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NEANDERTHAL ONTOGENY: A NEW SOURCE FOR CRITICAL ANALYSIS

ABSTRACT: As a result of the evolutionary perception of Neanderthals in human evolution, there has been a tendency to explain their distinctiveness by biological adaptive changes during their life. The present paper is an attempt to discuss some of the data used in discussions regarding Neanderthal ontogeny and to question the evidence for an accelerated maturation of Neanderthal children.

KEY WORDS: Neanderthal ontogeny – Dental development – Cranial growth

INTRODUCTION

From the early part of the Upper Pleistocene, Neanderthals emerged in Europe as a stage of human ancestry, with a long evolutionary history extending from 300.000 years to 35.000 years ago they constituted the largest sample available for any non-anatomically modern humans of the old Ancient World.

The origin of the concept of different ontogenetic patterns between Neanderthals and modern humans derives from the first publication of immature Neanderthal remains almost seventy years ago. When H. Martin published a monograph devoted to the La Quina child from Charente, France in 1926, he emphasized the differences between this child and a modern child of the same age, and underlined the « pithecoid » features of the fossil immature specimen. Over the past century, excavations have lead scholars to commonly associate Neanderthals with a Mousterian assemblage , and to see them as representatives of an evolutionary branch that became extinct with the emergence of modern humans. The recent discovery at Saint-Césaire in France (Levêque et Vandermeersch, 1981; Lévęque, 1989; Mercier et al., 1991) has provided evidence that Neanderthals were also tool-makers of an Upper Paleolithic industry. However it is suggested that this industry, i.e. the Chatelperronian in France, is completely different from other Upper Paleolithic assemblages (Pellegrin, 1995).

Indeed, the theory that, in Europe, a major bio-behavioral shift had occurred between Neanderthals and the first anatomically modern humans is supported by several scholars (e.g. Smith, 1983, 1991; Smith and Paquette, 1989; Trinkaus 1983a, 1989). Probably the main reason for this is that modern humans identified in Europe are associated with later Upper Paleolithic industries than the Chatelperronian. The morphological changes which occurred with the emergence of modern humans in Europe (i.e. emergence of the fully Upper Paleolithic technology for many scholars) might be essentially morphogenetic and adaptive. The possible identification of any ontogenetic differences between Neanderthals and anatomically modern humans could potentially be significant in understanding their distinctive adult anatomy, and was employed in arguments regarding their overall adaptive effectiveness.

Although the paleoanthropology of the last 100 century from the Mediterranean Levant has documented the association of early modern humans with a Mousterian assemblage (e.g. McCown and Keith, 1939; Vandermeersch, 1981; Tillier, 1984; Meignen et al., 1989), for a few scholars the distinctiveness of the Neanderthals, regardless of their proposed evolutionary position, is still associated with specific adaptive growth patterns (e.g. Keith, 1931; Vallois, 1937; Thoma, 1963; Vlček, 1970, 1973; Brothwell, 1975; Heim, 1982; Danilova, 1983; Trinkaus, 1983, 1984; Dean, Stringer and Bromage, 1986; Arsuaga et al., 1989; Trinkaus and Tompkins, 1990; Stringer, Dean and Martin, 1990).

Discussions regarding the non-modern-like growth and maturation pattern in Neanderthals have been assumed on several lines of evidence: gestation and maturation of neonates, dental development and brain growth in infants and children, and the early appearance of adult Neanderthal characteristics. While a better knowledge of the phylogenetic significance of some so-called Neanderthal features is still required, the investigation of the analysis of the postcranial ontogenetic development is rather more difficult than for the cranial skeleton (Tillier, 1986, 1989). By contrast, a reconsideration of some of the data used for the cranial skeleton in the discussion of Neanderthal ontogeny demonstrates that the assumption of an acceleration may be seriously questioned in light of the fossil evidence.

