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THE EVOLUTIONARY ORIGINS OF THE NEANDERTALS OR, WHY WERE THERE NEANDERTALS ?

by
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INTRODUCTION

This contribution and the set of papers which it introduces celebrate the centenary of one of the most important discoveries in the history of paleoanthropology. This is, of course, the paleoanthropological discovery at the Grotte de Bec-aux-Roches (or Betche-aux-Rotches) near Spy: the discovery, in secure archeological and geological contexts, of the partial skeletons of two adult Neandertals plus isolated fragments of other individuals (de PUYDT and LOHEST, 1887; FRAIPONT and LOHEST, 1886, 1887). In the one hundred years since that discovery, we have immensely increased our knowledge of those prehistoric humans, the Neandertals, of their biology, behavior, environmental context and distribution in space and time (SMITH and SPENCER, 1984). We have also come a very long way from having to document their existence as non-pathological archaic humans, and we are seeing them increasingly as an evolutionarily successful, though currently extinct, group of prehistoric humanity (TRINKAUS, 1986a, b). However, many issues concerning their evolutionary origins, their disappearance, their behavior and their role in the evolution of the genus *Homo* remain unresolved. Ongoing research is helping us to clarify many of these issues, but as past questions are resolved, new ones appear and our quest to understand the human evolutionary phenomenon we call "the Neandertals" continues. It is in this context that these introductory remarks and the accompanying papers are presented. I am sure that the individuals we know as the Spy Neandertals would be flattered if they knew of the attention they received at this conference and in this publication.

The focus here is upon the evolutionary origins of the Neandertals, or "L'Avènement de l'Homme de Néandertal". In considering the evolutionary origins of the Neandertals, several general questions emerge. First, what are the characteristics that are distinctive of the Neandertals, as opposed to ancestral traits and those shared with modern humans and non-

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Neandertal late archaic humans? Second, from whom did the Neandertals evolve? A corollary of this question is: where did they first evolve, or emerge, and to what extent was there geographical variation in the processes and chronology of their emergence? And third, what were the evolutionary processes, that is, biological and behavioral processes, which led to their emergence? In other words, "Why were there Neandertals?"

In this section, papers by CONDEMI, TILLIER and, to a lesser extent, ROTH and ORBAN *et al.* address the question as to the distinctive, or automorphous characteristics of the Neandertals, papers by PIVETEAU and CONDEMI, and CONDEMI review fossil samples relevant to the emergence of the Neandertals in Europe, and papers by BAR-YOSEF and CONDEMI present one interpretation relevant to the ongoing controversy as to the origins of the Near Eastern Neandertals. In these introductory comments, I am primarily concerned with a presentation of the issues relevant to our understanding of Neandertal origins.

THE NEANDERTALS

I am considering the Neandertals to have emerged sometime during the late Middle to early Upper Pleistocene. Since the evolutionary process of their emergence from more archaic members of the genus *Homo*, at least in western Europe, appears to have been gradual in tempo and mosaic in nature (see below; HUBLIN, this volume), a more precise determination of their time of appearance is probably impossible. Geographically, they were distributed, at one time or another during the early Upper Pleistocene, across Europe, south of approximately 52°N latitude, eastward at least as far as central Asia, and in the Near East. At approximately the same time period, there were other late archaic humans in eastern Asia, Australasia and Africa, members of the same grade of human evolution but representatives of different geographical clades. The extent of genetic separation of the Neandertals from these other members of the same grade remains open to question; it is best to consider members of these different clades as subspecies of the same species, possibly with relatively steep clinal gradients between the currently identified geogaphical groups but without any real genetic isolation between neighboring groups.

Morphologically, the Neandertals share features with both more archaic members of the genus *Homo* and modern humans, as well as possessing several unique features or combinations of features. They are most similar to other late archaic humans but are clearly sufficiently morphological distinct from them to be considered separately, regardless of their actual phylogenetic relationship to other hominid groups. Since one of the goals of this discussion is to assess what features of them are distinctive, a morphological definition is inappropriate at this point, but should emerge from the discussion of their characteristics of various phylogenetic polarities.

The Neandertals are usually included within *Homo sapiens*, as are most later Middle and early Upper Pleistocene archaic humans. Recently, there have been suggestions that they should be separated on a specific level and referred to as "*H. Neandertalensis*", given the morphological contrasts between them and subsequent populations of "anatomically modern" humans. Such a move would accentuate the differences between them and more recent humans, perhaps justifiably. However, it would also pose a series of questions regarding their taxonomic relationships to contemporaneous non-Neandertal and preceding populations of late archaic humans, relationships that will certainly defy definition through the non-evolutionary nature of the Linnean taxonomic system. Much as the Middle Pleistocene *H. erectus*/ archaic *H. sapiens* "boundary" has led to unresolvable nomenclatural debates given the apparent chronospecific relationships of these two groups and the mosaic nature of morphological change evident in the hominid fossil record (HUBLIN, 1986; STRINGER, 1984), so are nomenclatural distinctions, whether at the specific or the subspecific level, for later archaic humans likely to remain unclear and debatable given the geographically complex nature of later Pleistocene human evolution.

WHAT IS SPECIAL ABOUT THE NEANDERTALS?

Discussions of the evolutionary emergence of the Neandertals have focused primarily on geographical sequences of morphology, as represented in often scarce and predominately cranio-facial later Middle and initial Upper Pleistocene fossils, so as to determine their phylogenetic origins and the roles of preceding populations in those origins. Any resolution of the phylogenetic issues concerning Neandertal origins, as well as answers to the question posed above, namely "Why were there Neandertals?", requires a determination of what is special about the Neandertals. This must be done primarily with respect to their Lower and Middle Pleistocene predecessors and archaic contemporaries. Comparisons to anatomically modern, humans, who largely succeeded them in time, are of concern primarily to determine what traits were emerging as part of general later Pleistocene hominid evolution, as opposed to those traits that were unique to the Neandertals or generally ancestral for later Pleistocene humans. In other words, what were 1) the uniquely derived characteristics, or the autapomorphies, of the Neandertals, 2) their ancestral traits, or plesiomorphies, and 3) their traits derived in common with modern humans, or synapomorphies with modern humans.

