



Neanderthal Growth and Development: A Survey

Richard Clark

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Declaration

I, the author, confirm that the Thesis is my own work.

I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means).

This work has not previously been presented for an award at this or any other university.

Abstract

This thesis examines growth in size and morphological change with age in Neanderthal subadults. A catalogue and extended descriptions of the most informative individuals are provided. Some of the thesis is purely descriptive, but the subject is also approached from a life-history perspective and further draws upon brain and neurocranial development as well as the essential field of dental development.

Dental and skeletal attainment of Neanderthal subadults must be evaluated against chronological age, in some cases available from counts of dental microstriae. Growth studies of modern humans are referenced as a guide to growth processes, likely to apply to closely related species, and modern standards allow comparisons with Neanderthals.

Information from the physiological and dental fields and neuroscience is brought to bear on the question whether Neanderthals grew to adulthood more rapidly than living *Homo sapiens*, and main conclusions are as follows.

Brain growth affects timing of stages of ontogeny. Neanderthal endocranial volume range coincides with modern human range, which implies similar effects for both.

From infancy Neanderthals exhibited skeletal apomorphies which became more pronounced with age. By modern schedules subadults were dentally advanced but postcranially were small and grew slowly. By modern standards of percentage of adult size, using Neanderthal values, subadults were not skeletally advanced for their ages.

There is therefore an apparent dissociation between dental and skeletal/somatic growth rates in Neanderthals, in contrast to *Homo ergaster*, in which both systems are accelerated. Hypotheses regarding the dissociation are explored.

Rapid growth in recent humans is found to result principally from adequate or abundant nutrition and is therefore not always a sign of “live fast die young” life history. Ethnographical research suggests that even if adulthood were attained in fewer years the acquisition of subsistence and social skills would not be constrained.

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Preface

This thesis began life as a master's degree dissertation. The proposed degree would have been an MSc by research if that option had been available, but had to be an MPhil. The thesis was intended to be almost entirely descriptive but, with the introduction of life history theory, became more extensive and theoretical.

Graphs were produced using IBM® SPSS® Statistics and Microsoft® Excel®. An SPSS dataset containing alternative measurements by different scholars of Neanderthal and *Homo sapiens* fossil adults and subadults is available.

Section numbers allow cross-referencing within the text, e.g. §4.5.2. Tables and figures are numbered with a prefix of chapter number or appendix letter, e.g. Table 4.3, Figure C.2.

CHAPTER 1

INTRODUCTION

1.1 Rationale

There is a vast literature encompassing studies of individual Neanderthal subadults, growth processes, skeletal differences from *Homo sapiens*, life history theory, and the argument that Neanderthals reached adulthood at an earlier age. Here I attempt to bring together all these strands to provide a comprehensive account of Neanderthal ontogeny.

Much past research on Neanderthal ontogeny has focused on their distinctiveness or otherwise, as part of the debate about their phylogenetic relationship to modern humans. Some researchers have sought to show that Neanderthals were sufficiently similar to modern humans to be accounted members of the species *Homo sapiens* or that Neanderthals could have been ancestral to living humans of Western Asia and Europe (e.g. Brace 1967; Wolpoff 1980a; F.H. Smith 1983; Minugh-Purvis 1988; Bednarik 2014). Others have argued that Neanderthals were different enough to be a separate species, e.g. by dental differences (Bailey 2003), by craniofacial differences (Harvati 2003), and by overall morphology (Tattersall 1986; Stringer and McKie 1996; Tattersall and Schwartz 2008). Schwartz (2016) has argued for a separate genus.

Today, following genetic research uncovering differences in mitochondrial and nuclear DNA, it is widely agreed that Neanderthals are a separate species and that they contributed only limited ancestry to living humans by interbreeding with *Homo sapiens* populations (Krings et al. 1997; Green et al. 2010; Hawks 2012; Sankararaman et al. 2012, 2014, 2016; Sánchez-Quinto et al. 2015; Reich 2018).

Neanderthals were contemporaries of *Homo sapiens* in separate continents for more than 200,000 years. They are therefore treated here not as ancestral to, or a primitive form of, *Homo sapiens*, and not necessarily “less evolved” in the way that the earlier and smaller-brained *Homo erectus* can be regarded as such, but as a parallel or sister species to *Homo sapiens*, along with the more recently identified Denisovans (§1.3 and Chapter 2).

Now that evolutionary relationships have largely been clarified by genetic research, there is an opportunity to look again at Neanderthal ontogeny as a field in its own right, without the distraction of supporting or disputing a phylogenetic hypothesis.

Strictly, rather than *growth* it is ontogenetic difference with age that is investigated here, since the Neanderthal and other Palaeolithic immatures described cannot of course be reported longitudinally, nor do they represent a single defined population comparable with living populations (Tillier 2000:110). However, there is no other way to approach the subject of growth in extinct hominins than to treat the immature and adult remains that we have as if the individuals are typical of their ages.

