Cinq millions d'années, l'aventure humaine - Five Million Years, the Human Adventure
M. Toussaint éd., E.R.A.U.L. 56, 1992, Liège, pp. 151-176.

Paleontological Perspectives on Neandertal Behavior

Approche paléontologique du comportement des Néandertaliens

Erik Trinkaus *

Abstract

The study of the Neandertals has been increasingly dominated by a reluctance to admit that human ancestors might have been behaviorally different from ourselves. This has produced versions of the "Pre-Sapiens" approach, most denying modern human ancestry to anatomically archaic humans but others granting fully modern human behavioral patterns to all archaic human ancestors. To counter this non-evolutionary approach, it is suggested that there exist a sufficient number of uniformitarian patterns which enable us to interpret the functional morphology, development and degeneration of extinct human samples and to make reliable inferences regarding shifts in the distributions of past human behavioral patterns.

Résumé

L'étude des Néandertaliens a été de plus en plus souvent marquée par des difficultés à admettre que les ancêtres de l'homme aient pu avoir un comportement différent du nôtre. Cette manière de penser a engendré diverses versions de la théorie des "Pré-sapiens", dont la plupart ne voient pas les humains anatomiquement archaïques comme les ancêtres de l'homme moderne, tandis que d'autres attribuent un comportement pleinement moderne à tous les hommes archaïques. Pour parer à cette approche non évolutionniste, il est suggéré qu'il y a un nombre suffisant de modèles uniformisants qui nous permettent d'interpréter la morphologie fonctionnelle, le développement et la dégénérescence des échantillon humains éteints et de faire des déductions fiables à propos des changement dans la distribution des modèles du comportement des hommes du passé.

Key words : Neandertals, behavior, biomechanic, respiratory physiology, thermal regulation, dental attrition, pathological alterations.

Mots clés : Néandertaliens, comportement, biomécanique, physiologie respiratoire, régulation thermique, usure dentaire, modifications patlologiques.

Introduction

It has been almost a century and a half since the recognition of a Quaternary human existence (Grayson, 1983; Cohen and Hublin, 1989) and slightly more than a century since the acceptance of the association of archaic hominids (Neandertals) with Quaternary geological deposits and extinct fauna (Leguebe, 1986). Throughout this time period, different behavioral

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* Erik Trinkaus, Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA and UA 376 du C.N.R.S., Laboratoire d'Anthropologie, Université de Bordeaux I, 33405 Talence, France

models and phylogenetic schemes concerning the Neandertals have had periods of fashion. Out of this has emerged an intellectual legacy concerning what we are willing to accept for behavioral (and phylogenetic) schemes for these archaic hominids. At the same time, there have been attempts to identify uniformitarian principles which can be applied to the fossil record and recently to apply these principles to paleontological samples in the context of the intellectual paradigm of the evolutionary synthesis[1].

These trends have produced two partly conflicting movements; the first is based largely on the momentum of intellectual trends within paleoanthropology, and the second is influenced more the by emerging understanding of evolutionary biology and general anthropology (including biological anthropology, prehistory and ethnology). From these approaches to the behavioral interpretation of archaic human groups, conflicting views have arisen which are dichotomized along two axes.

The first axis concerns the degree to which we can make behavioral interpretations from human fossil remains. There are those who attempt to make reasonable interpretations (or hypotheses) concerning the changes in average patterns of hominid behavior through time and space, despite the limitations of the fossil record. These are opposed by those who maintain that the paleontologically documented morphology is too distant from the actual past behaviors of archaic hominids to allow behavioral interpretations. They also maintain that fossil samples are and will remain inadequate to permit such interpretations on a populational basis.

The second axis concerns the degree to which Pleistocene hominid behavior differed from that of extant humans. There are those who maintain that the consistent presence of nonmodern (or archaic) human morphology indicates that those fossil hominids must have had patterns of behavior that were significantly different from those of ethnographically and ethnohistorically documented recent humans. Others feel that it is unjustifiable to argue that archaic prehistoric humans differed behaviorally from modern humans in more than levels of overall strength and exertion. The latter would maintain that the process of hominization ("progress" towards us) consisted primarily of humans becoming more mechanically and energetically efficient, through the development of more effective technologies, and as a result, gradually losing their previous musculo-skeletal massiveness. The former would permit the existence of changes in basic patterns and frequencies of human behavior, in addition to changes in efficiency, during the course of human evolution.

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[1] "Uniformitarianism", and the resultant "uniformitarian principles," assume that processes which are identifiable in the natural world of the present are the same processes which were responsible for the formation of patterns and events in the past. This follows the original meaning of Lyell (1830). In the interpretation of human paleontological remains, the identification of the appropriate principles and associated processes is theoretically straight-forward, if frequently practically complex. We have sufficiently abundant extant humans, non-human primates, and other mammals and vertebrates to allow us to establish the biological baselines for interpreting hard tissue variation. In Paleolithic archaeology, it is seldom as straight-forward, even theoretically, since modern humans are the only extant culture-bearing primates. If we could establish that Middle Paleolithic or earlier hominids were fully culture-bearing, then we could theoretically apply uniformitarian principles derived from ethnographically-derived cultural universals among modern humans. However, it has not yet been adequately documented that all members of the genus *Homo* were indeed fully culture-bearing, which therefore limits our ability to use the ethnographic present for the direct interpretation of all of the Paleolithic past.

[2] "Late archaic humans" includes the Neandertals of the northwestern Old World (mostly Europe extending into central Asia, with some closely related but significantly different hominids present in the Near East [see Trinkaus, n.d.a.]) plus hominids of a similar grade but of different geographical clades in Africa, eastern Asia and Australasia. These hominids date generally from the later Middle Pleistocene until some time in the Upper Pleistocene, and are those which have been referred to as "Neandertal-like", "Neandertaloids", "archaic *Homo sapiens*" and "*Homo neanderthalensis*". Late archaic humans is here chosen as a non-regional, non-taxonomically formal term to describe these hominids which are generally similar in most aspects of their morphology, differing only in overall bodily proportions and aspects of facial and cranial base morphology.

In the context of these dichotomies, it has become necessary to resolve these basic issues before we are to proceed further in the analysis of the evolution of late archaic humans[2] and the emergence of modern humans. Paleontologically-documented evolution consists of geographical and temporal sequences of related biological forms, which underwent adaptive changes and adjustments to their environments (including culture in the case of hominids). Unless we can agree on how to approach the reconstruction of trajectories of past human behavior from the available evidence, we will never get past the philatelic curation of paleontological remains of past hominids.

A phylogenetic Digression

Most of the attention in later Pleistocene paleoanthropology has been focused on the controversies concerning the phylogenetic origins of modern humans and the phylogenetic fates of the late archaic humans such as the Neandertals (e.g., Trinkaus, 1982; Stringer and Andrews, 1988; Smith *et al*, 1989; Stringer, 1990; Smith and Trinkaus, 1991; papers in Smith and Spencer, 1984; Mellars and Stringer, 1989; Trinkaus, 1989a; Vandermeersch, 1989; Akazawa, n.d.). Despite the recent controversy, human paleontologists in fact agree on much of the sequence of human forms associated with the emergence of modern humans. They disagree primarily in the degree to which they see continuity from, as opposed to replacement of, regional groups of late archaic humans. Yet, from recent discussions, there appears to be little apparent hope of resolving many of the paleontological and genetic arguments concerning the details of regional sequences.