NEANDERTHAL GESTATION AND NEONATE MATURATION

While consistent growth analyses from living populations of children imply longitudinal studies, it must be emphasized that only cross-sectional studies are available for Neanderthals. In addition, the Neanderthal population was spread broadly across Europe and Western Asia *(Figure 1)*, and spanned more than 300.000 years. Therefore, possible evolutionary changes within the lineage over time and geographical variation always have to be considered.

Recent years have seen an increasing concern with different interpretations for the functional significance of the adult pubic morphology of Neanderthals (i.e. the medio-lateral elongation of the superior ilio-pubic ramus). Central to these interpretations is the role of obstetric requirements. It has been proposed that the elongated pubis may imply enlarged Neanderthal cephalo-pelvic dimensions, with regard to either a prolongation of gestation (Trinkaus, 1983a,1984) or to accelerated brain growth in utero (Dean et al., 1986). Further studies of adult Neanderthal pelvic size have discussed this idea of different pregnancy and specific obstetric requirements in Neanderthals (Rosenberg, 1986, 1988 ; Rak and Arensburg, 1987; Rak 1991).

The accelerated neonate maturation is based on the assumption that Neanderthal neonates are characterized by a bigger cranial size than modern neonates. It should be emphasized that this is assumed from the larger adult brain size by comparison with modern humans, and not on the basis of available data from immature specimens (Tillier, 1986, 1989; 1992). The presently available sample of Neanderthal neonates and infants includes six individuals from around the time of birth to about 7–9 months of age: La Ferrassie 4/4 bis and 5, L'Hortus I/Ibis from France; Shanidar 7 et 9 from Iraq; Kebara 1 from Israel (Heim, 1982; de Lumley, 1973; Trinkaus, 1983b; Smith and Arensburg, 1977). Among the cranial remains of these individuals, not even a single complete bone can be scientifically reconstructed, and a consideration of these remains does not permit the basic assumption of neurocranial dimension enlargement in Neanderthal neonates relative to modern neonates (Tillier, 1989, 1990).

The claim that Neanderthal infants were not born at the same stage of development as modern infants, and that they did not require a similar degree of parental care, as suggested by some scholars (e.g. Bunney, 1986; Trinkaus and Tompkins, 1990: 168-169; Smith, 1991), remains purely speculative. Interestingly, it shoud be

