



ANNE-MARIE TILLIER

PALAEOAUXOLOGY APPLIED TO NEANDERTHALS. SIMILARITIES AND CONTRASTS BETWEEN NEANDERTHAL AND MODERN HUMAN CHILDREN

ABSTRACT: Discoveries in Eurasia over the last two decades have focused attention on the significance of studies devoted to Neanderthal subadults. Ontogenetic studies are increasingly being employed to provide greater insight into the morphological features which distinguish adult individuals and thus to assist in the resolution of the controversies concerning the evolutionary relationships between Neanderthals and early modern humans.

Although the taxonomic assignment of immature individuals is complicated by changes in morphology brought about by growth and maturation processes, there is a clear tendency among some scholars to interpret morphological traits of subadults as relevant to taxonomic identifications (Neanderthals versus anatomically modern humans). Employing comparisons of Neanderthal, early modern human and recent children, this paper attempts to evaluate the relevance of some morphological and metric features that have been used in the identification of Neanderthal affinities.

KEY WORDS: *Neanderthals – Juveniles – Europe – Ontogeny – Palaeoauxology*

INTRODUCTION

Archaeological human samples often include a considerable number of children that permit the establishment of cohort ages and comparison of skeletal growth profiles between samples of similar temporal context and population affinity. By contrast, the reconstruction of growth and maturation patterns within prehistoric populations suffers from limited sample sizes. However, fossil immature skeletal remains are relevant to understand how growth-related processes may contribute to differences in adult morphology within and between prehistoric populations and consequently, they have the potential to provide important insights into the biology of these earlier populations.

In Europe, Neanderthals have been found in sites across western and central Europe and over a long time duration, probably more than 150,000 years. Most of the human

remains were associated with a Middle Palaeolithic archaeological context. By contrast, diagnostic European human remains identified as modern looking people have been found with Upper Palaeolithic industries, attributed to Aurignacian (e.g. the Cro-Magnon site in France) or Gravettian (e.g. Baoussé-Rousse in Italy; Předmostí in the Czech Republic).

It is commonly assumed by many scholars that the emergence of modern human growth patterns is correlated with an increase of cultural complexity, including progress in technology and social organisation, as well as extended human maturation patterns. While many studies attempt to establish different parameters of maturation between Neanderthal and modern human children, few examine the morphological variability observable within both groups or the lack of evidence for a biological shift in growth patterns between the two populations (Minugh-Purvis 1988, Tillier 1989, 1995, 1999).

Further, the traditional scenario of a strict correlation between the emergence of modern people and a bio-cultural revolution is seriously challenged by two major events. First is the identification of early modern humans associated with a Mousterian technology in the Mediterranean Levant, with the presence of 25 individuals in the Skhul and Qafzeh sites (McCown, Keith 1939, Vandermeersch 1981, Tillier 1999). Secondly, the persistence in western Europe of Neanderthals at the beginning of the Upper Palaeolithic is claimed to be well documented by the discoveries of human remains in Chatelperronian layers at the Saint-Césaire and Arcy-sur-Cure sites (Levêque, Vandermeersch 1980, Hublin *et al.* 1997).

This emerging complexity between biology and culture suggests that it may be more reasonable to discuss development from infancy to adulthood among Neanderthals without reference to their presumed bio-behavioural abilities. In this paper, some methodological aspects inherent to growth-related studies in Neanderthals are presented to illustrate the contrasts and similarities between Neanderthal and modern human children.

SAMPLING AND AGEING IMMATURE NEANDERTHALS

The anatomical differences between Neanderthals and early modern humans were initially recognised and defined on the basis of the European fossil record. The reasons for this include both the history of the discoveries and the distribution of fossils in Eurasia. Although the European specimens played the major role in addressing the question of morphological differences correlated to behavioural and adaptive contrasts between Neanderthals and modern humans, it should be noted that bone preservation and sampling limitations magnify the difficulties in the reconstruction of the skeletal biology of Neanderthals. In the analysis of subadult specimens there are theoretical and practical difficulties that cannot be overcome. The developmental reconstruction of the skeletal biology of Neanderthal children has to face several primary methodological problems:

First, the data are collected from specimens from sites often separated by hundreds (or thousands) of kilometres and thousands years in time. Yet these specimens are generally accepted as a representative sample, and are employed to document distinct developmental stages within the entire Neanderthal sample. Geographical and temporal variations should not be neglected in the analysis of the fossil record.

Secondly, non-adult individuals represent no more than 25% of the overall Neanderthal sample, and given the preservation of the fossil record, some skeletal growth stages are less well documented than others. For example neonate and infant skeletal morphology is still only partially known (Tillier 1995). Suggestions that Neanderthal infants

were not born at the same stage of maturation as modern infants (Trinkaus, Tompkins 1990), or that they had bigger heads than modern babies (e.g. Dean, Stringer, Bromage 1986, Stringer, Dean, Martin 1990) remain purely speculative for lack of a documented fossil record (Tillier, *ibid.*).

Thirdly, although the main goal in conducting growth-related analyses is to explore possible developmental differences between Neanderthals and modern humans, the accuracy of age at death estimations of fossil immature specimens is based on the use of chronological age estimators derived from studies of modern populations. Reference modern standards (e.g. enamel microstructure growth components, tooth calcification and erupting sequence, diaphyseal length, body size) may or may not be appropriate for the specimens under investigation.

In many cases, an accurate assessment of the overall body proportions of the Neanderthal children cannot be obtained, because the state of skeletal preservation does not permit such an evaluation.

Estimation of the age at death of Neanderthal subadults is most reasonably based on dental criteria. The last ten years have seen the publication of a number of studies on tooth surface enamel in Neanderthal and modern children, some of which remain controversial (Dean *et al.* 1986, Stringer *et al.* 1990, Mann, Lampl, Monge 1990). Several have emphasised individual variability and have questioned the accuracy of counting incremental lines in fossil teeth to estimate the age at death of Neanderthal children (Mann, Lampl, Monge 1991, Tillier *et al.* 1995, Vandermeersch *et al.* 1995).

Macroscopic and radiographic examinations of tooth formation times would appear to be the most relevant for age at death estimation, as differences in the timing of calcification and the eruption sequence in the dentitions of Neanderthals and living children cannot be substantially established (Tillier 1995, Tompkins 1996). However, in any individual case, with perhaps the exception of the third molar (Wolpoff 1979), the error of estimating age in this way may be magnified by the fact that the sex of the immature specimen remains unknown.

Finally, it is necessary to evaluate the morphological diversity of those children's skeletons which have been identified as Neanderthals. Only a few European sites have a large enough sample size to permit the evaluation of individual variation within a single sample. Furthermore, a comparison between the non-adult and adult skeletal morphologies is restricted to three sites¹⁾, Krapina in Croatia (Smith 1976), La Ferrassie (Heim 1976, 1982) and L'Hortus (de Lumley 1973) in France.

The human remains from the Krapina rock-shelter represent the largest Neanderthal sample (N = 874;

¹⁾ The important Simas de los Huesos collection from Spain (Arsuaga, Bermúdez de Castro, Carbonell 1997) will provide a unique opportunity for further investigation of this topic of research.