1.2 Objectives

The objectives of this study are:

1. To catalogue the hypodigm of immature Neanderthal remains;
2. To place Neanderthal ontogeny in a life-history perspective;
3. To describe the processes of Neanderthal ontogeny and, where necessary, critique claims made in the literature that appear to have insufficient evidence;
4. To present and critique the evidence for the widely held view that Neanderthal ontogeny was more rapid than in modern humans.

The thesis consists of eight chapters.

1. Introduction
2. Life history
3. Dentition
4. Brain and neurocranium
5. Development: Infant, child, juvenile, adolescent stages
6. Growth to adulthood
7. The argument for and against rapid growth in Neanderthals
8. Conclusions

Appendices supplement the main text, Appendix A being a catalogue of Neanderthal subadult remains, and the rest giving background information, tables of measurements, discussions of specialized topics, and illustrations.

Objectives are addressed throughout, but particularly emphasized as follows.

- Objective 1: Chapter 5 and Appendix A.
- Objective 2: Chapters 2, 7, 8.
- Objective 3: Chapters 3, 4, 5, 6, 8.
- Objective 4: Chapters 4, 7, 8.

1.3 Background

This section is intended to provide a context to the study. Recent widely known views of phylogeny and of morphological and behavioural differences between Neanderthals and modern humans are sketched. Supplementary information on phylogeny and morphology, and on *Homo* taxonomy and nomenclature, is given in Appendix B.

The Neanderthals were an anatomically distinct population of hominins which inhabited Western Asia and Europe for a period of greater than 200,000 years until around 40,000 years ago (40 ka), when they disappear from the fossil record (Higham 2021). They are generally assigned to a species *Homo neanderthalensis*.

During that period of Neanderthal existence, hominins identified as “anatomically modern” inhabited South, East and North Africa. They differed morphologically from Neanderthals and included the ancestors of all living *Homo sapiens* populations. Fossil skeletal remains from the Moroccan site Jebel Irhoud dated to approximately 315,000 years ago (315 ka) have been identified as the earliest exemplars assignable to our species (Hublin et al. 2017). Anatomically modern human groups migrated north-east from the African continent at least as far as South West Asia by 130 ka (Zaidner et al. 2025). Perhaps then but definitely after 80 ka, much wider migrations of modern humans east, north and west expanded their range over the whole of Eurasia, Oceania, and eventually North and South America. During that period of expansion, Neanderthals and other remaining archaic hominins (i.e. those not anatomically modern) became extinct.

Remains of hominins with incipient Neanderthal characteristics have been discovered dating to ~430 ka in Spain (Arsuaga et al. 2014), indicating that Neanderthals had a long ancestry in western Eurasia. DNA studies have shown that *Homo neanderthalensis* and *Homo sapiens* are descended from a common ancestral population which lived approximately half a million years ago (Sánchez-Quinto and Lalueza-Fox 2015; Reich 2018:30,54–55). The earliest fossils exhibiting almost the full suite of Neanderthal characteristics date from OIS6 and OIS7¹ levels (175–253 ka) at the site of Biache-Saint-Vaast (Guipert et al. 2011).

Neanderthals and *Homo sapiens* interbred at the margins of their ranges, probably in South West Asia, with the result that virtually all modern humans other than Sub-Saharan Africans carry a small quantity (only 1–2 %) of Neanderthal nuclear DNA (Green et al. 2010; Reich 2018:40–41).

Over the last century Neanderthals have often been presented as primitive hominins (Boule 1923) which, because of their primitiveness, necessarily were out-competed by modern humans: as in the stringent version of the “Out of Africa” scenario (e.g. the majority of contributions in Mellars and Stringer 1989). Other scholars have in the past proposed that they were a subspecies of *Homo sapiens* ancestral to anatomically modern *Homo sapiens*, as in the multiregional theory of human evolution (e.g. Coon 1962; Brace 1967; Wolpoff 1980a). While accepting the species distinction and that Neanderthals were not ancestral to modern humans, I seek to adopt an objective stance on their anatomical and behavioural characteristics.

Only in the last forty thousand years have we anatomically modern humans had the world to ourselves: previously some geographical areas supported populations of other hominins, of which Neanderthals were one and the relatively recently discovered Denisovans another (Higham 2021). They and the other archaic hominins became extinct. Even so, the two species *Homo sapiens* and *Homo neanderthalensis* were contemporaries for very much the greater part of the existence of both (Appendix B).

¹ Oxygen Isotope Stage.

Studies concerning Neanderthals and other archaic hominins frequently concentrate on their differences from modern humans, either on the basis of anatomy or on the archaeological evidence of their lithic technology and modes of subsistence, and seek to use these differences to infer that they were behaviourally, culturally and cognitively inferior, often concluding that is why Neanderthals became extinct (e.g. Binford 1982, 1985; Mellars 1996; Pearce et al. 2013; Gamble et al. 2014). Discussion of these wide-ranging arguments is beyond the scope of the present work. While enumeration and evaluation of differences and their consequences is entirely valid, it may equally be illuminating to adopt a perspective of considering Neanderthal characteristics and capabilities in their own right rather than exclusively contrasting them with ours. Inevitably one has to use information from biological and social anthropology concerning modern humans to fill gaps in the available evidence on Neanderthals, but the focus can be on them rather than just the differences.

