

# Chapter 12

## Facts and Ideas in Paleolithic Growth Studies (Paleoauxology)

### Evidence from Neanderthals in Europe

Anne-Marie Tillier

**Abstract** In the study of prehistoric populations, the identification of taxonomic markers derives from the study of preserved adult individuals. A complementary approach for understanding morphological differences between populations involves an investigation of ontogenetic and growth patterns. Within the Neanderthal population, the specimens employed to document distinct developmental stages originated from sites often separated by hundreds (or thousands) of kilometers and thousands of years in time. In the reconstruction of maturation patterns in Neanderthals, there are difficulties related to the availability of the fossil record itself, the evaluation of geographical and temporal variations, and the choice of appropriate comparative reference samples. Among Neanderthals, the importance of sexual dimorphism in the manifestation of morphological variation and age-related changes during the growth period cannot be evaluated. However, comparative analyses provide accurate information regarding the ontogenetic appearance of several diagnostic Neanderthal characteristics and reveal similarities and contrasts between Neanderthal and early modern children. This contribution attempts to address few aspects of the ongoing debate regarding maturational events and life history in non-adult Neanderthals from western and central Europe.

**Keywords** Children • Diagnostic traits • Health status • Middle Paleolithic • Ontogeny • Skeletal variation • Temporal and/or regional changes

### Introduction

Neanderthals have been found in sites geographically dispersed in Western Eurasia and over long time duration, probably more than 250,000 years. Most of the human remains

were associated with a Middle Paleolithic (i.e. Mousterian *sensu largo*) archaeological context; very few have been found with Lower Upper Paleolithic industries. The Neanderthal fossil record has played a major role in the development of studies from an auxological perspective that addressed the question of origin of modern human-like pattern of growth.

In the last two decades, paleoanthropologists have attempted to improve the methods of analyzing immature skeletons, and the impact of methodological advancements in dental and skeletal analyses has stimulated the emergence of paleoauxology. Hypothetical scenarios have emerged concerning life-history stages in Neanderthals and contradictory hypotheses have been produced focusing on growth and development. The specimens employed to document distinct developmental stages within the entire Neanderthal population originated from sites often separated by hundreds (or thousands) of kilometers and thousands of years in time. However, a general lack of appreciation for individual variation within and between groups (geographically and chronologically dispersed) characterizes studies comparing nonadult fossil specimens.

Comparative growth studies in extant populations have demonstrated that environmental differences and selective pressures have effects on the growing child. Accordingly, there is no guarantee that human groups, geographically distant in western Eurasia and evolving in different sites and habitats during several tens of thousands of years, shared similar growth patterns. In the present context, we think that there are limitations to the meaning of large-scale comparative analyses of immature fossil specimens in terms of paleoauxological reconstruction. This is the reason why this contribution will focus on individuals originating in western and central Europe.

### Sampling Nonadult Neanderthals in Europe

Besides the geographical and chronological dispersals, reconstruction of Neanderthal childhood from skeletal studies has had to face practical difficulties, such as bone preservation

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A.-M. Tillier (✉)

Laboratoire d'Anthropologie des Populations du Passé, UMR 5199-PACEA, Université Bordeaux 1, avenue des Facultés, 33405 Talence, France  
e-mail: am.tillier@pacea.u-bordeaux1.fr

and sampling limitations. While nonadult individuals represent no more than 25% of the overall Neanderthal sample, given the preservation of the fossil record, some skeletal growth stages are less well documented than others. Until the recent rediscovery of the Le Moustier 2 skeleton from South-western France (Maureille 2002), fetus and infant remains (i.e. individuals less than 1 year old) were really fragmentary. Age distribution (estimated age at death based on tooth development) of nonadult Neanderthal individuals from European sites shows a prevalence of the second age-class (1–4 year), followed by the class 10–14 year. At the present time, late adolescence is represented by a unique specimen, Le Moustier 1 (Ullrich 2005).

Within the fossil record, specimens with both skull and infracranial bones preserved are rare (e.g. Roc de Marsal, Le Moustier 1 and 2 in Southwestern France). There are a very small number of individuals represented by almost complete skulls or crania (e.g. Pech de l'Azé1, La Quina H18 in France, Engis 2 in Belgium, Subalyuk 2 in Hungary). A majority of Neanderthal immature finds are isolated bones, especially vault elements (e.g. Krapina 1 and 2 in Croatia) or mandibles (e.g. Scladina in Belgium). In a few cases, immature Neanderthals preserve only infracranial elements (e.g. La Ferrassie 6 in France, Kiik-Koba 2 in Crimea, few bones from Cova Negra in Spain) and consideration of the individual's growth profile is rather difficult to assess in the lack of close association with accurate age estimation.

Only a few sites restricted to western and central Europe have a large enough sample size to evaluate individual variation or to permit a within-site comparison between nonadult and adult skeletal morphologies. Yet, even within a single site, the question of contemporaneity arises, as illustrated by the Krapina and Le Moustier sites. At Le Moustier, the history of site excavations and circumstances of discoveries of the specimens led to confusion over the stratigraphical provenance and chronological attribution of the two nonadult individuals (Maureille 2002; Maureille and Turcq 2005). At the Croatian site, two partial immature skulls, Krapina1 and 2, have been unearthed: they originated respectively from level 8 in the upper part of the stratigraphic sequence and level 3 down in the sequence (e.g. Smith 1976; Radović et al. 1988).<sup>1</sup> Krapina1, geologically more recent, represents a single specimen (of unknown dental age estimates) within the large Krapina hominid sample, and the evaluation of several aspects of its peculiar morphology in terms of affinities to its predecessors remains questionable (see Minugh-Purvis et al. 2000; Sansilbano-Collilieux and Tillier 2006).

In this respect, intrapopulation variation might have occurred throughout time that cannot be neglected in the reconstruction of maturation patterns. Potential evolutionary trends in a regional Neanderthal sample are supported by the

Pech de l'Azé and Roc de Marsal children found in sites from the Dordogne separated by less than 25 km (Tillier 1996; Soressi et al. 2007). Evidence of ontogenetic variation in skull morphology between the two individuals of the same age class (differences in facial size and in robustness of the symphyseal region of the mandible) was emphasized by Tillier and radiometric dates recently obtained for both sites provides the basis for a new level of understanding of this individual variation. An early age around 70,000 years BP appears appropriate for the Roc de Marsal deposit associated to with a Mousterian assemblage (Sandgathe et al. 2005), while the Pech de l'Azé specimen (the only fossil hominid found in association with a Mousterian of Acheulean tradition type B) is more recent (Soressi et al. 2007), dated to the early part of oxygen isotope stage 3.

