EVOLUTION AT THE EUROPEAN EDGE: NEANDERTHAL AND UPPER PALEOLITHIC RELATIONSHIPS*

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INTRODUCTION

Present discussions about the contribution of European Neanderthals to subsequent human evolution have moved to a new level of analysis where various aspects of their social behavior have become important components in arguments accounting for their extinction. In many respects these new insights are dependent on a number of unfounded "facts" about the nature of Middle-Upper Paleolithic biological relationships. For example, it is taken for granted by numerous authors that European Neanderthals had little in common with the Upper Paleolithic groups who succeeded them and that metric and morphological differences are sufficient for labelling European Neanderthals as a species apart from *Homo sapiens*. Following from this taxonomic conclusion, a series of speculative models have been proposed to account for the extinction of European Neanderthals. The result is the Neanderthal issue is now riddled with a juxtaposition of fact and fiction, and the interpretative analyses have moved to a plane which no longer seek nor require reference to the original fossil material. In some cases rejected explanations about "unique" European Neanderthal morphology are treated as if they were never rejected; in others, speculations about the chronology or hypothetical behavior of European Neanderthals are often considered to be fact and have become critical to scenarios explaining European. Neanderthal extinction; and in others, undocumented claims about European Neanderthal morphological uniqueness are used to decide on their evolutionary fate. Thus, European Neanderthals continue to slide down the evolutionary scale, away from anything anyone would want to claim as ancestors.

Recent publications have produced a set of disjointed interpretations about what European Neanderthals represent morphologically and what they were capable of behaviorally (*e. g.,* Diamond 1989, Fischman 1992, Gargett 1989, Graves 1991). Trying to piece together all that has been recently written about European Neanderthals and the Upper Paleolithic people results in a picture resembling postmodernist art, where a series of incongruous, completely unrelated images are combined together in the same scene producing a phantasmagoria. For example, while there is still no human fossil evidence which supports the co–existence of Neanderthal and Upper Paleolithic forms in Europe, we now have a series of models and speculations about the details of this co-existence and why one group replaced the other, be it linguistic incompetence, spousal inattention, or inferior hunting practices. This is contrasted with analyses which have shown that European Neanderthals have modern-like brain configurations for producing language, some rudimentary art, and some evidence for participating in long–distance trade. There are also suggestions that Upper Paleolithic groups are directly derived from African migrants, despite the complete absence of any supportive analysis for the presence of ancient or modern African features in the earliest Upper Paleolithic humans. In short, the study of European Neanderthals has reached a state in paleoanthropology where the fossils themselves have been supplanted by speculations about them.

This paper re-opens the issue of the fate of the European Neanderthals by analyzing the actual fossils from the Mousterian and the Upper Paleolithic which constitute the primary evidence for and against continuity in the European paleontological sequence. The approach is concerned with testing evidence for a series

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of morphological and metric features which have been proposed by others to define the uniqueness of European Neanderthals. Klein (1992, 12) has observed that "the most important obstacle to progress on the issue of modern human origins is evidentiary." This paper is designed to test some of the statements made about the relationship (or lack of one) between European Neanderthals and the Upper Paleolithic, as judged from the morphological and metric details of the relevant fossils. As will be demonstrated, despite the presumptions in the popular and scientific literature, there is a substantial body of evidence which supports a direct contribution of European Neanderthals to later *Homo sapiens*.

BACKGROUND AND ISSUES

For some paleoanthropologists, European Neanderthals never figured prominently in the origin of Upper Paleolithic Europeans. This position was strongly reinforced with the new evolutionary phylogeny imposed on the fossil record by the results of mitochondrial DNA (mtDNA) analysis which, for some, provided the clinching evidence to rule that European Neanderthals were completely unconnected to later human evolution. Since the mitochondrial DNA hypothesis regards the origin of modern *Homo sapiens* as a replacement event with Old World–wide usurpation by African Eve populations (Cann, Stoneking and Wilson 1987, Delson 1988, Gould 1987, 1988, Lewin 1987, 1989, Stringer 1990, 1992a, Stringer and Andrews 1988, Vigilant *et al.* 1991, Wilson and Cann 1992), European Neanderthals have been relegated to a dead-end branch of human evolution. The mtDNA position is not without controversy with regard to the place and time of origin (Darlu and Tassy 1987, Excoffier 1990, Excoffier and Langaney 1989, Excoffier and Roessli 1990, Krüger and Vogel 1989, Langaney, Van Blyenburgh and Nadot 1990, Lewin 1990, Shreeve 1990 Templeton 1992, Thorne and Wolpoff 1992, Wolpoff 1988, 1989, 1992, Wolpoff *et al.* nd, Wolpoff and Thorne 1991) and Templeton (in press) has recently rejected virtually all the major tenets and conclusions of the African Eve argument. Yet, despite the apparent death of Eve, numerous paleoanthropologists presumably still accept the mtDNA predictions and continue to place the center of origin in Africa at about 100,000 years ago (Bräuer 1992, Fagan 1990, Klein 1989, Stringer 1990, 1992a, Stringer and Andrews 1988). Since modern humans arose outside Europe according to this perspective, European Neanderthals are considered irrelevant in their contribution to the evolution of subsequent European populations. Indeed, some workers consider European Neanderthals a different species from other Middle Paleolithic or Upper Paleolithic groups (Gould 1988, Rak 1991, Stringer 1990, Stringer and Grün 1991, Tattersall 1986).

The debate about the evolutionary place of the European (or Classic) Neanderthals has been longstanding, occupying many pages in the anthropological literature (*e. g.*, Brace 1964, 1968, Howells 1974, 1975, 1981, Hrdlička 1927, Radovčić 1985, Spencer 1984, Trinkaus and Howells 1979, Trinkaus and Smith 1985). The current rejection of European Neanderthals as ancestors to anyone is simply an extension, with a different twist, of an extended debate in paleoanthropology. Considering all that has been written, one might expect a resolution of this problem, but notwithstanding the popular press (*e. g.*, Allman 1991, Brown 1990, Diamond 1989, Fischman 1992, Fisher 1988, Tierney, Wright and Springen 1988) and certain statements made in the scientific literature (reviewed below), there is still considerable room for debate. Also, contrary to Klein's contention (1989, 263) that Neanderthals are the "best understood of all nonmodern fossil people," the recent literature on these hominids belies any kind of consensus (see for example, Frayer 1992, Frayer and Montet-White 1988, Gargett 1989, Smirnov 1989, Stringer 1990, 1992b, Wolpoff and Frayer 1992, Thorne and Wolpoff 1992). The implication of the arguments here is that Neanderthals continue to be the most *misunderstood* of nonmodern fossil people.

From their initial discovery much of the debate over European Neanderthals has related to judgments about morphological and metric variability in the skull, teeth, and postcranial skeleton. In many cases, there have been very limited comparisons of European Neanderthals with the humans who directly succeeded them. As Brace wrote almost thirty years ago "very few attempts have been made to compare Neanderthals as a group with other human populations" (1964, 6). Few papers have addressed the problem since 1964; instead, there has been return to what Weidenreich (1943, 1944) termed

> a sport of a certain group of authors to search the skeletal parts of Neanderthal Man for peculiarities which could be claimed as 'specialisation', thereby proving the deviating course this form has taken in evolution.

In questioning the adequacy of this approach, Weidenreich (1943, 44) gave as an example the "absolutely arbitrary handling" of taurodontism as a unique specialization in Neanderthals. He noted that taurodontism is not just found in European Neanderthals, but also occurs in the great apes, Eskimos, Bushmen, and the Mount Carmel material. In cladistic terminology this distribution means that taurodontism cannot be considered a European Neanderthal autapomorphy (uniquely derived feature), despite the fact that some authors still consider it as one. While Brace judged the search for specialized traits "abandoned" in 1964, it has certainly made a strong resurgence since then, primarily related to the importance of cladistic analysis in phylogenetic decisions.

It might seem ironic, given the debate stemming from the mtDNA results, but the geneticists have actually helped clarify the issues separating the gradualistic and replacement models on the fate of European Neanderthals. Since the mitochondrial arguments completely reject any interbreeding between the local fossil inhabitants and their replacers (Cann Stoneking and Wilson 1987, Wilson and Cann 1992), consideration of the persistence of morphological traits through time becomes a crucial facet for hypothesis testing over the "transition." No matter where the source population derives, if this group completely replaced the resident fossil groups with no operative gene flow, one would expect to locate the appearance of a suite of novel morphological features in the new, replacing species. Thus, characters considered to be markers of modern *Homo sapiens* should exclusively typify the new species and the same features should not be found in the hominid samples they were replacing, since the two groups were travelling different evolutionary trajectories. For Europe, Neanderthals should maintain archaic (plesiomorphic) features through time along with developing their own uniquely derived (autapomorphic) traits. If European Neanderthals are completely unrelated to subsequent humans, they should not show evidence for the development of modern traits, particularly those features considered to be uniquely derived in modern *Homo sapiens.* At the same time, uniquely derived traits ascribed to European Neanderthals would not be expected to occur in the descendants of the migrant group, unless one postulates another, separate evolutionary origin of the same autapomorphic features in the new species of Upper Paleolithic humans.

The patterning of metric and morphological variation in the European hominid sequence, then, is of fundamental importance for testing the validity of the replacement or gradual models. The presence or absence of what are considered unique European Neanderthal traits in subsequent European samples becomes a crucial issue in the Neanderthal debate. Moreover, comparison of traits between the Upper Paleolithic and the Skhul/Qafzeh (or African Eve) sample is also pertinent to this issue. If these skeletal samples exemplify the ancestral state (or are the true ancestors) of Upper Paleolithic Europeans, the derived features of the Levantine or African specimens should be well-represented in the Upper Paleolithic.

Besides the analysis of European Neanderthal traits over time and space, an issue related to the European Neanderthal-Upper Paleolithic question is the rate of evolutionary change between these fossil groups. For decades it has been proposed that European Neanderthals differed so profoundly from Upper Paleolithic hominids that there was insufficient time to allow them to evolve into Upper Paleolithic *Homo sapiens*. For example, Stringer (1984a, 66) argued:

> The recent discovery of the Saint-Césaire Neanderthal provisionally dated by archaeological correlation to *ca.* 31 - 35 kyr, 5 kyr, would seem to provide clear evidence that at least *some* Neanderthals were clearly too distinct and too late in time to have evolved into a[natomically] m[odern] *H. sapiens,* with whom they overlapped temporally and by whom they were replaced. To convert even the earlier last glaciation Neanderthals into the earliest a[natomically] m[odern] Europeans would require a tremendous acceleration in evolutionary change over a few thousand years, preceded and followed by relative (but not absolute) morphological stasis...

No data were offered to support any of these contentions, but this position typifies a longstanding, undocumented conclusion leading to the rejection of European Neanderthals from any sort of ancestral position.

Most recently with the first radiometric determinations of Saint–Césaire, Mercier *et al.* (1991) argue that with a thermoluminescence date of 36.3 kyr the hypothesis of European Neanderthals evolving into modern *Homo sapiens* becomes "chronologically untenable." Despite the fact that the new absolute dates are *older* than the initial dates inferred from the archaeology (Wolpoff and Frayer 1992), the dating of Saint-Césaire is now considered to settle the issue of European Neanderthal phylogeny. Yet, it is important to consider that no diagnostic human remains are currently associated with the Western European Aurignacian sites which "conclusively" demonstrate the overlap of Neanderthals and Upper Paleolithic hominids, contrary to the view expressed by Stringer (see above). The earliest complete Upper Paleolithic material from Western Europe (Cro-Magnon) may not even be Aurignacian, but Upper Perigordian (Bouchud 1966). Consequently, the presently known gap between Saint–Césaire and the earliest complete "modern" skulls from Western Europe (such as Cro-Magnon) may be as much as 12,000 years (Wolpoff and Frayer 1992). Furthermore, due to the nearly complete absence of human skeletal material associated with the earliest Aurignacian, we do not know who manufactured the earliest Aurignacian tools. Since archaeological assemblages do not predict human types in the Mousterian of Southwest Asia (Bar-Yosef 1992), there is no *a priori* reason to suspect they do in the earliest Aurignacian of Europe. Thus, the persistent reiterations that Neanderthal and Upper Paleolithic forms overlapped in Western Europe are completely unfounded and must be rejected until contemporary hominid forms, as opposed to archaeological industries, are found. The present state of knowledge about the earliest European Aurignacian hominids makes chronological arguments less "untenable" than one might expect from reading the recent literature.

Beyond this problem, none of the "not enough time" proponents provide evidence of evolutionary rates which would support contentions that a greatly elevated rate of evolution is required for allowing European Neanderthal ancestry to Upper Paleolithic Europeans. Yet, such declarations presuppose that evolutionary rates between other human lineages which are indisputably members of the same species do not exceed those between the Neanderthals and Upper Paleolithic Europeans.

In this paper the "Neanderthal problem" is addressed by reviewing a set of metric and morphological features considered unique in European Neanderthals and comparing them with frequencies of incidence in samples from Skhul/Qafzeh, the Upper Paleolithic, and more recent human groups. Where possible, data for the African Eve sample are also included. This type of analysis was heralded in a controversial paper by Stringer (1982, 435) who advocated

> an entirely different approach which could provide at least *some* unequivocal answers to the [Neanderthal] problem. An approach which might provide such evidence would be to investigate area-specific morphoclines and characters. If early a[natomically] m[odern] *Homo sapiens* populations evolved locally, directly and solely from Neanderthal precursors in Europe... then an analysis of purely local features should show incontrovertibly that they share derived characters which are unique to their clade only ("autapomporphies") and which cross the morphological divide between the two hominid groups (his italics).

Many of the same features Stringer considered relevant "towards a solution to the Neanderthal problem" in 1982 and assumed to settle the issue (Stringer, Hublin and Vandermeersch 1984, Stringer and Andrews 1988) are reviewed here. Until now, with the exception of only a few publications (Frayer 1992, Frayer *et al.* in press, Frayer, *et al.* n. d., Jelinek 1969, 1989, Smith 1978, 1982, 1984, Trinkaus 1976, 1981, Wolpoff 1989), no author has produced a broad statistical review of specific European Neanderthal traits compared to their representation in the humans from the Upper Paleolithic. This is somewhat surprising given the repeated statements that the traits associated with European Neanderthal do not continue from the European Mousterian to the Upper Paleolithic (Klein 1989, Stringer and Andrews 1988, Stringer, Hublin and Vandermeersch 1984, Stringer, Kruszynski and Jacobi 1981). In addition, evolutionary rates for the dentition and certain cranial measurements are calculated to assess the rapidity of change between Mousterian and early Upper Paleolithic groups compared to rates between groups of other possible lineal relatives. These are germane to the argument that not enough time exists for morphological or metric change to occur between European Neanderthals and the early Upper Paleolithic hominids.

SAMPLES

For the analysis of dental, cranial and postcranial metrics and morphological traits, I have compiled samples for European Neanderthals, Skhul/Qafzeh, and African Eves, the latter consisting of material from Border Cave and Klasies River Mouth. Metric data for these groups are based on measurements provided by M. H. Wolpoff and are supplemented by my morphological observations on numerous originals in various European museums and on casts located in the Laboratory of Paleoanthropology, University of Michigan. The European Neanderthal sample is composed of specimens for Central and Western Europe found in Mousterian or Chatelperronian contexts. For the purposes of this comparative analysis, I see no compelling reason for considering specimens from Central and Western Europe apart. Given the few number of specimens available from either area, prohibitively small sample sizes would be the main result. Sample sizes are not large for the Skhul/Qafzeh sample, but unlike most other considerations of the important fossils from these sites, data are included for *all* the specimens, rather than simply making comparisons to Skhul 5 or Qafzeh 9. Recently, Corruccini (1992) and Kidder, Jantz and Smith (1992) have shown that most specimens from these two sites do not fit within modern ranges of variation. Consequently, in evolutionary assessments of the material from Skhul/Qafzeh, it is important to include all the appropriate material from these two sites. Besides casts and Wolpoff's data set, I have relied upon the descriptions of McCown and Keith (1939) for Skhul and Vandermeersch (1981) for Qafzeh. Sample size is even smaller for the African Eve group (which lacks relevant postcranial remains), but deficiencies in sample size has not stopped others from utilizing this poorly preserved and questionably dated sample as representing the ancestors of all modern *sapiens* (*e. g.*, Bräuer 1992, Stringer 1990, 1992a). I use this African Eve sample with some trepidation and *only* to test statements made about it in the literature.

Data for the Upper Paleolithic, Mesolithic, and Neolithic come from my study of museum collections in Western and Central Europe. The Upper Paleolithic is divided into early and late periods, but unlike my earlier work (*e. g.*, Frayer 1978, 1981), I now use the glacial maximum (~18,000 B.P.) as the separation between the early and late Upper Paleolithic (see Gamble and Soffer 1990) and include the Azilian in the late Upper Paleolithic sample. In some cases, notably Predmostí and some of the Mladec remains, I have extracted metrics and observations from the literature or casts. Mesolithic and Neolithic samples include data collected only on original material. For cranial and postcranial features, the Hungarian Medieval sample consists of material from Zalavár (Sös and Bökönyi 1963), dated between the 9th-11th centuries. All measurements are based on my personal study of the material. I use this skeletal material to represent a recent human sample, but do not contend they are typical of all recent Europeans nor that they are direct, lineal descendants of any of the earlier samples.

CRANIAL FEATURES

European Neanderthals have specific cranial and facial features which have long been used to separate them from other contemporary and succeeding hominid groups. The standard presentation in the scientific and popular literature suggests these features are so distinct in European Neanderthals that they serve to completely distinguish them from all other populations. The fact is, however, that the majority of the presumed distinctive features also appear in the European Upper Paleolithic material, albeit not generally reaching the frequency or metric expression in the later time periods. In the following section a number of these so-called European Neanderthal autapomorphies are reviewed.

THE RETROMOLAR SPACE AND FACIAL PROGNATHISM

One of the more important European Neanderthal traits is facial projection measured by morphological criteria and metrics. Mandibles of European Neanderthals typically have a gap between the third molar and the anterior margin of the ramus called the retromolar space (Figure 1). This aspect of European Neanderthal morphology is interpreted as a requirement of midfacial prognathism in that the mandibular teeth were shifted forward to maintain functional occlusion with the anteriorly placed maxilla, leaving behind the retromolar space (Wolpoff 1980). Stringer, Hublin and Vandermeersch (1984, 55) list the retromolar space as a "detail of the usual morphology" of European Neanderthal facial prognathism, while Klein (1989, 273-4, 380) treats the presence of a retromolar space as a European Neanderthal feature and its absence as a modern characteristic. While these and other authors presume the retromolar space to be common in all European Neanderthals, Trinkaus (1987a, 438) lists five specimens (Krapina 57, La Naulette 1, La Quina 9, Vindija 206, and, probably, Hortus 4) which lack this "typical" feature, amounting to a frequency of 26.3% using his sample. Moreover, despite expectations that the retromolar space is absent in Upper Paleolithic hominids, this feature is far from rare, especially, in the early Upper Paleolithic material. For example, Wolpoff *et al.* (1981) describe a retromolar space in the Vindija 207 mandible associated with the early Aurignacian in Croatia (Figure 1), and wide retromolar spaces are also found in Predmostí 3, 4, and 21, Brno 2 , and Stetten 1 (Figure 1), all dated to the early Upper Paleolithic. Unfortunately, I did not collect the frequency of this trait in all the Upper Paleolithic and Mesolithic specimens, but the retromolar space is clearly not restricted to European Neanderthals. Rather, it occurs in a number of early Upper Paleolithic specimens which demonstrates that these specimens show evidence for the retention of some facial prognathism. In the Near Eastern and African material, Skhul 5 has a small retromolar space, but it is noteworthy that none of the mandibles from Qafzeh nor those attributed to African Eves have a retromolar space (McCown and Keith 1939, Rightmire and Deacon 1991, Vandermeersch 1981). The retromolar space, then, occurs sporadically at Skhul and in the Upper Paleolithic. Yet, the same feature is also variable in the European Neanderthals, demonstrated by its absence in about one-quarter of the specimens. While the retromolar space probably signals a measure of facial prognathism, it cannot be used as a feature which uniquely characterizes European Neanderthals. Nor is it a feature which heralds a discontinuity between European Neanderthals and the Upper Paleolithic, since it is clearly present in the Upper Paleolithic.