In particular, while comparison of morphology and material culture between *Homo sapiens* and *Homo neanderthalensis* populations who were broadly contemporary should be valid, comparison of Neanderthals from 130–50 ka with *Homo sapiens* from 27 ka is probably misleading. It would be misleading in much the same way as a comparison of North America in the year 1470 with North America in 1970. Wynn and Coolidge (2016:209–210) argue that the only valid comparison between modern human and Neanderthal cultures is between the Aurignacians and late Neanderthals in Europe, on the grounds that they were contemporary. However, contemporaneity is, to say the least, not proven here. Dating of the transition from Mousterian to Upper Palaeolithic and of the skeletal remains of Neanderthals and early moderns in Europe needs clearer resolution (Higham et al. 2014; Higham 2021). The latest Neanderthal fossils are dated to ≥ 40 ka, and by the time an Aurignacian stone tool culture is clearly established in any area of Europe no Neanderthal remains are found in that area, except perhaps at the site of Les Rois (Ramírez-Rozzi et al. 2009). More valid is the comparison of material culture at an earlier period when modern humans and Neanderthals definitely were contemporary but inhabiting different regions, as when, around ~ 130 ka, modern humans lived in East Africa while Neanderthals were in Europe, and groups met in the Levant (Zaidner et al. 2025). At that period and down to 50 ka both species exhibited a similar Mousterian lithic culture (Tattersall 1995:245).

Neither Neanderthals and their ancestors nor living *Homo sapiens* and our ancestors remained static but continued to evolve during the approximately half-million years of more or less separate existence. Neanderthals and anatomically modern humans contemporary with them were equipped with brains of comparable size: mean endocranial volume ~ 1350 – 1400 cm³ (Appendix E). The Middle Pleistocene species *Homo heidelbergensis*, which may have been our common ancestor with Neanderthals, evinced a lower mean cranial capacity, still well within modern human range at ~ 1200 cm³ (Appendix E). The Neanderthals' large endocranial volumes and relatively recent survival render them an especially intriguing subject in human evolution. They were like us in important respects but definitely not the same. Their ancestors and ours evolved in different continents, and their typical morphology is also distinctive. It is natural to inquire how alike or unlike they could be in their behaviour and mentality, although the evidence is necessarily limited to archaeology and skeletal anatomy.

Most publications on Palaeolithic populations, whether on *Homo sapiens*, Neanderthals or others, concentrate on adult specimens, partly because these are usually better preserved, and partly because they typically exhibit more distinguishing anatomical features. However, in recent years anthropologists have increasingly appreciated the importance of understanding ontogenetic processes as a mechanism of human evolution and also of investigating how children have contributed to past and present societies (Minugh-Purvis and McNamara 2002; Spikins et al. 2014; Meehan and Crittenden 2016; Mays et al. 2017).

In non-industrial recent societies and in prehistoric societies, children form a high proportion of any population. Such societies typically suffer higher infant mortality than in developed countries at the present day, so that immature remains are common in archaeological contexts (Wood et al. 1992). Of the Neanderthal hypodigm at the time of Trinkaus's (1995) analysis, approximately 51.6% of individuals were immatures. However, osteological remains of immatures are more susceptible to fragmentation and misidentification owing to small size, gracility and incomplete formation. In some cases recovered fragments of immature skeletons have been set aside for decades without being examined (Spikins et al. 2014:111–112; Maureille 2002). In recent hunter-gatherer societies children not only play among themselves but also participate in general community subsistence activities, and by extension would have done so in past populations, including extinct hominin species. In recent forager societies, children are generally expected to take care of younger siblings; they often contribute to food gathering from an early age, and sometimes to hunting (Mead 1928; Bogin 1999:199–200; Crittenden 2016; Lancy 2016).

Not only adults but also immature Neanderthals were typically more robust skeletally than modern humans. From this observation it has been argued that even young children in Neanderthal communities experienced high levels of physical activity (Kuhn and Stiner 2006). This in turn could be evidence that they not only participated in relatively safe activities, e.g. gathering or preparing food, as would be the case in recent hunter-gatherer societies, but also were actively involved alongside their elders in hunting expeditions. In such activities they would have incurred the dangers of potentially violent encounters with large prey animals such as bovids and cervids, and perhaps with competing predators.¹

¹ It could be argued that, as the target adult morphology of Neanderthals is robust, subadults would develop some degree of robusticity during ontogeny whether or not they were participating in adult activities.

1.4 The question of rapid growth

Prevailing opinion in palaeoanthropology is that Neanderthals grew to adulthood more rapidly than recent *Homo sapiens*. The argument has been advanced that a shorter subadult period –

- reduces the influence of experience on brain development, especially during infancy and early childhood;
- entails having less time to accomplish complex social and survival skills;
- coupled with high young adult mortality, is symptomatic of a species with low longevity.