## Becoming a Neanderthal

Neanderthals are commonly seen as a rather homogeneous group morphologically, and skull features traditionally play a major role in their anatomical definition (e.g. Stringer et al. 1984; Hublin and Tillier 1991; Hublin 1998; Condemi 2006). The taxonomic affiliation of immature remains is inferred from the identification of distinguishing anatomical features that have been proposed to describe adult Neanderthal skeletal morphology. However, it must be said that taxonomic identification of immature skeletal remains cannot avoid the significance of morphological changes directly related to growth and maturation processes.

## Fetus, Neonates, and Infants

Apart from Le Moustier 2 (still being studied), the first steps of the ontogenetic trajectory in Neanderthals are documented by fragmentary remains, the taxonomic assignment of which are rather difficult to assess. Based on the examination of a few Eurasian Upper Pleistocene specimens (La Ferrassie 5 and 4, L'Hortus I and Ib, Arcy-sur-Cure in France; Shanidar 7 and 9 in Iraq; Kebara 1 and Qafzeh 13 in Israel), scholars have not been able to identify in early infancy the specific population features that characterize adult cranial morphology (Vlček 1970; de Lumley 1973; Trinkaus 1983; Hublin et al. 1996; Tillier 1986, 1995, 1999; Tillier et al. 2003). On the contrary, Heim (1982: 16–17) described on the two La Ferrassie fragmentary frontal bones a faint thickening of the supraorbital region that was interpreted as an early development of a Neanderthal supraorbital torus. Heim argued that such a morphology had been previously identified on the Staroselye child from Crimea. Yet, this specimen from Crimea is fully

<sup>1</sup>Radiometric techniques applied to animal enamel tooth placed the section (Rink et al. 1999) between 110,000 and 137,000 years BP.

modern in its cranial morphology (Alekseev 1976; Tillier, in Ronen 1982: 315), and moreover its Mousterian attribution is no longer supported (Marks et al. 1997).

Apart from the Le Moustier 2 skeleton, infracranial evidence remains fragmentary and limits the inference of the early appearance of characteristics thought to be diagnostic of Neanderthals. Detailed descriptions of upper and lower limb remains belonging to Neanderthals under 1 year old exist in the literature: they mainly refer to French and Crimean specimens (Vlček 1973, 1975; Heim 1982). However, morphological features of the infant infracranial skeleton in modern humans are far from being well known; comparative studies between fossil and recent populations focus on a few infants who derive from sedentarized populations (i.e. regional osteological collections used in forensic anthropological studies): this can explain the general emphasis on diaphyseal robustness, curvature of long bones (ex: radius), or early appearance of muscle markings (see below, the example of the first metacarpal), in Neanderthal infant appendicular skeletons. In practice, some degree of morphological overlap between Neanderthal and Upper Paleolithic infant specimens cannot be avoided. Finally, the state of preservation of the postcranial skeleton limits body size and limb proportion reconstructions in Neanderthal babies.

### **Age-Related Changes in Individual Distinguishing Features**

At birth, only ear ossicles and the bony labyrinth within the temporal bone are fully grown and have their mature shape and size. There is clearly considerable variability in ear ossicle measurements among extant modern humans (Arensburg et al. 1981; Arensburg and Tillier 1983). The Neanderthal ossicles are preserved in three specimens (Biache St Vaast 1, La Ferrassie 3, and Le Moustier 1; Heim 1982; Ponce de Leon and Zollikofer 1999; Rougier 2003) and are described as different in size and shape from those of modern humans. But, as noted by Spoor (2002: 296), “a larger sample (...) would be required to come to definitive conclusions.”

Information concerning selected traits that can be used in the distinctiveness of Neanderthal bony labyrinth morphology can be obtained from recent publications (e.g., Hublin et al. 1996; Spoor and Zonneveld 1998; Thompson and Illerhaus 1998; Ponce de Leon and Zollikofer 1999; Spoor et al. 2003). The data collected from CT analyses reveal a certain degree of individual variation within the Neanderthal sample as illustrated by the Le Moustier 1 labyrinth. This specimen does not exhibit a “fully typical Neanderthal-like” morphology and it is suggested that such a morphology can be viewed, either as “(..) a sign of gene flow between Neanderthals and modern migrants,” or as a “more extreme form of

(*Neanderthal*) normal range of variation” (Spoor et al. 2003 :162). Related to the former proposal is the assumption that Le Moustier 1 might be considered as a late Neanderthal in the sample, a condition which cannot be established with regard to the historical context of the discovery, as mentioned before. As emphasized by Ponce de Leon and Zollikofer (2005: 256), the Le Moustier 1 labyrinth morphology questions the apomorphies of otic characters.