This exercise assumes, of course, that it is appropriate to identify derived versus ancestral, shared versus unique characteristics between samples of what is best considered as an evolving lineage of chronospecies with variable amounts geographic subspecific differentiation. Given that many of the expected differences between the samples will be in terms of trait frequencies, determination of polarity and phylogenetic usefulness of many traits is likely to be difficult. Yet, application of this approach to these fossil hominids should help to organize the data and highlight areas of uncertainty requiring further analysis and conceptual reformulation.

It should also be kept in mind that most discussions of Neandertal morphology assume that the Neandertal morphotype (or primary range of variation) is best represented by the "classic" western European Neandertals, especially those from the sites of La Chapelle-aux-Saints, La Ferrassie, La Quina, Spy, and, secondarily, Circeo and Neandertal. The dearth of associated skeletons for early last glacial central and eastern European Neandertals means that those remains are frequently given less consideration in evaluations of Neandertal morphology. In my assessments here, I use, to the extent possible, data from the full Neandertal range, even though the history of discoveries and research lend an inevitable bias toward the western European material.

Neandertal Autapomorphies

There is a limited number of definite autapomorphies among the Neandertals. They include primarily features of the cranial base, especially of the occipito-mastoid and temporal regions. However, even these must be employed cautiously, since aspects of them may represent merely reductions of some features associated with general cranial robusticity in earlier members of the genus *Homo*.

The clearest of their autapomorphous traits are those of the occipito-mastoid region (CONDEMI, this volume; HUBLIN, 1978a,b, 1980, this volume; SANTA LUCA, 1978). They include primarily their distinct, usually oval suprainiac fossae, their large juxta-mastoid eminences that usually extend below the tips of the mastoid processes and are separated from the mastoid process by a shallow sulcus, their tapering mastoid processes poorly separated from the petrous portion, and the presence of an anterior mastoid tubercle. These features of the mastoid process exist in the context of mastoid heights (from the Frankfurt horizontal) similar to those of recent humans (TRINKAUS, 1983a). They are combined with plesiomorphous traits of the occipital region, such as a continuous (although modest in size) transverse nuchal torus and the absence of a distinct external occipital protuberance (HUBLIN, 1978a, 1986, this volume).

These specific Neandertal traits, as well as the combination of automorphous and non-automorphous traits, occur with some variation in their degree of development in essentially all last interglacial and early last glacial European archaic human remains preserving the appropriate regions. In the Near East, they are more variable in their expression, and that degree of expression of individual traits does not appear to be chronologically ordered. For example, tapering mastoid processes (with or without anterior mastoid tubercles) are present on Shanidar 1 and Tabun 1 but are absent from Shanidar 2, Shanidar 5 and Amud 1.

It should be kept in mind, however, that juxta-mastoid eminences are generally robust in *H. erectus*, even though they are separated from the mastoid process by a deeper sulcus than among the Neandertals and do not always exend beyond the mastoid process tip (HUBLIN, 1978a; SARTONO, 1971; WEIDENREICH, 1943); is this a fundamentally different juxta-mastoid eminence morphology or a consequence of wider basi-crania in the context of less encephalization among *H. erectus* than among the Neandertals? Furthermore, suprainiac fossae do occur in recent humans, although the distinctive oval shape seen in mature and immature Neandertals is unknown or extremely rare among modern humans.

Several automorphous features of the Neandertal temporal region have been described, especially of the temporomandibular joint (TMJ) and external auditory meatus (EAM) (CONDEMI, this volume). Among the Neandertals, the TMJ has a mandibular (glenoid) fossa that is usually large, relative shallow, and poorly delimited anteriorly given their relatively flat and broad articular eminences. The articular tubercle is usually modest in size, although variable in size as it is among modern humans. The postglenoid process (posterior zygomatic tubercle) usually forms a significant part of the posterior wall of the mandibular fossa, rather than being a slight postero-lateral projection along the tympano-squamosal fissure. In addition, the EAM usually lies above the roof of the mandibular fossa, in the same horizontal plane as the zygomatic process of the temporal bone. Most of the other features that have been described as characteristic of the Neandertal temporal region appear to be plesiomorphous, variable and/or of uncertain polarity (CONDEMI, this volume).

Reconsideration of the fossil record and recent human variation, however, suggests that some caution is necessary in utilizing some of these traits as highly diagnostic of the Neandertals. The articular surfaces of TMJs are known to change shape and size in response to the altered stress trajectories associated with even modest levels of dental occlusal attrition (HINTON, 1979; HINTON and CARLSON, 1979; MONGINI, 1975), and the elevated level of dental occlusal attrition seen in most Neandertal adults suggests that a significant percentage of the observed morphology may be due to remodeling. Furthermore, at least three of the Neandertals with supposedly typical mandibular fossae, La Chapelle- aux-Saints 1, La Ferrassie 1 and Shanidar 1, experienced TMJ degenerative joint disease, which may well have altered their mandibular fossa configurations.