Radovic *et al.* 1988) from any site dated to the Riss-Würm within the Alpine glacial sequence or to oxygen isotope stage 5. The sample is very informative in many respects, but most of the remains are fragmentary and, based upon secondary morphological observations, the possibilities of associating them are extremely low. Besides ontogenetic aspects, the discussion of growth and development patterns within this Croatian sample is rather limited.

Relative dating of the two French sites, La Ferrassie and L'Hortus, is based upon the combined data of biostratigraphy and the archaeological context of the deposits (de Lumley 1973, Heim 1976), and these data place them within Würm II (oxygen isotope stage 4). In fact, the specimens found in these sites represent late Neanderthals associated with a Mousterian archaeological context, and consequently they represent an evolutionary pattern within the Neanderthal sample.

COMPARATIVE METHODS AND SAMPLES

Some recent studies have contrasted the morphology of Neanderthals and modern humans, focusing on functional interpretation using enlarged comparative samples from populations representing distinct lifeways. These studies have documented significant levels of inter-individual and inter-population variations in skeletal robusticity (e.g. Villemeur 1991, Hambucken 1993, Churchill 1994). By contrast, the juvenile human remains used in the comparison are restricted to samples mostly originating from regional collections used in forensic medicine studies (e.g. Madre-Dupouy 1992, Heim 1982, Dodo *et al.* 1998), and are thus not strictly appropriate in this regard. From an auxological perspective, skeletal biologists pay more attention to growth-related measurements of long bones in living populations rather than to the variability of morphological traits. It is clear that the investigation of post-cranial development in immature Neanderthals will benefit from an enlarged sample that will document the diversity of the subadult modern skeletal morphology within different populations. This will contribute to a better understanding of skeletal differences between Neanderthal and modern human morphologies. Previous examinations limited to individuals belonging to sedentarised and/or industrialised populations are, indeed, inadequate to define the contrasts in skeletal robusticity between Neanderthal and early modern children, or to discuss evidence of differences in muscularity or limb proportions.

Obviously, the comparative analysis should include the earliest representatives of modern people. In Europe, however, the earliest and later Aurignacian children are mainly represented by fragmentary skull remains and their biological identity is still poorly known (Martin 1936, Gen, Kczanowski 1982, Minugh 1983, Gambier 1989, this volume, Tillier 1990, Garralda *et al.* 1992). Consequently, the comparative sample should include later fossils such as Gravettian immature individuals, including Baoussé-

Roussé in Italy (Gambier *dir.*, n.d.) and Předmosti in the Czech Republic (Matiegka 1934–1938).

Outside of Europe, the specimens are the early anatomically modern children discovered in the Mousterian layers of the Qafzeh and Skhul caves in Israel (McCown, Keith 1939, Tillier 1999), and at the Aurignacian site of Ksar Aqil in Lebanon (Bergman, Stringer 1989).

Finally, it should be pointed out that skeletal data are assembled from infants and children who were the non-survivors in the population, a common situation in the study of archaeological samples (Saunders, Hoppa 1993). Such data are nevertheless employed to reconstruct growth patterns and maturational events within the Neanderthal lineage, although a majority of the non-adult skeletons may be the remains of children who suffered from greater levels of chronic stress in comparison with their surviving cohorts.

There is probably still much to be learned from investigating the relationships between childhood mortality and potential indicators of developmental disturbance in Neanderthals. Evidence of growth troubles, such as dental enamel hypoplasia (Skinner 1986, 1989, Ogilvie *et al.* 1989, Brennan 1991) and Harris lines (Brennan *ibid.*) have been examined within the Neanderthal sample. Hypoplastic defects have not been observed on Neanderthal deciduous teeth (Skinner 1986, Tillier *pers. obs.*). The results collected from the examination of the permanent teeth and long bones do not totally document a high degree of environmental stress factors among immature Neanderthals. Yet, the use of such data as adequate indicators of exclusive nutritional stress can be questioned for Neanderthal children, as it was previously done for living children (Neiburger 1990).

Despite the limitations on the study of Neanderthal growth patterns brought about by the differential preservation of anatomical regions and the representation of developmental stages within the fossil sample, studies have provided accurate information regarding the ontogenetic appearance of several diagnostic Neanderthal characteristics in the skull and post-cranial skeleton.

INVESTIGATING CRANIAL SIMILARITIES AND CONTRASTS

The assumption that the juvenile Neanderthal skull is essentially a small replica of the adult one seems to prevail in many ontogenetic studies, although such a view is in total contradiction to the data from growth studies of living populations. Comparisons between several Neanderthal children individuals, between them and recent children, reveal morphological differences documenting qualitative aspects of morphology related to age, sex or to both aspects of variation.

Skull morphometric variation and sexual dimorphism

While the indications of cranial robusticity are either absent or reduced on young specimens, it is rather difficult

to interpret the individual variation in terms of either age-related changes or sexual dimorphism.

Because of limited samples and relative lack of complete skeletons, patterns of skeletal sexual dimorphism in the Neanderthal adult sample are based on modern reference standards. Following such standard references, scholars have associated cranial gracilisation and small endocranial capacity with a female sex assignment, even though regional and temporal variations may be important factors involved in the manifestation of individual variation within the Neanderthal population.

Sex estimation of immature skeletons, based on morphometric criteria, remains a controversial question (Majo 1992, Majo, Tillier, Bruzek 1993). Identifying sexual dimorphism among Neanderthal children has been based on the same criteria as those employed for adult individuals, i.e. skull size, cranial bone gracilisation and dental metrics.

Thus, for instance, the Devil's Tower child from Gibraltar (ca 5-year-old at death), the Teshik-Tash individual from Uzbekistan (ca 9-year-old) and the Le Moustier 1 adolescent from France were described as male individuals (e.g. Buxton 1928, Klaatsch, Hauser 1909, Dean *et al.* 1986). By contrast a female sex was assigned to the Subalyuk 2 specimen from Hungary (ca 3-year-old) and to two French fossils, the La Quina 18 (ca 7-year-old) and the adolescent from Montgaudier (ca 12.5–14-year-old) (Thoma 1963, Dean *et al. ibid.*, Mann, Vandermeersch 1997).

Such sex estimations seem to disregard age-related changes as well as regional and/or temporal variation within the immature sample. For further discussion of the evidence for sexual distinction within the immature Neanderthal sample it should be important to have a more consistent basis.

Adult versus non-adult morphology, the search for phylogenetic traits

The taxonomic affiliation of immature cranial remains is inferred from the identification of distinguishing anatomical features that were used to describe the adult Neanderthal skeleton (e.g. Stringer *et al.* 1984, Hublin, Tillier 1991). Some skeletal traits appear to be more relevant than others for a phylogenetic assignment of immature Neanderthal remains.

Thus, a few diagnostic features of the cranial vault (e.g. "en bombe" cranial shape in posterior view; coexistence of a fully developed suprainiac fossa and a bilaterally protruding occipital torus) are known to be present in early ontogenetic stages (Tillier 1986).

By contrast, most of the traits of the upper face and mandible (e.g. midfacial projection, double-arched supra-orbital torus, retromolar space behind the third molar, mental foramina posteriorly located under the first permanent molar) appear later in age. Midfacial projection and inflated maxilla are associated with the two mandibular traits mentioned above that seem to develop later, when children have anterior and posterior permanent teeth (Tillier 1981, 1986). However, a recent comparison of the

developmental stages of mandibles in Neanderthals and modern humans demonstrates that a distinction in the location of the mental foramen can be identified earlier in ontogeny (Coqueugniot 1998, 1999, *versus* Tillier *ibid.*, Nara 1994).