It is nonetheless recognized that reasonable reconstructions of changes in past human behavioral patterns must be connected to appropriate phylogenetic schemes, or at least based on well founded geographical and temporal sequences of prehistoric humans. Yet, it appears appropriate to proceed with behavioral questions. Otherwise, the field is likely to stagnate in the already interminable phylogenetic arguments. This must be done, of course, bearing in mind that such behavioral interpretations may have to be modified in light of changing knowledge of past human phylogeny. Yet, since all such behavioral interpretations are little more than hypotheses, to be tested, modified and reformulated (such *is* the nature of science), these phylogenetic concerns bear only indirectly on the basic issues outlined above.

An Historical Background to Neandertal Behavior

Since current differences in behavioral interpretations of the Neandertals and the potential to make them from the fossil record are based in paleoanthropological traditions, it is appropriate to review the past century and a half of the study of the Neandertals. The more technical aspects of this history have been discussed by Trinkaus (1982) and Spencer (1984). However, those reviews have dealt little with changing perceptions of Neandertal behavioral reconstruction.

The first phase of the study of the Neandertals extends from the discovery of the Engis immature cranium in 1829 up to the eighth decade of the last century. This period was dominated, in both prehistory and human paleontology, by the establishment of a human antiquity and the recognition that there existed more archaic, both behaviorally and biologically, humans than were known in the modern world (Grayson, 1983; Cohen and Hublin,1989). The discussion was intimately related to the controversy over the acceptance of evolution and its applicability to humanity. It was, in particular, during this period that the discoveries at the Neandertal (Schaaffhausen, 1858), Forbes' Quarry (Gibraltar) (Falconer, 1864 : see Keith, 1911), and La Naulette (Dupont, 1866) were actively debated, with a few anatomists aligning themselves strongly on one side or the other of the issue of whether these fossils represented valid prehistoric and archaic humans. Many scientists simply reserved judgment given the absence of geological dating for the first two fossils and the incomplete nature of the third. For those who ventured a behavioral interpretation of these prehistoric humans, the inferences were based on phrenology, with the large brows, low neurocrania and robust constitution implying semi-human moral and cognitive characteristics. In fact, it was on the basis of such a phrenologically-inferred inferior moral stature that King (1864) proposed that the Neandertal individual belonged to a separate species, *Homo neanderthalensis.*

The following period, from the 1870s to approximately 1910, appears enlightened by comparison. During the late 1870s and early 1880s, a number of anthropologists (since such formally existed by then, largely through the Ecole d'Anthropologie de Paris of Broca and other national associations (Fletcher, 1882) came to accept the former existence of an archaic "race" of humans, usually including a strange mix of truly archaic forms, such as Neandertal, Forbes' Quarry and La Naulette, plus various robust, platycranic, recent human skulls of uncertain geological age. In fact, when Fraipont and Lohest (1887) described the Spy Neandertals and their Quaternary geological context, they were uncertain whether to assign them to a "Neandertal race" or to a "Canstadt race".

In this context, following on the general human social evolutionary models which were widespread in human intellectual circles of the late nineteenth century, and most clearly outlined by Tylor (1871) and Morgan (1877) (see Harris, 1968), anthropologists saw no difficulty in assigning "primitive" human biobehavioral characteristics to these archaic human remains (fig. 1). It was not surprising, therefore, that Collignon (1880) would infer that his Neolithic

Fig. 1 1873 artist's reconstruction of a Neandertal couple in their rockshelter (Anon., 1873, p. 617). Note the combination of large face and brows with otherwise Mesolithic/Neolithic features such as domesticated dogs and polished stone axes.

sample had habitually bent knees based on their marked tibial retroversion, and it was even less problematic for Fraipont (1888) to infer a similar bent knee gait and posture for the Spy Neandertals based on a similar anatomical feature. Morphologically more archaic humans, and especially those in the remote past, were simply behaviorally more archaic (fig. 2). They were in effect extending the period of "Savagery" of Morgan (1877) further into the past. At the same time, they saw little problem with integrating such biobehaviorally archaic human forms into the remote periods of human ancestry. After all "progress", with all of its potential to improve human existence (see Radovcic, 1988; Cohen and Hublin, 1989), made it possible for all humans to become civilized and European!

The only arguments against these behavioral schemes in the late nineteenth century came from a few anthropologists, who argued that these various early human groups were not so different from ourselves in their basic biobehavioral patterns. For example, Manouvrier (1893) so argued with respect to tibial retroversion, thereby narrowing the degree of change between archaic humans and ourselves but other-wise altering little in the overall unilineal scheme.

At the end of the first decade of the twentieth century in France and England reactions developed to this integration of biologically and behaviorally archaic humans into human ancestry (see Hammond, 1982 for France; Spencer, 1990 for England). Primarily through the work of Arthur Keith in England and Marcellin Boule in France, a school of thought emerged that has become known as *Pre-Sapiens*. These scientists, in their own separate fashions, argued that something as special as modern humanity must have a great ancestry, documentable through a long sequence of fossils essentially indistinguishable from ourselves. They never denied that we evolved from more archaic forms of humans, only that such forms must have been very remote in the past.

Fig. 2 Sketch reconstruction of one of the Spy Neandertals by Maximin Lohest about 1886 (Leguebe, 1986, p. 21).

In other words, they maintained that anything less human than ourselves could not have been a recent human ancestor. The Neandertals, being late Quaternary in age, were simply too archaic and too recent to fall within our acceptable ancestry. Boule (1911-13, 1921) maintained the functional anatomical and hence behavioral interpretations of Neandertal morphology already current, if occasionally contested (see Trinkaus, 1985), elaborating upon them with the more complete fossil material recently discovered at La Chapelle-aux-Saints and La Ferrassie, plus the Neandertal and Spy fossils. He used the anatomical contrasts between the Neandertals and early modern humans, rein-