The size of the postglenoid process and its participation in the posterior wall of the mandibular fossa is usually pronounced among European Neandertals (HEIM, 1976; MARTIN, 1923; VALLOIS, 1969). It is variable but usually smaller among their European predecessors (CONDEMI, 1985, this volume; PIVETEAU and CONDEMI, this volume), but it is also variable in *H. erectus*, being small in some crania (WEIDENREICH, 1943, 1945), large but not projecting in other fossils (LEAKEY and WALKER, 1985; RIGHTMIRE, 1979), and large and projecting in others (LEAKEY and WALKER, 1985). Its phylogenetic polarity is therefore uncertain, the European Neandertals differing from their predecessors primarily in their frequency of large postglenoid processes. Furthermore, its role as the region of the posterior insertion for the TMJ fibrous joint capsule suggests that its degree of projection and mediolateral extent may be functionally correlated with the overall shape of the mandibular fossa and the nature of habitual stresses on the TMJ. Therefore, even if Neandertal postglenoid process morphology is indeed autapomorphous, it may be but one reflection of their overall TMJ morphology.

In addition, the vertical position of the Neandertal EAM relative to the zygomatic process does not differ significantly from that of some *H. erectus* specimens (SARTONO, 1971; WEIDENREICH, 1943). The extreme development of the supramastoid crest in *H. erectus* crania gives the impression, especially on isolated or incomplete temporal bones (RIGHTMIRE, 1979; von KOENIGSWALD, 1940; WEIDENREICH, 1943), that the EAM is well below the level of the zygomatic process, even though many *H. erectus* EAM vertically overlap their zygomatic processes. It remains unclear whether whatever difference in EAM position relative to the mandibular fossa roof may exist between Neandertals and earlier hominids is due to changes in EAM position, mandibular fossa depth or zygomatic arch morphology; I suspect that the latter two are more important.

Possible Neandertal Autapomorphies

Among the generally recognized Neandertal autapomorphies are features of the facial skeleton and the configurations of the occipital profile in posterior and lateral views. Other features, such as their dental proportions and limb segment proportions, have also been seen as autapomorphous. However, these features, or rather complexes of features, are best viewed differently, especially when they are dissected into their components.

One of the more obvious of the Neandertal morphological complexes to be considered an autapomorphy is their mid-facial prognathism. This complex consists primarily of an anterior projection of the dentition and nasal aperture relative to their lateral facial skeleton (TRINKAUS, 1983a, 1987). It includes a variety of secondary characteristics of the facial skeleton that are spatial and/or biomechanical consequences of their overall facial configurations; these include their posteriorly located (M2-M3) anerior zygomatic roots, large mandibular retromolar spaes, posteriorly located mental foramina, antero-laterally flattened zygomatic bones, absence of a zygomatico-alveolar notch, absence of a canine fossa, relatively low zygomatico-maxillary angles indicating a slightly more parasagittal orientation of the infraorbital region, relatively horizontal and projecting nasal bones, anteriorly projecting nasion relative to the lateral orbital or supraorbital margins, reduced supratoral sulcus above glabella, and large frontal sinuses restricted to the middle half of the supraorbital torus (HEIM, 1978; HUBLIN, this volume; RAK, 1986; SMITH, 1983; TRINKAUS, 1983a, 1987). The first three secondary characteristics are spatial consequences of the antero-posterior separation of anterior dental region from the zygomatic/anterior ramal (masticatory muscle) region; the remainder are biomechanical consequences of the changed stress-resisting abilities of the Neandertal face relative to those of their predecessors. However, it should be kept in mind that this morphotype, although characterizing Neandertal faces in general, obscures considerable variation within the sample, only some of which is temporally ordered.

Furthermore, and most importantly, many of these traits, although unique to the Neandertals or rare in other human groups, are largely secondary consequences of two basic features: 1) a maintenance of Middle Pleistocene total facial (or dental) prognathism, and 2) a posterior retreat of the masticatory muscle region, relative to both neurocranial and postcranial dimensions (SMITH and PAQUETTE, in press; TRINKAUS, 1983a). The former is merely a plesiomorphous trait, a maintenance of an ancestral pattern than can be documented back at least as far as early, *H. erectus*. The latter is most likely a synapomorphy with modern humans, a shared derived condition of a relatively posterior position of the zygomatic bone and associated anterior mandibular ramal margin. Given the reduced ability of the Neandertal zygomatic region to resist bending moments placed upon the face through anterior dental loading, there has been a secondary change in a number of other features of the facial skeleton, which has resulted in the set of supposedly autapomorphous features of their facial skeleton. However, in any assessment of polarity of traits, it is mandatory to determine what are primary, as opposed to biomechanically, spatially and/or developmentally secondary, features. In the case of the Neandertal face, we have a unique (autapomorphous?) combination of one plesiomorphous trait with one that is synapomorphous with modern humans. Therefore, if the Neandertal face is to be considered evolutionarily autapomorphous (it is clearly morphologically unique), it is the *combination* of traits that must be so considered and *not* the traits themselves.

A similar situation is found with the Neandertal dentition, a related complex. Neandertal anterior teeth are large relative to their posterior teeth (TRINKAUS, 1983a), a presumably autapomorphous trait. However, their anterior teeth, one dental morphological field, have dimensions and morphologies (de LUMLEY, 1973; PATTE, 1959; TRINKAUS, 1983a; WOLPOFF, 1979; WOLPOFF et al., 1981) that most closely approximate those of their Middle and initial Upper Pleistocene European predecessors (WOLPOFF, 1979, 1982), sharing some traits even with earlier *H. erectus* (WALKER and LEAKEY, 1986; WEIDENREICH, 1937). Their post-canine teeth, in contrast, are morphologically and dimensionally indistinguishable from those of European and Near Eastern early modern humans (FRAYER, 1978; McCOWN and KEITH, 1939; TRINKAUS, 1983a; VANDERMEERSCH, 1981a). We therefore have, as with the facial skeleton, a plesiomorphous complex (the anterior teeth) combined with one that is synapomorphous with early modern humans (post-canine teeth), producing a unique proportional pattern.