A number of studies have employed a few skull traits in distinguishing Neanderthal from modern children, but the phylogenetic significance of these assessments has been recently criticised. Among the questionable traits are an elongated *foramen magnum* on the basicranium and on the mandible, a large medial pterygoid tubercle, a laterally expanded mandibular process (mentioned by Rak, Kimbel, Hovers 1994), and the lack of a mental trigone (used by Faerman *et al.* 1994, Rak *et al. ibid.*, Dodo *et al.* 1998, Duarte *et al.* 1999).

Qualitative observations collected from immature Neanderthal mandibles suggest that the development of the chin area manifests individual variation (Tillier 1981). An important limitation in the interpretation of this morphological variation refers to the fact that the fossil record is incomplete and scattered over considerable geographic distances and appreciable temporal levels. For example there is not a single site which preserves more than one immature mandibular specimen.

Some data collected from early modern human children associated with either Middle or Upper Palaeolithic industries established that such specimens display a degree of morphological variability in chin development. A few individuals originating from the Levant (Skhul, Qafzeh, Ksar Aqil) and Europe (Les Rois in France; El Castillo in Spain) may exhibit only a slightly prominent mental trigone (Garrauda *et al.* 1992, Gambier 1989, Tillier 1989, 1999). Discussing individual variation from a single site is possible in a unique case illustrated by the five immature mandibles from Qafzeh. In this site it appears likely that the differences between the individuals are due to age-related changes (Tillier 1999: 162, Fig. 77), recalling a growth pattern well known among recent children (Meredith 1957), even if we cannot exclude other factors.

Further recent comparative analyses of fossil and modern children demonstrate that the occurrence of an antero-posteriorly elongated *foramen magnum* can also be interpreted as age-related. The Amud 7 infant (ca 10 months old) from Israel and the Engis 2 child from Belgium ca 5 years at death (Figure 1B) indeed, exhibit an elongated shape of the *foramen magnum*, as shown by the values of the breadth/length index ($M.16 \times 100 / M.7$, following Martin's measurements) of 57.1 and 57.5 respectively. However, the older individual Teshik-Tash, as well as the two adults with a basicranium well preserved, i.e. La Ferrassie 1 (Figure 1A) and La Chapelle-aux-Saints from France, exhibit higher values of the index and thus do not document the persistence of this feature into adulthood (Tillier 1998: 387, Tab. 3). A similar conclusion can be reached from the data recently published on Le Moustier 1 adolescent (Ponce de Leone, Zollikoffer 1999) for whom an index value of 71.0 was given.



FIGURE 1. Variation in *foramen magnum* shape from childhood to adulthood: similarities between Neanderthals and medieval individuals from the Rajhrad site (Czech Republic). A: the La Ferrassie 1 man; B: the Engis 2 child (dental age at death ca 5 years); C: Rajhrad adult 270A; D: Rajhrad child 454 (ca 6-year-old). On both children the *synchondrosis intraoccipitalis anterior* is not closed. (Photographs by Tillier and Sellier.)

Interestingly, ontogenetic variation in the *foramen magnum* shape was also confirmed by the investigation conducted by Coqueugniot (1998) on two reference modern human samples (known ages and sex; $N = 103$), Spitalfields from England (Molleson *et al.* 1993) and Coimbra from Portugal (Anonymous 1985). This author identifies three morphotypes of the *foramen magnum* shape: elongated (breadth $\times 100$ /length ratio < 65), intermediate (ratio between 65 and 85) and rounded (ratio > 85). Among the youngest children, the rounded morphotype has a low frequency ($< 20\%$), while it occurs in more than 50% of the older individuals and prevails among adult individuals. Hence, the phylogenetic significance of the *foramen magnum* shape was rejected and similarities in age-related changes well established for both Neanderthals and modern humans (Figure 1 A to C).

Therefore, the identification of immature skeletal remains as part of the Neanderthal population should be regarded as a very specific approach. Additionally, the skull of the youngest Neanderthal children exhibits morphological traits, such as a vertical forehead, the absence of supraorbital torus, a relatively high and more rounded cranial vault and a relatively small mastoid process compared to the development of the juxtamastoid area, that make them more similar to modern children.

The use of fossil metric data

A basic aspect in comparative analyses of morphometric data from Neanderthal and recent children is the desire to draw conclusions about the distinctiveness of the former. However, such conclusions may be influenced by the specificity of the modern reference sample selected for comparative analysis.

Some researchers have suggested that Neanderthal children have a larger braincase than modern children and have directly addressed the question of a distinct growth rate of the skull (Dean *et al.* 1986, Stringer *et al.* 1990, Dodo *et al.* 1998). Others have demonstrated from the comparison between fossil (i.e. Neanderthal and Upper Palaeolithic specimens) and recent modern European children, that all Palaeolithic children may be within the distribution of the modern range of variation (e.g. Coqueugniot 1994, 1997, Minugh-Purvis 1998, Tillier 1998).

Comparative analysis of the endocranial volume between Neanderthal and recent children shows that the distinction is less evident than previously thought, as only one single specimen, the Teshik-Tash child, falls outside the range of variation of a modern sample from France (Coqueugniot 1994: 248, graph 5, Tillier, 1999: 169, Fig. 78). A similar conclusion was reached when Teshik-Tash was compared to the reference Coimbra sample from Portugal (Coqueugniot 1997). However, such a result was contradicted by the data collected from a sample originated from the Czech Republic: indeed, the range distribution of cranial capacities among children differs from one sample to another (Coqueugniot *ibid.*; Figure 2).

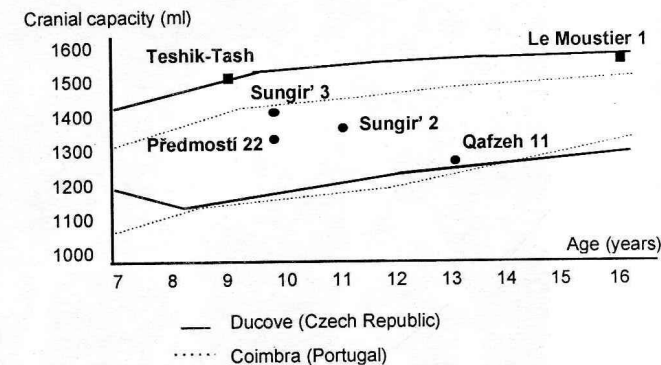


FIGURE 2. Age-related changes in cranial capacities. Neanderthal (black square) and early modern human (black dot) children compared to the range of distribution of the two European modern samples, Ducove and Coimbra (after Coqueugniot 1997).

Regional patterns of variation in cranial size and shape among recent modern children cannot be neglected and the choice of the particular recent sample has a major influence on attempts to establish differences between fossil and modern children.

METRIC GROWTH IN THE POST-CRANIAL SKELETON

Among adult Neanderthals many characteristics of post-cranial morphology reflect appendicular robusticity and body mass. They are absent or reduced in children, and thus, the search for striking differences between Neanderthal and modern human juvenile skeletons is rather difficult. In addition, the comparative analysis of Neanderthal and modern children is limited by the relative lack of data on the diversity of the skeletal morphology among recent human juvenile samples. Moreover, the assessment of morphological contrasts between Neanderthal and earliest modern human children in Europe is poorly documented.

