_x/I_y; I_{max}/I_{min}) since ratios do not need to be standardised. The significant increase seen in femoral cross-sectional circularity in the LUP sample suggests a reduction in activity level involving the lower limb, i.e. decreased mobility. This conclusion is consistent with archaeological evidence of increased territoriality and decreased residential mobility after the Last Glacial Maximum (Rozoy 1989).

7. Final considerations

The analyses reviewed here of temporal and geographic variance in cranial morphology, body shape and stature, and upper and lower limb skeletal robusticity in Upper Palaeolithic samples provide important information on the origins, microevolutionary trends, and biocultural adaptations of these populations. A number of issues raised in these summaries deserve comment.

Work carried out by Schumann on craniofacial form in the later Pleistocene, while detecting a small degree of morphological change (especially when the earliest modern humans of Europe are compared with the samples post-dating the Last Glacial Maximum), produces an overall picture of morphological stability during this time period. While the assumption that the Upper Palaeolithic was an insignificant or uninteresting period for human

Table 16. Differences in femoral and tibial geometric properties between Mid Upper Palaeolithic and Late Upper Palaeolithic.

	MUP		LUP		
Property[1]	Mean	SD	Mean	SD	% Difference[2]
Femur-50% (n=9 and n=14)					
CA	553.7	103.3	691.6	143.2	24.91*[3]
TA	709.3	102.3	866.4	164.1	22.15*
MA	155.6	72.5	174.8	54.7	12.34
Imax	298.9	80.0	373.4	119.1	24.92
Imin	187.8	56.2	267.3	80.5	42.33*
J	486.8	131.6	640.8	194.0	31.64*
Theta	84.2	10.4	69.9	16.2	-16.98*
Imax/Imin	1.6	0.2	1.4	0.2	-12.5**
Ix/Iy	1.6	0.2	1.3	0.2	-20.25***
Tibia-80% (n=6 and n=14)					
CA	1017.6	268.3	1101.2	200.1	8.22
TA	1980.6	347.6	1883.6	318.5	-4.90
MA	962.7	165.1	782.3	225.9	-18.74
Imax	2313.4	966.0	1966.8	636.1	-14.98
Imin	722.7	302.0	749.0	264.8	3.64
J	3036.1	1221.2	2715.7	850.1	-10.55
Theta	74.5	10.9	85.5	10.2	14.77*
Imax/Imin	3.4	0.9	2.7	0.7	-20.59
Ix/Iy	2.6	0.7	2.5	0.7	-3.85

[1] See below for abbreviations
All areas are standardized by L^3, multiplied by 10^8, all second moments of area are standardized by $L^{5.33}$, multiplied by 10^{12}

[2] [(MUP-LUP)/MUP]x100; a positive value indicates LUP>MUP

[3] * $P<0.05$; ** $P<0.01$; *** $P<0.001$

CA	cortical area
TA	total area
MA	medullary area
Imax	maximum second moment of inertia
Imin	minimum second moment of inertia
J	polar second moment of intertia
Theta	angle between M-L axis and direction of maximum bending rigidity

morphological evolution was clearly unfounded (Frayer 1984), it does appear that this period was characterised by a greater degree of stasis than change in craniofacial morphology. The lack of regional differentiation reported by Schumann is especially interesting, and may provide support for the idea of large-scale patterns of gene flow and cultural exchange across Europe during the Upper Palaeolithic (Gamble 1986). Regional differentiation during this period is low relative to living Europeans, raising the question of when (or over what period) the differences that characterise geographic populations of extant Europeans came into being. Schumann's work points to the major significance of the Last Glacial Maximum as a very dynamic phase during the Upper Palaeolithic, and it may be with the populations of post-glacial Europe, challenged by the climatic oscillations and large-scale environmental fluctuations of a warming world, that we should begin the search.