These apparent deficiencies of Neanderthals compared with *Homo sapiens* have been offered as an explanation for their extinction.

The principal support for the hypothesis of more rapid Neanderthal ontogeny comes from their dental development, which evidence indicates was notably advanced over that of modern *Homo sapiens*.

Previous arguments have tended, even if not explicitly, to take the form of this deductive sequence:

Premise: Neanderthal dental development accelerated;

Therefore: More rapid life history;

Therefore: More rapid somatic growth and brain growth;

Therefore: Less time for learning;

Therefore: Cognitively challenged relative to *Homo sapiens*;

Therefore: Modes of subsistence and survival inferior;

Therefore: Selectively disadvantaged and became extinct.

Much of this reasoning uses as an initial basis the illuminating work of B.H. Smith (1989a, 1989b, 1991, 1992), who produced regressions which show strong correlations in primates between age at first permanent molar emergence and adult brain size, adult female body weight, age at first reproduction, life span and other *life-history-related variables* (§2.4.1). More recently, authors have suggested that these correlations may successfully distinguish groups at family, subfamily and perhaps genus level, but have questioned whether they are applicable to closely related species such as modern humans and extinct hominins (Dirks and Bowman 2007; Guatelli-Steinberg 2009), although the correlations are still foregrounded in recent papers (e.g. Modesto-Mata et al. 2020).

In the thesis, subadult ages at death calculated from counts of dental microstructure (§C.3, §C.4), whenever available, are treated as chronological ages. Only in the absence of such values are previous ages determined from recent human dental standards used. This means that advancement or delay of both *skeletal* and *dental* maturity are assessed in relation to these *chronological* ages, rather than skeletal maturity being judged only by dental age.

The present work seeks to collate and evaluate evidence for and against the hypothesis of more rapid ontogeny. To deal with this question it is necessary to examine the whole subject of human growth and life history as far as it can be applied to an extinct population, including not only dental development but also brain growth, somatic growth, nutrition, pathology, and information from ethnography. I suggest that the overall question cannot be answered by a single result from the dental or other fields. Instead it has to be approached as comprehensively as possible from many angles, taking into account the wide variation observed among modern humans and the effects of environment during ontogeny. This thesis is an attempt to provide such a comprehensive study.

CHAPTER 2

LIFE HISTORY

2.1 Introduction

“Life history may be defined as the strategy an organism uses to allocate its energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death.... Life history, in this definition, encompasses the major growth, development, and reproductive events that occur between the conception and death of an organism” (Locke and Bogin 2006:303).

This chapter seeks to examine the concepts of life history theory and assess the evidence available for Neanderthal life history. Demographic, nutritional, pathological, environmental and other factors that may affect life history are discussed.

Initially, life history theory is outlined as applied to primates, and the commonly defined stages of postnatal life are detailed, which will be extensively referred to in subsequent chapters. Here, life history theory together with information from ethnography and archaeology are brought to bear to clarify why some populations may have more rapid or more extended ontogeny than others, and insights from these results are applied to Neanderthals.

2.2 Life history outline

2.2.1 Trade-offs, fast and slow schedules

Body size (measurable as body mass) can be viewed as the primary determinant of an animal's ecological opportunities, physiology, morphology and rate of living (Lindstedt and Calder 1981:2; Harvey and Clutton-Brock 1985:559,579). Larger animals tend to live longer and take more time growing to reach adult size than smaller animals. Among mammals generally, and specifically within the primate order, the same principle largely applies (Lindstedt and Calder 1981).

Much of life history theory is built around the concept of *trade-offs* (Stearns 1992:72–89; Lee 1993; Hill 1993). Any organism has to consume sources of energy from the environment in the form of food, water, air and light, in quantities limited by its existing size and capability. Energy can serve such uses as body maintenance and repair, growth, locomotion, reproduction, and reserve or storage (e.g. fat). Energy used for one purpose cannot be used for another, except that stored energy can be accessed in time of need. These limitations give rise to trade-offs during life between one use and another. Energy invested in early reproduction is no longer available for body maintenance which might have permitted greater longevity. On the other hand, energy invested in a strong immune system may permit avoidance of disease and more years of reproduction (Lee 1993:80). The life history *strategy* of a species is partly determined by the trade-offs which it characteristically adopts. A successful strategy is one which enables reproduction at a rate which allows survival or even expansion of the species.

Mammals are born relatively small, have to feed to stay alive and to grow, and availability of food is limited by environmental conditions and the ability of the organism to obtain it. For a mammal at a subadult stage of life there is a trade-off between (a) investing energy in growing to attain a larger body size and (b) investing energy in early reproduction to ensure continuity of the population. This is one of several trade-offs. The survival strategies of species, genera and subfamilies are derived from the success to date of the trade-offs characteristic of their lineage.