In the comparison of limb segment and body proportions, Neanderthal immature specimens may provide evidence for similarities during growth with recent children and consequently, for distinct patterns between adult and non-adult Neanderthal specimens.

Claviculo-humeral index and trunk size

The trunk of adult Neanderthals is commonly described as broad compared to that of modern humans (e.g. Heim 1976, Vandermeersch 1981, Trinkaus 1983). None of the Neanderthal immature individuals retain a complete trunk. A large part of the thorax is preserved in the Roc de Marsal child, ca 3 years old at death, and its overall dimensions fall within the modern human range of variation (Madre-Dupouy 1992, Tillier pers. obs.). Among other immature European Neanderthals, i.e. La Ferrassie 4bis, 6 and 8 (Heim 1982), Kiik-Koba 2 (Vlček 1973), Subalyuk 2 (Pap

et al. 1995), and Ehringsdorf G (Vlček 1993), the fragmentary state of preservation of the ribs does not permit, in our opinion, any accurate evaluation of trunk size. Similar cautionary comment should be applied to the ca 9-year-old Teshik-Tash specimen having only the second and seventh ribs preserved: following Sinelnikov (in: Gremjatskiy, Nesturkh 1949: 134), the ribs are quite similar in size to those of recent children.

A complementary indication of trunk volume may derive from the estimation of the relative elongation of the clavicle, evaluated by the value of the claviculo-humeral index (clavicle length $\times 100$ /humerus length). This value for two adult European Neanderthals, i.e. Regourdou (51.0; Vandermeersch, Trinkaus 1995), and La Ferrassie 1 (53.5; Heim 1976) is above the mean of five Aurignacian adults from Předmostí (46.5 ± 1.4 ; after Matiegka 1934–1938).

Two Neanderthal children from Eurasia, Roc de Marsal and Teshik-Tash, have complete clavicles that were described as being exceptionally long (Madre-Dupouy 1992). However, for these individuals the claviculo-humeral index cannot be estimated on the basis of the inadequately preserved humeri. The bones of other European immature specimens are also too fragmentary (e.g. Kiik-Koba 2; Ehringsdorf G) or missing and no quantitative comparison of clavicle length to humeral length can be conducted. Additional support for the idea that Neanderthal children have long clavicles might be provided by the recent report on the Dederiyeh child from Syria. This 2-year-old child has a high claviculo-humeral index (Dodo *et al.* 1998: 336, Fig. 14).

Interestingly, two early anatomically modern humans from Skhul and Qafzeh exhibiting preserved clavicles and humeri (Skhul 1, ca 3-year-old, Qafzeh 10, ca 6-year-old) also possess high claviculo-humeral indices (respectively 46.8 and 49.4), and this suggests that they share in common with Neanderthals a relatively long clavicle (Tillier 1999).

In fact study of recent samples suggests that long clavicles and short arms appear to be normal features for infants and young children. Table 1 shows a comparison of the developmental stages of the claviculo-humeral index within the Spitalfields and Coimbra samples. The two samples include distinct age groups: 90 percent of the Spitalfields sample is represented by young individuals (from birth to 5 years), while all of the Portuguese children are older than 7 years.

TABLE 1. Age variation of the claviculo-humeral indices in the Spitalfields immature sample ($N = 44$).

Birth – less than 1 year	65.20 ± 2.75	$N = 17$
From 1 to 5 years	57.31 ± 4.96	$N = 24$
From 6 to 10 years	53.26 ± 5.38	$N = 2$
From 10 to 16 years	47.59	$N = 1$

Within the Spitalfields sample, the older children possess values closer to the mean index of the Coimbra children (47.0 ± 2.0 ; $N = 20$). Such observations suggest that the values of the claviculo-humeral index within these two European samples may represent an age-related trait.

Indeed, this conclusion is confirmed by data collected on adult individuals belonging to the two reference samples. A mean value of the index (46.80 ± 0.02 , $N = 30$) can be calculated on a sample from Spitalfields. Previous estimations of the clavicle/humerus length ratios published for the Coimbra adults (females: 0.46 ± 0.02 , $N = 153$; males: 0.46 ± 0.01 , $N = 156$; Xavier da Cunha, Xavier de Morais 1961) are in agreement with the Spitalfields data.

Lower limb segment proportions

Adult Neanderthals manifest a shortening of the distal segment of their lower limbs (leg / thigh length ratio), that is thought to reflect a certain degree of cold adaptation, as a similar condition is displayed by subarctic recent populations such as Lapps and Inuits. This is well illustrated by the values of the crural index (maximal tibial shaft length $\times 100$ /maximal femoral shaft length). Although our knowledge of the limb proportions among the Earliest Upper Palaeolithic hominids from Europe is quite limited, the fact that Neanderthals and early modern humans differed in the value of their crural indices was employed in the debate concerning the origins of the modern humans in Europe (Trinkaus 1983, Stringer, Hublin, Vandermeersch 1984, Wolpoff 1989, Hublin, Tillier 1991, Frayer 1992, Holliday 1995, 1999, Duarte *et al.* 1999).

Among adult European Neanderthals, the crural indices can be directly estimated for two specimens, e.g. Spy 1 (76.2, after Fraipont, Lohest 1887), La Ferrassie 2 (74.0, after Heim 1976), and in both cases they are low. Other individuals (La Chapelle-aux-Saints and La Ferrassie 1) possess incomplete bones which can provide only approximative values of the crural index, respectively 79.1 (Boule 1911–1913) and 80.7 (Heim *ibid.*).

By contrast, an early anatomically modern human from the Levant, Skhul 4, exhibits a high value (88.5, after McCown, Keith 1939), above the mean value of the crural indices estimated from the Gravettian Předmostí adult sample (86.4 ± 2.3 ; $N = 5$, after Matiegka 1934–1938).

Analysis of post-cranial development in Neanderthals is rather difficult in Europe²: immature bones are scarce and when found always partially preserved. As mentioned previously the La Ferrassie site is quite unique for providing data on both children and adults. The La Ferrassie 6 child brings evidence of shortened hindlimb proportions with a femoro-tibial length ratio (78.6) slightly above the value of the adult La Ferrassie 2 index.

² In this aspect the recent discovery of the Mezmaiskaya child in Northern Caucasus (Golanova *et al.* 1999) has the potential to significantly contribute to our knowledge of the post-cranial morphology of Middle Palaeolithic children.

All of the other European Neanderthal children are represented by incomplete bones and any estimations of their crural indices, in our opinion, remain quite speculative due to the state of preservation of the femoral and tibial diaphyses. Such cases are represented by the Roc de Marsal child (Madre-Dupouy 1992: 220, Figs. 120, 121, 122) and the Le Moustier 1 adolescent (Herrmann 1977: 135, Figs. 3a, 137, 4) in Europe, or by the Asian Teshik-Tash child (Sinelnikov in: Gremiatskiy, Nesturkh, 1949: 133, Fig. 4 and Tab. 3). Thus, within the European sample, the discussion about the early appearance of the lower limb shortening in development in immature Neanderthals is based on one single specimen, the La Ferrassie 6 child. Because stages of dental calcification and eruption are unknown for this child, there have been different estimates proposed for its age at death: ca 3 years (Heim 1982), between 3 and 5 years (Tompkins, Trinkaus 1987, Tillier 1999).