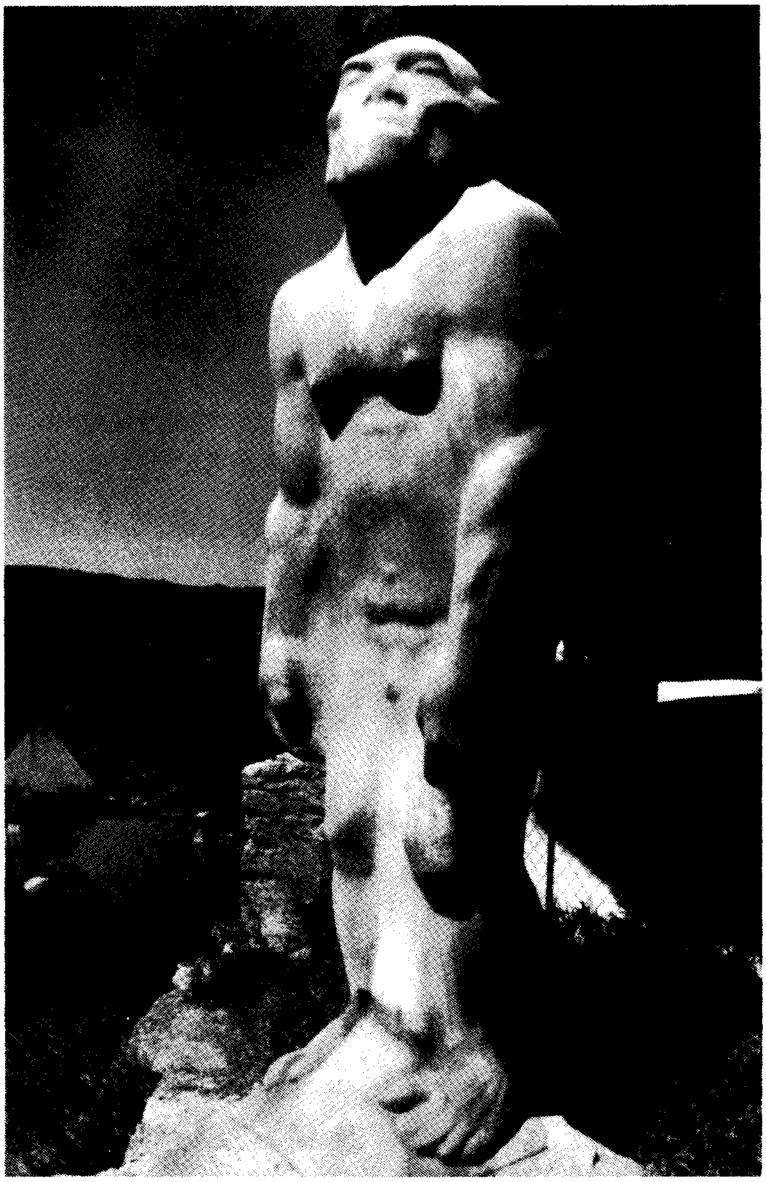

Fig. 3 Statue of a Neandertal made in 1931 by P. Dardé, currently in front of the the "Musée National de Préhistoire", les Eyzies-de-Tayac. It represents the postural reconstruction detailed by Boule (1911-1913), with the habitually bent knees and divergent hallux.

forced by behavioral inferences, to exclude them from modern human ancestry. Keith (1912, 1915) accepted a rogue's gallery of dubious "early modern humans" of supposed Quaternary age (many considered of dubious antiquity at the time; e.g., Moulin Quignon) and built his ancestry for modern humans upon them, integrating Piltdown when it became available.

This school of thought, best referred to as the "Anatomical Pre-Sapiens" school, became dominant during the first half of the twentieth century, with most European and North American anthropologists subscribing to some version of its phylogenetic tenets. There were a few challenges, such as those of Hrdlicka (1927, 1930). He tried to update the unilineal schemes of the late nineteenth century using more complete fossil material and a more explicit role for changing human behavior and environment in the observed morphological alterations, but he convinced few of his contemporaries. Basically, the behavioral interpretations of the Neandertals remained an updated version of the archaic, semi-human creature that had begun in the late nineteenth century, being modified in detail but remaining the same in its core aspects as more complete fossil material became available and it was possible to integrate material from a rapidly expanding Paleolithic archaeological record (fig. 3). The main contribution of Boule and Keith and their contemporaries in human paleontology was to champion the idea of phylogenetic replacement. The behavioral aspects were secondary and, in many ways, self-evident to anyone with the "correct" perspective.

This view started to change on the eve of World War II, with Kleinschmidt (1938) and Coon (1939) questioning some aspects of Boule's well established (if incorrect) postural reconstruction of the Neandertals. The strict "Pre-Sapiens" phylogenetic school started to evolve into a *Pre-Neandertal* school. In this, some recently discovered archaic fossils pre-dating the "classic" Neandertals, such as the Swanscombe and Saccopastore remains, were seen as reasonable ancestors for modern Europeans even if the early last glacial "classic" Neandertals remained phylogenetically separate. In the post-war period and through the 1950s, there was an increasing acceptance of a "Pre-Neandertal" phylogenetic scheme (e.g., Howell, 1951; Sergi, 1953; Breitinger, 1957), despite the efforts of Vallois (1958) to revive the old "Pre-Sapiens" argument. This was associated with the acceptance of *Homo erectus* into human ancestry, through the work of Weidenreich (1936, 1937, 1941, 1943) and v. Koenigswald (1940), and the gradual admission that *Australopithecus* might be a hominid (LeGros Clark, 1947, 1967).

As a result of these changes in the perception of human phylogeny, the Neandertals became close relatives, if not direct ancestors, of modern humans (fig. 4). This prompted reconsiderations of Boule's semi-human postural reconstruction of the Neandertals and clear demonstrations that the Neandertals fell well within modern human ranges of variation with respect to posturally significant aspects of their morphology (Arambourg, 1955; Patte, 1955; Schultz, 1955; Toerien, 1957; Straus and Cave, 1957). Consequently, the Neandertals came to be considered as behaviorally essentially indistinguishable from modern humans (see esp. Straus and Cave, 1957). They were even placed in *Homo sapiens* (Dobzhansky, 1944; Mayr, 1951), following the tradition established by King (1864) of using general theoretical considerations rather than paleontological analyses to determine their specific status.

Fig. 4 1939 reconstruction of a Neandertal by Carleton S. Coon (Coon, 1939, p. 24). The drawing was made to emphasize the role of clothing in influencing racial attributions, as well as to demonstrate the general similarities of the Neandertals and modern Europeans.

This change of behavioral perspective of the Neandertals emerged through the 1960s into what is best referred to as the "Behavioral Pre-Sapiens" school. Whereas Boule, Keith and others in the early twentieth century refused to have a being that was anatomically less human than ourselves as a close relative, most paleoanthropologists in the 1950s and subsequently were uncomfortable with a close relative that was behaviorally less human than ourselves[3].

This trend started with the correction of the functional morphological errors of Boule and his predecessors. It continued with attempts to explain away aspects of Neandertal morphology, such as their large noses and short distal limb segments as due to cold adaptations or their large anterior teeth as due to less elaborated tool kits (e.g., Howell, 1951; Coon, 1962; Brace, 1962; Badoux, 1965; Brose and Wolpoff, 1971). However, what began with the establishment that they had the same basic kinesiology and cognitive capabilities as ourselves, quickly evolved into maintaining that they were simply robust versions of ourselves. Then, for some anthropologists (e.g., Brace, 1962; Brose and Wolpoff, 1971), they only had to wait for biological evolution to catch up with their already modern behavioral patterns and turn them into modern humans. After all, they were the first flower people (Solecki, 1971)!

The net result was to minimize the possible behavioral significance of morphological contrasts, even while admitting that such contrasts existed. Few of the above mentioned functional analyses actually compared Neandertal morphology in depth to that of modern humans; most were content merely to generalize from existing descriptions and hypothesize in general as to why the Neandertals were behaviorally, if not always phylogenetically, so close to ourselves. Consequently, human evolution had become similar to a Russian comedy, in which, at the end, everyone dies happy (or at least just like us)!

The proximate problem with this "Behavioral Pre-Sapiens" approach is that it denies the abundant evidence from functional morphology, dental attrition and paleopathology, much of it present in the literature by the late 1960s and 1970s, that significant changes in human behavior had taken place between late archaic and early modern humans.

The more ultimate difficulty raised by a "Behavioral Pre-Sapiens" approach is that, in its logical extreme (e.g., Wolpoff, 1971; Mann, 1972; Isaac, 1978), it denies the possibility of any meaningful human biological evolution during much of human evolutionary history. It implies that little that was adaptively important in the hominid biobehavioral system could have changed during much of the existence of the genus *Homo*, if not for all of the Hominidae. Consequently, since any significant behavioral changes are denied, any differential reproduction as a result of adaptively meaningful behavioral contrasts becomes impossible. This leaves us with a stochastic process in which similar directional trends in morphology over many tens of millennia in different regions of the Old World are explainable only through genetic drift, possibly in the context of relaxed selection, combined with developmental plasticity in the overall level of musculo-skeletal massiveness.