In addition to the occurrence of the retromolar space, metric evidence demonstrates that European Neanderthals have anteriorly projecting faces (Rak 1986, Trinkaus 1989a). But, this condition also characterizes the Upper Paleolithic samples which follow Neanderthals in Europe. Table 1 reviews data for 16 points on or near the face taken from the auricular point. The auricular point was used in place of a more traditional one (like *basion*) since crucial parts of the basal region are often missing in European Neanderthals and later specimens. From Table 1 is apparent that European Neanderthals show considerably greater (and statistically significant) facial projections for a number of standard points compared to the early Upper Paleolithic sample.

Yet, the overall percent change (%Δ) to the early Upper Paleolithic for these 16 measurements is less than average amount of change from the early Upper Paleolithic to the Mesolithic (7.8%) or from the early Upper Paleolithic to the Medieval sample (7.7%). While the pattern of change among the various comparisons is dissimilar through time, these data clearly show that reduction in facial prognathism characterizes Europeans who follow the Neanderthals. Some of these reductions reach a maximum between European Neanderthals and the early Upper Paleolithic, but the overall percent reduction is greater in later time periods than between the European Neanderthals and the early Upper Paleolithic sample. It is also noteworthy that if the Skhul/Qafzeh sample represents the ancestors of Upper Paleolithic Europeans, overall facial projection would have to increase slightly in the early Upper Paleolithic, but generally not at statistically significant levels, then reverse this pattern and reduce throughout the remainder of European prehistory.

Besides these measures of prognathism, Europeans from all time periods have upper faces that project like European Neanderthals, unlike comparative samples of the Near East *sapiens* or African Eves. Previously, Wolpoff (1989, 132) has discussed the projection of *nasion* in front of the bi-*fmt* (*frontomalaretemporale*) line and argued that European Neanderthals and early Upper Paleolithic Europeans have anteriorly angled upper faces, while the Skhul/Qafzeh upper faces are flat. This more anterior position of *nasion* in European Neanderthals is consistent with Rak's argument (1986) of a more sagittal orientation of the midface or Trinkaus' explanation of zygomatic retreat (1987a). Figure 2 shows the browridge region from above in La Chapelle-aux-Saints, Mladeč 5 and Skhul 5. In La Chapelle-aux-Saints there is a great deal of anterior projection at the midline, with the lateral supraorbital region angling strongly in the posterior direction. In Skhul 5, the upper facial region is relatively flat from *nasion* to *fmt*, showing little midline projection and minor posterior-lateral angulation. Of these two, Mladeč 5 is most like La Chapelle-aux-Saints, with a high degree of anterior midline projection, coupled with a posteriorly angled lateral supraorbital margin.

TABLE 1

Percent Differences (% Δ) for Facial Measurements from the Auricular Point for Transition Comparisons

(§ - p < .05; ‡ p < .01 for significant differences in means with two-tailed student's t)

Auricular point to :	European Neands / Early Upper Paleo. % Δ	Skhul/Qafzeh /Early Upper Paleo. % Δ	Early / Late Upper Paleolithic % Δ	Early Upper Paleo. /Mesolithic % Δ	Early Upper Paleo. /Medieval % Δ
prosthion	11.8‡	4.3	6.2‡	7.1‡	6.9‡
nasospinale	10.3‡	-4.6	6.0‡	8.2‡	8.4‡
nasion	9.2‡	-.4	4.3§	5.7‡	5.9‡
glabella	8.5‡	1.8	4.3§	5.8‡	6.6‡
Zygomaxillarae	0.0	-4.8	4.7	9.6‡	9.5‡
M1/M2	20.2‡	1.1	2.8	3.3	4.1
P3/P4	12.6‡	.7	6.3§	5.7	6.4‡
I2/C	11.9‡	2.0	5.1‡	5.3‡	5.9‡
Inferior Nasomaxillary Suture	6.5§	-7.2	4.8§	7.9‡	7.8‡
jugale	4.9	-3.6	11.1‡	13.8‡	13.0‡
frontomalareorbitale	3.7	-3.4	6.2‡	8.7‡	9.7‡
alare	8.1‡	1.9	5.0‡	7.0‡	8.2‡
Anterior Temporal Fossa	-1.2	-5.5	6.4§	10.3‡	5.6‡
zm Suture at Orbit Margin	-.5	-13.1	4.9§	8.1‡	8.0‡
Palatine Suture Cross	6.0	12.8§	6.6‡	8.5‡	-8.1‡
Post-*orale*	5.5	-	8.0‡	9.1‡	8.9‡
Average Change	7.3	-2.9	5.8	7.8	7.7

TABLE 2

Nasion Projection from the Bi-*FMT* line (in mm)

	MEAN	(N)	RANGE
European Neanderthals	29.3	(11)	26.5 -35.8
Skhul/Qafzeh	12.4	(3)	6.6 -21.7
African Eves (Border Cave 1)	17.8	(1)	-
Early Upper Paleolithic	21.9	(16)	14.6 -31.9
Late Upper Paleolithic	19.3	(23)	10.4 -30.7
Mesolithic	19.4	(114)	3.7 -32.4
Medieval Hungarians	20.2	(40)	7.9 -29.0

This visual impression can be evaluated using measurements from *nasion* and *fmt* to calculate the projection of *nasion* in front of the bi-*fmt* line. In Table 2, European Neanderthals show an average projection of 29.3 mm and all four post-Neanderthal European samples are clustered together with *nasion* projections ranging between 19.3mm and 21.9mm. Each of these European samples is well below the European Neanderthal mean, but they also differ considerably from the Skhul/Qafzeh condition which shows little anterior projection at the midline. In addition, the single African Eve specimen shows a lower *nasion* projection than the means for any of the European samples, although it overlaps with the European range. Differences among the samples clearly show that European samples have projecting faces directly above the nose as a typical feature, while in the Near East material the region at *nasion* projects little and the upper face tends to be flat. Although statistically significant differences are not shown in this table, European Neanderthal projections at *nasion* are significantly greater than all the other samples, excluding the African Eve group with a sample size of one. However, the Skhul/Qafzeh sample shows a statistically significant flatter upper facial region compared to all other groups (except the African Eves). Thus, while European Neanderthals have significantly more projecting faces at *nasion*, the Skhul/Qafzeh sample has a significantly less projecting region at *nasion* compared to all the European samples. The importance of this variable morphology between Europe and the Near East (or Africa) is that if Skhul/Qafzeh (or the African Eves) represent the ancestral form, the Upper Paleolithic descendants experienced a substantial increase in upper facial projection, moving in the direction of the European Neanderthals whom they supposedly replaced. On the other hand, if European Neanderthals are the ancestral forms, the upper facial projection decreased substantially over time. One can ask, is it reasonable to propose (or to expect) that the hypothesized replacing populations from the Near East somehow developed the projecting upper faces which characterize the people they were replacing ? Or, is it more likely that the upper facial projection in the Upper Paleolithic is a retention of an archaic, regional European marker ?

In summary, for these measures of facial and supraorbital projection, there is nothing which convincingly rejects European Neanderthals as an ancestral group to the Upper Paleolithic people of Europe. While the Skhul/Qafzeh sample shows greater similarity in certain facial measurements to the early Upper Paleolithic, they show a considerably flatter upper face which is distinct from early Upper Paleolithic and later Europeans. At the same time European Neanderthals have a variable expression in the retromolar space and upper faces which project more than the Upper Paleolithic and later Europeans. Finally, the distinctive facial dimensions should be viewed with respect to changes in the same dimensions from the early Upper Paleolithic onwards. Seen in this context, dimensional reduction from European Neanderthals to the early Upper Upper Paleolithic is completely within the range of percentage reductions in post-Neanderthal Europeans.

NASAL BREADTH

The large size of the nasal aperture has long been recognized as a salient feature of European Neanderthals, distinguishing them from the European Upper Paleolithic samples (Boule and Vallois 1957, Coon 1962, Trinkaus 1987b, Wolpoff 1980). Size of the European Neanderthal nasal aperture is evident by its anterior projection from the coronal plane, by its maximum height, and the breadth across the lower margin. As reviewed above (Table 1) European Neanderthals have substantially larger chords from the auricular point to *nasospinale*, *nasion*, the inferior nasomaxillary suture, and the lateral aspect of the lower nasal aperture (*alare*) compared to the early Upper Paleolithic sample. However, the same dimensions reduce significantly within the Upper Paleolithic and from the early Upper Paleolithic to the Mesolithic. Thus, while European Neanderthals have distinctively projecting noses, this aspect of European faces also decreases markedly though time after the appearance of the Upper Paleolithic. Compared to the Skhul/Qafzeh sample, these same four dimensions are slightly larger in the early Upper Paleolithic (except for the auricular point-*alare* chord), but none of the differences reach statistical significance (Table 1). Obviously, these data show a greater similarity between the Near Eastern and Upper Paleolithic samples in nasal projections along the sagittal midline, which is consistent with other published studies.

Heights and breadths of the nose for the comparative samples are presented in Table 3. In addition to maximum nasal height and breadth, indices of these nasal dimensions relative to the *fmt-fmt* (*frontomalaretemporale*) chords are also given. Clearly, absolute and relative nasal heights are substantially greater in the European Neanderthal sample compared to any of the other groups. Mean nasal height in the early Upper Paleolithic (51.6 mm) is some 10mm smaller than in the European Neanderthals (62.0 mm) and no substantial changes occur in nasal heights once the Upper Paleolithic is reached. Relative nasal height is also considerably smaller in the early Upper Paleolithic (compared to the European Neanderthals) and shows a slight trend for increasing into the later populations, which have generally narrower upper facial breadths. In this regard, it is perhaps interesting that the Mesolithic and Medieval samples have relative nasal heights closer to the European Neanderthals than either the early or late Upper Paleolithic samples.

TABLE 3

Absolute and Relative Nasal Heights and Breadths for European Neanderthal, Skhul/Qafseh[1]

Early Upper Paleolithic, Late Upper Paleolithic, Mesolithic, Neolithic, and Medieval Samples.

	Nasal Height Mean (n)	Nasal Ht/*Fmt-Fmt* Mean (n)	Nasal Breadth Mean (n)	Nasal Br/*Fmt-Fmt* Mean (n)
European Neanderthals	62.0 (6)	51.7 (6)	31.7[2] (12)	27.7 (7)
range	(57.9-66.6)	(49.8-55.5)	(26.2-35.1)	(25.3-29.7)
Skhul/Qafzeh	54.2 (4)	44.2 (4)	31.8 (3)	26.1 (3)
range	(53.0-55.6)	(40.6-48.5)	(30.8-32.5)	(23.2-29.2)
Early Upper Paleolithic	51.6 (17)	46.5 (14)	26.3 (23)	24.3 (19)
range	(45.6-61.1)	(41.8-52.3)	(20.2-29.7)	(20.4-28.8)
Late Upper Paleolithic	49.7 (29)	46.2 (21)	23.7 (33)	22.3 (20)
range	(43.0-60.1)	(41.8-53.6)	(15.8-27.2)	(15.0-25.7)
Mesolithic	50.6 (90)	47.9 (79)	23.8 (118)	22.4 (84)
range	(40.4-62.8)	(40.3-55.6)	(18.8-30.0)	(18.3-28.4)
Neolithic	49.0 (231)	46.8 (217)	24.0 (222)	22.9 (208)
range	(35.2-61.0)	(39.1-56.8)	(18.6-28.9)	(17.0-28.0)
Medieval Hungarians	49.9 (67)	48.0 (66)	24.3 (70)	23.3 (68)
range	(41.9-58.7)	(42.2-56.3)	(20.2-27.9)	(20.4-26.5)

1 Since all the Skhul/Qafzeh specimens (except Qafzeh 6) lack either *nasion* or *nasospinale*, the estimates of McCown and Keith (1939) and Vandermeersch (1981) are used.
2 Vindija 225 = 28.5mm.; Vindija 259 = 26.2mm.

At the same time, absolute and relative nasal heights are similar between the Skhul/Qafzeh and early Upper Paleolithic sample, consistent with some arguments that certain aspects of the faces of these two groups are derived in the direction of recent humans.

While there is a similarity in the nasal height between the Skhul/Qafzeh and early Upper Paleolithic samples, this similarity certainly does not extend to the nasal breadths. For some, it may be surprising to find that maximum breadths of the nasal aperture are indistinguishable between the European Neanderthal (31.7mm) and Skhul/Qafzeh (31.8mm) samples. Thus, while the Skhul/Qafzeh samples exhibit shorter faces and substantially less facial projection than European Neanderthals, they maintain absolutely large maximum nasal breadths. Most likely, this is related to the large maxillary incisor size found in both European Neanderthals and the Skhul/Qafzeh sample (see below). Differences between sample means for the nasal breadth in these two samples does not reach statistical significance, but both European Neanderthals and the Skhul/Qafzeh samples are significantly larger than any of the Early Upper Paleolithic and later samples. It is also apparent that both measures of relative nasal breadth show little separation between the European Neanderthals and Skhul/Qafzeh sample. Although Skhul/Qafzeh displays lower nasal breadth indices, like the European Neanderthals, relative nasal breadths are larger in both these samples than found in the early Upper Paleolithic and later groups. Thus, arguments that European Neanderthals have substantially larger absolute or relative breadths compared to the so-called "proto–Cro–Magnons" from the Near East draw little support from the available data.

Compared to these samples, the early Upper Paleolithic exhibits reduced absolute nasal dimensions, about 20% smaller than either the Skhul/Qafzeh and European Neanderthal sample. With in the Upper Paleolithic, further reduction occurs in nasal breadth which is about 9% larger in the early Upper Paleolithic compared to all the subsequent samples. This is a statistically significant reduction with a probability <.001 for each case. After the late Upper Paleolithic there is little change in this dimension. Relative nasal breadths in the early Upper Paleolithic are also 14% smaller than the European Neanderthals and 7% smaller than the Skhul/Qafzeh sample. Whether European Neanderthals or Skhul/Qafzeh are the ancestral group, nasal breadth indices decrease substantially once the early Upper Paleolithic is reached and continue to reduce to the Mesolithic. For example, relative nasal breadths decline about 9% from the early Upper Paleolithic to the Mesolithic. Marked reductions in relative nasal breadth from the early to the late Upper Paleolithic (or Mesolithic) are accompanied by reductions in lateral nasal projections from the auricular point, ranging from 4.3% - 8.2% (Table 1). Taken together, the available data indicate that as the face retreated under the brows in the post–Neanderthal European groups, absolute and relative nasal breadth also decreased. Moreover, as maxillary incisor size decreased, nasal breadth showed concomitant reductions.

Finally, given the smaller absolute and relative dimensions of the nasal aperture in the early Upper Paleolithic, are there trends for nasal breadth reduction in European Neanderthals? Because of the limited facial remains from late Neanderthals, the question cannot be definitively answered. However, two published specimens from the late Mousterian site of Vindija (#225 and #259) represent the bottom of the European Neanderthal range for maximum breadth (Footnote, Table 3) and their average size is much closer to the early Upper Paleolithic than to the European Neanderthal mean (see also, Smith 1992a, 151-152). As pointed out by Wolpoff, *et al.* (1981, 505) with respect to these specimens from Vindija, "[s]ince facial size reduction is one of the major morphological alterations associated with the transition from Neandertals to anatomically modern *Homo sapiens*, the fact that the Vindija G3 hominids tend to approach the early modern condition is indeed significant." Furthermore, the late Neanderthal from Saint Césaire (when fully published) will demonstrate that this specimen also has a reduced maximum nasal breadth compared to the earlier European Neanderthal sample. From the three late Neanderthal specimens now known, nasal breadth reduces over time away from the earlier European Neanderthal mean and toward the early Upper Paleolithic mean whether the specimens are sampled from Central or Western Europe. In this metric feature, late Neanderthals from Vindija and Saint-Césaire are taking on features assumed to be modern attributes in Upper Paleolithic hominids. In sum, while nasal height shows a clear distinction between the European Neanderthals and the Upper Paleolithic, differences in nasal breadths are much less divergent, reducing into the late Mousterian, then show further reduction within the Upper Paleolithic.

LAMBDOIDAL FLATTENING AND THE OCCIPITAL BUN

Lambdoidal flattening and the presence of an occipital bun resulting in a posteriorly projecting occipital are features found in European Neanderthals (with the exception of Saccopastore 1) and in many Upper Paleolithic, Mesolithic and later specimens (Frayer 1986, Smith 1983, 1984, 1991, Trinkaus and LeMay 1982, Wolpoff 1980). It is important to note, however, that La Ferrassie 1 and Spy 2 have a very weakly developed bun and minor lambdoidal flattening. Thus, while Stringer, Hublin and Vandermeersch (1984, 54-55) list this aspect of occipital morphology as a "common" European Neanderthal feature and a nonprojecting occipital as a derived feature in recent *Homo sapiens*, by this criterion alone at least three European Neanderthals do not fit the typical pattern, but diverge toward the "modern" morphology. Moreover, many post–Neanderthal crania from Europe possess both lambdoidal flattening and the occipital bun. On the other hand, specimens from Skhul/Qafzeh lack development of either lambdoidal flattening or occipital buns (McCown and Keith 1939, Vandermeersch 1981). Such features are also absent in the few African Eve specimens, which like the Skhul/Qafzeh hominids have much more rounded posterior occiputs. The morphology of the posterior occipital, then, is discontinuous between the early Upper Paleolithic and either the Skhul/Qafzeh (or African Eve) samples in that neither of these potential ancestors have the typical morphology found in the early Upper Paleolithic.

Yet, the morphology of this region exhibits continuity between European Neanderthals and the early Upper Paleolithic. To illustrate this similarity, Figure 3 provides lateral cranial contours of the posterior vault for a selection of European Neanderthal, Skhul/Qafzeh, and early Upper Paleolithic specimens. Like the Skhul/Qafzeh specimens, the Upper Paleolithic skulls show higher posterior cranial vaults, but like the European Neanderthals, in most of the early Upper Paleolithic specimens the occipital squama is oriented posteriorly forming a marked bun (chignon). Furthermore, as in European Neanderthals (and unlike the Skhul/Qafzeh occiputs), some Upper Paleolithic skulls have flattening on the posterior parietals,, sometimes extending onto the superior-most occipital squama. Lambdoidal flattening and the formation of the occipital bun are especially evident in the three Mladeč vaults which represent the earliest specimens in the Upper Paleolithic series (Figure 3) and are more like European Neanderthals than any of the later specimens (see also, Caspari 1991, Smith 1982, Wolpoff 1980). Later specimens from Western Europe (Cro-Magnon and Abri Pataud) show a marked reduction in posterior parietal flattening, but preserve in most cases a pronounced occipital bun.

Finally, Caspari (1991) has reviewed aspects of occipital squama morphology in Central Europe and argues that, while there is gross morphological similarity in European Neanderthals and the early Upper Paleolithic, the European Neanderthals tend to have greater flattening on the occipital, more acute angles between the occipital and nuchal planes, and a more transversely elongated bun with a narrower posterior face compared to the early Upper Paleolithic material. With respect to these features Mladeč 6, dated to the early Aurignacian of Moravia (Frayer 1986, Jelínek 1969, 1976, Smith 1982), is virtually identical to the European Neanderthal condition (Caspari 1991, 179-181). Certainly, no specimens from the Near East or Africa provide a reasonable ancestral state to Mladeč 6 or virtually any of the other early Upper Paleolithic material. Whether the morphology of this region is mediated by ontogenetic processes (Trinkaus and LeMay 1982) or is a functional, adaptive response (Smith 1983, Caspari 1991), the morphology of the occipital region provides indisputable links between European Neanderthals and the Upper Paleolithic.

SUPRAINIAC FOSSA

The suprainiac fossa is a pit located in the occipital plane just above the nuchal plane (Figure 4). First noted by Gorjanović-Kramberger (1902) and Klaatsch (1902), the feature has been studied recently in greater detail by Caspari (1991), Heim (1982), Hublin (1978a), and Santa Luca (1978). Primarily resulting from the work of Hublin (1978a) and Santa Luca (1978), the suprainiac fossa is considered a European Neanderthal autapomorphy (Hublin 1978b, 1980, Stringer, Hublin and Vandermeersch 1984). While such a designation is technically inaccurate since the identical feature occurs in a number of pre–Neanderthal European fossils (*e. g.*, Swanscombe) and in specimens from outside Europe (*e. g.*, Qafzeh 6, Skhul 9, Zhoukoudian 3), the high frequency of this trait for European Neanderthals suggests it is a common feature of the group. Yet, this does not mean there is a consistent morphology in European Neanderthals. In fact, the suprainiac fossa shows considerable variation, ranging from a small, single pit in Gibraltar 1 to a doubled structure in La Quina 5 to an extensive fossa in Salzgitter–Lebenstedt (Hublin 1978a). In the majority of specimens, the suprainiac fossa is roughly triangular in shape, with the apex directed away from the nuchal plane (Caspari 1991, Frayer 1992). In the post–Neanderthal European samples, no specimen exactly matches the European Neanderthal condition, although Caspari (1991, 152-3) describes "a resorptive surface, very similar to the suprainiac fossa of Neandertals, though much less clearly expressed" in the Mladeč 6 male. However, in most other specimens from Upper Paleolithic, Mesolithic, and recent samples the suprainiac fossa tends to be (1) small, shallow, and confined to the sagittal midline and (2) shaped differently, with the apex of the triangular fossa pointing toward the nuchal plane (Figure 4; Caspari 1991, Frayer 1992). When present in these specimens the suprainiac fossa appears to be the result of a strong expression of the convergence of the supreme and superior nuchal line coupled with a marked projection of the external occipital protuberance (*inion*). For these reasons, it is apparent that this structure (except possibly for Mladeč 6) is not identical between Neanderthal and post-Neanderthal Europeans (Caspari 1991, Frayer 1992).