The rounded profiles of their neurocrania in posterior view *(norma occipitalis)* ("forme en bombe") have also been considered an autapomorphous trait of these Upper Pleistocene hominids (BOULE, 1911-13; HUBLIN, 1978b, 1982, this volume; TILLIER, 1986, this volume). Although distinct from the more angled (semi-pentagonal) neurocrania of both *H. erectus* and modern human crania, it is not clear to what extent this shape should be considered uniquely derived in a cladistic sense. The Neandertal rounded neurocranial profile is produced by 1) a reduction and medial curving of the mastoid region, 2) a moderately high maximum neurocranial breadth, 3) indistinct parietal bosses in the adult, 4) modest to small temporal lines and 5) no sagittal keel. These features need to be evaluated separately, since the rounded occipital profile of the Neandertals is clearly a combination of functionally and developmentally separate (cranial base, masticatory and cerebral) features.

The reduction of cranial base breadth across the mastoid region is shared with modern humans, even though the actual curve of the mastoid process (of some Neandertals) may be uniquely derived (however, it is already counted as a Neandertal autapomorphy above, and besides, it is a developmental retention of an immature state). The height of maximum neurocranial breadth is a product of encephalization associated with platycephaly, a trait shared with many modern humans even though the frequency of platycephaly combined with a large endocranial capacity is more frequent among the Neandertals. The supero-lateral parietal angling (producing a semi-pentagonal shape) seen in *H. erectus* and modern humans, although superficially similar, is in fact different in the two groups. In *H. erectus* it is the result of pronounced temporal lines and cranial vault thickening along them (RIGHTMIRE, 1979; WEIDENREICH, 1943, 1945); in modern humans it is the result of the persistence into the adult of the angulation produced by the parietal bosses (or ossification centers) of the developing cranial vault. The Neandertals have lost the former, without having the latter. And finally, the Neandertals, along with modern humans, have lost the neurocranial superstructures, such as sagittal keels, frequently found on *H. erectus* crania (WEIDENREICH, 1943, 1945).

Therefore the Neandertal "forme en bombe", is a combination of traits which are: 1) plesiomorphous (platycephaly and developmental loss of parietal bosses), 2) synapomorphous with modern human (encephalization, cranial base reduction and neurocranial superstructure reduction) and 3) apparently uniquely derived (mastoid profile). It is another mosaic of ancestral and differentially derived traits, the components of which are best evaluated separately.

The posterior crania of the Neandertals have also been distinguished from those of other members of the genus *Homo* on the basis of their profiles in lateral view *(norma lateralis)* (CONDEMI, this volume; HUBLIN, 1978b, this volume; STRINGER, 1980). In particular, European Neandertals usually have large occipital buns (or "chignons") associated with supralambdoid depressions and reduced transverse occipital tori, a pattern that appears in lower frequencies in the late Middle Pleistocene of western Europe. Unfortunately, no one Near Eastern Neandertal cranium is sufficiently complete and undistorted in the occipital region to indicate whether they possessed occipital buns, but the central Asian Teshik-Tash 1 specimen clearly possesses one. The buns and supralambdoid depressions are products of the same growth process (TRINKAUS and LeMAY, 1982), and they are well known for both Neandertals and more recent humans (JELINEK, 1959; McCOWN and KEITH, 1939; SZOMBATHY, 1925; TRINKAUS and LeMAY, 1982; VALLOIS and BILLY, 1965; VLČEK, 1961; WOLPOFF and JELINEK, 1987). They are thus a synapomorphy with early modern humans and are probably associated, through growth, with marked encephalization combined with platycephaly. The reduction of the transverse occipital torus and its contrasts with both earlier and later hominids are part of their occipito-mastoid complex.

It has also been suggested that their short distal limb segments, or low brachial and crural indices, represents an autapomorphy (VALLOIS, 1954). Although they are certainly derived with respect to earlier equatorial hominids (BROWN et al., 1985; STRINGER, 1986; WALKER and LEAKEY, 1986), they are nonetheless well within modern human ranges of variation (TRINKAUS, 1981). They are best seen in the context of the biogeographical patterning and thermal adaptation characteristic of all human groups, and not as unique to the Neandertals. The interesting question concerning Neandertal limb segment proportions involve why they appear so "arctic" (in a modern human sense) given their lower latitudes of occupation, especially in the Near East (even though those of the Near Eastern Neandertals are less extreme than the limb segment proportions of the European ones [TRINKAUS, 1981]).

Plesiomorphous Characteristics of the Neandertals

There are a number of clearly plesiomorphous Neandertal traits. These include most reflections of postcranial robustness, including femoral and tibial shaft hypertrophy and cross-sectional morphology, talar articular enlargement, humeral muscular insertion development, ulnar trochlear notch orientation, and probably hand and foot phalangeal proportions (DAY, 1971; HEIM, 1982a; LEAKEY et al., 1978; ROSAS, 1985; SANTA LUCA, 1980; TILLIER, this volume; TRINKAUS, 1983a, b, 1984a,c, 1986a, b; WALKER, pers. comm.; WEIDENREICH, 1941). Also plesiomorphous is their platycephalic neurocranial shape and general cranial robusticity, including supraorbital torus development and cranial vault thickness (STRINGER, 1984; WEIDENREICH, 1943). If anything, these various reflections of robusticity show some reduction relative to their predecessors, hence changes in the direction of anatomically humans. Their nasal aperture projection, to the extent that it is independent of masticatory constraints, would also be best seen as plesiomorphous (FRANCISCUS and TRINKAUS, 1988).