Although genetic drift and developmental plasticity might explain some regional patterns in morphology and some changes in robusticity, it is difficult to account for the multitude of hominid morphological changes throughout the later Pleistocene simply in terms of developmental and stochastic processes. Therefore, in effect, to deny that there were significant behavioral

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[3] Vandermeersch (1981b) has used the term "Pre-Sapiens" in what is best referred to as a "Phylogenetic Pre-Sapiens" approach. In this, he used the term "Pre-Sapiens" to refer to those late archaic humans whom he considered to have been directly ancestral to modern humans, distinct from the Neandertals and their late Middle Pleistocene ancestors. His usage, although unfortunate given the historical connotations of the term "Pre-Sapiens", does not appear to carry the morphological or behavioral implications of the "Anatomical Pre-Sapiens" or "Behavioral Pre-Sapiens" schools. In fact, his construct is a purely phylogenetic one similar to those proposed by a number of authors recently (e.g., Stringer and Andrews, 1988; Hublin, 1990; Bräuer and Rimbach, 1990; Smith and Trinkaus, 1991) which see most modern humans arising from non-Neandertal late archaic humans with varying degrees of admixture with the Neandertals, depending upon the author involved, all of which can be viewed as more globally oriented versions of the basic tenets of the former eurocentric "Pre-Neandertal" models of modern human origins.

changes through later Pleistocene human evolution is to deny that the observable morphological changes have any evolutionary significance. The paleontology of the genus *Homo* becomes, as a consequence, only the cataloging of fossils and arguments over their phylogeny. Any investigation of evolutionary processes and significance becomes *a priori* impossible.

The behavioral perspective presented by the "Behavioral Pre-Sapiens" approach became complicated during the 1970s and 1980s as a result of two trends. Each arose from attempts to go beyond the restricting effects of generalizations, such as are provided by the "Behavioral Pre-Sapiens" approach, and to investigate on a system-by-system basis the probable behavioral similarities and differences between Neandertals and modern humans.

The first trend was a series of attempts to analyze the morphological similarities and differences between the Neandertals and ourselves and to give functional meaning to them (e.g., Musgrave, 1971; Lieberman and Crelin, 1971; Trinkaus, 1975a, b, 1976, 1977, 1978a, b, 1981, 1983a, b, c, 1984a, b, 1986, 1987; Lovejoy and Trinkaus, 1980; Stoner, 1981; Smith, 1983; Rak, 1986; Trinkaus and Churchill, 1988; Smith and Paquette, 1989; Ruff and Trinkaus, 1989a, b; Churchill and Trinkaus, 1990). Some of these functional interpretations have been rejected or retracted (e.g., Lieberman and Crelin, 1971 versus Arensburg *et al.*, 1990; Trinkaus, 1977 versus Churchill and Trinkaus, 1990; Trinkaus, 1984a versus Trinkaus and Tompkins, 1990), others modified (e.g., Musgrave, 1971 versus Stoner and Trinkaus, 1981) and others remain debated (e.g., Smith, 1983; Rak, 1986; Trinkaus, 1987; Smith and Paquette, 1989). Yet, all of them have led to interesting hypotheses and further research into Neandertal functional morphology. These have been supplemented by dental attrition and paleopathological analyses (e.g., Ryan, 1980; Ogilvie *et al.*, 1989; Brennan, 1991; Trinkaus, n.d.b.). Most importantly, these studies have documented beyond a doubt that while there are numerous functional similarities between Neandertals and modern humans, there are also clear differences, ones that go beyond simple contrasts in musculo-skeletal massiveness (see Trinkaus *et al.*, n.d.).

The second trend has been an increasing integration of Paleolithic archaeology with human paleontology. There had always been some communication between these two related fields (more than similar concerns with chronology), but little of it had taken the form of explicit attempts at correlations between the behavioral inferences derived from the two prehistoric records, one archaeological and the other paleontological. This trend started as attempts to use the Middle Paleolithic archaeological record to explain human biological changes (e.g., Brace, 1962; Brose and Wolpoff, 1971), and has led to efforts to integrate the inferences from both human fossils and the associated Paleolithic archaeological record as they related to specific behavioral complexes (e.g., Trinkaus, 1986, 1989b). In these, a general correlation had been assumed between the Neandertals and the Middle Paleolithic and between early modern humans and the Upper Paleolithic (appropriately qualified to some extent [e.g., Trinkaus, 1986, 1989b]).

Yet, it is now known that Middle Paleolithic technology emerged in Europe before the appearance of "classic" Neandertals (Tuffreau and Sommé, 1988; Rigaud, 1989), that late western European Neandertals were associated with early Upper Paleolithic assemblages (Lévêque and Vandermeersch, 1980), and that central European and Near Eastern early modern humans were associated with Middle Paleolithic assemblages (Vandermeersch, 1981a; Trinkaus, 1984b; Smith and Trinkaus, 1991). These realizations place restrictions on using behavioral inferences from the Middle Paleolithic archaeological record as a basis for understanding Neandertal morphology. Yet, they have also been used to question the validity of any behavioral contrasts between Neandertals and modern humans (Tillier, 1989; Wolpoff *et al.*, 1991).

Even though these reservations are legitimate and raise important interpretive issues, they also hark back to the ongoing "Behavioral

Pre-Sapiens" perspective : can we legitimately propose that the Neandertals (or any other late archaic humans) were behaviorally different from ourselves? As a consequence, and by extension, the foundations of those paleontologically-based behavioral inferences have been questioned. Yet, these extreme reservations appear more as general, *a priori* dismissals of any functional analysis of paleontological remains, rather than as serious critiques of clearly proposed and substantiated interpretations. They raise, once again, the two issues presented above : 1) can we make reasonable inferences concerning changes in past human behavioral patterns based on functional interpretations of human paleontological remains, and 2) it is appropriate to assume that there may have been significant differences in the habitual behaviors of past human groups?

Bones and Behavior

The interpretation of behavior from paleontological morphology is based on the application of uniformitarian principles from modern humans and other mammals to the fossil record. These include bone biomechanics, respiratory physiology and thermal regulation, dental attrition, and pathological alterations. Before each is examined, a few principles need to be reviewed.

First, it is not possible to state the actual, or absolute, behavioral patterns of prehistoric human groups from their fossil remains or their discarded material remains (the archaeological record). We do not have Paleolithic Pompeiis, and only in extremely rare cases can we even determine such factors as probable cause of death. What we can assess with reasonable reliability is the degree of behavioral difference between a paleontological sample and either another paleontological sample or modern human samples. Ideally, we would like to have modern human reference samples of known behavioral patterns, against which we can compare both late archaic (Neandertal) and early modern human samples. In any case, what is assessed is the *amount of difference in behavior* between the two groups with respect to the feature investigated.

Secondly, it is unlikely that the ranges of potential behavior between any two human groups, or the basic capabilities of the average individuals in the groups, were significantly different. However, the *frequencies* with which different behaviors were performed can be quite pronounced. To take an extreme example, chimpanzees and modern humans have essentially the same ranges of locomotor behavior, from full bipedalism to brachiation, but no one would argue that the habitual locomotor behaviors of these two closely related species are the same. This is important, since small changes in the frequencies of specific behaviors can have significant effects on bone mass and shape (Matsumura and Okada, 1987; Lanyon, 1990) and on the rates of wear, malformation or degeneration of biological structures (Radin, 1972; Serink *et al.*, 1977; Goodman *et al.*, n.d.). Therefore, any behavioral inferences from morphological differences will most likely represent differences in *habitual behavior* patterns, ones which nonetheless might be pronounced.

Third, since it is differences in the *frequencies* of behaviors which are of interest, all analysis must consist of probabilistic, or statistical, comparisons of relevant factors between samples. Given the close relationship between Neandertals and modern humans, whatever their phylogenetic relationships, it is likely that the ranges of variation in most features of interest will overlap. However, there may exist highly significant differences between the samples, and it is that probabilistic degree of difference which is of interest, not whether there is an overlap in their ranges of variation.