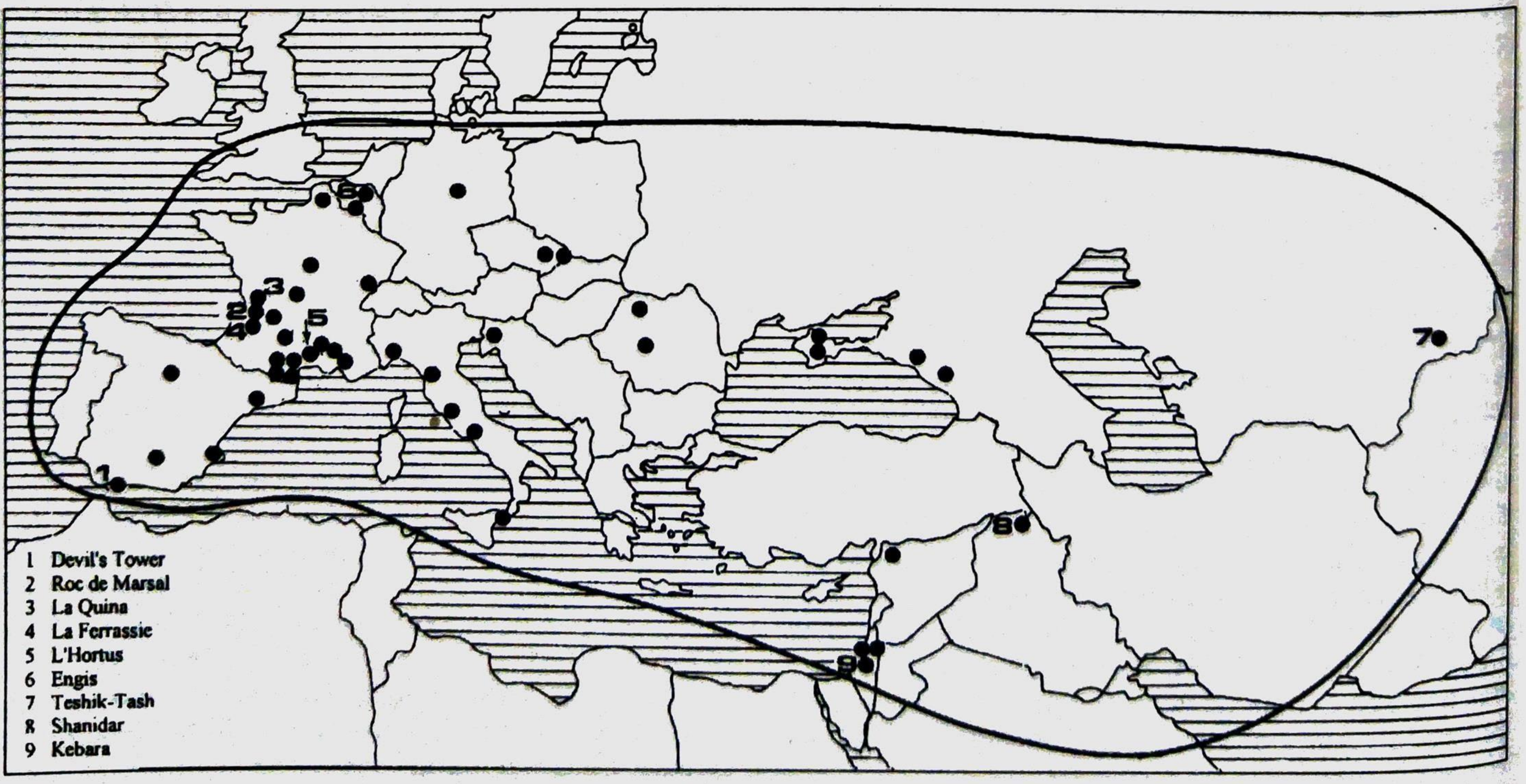

FIGURE 1. Geographic position of the major sites with immature individuals attributed to the Neanderthal population. The sites numbered refer to the fossil individuals cited in the text.

recalled that European Upper Paleolithic hominids (e.g. Vandermeersch, 1981 ; Matiegka, 1934; Vallois and Billy, 1965) also had large adult brain size, in terms of the average usually employed. However a non-modern neonate maturation pattern has never been proposed, as these hominids, exhibiting modern morphological affinities, are thought to be bio-behaviorally modern, and thus to have been more efficient than Neanderthals at taking care of premature babies.

At the present time, in our opinion, the precise taxonomic identification of neanderthal neonate and infant morphology remains an open question given the preservation of the fossil record. As we have mentioned already, exploration of the first Neanderthal ontogenetic stages lies in the examination of a few specimens. The cranial skeletal remains are incomplete and damaged , and it is virtually impossible to assess the phylogenetic significance of some features, such as bone thickness, when comparative analysis is restricted to European recent neonates and infants (due to the lack of Upper Paleolithic neonates available for comparison). It is difficult to identify features in the cranial and postcranial skeleton of these individuals that might allow us to align them with the Neanderthal group. However, regardless of the anatomical features they manifest, all the specimens uncovered were associated with Mousterian assemblages, and were considered members of the same group as the other individuals found in the sites.

NEANDERTHAL ONTOGENY FROM INFANCY TO ADULTHOOD

Knowledge of the later stages of Neanderthal ontogeny is based on the analysis of numerous immature specimens (a minimum of sixty individuals) that allow us to evaluate the variation potentially present in these extinct hominids. Arguments in favor of an acceleration in Neanderthal childhood development are based on the timing of dental crown calcification, metrics, and early identification of adult morphological characteristics.