There are also a few traits known for the Neandertals that distinguish them from modern humans that are of uncertain phylogenetic polarity, given the dearth of postcrania for Middle and Lower Pleistocene members of the genus *Homo*. These include several aspects of hand morphology, shoulder proportions, and possibly pelvic (especially pubic) morphology. The first two are likely to be plesiomorphous, given their probable functional correlations with overall appendicular robusticity (TRINKAUS, 1983a, b) (see above). The polarity of Neandertal pubic morphology (HEIM, 1982a; McCOWN and KEITH, 1939; RAK and ARENSBURG, 1987; TRINKAUS, 1983a, 1984b) remains uncertain. However, the only sufficiently complete earlier hominid pelvic remains, those of *Australopithecus*

(JOHANSON et al., 1982; ROBINSON, 1972) (pelvic remains of *H. erectus*, despite claims to the contrary, are too incomplete to provide an indication of pelvic aperture dimensions and pubic morphology [BROWN et al., 1985; DAY, 1971]), show the same pubic enlargement and more posterior iliac orientation that is present among the Neandertals. This suggests, but does not confirm, the Neandertal pelvic morphology is plesiomorphous.

Neandertal Synapomorphies with Modern Humans

Among the remainder of their morphological characteristics, there are a number of synapomorphies with modern humans. These include their endocranial capacities (HOLLOWAY, 1981; TRINKAUS and LeMAY, 1982), general vertebral morphology (HEIM, 1976; TRINKAUS, 1983a) and posterior permanent and deciduous dental dimensions and morphology (FRAYER, 1978; TILLIER, 1979; TRINKAUS, 1983a). Most of the other traits shared between Neandertals and early modern humans, such as many aspects of appendicular articular and diaphyseal morphology, nasal configuration, cranial base morphology and cerebral circulation, are probably symplesiomorphies, since they are present or are likely to be present in Middle and Lower Pleistocene members of the genus *Homo*.

The Role of Development

The analysis of immature remains among the Neandertals (despite their scarcity for earlier hominid groups) might assist in the determination of what is special about the Neandertals, since adult morphology is after all the product of differential development (TILLIER, 1986, this volume). It is now apparent that many of the above mentioned basi-cranial traits appear early in Neandertal development (HEIM, 1982b; HUBLIN, 1980; TILLIER, 1983a, 1986, this volume), suggesting importance in overall Neandertal morphology. However, a number of aspects of Neandertal postcranial morphology, which are known to be or are likely to be plesiomorphous for them (especially reflections of postcranial robusticity and proportions) also appear early in development (HEIM, 1982b; TOMPKINS and TRINKAUS, 1987; VLČEK, 1973). Yet, interestingly, the characteristic Neandertal midfacial prognathism appears primarily with the eruption of the permanent dentition (TILLIER, 1983a, b, 1986, this volume), lending support to the above described roles of the dental and masticatory regions in producing this facial configuration (see TRINKAUS, 1987). The analysis of Neandertal development may thus shed light on the interrelationships between units forming unique combinations of morphology among these prehistoric humans, but it is unlikely to furnish, by itself, a clear differentiation between derived and ancestral traits.

Summary

Therefore, the only definitely uniquely derived traits, that is autapomorphous characteristics, of the Neandertals are aspects of their temporal and occipito-mastoid regions. Their anterior dental dimensions, mid-facial prognathism, and rounded occipital contours combine plesiomorphous traits, synapomorphies with modern humans and above mentioned occipito-mastoid autapomorphies to create apparently unique configurations. It remains open as to whether these unique combinations warrant the weight frequently given to them in phylogenetic analyses, since few of the primary, individual characteristics of them are truely uniquely derived. The remainder of the morphological characteristics which are frequently used to distinguish the Neandertals from modern humans are either clearly plesiomorphous or likely to be plesiomorphous.

A QUESTION OF ORIGINS

One of the primary concerns of paleoanthropologists regarding the Neandertals remains the phylogenetic issue. With respect to this session, the questions is: "From whom did they evolve, where and when?".

Europe

For western Europe, there is now a consensus that the Neandertals evolved gradually from their western European Middle Pleistocene predecessors during the later Middle and initial Upper Pleistocene (CONDEMI, 1985, this volume; HUBLIN, 1978a, b, this volume; STRINGER, 1985; TILLIER, this volume; TRINKAUS, 1982; VANDERMEERSCH, 1985; WOLPOFF, 1980). There is simply no evidence, paleontological or otherwise, for a "Pre-Sapiens" lineage in western Europe (HUBLIN, 1978b, 1982, this volume; SANTA LUCA, 1978; STEWART, 1964; TRINKAUS, 1973; VANDERMEERSCH et al., 1976). In central and eastern Europe the fossil evidence is less complete, but a similar pattern appears evident (SMITH, 1982; STRINGER, 1985; STRINGER et al., 1979).

In Europe, there is an earlier Middle Pleistocene sample (including specimens from Arago, Bilzingsleben, Mauer, Petralona and Vértesszöllös) that shows few Neandertal autapomorphies (as traits or combinations). By the later Middle Pleistocene, the sample (including specimens from Biache, La Chaise [Suard], Swanscombe and possibly Steinheim) show clear Neandertal affinities, and specimens from the last interglacial time period (e.g., La Chaise [Bourgeois-Delaunay], Ehringsdorf, Krapina and Saccopastore; the "proto-Neandertal" sample) are clearly Neandertal-related, but lack the full "classic" morphological configuration of the later, early last glacial, remains. Given normal ranges of variation and difficulties in precise geological dating of many of the specimens (especially for the Middle Pleistocene sample), the most parsimonious interpretation is to see a gradual emergence of a Neandertal morphology within a single European lineage during this time frame.