Such statistical analyses ideally require, of course, adequately large samples of both fossil hominids and recent humans. It is unlikely that we will ever have fossil samples of sufficiently large size and completeness for temporally and geographically restricted groups of hominids. However, statistical techniques exist which permit the probabilistic evaluation of the differences between small samples or the comparison of individual data points to larger reference samples. Furthermore, all samples should be defined based on the problem involved, and all consequent results (as in all statistical or paleontological analyses) are, by their very nature, dependent upon the sample composition employed, modifiable as new data become available, and providing only relative assessments of the available morphological patterns.

Fourth, the degree to which morphological differences are due to genetic effects of little behavioral significance, such as pleiotropy and phylogenetic baggage, should be assessed. It is difficult to assess skeletal pleiotropy in living populations and much more so in fossil samples. The only probable case currently known involves hallucial and pollical interphalangeal proportions, in which the hallucial pattern is likely to be secondary to the pollical one (Trinkaus, 1984c). Other possible pleiotropic effects must remain unknown or, such as this one, merely postulated. However, since possible intercorrelations between traits can be tested and accounted for in analyses, introduced biases from pleiotropy are likely to be minimal. Phylogenetic baggage, or the persistence of traits that have little behavioral implication for groups like the Neandertals, are more relevant. They are also more amenable to consideration. First, the growing Middle and Lower Pleistocene *Homo* fossil record is allowing us to assess the nature of the morphological changes that led up to the Neandertals and thereby identify possible plesiomorphies (e.g., Trinkaus, 1988). Second, many of the features involved are developmentally and degeneratively plastic (see below), and hence unlikely to be maintained in their condition without similar behavioral patterns. Third, many of the features are energetically costly (e.g., massive musculo-skeletal features), and hence selectively disadvantageous unless maintained by stabilizing selection; they will therefore reflect current selective pressures and not be merely phylogenetic baggage from earlier hominids. And fourth, those features which are perceived as being selectively neutral and of little behavioral significance are not likely to be those used for the functional morphological analysis of fossil hominid samples.

There have been attempts to use the developmental morphology of the Neandertals to assess the genetic (or phylogenetic) significance of traits (e.g., Tillier, 1984, 1988; Tompkins and Trinkaus, 1987; Minugh-Purvis, 1988). However, few fossils which are sufficiently complete for functional analysis exist for individuals before the age of about 3 years. Yet, it is during those first few postnatal years that most selection is takes place, and the skeleton is most responsive to stress and activity patterns at that time. Therefore, the presence of functionally relevant contrasts between Neandertal children and those of modern humans does not necessarily mean that they are highly genetically determined or of little relevance to behavioral inferences about the Neandertals; in fact, their presence can only reinforce interpretations based on the larger and more complete samples of adult remains.

Ideally, comparisons should employ those features which are known to be produced by developmental and degenerative processes that affect all individuals. However, given the probable roles of directional and stabilizing selection on Pleistocene hominid morphology, most features which can be reasonably related to functional aspects of the organism should be amenable to such behavioral analyses.

Therefore, the behavioral interpretation of Neandertal remains involves the *comparative* analysis of *statistical distributions* of morphological features, as related to *habitual patterns* of behavior during the life cycles of the *populations* involved. It should therefore be possible to ascertain the patterns of behavioral change between phases of hominid evolution and thereby investigate the evolution of the Hominidae rather than just a sequence of morphological forms.

1. Bone Biomechanics

The functional interpretation of bone as a structural system assumes that bone, unless nutritionally or epidemiologically compromised, will provide the necessary mechanical structures to perform habitual activities and to resist habitual mechanical forces placed upon it. The former include primarily the osteological portions of articulations, especially diarthrodial ones, as well as structures for muscle and connective tissue attachment. The latter includes protective structures, such as the internal neurocranium, the orbits and (to a lesser extent) the thoracic cage. However, it consists mostly of structures, such as much of the facial skeleton, the external neurocranium, the vertebrae and rib cage and appendicular skeleton, which provide levers and mechanical structures for the generation of bodily movement and mechanical resistance of habitual forces placed upon it by muscle contraction and body momentum.

The basic form of the skeleton is developmentally determined by the individual's genotype (Ascenzi and Bell, 1972; Lanyon, 1990). However, abundant and ongoing research has documented the marked potential for plasticity of the vertebrate (including human) skeleton (e.g., Arkin and Katz, 1956; Riesenfeld, 1966; Houston and Zaleski, 1967; Tschantz and Rutishauser, 1967; Liskova and Hert, 1971; Doyle, 1977; Goodship *et al.*, 1979; Katz, 1980; Lanyon, 1980, 1982, 1990; Lanyon *et al.*, 1982; Matsumura and Okada, 1987). Most of the research has emphasized the nature, degree, and causes of changes in diaphyseal dimensions and morphology in response to altered mechanical environments. Other studies have documented the degree to which muscular attachments can affect osteological morphology, whereas others have documented differential metaphyseal deposition in response to altered articular forces and the resultant changes in epiphyseal orientation.

This research combines with the abundant literature on human squatting morphology (see Trinkaus, 1975b and references therein) and cranial deformation (Anton, 1989 and references therein) to illustrate the degree to which human diaphyseal, articular and craniofacial morphology can be altered by modest changes in habitual behavioral patterns. In addition, two cases of Neandertal post-traumatic remodeling (Schwalbe, 1901; Trinkaus, 1983a; Trinkaus *et al.*, 1990) plus levels of upper limb bilateral asymmetry (Trinkaus *et al.*, 1990) document the degree to which the observed morphology of these Pleistocene hominids, as with modern mammals, is largely determined by levels and patterns of habitual biomechanical force through the skeleton. The genetically determined growth trajectories are thus modified through development, with continued alteration in adulthood.

Consequently, it is possible to employ a few basic principles in the interpretation of paleontological osteological morphology. First, the quantity and distribution of cortical bone in diaphyses will reflect the habitual levels and patterns of mechanical forces through those tubular structures. In general, genetically determined growth processes and subsequent remodeling combine to keep strain levels from habitual activity within an acceptable range with a minimum amount of osteological material. The amount of such material in diaphyses can be approximated paleontologically through geometric analyses of diaphyseal cross-sections taken at specified percentages of diaphyseal beam length (e.g., Endo and Kimura, 1970; Lovejoy and Trinkaus, 1980; Trinkaus and Ruff, 1989a) (fig. 5), or less accurately through diaphyseal external diameters (e.g., Twiesselmann, 1961; Trinkaus, 1976). Secondly, the orientations of trabecular bone in select regions will reflect the orientations of habitual forces through those regions of the skeleton (Smith, 1962; Lanyon, 1974). This is assessable through finite element analyses of trabeculae in three-dimensions, or on carefully oriented two-dimensional radiographs of the bones (e.g., Heller, 1989). Third, the orientations of articular surfaces will reflect the habitual directions of joint reaction forces across those joints, with the joints being oriented so as to minimize shear stress across the articular surfaces. Given appropriate knowledge of joint reaction force patterns through any given joint system, plus the basic similarity of the subchondral bone morphologies of Neandertal and modern humans, it is possible to use articular orientation and proportions to assess habitual differences in joint loading positions (e.g., ulnar trochlear notch orientation [Trinkaus, 1983a, n.d.b.] and scapular glenoid proportions

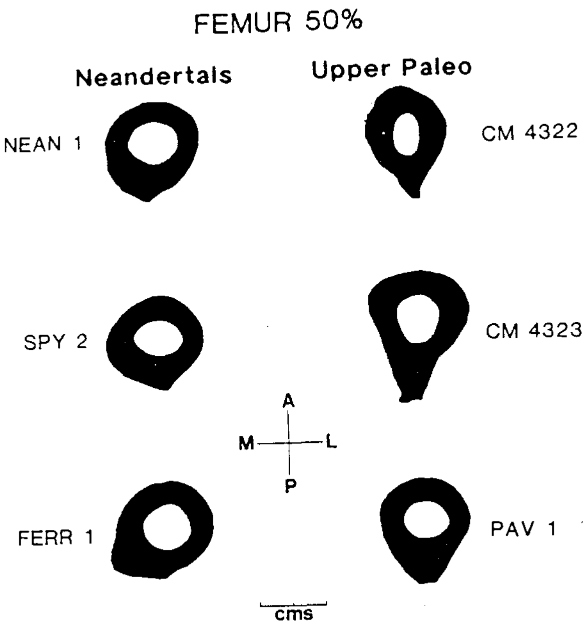

Fig. 5. Reconstructed cross-sections of the femoral midshaft, providing the subperiosteal and endosteal contours, for European Neandertals (Neandertal 1, Spy 1 and La Ferrassie 1) and early Upper Paleolithic humans (Cro-Magnon 4322 and 4323 and Paviland 1).