An early presence in Neanderthal ontogeny, i.e. ca 2 years of age, of lower limb shortening seems to be confirmed by the preliminary report on the Dederiyeh child from Syria (Dodo *et al.* 1998: 336, Fig. 14). Therefore the assessment of short distal limb segment for Neanderthal children is supported by the examination of two immature individuals separated by thousands of kilometres.

There is not a great deal of additional comparative data from other samples of immature individuals, i.e. members of the genus *Homo* and modern human groups. Within the Skhul-Qafzeh immature sample, a high value of the crural index (85.7) can be estimated for a single specimen which possesses lower limb bones sufficiently complete to permit such an estimation, i.e. the Skhul 1 child ca 3 years old. This value is slightly below that of the adult Skhul 4.

Unfortunately, no information on limb proportions is available for the Předmostí subadults in Matiegka's monograph³. The two children from the Gravettian Baoussé-Rousse site in Italy, ca 18 months and ca 3 years old at death (Gambier 1997, dir. n.d.) respectively, have lower values for the crural index than that of Skhul 1, and one of them is very close to that of La Ferrassie 6 (Gambier, pers. comm.). Two other individuals from Baoussé-Rousse that have previously been studied, a female and an adolescent skeletons, seemed to exhibit higher crural indices (respectively 84.1 and 83.8, after Verneau 1906).

The crural index for juveniles is calculated by using inter-metaphyseal lengths, while inter-epiphyseal lengths are measured for adolescents and adults. Data assembled from recent European subadult samples in western Europe document individual variation in terms of the crural index. The mean of the crural indices for the Spitalfields sample (83.2 ± 3.0 ; $N = 26$) is above that of the Coimbra sample

(77.0 ± 4.2 , $N = 20$). The former includes a majority of young individuals (less than 5 years old at death) while the latter is composed of children between 7 and 16 years of age at death. The mean value calculated for a group of Spitalfields adults (81.5 ± 2.2 ; $N = 64$) mirrors the index calculated for the sample of children, but no data are available at the moment for the Coimbra adults.

Although modern samples employed in these preliminary analyses of lower limb proportions in modern children are small and probably inadequate, it is clear that individual and population variations are present. More substantial data on modern children (i.e. fossil and recent specimens) are required to support the notion that Neanderthal children are unique in possessing lower limb shortening. Furthermore it is also possible that future research results on enlarged samples of living children will document ranges of variation which encompass the short lower limb proportions now known from the few Neanderthal children.

Elongation of superior pubic ramus

Compared to recent modern bones, the Neanderthal adult pelvis shows a medio-lateral elongation of the superior pubic ramus accompanied by its relative vertical thinning (Stewart 1960, Trinkaus 1976, Rosenberg 1988). Although no complete Neanderthal adult pelvis has been recovered in Europe, it has been suggested that this elongation of the superior pubic ramus is morphologically associated with a narrowing of the greater sciatic notch (Rak 1990, Tillier, Majo, Bruzek 1995).

Immature Neanderthal pelvises sufficiently complete to permit the calculation of proportional indices and to evaluate the correlation between pubic and body size are rare. Again, the best specimen for such quantitative comparison in Europe is represented by the La Ferrassie 6 child. The medio-lateral elongation of the pubic ramus can be identified on this specimen (Heim 1982, Tompkins, Trinkaus 1990, Tillier *et al.* 1995). This pattern can be illustrated by a superior pubic ramus/femur length ratio of 22.4. From the preliminary observations published on the Dederiyeh young child (Dodo *et al.* 1998: Tab. 3, Fig. 13), it appears that its superior pubic ramus is also medio-laterally elongated.

Among the early modern humans from Skhul and Qafzeh, the ca 3-year-old child, Qafzeh 21, had a shorter pubis than that of La Ferrassie 6 (Tillier 1999: Tab. 20), but pubic elongation relative to stature cannot be compared to that of the European Neanderthal child. Pubic and femoral measurements are available for an older child, Qafzeh 10 ca 6-year-old at death, and it possesses a lower value of the pubo-femoral index (17.2) than that of La Ferrassie 6. No data are available at the present time that examine the relationships between pubic measurements and body size in early European modern children.

Within modern samples, preliminary studies have discussed age-related changes in pubic and femur growth pattern and the influence specific of the population sample

selected for the analysis (Majo 1995, 1997). Since La Ferrassie 6 and Qafzeh 10 may represent two stages of development, the differences in the two values of the pubic-femur length ratio may reflect an age-related change during growth. Indeed, when the two fossils are compared to immature individuals originating from two European reference samples, grouped together to form a series of age at death categories (Musée de l'Homme and Coimbra collections, $N = 40$; Tillier *et al.* 1995, Tillier 1999: Fig. 49), they appear to fall within the modern range of variation for the comparative pubic and femoral measurements.

Furthermore, within the French-Portuguese sample, the mean value of the pubis-femur length ratio for young children (i.e. between 0.5 and 7-year-old; $N = 17$) is significantly higher (21.5 ± 1.6 ; Student *t* test $p = 5.E-04$) than that (19.1 ± 2.2) of older children (i.e. between 8 and 16-year-old; $N = 23$). Clearly these metric comparisons represent only a preliminary investigation but they suggest that inter- and intra-population variations affecting pelvic ontogeny need to be better documented.

CONCLUSIONS

The preceding discussion has attempted to address important aspects of the ongoing debate over the presence or absence of differences in growth and development patterns between Neanderthals and early modern humans. Palaeoanthropology applied to Neanderthals is restricted to cross-sectional comparisons between specimens that are geographically scattered and the temporal distance between them and anatomically modern children cannot be neglected. Within the Neanderthal sample, the analysis of within-site variation in growth-related features cannot be accurately conducted and for the moment we are not able to interpret morphological differences as reflections of temporal and/or regional changes. Studies of Neanderthal immature remains have the potential to reveal similarities and contrasts between them and recent children. But it is clear that we have to recognise the difficulties in attempting to build a biological model of Neanderthal growth.

We are still far from a consensus on the nature of the patterns and biological processes that contributed to the development of Neanderthal skeletal morphology. Nevertheless it is obvious that many palaeoanthropologists will undoubtedly continue to search for differences in growth rate and maturation events between Neanderthal and early modern children.

ACKNOWLEDGEMENTS

Thanks are due to Eugenia Cunha, Maria-Augusta Rocha (Dept. of Anthropology, Coimbra University), and to Theya Molleson (BMNH, London) for free access to the collections under their care. I am deeply grateful to Theya Molleson for providing me the data base on the Spitalfields

sample, to Tona Majo and Pascal Sellier for their friendly contribution in collecting additional data from Spitalfields and Musée de l'Homme subadult collections, to Hélène Coqueugniot for providing me an unpublished figure, and finally to Alan E. Mann for the fruitful discussions that we had during the preparation of this manuscript.