Like other features rarely found in recent populations, the genetics and function of this character are open to question. According to work by Heim (1982), the suprainiac fossa occurs in all juvenile and adult European Neanderthals as well as in some contemporary human infants. But, in modern infants this feature is later lost due to bone remodelling. Based on comparative ontogeny, Heim infers that the suprainiac fossa is related to retarded osteogenic growth in European Neanderthals. On the other hand, Hublin (1978a, 1980) regards the suprainiac fossa as homologous to the external occipital protuberance (*inion*) which is absent in European Neanderthals. Hublin contends that the fossa is created by contraction of the space between the superior and supreme nuchal lines. Most recently, Caspari (1991) has reviewed the incidence of this feature in Upper Pleistocene Central European fossils and concludes that the suprainiac fossa is a resorptive surface created by bending stresses along the nuchal torus. Loss of the distinctiveness of this feature in post–Neanderthal groups is judged by her as a reflection of changes in the distributions of loads on the nuchal torus.

Given these differences in opinion about the origin of the suprainiac fossa and questions concerning the comparability across various samples, it is perhaps phylogeneticly meaningless to compare the incidence of this trait in European Neanderthals with other samples. Yet, if as Caspari (1991) argues, the suprainiac fossa is simply a resorptive surface, the shape of the region is less important than the fact that it exists in all the samples. In addition, Hublin (1978a) has provided statistics for the occurrence of the suprainiac fossa in European Neanderthals and modern French, which leads to the impression that he considers the differing morphologies comparatively equivalent.

With these reservations in mind, I present data for the incidence of the suprainiac fossa for European Neanderthals and other samples in Table 4. The incidence of the suprainiac fossa in the European Neanderthals is nearly 100%. The only currently known Mousterian associated specimen which lacks this feature is an occipital from Krapina (11.5), deriving from an upper level (8) at this site (Radovčić *et al.* 1988). Since Simek (1991) regards this level as Mousterian, I have included it with the European Neanderthals, for lack of any other sample to place it (1). While the frequencies of a suprainiac fossa in all other samples are considerably lower than in the European Neanderthals, a resorptive surface above *inion* is obviously not absent in these groups. Upper Paleolithic and Mesolithic groups show an incidence between 19.3% and 30.0% which is considerably higher than the Medieval Hungarian and modern French samples. It is also apparent that the suprainiac fossa is found in the Near Eastern samples at frequencies well below the European Neanderthals, but within the Upper Paleolithic-Mesolithic range.

The incidence of a resorptive surface above *inion* in these samples provides no support for the contention that this feature is limited to the European Neanderthals. To the contrary, it is found at frequencies between 2% and 30% in other European samples. In one perspective, the near equivalent frequencies of the Skhul/Qafzeh and early Upper Paleolithic samples may signal a close relationship, but given the fact that the incidence of suprainiac fossa decreases to near 0% in the modern French sample, it is apparent that there is a major shift in frequency within so–called anatomically modern *Homo sapiens*. This observation, coupled with Caspari's functional explanation (1991), may mean that frequency differences between European Neanderthals and the early Upper Paleolithic reflect the consequences of a behavioral shift (which continues through prehistoric into historic Europe), rather than signalling a phylogenetic divergence. Whatever the case, a resorptive surface above *inion* cannot be considered a uniquely derived trait in European Neanderthals and cannot be used to disqualify them from leaving European descendants.

(1) Another specimen from this level (Krapina is considered a "transitional specimen" between Neanderthals and the early Upper Paleolithic, but classified as neither (Minugh and Radovčić 1991, 132).

TABLE 4

Frequencies of the Suprainiac Fossa in European Neanderthal, Skhul/Qafzeh, Upper Paleolithic, Mesolithic, and recent European Adult Samples.

	PRESENT % INCIDENCE (N)	ABSENT % INCIDENCE (N)
European Neanderthals[1]	95.7 (23)	4.3 (1)
Skhul/Qafzeh	28.6 (2)	71.4 (5)
Early Upper Paleolithic[2]	38,5 (10)	61,5 (16)
Late Upper Paleolithic	23.7 (9)	76.3 (29)
Mesolithic	19.3 (31)	80.7 (130)
Medieval Hungarians	5.9 (14)	94.1 (223)
Modern French[3]	2.0 (2)	98.0 (98)

1 Since Simek (1991) considers level 8 at Krapina as Mousterian, I now include the occipital (11.5) which lacks a suprainiac fossa as a Neanderthal (unlike Frayer 1992: Table 1).
2 Following Caspari (1991) I now recognize a suprainiac fossa in Mladec 1 & 6. This accounts for the different frequencies in Frayer (1992: Table 1).
3 From Hublin (1978a).

TABLE 5

Frequencies of the Mastoid Tubercle in European Neanderthal, Skhul/Qafzeh, Upper Paleolithic, and Mesolithic Samples

	PRESENT % INCIDENCE (N)	ABSENT % INCIDENCE (N)
European Neanderthals	34.8 (8)	65.2 (15)[1]
Skhul/Qafzeh	40.0 (2)2	60.0 (3)
Early Upper Paleolithic	20.0 (5)[3]	80.0 (20)
Late Upper Paleolithic	0.0 (0)	100.0 (19)
Mesolithic	0.0 (0)	100.0 (179)

1 Specimens not possessing a mastoid tubercle include Gibraltar, Quina 27, Saccopastore 1, and all eleven adult mastoids from Krapina.
2 Specimens possessing a mastoid tubercle include Skhul 4 and Qafzeh 3.
3 Specimens possessing a mastoid tubercle include Cioclovina, Combe Capelle, Dolni Věstonice XIII, Pavlov, and Stetten 1.

MASTOID TUBERCLE

The mastoid tubercle is a prominent bump on the anterior-lateral face of the mastoid, just posterior to the external auditory meatus (Figure 4). The trait was first quantified by Santa Luca (1978) who argued it was consistently found in European (and Levantine) Neanderthals, but absent in Skhul/Qafzeh and other specimens from Africa and Asia. Although Santa Luca provided no data for the incidence of this trait in post-Neanderthal groups, from his paper one assumes a total absence of the mastoid tubercle in non-Neanderthals. Six years later a similar tact was taken by Stringer, Hublin and Vandermeersch (1984, 55), who list the presence of a mastoid tubercle as a European Neanderthal feature, considering it a "probable autapomorphy," a view shared by Klein (1989) and Condemi (1988) among others. Except for the limited sample reviewed by Santa Luca (1978), no one has determined the frequency of this trait in a large sample of European Neanderthals (2) nor reviewed the incidence of the trait in Upper Paleolithic and more recent *Homo sapiens.* Based on my study of original specimens and casts, the mastoid tubercle cannot be considered a uniquely derived trait in European Neanderthals. Besides the fact that the mastoid tubercle occurs in less than half the European Neanderthals, it is present in two of the four Skhul/Qafzeh specimens (Table 5). By this alone, it cannot be a European Neanderthal autapomorphy, probable or otherwise. Moreover, the trait reaches an expression of 20% in the early Upper Paleolithic, further indicating that it is not a uniquely derived feature in European Neanderthals. What is interesting is the total absence of this feature in late Upper Paleolithic and Mesolithic groups, so like other presumed autapomorphic European Neanderthal features, this trait shows a marked dichotomy between the Upper Paleolithic groups, with some evidence for continuity between the European Neanderthals (and in this case, Skhul/Qafzeh) and the early Upper Paleolithic. Consequently, regardless of previous attributions of the mastoid tubercle as an autapomorphic feature separating European Neanderthals from other earlier and later hominid groups, this feature has little taxonomic or phylogenetic valence in discriminating Upper Pleistocene and recent hominids.

CRANIAL BASE ANGULATION

Flattening of the cranial base of European Neanderthals is a feature which can be traced to the original reconstruction by Boule of the La Chapelle-aux-Saints skull. Based on his reconstitution of the parts, Boule (1911-13, 25-27) argued that the skull was flattened along the sagittal profile, occupying an intermediate morphological position between the extremely flattened skulls of chimpanzees and the arched condition seen in modern *Homo sapiens.* Since apes are characterized by unflexed skull bases, the presence of this condition in European Neanderthals was considered by Boule as a primitive feature, expressly indicating incomplete bipedalism. Long after the bipedal locomotion was no longer questioned in European Neanderthals (Straus and Cave 1957), the flattening of the cranial base still remains as either a primitive retention or a uniquely derived trait. For example, Stringer, Hublin and Vandermeersch (1984, 55) list a "flattened cranial base" in their compilation of proposed European Neanderthal autapomorphies and common characteristics, but consider its "phylogenetic status uncertain".

In addition to the regarding basicranial flattening as a possible taxonomic marker, since the publication of Lieberman and Crelin (1971), this feature has been used to argue that European Neanderthals lacked the essential anatomy to produce the full range of sounds typical of human speech. Despite numerous objections to this conclusion (Duchin 1990,

(2) It is interesting to note that Santa Luca lists Gibraltar 1 (Forbes Quarry) as part of his "core" Neanderthal sample (1978, 622), but does not include a figure of it nor mention that Gibraltar 1 lacks the mastoid tubercle. Saccopastore 1 also lacks this feature, as probably does Saccopastore 2.

Falk 1975, Holloway 1983, 1985, LeMay 1975, Wind 1981, 1988), incompetent vocal ability has become a component of the argument that European Neanderthals could not be ancestral to Upper Paleolithic Europeans. In fact, reduced language ability in European Neanderthals has been used in popular scenarios to account for their demise (Diamond 1989, Fischman 1992, Fisher 1988, Kolata 1974). Most recently, Laitman *et al.* (1992) have argued that a flat cranial base coupled with large craniofacial sinuses indicate that European Neanderthals were more susceptible to upper respiratory tract infections which contributed to their extinction.

In many respects, these arguments about European Neanderthals or at least for La Chapelle-aux-Saints have been negated by the publication of Heim's new reconstruction. According to Heim (1989, 99-100)

> The [right] pterygoid process, which allows for the union between the cranial floor and the face, was originally poorly positioned [by Boule] bestowing to the cranial base a strangely flattened aspect and causing erroneous interpretations about the carriage of the head as well as the almost certain imporbability of articulated language in Neandrthals! *Our reconstruction, then, should put an end to the controversies about the existence of articulated language among Neandertals. These humans were anatomically capable of producing the same vowels and the same consonants as us*. Did they do so in reality ? This is something the anthropologist alone cannot answer (my translation and emphasis).

To support his contention that the cranial base is within the modern range of variation, Heim reports that the Welcker angle (*basion-ephippion-nasion*) for the new reconstruction of La Chapelle-aux-Saints is 137.5°. In modern humans, this angle shows a range of 126° - 150°, so La Chapelle-aux-Saints occupies the center of the modern human range. It also is not dissimilar from Gibraltar 1 (142°) and La Ferrassie 1 (135°), both of which fall completely within the range of modern human variation (Heim 1989, 105).

While the Welcker angle measures flexion of the cranial base, since it crosses through the base of the skull and into the hypophyseal fossa, it is not directly comparable to the portion of the cranial base used to infer vocal ability. This region, the supralaryngeal space, has been reconstructed in a series of papers using the basicranial profile (Laitman 1981, 1984, 1985, Laitman, Gannon and Reidenberg 1989, Laitman, Heimbuch and Crelin 1979, Laitman and Reidenberg 1987, Laitman *et al.* 1991). Based on the angles made among five standard landmarks on the skull base, Laitman and his colleagues have argued that European Neanderthals have flatter cranial bases than hominids that preceded and succeeded them. Furthermore, since in living mammals and nonhuman primates a flat skull base is associated with a highly placed larynx, the European Neanderthal condition is thought to represent a restriction of the supralaryngeal space.

Despite the evidence presented above for La Chapelle-aux-Saints, even if one accepts that European Neanderthals have flat cranial bases and that this is indicative of subhuman vocalization, one must assume the same relationship holds for other hominids. That is, if cranial base flattening is related to a highly positioned larynx which correlates with reduced language capacity, one would not expect to find flattened craniobasal regions in Upper Paleolithic, Mesolithic, and more recent European hominids for whom no one denies fully articulate speech.

In a separate paper I have reviewed techniques for reconstructing the basicranial profile (Frayer , n.d.) using the angle made between the *basion–sphenobasion* and the *basion–prosthion* chords. While this angle only represents a portion of the total profile reconstructed by Laitman and his colleagues, the other two points used by them (*hormion* and *staphylion*) are so commonly missing in European Neanderthals and most of the other hominids that it is difficult to justify including them. As argued by Frayer (n.d.) the angle made between the points *basion, sphenobasion,* and *prosthion* is a reliable measure of the degree of basicranial flexion.

Table 6 provides descriptive statistics for the basicranial angle for four European Neanderthals, Skhul 5, and samples from the early and late Upper Paleolithic, Mesolithic, and Hungarian Middle Ages (3). From these data it is clear that European Neanderthals have the lowest angles of the six samples. However, their ranges mostly overlap with the early Upper Paleolithic and completely overlap with the late Upper Paleolithic and Mesolithic. Levels of statistical significance are not shown in this table, but European Neanderthals are significantly different from *only* the Medieval sample, as measured by a two-tailed student's t. Yet, the Mesolithic mean (42°) is also significantly different from the Medieval Hungarian sample and no one would seriously argue that these Holocene people lacked language capability. For individual specimens, it is interesting to note that La Ferrassie 1 has a basicranial angle which exceeds the early Upper Paleolithic range and is near the top of all other sample ranges. This result is consistent with Laitman, Heimbuch and Crelin's (1979) reconstruction of the highly angled craniobasal profile of La Ferrassie 1. On the other hand, La Chapelle-aux-Saints has an angle at the very bottom of the Medieval Hungarian range, but well above numerous specimens from the late Upper Paleolithic and Mesolithic. No one doubts that these post-Mousterian human populations had speech and, based on the overlap of European Neanderthals with these samples, there is no reason to suspect these Middle Paleolithic people were incapable of speech.

(3) Thanks to measurements provided by Professor Jean-Louis Heim, I have been able to reconstruct the craniobasal angle using the new reconstruction of La Chapelle–aux–Saints. While the European Neanderthal and Skhul/Qafzeh samples are small, these specimens represent the only crania which preserve the essential anatomical details for reconstructing the basicranial angle.

Thus, in addition to the fact that craniobasal flattening can no longer serve as taxonomic feature separating European Neanderthals from subsequent Europeans, it is equally unjustifiable to incorporate speculations about linguistic deficiencies in European Neanderthals with regard to questions of extinction and replacement. Moreover, since Skhul 5 has an angle which fits comfortably within the European Neanderthal and the Upper Paleolithic range, there is no evidence that basicranial characteristics of this specimen confer any important taxonomic information or a closer relationship to the Upper Paleolithic hominids.

SINUS SIZE AND MORPHOLOGY

Associated with the large facial size of European Neanderthals are well–developed frontal and maxillary sinuses. According to Stringer, Hublin and Vandermeersch (1984, 55) in European Neanderthals "the frontal sinus extends laterally, not superiorly [and the] zygomatic process of [the] maxilla is inflated". This morphology would appear to constitute a significant difference from more recent *Homo sapiens,* simply based on the definition of European Neanderthal uniqueness. However, Stringer, Hublin and Vandermeersch (1984) include no data to support such a contention about the form of the frontal and maxillary sinuses in European Neanderthals.

In a paper by Szilvássy, Kritscher and Vlček (1987) on sinus variation in fossil and recent humans, the authors conclude that there are no differences in paranasal sinus morphology between modern *Homo sapiens* and European Neanderthals. In this study depicting more than 700 facial profiles in the coronal plane of Europeans, Asians, Africans, Australians, Oceanians, and Patagonians, consistent differences were found among geographic groups. For example, as shown in Figure 5, the typical European pattern combines the largest frontal sinuses with intermediately sized maxillary sinuses; the typical Asian pattern combines the smallest frontal sinuses with the largest maxillary sinuses; and the African pattern is typified by intermediate sized frontal sinuses.

TABLE 6

Descriptive statistics for the angle of the *basion-sphenobasion* chord away from the *basion-prosthion* line

	mean (n)	range
European Neanderthals	42° (4)	32° - 58°[1]
Skhul/Qafzeh (Skhul 5)	47° (1)	-
Early Upper Paleolithic	46° (4)	37° - 51°[2]
Late Upper Paleolithic	48° (6)	26° - 68°
Mesolithic	43° (30)	23 °- 68°
Medieval Hungarians	53° (35)	36° - 64°

1 Saccopastore 1 - 32°; La Chapelle–aux–Saints - 36°; Gibraltar 1 (Forbes Quarry) - 41°; La Ferrassie 1- 58°.
2 Abri Pataud 1 - 37°; Cro-Magnon 1 - 47°; Předmostí 4 - 48°; Mladeč 1 - 51°

associated with the smallest maxillary sinuses. With respect to height and lateral extension of the frontal sinuses, modern Europeans as a group tend to have the highest and the most laterally directed sinuses.

Like the modern samples, the European Neanderthals show considerable variation in frontal sinus size and morphology. However, as Szilvássy, Kritscher and Vlček (1987, 346) state: "the characteristics of the Neanderthal sinuses are within the range of variation of modern *Homo sapiens*, and especially resemble the European pattern". This observation can be confirmed in Figure 5. European Neanderthals, as well as the single Upper Paleolithic specimen (Mladeč 1) included in their study, have large frontal sinuses combined with proportionately intermediate sized maxillary sinuses. Moreover, the contention that European Neanderthals typically have low, laterally extended frontal sinuses can be rejected. For example, the left or right frontal sinuses vary considerably within any individual European Neanderthal (*e. g.*, Monte Circeo) and three European Neanderthals have at least one frontal sinus in which the maximum vertical sinus height exceeds the maximum horizontal sinus length *(i. e.*, Šala [left], Gibraltar [left], and La Chapelle-aux-Saints [right)(4) While

(4) The frontal sinus patterns of La Chapelle-aux-Saints are based on the old reconstruction of this specimen. According to Heim (1989) the frontal and maxillary sinuses La Chapelle-aux-

European Neanderthals indisputably have large maxillary sinuses, they do not fundamentally differ from the pattern found in Europe. Certainly, they do not resemble the small maxillary sinuses typical of Africans, nor the proportionally large maxillary sinuses typical of Asians. For the single Upper Paleolithic skull illustrated (Mladeč 1), the frontal sinus is high and extends laterally past the midorbital point. Mladeč 1, then, has a typical European pattern for the frontal sinuses and closely resembles European Neanderthals. Maxillary sinus size in Mladeč 1, as judged proportionately to the frontal sinuses, is also most like the European pattern and is especially different from the typical modern African configuration. Finally, there is no evidence that the Qafzeh 6 sinus patterns are especially similar to Europeans, whether Mladeč 1 or any of the modern samples are considered. From Figure 5, it is apparent that this purported "proto–Cro–Magnoid" has considerably smaller frontal sinuses and considerably larger maxillary sinuses than Mladeč 1. If anything, Qafzeh 6 is more reminiscent of the Asian, rather than the European pattern.

In summary, despite contentions in the literature, European Neanderthals have frontal and maxillary sinuses typical of the patterns found in people who follow them chronologically. Thus, based on the extensive comparative samples generated by Szilvássy, Kritscher and Vlček (1987), sinus patterns show continuity rather than discontinuity from the European Neanderthals to the subsequent populations. Like in other features discussed in this paper, if Upper Paleolithic people are solely related to Levantine (or African) people, they deviate from the patterns found in these proposed ancestral forms and, this deviation is precisely in the direction of the features typical of the European Neanderthals.