[Churchill and Trinkaus, 1990]). And fourth, the distribution of cortical bone in the facial skeleton, as in the diaphyses, will reflect the nature of forces through the facial skeleton during mastication, bearing in mind that the facial skeleton also performs respiratory (oral and nasal) and protective (orbital and neurocranial) functions. Clearly the patterns of force in each case, being generated by multiple structural and behavioral features, will remain complex. However, and more importantly, emphasis on the differences between samples will provide greater information concerning the forces responsible for the changes between the samples.

2. Respiratory Physiology and Thermal Regulation

Respiration, as a primary physiological function of the organism and one of the few that impinges directly upon the skeleton (e.g., the nose and the thorax), places demands and constraints upon the skeletal morphology. Lung volume, as determined developmentally by altitude and (probably) activity levels, determines aspects of thoracic morphology, including sternal length and rib curvature (Beall, 1982; Malhotra, 1986; Eckhardt and Eckhardt, 1987). Nasal morphology (fig. 6), which is related to thermal adaptations and the related aspect of moisture retention through respiration (Courtiss *et al.*, 1984), is correlated with climatic parameters and (probably) activity levels (Weiner, 1954; Wolpoff, 1968; Carey and Steegmann, 1981; Crognier, 1981). Furthermore, nasal morphology is developmentally primary in the facial skeleton (Chierici *et al.*, 1973; Steegmann and Platner, 1968; Anton, 1989), and biomechanical considerations of facial morphology relating it to mastication must take nasal variation into account.

In addition, bodily thermal regulation is mediated through body mass and proportions, including overall body mass relative to stature,

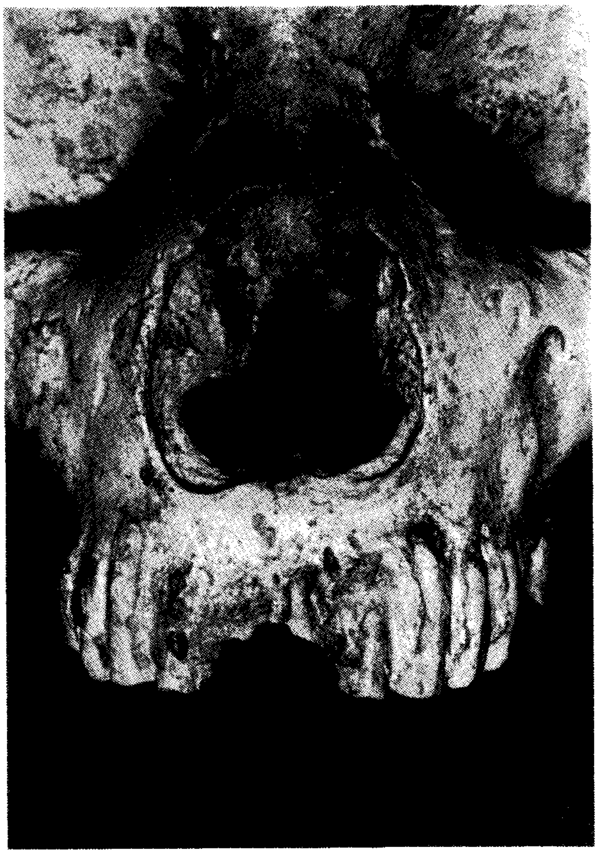

Fig. 6 Anterior view of the Forbes' Quarry 1 nasal aperture, showing the broad aperture, prominent turbinate crests and sharply angled interior margin characteristic of Neandertals.

head size, limb to body core proportions and limb segment proportions (Trinkaus, 1981; Beals *et al.*, 1984; Holliday and Trinkaus, 1991; Ruff, n.d.), and it is likely that at least some aspects of Neandertal morphology are related to such considerations (Badoux, 1965; Trinkaus, 1981; Ruff, n.d.). Furthermore, aspects of body mass and proportions are known to be plastic during development in mammals (Weaver and Ingram, 1969; Riesenfeld, 1973; references in Trinkaus, 1981). Although the extent to which observed patterns are developmentally determined remains uncertain, the potential for such developmental alterations under thermal stress reinforces these climatic interpretations of the observed proportions.

3. Dental Attrition

The enamel and dentin of teeth wear down during the lifetime of an individual as a result of contact with abrasive materials in the diet and use of the teeth (primarily anterior ones) as a grasping devise on hard abrasive materials (Molnar, 1971). The rate and nature of molar and premolar wear is determined primarily by the level of abrasive grit in the diet (Gordon, 1990). In the absence of dental lesions (caries, abscesses, tooth loss), it will be relatively uniform in an environmentally homogeneous population (Miles, 1963; Lovejoy, 1985). The rate and patterns of anterior tooth wear will be a combination of dietary abrasion plus the extent to which the anterior teeth are employed in non-dietary activities (Wallace, 1975, and comments therein). Most anterior teeth will wear in a similar pattern, becoming relatively flat in the occlusal plane as the crown is partially worn away and then becoming rounded labially and lingually as the enamel wears away and resistance to marginal rounding is lost (Smith, 1976; Wallace, 1975).