Rodents such as mice and rats are small-bodied, reproduce early and often, and give birth to litters of several offspring. The offspring in turn are small, “low-quality” or relatively expendable in that each singly represents very limited investment of energy by the parent. Some may die young, but sufficient numbers live long enough to reproduce. At the opposite extreme are the largest-bodied primates, i.e. the three great ape genera and humans. They reproduce only after at least ten years of growth, give birth usually to single “high-quality” offspring (Schultz 1969:184), and typically do not reproduce again until the most recent offspring has been weaned, which may be several years after birth. Great apes and humans invest available energy in their individual protracted growth and in producing large offspring by relatively postponed and infrequent reproduction.

Earlier work on life history emphasized a “fast-slow continuum”. Representing the fast end are complexes of physiological traits giving rise to rapid development and maturation, early reproduction and early death, so that the organism lives fast and dies young, while the slow end is represented by trait complexes which produce a long subadult period, late attainment of reproductive maturity and a long adult lifespan, so that the organism lives slow and dies old (Promislow and Harvey 1990; B.H. Smith 1992:139; B.H. Smith and Tompkins 1995:263; Kelley 1997:192).

For chimpanzees, genetically the closest living genus to *Homo*, recent studies in the wild have discovered greater variation than previously known in ages of attainment of dental and other maturational milestones (Zihlman et al. 2004, 2007; Bolter and Zihlman 2007; Kelley and Schwartz 2010, 2012; T.M. Smith et al. 2013; Machanda et al. 2015; Walker et al. 2018). For species of australopithecines and early *Homo*, evidence is accumulating that life history encompassed considerable variation according to environmental differences such as climate, habitat, diet, and predation risk, so that a mosaic model of life history may be more appropriate than the fast-slow continuum concept on its own (Leigh and Blomquist 2007:402; Schwartz 2012:S395; Kelley & Schwartz 2012; Kuykendall 2003, 2020). The fast-slow concept continues to be applied as one of the distinctions between Neanderthals and modern humans (e.g. Ramírez-Rozzi and Bermúdez de Castro 2004), and therefore is discussed further.

2.2.2 Life history of hominids

Among living primates, modern humans are the outstanding exemplars of the “live slow die old” strategy. Although chimpanzees are slow growing relative to monkeys and the lesser apes, they have shorter lifespans and progress more rapidly through subadult stages to adulthood than living humans (Figure 2.1, Table 2.2). Within the chimpanzee-hominin clade, chimpanzees can be seen as occupying the fast end of the life history spectrum and living humans the slow end. For the various species of hominin that have existed since the last common ancestor of chimpanzees and humans (6–7 Ma), the question arises of their chimpanzee-like or human-like position on the putative spectrum and which, if any, had a life history resembling that of modern humans.

A reasonable null hypothesis would be that the earliest hominins must have been more similar to chimpanzee ancestors than living humans are, and therefore that their life history was relatively fast. It is also reasonable to expect that later hominins, whose fossil remains over time come to resemble modern human morphology more closely, may have had life history schedules approaching those of modern humans. Over the last three decades research has tended to date the attainment of “slow” modern-human-like life history later and later, and to confine it to *Homo sapiens*.

The earliest hominins up to ~2.5 Ma had chimpanzee-like endocranial volumes and body size. Studies of *Australopithecus*, *Paranthropus* and early *Homo* have led to a consensus that their life history schedules were more similar to those of chimpanzees than living humans (Bromage and Dean 1985; Bromage 1987; Beynon and Dean 1988; B.H. Smith 1989a, 1989b; Kuykendall 2020). The case has been made that specimens assigned to *Homo habilis* and *Homo rudolfensis* were more similar in body size, morphology and possibly life history to australopithecines than to *Homo ergaster/erectus* and should be relegated to *Australopithecus* (Wood and Collard 1999a, 1999b).

Analyses of the fairly complete subadult *Homo ergaster* specimen KNM-WT15000, dated to ~1.5 Ma, determined that its pattern of growth was different from that of modern humans, with faster dental development and conspicuously greater skeletal growth for its age (B.H. Smith 1993; Ruff and Walker 1993; Dean and Lucas 2009). This result was surprising, because *Homo ergaster/erectus* is the earliest hominin to have a large body size and stature similar to those of modern humans (Ruff et al. 1997), and among primates larger body size is correlated with slower life history (Harvey and Clutton-Brock 1985; B.H. Smith 1989a, 1991). It has been argued that in *Homo erectus s.l.* third molar eruption was at ~14 years (Dean and Lucas 2009; Dean and Smith 2009; Dean 2010), which, if somatic and dental development are tightly correlated, would indicate that adult stature was attained shortly after that age, i.e. ~5 years earlier than in living human males.