Saints are "huge," but it is impossible to make direct comparisons between the profiles illustrated in my Figure 5 and the sinus morphology as depicted by Heim for the new La Chapelle-aux-Saints reconstruction.

MANDIBULAR FORAMEN TYPES

Since first reported by Gorjanović-Kramberger (1906), the shape of the mandibular foramen has figured as an important morphological marker in the European Neanderthals. For example, Stringer, Hublin and Vandermeersch (1984, 55) consider the horizontal-oval (H-O) foramen a "common feature" of European Neanderthals. In recent hominids the mandibular foramen is V–shaped, with a groove separating the anterior from the posterior aspects of the region, but in some European Neanderthals the region takes on a H-O form (Figure 1). In the H–O type, the anterior and posterior borders are connected by a broad band of bone which appears to be a posterior extension of the mandibular lingula. This morphological pattern is distinct from mylohyoid bridging since it occurs well above the point where the mylohyoid groove begins. Moreover, as Smith (1976, 1978) has argued, the bridge corresponds to the attachment of sphenomandibular ligament and the larger insertion area is probably related to an expansion of this ligament. While the genetics of this trait are unknown, it seems unlikely that it is solely the product of masticatory stress. For example, australopithecines totally lack the trait, and the H-O foramen is exceptionally rare in the fossil record of *Homo* before the Neanderthals. In pre–Mousterian Europe the H–O form is absent in specimens such as Mauer and Arago 2 and 13. Each of these have the normal, V–shaped morphology. From my survey of the literature and inspection of casts and original specimens, the only non–European fossil which possesses the H–O trait is an archaic *Homo* mandible from Olduvai Gorge (OH-22).

Using Smith's definition (1978), frequencies of the two mandibular foramen types are presented in Table 7. These figures represent the presence of the trait with regard to either side, rather than counting left and right sides separately as done by Smith (1978, 526). In the few cases where the mandibular foramen type is asymmetrical, the H–O type was scored as present if at least one side exhibited the trait. Frequencies of this trait show that just more than half of the European

Neanderthals have the H–O type, so it is clear they are not monomorphic with regard to the shape of the mandibular foramen. For example, La Chapelle-aux-Saints has a "normal" type mandibular foramen (Figure 1). The trait is completely absent in the Skhul/Qafzeh sample, as it is in the single mandible which preserves this area in the African Eves (KRM 16424). For the early Upper Paleolithic, the frequency of the H–O pattern reaches 18% (5) which is clearly distinct from the low occurrences (1.4% - 6.7%) in the late Upper Paleolithic, Mesolithic, and Medieval comparative samples. Thus, this so-called "common" characteristic of European Neanderthals (Klein 1989, Stringer, Hublin and Vandermeersch 1984) is also "common" in the early Upper Paleolithic sample. In fact, the early Upper Paleolithic frequencies are as distinct from the other samples as European Neanderthals frequencies are from the early Upper Paleolithic. Moreover, if the trait has a genetic basis, its absence in the proposed non–European ancestors to modern *Homo sapiens* (African Eves and Skhul/Qafzeh) would mean that the trait would have had to evolve twice - once in the European Neanderthals, then again in the early Upper Paleolithic.

CHINS

The presence of a well–developed chin has long been considered the mark of modern humanity (duBrul and Sicher 1954), and decisions about the place of European Neanderthals have generally included a consideration of the expression of the chin. For example, Boule and Vallois (1957) regarded the absence of a chin (or its receding nature) in European Neanderthals as an indication of their overall primitiveness and as evidence for their exclusion from the human line. The same line of reasoning is advanced by Klein (1989, 273) who describes the chin in Neanderthals as "variably developed, but usually absent". On the other hand, definitions of modern *Homo sapiens* usually include the presence of a distinct chin as a fundamental trait (Klein 1989, Stringer, Hublin and Vandermeersch 1984) which sets up the dichotomy between the supposedly chinless European Neanderthal and the typically chined recent humans. Here, I follow the definition of a chin proposed by duBrul and Sicher (1954, 12-13)

> The true chin as we understand it is structured in relief on the upward and backward slanting outer surface of the jaw at the midline. Upon this plane a swelling ridge cants sharply out of the hollow just below the sockets of the incisor teeth. The ridge divides below to enclose a triangular bulge whose slightly concave base forms the lower border of the jaw and ends on either side in a little blunt knob, drawn out laterally into a daintily upturned point, the mental tubercle.

The important aspects of this definition relate to the incurved area (incurvatio) beneath the incisor alveoli, the mental protuberance or mental trigone, and the laterally placed mental tubercles (Figure 6). By this definition, numerous Neanderthals have a chin, as measured by the possession of the first two of these traits which show a variable degree of expression. For example, Heim (1976, 253-254) describes the La Ferrassie 1 mandible as follows:

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(5) When the early Upper Paleolithic sample is limited to the Aurignacian and eastern Gravettian (Frayer 1992, Table 2), frequencies for the H–O pattern are 44.4%.

TABLE 7

Mandibular Foramen Types in European Neanderthal, Skhul/Qafzeh, Early Upper Paleolithic, Late Upper Paleolithic, Mesolithic, and Medieval Samples[1]

	HORIZONTAL-OVAL % (N)	NORMAL % (N)
European Neanderthals	52.6 (10)	47.4 (9)
African Eves	0.0	100.0 (1)
Skhul/Qafzeh	0.0	100.0 (2)
Early Upper Paleolithic[1]	18.2 (4)	81.8 (18)
Late Upper Paleolithic[1]	6.7 (2)	93.3 (28)
Mesolithic	1.9 (3)	98.1 (158)
Medieval Hungarians	1.4 (3)	98.6 (205)

1 These frequencies differ from Frayer (1992: Table 2) due to expanding the time range of the early Upper Paleolithic sample and the inclusion of additional matarial from Central Eruope.

The most peculiar trait of the La Ferrassie 1 mandible concerns the existence of a rough chin. In spite of its rudimentary aspect, the chin occurs in the form of a large swelling and slight projection which occupies all the inferior half of the anterior symphyseal region. It also slightly projects in front of the alveolar border (my translation).

Even Boule and Vallois (1957, 226) recognized the presence of a chin in La Ferrassie 1 ("there really is an indication of a chin triangle"), although in the same source they proclaimed that European Neanderthals have "no chin."

In addition to La Ferrassie 1, a patent sub-incisal curvature and/or mental protuberance occur in La Quina 9, Montgaudier, Regourdou, Spy 1, Monte Circeo 3, Vindija 206, Vindija 231 and Zafarraya. From published photographs, Saint-Césaire also appears to show the development of the mental protuberance and indications of a sub-incisal depression (Vandermeersch 1984). These represent about a third of the adult European Neanderthal mandibles which retain the symphyseal region, so it is apparent that chins are not rare in these humans (Wolpoff 1975). Moreover, as Wolpoff has noted (1980, 284), "the [true chin] first appears in the Riss/Würm European sample, [and] the Würm [Neanderthal] morphology represents a shift in frequencies rather the sudden appearance of a new feature". Thus, compared to the pre-Würm mandibles, many European Neanderthals have a symphyseal region which is evolving in the modern direction. It is also interesting to note that two of the four African Eve mandibles from Klasies River Mouth lack a chin (Caspari and Wolpoff 1980) and show considerably less development of this region than numerous European Neanderthals. Nevertheless, these fragmentary specimens are routinely considered thoroughly modern (Klein 1989; Rightmire and Deacon 1991). Finally, the specimens from Skhul and Qafzeh each have a well–developed mental eminence associated with sub-incisal curvature and in this regard, they are morphologically closer to the Upper Paleolithic morphology than any European Neanderthal.

An important factor in the development of the chin is that the laterally placed mental tubercles (Figure 6) appear after the incurved sub-incisal curvature and the mental prominence become common (Smith, pers. comm.). For example, while numerous European Neanderthals have a chin, with the possible exception of Spy 1, none exhibit any development of the mental tubercle. These are also rarely present in the Skhul/Qafzeh or Klasies River Mouth mandibles. In the early Upper Paleolithic sample, some specimens (Stetten 1, Brno 2) show well–developed mental tubercles, while in others (Předmostí 3, Zlatý Kůň, Dolní Věstonice 3) the inferior mandibular border lacks any mental tubercle development. Compared to the late Upper Paleolithic, Mesolithic, and later human specimens which almost always show some development of the mental tubercles, some of the early Upper Paleolithic mandibles express a more primitive morphological pattern. Thus, despite the fact that all Upper Paleolithic (and later) specimens exhibit deeper sub–incisal curvature and a more prominent mental protuberance compared to European Neanderthals and most of the Skhul/Qafzeh and African Eve specimens, some early Upper Paleolithic specimens lack the development of the mental tubercles. In this regard, the frequency shift to the completely modern chin morphology occurs over the Upper Paleolithic. European Neanderthals can be viewed as representing an intermediate stage between the Middle Pleistocene and Late Würm morphologies.

POSTCRANIAL FEATURES

Measures of Body Size and Proportions

There is a general consensus in the popular and scientific literature that European Neanderthal populations are all short and Skhul/Qafzeh and Upper Paleolithic populations are all tall. For example, Ross (1991, 42) describes European Neanderthals as "stocky wrestlers" and Upper Paleolithic groups as "lanky basketball players". To a certain extent some of this is true, especially with reference to stockiness as measured by various joint and shaft dimensions (Trinkaus 1976, 1983, 1989, but see Wolpoff 1989, 134-136). Yet, stature differences are not as clear-cut as commonly assumed. Using the stature estimating technique of Feldesman, Kleckner and Lundy (1990), Figure 7 plots stature against time for Skhul/Qafzeh, European Neanderthals, Upper Paleolithic (6), and Mesolithic specimens. Although differences are obvious, it is apparent that the European Neanderthal and Skhul/Qafzeh samples extensively overlap in stature, typological statements notwithstanding. More interesting are trends in stature over the Upper Paleolithic and Mesolithic. Body height increases from about 30kya to 20kya, then decreases into the late Upper Paleolithic and Mesolithic. Thus, the earliest populations from Upper Paleolithic Europe are not especially tall compared to those just before the glacial maximum. This demonstrates that generalizations about great body height in all Upper Paleolithic groups are oversimplifications of the variation found within the Upper Paleolithic. Viewed with respect to changes in body height over the Upper Paleolithic, stature estimates for the earliest Upper Paleolithic specimens are more like the "short" European Neanderthals than like the "tall" Skhul/Qafzeh hominids. Like

(6) In Ross (1991) Stringer suggests the body casts from Cueva Morín (Freeman and Gonzalez Echegaray 1973) provide evidence for tall individuals in the earliest Upper Paleolithic. Rather than relying upon these enigmatic discoveries, I use the available femur lengths to estimate stature.

numerous other features reviewed in this paper, if the Skhul/Qafzeh sample represents the ancestors (or the ancestral state) of the early Upper Paleolithic people, the proposed ancestral pattern was modified substantially toward the resident European Neanderthals they are assumed to have replaced.

While stature estimates do not delineate European Neanderthals from the earliest Upper Paleolithic, limb proportions clearly show that distal limbs segments were relatively long in Upper Paleolithic groups (Trinkaus 1981, 1986, 1989). The brachial index (maximum radius length*100/maximum humerus length) plotted against time is shown in Figure 8. The earliest Upper Paleolithic specimens are markedly different from the European Neanderthals, and, while the ranges of the two overlap, sample differences are readily apparent. On the other hand, it is worthwhile noting that the so-called tropically adapted Skhul/Qafzeh specimens show a broad range in these indices, from one of the lowest recorded to one of the highest recorded for any of the samples. The crural index (maximum tibia length*100/maximum femur length) better fits traditional expectations (Figure 9) with European Neanderthals exhibiting very low indices and the Skhul/Qafzeh hominids showing more modern-like proportions. Yet, it is noteworthy that one of the Skhul/Qafzeh specimens is well within the European Neanderthal range.

These distributions for brachial and crural indices have been interpreted as evidence for cold adaptation in European Neanderthals and heat adaptation in the Near Eastern material (Trinkaus 1981, 1986). But, as first argued by Wolpoff (1989, 122-123), if such correlations exist between climate and distal limb proportions, "why didn't the succeeding [Upper Paleolithic] European populations also eventually develop short distal limb segments, adapted as they were to the coldest portion of the Würm ?" As is unambiguously shown in Figures 8 and 9, there are no changes in distal limb segment proportions from the Upper Paleolithic to the Mesolithic. Mean brachial indices hover around 77.5 and crural indices around 84.5 for the whole period and there is absolutely no trend through time for either index. Applying mean indices for the Upper Paleolithic limb segments to Trinkaus' regression on temperature (1981, 212-213), these populations should be living in an environment with a mean annual temperature of about 22°C for the brachial index and about 16°C for the crural index. Rather than accept the *possibility* of gene flow from tropical areas for explaining these high indices in the Upper Paleolithic (Trinkaus 1981, 1983, 1989) or the *certainty* of it (Stringer, as quoted in Ross 1991), it seems more likely that distal limb proportions have little (or nothing) to do with climatic adaptation in Late Pleistocene Europe or the Near East.

The climatic relationship to body size or limb segment proportions is not just a problem for the European samples. Aspects of the Skhul 5 postcranial skeleton provide such a contradiction in expectations to make one question any association. It has the highest stature (192.9 cm) of any of the Near Eastern specimens, but a brachial index (70.5) below and a crural index (80.0) at the European Neanderthal mean (Trinkaus 1981, 194) (7). As Trinkaus (1981, 218) has argued, *[t]he associations between the brachial and crural indices and mean annual temperature have to be accepted for all or none of the Pleistocene hominid samples*" (his italics). Given the inconsistencies in the Middle and Upper Paleolithic, it is time to finally reject any kind of climatic explanation for limb segment proportions, as well as for the tropical origins for the earliest Upper Paleolithic people.

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(7) While Near Eastern Neanderthals have not been considered in this paper, it is important to note that they have brachial indices identical to the Skhul/Qafzeh mean and crural indices identical to the European Neanderthal mean (Trinkaus 1981, Wolpoff 1989). If the climatic hypothesis is correct, Near Eastern Neanderthals are warm-adapted in their upper limbs and cold-adapted in their lower limbs.

Eliminating climatic adaptation does not resolve the problem of discontinuity in the brachial and crural indices among the Skhul/Qafzeh, European Neanderthal, and Upper Paleolithic/Mesolithic samples. Trinkaus (1983, 1986, 1989) suggests behavioral patterns may be involved, but this explanation also has problems since the Skhul/Qafzeh hominids show no fundamental differences in technological or behavioral capacity with Neanderthals from the Near East (Bar-Yosef 1992, Marks 1988, Shea 1988, 1989). Moreover, the European Mousterian shows a greater diversity in hunting patterns, raw material usage, core reduction techniques, and ecosystem extraction than is commonly appreciated, especially by biological paleoanthropologists (see, for example, Clark and Lindly 1988, Jelinek 1988, Müller-Beck 1988, Rensink *et al.* 1991, Roebroeks *et al.* 1988). Besides this, during the period of fundamental change within the Upper Paleolithic involving technological innovations and major shifts in hunting practices (Frayer 1981), there appears to be no correlative change in the postcranial skeleton specifically related to distal limb segment indices. Consequently, based on the evidence from the Upper Paleolithic, where well-documented technological changes associated with hunting have occurred with no biological consequences on limb indices, it is difficult to attribute specific brachial and crural differences between Neanderthals and other groups to economic differences. Whatever the reasons for stature or distal limb segment differences through time and space, it is inappropriate to use them as indicators of phylogenetic separation and completely unjustified to argue that Upper Paleolithic groups are direct descendants of tropical ancestors.

Measures of Femoral Robusticity

Trinkaus (1976) has reviewed the femoral metric characteristics in Upper Pleistocene hominids from the Near East and Europe, documenting major differences between European Neanderthal and Upper Paleolithic samples in meric (subtrochanteric anterior–posterior *100/ subtrochanteric medial–lateral), pilastric (midshaft anterior–posterior*100/ midshaft medial–lateral), and robusticity (100* √ midshaft anterior–posterior * midshaft medial–lateral / bicondylar length) indices. While Trinkaus (1976) declined to draw phylogenetic conclusions from these differences, this study and others, (Trinkaus 1986, 1987b, 1989) have emphasized the greater muscular robusticity in European Neanderthals, leading to their "wrestler" image.

It is impossible here to review all the features established by Trinkaus to indicate hyper–robusticity in European Neanderthals; instead, I present data only for the three femoral indices listed above (Table 8). For the meric index, the European Neanderthals are not substantially different from the other European samples, which as a group all have flatter subtrochanteric cross–sections compared to the mean index for Skhul/Qafzeh (see below). In the pilastric index, European Neanderthals have round midshafts, while the Skhul/Qafzeh, Upper Paleolithic, and Mesolithic samples have larger anterior–posterior dimensions, presumably related to the greater development of the *linea aspera* in these hominids. The early Upper Paleolithic condition is about midway between the European Neanderthal and Skhul/Qafzeh means, and after the early Upper Paleolithic, considerable reduction in the pilastric index occurs over time. For both the meric and pilastric indices, the Medieval sample is curiously like the European Neanderthal condition. For only the robusticity index is there any similarity between the early Upper Paleolithic and Skhul/Qafzeh conditions. In this index, European Neanderthals exhibit larger means than any of the other samples.

TABLE 8

Meric, Pilastric, and Robusticity Indices for Femurs of Comparative Samples

	MERIC		PILASTRIC		ROBUSTICITY[1]	
	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE
European Neanderthals [2]	79.6	73.0-89.1	99.5	86.7-108.9	7.1	6.8-7.4
Skhul/Qafzeh[2]	83.1	76.5-90.4	125.8	109.7-140.1	6.3	5.4-7.0
Early Upper Paleolithic	77.6	60.2-98.5	115.7	99.0-142.3	6.3	5.6-7.1
Late Upper Paleolithic	78.0	65.5-90.9	112.7	93.2-135.7	6.4	5.4-7.5
Mesolithic	78.0	59.8-98.5	108.3	83.3-140.0	6.5	5.7-7.5
Medieval	80.4	64.6-98.9	101.0	83.3 - 123.2	6.2	5.4 - 8.1

1 For Upper Paleolithic, Mesolithic and Medieval samples, the maximum femur length is used in calculating this index, since I did not measure bicondylar length. Because maximum femur length is larger, this substitution has the effect of lowering the index, but not enough to greatly affect the resulting statistics.
2 Data from Trinkaus (1981, 1976), Vandermeersch (1981), Wolpoff (pers. comm.)

No attempt is made here to draw phylogenetic relationships, but it is noteworthy that these femoral indices do not provide simple distinctions about robusticity through time or across samples. In particular, there is little in these statistics which would indicate a greater similarity in these three measures of femoral robusticity (or any correlates to behavioral patterns) between Skhul/Qafzeh and the early Upper Paleolithic. If anything, the Skhul/Qafzeh sample is odd (see also Trinkaus 1976, 313), since it shows considerably higher indices for the meric and pilastric indices compared to any of the European samples. Finally, given the nearly identical mean values of the European Neanderthals and the Medieval Hungarians for the meric and pilastric indices, one wonders what these signal with respect to the presumed uniqueness of European Neanderthals.

Proximal Femoral Flange

As discussed by Kidder, Smith and Jantz (1991, 1992b) European Neanderthals possess a flattened subtrochanteric area which is accentuated by a "proximo-lateral flange". This flange occurs lateral to the fascial rugosities of *vastus lateralis* and *gluteus maximus* in the proximal aspect of the femur and can be readily observed from the anterior surface (Figure 10). The low meric index in European Neanderthals compared to the Skhul/Qafzeh hominids (Table 8) which lack the lateral proximal flange, apparently relates to the marked development of this feature in European Neanderthals. All known early Upper Paleolithic specimens possess the proximal femoral flange, as do a number of later Upper Paleolithic and more recent specimens. Kidder, Smith and Jantz (1991, 104) argue that this flange is likely a genetic trait since the presence of the feature is not correlated with a specific size or shape of the proximal femur. Also, according to them, the flange is found in infant femurs indicating "a non-adaptive" etiology for the trait. The high frequency of this feature in European Neanderthals and in the subsequent Upper Paleolithic hominids, along with its apparant absence in the Skhul/Qafzeh femurs, provides evidence for evolutionary continuity in Europe (Smith 1992b) and discontinuity between Skhul/Qafzeh and the Upper Paleolithic. If the Skhul/Qafzeh humans are the sole ancestors, the identical trait would have had to evolve again in the early Upper Paleolithic.