Dental development

Based on dental calcification and eruption data, a number of scholars have suggested that Neanderthals showed accelerated dental development (e.g. Thoma, 1963; Dean et al., 1986; Stringer et al., 1990; Arsuaga et al., 1989). However, a substantial variability within individuals in the immature Neanderthal sample exists in the tooth calcification sequence and in the tooth eruption sequence (Legoux, 1965, 1966, 1970; Tillier, 1988, 1989, 1993). A recent study of incremental lines in tooth enamel, using one single central permanent incisor, was employed in arguments regarding accelerated dental development in Neanderthals, consistent with the premises of accelerated growth (Dean et al., 1986; Stringer et al., 1990).

Cautionary remarks were published regarding this histological study (Tillier, 1988; Trinkaus and Tompkins, 1990), as a conclusion derived from one single Neanderthal tooth had to be considered as premature. In fact, further studies of surface enamel increments in an enlarged sample of Neanderthal and modern human teeth (Mann et al., 1990, 1991; Lampl et al., 1991) demonstrate that any assumption about differences between Neanderthals and modern humans in terms of dental development rate, based on dental enamel histological studies, is suspect. Additionally, enamel incremental studies reinforce conclusions previously made by scholars employing tooth calcification and eruption sequence in Neanderthals, which means that one single specimen cannot be considered as representative of the total Neanderthal population.

Cranial metrics

Recent studies of immature Neanderthal individuals have emphasized the importance of considering the cranial measurements, or other morphometric data on the postcranial bones in an analysis of maturation patterning (e.g. Vlček; 1972; Heim, 1982; Dean et al., 1986; Tompkins and Trinkaus, 1987; Stringer et al., 1990). In fact, assessment of maturation patterns derived from one individual can, again, be debated, as data for Neanderthal children provide more reliable evidence of biological variability, although some ontogenetic stages are missing.

Compared to growth studies undertaken using living populations of humans, our knowledge of Neanderthal cranial growth, for instance, is necessarily based on a few individuals. But even a limited sample of Neanderthal children provides evidence of variability consistent with individual maturation patterns between children in living populations (Tillier, 1988, 1991, in press). Thus, in the absence of longitudinal studies for extinct children, only the consideration of all the available juvenile specimens may provide a better, appropriate comparative framework for growth studies on Neanderthals.

Indeed, evidence for individual cranial variation in size can be easily taken from an examination of the fossil record (Tillier, 1988, 1993). For instance, two Neanderthal juveniles with close dental ages (ca. 5 years) exhibit different cranial dimensions, as shown by Engis 2, from Belgium, and Devil's Tower, from Gibraltar. Equally important, Neanderthal children with different individual ages at death can display similarities in cranial size : this is the case for Devil's Tower (ca. 5 years old) and Teshik-Tash (ca. 9 years old) from Uzbekhistan.

The Upper Paleolithic children share with Neanderthals a cranial dimension enlargement, when a comparison is made with a recent sample of known age *(Figure 2)*. At close individual dental ages, Neanderthal and Upper Paleolithic children from a restricted area such as the southwest of France exhibit similarities in cranial size; this can be illustrated by the Roc de Marsal Neanderthal child ca. 3 years old, compared to the La Madeleine and Le Figuier children (Billy, 1979; Tillier, 1983b; Heim, 1991).