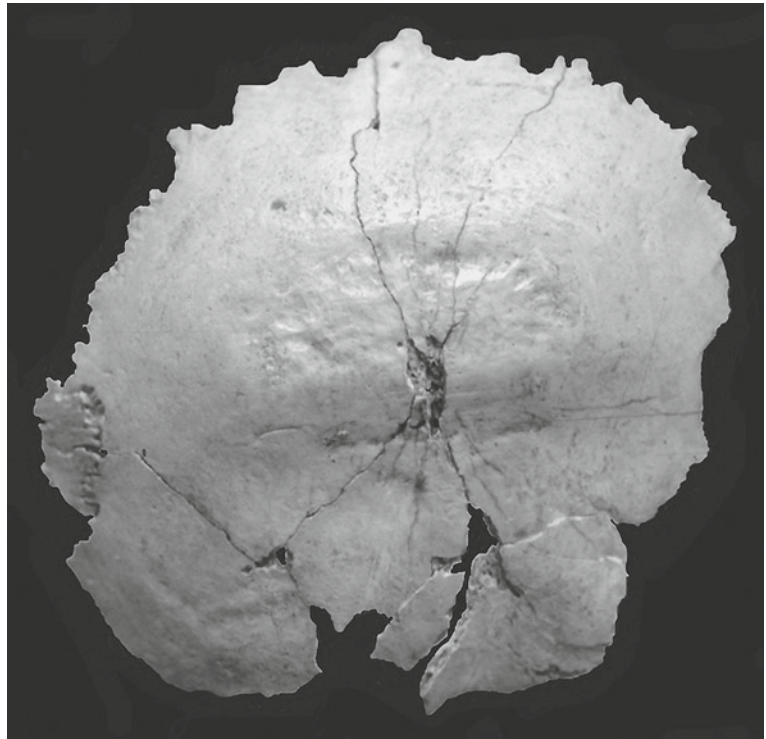
With regard to the external skull development, Vlček (1970) was the first to suggest that individual distinguishing features can be recognized in immature Neanderthals of at least 2 years of age. Hublin (1980), Heim (1982), Tillier (1986), and Minugh-Purvis (1988) have come to a similar conclusion. For instance, the occipital morphologies of young specimens from La Chaise Abri-Suard and La Ferrassie sites (Fig. 12.1) exhibit coexistence of a fully developed suprainiac fossa and bilaterally protruding occipital torus, a low occipital height, a highly convex occipital squama. Similarly, compared to that of modern children, the size of the Neanderthal mastoid process relative to that of the juxtastoid eminence changed less during ontogeny; in other words, adult Neanderthals accentuated a juvenile trait in this part of the temporal bone (Tillier 1983, 1988).

Few researchers argued that similarities and contrasts between Neanderthal and modern human skull morphology evolved as postnatal bone maturation progressed (e.g. Tillier 1983, 1986; Coqueugniot 1999; Williams 2001). Neanderthal juveniles have an absent or reduced supraorbital torus, a more vertical forehead, a more rounded cranial vault (Fig. 12.2).

Similarly, the shape of the foramen magnum in juvenile Neanderthals shows some degree of morphological overlap with modern humans. The Engis 2 child skull from Belgium (ca. 4 years at death), exhibits an elongated foramen magnum, as shown by the value of the breadth/length index (Tillier 1983). On this young specimen, neither the anterior nor the posterior intra-occipital synchondroses are fused. Older Neanderthals from France with a well-preserved basi-cranium, such as the two adults, i.e. La Ferrassie 1 and La Chapelle-aux-Saints, exhibit higher values of the index than that of the Belgian child (Creed-Miles et al. 1996; Tillier 1998, 2000).

Interestingly, Arsuaga et al. (1997) documented within-site age-related individual variation of the foramen magnum shape at Sima de Los Huesos (Spain) that supported similar conclusions about age-related changes among other archaic members of the genus *Homo*. Furthermore, comparative data deriving from analyses of modern children demonstrate that the occurrence of an elongated foramen magnum can be, indeed, interpreted as an age-related trait (Coqueugniot and Le Minor 2002). The changing proportions of the foramen magnum throughout life are in fact partly related to complete closure of both intra-occipital and spheno-occipital

**Fig. 12.1** External view of the occipital bone of the La Ferrassie 8 child showing the development of the suprainiac fossa and bilateral protruding torus on a young child, ca. 2 years old at death (Photo J.-L. Heim)



synchrondroses. On the basis of this constancy through the juvenile years, the presence of an elongated foramen magnum on a very young fossil specimen does not necessarily align it with Neanderthals (Creed-Miles et al. 1996; Tillier 1998; Coqueugniot 1999; versus Rak et al. 1994).

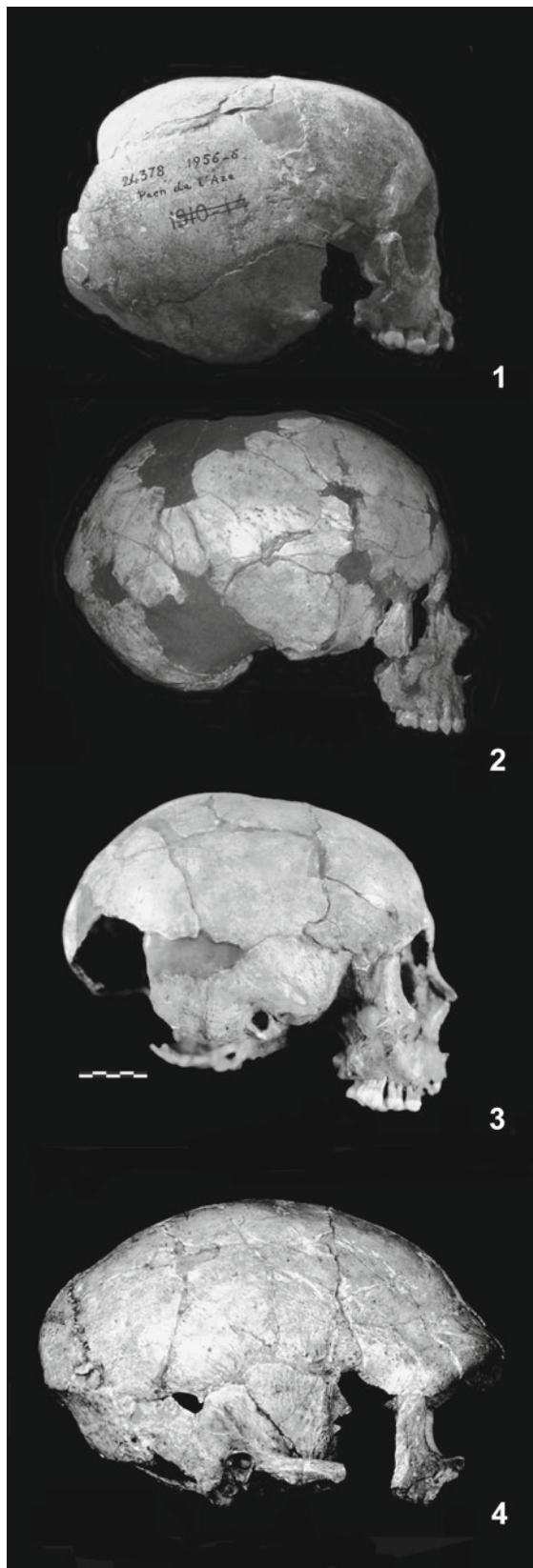
Anatomical traits of the Neanderthal facial skeleton (e.g. midfacial projection, anterior maxillary inflation and straightness of the maxillo-zygomatic profile in norma facialis, double-arched browridge with large pneumatization, posterior positioning of the mental foramen) appear later in ontogeny. A posterior localization of the mental foramen can be observed before the eruption of the first permanent molar in young Neanderthals (Fig. 12.3, Coqueugniot 2000). By contrast, other facial features seem to be fully developed in late childhood (Tillier 1983, 1986, 1987; Minugh-Purvis 1988; Williams 2001) and these changes in developmental patterns occur when children have anterior and posterior permanent teeth (Fig. 12.4a, b).