Central Asia

It is difficult to evaluate the evidence for the origins of the central Asian Neandertals, who are represented solely by the Teshik-Tash 1 immature skeleton (GREMYATSKIJ and NESTURKH, 1949). This specimen, however, shares many morphological characteristics with European Neandertals (including those from the Crimea), thereby extending the range of the Neandertals at least as far as central Asia. It is preceded in that region generally only by Azykh 1 Middle Pleistocene mandible, which appears to exhibit only archaic features for later Pleistocene hominids (ROGINSKIJ and LEVIN, 1978). It is therefore not possible to establish either a local origin for the central Asian Neandertals or an expansion of their range to the east from Europe during the early Upper Pleistocene or to determine when the Neandertal morphological patterns emerged there.

The Near East

The origins of the Neandertals in the Near East are more complicated and more controversial. There are currently two major interpretations of Neandertal origins in the Near East. These can be referred to as the "in-migration hypothesis" and the "local emergence hypothesis". The differences of interpretation are due in part to different interpretations of certain rather incomplete fossil specimens and in part to different approaches to the fossil record. However, the differences of interpretation remain in large part due to the extreme chronological uncertainty for most of the Near Eastern Middle Paleolithic fossil hominids. In my opinion, there are currently *no* securely dated Near Eastern Middle Paleolithic fossil hominids, despite valiant, varied and continuing efforts to date them, and at only two sites, Shanidar and Tabun, do we have separate human fossil samples with secure relative chronological (that is stratigraphic) relationships for this general time period, and there is uncertainty as to the stratigraphic position of the Tabun 1 skeleton. Clearly some resolution of chronological problems is required before we can hope to reach a consensus on the origins of the Near Eastern Neandertals.

The "local emergence hypothesis" (TRINKAUS, 1983a, 1984a, 1986a) sees a morphological continuity starting with the pre-Middle Paleolithic archaic specimens from Zuttiyeh, Gesher-Benot-Ya'acov and Tabun Layer E, all of whom exhibit *only* ancestral, or plesiomorphous, traits with respects to both the Neandertals and anatomically modern humans. They are followed in this sequence by the somewhat archaic sample including the earlier Shanidar remains and probably Tabun 1. The last, and fully Neandertal, sample includes the later Shanidar remains, the Amud fossils, and probably Tabun 2 (this assumes [but does not rely upon] that the Tabun 1 skeleton comes from the equivalent of Garrod's "Layer D" and that the Tabun 2 mandible derives from Garrod's "Layer C"; the stratigraphic position of the [in some ways enigmatic] Tabun 2 mandible appears secure, whereas that of the Tabun 1 skeleton is less certain).

This interpretation is based in large part on the apparently gradual shifts from an archaic upper facial morphology in Zuttiyeh 1, to an intermediate archaic/Neandertal ("proto-Neandertal") facial morphology in Shanidar 2 and 4 (and Tabun 1), to the fully Neandertal facial morphology seen in Amud 1 and Shanidar 1 and 5 (a sequence very similar to the late Middle to early Upper Pleistocene sequence seen in Europe). At the same time, there was postcranial stasis and non-chronologically ordered (even at Shanidar) variation in the occipito-mastoid and temporal regions among these Near Eastern late archaic humans. Given the tenuous dating of most of these specimens, this interpretation must rely heavily on the evidence from Shanidar, evidence which the Levantine data, in general, supports.

This sequence through time is *not* (nor ever was) viewed as an autonomous lineage leading to Near Eastern Neandertals independent of the European sequence. It is viewed as one that was, through time, in clinal genetic contact with neighboring Neandertal populations to the north and west. Furthermore, given the geographical distance between them and western European populations, some morphological differences between these Near Eastern Neandertals and the western European ones would be expected. In fact, the degree of similarity between these Near Eastern Neandertals and their western European counterparts is rather surprising, given the contrasts between them and their not very distant north African contemporaries.

It also needs to be emphasized that the absolute ages of most of these fossils remain unknown. Although it is possible that the Near Eastern Neandertals appeared later than their European counterparts, it is also possible that fully Neandertal populations emerged roughly contemporaneously in both regions. The early Shanidar sample may well have been contemporaneous with the samples from Ehringsdorf, Krapian and Saccopastore, all of whom exhibit a similar degree of archaicness relative to later "classic" Neandertals. Furthermore, the truly "classic" Neandertal morphology is well known in western Europe only for the latter half of the early last glacial (Würm I/II and Würm II), well after the probable time of the early Shanidar sample and most likely about the same time as the later, more Neandertal, Shanidar sample.

The "in-migration hypothesis" (BAR-YOSEF in press, this volume; CONDEMI, 1985, this volume; VANDERMEERSCH, 1981a, b), in contrast, would see the Near Eastern Neandertals as the product of a population movement from the north and west, deriving primarily from the last interglacial populations represented by samples such as those from Saccopastore and Krapina. This derivation from these last interglacial "proto-Neandertals" would explain the higher frequency of supposedly more generalized features in the Near Eastern Neandertals.

In this scenario, the Near Eastern Neandertals would be seen as either alternating with early modern humans in the Near East or ecologically separated from those early modern human populations, perhaps driven into that region by climatic deterioration to the north and west during the early last glacial (especially during oxygen isotope stage 4) (BAR-YOSEF, this volume) but nonetheless able to compete successfully with early modern humans for resources in the Near East for several tens of millenia.

This scenario is based largely on some combination of: 1) perceived derived modern human traits in the Zuttiyeh anterior cranium, 2) an acceptance of a date of 80-90 kyr BP for the early modern human sample from Qafzeh (without the presence of early modern humans in the Levant before 40-50 kyr BP, there is no need to derive the Near Eastern Neandertals from elsewhere), 3) a tight and late chronological culstering of the Near Eastern Neandertals, and 4) the presence of only more generalized "proto-Neandertal" morphological configurations in the Near Eastern Neandertals. All of these interpretations have weaknesses.