REFERENCES

- AKAZAWA T., MUHESEN S., DODO Y., KONDO O., MIZOGUCHI Y., 1995: Neanderthal infant burial from the Dederiyeh Cave in Syria. *Paléorient* 21,2: 77-86.
- ANONYMUS, 1985: *Cem anos de antropologia em Coimbra*. Museu e Laboratorio Antropologico, Coimbra. 261 pp.
- ARSUAGA J. L., BERMUDEZ DE CASTRO J. M., CARBONELL E., 1997: Preface. *J. of Hum. Evol.* 33: 105-108.
- BERGMAN C., STRINGER C. B., 1989: Fifty years after: Egbert, an early Upper Palaeolithic juvenile from Ksar Aqil, Lebanon. *Paléorient* 15,2: 99-111.
- BOULE M., 1911-1913: L'homme fossile de La Chapelle-aux-Saints. *Ann. Paléontol.* 7:21-56, 85-192, 8: 1-70.
- BRENNAN M. U., 1991: *Health and disease in the Middle and Upper Paleolithic of southwestern France*. Ph.D. Dissertation, New York University.
- BUXTON L. H. D., 1928: Excavations of a Mousterian rock-shelter at Devil's Tower, Gibraltar. Chap. II: Human remains. *J. Roy. Anthr. Inst.* 58: 57-85.
- BRUZEK J., TILLIER A.-M., 1996: A reconsideration of the Předmostí pelvis (Gravettian, Czech Republic). *Anthropologie* XXXIV, 3: 231-238.
- CHURCHILL S. E., 1994: *Human upper body evolution in the Eurasian Later Pleistocene*. Ph.D. Dissertation, University of New Mexico.
- COQUEUGNIOT H., 1994: Equations d'estimation de la capacité crânienne chez l'enfant: application paléanthropologique. *Anthropologie* XXXII, 3: 243-250.
- COQUEUGNIOT H., 1997: Variabilité diachronique des dimensions crâniennes de l'enfant en Europe Centrale. *Communication to the 1819th meeting of the Société d'Anthropologie de Paris, January 20th*.
- COQUEUGNIOT H., 1998: Variabilité morphologique de la tête osseuse au cours de l'ontogenèse. L'exemple des enfants de l'espèce *Homo sapiens*. Thèse de l'Université Bordeaux 1, spécialité Anthropologie (unpublished).
- COQUEUGNIOT H., 1999: *Le crâne d'Homo sapiens en Euroasie: croissance et variation depuis 100.000 ans*. BAR International Series 822, Oxford.
- DEAN M. C., STRINGER C. B., BROMAGE T. G., 1986: Age at death of the Neanderthal child from Devil's Tower, Gibraltar, and the implications for studies of general growth and development in Neanderthals. *Amer. J. of Phys. Anthropol.* 70: 301-309.
- DODO Y., KONDO O., MUHESEN S., AKAZAWA T., 1998: Anatomy of the Neanderthal infant skeleton from Dederiyeh Cave, Syria. In: T. Akazawa, K. Aoki, O. Bar Yosef (Eds.): *Neanderthals and modern humans in Western Asia*, pp. 323-338. Plenum Press, New York.
- DUARTE C., MAURICIO J., PETTITT P. B., SOUTO P., TRINKAUS E., VAN DER PLICHT H., ZILHÃO J., 1999: The Early Upper Paleolithic human skeleton for the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia. *Proc. Nat. Acad. of Sciences* 96: 7604-7609.

³ The human remains of 29 adult and non-adult individuals were found in the Gravettian Moravian site of Předmostí, but they were destroyed during the 1945 fire at Mikulov Castle.