In conclusion, it is clear that the phylogenetic assignment of immature Neanderthal cranial remains is easier for some skeletal parts than for others, as age-related changes affect the skull morphology (e.g. cranio-facial shape). Only few diagnostic features of the cranial vault are known to be present at early childhood (e.g. Heim 1982; Hublin 1980; Tillier 1983).

### ***Infracranial Skeletal Morphology and Neanderthal Traits Revisited***

The appendicular skeleton and the pelvic girdle are thought to document morphological differences between human groups within the Late Pleistocene hominid sample (e.g. Churchill 1994; Trinkaus 1992; Trinkaus et al. 1998). Most of the features described on the Neanderthal upper and lower limbs can be seen as reflections of the high level of muscularity of these hominids. Consequently, it is not surprising that their differentiation on subadult upper and lower limbs cannot be identified in the early stages of development. Each new discovery of specimens contributes to the knowledge of the range of variation in postcranial skeletal morphology among nonadult Neanderthals and ontogenetic appearance of features currently found in adults (Arsuaga et al. 2007).

As a matter of fact, comparative analysis of Neanderthal and Upper Paleolithic adult skeletal remains provide evidence that some of the diagnostic features described on the Neanderthal appendicular skeleton (i.e. morphology of the scapular axillary border, muscular markings on long bones, claviculo-humeral index, etc.) have also been identified in Lower or Middle Upper Paleolithic skeletons from Europe (e.g. Jelinek 1992; Frayer 1992; Trinkaus et al. 2006).



**Fig. 12.2** Skull development in Neanderthals from Southwestern France. 1 Pech de l'Azé child (ca. 2 years old at death), 2 Roc de Marsal (ca. 3 years old), 3 La Quina H18 (ca. 7 years old), and 4 the adult La Quina 5. Besides age-related changes in skull morphology (supraorbital torus,

Until recently, the comparison between Neanderthal and modern children excluded Upper Paleolithic specimens. Furthermore, given the scarcity of available comparative material of earlier European archaic humans, it remains to be seen what features were already present in earlier, pre-Neanderthal populations in order to clarify the polarities of the traits.

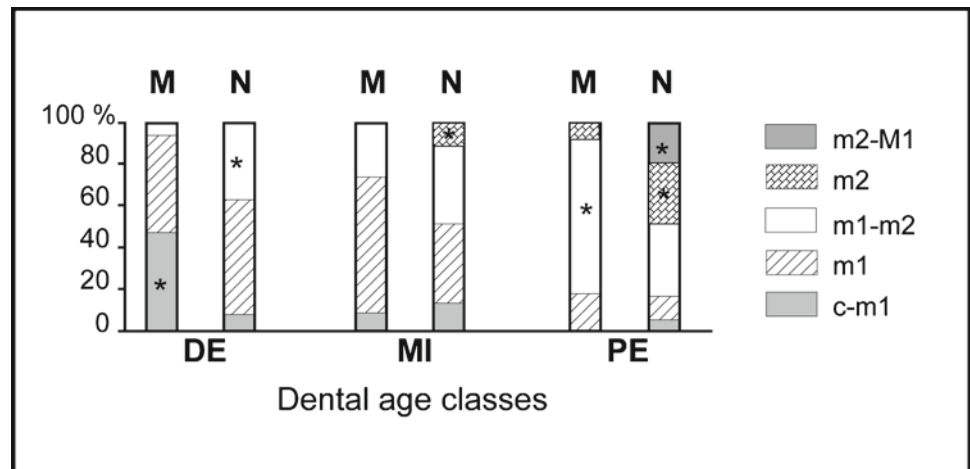
### The Superior Pubic Ramus

Of particular interest here, a few scholars (e.g. McCown and Keith 1939; Stewart 1960; Trinkaus 1976; Rosenberg 1988; Rak 1990) have identified diagnostic features of the Neanderthal hipbone. Special emphasis was given to the superior pubic ramus which, according to the authors, was described as very long and vertically flat among Neanderthals, while short and thick in modern humans. Consequently, the superior pubic ramus was thought to have a shape which had a potential in assessing the Neanderthal affinities of a specimen. Additional data and new discoveries led to a revision of the phylogenetic status of pubic characteristics and an elongated pubic ramus should be regarded as plesiomorphic: it was already present on earlier fossil remains than Neanderthals, as documented by australopithecines, the Sima de Los Huesos specimens in Spain, and was described in early Levantine hominids from Tabun and Skhul (e.g. Arensburg and Belfer-Cohen 1998; Arsuaga et al. 1999; Bonmati and Arsuaga 2005; Tillier 2005a).