Obviously, the cranial size of one single specimen can not form the focus of an argument for accelerated growth. Moreover measurements are insufficient for aging skulls

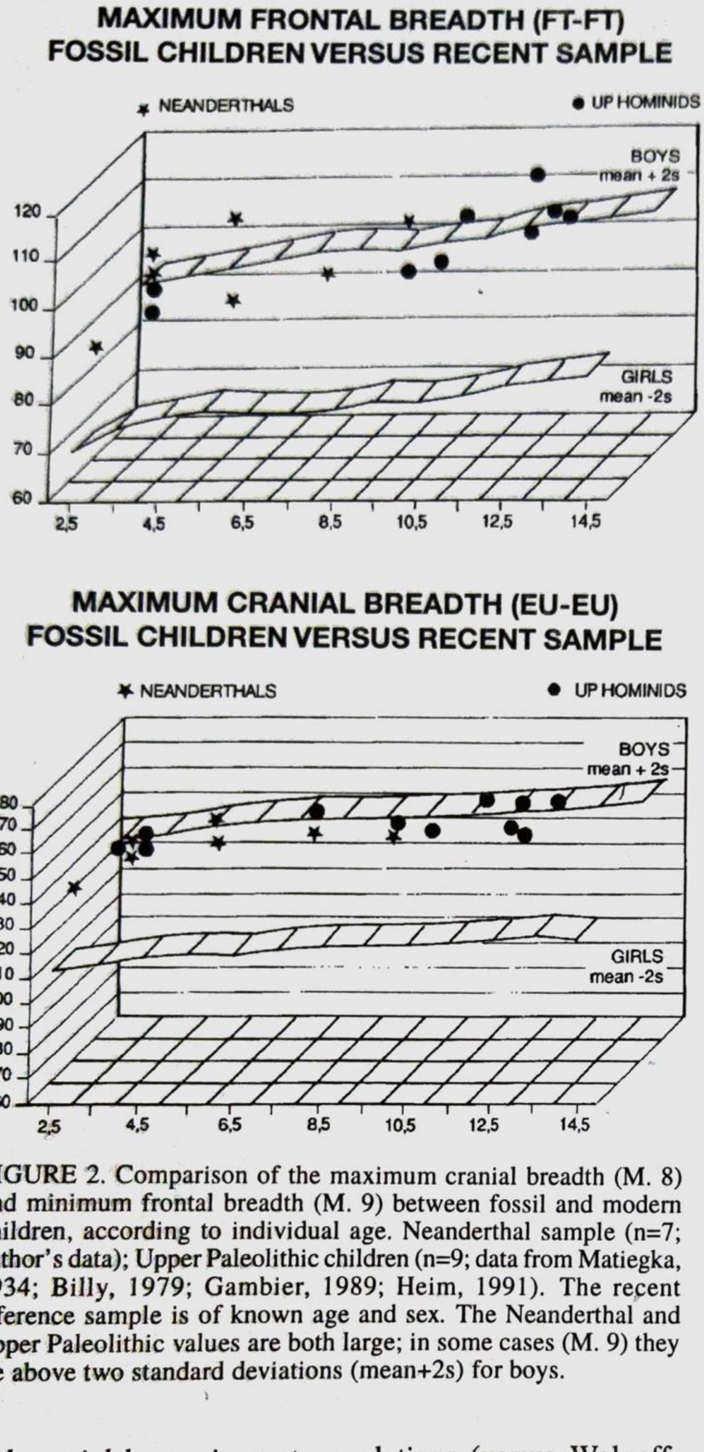

FIGURE 2. Comparison of the maximum cranial breadth (M. 8) and minimum frontal breadth (M. 9) between fossil and modern children, according to individual age. Neanderthal sample (n=7; author's data); Upper Paleolithic children (n=9; data from Matiegka, 1934; Billy, 1979; Gambier, 1989; Heim, 1991). The recent reference sample is of known age and sex. The Neanderthal and Upper Paleolithic values are both large; in some cases (M. 9) they are above two standard deviations (mean+2s) for boys.

and cranial bones in past populations (versus Wolpoff, 1980:314; Minugh Purvis and Radovcic, 1991).