- FRAIPONT J., LOHEST M., 1887: La race humaine de Néanderthal ou de Canstadt en Belgique. *Archives de Biologie* VII:587-757.
- FRAYER D. W., 1992: The persistence of Neanderthal features in post-Neanderthal Europeans. In: G. Bräuer, F. H. Smith (Eds.): *Continuity or replacement? Controversies in Homo sapiens evolution*, pp. 179-188. Balkema, Rotterdam.
- GAMBIER D., 1986: Etude des os d'enfants du gisement aurignacien de Cro-Magnon, Les Eyzies (Dordogne). *Bull. Mém. Soc. Anthropol.* 3,1: 13-26.
- GAMBIER D., 1989: Fossil hominids from the Early Paleolithic (Aurignacian) of France. In: P. Mellars, C. B. Stringer (Eds.): *The Human revolution. Behavioral and biological perspectives on the origins of modern humans*, pp. 194-211. Edinburgh University Press, Edinburgh.
- GAMBIER D. (Ed.) n.d.: *Anthropologie et paléontologie funéraire des populations du Paléolithique supérieur d'Italie: l'exemple de la double sépulture d'enfants du site de Baoussé Roussé*. Antiquités Nationales, Réunion des Musées Nationaux.
- GARRALDA M.-D., TILLIER A.-M., VANDERMEERSCH B., CABRERA V., GAMBIER D., 1992: Restes humains de l'Aurignacien archaïque de la Cueva del Castillo (Santander, Espagne). *Anthropologie* XXX, 2: 159-164.
- GEN E., KACZANOWSKI K., 1982: Human remains. In: J. K. Kozłowski (Ed.): *Excavations in the Baco Kiro Cave. Final Report*, pp. 75-79. Panstwone wydawnictwo naukowe, Warszawa.
- GOLANOVA L. V., HOFFECKER J. F., KHARITONOV V. M., ROMANOVA G. P., 1999: Mezmaiskaya Cave: a Neanderthal occupation in the Northern Caucasus. *Curr. Anthropol.* 40, 1: 77-86.
- GREMIATSKIY M. A., NESTURKH M. F. (Eds.): 1949: *Teshik-Tash, paleoliticheskiy tshelovek*. Trudi nauchno-issledovatel'skovo instituta antropologii (in Russian).
- HAMBUCKEN A., 1993: Variabilité morphologique et métrique de l'humérus, du radius et de l'ulna des Néandertaliens. Comparaison avec l'homme moderne. Thèse de Doctorat, Université Bordeaux 1, Talence (unpublished).
- HEIM J.-L., 1976: *Les Néandertaliens adultes de La Ferrassie (Dordogne). Etudes anthropologique et comparative*. Archives de l'Institut de paléontologie humaine, Mém. 35. Masson, Paris.
- HEIM J.-L., 1982: *Les enfants néandertaliens de La Ferrassie*. Fondation Singer Polignac, Paris: Masson.
- HERRMANN B., 1977: Über die Reste des postkranialen Skelettes des Neanderthals von Le Moustier. *Z. für Morph. und Anthropol.* 68, 2: 129-149.
- HOLLIDAY T. W., 1995: *Body size and proportions in the Late Pleistocene Western Old World and the origins of modern humans*. Ph.D. Dissertation, University of New Mexico.
- HOLLIDAY T. W., 1999: Brachial and crural indices of European Late Upper Palaeolithic and Mesolithic humans. *J. of Hum. Evol.* 36: 549-566.
- HOVERSE E., RAK Y., LAVIR., KIMBEL B., 1995: Hominid remains from Amud cave in the context of the Levantine Middle Paleolithic. *Paléorient* 21,2: 47-62.
- HUBLIN J.-J., SPOOR F., BRAUN M., ZONNEVELD F., CONDEMI S., 1996: A late Neanderthal associated with Upper Paleolithic artefacts. *Nature* 381: 224-226.
- HUBLIN J.-J., TILLIER A.-M., 1991: L'Homo sapiens en Europe occidentale: gradualisme et rupture. In: J. J. Hublin, A.-M. Tillier (Eds.): *Aux Origines d'Homo sapiens*. Pp. 291-327. Nouvelle Encyclopédie Diderot. Presses Universitaires de France, Paris.
- KLAATSCH H., HAUSER O., 1909: *Homo mousteriensis Hauseri*. *Arch. Für Anthropol.* 3: 287-297.
- LEVEQUE F., VANDERMEERSCH B., 1980: Découverte de restes humains dans un niveau castelperronien à Saint-Césaire (Charente-Maritime). *C. R. Acad. Sci. de Paris* 291: 187-189.
- LUMLEY M.-A. de, 1973: *Anté-néandertaliens et Néandertaliens du Bassin Méditerranéen occidental européen*. Etudes Quaternaires, Mém. 2. Université de Provence, Marseille.
- MADRE-DUPOUY M., 1992: *L'enfant néandertalien du Roc de Marsal. Etude analytique et comparative*. Cahiers de Paléanthropologie. Editions du CNRS, Paris.
- MAJO T., 1992: Ontogénèse de l'os coxal et détermination sexuelle: l'importance de l'ilium. *Bull. Mém. Soc. Anthropol. Paris* 1-2:61-74.
- MAJO T., 1995: Quelques aspects de la croissance de l'os coxal. Application aux Néandertaliens de la Ferrassie. *Anthropologie et Préhistoire* 106: 57-64.
- MAJO T., 1997: Diagnostic auxologique de l'os coxal. In: L. Buchet (Ed.): *L'enfant, son corps, son histoire*. Actes des 7es Journées anthropologiques de Valbonne, 1-3 juin 1994, pp. 165-175. APDCA, Paris.
- MAJO T., TILLIER A.-M., BRUZÉK J., 1993: Test des fonctions discriminantes de Schutkowski impliquant l'ilium pour la détermination du sexe dans des séries d'enfants de sexe et d'âge connus. In: A.-M. Tillier, E. Crubézy, B. Vandermeersch (Eds.): *Croissance et Vieillesse*. Actes du 21e Colloque du groupement des anthropologistes de langue française. *Bull. Mém. Soc. Anthropol. Paris*, 5: 61-68.
- MANN A. E., LAMPL M., MONGE J., 1990: Décompte de périkyrmies chez les enfants néandertaliens de Krapina. *Bull. Mém. Soc. Anthropol. Paris* 2: 213-224.
- MANN A. E., LAMPL M., MONGE J., 1991: The uses of scanning electron microscopy in the reconstruction of neanderthal lifeways. *Amer. J. of Phys. Anthropol.* suppl. 12: 124.
- MANN A. E., VANDERMEERSCH B., 1997: An adolescent female mandible from Montgaudier (Charente, France). *Amer. J. of Phys. Anthropol.* 103: 507-527.
- MARTIN H., 1936: Nouvelles constatations faites dans la station aurignacienne de La Quina (Charente), tranchées X et Y. *Bull. de la S. P. F.* 33: 177-216.
- MATIEGKA J., 1934-1938: *Homo Předměstensis. Fossilní člověk z Předměstí na Moravě*. Vol. 1: *Lebky*, Vol. 2: *Ostatní části kostrové*. Česká akademie věd a umění. Praha (in Czech).
- MCCOWN T. D., KEITH A., 1939: *The Stone Age of Mount Carmel*. Vol. II. Clarendon University Press, Oxford.
- MEREDITH H. V., 1957: Change in the profile of the osseous chin during childhood. *Amer. J. of Phys. Anthropol.* 15, 2:247-252.
- MINUGH N., 1983: The Mladeč 3 child: Aspects of cranial ontogeny in early anatomically modern Europeans (abstract). *Amer. J. of Phys. Anthropol.* 60: 228.
- MINUGH PURVIS N., 1988: *Patterns of craniofacial growth and development in Upper Pleistocene Hominids*. Ph.D. Thesis. UMI Dissertation Information Service, Ann Arbor (USA).
- MINUGH PURVIS N., 1998: The search for the Earliest Modern Europeans. In: T. Akazawa, K. Aoki, O. Bar Yosef (Eds.): *Neandertals and Modern Humans in Western Asia*. Acts of the Tokyo University Museum Symposium, Neanderthals and Modern Humans in West Asia, 20-25 November 1995. Pp. 339-352.
- MOLLESON T. I., COX M., WALDRON A. H., WHITAKER D. K., 1993: *The Spitalfields project. Vol. 2: The Anthropology CBA Research Report*. 86, York.
- NARA T., 1994: Etude de la variabilité de certains caractères métriques et morphologiques des Néandertaliens. Thèse de l'Université Bordeaux 1, spécialité anthropologie (unpublished).
- NEIBURGER D. D. S., 1990: Enamel hypoplasias: poor indicators of dietary stress. *Amer. J. of Phys. Anthropol.* 82: 231-233.
- OGILVIE M. D., CURRAN B. K., TRINKAUS E., 1989: The incidence and patterning of dental enamel hypoplasias among the Neandertals. *Amer. J. of Phys. Anthropol.* 79: 25-41.
- PAP I., TILLIER A.-M., ARENSBURG B., CHECH M., 1996: The Subalyuk Neanderthal Remains (Hungary): a re-examination. *Annales historico-naturales (Musei nationalis Hungarici)* 88: 233-270.