Within the immature Neanderthal sample, the number and state of preservation of the hip bone remains limit consistent metric analysis (Majó 2000; Majo and Tillier 2003). Unfortunately, the pubic skeletal part is lacking or poorly preserved among four specimens (Roc de Marsal, Le Moustier 1 and 2, Kiik-Koba 2 in Crimea). From the La Ferrassie rockshelter, two of the immature individuals provided information on the development of juvenile pubic bones (Heim 1982). La Ferrassie 8, a child ca. 2 years old, preserves a large portion of the two superior pubic rami, besides the two nearly complete ilia and one fragment of the left ischium. La Ferrassie 6 hipbone consists of a right pubis and ischium (minus the superior part of the acetabulum), two thirds of the left ilium, as well as fragments of the left ischium and right ilium. No teeth were preserved for this specimen and the age at death of the child was estimated between 3 (Heim 1982) and 4–5 years (Tompkins and Trinkaus 1987; Majo and Tillier 2003).

frontal curvature, height/length skull ratio, occipital bun), it should be reminded that Roc de Marsal and the two La Quina specimens are earlier (attributed to oxygen isotope stage 5 and 4 respectively) than Pech de l'Azé1 (Photos A.-M. Tillier)

**Fig. 12.3** Position of the mental foramen and evolution during growth in Neanderthal (*N*) and Modern (*M*) mandibles. Classes in dental development: DE=deciduous dentition (c, m1, m2), MI=deciduous dentition+first permanent molar (M1), PE=Permanent dentition. A posterior positioning of the mental foramen in Neanderthal mandibles is not dependent on the first permanent molar (\*) statistically significant difference (After Coqueugniot 2000)



**Fig. 12.4** Roc de Marsal (1) and La Quina H18 (2) skulls in frontal view. The skull of the oldest child (La Quina 18, ca. 7 years old at death) is narrower but exhibits supraorbital torus, supraglabellar depression,

and straight maxillo-zygomatic inferior profile, three features absent on Roc de Marsal (Photo A.-M. Tillier)

On the basis of a comparative analysis between the La Ferrassie specimens and modern children, the assumption of age-related changes in the pubic shape among Neanderthals cannot be rejected.<sup>2</sup> The elongation of the superior pubic ramus is present only on La Ferrassie 6, obviously older in developmental age than La Ferrassie 8 (considering bone maturation and diaphyseal lengths). But, in contrast with the

adult shape, the immature La Ferrassie 6 pubis exhibits no variation in height between the ventral and dorsal margins of the superior ramus (Tompkins and Trinkaus 1987; Majó 2000; Majo and Tillier 2003). The age at which this last pubic change occurs in Neanderthals before adulthood is unknown, due to the lack of bones from older individuals.

Interestingly, comparative analysis of hipbone growth conducted between the La Ferrassie individuals and Levantine early modern humans from Qafzeh (Majo and Tillier 2003) revealed a certain degree of morphological

<sup>2</sup>It is clear that drawing definitive conclusions on the basis of two specimens is premature.

overlap in ramus pubic elongation between the two groups within similar age-classes. Such results lead one to reconsider the use of the pubic morphology in the assessment of Neanderthal affinities in Eurasian Middle Paleolithic children. Hipbone remains of Upper Paleolithic specimens belonging to similar age-classes (Henry-Gambier 2001; Bruzek and Trinkaus 2002) are not complete enough to permit metrical comparisons. The incomplete pubic bone of Lagar Velho (age 4.5–5 years) from Portugal is described as “relatively short compared to those of both Late Pleistocene and recent children of similar age” (Bruzek and Trinkaus 2002: 431), while the Late Upper Paleolithic specimen from Grotte des Enfants in Italy (GE2, age ca. 2 years, Henry-Gambier in Henry-Gambier (Ed) 2001: 78) possesses a pubic length that falls within the range of variation of modern children of similar ages (Tillier 1999).

### Lower Limb Segment Proportions

Adult Neanderthals exhibit (to maintain the same tense) relatively short tibial length relative to femoral length and such segmental proportions of the lower limb are commonly

seen as a possible reflection of cold-climatic adaptation (e.g. Trinkaus 1981; Holliday 1995). Measurements defined on adult long bones are not applicable for immature specimens, due to patterns of bone maturation (Tillier 2005b). Furthermore, secondary ossification centers are mainly lacking (i.e. proximal and distal epiphyses) and diaphyseal lengths incompletely preserved in a majority of Neanderthal children (e.g. Kiik-Koba 2, Roc de Marsal, la Ferrassie 3, etc.).

A single child, La Ferrassie 6 (Fig. 12.5) allows an accurate evaluation of segment proportions, illustrated by the value of the crural index (tibio-femoral intermetaphyseal length ratio). Despite the lack of reliable age estimation for La Ferrassie 6 (no teeth are preserved), comparison between fossil and recent children provides evidence of individual and interpopulation variations (Table 12.1). The crural index, lower in La Ferrassie 6 than in the two Levantine early modern immature skeletons, is closer to few values in European Upper Paleolithic individuals. Furthermore, data collected from recent populations document large variability. Given the range of variation reported in crural index values, it would be fruitful to increase the sample of data collected for Neanderthals with new discoveries.



**Fig. 12.5** Within-site pattern of lower limb growth in Neanderthals from Southwestern France. Both La Ferrassie 6 child ca. 4 years old (1) and La Ferrassie 2 adult (2) exhibit short tibial length relative to femoral length; however, the crural index (using maximum lengths including

epiphyses) is lower on the adult (74.6) than on the child (77.6 minus cartilage thickness). The percentage of adult size attained is 45% for the juvenile femur (maximum length including epiphyses) and 47% for the tibia (Photo J.-L. Heim and A.-M. Tillier)

**Table 12.1** Variation in crural index values (tibio-femoral intermetaphyseal length ratio) among children. Comparison between the Neanderthal La Ferrassie 6 child, other Paleolithic specimens, and recent children

Children and their geographical provenance	Ages at death	Crural index
Europe: Middle (MP) and Upper Paleolithic (UP)		
La Ferrassie 6 (MP)	ca. 4 years?	76.5 (1)
Grotte des Enfants 2 (UP)	ca. 2 years	82.0 (2)
Grotte des Enfants 1 (UP)	ca. 3 years	79.0 (2)
Arene Candide 11 (UP)	ca. 3 years	83.0 (2)
Lagar Velho (UP)	ca. 4 years	79.0 (3)
Arene Candide 8 (UP)	ca. 7 years	78.4 (2)
Southwestern Asian: Middle Paleolithic		
Dederyeh 1	ca. 2 years	80.5 (4)
Skhul 1	ca. 3 years	85.7 (1)
Recent samples geographically dispersed		
Coimbra (Portugal, $N=20$ )	7–16 years	$77.0 \pm 4.2$ (1)
Japanese children ( $N=46$ )	Unknown	$79.2 \pm 2.8$ (4)
Spitalfields (Great Britain, $N=26$ )	0–5 years	$83.2 \pm 3.0$ (1)
South African black children ( $N=61$ )	Unknown	$83.5 \pm 2.4$ (4)