The Zuttiyeh 1 anterior cranium exhibits traits which I believe can *only* be seen parsimoniously as symplesiomorphies for Upper Pleistocene hominids in general (KEITH, 1927; HUBLIN, 1976; TRINKAUS, 1983a). They occur in Middle Pleistocene African, east Asian and European specimens, and are even present to some extent in the Shanidar 2 and 4 fossils. It therefore cannot be employed to decide between competing hypotheses as to be origins of the Near Eastern Neandertals; it could be ancestral to the Neandertals, early modern humans or both separately.

The early anatomically modern human Qafzeh sample, despite valiant efforts, remains undated more precisely than to the Levantine Middle Paleolithic. There are no reliable radiometric dates for the hominid levels (BAR-YOSEF and VANDERMEERSCH, 1981), lithic remains (although suggesting a relatively late date [JELINEK, 1982]) are inconclusive chronologically, sedimentological paleoclimatic dating (FARRAND, 1979) provides only a general bracketing, and microvertebrate chronologies (BAR-YOSEF, in press; TCHERNOV, this conference), potentially the most reliable of current data, are weakened by the faunal corridor nature of the Levant and the difficulties in choosing between potential faunal events represented by the limited number of samples. If the Qafzeh sample should date to ca.40-50 kyr BP, similar in age to the morphologically similar Skhul sample and later than (although possibly very close to) the later Shanidar sample, several problems would be eliminated: 1) the need to derive the Neandertals from the north and west, 2) the need to explain how Neandertals and early modern humans remained genetically separate in an area as small as the Levant for upwards of 30 kyr, and 3) the need to determine how the Neandertals were able to out-compete early modern humans in the Levant when those same early modern humans were able successfully and relatively rapidly to displace/absorb Neandertals across the Near East and Europe in the middle of the last glacial.

It remains difficult to evaluate the chronological clustering, or lack thereof, of the Near Eastern Neandertals. All are from levels that predate reliable radiocarbon determinations, and those published for sites such as Shanidar and Tabun should be viewed as no more than minimum ages. Furthermore, we cannot even agree on from what stratigraphic levels important specimens, like Tabun 1, derive. It is likely that the earliest of the Near Eastern Neandertals (the early Shanidar sample) derive from the beginning of the early last glacial (early stage 4), but they may easily come from a cool phase of the last interglacial. The latest of the Near Eastern Neandertals (probably Tabun 2 and the later Shanidar sample, possibly with Amud 1) may well date to ca.50 kyr BP, although current data prevent confirmation of that. If these assessments are even approximately accurate, there is no more clustering in time of the Near Eastern Neandertals than there is of the European ones.

There are indeed similarities, as CONDEMI (this volume) and VANDERMEERSCH (1981a) have emphasized, between *some* of the Near Eastern Neandertals and the European "proto-Neandertals", such as Saccopastore 1 and 2, suggesting a liaison between the two geographical regions during the last interglacial with some genetic separation subsequently. The similarities are primarily limited to the occipital and temporal regions, given the more "generalized", or ancestral, configurations of Near Eastern Neandertal suprainiac regions, the absence of tapering mastoid processes dwarded by juxtamastoid eminences in some (3 of 5) Near Eastern Neandertals, the vertical position of the temporal zygomatic root relative to the external auditory meatus, deep mandibular fossae in some specimens, and the less developed midfacial prognathism of some Near Eastern specimens (see above for secondary features).

Yet, when the Near Eastern Neandertals are examined closely, it is seen that 1) there is considerable variation in mastoid and juxta-mastoid morphology, with two out of five specimens (Shanidar 1 and Tabun 1) exhibiting European Neandertal configurations, 2) the vertical position of the zygomatic root is variable, 3) mandibular fossae are variable in depth, in part due to differing degrees of TMJ degenerative joint disease, and 4) the degree of development of midfacial prognathism, as in Europe, is chronologically ordered, becoming more pronounced during the early last glacial. Furthermore, although Near Eastern Neandertals appear to lack large occipital buns (all are damaged in that region), there is considerable variation in this region in European late Middle Pleistocene and last interglacial hominids, with four specimens (Biache 1, Ehringsdorf 9, and Krapina B and D) possessing buns and three (Saccopastore 1, Steinheim 1, and Swanscombe 1) lacking them, and there is variation in the degree of occipital bun development even within samples of "classic" European Neandertals (compare Spy 1 and 2 [FRAIPONT and LOHEST, 1887]). Only the more generalized suprainiac regions of the Near Eastern Neandertals consistently support a morphological liaison between them and some European "proto-Neandertals", although distinct suprainiac fossae were well established in Europe by the late Middle Pleistocene (HUBLIN, 1978a, 1980, this volume).

It is therefore apparent that the "in-migration hypothesis" is not well supported by secure data or interpretations. However, the inadequate chronological control correctly available for many Near Eastern late Middle and early Upper Pleistocene human remains, combined with the absence of non-plesiomorphous anatomical regions for Middle Pleistocene hominids from the Near East, make it impossible to reject fully either interpretation. The "local emergence hypothesis", in which Near Eastern late archaic human populations, in genetic contact with their European and central Asian relatives throughout the late Middle and early Upper Pleistocene, became increasingly Neandertal-like in morphology during this time period, appears to fit the available secure data best and requires the fewest unusual population dynamics. It is therefore preferable as an interpretation of the origins of the Near Eastern Neandertals.