- PONCE DE LEONE M. S., ZOLLIKOFFER C. P. E., 1999: New evidence from Le Moustier 1: Computer-assisted reconstruction and morphometry of the skull. *The Anatomical Record* 254: 474-489.
- RADOVIC J., SMITH F. E., TRINKAUS E., WOLPOFF M. H., 1988: *The Krapina Hominids. An illustrated catalog of skeletal collection*. Mladost, Zagreb.
- RAK Y., 1990: On the differences between two pelvises of Mousterian context from Qafzeh and Kebara Caves, Israel. *Amer. J. of Phys. Anthropol.* 81: 323-332.
- RAK Y., 1991: The pelvis. In: O. Bar-Yosef, B. Vandermeersch (Eds.): *Le squelette mousterien de Kébara 2*. Pp.147-156. Cahiers de Paléanthropologie. Editions du CNRS, Paris.
- RAK Y., KIMBEL B., HOVERSE E., 1994: A Neanderthal infant from Amud Cave, Israel. *J. of Hum. Evol.* 26: 313-324.
- ROSENBERG K. R., 1988: The functional significance of the Neanderthal pubic length. *Curr. Anthropol.* 29, 4: 595-617.
- SKINNER M. K., 1986: An enigmatic hypoplastic defect of the deciduous canine. *Amer. J. of Phys. Anthropol.* 69: 59-69.
- SKINNER M. K., 1989: Developmental stress in immature hominids from the Late Pleistocene of Western Europe: Evidence from dental attrition and enamel hypoplasia (abstract). *Amer. J. of Phys. Anthropol.* 78: 303-304.
- SMITH F. H., 1976: *The neanderthal remains from Krapina. A descriptive and comparative study*. Report of investigations Number 15, University of Tennessee.
- SAUNDERS S. R., HOPPA R. D., 1993: Growth deficit in survivors and non-survivors: biological mortality bias in subadult skeletal samples. *Yearbook of Phys. Anthropol.* 36: 127-151.
- STEWART T. D., 1960: Form of the pubic bone in neanderthal man. *Science* 131: 1437-1438.
- STRINGER C. B., DEAN M. C., MARTIN R. D., 1990: A comparative study of cranial and dental development within recent British sample and among Neandertals. In: C. E. J. Rousseau (Ed.): *Primate life history and evolution*. Pp. 115-152. Wiley Liss Inc.
- STRINGER C. B., HUBLIN J.-J., VANDERMEERSCH B., 1984: The origin of anatomically modern humans in Western Europe. In: F. H. Smith, Spencer (Eds.): *The origin of modern humans*. Pp. 51-135. Alan R. Liss Inc.
- THOMA A., 1963: The dentition of the Subalyuk Neanderthal child. *Z. Morph. Anthropol.* 54, 2: 127-150.
- TILLIER A.-M., 1986: Quelques aspects de l'ontogénèse du squelette crânien des Néandertaliens. In: V. V. Novotný, A. Mizerová (Eds.): *Fossil Man - New Facts, New Ideas*. Anthropos (Brno) vol. 23: 207-216. Brno.
- TILLIER A.-M., 1989: The evolution of modern humans: Evidence from young Mousterian individuals. In: P. Mellars, C. B. Stringer (Eds.): *The Human revolution. Behavioral and biological perspectives on the origins of modern humans*. Pp. 286-297. Edinburgh University Press, Edinburgh.
- TILLIER A.-M., 1990: Néandertaliens et origine de l'homme moderne en Europe, quelques réflexions sur la controverse. In: C. Farizy (Ed.): *Paléolithique moyen récent et Paléolithique supérieur ancien - ruptures et transitions*. Mémoires du Musée de Préhistoire d'Ile-de-France. Musée Ile-de-France, 3: 21-24. Paris.
- TILLIER A.-M., 1995: Neanderthal ontogeny: a new source for critical analysis. *Anthropologie (Brno)* XXXIII, 1-2: 63-68.
- TILLIER A.-M., 1998: Ontogenetic variation in Late Pleistocene *Homo sapiens* from the Near East: Implications for methodological bias in reconstructing evolutionary biology. In: T. Akazawa, K. Aoki, O. Bar Yosef (Eds.): *Neandertals and Modern Humans in Western Asia*. Acts of the Tokyo University Museum Symposium, Neanderthals and Modern Humans in West Asia, 20-25 November 1995. Pp. 381-390.
- TILLIER A.-M., 1999: *Les enfants moustériens de Qafzeh. Interprétation phylogénétique et paléoaurologique*. Cahiers de Paléanthropologie, CNRS Editions, Paris.
- TILLIER A.-M., MAJO T., BRUZÉK J., 1995: Limites d'une approche "bio-culturelle" des populations anciennes: l'exemple du complexe fémoro-pelvien des Néandertaliens. Actes du Colloque "Nature et Culture" 1993. *ERAUL* 68: 579-595. Liège.
- TILLIER A.-M., MANN A. E., MONGE J., LAMPL M., 1995: L'ontogénèse, la croissance de l'émail dentaire et l'origine de l'homme moderne: l'exemple des Néandertaliens. *Bull. Soc. Royale Belge d'Anthropologie et Préhistoire* 106: 97-104.
- TOMPKINS R. L., 1996: Relative dental development of Upper Pleistocene hominids compared to human population variation. *Amer. J. of Phys. Anthropol.* 99:103-118.
- TOMPKINS R. L., TRINKAUS E., 1987: La Ferrassie 6 and the development of Neanderthal pubic morphology. *Amer. J. of Phys. Anthropol.* 73: 223-239.
- TRINKAUS E., 1976: The Morphology of European and Southwest Asian Neanderthal pubic bones. *Amer. J. of Phys. Anthropol.* 44: 95-104.
- TRINKAUS E., 1983a: Neanderthal postcrania and the adaptive shift to modern humans. In: E. Trinkaus (Ed.): *The Mousterian legacy*. BAR Intern. Series, 164: 165-200. Oxford.
- TRINKAUS E., 1983b: *The Shanidar Neandertals*. Academic Press, New York.
- TRINKAUS E., 1990: Morphological contrast between the Near Eastern Qafzeh/Skhul and late archaic human samples: grounds for a behavioral difference? In: T. Akazawa, K. Aoki, T. Kimura (Eds.): *The Evolution and dispersal of Modern Humans in Asia*, pp. 277-295. Hokusen-Sha, Tokyo.
- VANDERMEERSCH B., 1981: *Les hommes fossiles de Qafzeh (Israël)*. Cahiers de Paléanthropologie. Editions du CNRS, Paris.
- VANDERMEERSCH B., TILLIER A.-M., MANN A. E., LAMPL M., MONGE J., 1995: Variation in the dental enamel of living populations: implications for human origins. *Amer. J. of Phys. Anthropol.*, annual meeting issue, supplement. 20: 129.
- VANDERMEERSCH B., TRINKAUS E., 1995: The postcranial remains of the Regourdou 1 Neanderthal: the shoulder and arm remains. *J. of Hum. Evol.* 28, 5: 439-476.
- VERNEAU R., 1906: *Les grottes de Grimaldi (Baoussé-Roussé). Tome II, Fascicule 1: Anthropologie*. Pp. 1-209. Imprimerie de Monaco.
- VILLEMEUR I., 1994: *La main des Néandertaliens. Comparaison avec la main des hommes de type moderne. Morphologie et mécanique*. Cahiers de Paléanthropologie, CNRS Editions, Paris.
- VLČEK E., 1973: Post-cranial skeleton of a Neanderthal child from Kiik-Koba, USSR. *J. of Hum. Evol.* 2: 537-546.
- VLČEK E., 1993: *Fossile Menschenfunde von Weimar-Ehringsdorf*. Thüringisches Landesamt für Archäologische Denkmalpflege, Kommissionsverlag. Konrad Theiss Verlag, Stuttgart.
- WOLPOFF M. H., 1979: The Krapina Dental remains. *Amer. J. of Phys. Anthropol.* 50: 67-114.

- WOLPOFF M. H., 1989: The place of the Neandertals in human evolution. In: E. Trinkaus (Ed.): *The emergence of Modern Humans*. Pp. 97-141. University Press, Cambridge.
- WOLPOFF M. H., 1992: Theories of modern origins. In: G. Bräuer, F. H. Smith (Eds.): *Continuity or replacement? Controversies in Homo sapiens evolution*. Pp. 25-63. Balkema, Rotterdam.
- YOUNG R. W., 1957: Postnatal growth of the frontal and parietal bones in white males. *Amer. J. of Phys. Anthropol.* 15, 3: 367-386.
- XAVIER DA CUNHA A., XAVIER DE MORAIS M. H., 1961: Estudo antropológico da clavícula nos Portugueses. *Cont. Para o Estudo da Antrop. portuguesa*. Vol. VII, Fas. 5. Coimbra.

Anne-Marie Tillier
UMR 5809 CNRS
Laboratoire d'Anthropologie des Populations
du Passé
Université Bordeaux 1
Avenue des Facultés
33405 Talence
Tel.: 0033 55684 8935
Fax: 0033 55796 2545
E-mail : am.tillier@anthropologie.
u-bordeaux.fr