Scapular border types

Scapular border morphology has long been considered an important trait marking differences between European Neanderthals and subsequent groups (*e. g.*, Boule 1911-13, Stringer, Hublin and Vandermeersch 1984). Based on the work of von Eickstedt (1925) axillary borders are classified into three main types : dorsal (*sulcus axillaris teretis*), bisulcate (*sulcus axillaris bisulcata),* and ventral *(sulcus axillaris subscapularis).* Trinkaus (1977) has reviewed the frequencies of these three types in Middle Paleolithic, Upper Paleolithic, and recent hominids, concluding that the types are correlated with levels of muscular stress and, based on the samples available at the time, that the dorsal pattern typical in European Neanderthals was absent in Upper Paleolithic groups. Like the other nonmetric features discussed above, the trait's heritability is uncertain. Trinkaus (1977) assumes an interplay of genetics and muscular activity in producing the various types, but evidence from Neanderthal children suggests the trait may have an important genetic component. For example, Vlcek (1973, 543) argued that the neonate from Kiik-Koba has a scapular morphology "practically of the same nature as found in the adult [Neanderthal] individuals". As for its axillary border, Vlcek (1973) observed that "the axillary border is thicker and there is a suggestion of the development of the *sulcus marginalis* [*teretis*]". On the other hand, while Heim confirmed the thickened axillary border in his study of the La Ferrassie 4b neonate (1982, 24), he found no evidence for the dorsal groove on this similarly aged infant. Yet, he speculated the dorsal pattern would develop soon afterwards, correlated with muscular action. This, it would appear that the axillary border in subadults shows a predisposition to the adult state, and if this occurs as early as the age of the Kiik–

Koba infant (5-7 months), there likely is a significant genetic component to its type of expression, since powerful muscular activity is presumably minor in infancy.

Table 9 provides frequencies for scapular border types in the Skhul/Qafzeh sample, European Neanderthals, and subsequent Europeans. It is apparent that the dorsal pattern is not absent in the early Upper Paleolithic, but reaches a frequency of nearly 17%. Differences among the samples are apparent, with European Neanderthals dominated by the dorsal pattern and late Upper Paleolithic, Mesolithic, and modern Europeans exhibiting primarily the ventral type. The bisulcate pattern is found in four of the five scapulas from Skhul/Qafzeh (which lack any dorsal example). It is also the most common type in the early Upper Paleolithic sample, but does not closely approach the 80% frequency in Skhul/Qafzeh. In some ways, the early Upper Paleolithic sample is just as distinct from the later European samples as European Neanderthals are different from the early Upper Paleolithic. For example, while the frequency of the dorsal type is well below the European Neanderthal occurrence, only about 30% of the early Upper Paleolithic specimens show the ventral type compared with a range of 68.1% - 75.8% for all later samples. If the bisulcate condition is considered to be intermediate between the dorsal and ventral patterns, early Upper Paleolithic specimens are clearly intermediate between Neanderthals and later European samples in their high frequency of this pattern. However one interprets these data, it is clear that the supposed common pattern in European Neanderthals shows variable expression and that the dorsal axillary trait is not absent (nor even rare) in the early Upper Paleolithic sample. Like other features discussed above, the dorsal axillary border is not unique to the European Neanderthals. Therefore, this trait provides no support for a hiatus between European Mousterian and Upper Paleolithic samples.

TABLE 9

Scapular Border Types for European Neanderthal, Skhul/Qafzeh, Early Upper Paleolithic, Late Upper Paleolithic, Mesolithic, and Modern European Samples[1]

	DORSAL		BISULCATE		VENTRAL	
European Neanderthals	64.7%	(11)	23.5%	(4)	11.8%	(2)
Skhul/Qafzeh[2]	0.0%	(0)	80.0%	(4)	20.0%	(1)
Early Upper Paleolithic	16,7%	(3)	55.6%	(10)	27.8%	(5)
Late Upper Paleolithic	0.0%	(0)	29.4%	(5)	70.6%	(12)
Mesolithic	10.6%	(5)	21.3%	(10)	68.1%	(32)
Modern Europeans[4]	.4%	(1)	23.8%	(28)	75.8%	(91)

1 These frequencies differ slightly from Frayer (1992, Fig. 1) due to the re–analysis of some specimens and the addition of the new Dolní Věstonice material.

2 From Vandermeersch (1981, 200)

3 Early Upper Paleolithic specimens with the dorsal pattern consist of Barma Grande 2, Dolní Věstonice and Předmostí 14.

4 From Trinkaus (1977, 232)

RATES OF EVOLUTIONARY CHANGE

Since the early 1900s, there has been a persistent argument that European Neanderthals could not be the ancestors of Upper Paleolithic groups, since not enough time exists between the two groups to allow for metric or morphological change (Boule 1911-1913, Klein 1992, Mercier *et al.* 1991, Stanley 1981, Stringer 1984a, 1984b, Vallois 1958). This argument has been made despite the fact that few have calculated rates of evolution between European Neanderthals and the early Upper Paleolithic nor compared these rates with other chronologically successive series. More than thirty years ago Howell (1957, 341) argued that "the fossil record can afford direct evidence which would give an indication of evolutionary rates and the time necessary for any such transformation," yet from then to now, such studies have been sparse. In 1978, I computed rates of change, measured by mm (or mm^2) per millennium and found that rates between the early and late Upper Paleolithic exceeded those between the European Neanderthal and early Upper Paleolithic. In 11 of 16 (69%) mandibular tooth lengths and breadths and in 4 of 6 (67%) mandibular canine and posterior tooth areas, rates of evolution were greater within the Upper Paleolithic than between the Mousterian and Upper Paleolithic samples (Frayer 1978, 126). A similar pattern was evident in the maxillary tooth lengths, breadths, and areas.

Few paleoanthropologists would argue that early and late Upper Paleolithic humans are unrelated to each other, much less members of the different species. However, Stringer (1989, 241) suggests that "[m]odern Europeans certainly had ancestors, but that does not mean we must accept, without further proof, that the whole EUP [early Upper Paleolithic] sample represents those ancestors". Despite this enigmatic statement, I still contend that the rates of change for most dental dimensions within the Upper Paleolithic are greater than the dimensional changes between European Neanderthals and the early Upper Paleolithic sample. This fact provides no support for the "not enough time" arguments. However, commenting on my 1978 work, Stringer (1982, 432) argued that re-arranging my published Upper Paleolithic sample "in alternate and equally or more justifiable ways [would] produce different trends in some cases, nullify[ing] the claimed evolutionary trends" within the Upper Paleolithic. Stringer presented no data to support this contention (8), but in 1984 I divided the Upper Paleolithic sample following his intimations and concluded that "there is no basis to argue that there is no strong trend for considerable tooth size change within the Upper Paleolithic" (Frayer 1984, 223). From my work on the Upper Paleolithic dental sample, the only way to support Stringer's statement for a nullification of dental trends over this period would be to randomize the Upper Paleolithic and Mesolithic samples with respect to time.

To update the consideration of evolutionary rates, data were collected for several different samples (Tables 10 -13) with rates of change calculated by the equation

$$\frac{\log_e x_2 - \log_e x_1}{t}$$

Which is Haldane's (1949) formula for the computation of darwins. In this formula x_1 and x_2 are the sample means and t is the time interval between the two groups. The effect of this commonly used algorithm is to normalize

(8) Gambier (1989, 207) apparently accepts Stringer's datafree argument, although she also provides no data to support the contention that tooth size is stable over the Upper Paleolithic. In the same article Gambier also expresses a concern about small sample size and that the discovery "of a few additional teeth could completely alter the picture" (1989, 209). Compared to most studies in paleoanthropology, the samples used in Frayer (1978) are large and, if new discoveries have "altered" the results, the discovery of Saint-Césaire has made Neanderthal dental dimensions more like the early Upper Paleolithic condition.

size changes over time. Here, time was calculated as the estimated average period of separation between any two samples using the modal dates given below. To facilitate tabular presentation, time was measured by 10,000 year segments rather than the million year interval normally used in calculating darwins. Those wishing to convert the rates in Tables 10-13 to darwins should divide each by 1000. Finally, it is important to note that changes in dental or craniofacial size are not used as cladistic traits here. On the contrary, rates of change in these features are presented solely to test arguments about the amount of change occurring between various samples from the late Würm and Holocene.

DENTAL SAMPLES

The dental rate comparisons involve three groups considered to be possible ancestors of the early Upper Paleolithic Europeans (African Eves, Skhul/Qafzeh, European Neanderthals), the early Upper Paleolithic, and four subsequent groups deriving from the late Upper Paleolithic, Mesolithic, Neolithic, and Medieval periods. The African Eve sample includes Border Cave, Klasies River Mouth, and Mumba, based on measurements of the originals by M. H. Wolpoff, except the lower and upper M2s from Mumba which come from Bräuer and Mehlmann (1988). Following estimates in the literature (Klein 1989), I use 90,000 years as the modal date for the African Eve sample. The Skhul/Qafzeh data set comes from measurements on the originals by M.H. Wolpoff and is also given a modal date of 90,000 years, consistent with recent TL dates published for both sites (Schwarcz *et al.* 1988, Stringer *et al.* 1989). The bulk of the European Neanderthal sample derives from Wolpoff's measurements on the originals, but I have also supplemented his data set with some new specimens described in the literature, for example, La Bréche de Genay (deLumley 1987). As a modal date for this group, I use 70,000 years, which corresponds to the midpoint of the span of Mousterian industries in Europe (Mellars 1986). From the total European Neanderthal sample, I have also compiled a late Neanderthal sample which consists of Arcy-sur-Cure, Hortus, Saint-Césaire, Vindija, Šipka, Kůlna, and Le Moustier; the latter which presumably has a TL date of about 40,000 B.P. (Valladas *et al.* 1986). I have estimated a modal date for this late Neanderthal sample of 37,000 B.P. which corresponds to the recently published date for Saint-Césaire (Mercier *et al.* 1991). The Upper Paleolithic and Mesolithic measurements derive primarily from my review of the original material, except for a few specimens which have been lost, destroyed, or to which I otherwise did not have access. These include such sites as Predmostí (Matiegka 1938) and Romito (Fabbri and Mallegni 1988). Modal dates for these three samples are 26,500 B.P. for the early Upper Paleolithic, 14,000 B.P. for the late Upper Paleolithic, and 8000 B.P for the Mesolithic. The Neolithic samples come from my measurements of specimens from Western and Central Europe, including material from the earliest to the latest Neolithic, the latter represented mainly by Danish and Swedish material. Given the differences in time of the earliest appearance of the Neolithic in Western and Central Europe (Champion *et al.* 1984), the modal date for the Neolithic is difficult to determine. In this analysis, I have used 6500 B.P. as the estimated modal date. The actual modal date may be somewhat earlier, and if so, the calculated evolutionary rates would be even higher than reported here. Finally, data for the Medieval sample are from my measurements from the 9th–11th century site at Zalavár (Sös and Bökönyi 1963) along with Wolpoff's measurements of the large cemetery at Halimba (Nemeskéri and Acsádi 1957). A modal date of 800 B.P. is used.

RATES OF MANDIBULAR AND MAXILLARY DENTAL CHANGE

For the mandibular teeth, of the nine sample comparisons the most rapid rates of change in anterior tooth lengths and breadths (Table 10) and tooth areas (Table 11) are *not* found for the European Neanderthal–early Upper Paleolithic transition nor in the late Neanderthal-early Upper Paleolithic comparison. Rather, the highest rates occur between the Mesolithic and Neolithic with an average darwin of .1576 in the anterior lengths and breadths (Table 10) and .2302 for the posterior tooth areas (Table 11). While this transition may constitute an influx of people and/or genes from the east (Ammerman and Cavalli-Sforza 1984, Sokal, Odin and Wilson 1991), it certainly was not a total population replacement given the slow adoption of agriculture in some areas and the wealth of evidence for interaction between Mesolithic and Neolithic people (Price 1987, Zvelebil 1986, Zvelebil and Zvelebil 1988). Also, the population transition did not involve the invasion of a new species, so rates of evolution for these teeth represent a measure of dental change within an evolving species. From Tables 10 and 11, it is clear that the average rates for the European Neanderthal/early Upper Paleolithic sample (.0070 and .0119) are consistently lower than any of the average darwins for sample comparisons after the appearance of the Upper Paleolithic, whether anterior tooth lengths and breadths or tooth areas are considered. This observation falsifies both the contention that differences between the European Neanderthals and the early Upper Paleolithic require a rapid rate of change and the unsupported claim that tooth size shows little absolute or relative change after the appearance of the Upper Paleolithic (Stringer 1982).

TABLE 10

Rates of Change in Mandibular Anterior Tooth Lengths and Breadths Between Selected Groups, as Measured by Darwins per 10,000 Years
(Significant difference in means: § p<.05; ‡ p<.01 with one tailed student's t)

	I1 LT	I1 BR	I2 LT	I2 BR	C LT	C BR	MEAN
African Eves -> Early Upper Paleolithic	-	-	-.0198‡	-.0041	.0087§	-.0075	-.0057
Skhul/Qafzeh -> Early Upper Paleolithic	.0024	.0032§	.0042	.0039§	.0079‡	.0000	.0036
Neanderthals -> Early Upper Paleolithic	.0017	.0147‡	.0031	.0111‡	.0079‡	.0034§	.0070
Late Neanderthals -> Early Upper Paleolithic	.0150	.0689‡	.0326	.0477‡	.0446‡	-.0152	.0323
Early -> Late Upper Paleolithic	.0168	.0099	.0149§	.0091§	.0217‡	.0184‡	.0151
Early Upper Paleolithic -> Mesolithic	.0079	.0107‡	.0107‡	.0133‡	.0156‡	.0243‡	.0138
Mesolithic -> Neolithic	.2187‡	.1460‡	.1960‡	.1367‡	.1727‡	.0753‡	.1576
Early Upper Paleolithic -> Neolithic	.0230‡	.0204‡	.0240‡	.0221‡	.0268‡	.0280‡	.0241‡
Early Upper Paleolithic -> Medieval	.0121‡	.0135‡	.0163‡	0.151‡	.0190‡	.0224‡	.0164

TABLE 11

Rates of Change in Mandibular Tooth Areas Between Selected Groups,
as Measured by Darwins per 10,000 Years
(Significant difference in means: § p<.05; ‡ p<.01 with one tailed student's t)

	Canine	P3	P4	M1	M2	M3	Mean
African Eves -> Early Upper Paleolithic	-.0087	.0094	.0091	.0058	-.0081	-.0089	-.0023[1]
Skhul/Qafzeh -> Early Upper Paleolithic	.0072§	.0111‡	.0095‡	.0075‡	.0039	.0079§	.0079
Neanderthals -> Early Upper Paleolithic	.0121‡	.0174‡	.0127‡	.0017	.0124‡	.0153‡	.0119
Late Neanderthals -> Early Upper Paleolithic	.0200	.0466‡	.0406§	-.0059	.0327	.0528§	.0311
Early -> Late Upper Paleolithic	.0355‡	.0249‡	.0222‡	.0099	.0098	.0055	.0180
Early Upper Paleolithic -> Mesolithic	.0371‡	.0234‡	.0129‡	.0061§	.0127‡	.0131§	.0176
Mesolithic -> Neolithic	.2227‡	.2420‡	.1567‡	.2847‡	.2560‡	.2193‡	.2302
Early Upper Paleolithic -> Neolithic	.0504‡	.0390‡	.0232‡	.0260‡	.0300‡	.0279‡	.0328
Early Upper Paleolithic -> Medieval	.0391‡	.0373‡	.0253‡	.0218‡	.0280‡	.0267‡	.0297

1. For samples greater than 1, mean = -.0037; when greater than 3, mean = -.0085.

Since the length of the time interval has an effect on evolutionary rates (Gingerich 1983), it is important to recognize that the longer time interval between the European Neanderthal/early Upper Paleolithic (as compared to the Mesolithic/Neolithic) samples may contribute to the differences in the rates of evolution (9). Yet, when the Neanderthal/early Upper Paleolithic rates are judged relative to the longest post-Mousterian comparison (early Upper Paleolithic/Medieval), the average rates occurring over the "modern" *Homo sapiens* comparison (.0164 for anterior mandibular teeth; .0297 for mandibular areas) are about double those between Neanderthals and the early Upper Paleolithic (.0070 and .0119, respectively). For the late Neanderthal/early Upper Paleolithic comparison, the average rates of .0323 for the anterior teeth and .0311 for the areas are indisputably larger than found within the Upper Paleolithic (.0151 and .0180, respectively) and both are sampled over a similar period of time. For the mandibular anterior teeth, the average rate of reduction between the late Neanderthal/early Upper Paleolithic comparison exceeds all but the Mesolithic/Neolithic case, which is sampled over a considerably shorter time period. On the other hand, while the late Neanderthal/early Upper Paleolithic rates for mandibular tooth areas exceed those found within the Upper Paleolithic, they are lower than the early Upper Paleolithic/Neolithic and early Upper Paleolithic/Medieval comparisons, both

(9) Sex ratios also undoubtedly affect these rate comparisons and both Neanderthal samples have an over-representation of males. Consequently, the elevated rates (especially for the late Neanderthal sample) are likely higher due to the inclusion of more males than in the early Upper Paleolithic samples.

of which are sampled over a longer period of time. While it is apparent that anterior tooth dimensions (especially mandibular incisor breadths) reduce substantially from the late Neanderthal to the early Upper Paleolithic, average darwins for the mandibular teeth indicate that rates of evolution between late Neanderthals and the early Upper Paleolithic are not beyond the magnitude of change seen in the evolution of *Homo sapiens*, especially for the mandibular tooth areas. Based on these average rates, mandibular dental change from the total (or late) Neanderthals to the early Upper Paleolithic does not require an exorbitant rate of evolution.

In addition to the average rates for the mandibular teeth, it is relevant to consider the maximum darwin for tooth dimensions to determine if any represent an inordinate amount of change between the European Neanderthals and the early Upper Paleolithic. Here again, there is no evidence to support contentions that a rapid rate of evolution is required for the European Neanderthal/early Upper Paleolithic transition. For example, in the mandibular anterior lengths and breadths between the European Neanderthal and the early Upper Paleolithic samples, the maximum darwin is .0147 for the I1 breadth (Table 10). This rate is lower than four of the six rates of change within the Upper Paleolithic or between the early Upper Paleolithic and Medieval Hungarians. It is also below every darwin calculated for the early Upper Paleolithic/Neolithic comparison. In the late Neanderthal/early Upper Paleolithic case the I1 breadth has a maximum darwin of (.0689) which is large compared to all other samples, except again the Mesolithic/Neolithic rate for this dimension (.1460). For mandibular tooth areas, .0174 (P3) represents the highest rate for the European Neanderthal/early Upper Paleolithic comparison. This is lower than all Upper Paleolithic and later sample rates for the same tooth, and more than ten times below the darwin for mandibular P3 in the Mesolithic/Neolithic comparison. In the late Neanderthal/early Upper Paleolithic comparison, the highest darwin is .0528 for the M3 area. While this is above the rates for most other samples, the .2193 rate for the M3 reduction between the Mesolithic and Neolithic is nearly four times as rapid, although the time interval is much shorter. Thus, in the mandibular dentition, whether average darwins or maximum darwins are considered, rates of tooth size change between European Neanderthals and the early Upper Paleolithic are not beyond the values documented for other evolutionary transitions.

In the maxilla basically the same pattern is evident, with rates for the European Neanderthal/early Upper Paleolithic comparison well below those for other transitional cases, especially the extremely high Mesolithic/Neolithic darwins (Tables 12 and 13). For the incisor/canine lengths and breadths (Table 12), the highest rate of change observed in the European Neanderthal/early Upper Paleolithic case is .0170 for the maxillary I2 breadth, which is small in comparison to the magnitude of change found for the same tooth within the Upper Paleolithic (.322) and extremely low compared to the maximum rate in the Mesolithic/Neolithic (.2980). The maximum rate observed for the late Neanderthal/early Upper Paleolithic comparison is .0572 (I2 br), which represents the highest darwin for any of the sample comparisons except those for the Mesolithic/Neolithic. Overall, the average rate of dimensional change in these three anterior teeth is .1543 in the Mesolithic/Neolithic transition about fifteen times the European Neanderthal/early Upper Paleolithic rate (.0098) and about seven times the rate of the late Neanderthal/early Upper Paleolithic comparison (.0252). However, except for the Mesolithic/Neolithic case, the late Neanderthal/early Upper Paleolithic comparison shows a higher rate (.0252) than found in any other sample comparisons. Thus, as in the mandible, the maxillary anterior teeth show a high average rate of change for the late Neanderthal/early Upper Paleolithic comparison.