Although *Homo erectus s.l.* did not have a modern human life history, it is conceivable that some later non-sapiens species remain candidates for a life history more nearly resembling ours: *Homo antecessor*, *Homo heidelbergensis*, Denisovans, and Neanderthals. As discussed in Chapter 1 and Appendix B, the view of Neanderthals as ancestors of modern humans is no longer tenable, except for their minimal contribution of DNA by limited episodes of interbreeding. For this reason, and because the lineages of *Homo sapiens*, Neanderthals, and presumably Denisovans coexisted in geographically separate areas for ~500 ka, Neanderthals and Denisovans should be regarded as parallel or sister species to *Homo sapiens*, each with their own apomorphies and adaptations to environment. As such, they were not intermediate between *Homo heidelbergensis s.l.* and *Homo sapiens* and therefore did not necessarily embody a “primitive” plesiomorphic life history.

2.3 Stages of hominid growth and development

2.3.1 Ages and stages

Stages of growth for *Pan troglodytes*, *Australopithecus africanus*, *Homo habilis*, *Homo erectus*, and recent *Homo sapiens* are shown in Figure 2.1. It is derived from Bogin (2003), after Schultz (1969) with Bogin's addition of *Homo habilis* and *Homo erectus s.l.*. Bogin distinguishes *Homo erectus* early and late. Average ages of stage transitions are shown at full years, a stage beginning at attainment of that year. Bogin's original has some transitions at half years. Average transitions of living *Homo sapiens* to adolescence at 10+ years and adulthood at 17+ years represent female stages better than male, for which they seem early, especially the end of adolescence, in comparison with ages from Tanner (1962) and Bogin (1999).

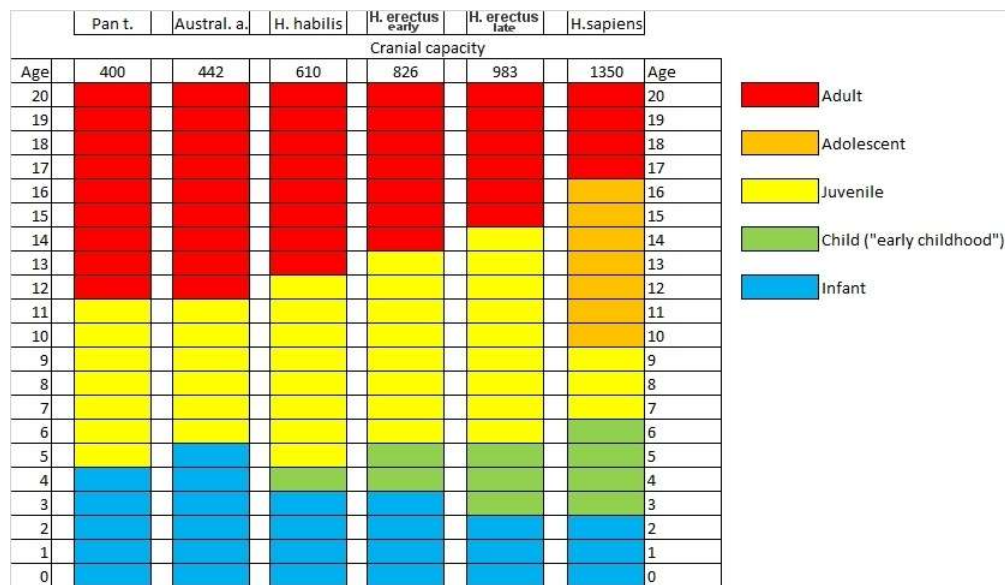


Figure 2.1: Ages and stages of hominid growth

According to this schema, great apes and the australopithecines have only two preadult stages: infant and juvenile. In apes, the juvenile stage is introduced by cessation of suckling. Adulthood is achieved when the hitherto juvenile ape, having not much earlier reached sexual maturity, finishes growth in length with long-bone epiphyses closing and third molar teeth reaching apex closed. In the genus *Homo* an extra stage, (*early*) *childhood*, replaces the later part of infancy. It is hypothesized (Bogin 1999, 2003) that *childhood* in this technical sense appeared first in *Homo habilis* or at least *Homo ergaster/erectus*, and became lengthened in later hominins. Living humans have a further stage, *adolescence*, which replaces the later part of the juvenile stage and extends into what would otherwise be years of early adulthood. In modern humans adolescence typically includes a growth spurt of 2–5 years, when somatic growth proceeds more rapidly than at any time since infancy.

The question arises whether the adolescent stage as found in modern humans was present in the sister species *Homo neanderthalensis* – and the other sister species the Denisovans, and the likely common ancestor species *Homo heidelbergensis (s.l.)* – and whether any of those species' preadult life was as lengthy as that of *Homo sapiens*.

Bogin's stages of development as defined here are used throughout later chapters, and Neanderthal subadult remains are classified as *infant*, *early child*, *juvenile* and *adolescent* according to their age stage as if they were modern humans. As will be argued later, such a classification is most likely accurate up to and including early adolescence. Arguments are dealt with in Chapter 7, and in other chapters developmental issues relevant to this question are covered in some detail.