Bone length measurements of fossil specimens employed in the comparison derive from the following sources: (1) Tillier 2000, (2) sources in Henry-Gambier 2001, (3) Ruff et al. in Zilhao and Trinkaus 2002, (4) Kondo and Dodo in Akazawa and Muhesen 2002). Individual data from cross-sectional reference samples were collected either by the author (Spitalfields and Coimbra collections) or by her Japanese colleagues

### Thumb Proportions and Morphology

On the first metacarpal, adult Neanderthal handbones exhibit hypertrophied insertion of the opposing muscle of the thumb (*opponens pollicis musculus*), and a long distal phalange relative to the proximal phalange of the pollex. It was suggested that such features influenced the effectiveness of manipulative movements and precision grip (Vlček 1973; Trinkaus 1983; Villemeur 1994). Preservation of handbones in immature specimens is quite exceptional, especially complete thumbs, as shown by Roc de Marsal (ca. 3 years old at death) and La Ferrassie 3 (skeletal age presumed to be close to 10 years, according to Heim 1982) specimens. Young individuals such as Kiik-Koba 2 (less than 1 year old) and Roc de Marsal do not manifest specific development of attachment for the opposing muscle of thumb in the first metacarpals (Madre-Dupouy 1992 and author's observations versus Vlček 1973), in contrast with the oldest child, La Ferrassie 3. This specimen also exhibits an elongated distal pollical phalange ( $I=91.3$ , versus 69.8 for Roc de Marsal) similar to that of adult Neanderthals (between 85.2 and 89.3 for La Ferrassie 1; 84.3 La Ferrassie 2). However, as already noted in the case of pubic growth, additional data are required to confirm an age-related change for the appearance of specific pollical features during childhood and to precisely determine the age trends in timing of their appearance.

Yet, this short review suggests that variation in the appearance of traits during infracranial skeleton growth in Neanderthals cannot be ignored. To a certain degree, the skeletal remains of very young Neanderthals are generally similar to those of modern humans of the same developmental age. Additional insight into the variation of ontogenetic pattern and age-related differences in skeletal morphology among young Neanderthals is necessary to draw definitive conclusions. Most of the bone features related to the requirements of manipulation and locomotion are associated with late development of interosseous ligamentous areas and muscle attachments. The reconstruction of skeletal maturational events would benefit from the accumulation of data with new discoveries and further studies.

### Is There a Neanderthal Growth Pattern?

Central to the argument in favor of a distinct Neanderthal growth pattern is the idea of a unique modern-like pattern denied by the existent data bringing evidence of interpopulation diversity. Differences in population patterns of growth and development are well documented in modern living population samples (e.g. Eveleth and Tanner 1990; Bogin 1991). Nutritional, social, and environmental factors contribute to the differences in growth rate and development. It would not be surprising that Neanderthals living over a period of tens of thousands of years should manifest differences in growth patterns.

### Cranial Size

The last two decades have seen an increasing concern with distinct interpretations of ontogenetic patterns in Neanderthals that have employed brain growth and cranial size. Few scholars (e.g. Trinkaus 1984; Dean et al. 1986) have asserted that a nonmodern human-like pattern in Neanderthal fetal growth resulted in an enlarged brain size at birth, while others (e.g. Tillier 1986, 1995; Minugh-Purvis 1988) have argued that such an assertion could not be supported by the available fossil record.

The Devil's Tower child from Gibraltar has also served as a model to assume larger braincases in juvenile Neanderthals than in recent children, and to suggest (e.g. Dean et al. 1986; Stringer et al. 1990; Trinkaus and Tompkins 1990) a distinct growth rate of the skull in Neanderthals. Other scholars (e.g. Tillier 1988; Coqueugniot 1994; Minugh-Purvis 1988) have argued from a larger comparative sample that individual variation in skull size existed among Neanderthal subadults, within the same age-class as Devil's Tower (as shown by



Pech de l'Azé, Subalyuk 2, Engis 2) or in older specimens (e.g. La Quina H18). Cranial size assessments of Neanderthal were based on direct measurements of sufficiently preserved specimens. Moreover, the specificity of the modern reference sample selected in the comparison to Neanderthals influenced the results of the analysis, as all recent children did not show similarly-sized braincases (Coqueugniot 1994, 1999).

New endocranial volume estimations were proposed for three Neanderthal children (e.g. Roc de Marsal, Devil's Tower, and Engis 2), using computer-assisted analysis and reconstruction of missing skeletal parts (Zollikofer et al. 1995; Coqueugniot and Hublin 2007). Based on their results, the authors suggested that brain growth could be faster during early childhood in Neanderthals than in early modern humans. However, one should keep in mind that there is a discrepancy between authors's results and cranial size for Engis 2, and that the data employed in the comparative analysis were collected by different techniques. Furthermore, the influence of sexual dimorphism in the manifestation of cranial size variation during the growth period cannot be evaluated among young Neanderthals.

## Dental Development

During the last two decades, dental studies have been employed to suggest a non-modern-like pattern of growth in Neanderthals. Scholars have explored tooth enamel microstructures and timing of permanent crown formation (incisors and/or molars) to support a shorter period of dental growth in Neanderthals (e.g. Dean et al. 1986; Stringer et al. 1990; Ramirez-Rozzi and Bermudez de Castro 2004). Others studies have revealed similarities in perikymata counts between Neanderthal and modern human teeth (e.g. Mann et al. 1990, 1991; Tillier et al. 1995; Guatelli-Sternberg et al. 2005; Ramirez-Rozzi 2005; Monge et al., 2005). The resulting consequence is a clearer picture of the Neanderthal position within this modern human range.

Furthermore, better knowledge of modern human diversity, including both extant and fossil samples (e.g. Liversidge 2003; Liversidge and Molleson 2004; Monge et al. 2006; Reid and Dean 2006) reinforces the idea that in modern populations, significant variation exists in enamel incremental markings and perikymata packing patterns.