TABLE 12

Rates of Change in Maxillary Anterior Tooth Lengths and Breadths Between Selected Groups, as Measured by Darwins per 10,000 Years
(Significant difference in means: § p<.05; ‡ p<.01 with one tailed student's t)

	I1 LT	I1 BR	I2 LT	I2 BR	C LT	C BR	MEAN
African Eves -> Early Upper Paleolithic	-	-	-	-	-	-	-
Skhul/Qafzeh -> Early Upper Paleolithic	.0063‡	.0035‡	.0090‡	.0056‡	.0041‡	.0022	.0051
Neanderthals -> Early Upper Paleolithic	.0032	.0100‡	.0119‡	.0170‡	.0071‡	.0095‡	.0098
Late Neanderthals -> Early Upper Paleolithic	.0093	.0111§	.0348§	.0572‡	.0156	.0233	.0252
Early -> Late Upper Paleolithic	.0204 §	.0041	.0132	.0322‡	.0155‡	.0139 §	.0166
Early Upper Paleolithic -> Mesolithic	.0048	.0089‡	.0031	.0231‡	.0083‡	.0126‡	.0101
Mesolithic -> Neolithic	.2980‡	.1193‡	.2560‡	.0000	.1500‡	.1027‡	.1543
Early Upper Paleolithic -> Neolithic	.0257‡	.0168‡	.0211‡	.0215‡	.0184‡	.0190‡	.0204
Early Upper Paleolithic -> Medieval	.0167‡	.0111‡	.0144‡	.0172‡	.0148‡	.0152‡	.0149

TABLE 13

Rates of Change in Maxillary Tooth Areas Between Selected Groups, as Measured by Darwins per 10,000 Years
(Significant difference in means: § p<.05; ‡ p<.01 with one tailed student's t)

	Canine	P3	P4	M1	M2	M3	Mean
African Eves -> Early Upper Paleolithic	-	-	-	-	.0056(1)	-	-
Skhul/Qafzeh -> Early Upper Paleolithic	.0068§	.0086‡	.0049	.0066‡	.0048	.0045	.0060
Neanderthals -> Early Upper Paleolithic	.0179‡	.0145‡	.0171‡	.0083‡	.0091‡	.0157‡	.0138
Late Neanderthals -> Early Upper Paleolithic	.0373	.0227	.0409§	.0101	.0317	.0417	.0307
Early -> Late Upper Paleolithic	.0264§	.0338‡	.0259‡	.0081	.0195§	.0242§	.0230
Early Upper Paleolithic -> Mesolithic	.0212‡	.0215‡	.0165‡	.0120‡	.0199‡	.0156‡	.0178
Mesolithic -> Neolithic	.2580‡	.3193‡	.2507‡	.2573‡	.2927‡	.2493‡	.2712
Early Upper Paleolithic -> Neolithic	.0381‡	.0428‡	.0333‡	.0295‡	.0394‡	.0323‡	.0359
Early Upper Paleolithic -> Medieval	.0303‡	.0352‡	.0295‡	.0259‡	.0397‡	.0285‡	.0315

1 Sample size for African Eves = 1.

Rates for the maxillary canine and posterior teeth (Table 13) are similar to the degree and pattern of change in the mandibular tooth areas. The average rate (.0138) and the maximum rate (.0179) of change between the European Neanderthals and the early Upper Paleolithic are below the average rate (.0230) and the maximum rate (.0338) found within the Upper Paleolithic. They are also magnitudes smaller than the rates between the Mesolithic and Neolithic which has an average rate of reduction of .2712 and a maximum rate of .3193. For the late Neanderthal/early Upper Paleolithic comparison, the rates of dental change do not differ fundamentally from those found between the Upper Paleolithic and Medieval Hungarians and each are magnitudes below the specific rates in the Mesolithic/Neolithic transition. As is apparent from the average rates of change for these six teeth, compared to the early Upper Paleolithic, the European Neanderthal (.0138) or late European Neanderthal sample (.0307) average rates are well within the limits of most of the later sample comparisons. For example, a greater amount of change occurs from the Mesolithic to the Neolithic (.2712), from the early Upper Paleolithic to the Neolithic (.0359), and from the early Upper Paleolithic to the Middle Ages (.0315).

Based on these comparative evolutionary rates, the average darwins between European
Neanderthals (or late Neanderthals) and the early Upper Paleolithic are not especially rapid. Rather, rates of change between either European Neanderthal samples and the early Upper Paleolithic are within the magnitude of change found for recent *Homo sapiens*, whether average rates of change or highest rates for any tooth dimension are considered. Figures 11 and 12 summarize the European data presented in tables 10-13 and demonstrate visually that there was no "tremendous acceleration" in rates of dental change (Stringer 1984a, 66). These data convincingly falsify the argument that European Neanderthals as a group cannot be ancestral to subsequent *Homo sapiens* in Europe (at least with respect to dental evolution) because "too much change is required over too little time". Moreover, based on the rates of dental evolutionary change, there is nothing to support the contention that European Neanderthals represent a separate species. Such a conclusion would only hold if one is also willing to accept a speciation event between the early and late Upper Paleolithic, between the Mesolithic and Neolithic, between the early Upper Paleolithic and Neolithic, or between the early Upper Paleolithic and Middle Ages, since all of these comparisons have similar or considerably higher evolutionary rates in the various comparisons.

With respect to the other possible ancestors, mandibular rates between the African Eve/early Upper Paleolithic samples require an increase in average tooth size between the two samples, especially due to the considerably smaller M2 and M3 areas in the African Eve sample. Sample sizes are minimal (n= 1-2) for all other teeth (and even for the lower M2 and M3 areas sample size only equals 4), so the significance of this required trend for tooth size increase over time is fuzzy. Since there is only one upper tooth attributed to the African Eve sample, even less can be determined about maxillary rates. Yet, even with these tiny samples, there is nothing to suggest that African Eves constitute a more likely ancestor, especially given the general trend for dental reduction in human evolution. For African Eves to be the ancestors, tooth size would have to increase in the early Upper Paleolithic, then decrease substantially through time.

Following the African Eve sample, the average rates between Skhul/Qafzeh and the early Upper Paleolithic represent the smallest overall change for any of the samples. Some may point to these low rates as evidence for the greater likelihood of a lineal relationship between the Near East and Europe. But, by the same reasoning European Neanderthals are more likely to be ancestral to the early Upper Paleolithic than is the early to the late Upper Paleolithic, since the latter requires higher rates of overall change in all mandibular and maxillary comparisons. Thus, while the rates of change between

Skhul/Qafzeh and the early Upper Paleolithic are lower than the European Neanderthal/early Upper Paleolithic rates, this fact alone does not necessarily signify a closer evolutionary relationship.

In summary, while rates of dental evolutionary change by themselves do not allow the identification of which group is ancestral to the early Upper Paleolithic Europeans, they do indicate that European Neanderthals cannot be eliminated as possible ancestors, based on speculations of grossly elevated evolutionary rates. Moreover, the period following the Neanderthals in Europe is not characterized by absolute or relative stasis (*contra* Stringer 1982, 66) with regard to the metrics of the dentition. If there is a transitional period which is markedly different in these comparisons, it is the Mesolithic/Neolithic case which indisputably shows a marked degree of rapid evolutionary change.

RATES OF CRANIO-FACIAL CHANGE

Using the samples presented in Table 1, evolutionary rates were calculated for facial measurements using the same intervals as for the dentition (Table 14).

TABLE 14

Rates of Change (in darwins) for Facial Measurements from the Auricular Point for Transition Comparisons

Auricular Point to :	European Neanderthal/ Early Upper Paleolithic darwins	Skhul/Qafzeh Early Upper Paleolithic darwins	Early/Late Upper Paleolithic darwins	Early Upper Paleolithic/ Mesolithic darwins	Early Upper Paleolithic Medieval darwins
prosthion	.0113	.0030	.0208	.0162	0.113
nasospinale	.0097	-.0031	.0208	.0189	.0136
nasion	.0087	-.0003	.0152	.0130	.0097
glabella	.0083	.0013	.0144	.0130	.0105
zygomaxillarae	.0000	-.0031	.0160	.0216	.0152
M1/M2	.0184	.0008	.0088	.0076	.0066
P3/P4	.0120	.0005	.0208	.0130	.0105
I2/C	.0113	.0014	.0176	.0124	.0097
Inferior Nasomax. Suture	.0062	-.0049	.0168	.0178	.0128
jugale	.0048	-.0025	.0368	.0308	.0206
frontomalareorbitale	.0034	-.0024	.0216	.0200	.0160
alare	.0078	.0013	.0168	.0157	.0132
Anterior Temporal Fossa	-.0011	-.0036	.0208	.0227	.0089
zm Suture at Orbit Margin	-.0007	-.0083	.0168	.0184	.0132
Palatine Suture Cross	.0057	-.0083	.0224	.0195	.0132
Post-*orale*	.0055	-	.0264	.0205	.0144
Average Change	.0070	-.0019	.0196	.0176	.0125

Since the only late Neanderthal with reliable facial measurements is unpublished (Saint-Césaire) and there are few comparative measurements for the African Eve sample, it is impossible to calculate rates for these sample comparisons. In addition, most of these measurements for the Neolithic sample are lacking in my data set. Consequently, rates for the Mesolithic/Neolithic transitional case are not included.

As with the dental rates, changes in facial measurements from the auricular point provide absolutely no evidence for an elevated rate of evolution between European Neanderthals and the earliest Upper Paleolithic. The average rate of change between the European Neanderthals and the earliest Upper Paleolithic for these 16 facial measurements is .0070, which is substantially below the average rates or all three post-Mousterian comparisons. For example, the early/late Upper Paleolithic average rate is .0196, the early Upper Paleolithic/Mesolithic average rate is .0176, and the early Upper Paleolithic/Medieval average rate is .0125. In addition, the maximum rate observed for the European Neanderthal/early Upper Paleolithic comparison is .0184 which is lower than 8 of the 16 rates for the early/late Upper Paleolithic transition. Thus, like the dentition, these measures of facial projection demonstrate that rapid evolutionary rates do not characterize the possible transition of European Neanderthals into the early Upper Paleolithic. These rates of change also show that anything but stasis characterizes the post-Neanderthal period in Europe.

As for rates between the Skhul/Qafzeh and early Upper Paleolithic samples, it is apparent that very minor change in these dimensions is required. The majority of these differences involve an increase in the projection of facial points, although few are associated with significant differences (Table 1). If the Skhul/Qafzeh hominids are the actual ancestors to the early Upper Paleolithic Europeans, it is interesting that the transitional period is characterized by relative stasis in these measurements, followed by markedly elevated rates of reduction within (and after) the Upper Paleolithic.

As in the case of the dentition, it is important to recognize that rates of evolution do *not* identify the most likely ancestor. Rather, they are *only* relevant in eliminating possible ancestors in situations where the rate of evolution requires an exorbitant amount of change over time. As shown for the facial measurements from the auricular point, the overall and maximum rates of change from the Mousterian to the Upper Paleolithic groups are within the range of variation for darwins between subsequent populations. In short, there is no evidence to suggest that the European Neanderthal/early Upper Paleolithic rates are so high to require eliminating European Neanderthals from a possible ancestral position.

CONCLUSIONS

Review of numerous so-called autapomorphic features and rates of evolution does little to confirm pronouncements that European Neanderthals have no phylogenetic relationship to subsequent Upper Paleolithic hominids. For many of the morphological features which have been used to characterize the uniqueness of European Neanderthals, there is strong evidence for the persistence of European Neanderthal traits into the Upper Paleolithic. These include nonmetric features such as the retromolar space, mastoid tubercle, suprainiac fossa, lambdoidal flattening and the presence of an occipital bun, maxillary and frontal sinus patterns, H-O mandibular foramen, proximal femoral flange, and dorsal scapular border. The persistence of these traits over the European fossil record closes the hiatus between the Mousterian and Upper Paleolithic groups. At the same time many of these identical features are absent in the Skhul/Qafzeh hominids or the African Eve sample; in fact, it is the absence of these features which lead some to recognize these groups as "anatomically considered in any detail and the metric comparisons were not constructed to reflect presumed autapomorphic differences. Consequently, the utility of these studies in demonstrating paleobiological relationships between the European Middle and Upper Paleolithic humans is dubious, and both should be viewed as insufficient tests of the hypothesis of a Neanderthal–Upper Paleolithic lineal relationship.

That there are Neanderthal features in especially the early Upper Paleolithic Europeans does not make these skeletal remains Neanderthals, just as the occurrence of "modern" features in Neanderthals does not make them "modern". While not considered here, there are a number of features typical of Neanderthals that do not appear to make an appearance in the European Upper Paleolithic. From the list of Stringer Hublin and Vandermeersch these include the *en bombe* (spherical) cranial shape, a large occipitomastoid crest (although this is present in, at least, Mladeč 5 [Frayer *et al.*, n.d.]), a double arched supraorbital torus, an elongated superior pubic ramus, and low distal limb segment indices. Other specific features associated with facial size and morphology (Heim 1976, Rak 1986, Trinkaus 1987a) are also not common in the Upper Paleolithic. However, just based on the absence (or reduced nature) of these features in the Upper Paleolithic, it is unwarranted to disclaim any affiliation between European Mousterian and Upper Paleolithic groups, given the presence of many, other clear links. A similar set of features can be compiled which would eliminate the Skhul/Qafzeh hominids or the paltry African Eve fossils from any sort of evolutionary link to the Upper Paleolithic Europeans (*e. g.*, upper facial flatness, absence of lambdoidal flattening/occipital buns, absence of the H-O mandibular foramen, absence of the proximal femoral flange). Moreover, the presence of "modern-like" features in the Neanderthal sample (*e. g.*, chins, reduced nasal dimensions, loss of the retromolar space, and bisulcate and ventral scapular borders) demonstrates that at least some of the Neanderthal features were becoming modified in the direction of the morphology found in later Europeans.

In summary, given the (1) presence of many of the identical morphological features throughout the Late Pleistocene of Europe and (2) the presence of more "modern" features in the late European Neanderthals, it is unjustified to assume that European Neanderthals had no relationship to the Upper Paleolithic Europeans. Given numerous fundamental differences between the so-called "proto-Cro-Magnons" of the Near East and the European Upper Paleolithic sample, it is also unnecessary to postulate that the origin of more modern features in the Upper Paleolithic was significantly influenced by extra-European forces (Smith, Falsetti and Donnelly 1989). For many features, the Upper Paleolithic Europeans, especially those from the early Upper Paleolithic, bear the mark of the Neanderthals who preceded them. In looking for Upper Paleolithic origins outside Europe, one encounters at least as many problems as attempting to determine the mechanism and course of the changes occurring solely within the European sequence. For example, given the new dates of about 90 kya for the Skhul/Qafzeh specimens, even if a few modern-like features are present in some skulls from these sites, there are no known, chronologically intermediate specimens from the Near East or Europe which represent the continuation of these supposed more modern morphologies. Just as it may be relevant to pose questions about the discontinuity of certain features between European Neanderthals and the Upper Paleolithic, it is also reasonable to wonder about the 60,000 year hiatus between the Skhul/Qafzeh hominids and the early Upper Paleolithic of Europe. In other words, is it reasonable to propose a model which requires modernizing features deriving from the Near East for the formation of the Upper Paleolithic, when there is such a huge time gap between the Middle Paleolithic and Upper Paleolithic appearance of the features? Moreover, since the majority of these features (such as increase in cranial height) are general evolutionary trends occurring world-wide over the entire course of human evolution, these "modernizing" features are not especially sensitive in determining (or eliminating) regional phylogenetic sequences. Thus, the perspective that the modern" or "proto-Cro-Magnons" (Klein 1989, Stringer, Hublin and Vandermeersch 1984, Vandermeersch 1989). It is important to consider the problem the European continuity in these traits poses for models which specify the Near East (or Africa) as the unique source for Upper Paleolithic Europeans. If the Near Eastern (or African Eves) are solely ancestral to Upper Paleolithic Europeans, there is no choice but to assume that each of these traits had another, separate evolutionary origin in the European Upper Paleolithic. That is, since a number of these traits are typically found in European Neanderthals and are absent in either the Skhul/Qafzeh or the African Eve sample, they must have evolved again in the early Upper Paleolithic, then dropped out quickly in the succeeding European populations. However, the probability of a suite of the exact same traits evolving twice within the European sequence is so infinitesimal that it seems reasonable to reject any model which necessitates such an unlikely series of evolutionary events. If European Neanderthals had no place in the origin of later Europeans, proponents of the total replacement view must either eliminate these "defining" characters of European Neanderthals or develop a model accounting for the persistence of European Neanderthal traits in subsequent Europeans without genetic continuity between the European Middle and Upper Paleolithic. The latter will be a formidable task. Inquiries into the relationship between European Neanderthals and the Upper Paleolithic groups, then, must consider the substantial evidence for the persistence of morphological traits through time. Moreover, the absence of most of these same traits in the hypothetical ancestors from Africa or the Near East is not an inconsequential matter and demands an explanation if these forms continue to be considered as ancestral to the European Upper Paleolithic people.

Recently, Bräuer (1992, 95) has suggested that the use of such features is flawed and that analysis of these kinds of traits "involve[s] questionable frequencies of features whose relevancies are themselves frequently questionable". Besides providing no data to support such a contention, this is an ironic, contradictory statement. Earlier in the same paper Bräuer assumes "that the conception of numerous indigenous evolutionary lines leading to modern humans is not well supported by the present evidence" (1992, 84) citing papers which use some of these same traits to "prove" discontinuity. For Bräuer, a bivariate plot of principal components factor scores for craniofacial variables which includes only four Upper Paleolithic specimens (two of which come from the very end of the Upper Paleolithic) is evidence enough for replacement. These kinds of plots neither represent the variation found in the fossil samples nor, necessarily, reflect biological reality (cf, Kidder, Jantz, and Smith 1992). Rather, Bräuer's multivariate analysis is simply a convenient way to reduce complex variation to a couple of axes. Such an analysis provides no support for contentions that European Neanderthals are a species apart from *Homo sapiens* nor that traits commonly found in European Neanderthals are trivial to the question of the relationship of European Neanderthals to the Upper Paleolithic.

This review of the persistence of supposed Neanderthal autapomorphies also differs from the conclusions of Gambier (1989, 206), who could "recognize neither derived Neanderthal features nor appropriate intermediate morphologies in [her French] Aurignacian sample". The inability of Gambier to find Neanderthal autapomorphies is not surprising since her sample was limited to France and included Cro-Magnon as the pivotal site. Since Cro-Magnon may be from the latest part of the early Upper Paleolithic (Bouchud 1966), the importance of the material from this site in determining Mousterian–Upper Paleolithic relationships is debatable. Beyond this problem, when Gambier did find a Neanderthal feature in an Upper Paleolithic specimen (such as occipital bunning), the similarity was discounted because it was "not consistently present" (Gambier 1989, 204) or differed slightly in its morphology. Stringer (1989) came to basically the same conclusion in an analysis of selected cranial metrics. In both these studies, the specific derived features listed by Stringer, Hublin and Vandermeersch (1984, 55) were not

Near East (or Africa) is the unique or catalytic source is actually more difficult to demonstrate than accounting for an *in situ* change among the European Late Pleistocene humans. Modern–like features in some of the Skhul/Qafzeh specimens may be localized occurrences, which, although interesting, are inconsequential to the evolutionary developments in Europe. Until unique links can be shown to exist between the Skhul/Qafzeh (or African Eve) and the Upper Paleolithic hominids, these groups must be viewed as unlikely ancestors.

Beyond these morphological and metric considerations, rates of evolutionary change in dental and craniofacial metrics show no evidence of an abrupt shift between the European Neanderthals and the Upper Paleolithic. While there was marked metric change between Mousterian and Upper Paleolithic samples, measured with respect to the magnitude of change over the Upper Paleolithic or between subsequent periods, the rates of evolutionary change are generally higher in populations for which few would deny an ancestral–descendant relationship. Consequently, the longstanding argument that "not enough time" exists between the Neanderthal and Upper Paleolithic periods for allowing evolutionary change from one to the other is demonstrably without support from the available evidence.

In short, there are many unique morphological links between the European Middle and Upper Paleolithic hominids and few between the Skhul/Qafzeh (or African Eve) sample and the Upper Paleolithic. These factors, coupled with data on rates of evolution, suggest it is now time to consider European Neanderthals as the probable ancestors of the people in the Upper Paleolithic.