2.3.2 Infant stage

During the infancy stage, in living humans growth in body length decelerates from an early near-fetal rate of ~22 cm/y to 6 or 7 cm/y by age ~3 years. The offspring is dependent on its mother or other older caregivers for all kinds of care and feeding. This stage ends with the completion of weaning, i.e. cessation of suckling. In humans this takes place at ~3 years, when the offspring enters early childhood, with continued dependence, and in chimpanzees at ~5–6 years when the offspring enters the juvenile stage, during which offspring are fully capable of feeding themselves (Bogin 1999:30).

Human neonates and infants are fatter than the young of other terrestrial mammals (Leonard et al. 2003:11), and at all ages humans have much larger adipose depots (14–26% of adult body mass) than chimpanzees or bonobos (3–10%) (Navarrete et al. 2011:92). During the first postnatal year infants accumulate further adipose tissue (Kuzawa 2019:13267), which in later infancy begins to decrease as a percentage of body mass. Such fat stores may provide an energy reserve for weaning when the child becomes dependent on extrinsic food of lower nutritional value (Leonard et al. 2003:11; Kuzawa 2010:521).

Weaning onset, the introduction of extrinsic foods at ~6 postnatal months, may bring about ingestion of parasites and bacteria, and in some environments replacement food is low in nutritional value. From cessation of suckling at ~2.5–3 years, the child depends entirely on extrinsic food. In subsistence-level societies the infant and early childhood stages therefore carry a high risk of mortality (Kuzawa 2010:521; Bogin 1999:175,274).

2.3.3 Early childhood stage and weaning

The human *early childhood* stage follows cessation of suckling but with continued dependence on adults for provisioning with largely adult foods. Although, as with humans, complementary foods are introduced within the first postnatal year and become an increasingly larger portion of their diet, chimpanzee mothers continue to suckle their young up to 4–7 years (T.M. Smith et al. 2013:2788–2789) during which time the young remain technically infants.

Effectively in *Homo sapiens* this new stage extends infancy but without the suckling component, because infantile dependency continues after what is a very early weaning by ape standards. For modern humans in subsistence-level societies, cessation of suckling is expected at 2.5–3 years (Humphrey 2010), approximately half the age of fully weaned chimpanzees, although continued suckling has been observed in humans as late as 5 years (Sellen 2006:186,189).

The childhood stage enables cessation of suckling while the offspring is still too weak and unskilled to provision itself fully. It permits the mother to cease lactation, so that lactation-induced hormones which can inhibit ovulation, specifically prolactin, are reduced and the mother is able to conceive again (Konner 2005:35; but see §2.4.2). The potential arises for a shorter inter-birth interval (IBI) than in an ape-like population with prolonged infancy. A short inter-birth interval is typical of recent humans in both developed and subsistence-level societies

(Kuzawa and Bragg 2012). Early weaning thus promotes *stacking* of infants, i.e. several offspring aged very few years apart can be growing up simultaneously (Humphrey 2010). Among recent humans, stacking is enabled by alloparenting, whereby the weaned child is provisioned not only by the mother but by other members of the family, such as fathers,¹ older siblings, and others in the wider community, as seen in both developed and subsistence-level societies. Such substitution enables the mother to attend to a new infant without being overwhelmed by the demands of the weanling. This process requires a degree of social cooperation, commitment and communication beyond that observed among chimpanzees.

Development of the childhood stage opens up the potential for population increase, since births can be more closely spaced, permitting more births before menopause. Shorter inter-birth intervals enhance the mother's reproductive fitness. Bogin (1999:192, 2006) argues that this consequence, not elongation of immaturity for putative extended learning, is what confers selective advantage to a population which develops a childhood stage. For the infant, early cessation of suckling is not itself an advantage, because it may lead to dietary stress, loss of passive immunity and the ingestion of parasites (Skinner 1997a:690) and often, though not always, causes dissatisfaction or distress (Takada 2005; Fouts and Lamb 2005). Even at onset of weaning infection and malnourishment may begin to occur (Owen et al. 1974:597). The selective advantage to the community of shorter inter-birth intervals therefore must outweigh the risk to individual offspring.

2.3.4 Juvenile stage

Some animals such as rodents reach reproductive maturity soon after weaning. Technically, then, they pass straight from infancy to adulthood,² whereas social animals such as carnivores, elephants and primates have a juvenile stage during which they remain immature and relatively small but largely fend for themselves (Bogin 1999:200). The juvenile offspring is capable of provisioning itself and preserving its life. Bogin (1999:75) remarks that young individuals commonly called "street children" are juveniles, rarely younger than ~7 years.

Juveniles, unlike infants, are large and strong enough to be able to forage for food, although among chimpanzees they stay close to the mother for ~10 further years. Juvenile chimpanzees with a surviving mother thrive and gain more muscle mass than those whose mother dies (Samuni et al. 2020). Juvenile chimpanzees can survive the death of the mother, particularly if adopted by another adult female, whereas infants still being suckled, even older ones, are likely to languish and die (Van Lawick-Goodall 1971; Robson et al. 2006:40).