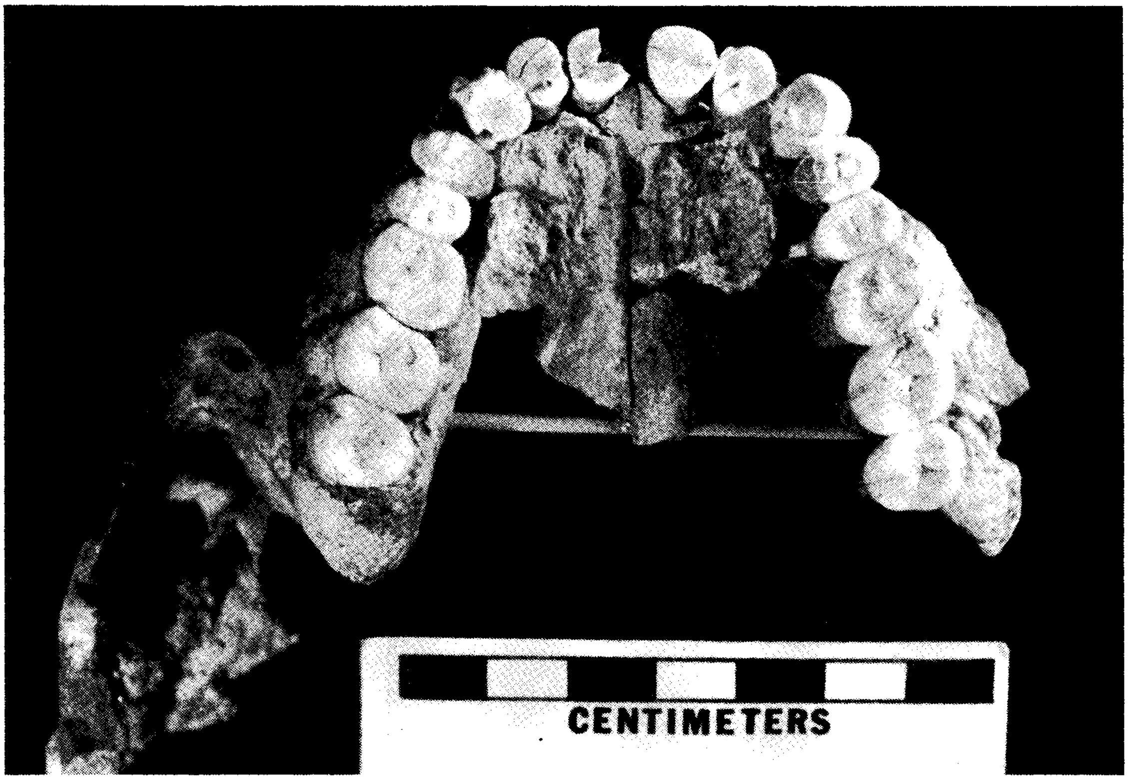

Fig. 7 Occlusal view of the Shanidar 2 maxillary dentition, showing the pronounced wear on the shovel-shaped anterior teeth relative to that on the associated posterior teeth.

In a behavioral sense, therefore, dental attrition can be employed in two ways. First, the quantified microscopic occlusal wear of the posterior dentition (e.g., Gordon, 1990) can provide indications of dietary differences, despite undoubted environmental differences between populations. Second, the extent of anterior wear, *relative to* the posterior wear, will provide an indication of the degree to which the anterior teeth were used for more than dietary purposes (e.g., Trinkaus, n.d.b.) (fig. 7). However, the comparison of anterior dental wear to posterior wear must be adjusted for relative tooth size, since Neandertals have larger anterior teeth (compared to cheek teeth) than most modern humans (Trinkaus, 1983a).

It is not the degree of wear present on individual teeth that is important (all humans can achieve the same degree of wear on a given tooth given sufficient time and abrasion); it is the amount of wear on the anterior teeth *relative to* that on the posterior teeth (adjusted for tooth size) which provides an indication of similarities and differences in the amount of anterior tooth wear greater than that which would be expected from the dietary intake of the individual. The differences between samples in relative anterior dental attrition will be more apparent in older individuals with more advanced dental wear, and all younger individuals will have similarly low levels of both anterior and posterior wear. For this reason, it is important to compare the *rates* of anterior versus posterior wear across samples and not merely to compare individuals who might have been of very different ages at death.

Ideally (see Trinkaus and Thompson, 1987), it will be possible to assign reasonably accurate ages at death to the specimens in different samples. This would add the possibility of providing an average absolute rate of wear, rather than merely the relative rates of wear provided by anterior to posterior wear comparisons.

4. Developmental and Degenerative Pathological Alterations

Recent research in modern human and skeletal biology (Goodman *et al.*, 1988; Goodman and Rose, 1990) has demonstrated the potential of various stress indicators for providing insights into the morbidity of past human groups. Since differential morbidity translates into differential mortality, which can have profound effects on the differential survival of human groups (Zubrow, 1989), the analysis of stress indicators in past human groups becomes important.

The resultant paleopathological analyses on samples of fossil human remains (e.g., Trinkaus and Zimmerman, 1982; Ogilvie *et al.*, 1989; Brennan, 1991), in addition to those that merely diagnose and list lesions (e.g., Dastugue, 1960; Dastugue and Lumley, 1976; Trinkaus, 1983a, 1985), divide the lesions into two categories : developmental and degenerative. The former, which include primarily dental enamel hypoplasias (fig. 8) and transverse (Harris) lines, can be scaled to the age of the individual but are limited to events from birth to early adolescence. The latter, which include all lesions that leave traces on hard tissue (but consist most commonly of trauma and degenerative joint disease), can provide indications of overall levels of stress throughout life. However, degenerative lesions need to be scaled to the age at death of the individual so as to provide indications of differential levels of risk (Lovejoy and Heiple, 1981), since longer lived individuals will have had more opportunity to accumulate lesions.

Most of the paleopathological comparisons between Neandertals and modern humans have focused on dental enamel hypoplasia and trauma. Transverse lines remodel during life and are poorly preserved through fossilization and specimen preparation, and degenerative joint disease is difficult to assess without large samples of associated skeletal remains. Dental enamel hypoplasias, however, remain until the tooth enamel is worn away, and evidence of trauma can be clearly identified and tabulated even though its analysis suffers as well from small samples, unassociated remains and imprecise ages at death of the individuals.

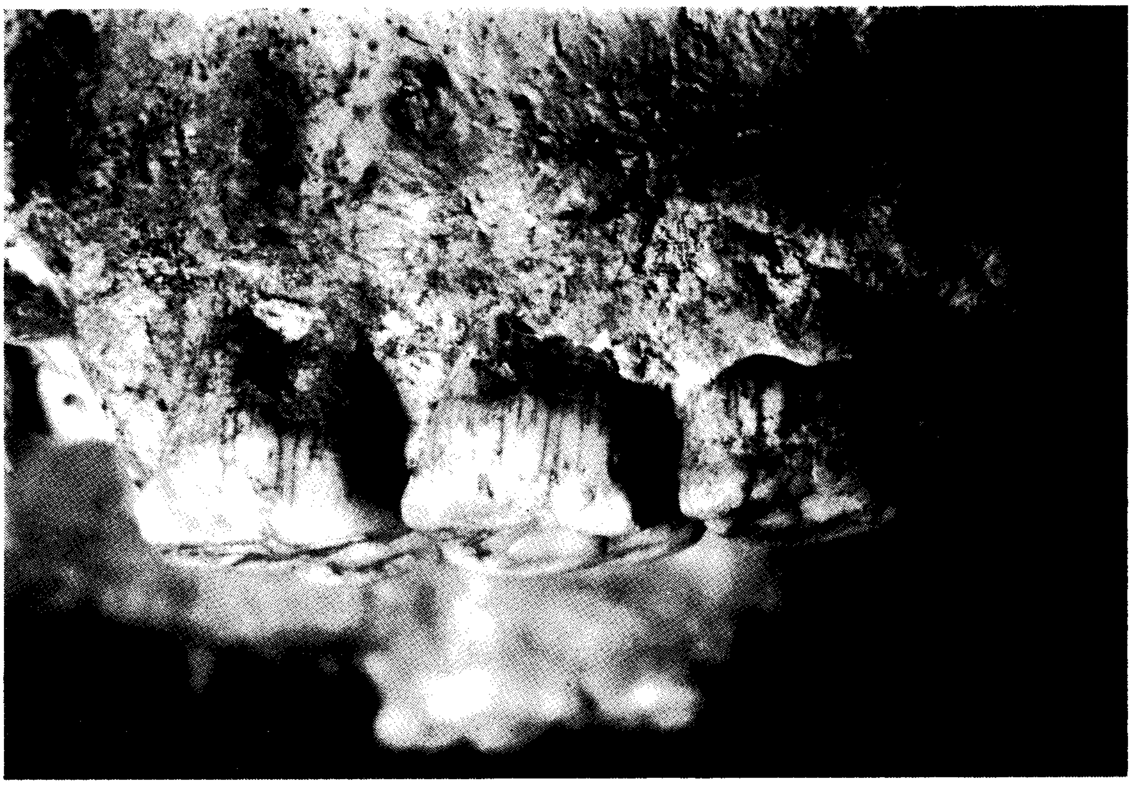

Fig. 8 Buccal view of the Saccopastore 1 left maxillary molars, illustrating its pronounced dental enamel hypoplasia. Note that the degree of hypoplastic alteration increases from the M1, to the M2, to the M3, as with the Neandertal sample as a whole.