ACKNOWLEDGEMENTS

This paper was made possible through NSF grant BNS 84-49057 and several awards from the National Academy of Science and the University of Kansas General Research Fund. Without the support of these agencies, the work could not have been accomplished. I also thank the curators of European skeletal material for allowing me the privilege of examining their collections. R. E. Caspari, K. Fuller, J.L. Hofman, F.H. Smith, and M.H. Wolpoff provided critical comments on the manuscript, but do not necessarily agree with all that is written here, as they may indicate in public or private. C. Nicolay produced most of the figures and D. Keslar helped in some of the computations. Finally, much of the perspective of this paper derives from a joint work (Frayer *et al.* nd) involving the description of the Mladeč human remains from Moravia. While the principal authors (Wolpoff, Smith, and Jelínek) of this still unfinished study may not completely concur with my analysis, they deserve credit in forming some of the basic ideas for which we can all agree. Finally, this paper was originally begun as a solicited contribution for a *Journal of Anthropological Research* volume edited by L. G. Straus (Summer 1991). For a variety of reasons, I was regretfully unable to make their deadline.

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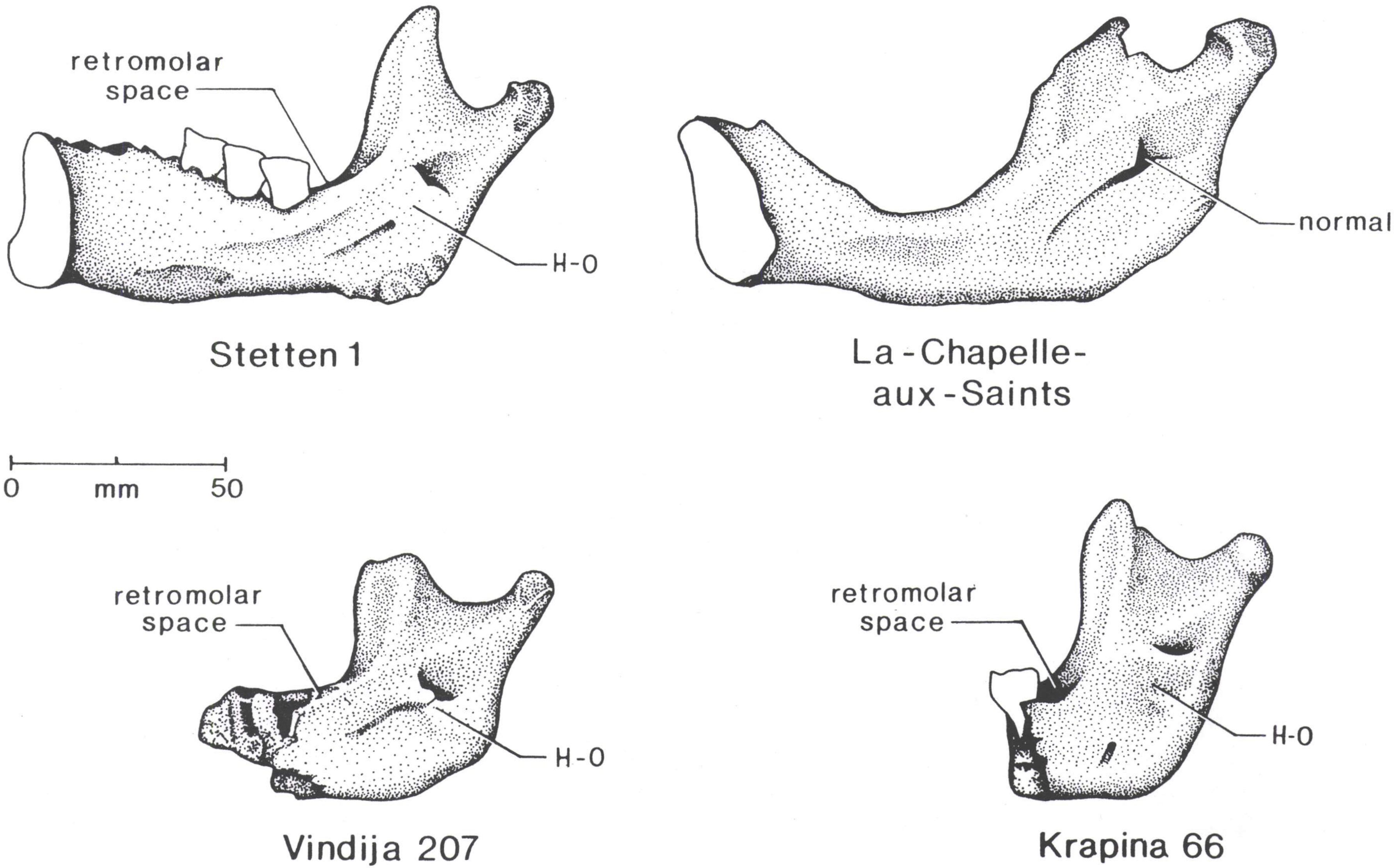

Figure 1.
The retromolar space and mandibular foramen types in two European Neanderthal (La Chapelle-aux-Saints and Krapina 66 [reversed]) and two Upper Paleolithic mandibles (Stetten 1 and Vindija 207).

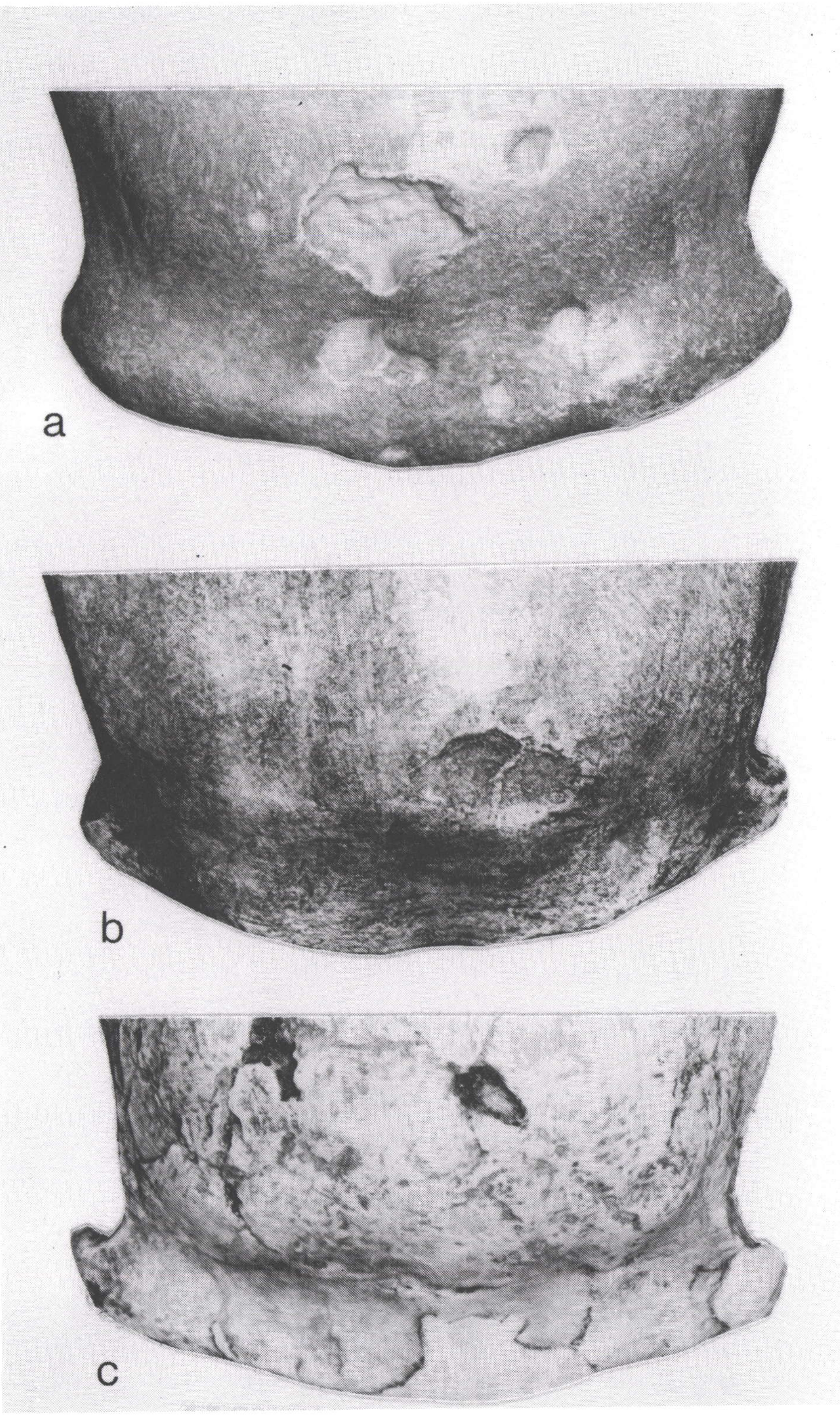

Figure 2.
Superior views of the anterior frontals of La Chapelle-aux-Saints (a), Mladeč 5 (b), and Skhul 5 (c).

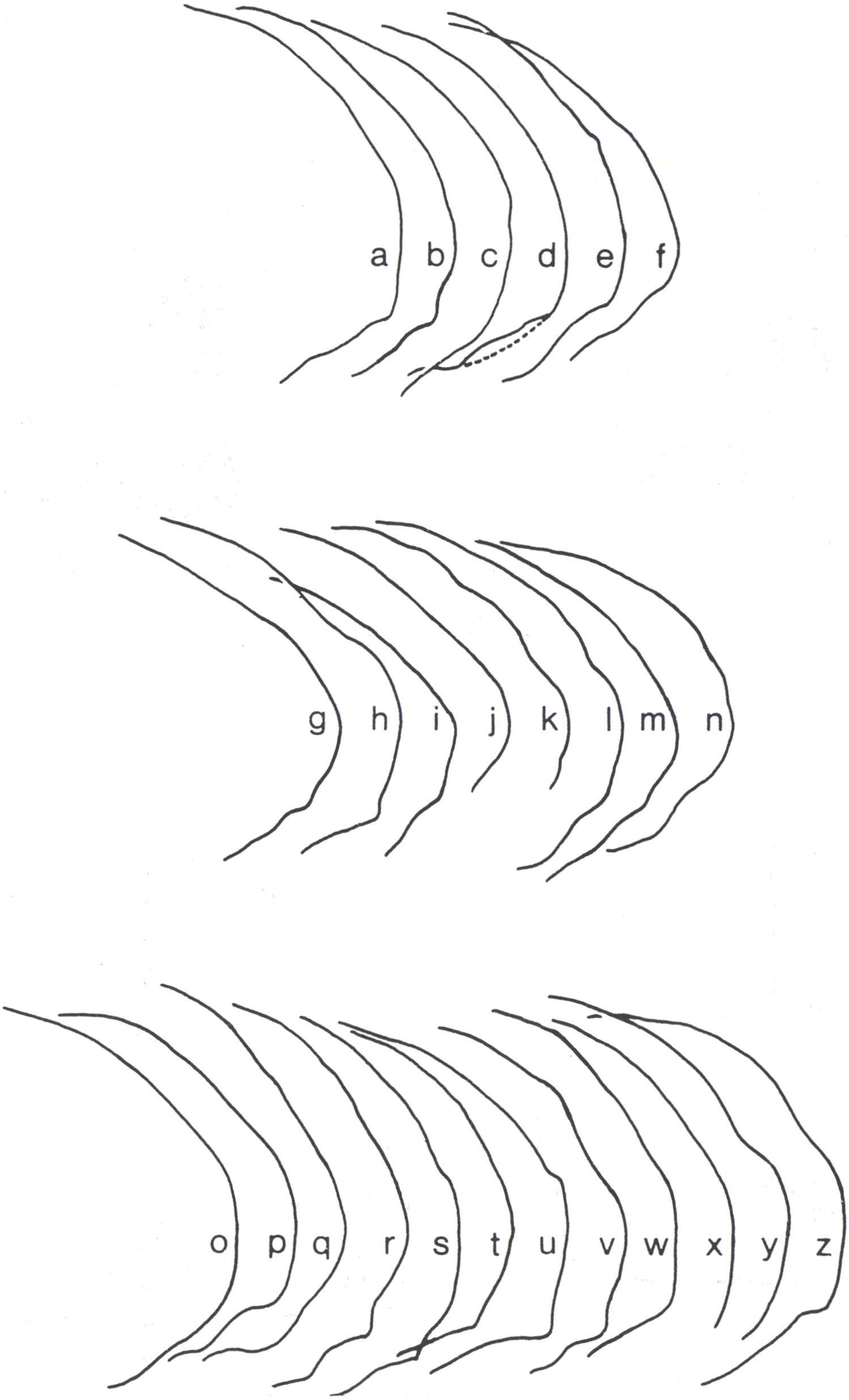

Figure 3.
Lateral posterior cranial profiles of Skhul/Qafzeh, European Neanderthals, and early Upper Paleolithic specimens. a Qafzeh 3; b Qafzeh 6; c Qafzeh 9; d Skhul 4; e Skhul 5; f Skhul 9; g La Chapelle-aux-Saints; h Monte Circeo; i La Quina 5; j Neanderthal; k Spy 1; l Spy 2; m La Ferrassie 1; n Saccopastore 1; o Mladeč 1; p Mladeč 5; q Mladeč 6; r Předmostí 3; s Předmostí 4; t Předmostí 9; u Pavlov 1; v Brno 2; w Cro-Magnon 1; x Cro-Magnon 2; y Cro-Magnon 3; z Abri Pataud 1. (a-c from Vandermeersch 1981; d-f from McCown and Keith 1939; g from Heim 1989; h-m from Heim 1978; n from Sergi 1944; o-q from Szombathy 1925; u-v from Vlček 1944, 1991; w-y from Vallois and Billy 1965; z from Billy 1975).

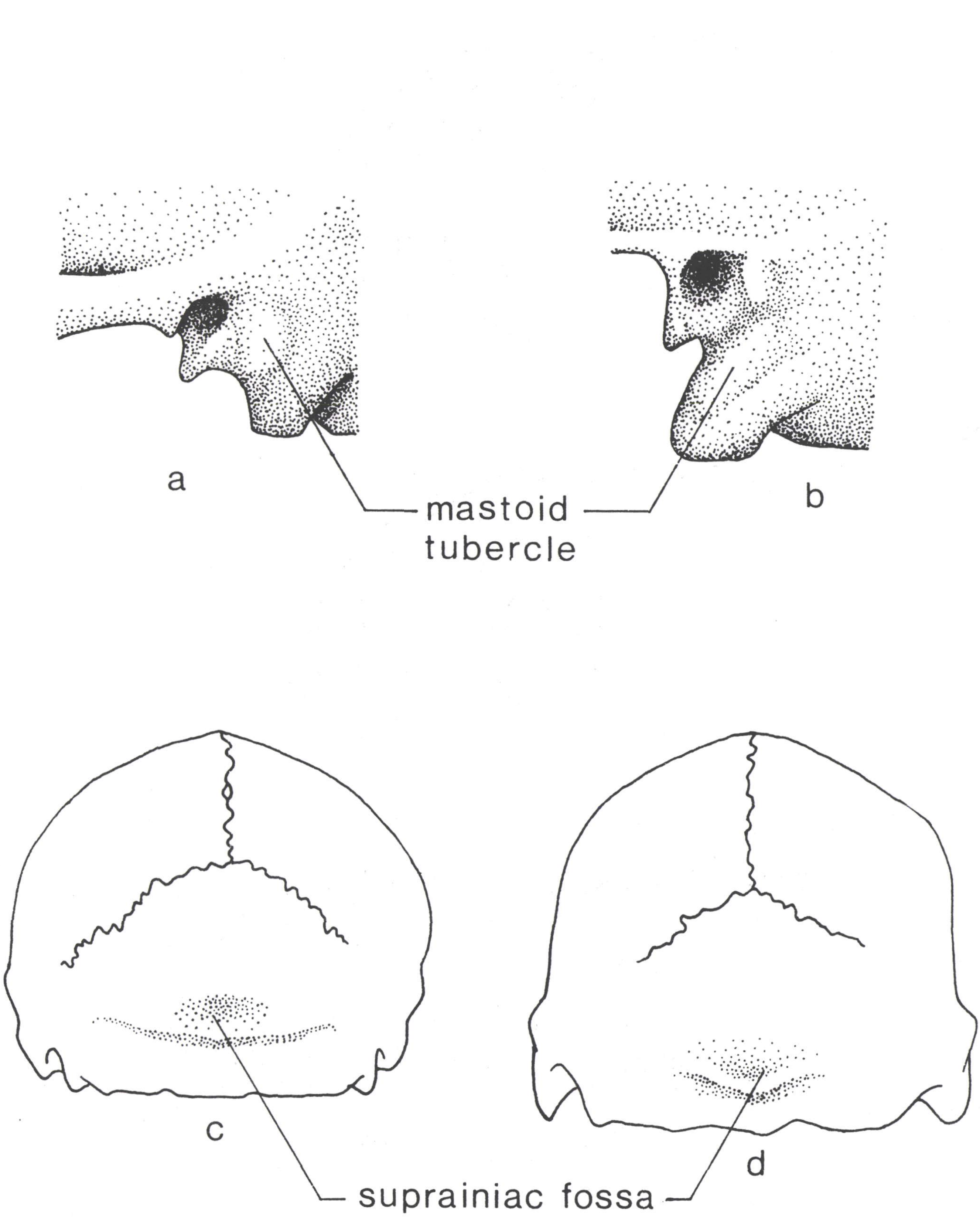

Figure 4.
Mastoid tubercle in La Quina 5 (a) and Combe-Capelle (b) and the suprainiac fossa in La Quina 5 (c) and Předmostí 3 (d).