Following Reid and Dean (2006), more useful information can be accrued using molar microstructures that appear to be less variable than those of incisors. Using high-resolution micro-computed tomography analysis of two molars from La Chaise-de-Vouthon in France (one deciduous and one permanent), Macchiarelli et al. (2006) suggested that distinctiveness of tooth formation and dental growth in Neanderthal children is questionable.

Recently, Smith et al. (2007), from their analysis of the Belgian Neanderthal specimen from the Scladyna Cave, concluded that postcanine teeth had probably different formation times in Neanderthals, in contrast with anterior teeth. Following these authors, the Scladyna Neanderthal child presents molars that were "(...) characterized by shorter periods of overall crown formation than modern humans (...)" (Smith et al. 2007: 20221).

## Discussion

As we already mentioned (Tillier 2000), patterns of growth in Neanderthals are difficult to assess without reference to larger comparative samples. It is clear, from an auxological perspective, that investigations of Neanderthal growth trajectories can benefit from the use of enlarged samples that document the diversity of subadult modern dental and skeletal morphologies within past (i.e. Middle and Upper Paleolithic specimens) and recent populations geographically dispersed. Recent modern human samples used in comparative analyses mostly originate from regional collections, i.e. mainly European ones. The interpretation of observed differences (cranial size, number and packing pattern of perikymata on teeth, development of muscle markings, limb proportions, etc.) between Neanderthals and modern children must consider the significance of inter- and intrapopulation variation within distinct samples, following in this sense a methodological approach generalized in the study of adult individuals. Such data will markedly contribute to our ability to better assess the phylogenetic status of the features associated with Neanderthals and to more fully understand their biological implications.

Various lines of evidence dealing with variation of dental maturation in living humans and fossil hominids (e.g. Liversidge 2003; Liversidge and Molleson 2004; Monge et al. 2006; Guatelli-Sternberg et al. 2005; Reid and Dean 2006; Macchiarelli et al. 2006) challenge the use of data collected from studies of individual cases (Ramirez-Rozzi and Bermúdez de Castro 2004; Smith et al. 2007) in the identification of species or lineages, and the reconstruction of life history in past populations. Scholars professionally concerned with odontology studies know that there are ethnic differences in the eruption schedules for deciduous and permanent dentition; there is a wealth of literature on interpopulation variations. Huge differences in tooth emergence between captive and wild chimpanzees recently documented (Zilhman et al. 2004) also questions the use of tooth emergence times as population biological markers.

Finally, it is clear that the paucity of well-preserved skeletons (a common problem for growth-related researches) limits (1) the evaluation of individual variation among Neanderthals, and (2) the reconstruction of Neanderthal

trajectories of limb bone lengths related to dental age (versus Thompson and Nelson 2000). In addition, the influence of sexual dimorphism in the manifestation of morphological variation during the growth period cannot be evaluated. It is widely accepted that there are no accurate morphological criteria and reliable methods for a sex estimation of immature skeletons. For Paleolithic specimens, including Neanderthals, investigation in genetic markers on X/Y chromosomes remains rather problematic.

In most cases, the relationship between individual variation and anomalies in developmental patterns is rather difficult to assess. From limb bone lengths and body size reconstruction of the Neanderthal Le Moustier 1 adolescent, Thompson and Nelson (2000: 489) suggested that this individual had experienced a very late growth spurt. Besides the fact that "(...) all measurements included herein must be considered to be estimates" (Thompson and Nelson 2005:280), it is of concern to consider that the delay in skeletal growth achievement might reflect either prolonged growth related to sex or individual developmental disturbances in this individual (dental age estimates of  $15.5 \pm 1.25$  years, according to Thompson and Nelson 2005) rather than delayed intracranial growth in Neanderthals relative to modern humans.

## Life History of Neanderthal Children

The Neanderthal immature sample under examination includes infants and children who were the nonsurvivors in the population, a common situation in the study of archaeological samples (Saunders and Hoppa 1993). Although they serve to reconstruct growth patterns and maturational events during childhood within the Neanderthal lineage, it should be kept in mind that they might illustrate cases of abnormal developmental processes. The European Neanderthal sample represents a relative abundance of immature individuals to whom an age less than 10 years can be assigned, but the real level of infant mortality cannot be established from the small number of individuals (less than 1 year) uncovered.

## Indicators of Nonspecific Stress

Evidences of growth difficulties, such as tooth enamel hypoplasia (Ogilvie et al. 1989; Brennan 1991; Garcia-Sanchez et al. 1994; Skinner 1996; Guatelli-Sternberg et al. 2004), have been examined among Neanderthals. But authors have employed different scoring techniques (i.e. all types of enamel hypoplasia checked or examination limited to linear enamel hypoplasia, number of teeth scored, etc.) and this could easily explain the varying results in the analysis of

permanent teeth. A crucial test in the discussion of nonspecific stress markers lies in the developmental degree of enamel defects and the number of teeth affected.

Neanderthal children exhibit a low frequency of hypoplastic enamel defects on deciduous teeth (Skinner 1996; author's observations). The Devil's Tower child is quite unique in the number of teeth affected, three of the four deciduous teeth preserved and two of the four permanent molars, a condition that indicates, according to Skinner (1996: 844), two stress episodes, at birth and around 3.5 years. Guatelli-Sternberg et al. (2004) focused on linear enamel hypoplasia affecting permanent teeth (from Southern France individuals and Krapina sample); they reported a low percent (less than 40%) of individuals bearing at least two (or more) teeth affected, a result that did not support higher levels of environmental stress episodes among Neanderthals than in the comparative sample of Inuit foragers.