As with most of these behaviorally related comparisons, it is the differences between the *patterns within samples* that are important, not the presence or absence of given lesions in the fossil samples of interest. For these reasons, the analysis of morbidity in paleontology should employ the largest samples available. It should also focus on patterns in the lesions, rather than on the presence/absence of the lesions or even the overall frequency of them. For example, the frequency distribution of dental enamel hypoplasias across the dentition among the Neandertals, which is the opposite of that found among modern humans (increasing, rather than decreasing, in incidence in the later calcifying teeth [Ogilvie *et al.*, 1989]), is much more significant than even the high frequency of the lesions in Neandertal samples.

It must be kept in mind that all lesions on fossil material indicate survival of the stressful episode, since all identifiable lesions represent tissue repair and/or additional growth of the structure in question. It is therefore possible to have lower levels of lesions indicate greater morbidity, associated with very high mortality. This, however, is rare except in cases of chronically severely stressed populations, ones that are unlikely to have persisted for long periods of time in the Pleistocene.

It is also important to note that the precise etiology of each lesion is not necessarily relevant. Whether a specific dental enamel hypoplasia, for example, was caused by nutritional imbalance, disease or localized trauma (or others, see Goodman and Rose, 1990), it represents a period of morbidity for the individual, which will effect that individual's potential to contribute to the survival and continuation of the population. Although indirect arguments can be made for one cause being the probable most common one (e.g., Ogilvie *et al.*, 1989), the general level of stress, and its implications for populational morbidity, remains the same.

5. Putting the Body Together

The individual means of assessing similarities and differences in the behavioral patterns of fossil and modern samples can provide insights into regional anatomically based behavioral patterns or overall levels of activity or stress. However, given the limited range of developmental and remodeling responses for bone and teeth, it is possible to have multiple factors influencing single structures. This was mentioned with respect to the nasal morphology, as influenced by respiratory demands, relative to facial structure, as influenced by masticatory biomechanics. It also occurs with respect to trauma, in which post-traumatic remodeling of otherwise normal bone can seriously alter the biomechanical implications of the observed morphology. Similarly, changes in body proportions as an aspect of thermal adaptation can modify the moment arms of body mass and muscles, affecting both the mechanical advantages of the muscles and the forms of the structural reinforcements of associated bones. For this reason, it becomes necessary to sort out the relative importances of the different parameters affecting the observed structures. Naturally, as our knowledge progresses, we start by formulating monocausal interpretations of observed morphological differences, and then modify them as our understanding of associated structures and other physiological systems improves. Given the relative recency of the efforts to apply uniformitarian principles to the functional interpretation of the later Pleistocene paleontological record, it is to be expected that many of our interpretations appear simplistic. That is already changing.

Human Paleontology versus Paleolithic Archaeology

Following these general principles, it should be possible to generate hypotheses regarding the patterns and degree of change in biologically relevant behavioral patterns between Neandertals (or other late archaic humans) and modern humans. However, as pointed out above, a late western European Neandertal is associated with an early Upper Paleolithic industry (the Castelperronian), whose elements indicate behavioral constrasts with the Middle Paleolithic and affinities to other early Upper Paleolithic industries (Farizy, 1990). In addition, in central Europe and the Levant, there are cranio-facially robust early modern humans associated with Middle Paleolithic industries, which, so far in the Levant, have appeared similar to those associated with Near Eastern late archaic humans (Shea, 1989; but see Jelinek, 1982). Furthermore, the behavioral interpretations from the Neandertal fossil record have not always corresponded to those proposed by Middle Paleolithic archaeologists.

These problems appear serious to some (e.g., Tillier 1989; Wolpoff *et al.*, 1991) and have consequently led them to reject most behavioral inferences made from human fossil remains. Ideally one would hope that the behavioral inferences from the human paleontological and Paleolithic archaeological records would correspond closely, since the hominids whose remains are being studied are, presumably, the same ones that were leaving behind the debris that makes up the archaeological record. However, some non-correspondance is not surprising. Indeed, the degree of correspondance that is currently obtainable between behavioral inferences from Neandertal anatomy and the Middle Paleolithic archaeological record (e.g., Trinkaus, 1986, 1989b) is heartening. The other discordances occur around times of evolutionary transition (the latest Neandertals or the earliest modern humans in the region in question), at which times it is expected to find additional complexities.

The discordances between behavioral inferences made from Neandertal biology and the Middle Paleolithic record are undoubtedly due largely to two factors. First, our potential behavioral interpretations of fossil anatomy must remain on a general level and be focused on *rates and patterns of change* rather than on "reconstructing" behavior. There will therefore always be a certain degree of generalization regarding the inferences that can be made from the fossils.

Secondly, although there are uniformitarian principles established for the interpretation of human paleontological remains, comparable uniformitarian principles for the interpretation of Paleolithic archaeological materials remain more elusive.

Technology can be analyzed with similarly robust techniques, but human behavior, even as documented in the Paleolithic archaeological record, consists of far more than technology. Furthermore, given the uniqueness of many human behaviors, the analysis of evidence for similar ones in the Paleolithic archaeological record must depend upon empirical generalizations from modern humans (but never on direct analogies with specific human groups). Even if these empirical generalizations arrive at revealing universal patterns for modern humans, their application to the Middle Paleolithic assumes, rather than demonstrates, that the basic behavioral/adaptive patterns of those prehistoric humans fell within the range of variation of modern humans. There is sufficient evidence, both paleontological and archaeological, to question whether Middle Paleolithic (or earlier) hominids were indeed so behaviorally similar to ourselves. Furthermore, such assumptions, implicit or explicit, make any such interpretation part of the "Behavioral Pre-Sapiens" approach with its nonevolutionary implications.

All of these problems are currently being addressed in both human paleontology and Paleolithic archaeology. Furthermore, the current situation, with incomplete correspondence (or incomplete discordance) between behavioral inferences from the paleontological and archaeological records, provides the ideal scientific forum for progress. There are sufficient behavioral inferences from each sphere to provide hypotheses to be tested against additional data from its own area and, especially, from the other area. Discordances should be seen as opportunities to further our understanding, rather than as occasions to reject that which one does not understand.

Conclusion

These historical and methodological considerations indicate that we have come a long way from the early attempts to describe Neandertal behavior, in which they were seen as one more primitive stage in human evolutionary progress. Despite the limitations of sample size, fossil preservation, and the applicability of analytical techniques to paleontological remains, it is increasingly feasible to make reasonable statements regarding the behavioral evolution which took place between the Neandertals and modern humans. However, this will be possible only by rejecting the "Behavioral Pre-Sapiens" approach which continues to dominate much of paleoanthropology. It will be possible only once paleoanthropologists recognize the probabilistic and scientific nature of the endeavor and, using the materials and hypotheses currently available, continue to explore new ways in which we can apply uniformitarian principles to the understanding of past human evolutionary patterns.

Acknowledgments
I would like to thank Dr. Michel Toussaint and Dr. J.-M. Cordy for inviting me to participate inthe symposium on "Cinq millions d'années, l'aventure humaine" and to contribute to this volume. This paper is based in part on ongoing research since 1973, which has been funded by the Wenner-Gren Foundation, the National Science Foundation, the L.S.B. Leakey Foundation, Harvard University, the University of New Mexico, and the Centre National de la Recherche Scientifique; to all I am grateful. Dr. K.M. Trinkaus kindly provided helpful comments during the preparation of this paper.

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