Relative morphological stability across regions, and support for the idea of 'open systems' (Gamble 1986), during the Mid Upper Palaeolithic is also suggested by analysis of stature. Formicola's work shows that both Ligurian (Grimaldi) and Moravian gravettian samples are characterised by very tall stature, considerably higher than that in later samples. Apparently, the most dramatical effects on height occurred at the end of the Last Glacial Maximum, rather than at the transition from the Palaeolithic to the Mesolithic. Factors generally invoked to explain the negative trend from Mid to Late Upper Palaeolithic include changes in functional requirements (a reduction in activity levels) and/or dietary sufficiency (a reduction in protein intake) related to changed subsistence strategies or increased populational demand on resources. A less often considered but potentially important factor could be decreased gene flow (and attendant inbreeding effects) in the Late Upper Palaeolithic in a context of decreased residential mobility and development of more restricted mating networks. Almost everyone who has viewed the Mid Upper Palaeolithic from a European (rather than more narrow regional) perspective has been struck by the cultural and morphological similarities of geographically separate populations. Formicola points to these broad geographic patterns as indicating a social and economic framework based on high levels of mobility and intergroup contact over vast areas – leading to the maintenance of networks of gene flow and cultural exchange. The Last Glacial Maximum may represent a watershed in the evolution of European social systems, in which increased territorialism and reduced intergroup exchanges (of perhaps both genes and material goods) resulted from the broadening of resource exploitation and greater control over the environment (thus obviating the need for extended social 'safety nets').

The biomechanical analyses of the upper and lower limb produce a somewhat contrasting picture. Holt's results point to a decrease in mobility and, thus, are in agreement with the model developed by Formicola. Churchill's analysis, however, reveals a significant increase in strength and robusticity in LUP upper limb. The wide-spread ecological changes that accompanied the post-Glacial Maximum created a complex situation, requiring broad ranges of biological and cultural adaptations. Trends exhibited by biomechanical data may be reflections of this complexity. The increase in body-size standardised upper limb bone strength, reflecting changes in labour intensity (most likely but not necessarily related to subsistence economy), occur in the context of a flourishing material culture. The emergence of solutrean, magdalenian and epigravettian cultures includes a rapid development of foraging tools, as well as objects of art and personal adornment possibly denoting increasing complexity in social organization. The traditional paradigm (traditional in American anthropology, at least) of a direct connection between technological evolution and reduction in bone and muscle strength is not borne out by these analyses. Instead, it appears that both technology and somatic strength may be reflecting a period of increased resource stress (and hence greater foraging intensity) in the Late relative to the Mid Upper Palaeolithic. This stress may have been driven by demographic (exponential population increase and increased population density) or ecological (deteriorating conditions associated with the onset of the Last Glacial Maximum) factors. This contrasts with Formicola's view of social and demographic factors responding to increased diversification in extracting resources from the environment. These differing viewpoints should stand as a focal point for further research. It is also noteworthy that the changes documented by Holt and Churchill in the postcranial skeleton are not reflected by changes in the presence or expression of features of cranial 'robusticity' (e.g., cranial vault superstructures). Taken together, the cranial and postcranial data paint a picture of mosaic evolutionary trends in skeletal morphology.

As concerns body shape, Mid Upper Palaeolithic remains tend to possess a long, linear physique more closely approximating the Sub-Saharan African condition than that of recent Europeans. The results of Holliday's analysis fit more easily within a Replacement (or Intermediate model) framework than within a model of Regional Continuity. This work also points to the absence of strong evidence for cold adaptation in the European modern human populations of the pre-Glacial Maximum. Interestingly, it is only after the Last Glacial Maximum that changes towards a more cold-adapted body shape (one that characterises living Europeans) can be detected. Thus, as with the work of Schumann, this points to the Last Glacial Maximum and the subsequent period as being key in the evolution of modern patterns of morphological variation in Europe. The absence of clear evidence for increased cold adaptation during the Mesolithic could be due to the rise of temperatures with the onset of the Holocene, or perhaps to improved cultural means (through clothing, shelter and pyrotechnology) of environmental buffering.

The results summarized in this paper point once more to the complex and dynamic nature of human adaptive, social and economic systems in the Upper Palaeolithic. If we are to arrive at a fuller and more accurate picture of the ecological, cultural, and biological aspects of late Pleistocene European populations, we must endeavour to integrate and synthesize the various approaches outlined here, and work towards a greater degree of interactive work with those investigating the dynamics of cultural evolution (through the archaeological rather than the fossil record) of this time period. We hope that this paper will serve to stimulate work of this nature in the future.

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