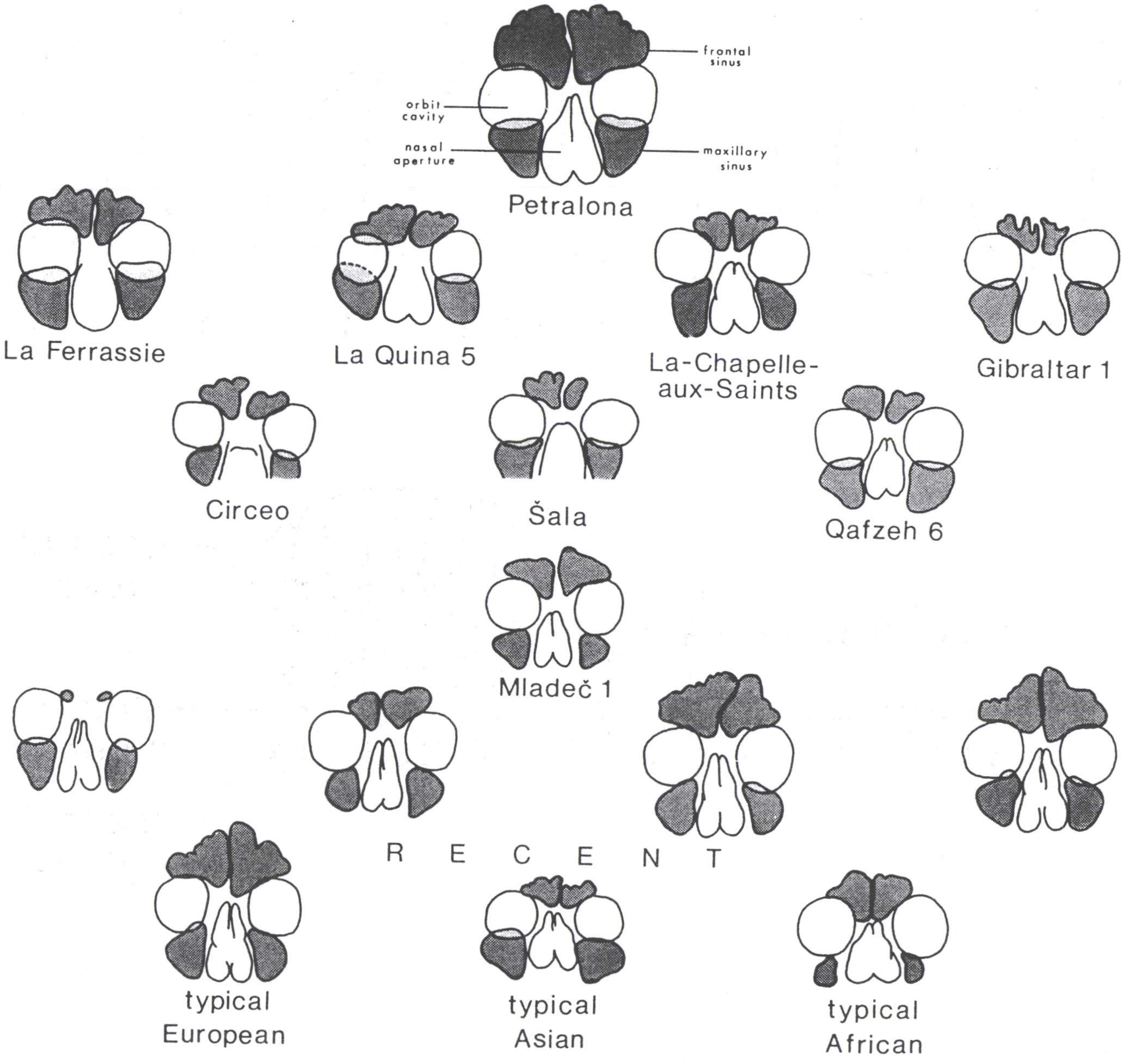

Figure 5.
Frontal profiles of paranasal sinuses (modified from Szilvássy, Kritscher and Vlček 1987)

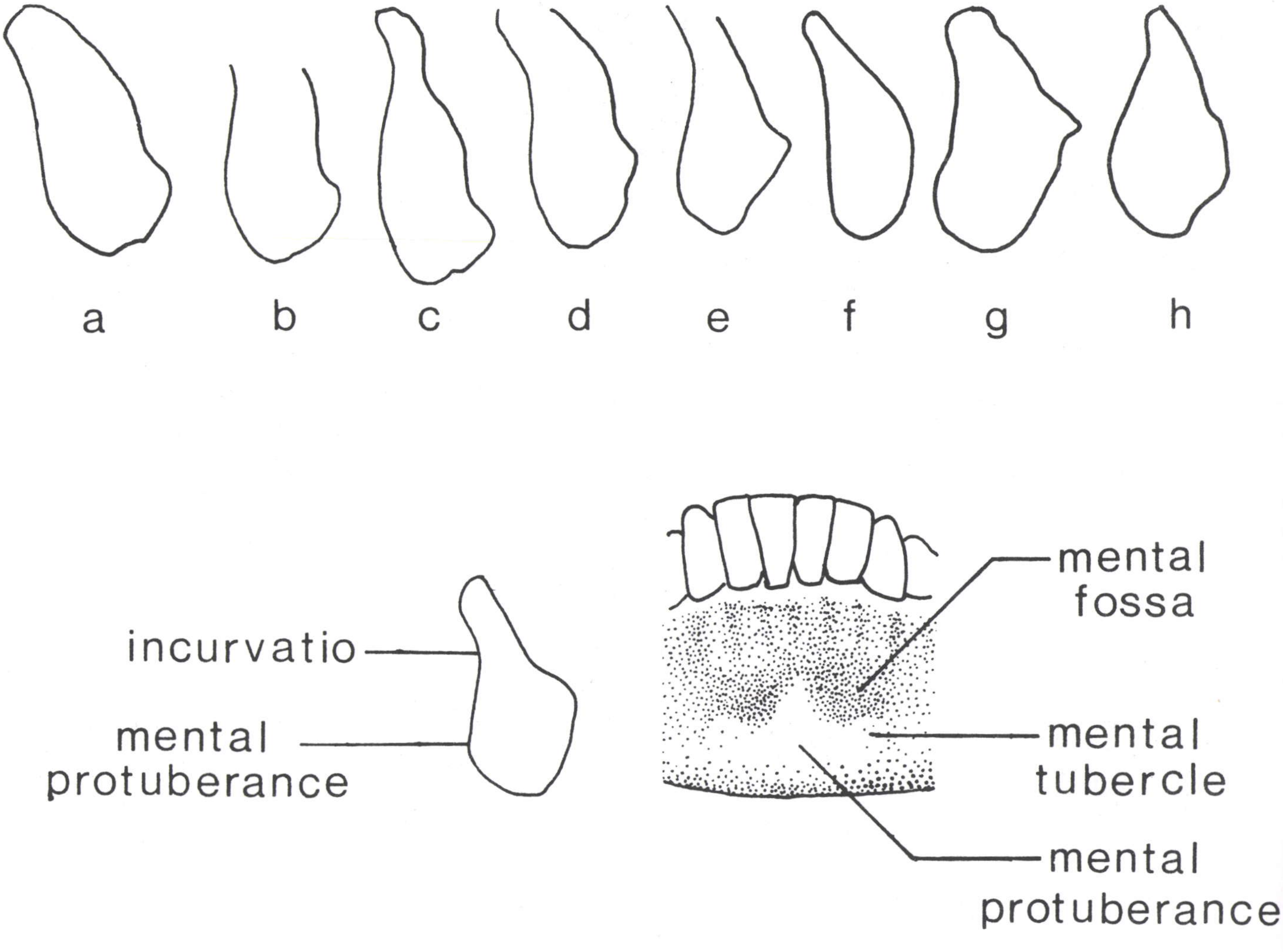

Figure 6.

Symphyseal cross-sections (oriented in the alveolar plane) and major anatomical features of the chin. a La Chapelle-aux-Saints; b Circeo 3; c La Ferrassie 1; d Skhul 5; e Předmostí 3; f Pavlov 1; g Cro-Magnon 1; h modern French. (a-d , h from Heim 1978; e from Matiegka 1934; f from Vlček 1991; g from Vallois and Billy 1965). Other diagrams modified from DuBrul and Sicher 1954.

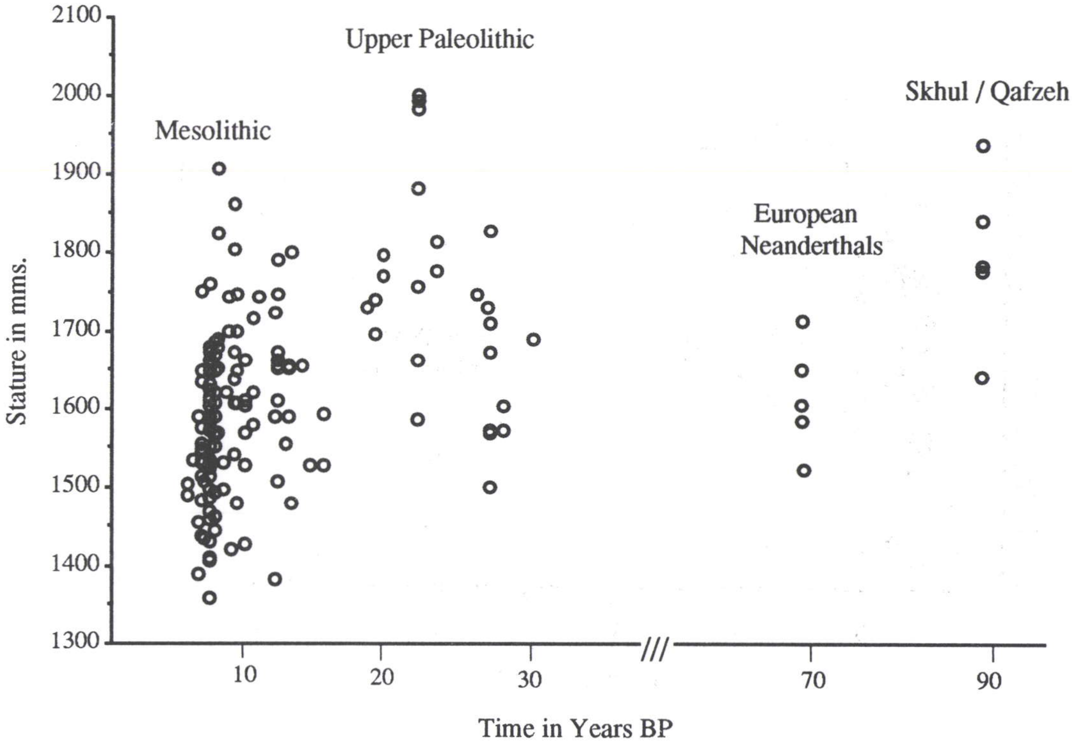

Figure 7.
Stature estimates based on the technique of Feldesman Kleckner and Lundy (1990) for the Skhul/Qafzeh, European Neanderthal, Upper Paleolithic, and Mesolithic samples.

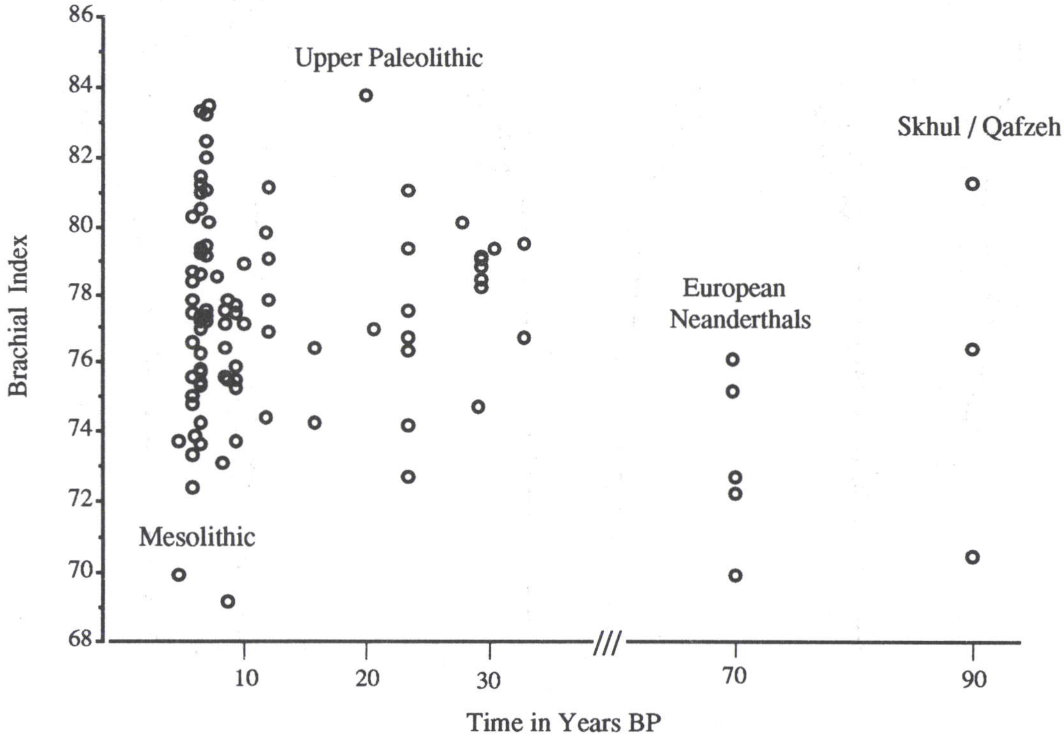

Figure 8.
Brachial indices for the Skhul/Qafzeh, European Neanderthal, Upper Paleolithic, and Mesolithic samples.

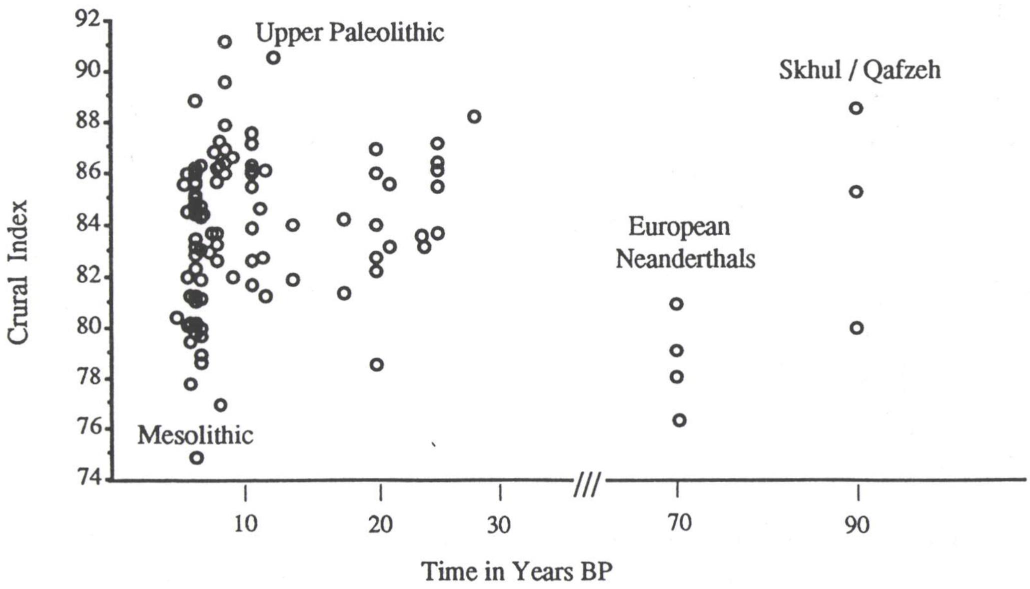

Figure 9.
Crural indices for the Skhul/Qafzeh, European Neanderthal, Upper Paleolithic, and Mesolithic samples.

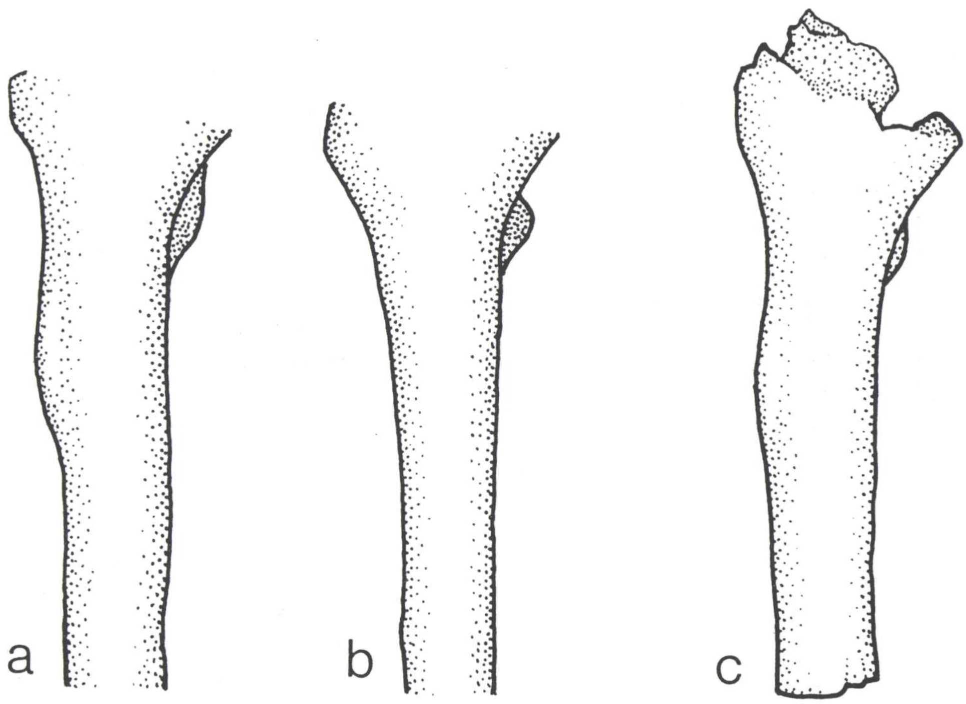

Figure 10.
Proximal femoral flange in Spy 2 (a), Skhul 4 (b), and Mladec 28 (c), from casts.

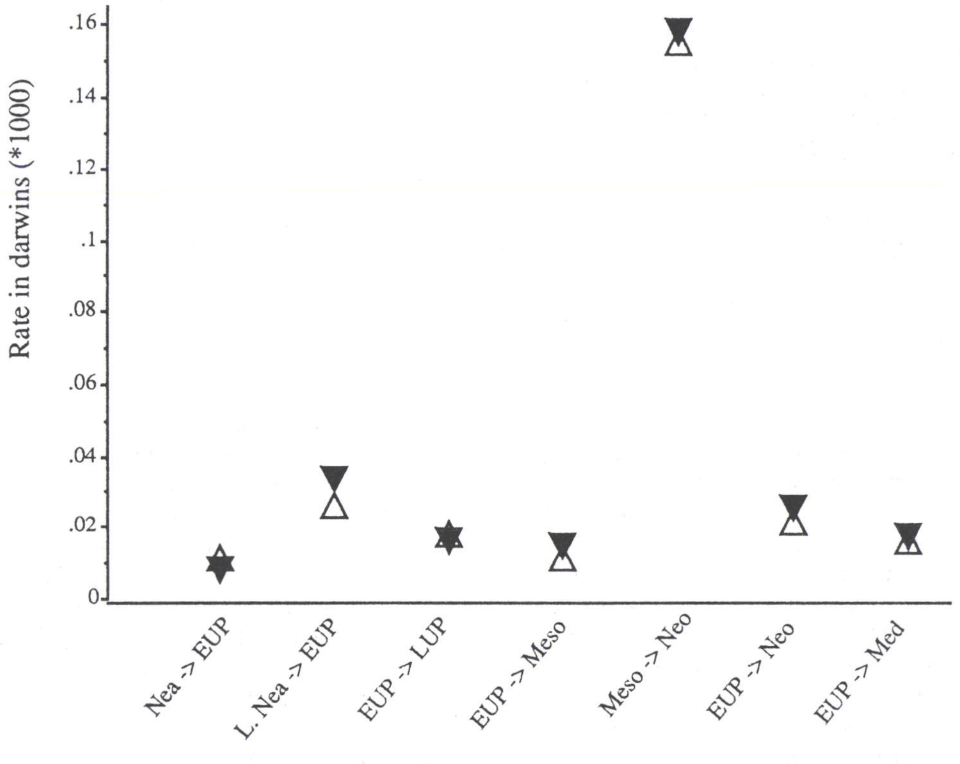

Figure 11.
Evolutionary Rates of the Comparative European Samples for the Anterior Tooth Dimensions ▼ - mandibular average rate; △ - maxillary average rate.

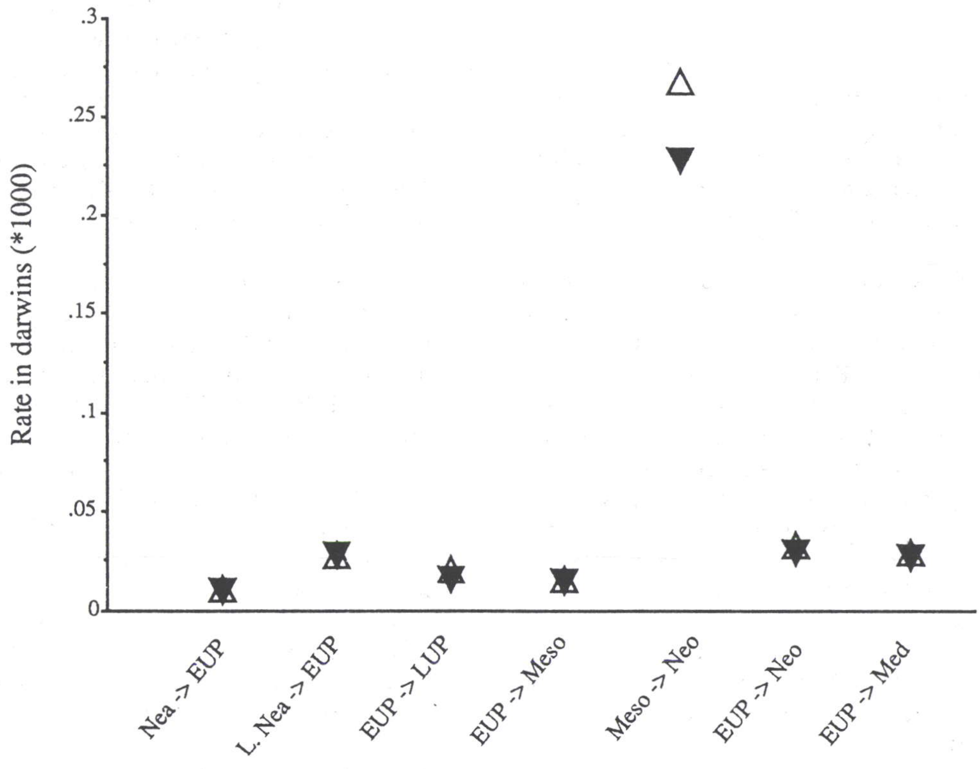

Figure 12.
Evolutionary Rates of the Comparative European Samples for the Canine and Posterior Tooth Areas ▼ - mandibular average rate; △ - maxillary average rate