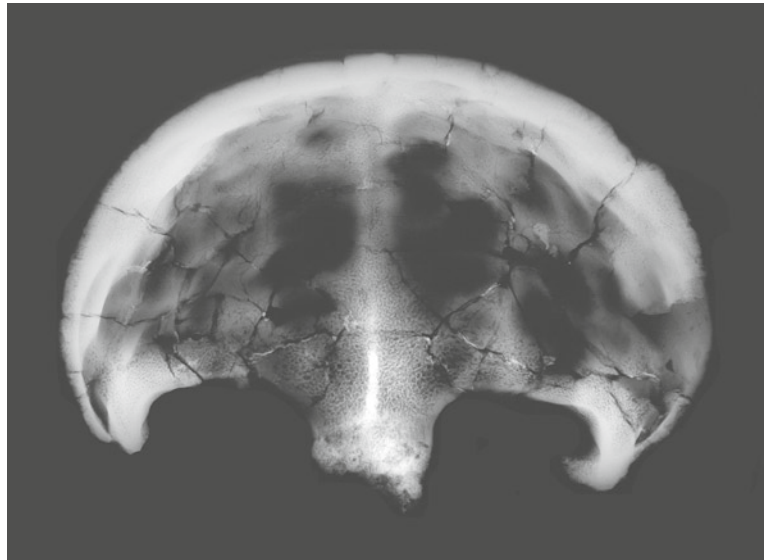
## Anomalies, Bone Lesions

If associated skull and intracranial remains are taken into consideration, the fossil evidence in support of developmental defects of bones comes from a small number of young individuals. This evidence, however, is not complete enough at the moment to allow us to draw definitive conclusions about the mortality and stress patterns in the Neanderthal immature sample from Europe. Furthermore, due to their structure, immature cranial bones tend to be less resistant to postmortem soil pressure than adult ones and postmortem skull deformations may occur. Such postmortem alterations cannot be rejected in the case of postbregmatic depression observed on the Krapina 1 and Subalyuk 2 specimens (Pap et al. 1995; Sansilbano-Collilieux and Tillier 2006).

The number of reported cases of antemortem cranial alterations is small. The Devil's Tower cranium is represented by three bones, and among them the frontal is well preserved with the exception of the orbital roofs. The inner table of this bone exhibits a rugged surface with digital impressions clearly visible on a frontal X-ray (Fig. 12.6). Such impressions affecting the bone are known in recent children to be associated with increased intracranial pressure; they usually vanish around the age of 4 years (Maroteaux 1982). An examination of Neanderthal children indicates that similar alteration of the inner frontal surface is present on (at least) two other specimens, Krapina 1 and La Chaise-Abri Suard 17 (Sansilbano-Collilieux and Tillier 2006). In both cases, individual age at death of the children is unknown,<sup>3</sup> while the

<sup>3</sup>We personally feel that, in the absence of the dentition, the reliability of age estimates in children older than perinates, based on single cranial measurements, is questionable.

**Fig. 12.6** X-ray picture of the Devil's Tower frontal bone (by courtesy of T. Molleson, BMNH, London) showing the distribution of the digital impressions



Devil's Tower child died during the fifth year postnatal (dental age estimates). Interestingly, the developmental pattern observed on Devil's Tower and Krapina 1 frontal bones is associated with enlarged cranial size relative to other specimens (e.g. Dean et al. 1986; Tillier 1988; Minugh-Purvis et al. 2000), and, to dental indication of a stress episode around 3 years for Devil's Tower, while the Krapina 1 temporal exhibits peculiarities in the internal sinus patterns (Minugh-Purvis et al. 2000; Sansilbano-Collilieux and Tillier 2006).

A second immature individual recovered from the Krapina rockshelter, Krapina 2, is represented by the posterior region of the cranium and possesses internal features that deviate substantially from the condition found in adults from the site. In this specimen, the occipital bone exhibits displacement of endocranial structures with dissociation between external and internal axes of the bone, absence of the occipital crest and large vermian fossa (Sansilbano-Collilieux and Tillier 2006).

On the basis of a new computerized reconstruction of the Le Moustier 1 skull, Ponce de Leon and Zollikofer (2005) state that this adolescent shows evidence of mild plagiocephaly and healed condylar neck fracture of the left side of the mandible.

The relationships between the aforementioned various bone abnormalities and the death of the individuals is rather difficult to assess, as most of them are not lethal in extant human populations. The only available evidence of bone lesion related to the cause of death might come from the Lazaret specimen in Southeastern France. The preserved portion of the cranium, a right parietal bone, showed evidence of a localized bone lesion on both external and internal surfaces

which has been interpreted as a meningioma-induced tumor (de Lumley 1973; Dastugue and de Lumley 1976), a condition quite exceptional for a child supposed to be less than 10 years old at death and dated to oxygen isotope stage 6.

## Concluding Remarks

Comparative analyses provide accurate information regarding the ontogenetic appearance of some diagnostic Neanderthal characteristics in the skull and infracranial skeleton. Collected data reveal similarities and contrasts between Neanderthal and modern children, but additional information is needed to confirm an age-related change for the appearance of specific features during childhood and to precisely determine the timing of their appearance. The interpretation of morphological differences as reflections of temporal and/or regional changes, as well as an investigation of within-site variation in growth-related features, would benefit from the accumulation of data with further studies and new discoveries.

In view of the aforementioned problems, we feel that the definition of a Neanderthal growth pattern and the characterization of within-population variation are far to be reached. Future research that incorporates juvenile skeletons from geographically distinct populations including hunter-gatherers will undoubtedly lead to a greater understanding of the evolutionary significance of juvenile Neanderthal skeletal remains.

Comparative growth studies in extant populations have demonstrated that environmental differences and selective

pressures have effects on the growing child. Accordingly, there is no guarantee that Neanderthals, evolving in different sites and habitats during several tens of thousands of years, shared similar growth patterns with living humans. There is no need to assert that possible variability in developmental pattern and somatic growth in Neanderthals was due to limitations in social and cognitive faculties. In 2007 we are still far from a consensus on the nature of the biological patterns that contributed to the development of Neanderthal skeletal morphology.

N. B. Since the acceptance of the manuscript, a new study of neurocranial size growth has been performed, using virtual reconstruction of incomplete infant and juvenile skulls (Ponce de Leon et al. 2008). Based on their reconstruction of the neonate specimen from the Mezmaiskaya Cave from Russia, considered as a Neanderthal (a questionable attribution, see Barriel and Tillier 2002), the authors established that “Neanderthal brain size at birth was similar to that in recent *Homo sapiens* (...)”. Data from older specimens lead the authors to conclude that postnatal brain growth rate was different between the two samples (i.e. Neanderthals and recent children) used in the comparative analysis. In this context, these authors suggest that additional evidence for brain size growth in early anatomically modern humans is still requested, joining us in this point (Tillier 1995: 65).

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