Development of the adult morphology

Several studies (e.g. Vlcek, 1970, 1973; Heim, 1982; Danilova, 1983; Arsuaga et al., 1989; Tompkins and Trinkaus, 1987) have suggested that the early ontogenetic appearance of adult Neanderthal morphological characteristics may be indicators of growth pattern distinctiveness between Neanderthals and modern humans. A few studies (Tillier, 1981, 1983a et b, 1986, 1993 ; Minugh-Purvis, 1988; Madre-Dupouy, 1991) have focused on the ontogenetic appearance of adult morphology in an attempt to understand the phylogenetic history of the Neanderthals. In fact, the identification of one single feature of adult Neanderthal morphology can not form the focus of an argument for accelerated maturation of the individual Neanderthal child.

In documenting Neanderthal ontogeny, we now have evidence that the appearance of adult Neanderthal features during development exhibit heterochrony, in both the cranial and post-cranial skeleton. This means that the growth processes eventually resulting in distinct Neanderthal adult cranial morphology seem especially intensified in the chronologically oldest individuals, such as Teshik-Tash, ca. 9 years old (Tillier, 1986, 1991, 1993). Thus, most of the characteristics commonly employed for the distinctiveness of a Neanderthal adult mandible (e.g. retromolar space, backwards positioning of the mental foramina below the first permanent molar, horizontal-oval shape of the mandibular foramen) are related to the achievement of permanent dentition. By contrast, only plesiomorphic retentions can be recognized on immature mandibles, i.e. receding symphysis, lack of a chin, planum alveolare, body robusticity. These immature mandibles cannot be distinguished from bones attributed to other archaic *Homo sapiens* than Neanderthals. This means that the taxonomic assignment of immature Neanderthal specimens is complicated by the changes in morphology brought about by the process of growth itself. The eruption and achievement of permanent dentition are accompanied by a dental arch and mandibular body remodelling that gives place to retromolar space and posterior positioning of the mental foramina (Tillier, 1981).

Although the exploration of the development of Neanderthal cranial morphology is subject to the lack of some ontogenetic stages, it is quite clear that some of Neanderthal features appear later on the face than on the braincase (Tillier, 1986). However, in addition to age-related changes, individual variation affects the cranial morphology of non-adult Neanderthals. This variation can be illustrated by examination of the morphology of the immature Neanderthal supraorbital torus on four individuals. Engis 2 (ca. 5 years old) and La Quina 18 (ca. 7 years old, Southwest of France) manifest no supraorbital proeminence in the lateral areas, while Devil's Tower (ca. 5 years old) and Teshik-Tash (ca. 9 years old) display a continuous bulbing of the supraorbital region. The difference between Devil's Tower and Teshik-Tash refers to age-related changes, with an increase of the supraorbital proeminence well separated from the squamous part of the frontal bone on the later (Tillier, 1983a). Other aspects of individual variation can be noted on the skull and the mandible (Tillier, in press). It seems at the present time quite impossible to factor out the influence of sexual dimorphism or/and geographical changes in individual variation affecting Neanderthal ontogeny.

CONCLUSION

In conclusion, most of the arguments brought in favor of accelerated Neanderthal ontogeny were advanced on the basis of single specimens, and the existing biological variability has been overlooked. However, it should be recalled that this variability is observed within a fossil population that manifests, a large geographical dispersal and a large chronological distribution.

The other conclusion refers to the heterochrony affecting the development of the features during Neanderthal ontogeny. Thus the taxonomic assignment of immature Neanderthal specimens is complicated by changes in morphology brought about by the process of growth itself.

Actually, the assumption that Neanderthal ontogeny was accelerated with regard to that of modern humans can be seriously questioned. There are still many problems inherent in attempting to reconstruct an ontogenetic model peculiar to Neanderthals, on the basis of information exclusively derived from living populations. Although there are great difficulties in growth analyses from extinct populations, detailed studies are indeed fruitful, and there is no doubt that the key to problems of recent hominid evolution stage rests, to some extent, with ontogenetic studies of Neanderthals and early anatomically modern humans.

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