Summary

The debate over the phylogenetic origins of the Near Eastern Neandertals will undoubtedly remain with us for some time, given the state of the fossil record and problems in dating the earlier Upper Pleistocene. However, a consensus is emerging on the evolutionary origins of the Neandertals in Europe, and the current alternative hypotheses concerning their Near Eastern origins are making of us consider and evaluate different hypotheses and seek data to test them. In the meantime, a general view of local emergence of the Neandertals, with no local lineage in genetic isolation, across the Neandertal range during the late Middle and initial Upper Pleistocene fits the available data best.

Let me emphasize that this does *not* mean that the emergence of the Neandertals across Europe, the Near East and central Asia was entirely uniform. As BAR-YOSEF (in press, this volume), CONDEMI (1985, this volume), VANDERMEERSCH (1981a, b) and I (1983a, 1984a) have emphasized for the Near East and as SMITH (1982, 1984) and STRINGER (1980) have documented for central and eastern Europe, the sequences of morphological changes in those regions were not identical to the well documented western European sequence, in either the exact morphological results or the chronological timing of changes. Some geographical variation *is to be expected,* given the geographical distances involved, the included topographic relief and ecological variation, and the cul-de-sac nature of western Europe contrasting with the faunal corridor nature of the Near East. What is surprising is that, given a null hypothesis of similar morphological and chronological patterns of Neandertal emergence across this region, it is not possible to reject this null hypothesis. In fact, as discussed above, such an hypothesis most parsimoniously fits the available secure data.

WHY WERE THERE NEANDERTALS?

Why, then, did we have the emergence across Europe, central Asia and the Near East, during the late Middle and early Upper Pleistocene, of the basi-cranial, facial and dental morphology that we associate with the Neandertals? Was this the result purely of random, selectively neutral genetic variation that became fixed through genetic drift in this geographical area? Given its geographical extent, its temporal duration, and the involvement of several important functional anatomical complexes, it seems unlikely that it was entirely selectively neutral. If that is the case, then what were its functional significances in the context of the late Middle and early Upper Pleistocene and associated human cultural systems?

Let me emphasize that this question is relevant across the entire Neandertal geographical range, regardless of one's preferred scenario for the origin of the Near Eastern Neandertals. For the Near East, one still has to explain why the Neandertal morphology and its associated behaviors either were selected for within populations during the earlier Upper Pleistocene or were capable of competing successfully with early modern human populations in that same restricted geographical area.

Many of the characteristics that distinguish the Neandertals from modern humans are plesiomorphous, or shared generally with archaic members of the genus *Homo* from the Middle and Lower Pleistocene. However, in several features, particularly aspects of the locomotor apparatus and of the skull as a whole, they exhibit a slight to modest descrease in overall robusticity relative to that of their predecessors. This implies that, despite morphological similarities between them and earlier hominids which indicate similar behavioral patterns, the Neandertals were reducing the levels of habitual biomechanical stress (both peak levels and levels of repetition) on their anatomies. This implies gradual ameliorations in their overall adaptive pattern, something which is generally indicated by the associated archeological record.

Since some of the unique configurations of Neandertal skeletal morphology involve differential reductions of regions that are hyperrobust in earlier hominids, these gradual changes in otherwise plesiomorphous regions are in part responsible for the morphology we recognize as Neandertal. However, there are traits and combinations of traits that are uniquely Neandertal, which must be considered.

Interestingly, all of the apparently autapomorphous traits or combinations of traits of the Neandertals can be related directly or indirectly to their continued use of large anterior teeth in the context of reductions in overall cranio-facial robusticity. Most aspects of their facial morphology are best seen as means of resisting forces generated through the facial skeleton by elevated levels and/or frequencies of anterior dental loading (HEIM, 1978; RAK, 1986; SMITH, 1983; SMITH and PAQUETTE, in press; TRINKAUS, 1983a, 1984a, 1987). Their temporomandibular joint morphology is undoubtedly related to joint reaction and musculoligamentous forces through that region, forces that were undoubtedly altered by their unique facial configurations. Their large juxta-mastoid eminences are probably due to hypertrophy of the digastric muscles for mandibular retraction and stabilization. And other aspects of their occipito-mastoid region may well be reflections of altered attachments for head stabilization muscles, muscles that would counteract anteriorly directed forces on cranium from the dentition.

The above question as to "Why were there Neandertals?" can therefore be rephrased as: "What were they doing with their teeth that neither non-Neandertal archaic *H. sapiens* nor anatomically modern humans habitually did?" Or, alternatively, since large anterior teeth and associated prognathic faces appear to be plesiomorphous for *H. sapiens*, "What ancestral behaviors involving the anterior teeth persisted among the Neandertals in the context of reducing masticatory and cranio-vertebral muscles, while those behaviors were decreasing among non-Neandertal archaic *H. sapiens* and early moderne humans?". The answers to these questions will not come from continual phylogenetic resorting of the fossils. They lie instead in greater understanding of Neandertal cranio-facial biology, an integration of the behavioral implications of the anterior dental use with those derived from their upper links, analysis of associated archeological remains (especially as regards its implications for the manipulative mechanics), and the placement of both of these in more secure chronological contexts.

CONCLUSION

I believe that we have come a long ways toward providing the phylogenetic and contextural background needed to address these more behaviorally oriented questions. Although disagreement remains as to how to interpret cladistically some aspects of Neandertal morphology and on the nature of the origins of the Near Eastern Neandertals, there is considerable agreement on the significant morphological attributes of the Neandertals and the evolutionary course of their emergence in Europe. Hopefully the contributions to this section, this consideration of "L'Avènement de l'Homme de Néandertal", will help us to focus in on topics of disgreement so that we can begin to test alternative interpretations with new data, rather than merely restating of previous positions. Regardless of the eventual outcomes of that research, the associated discussions are guaranteed to provide more of the lively exchanges that have characterized studies of these distant relatives of ours, the Neandertals.

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