At the transition to the juvenile stage in humans there is a short period of accelerated growth, the mid-growth spurt, of smaller magnitude than the adolescent growth spurt (Tanner 1947:305; Leigh and Park 1998:344; Bogin 1999:69,78). Following this small spurt in humans growth slows again until adolescence.

The juvenile stage leads to either adulthood for chimpanzees or the adolescent stage for humans.

¹ In some recent hunter-gatherer societies, mothers provide up to ~90% of the time spent caring for an infant and fathers up to ~25%, making fathers the principal providers after mothers (Konner 2005). Contrastingly, Hrdy (2005) and Hawkes (2006) emphasize the provisioning role of grandmothers and allomothers.

² However, in rats adolescence has been defined as weeks 28–42 of life (Juraska and Willing 2017:88).

2.3.5 Adolescent stage

In modern humans an *adolescent* stage can be defined as that period between puberty, the initiation of the process of developing reproductive capability, and the attainment of adult height.

A distinctive characteristic of the adolescent stage of human life history is the adolescent growth spurt, which in its genuine form is said to be unique to our genus (Bogin 1999:201; but see Leigh 1996, 2001; Leigh and Shea 1995; Dean 2016). Locke and Bogin (2006:302) argue that growth spurts during the late preadult years in other primates are not comparable: in particular, those observed in laboratory chimpanzees following periods of arrested growth during experimentation, presumably due to trauma, appear to be catch-up growth.

The life stage of adolescence has generally been reckoned to begin with visible changes to the reproductive system (Tanner 1962; Marshall 1978). Internally, reproductive development is effected by the hormonal output of the hypothalamic-pituitary-gonadal axis.

The adolescent growth spurt in somatic growth lasts several years, accelerating to *peak height velocity* (PHV) then tailing off gradually toward the cessation of statural growth. Adolescent changes in the individual altogether span 7–10 years, males typically exhibiting slower progress through the various developments (Tanner 1962; Winter 1978; Taranger and Hägg 1980). Changes in females become visible on examination typically at ~10–10.5 years, in males only ~1 year later, whereas for the growth spurt PHV is reached 2 years apart, in females at ~12 years and in males ~14 years (Tanner 1962; Marshall 1978). Evidence has been presented that, in girls only, the growth spurt occurs ~1 year earlier than previously stated, with onset at ~9.5 years and peak in statural and facial growth at ~10.9–11.5 years (Mellion et al. 2013). Obesity and rapid weight gain in prepubertal years is associated with earlier puberty in girls, but in boys the association is less clear (Wagner et al. 2012). The growth spurt itself lasts up to ~4.8 years (Taranger and Hägg 1980:63). Menarche typically occurs ~1 year after PHV (Tanner 1962),¹ while spermarche occurs ~1 year before PHV (Nielsen et al. 1986; Ma et al. 2011).

Adolescence is initiated by reproductive hormonal processes, whereas its conclusion is identified by cessation of an essentially skeletal growth process. Reproductive capability is attained before attainment of adult stature or length (Table 2.1). Attainment of adult stature in humans generally occurs at 17–21 years (Tanner 1989), males later than females, but skeletal and soft tissue growth continues, and in males the medial clavicle and elements of the pelvis may not fuse until the mid or later twenties, i.e. well into adulthood (Cunningham, Scheuer and Black 2016; Webb and Suchey 1985).

Table 2.1: Adolescent stage milestones, modern humans

Event/milestone	Ages attained (y)	
	Male	Female
Gonadarche	10–11	9–10
Puberty (visible changes)	11–12	10–11
Spermarche	13	
Peak height velocity	14	12
Menarche		13
Cessation of statural growth	18–21	17–19
Data from Tanner 1962, 1989; Marshall 1978; Winter 1978; Nielsen et al. 1986; Ma et al. 2011; Bogin 1999; Cunningham, Scheuer and Black 2016.		

¹ Björk and Helm (1967:136) reported it on average 17 months after PHV.

Adolescence in modern humans is at least as long as any two of the earlier subadult stages put together. If other primates do not have an adolescent stage, then since the sexual development and growth which take place during human adolescence occur in other primates, with the possible exception of a growth spurt, these developments have to be assigned to their juvenile stage or early adulthood.

The adolescent growth spurt is almost universal among recent humans, but may be undetectable or barely detectable in some groups living with challenging conditions, e.g. chronic stress, undernutrition, or high-altitude hypoxic environments. Such groups tend to have gradual and extended growth of stature and body mass up to adulthood, finishing as late as the middle of the third decade of life (Gurven and Walker 2006:840; Blurton Jones 2006:251).

2.4 Life history variables: comparison of apes, recent humans and Neanderthals

2.4.1 Life history and life history related variables

Measures of size, duration and rate related to body dimensions, stages and events of life across taxa can be expressed as numerical variables which exhibit correlation with each other and allow patterns to be detected in the life histories of those taxa (Harvey and Clutton-Brock 1985; B.H. Smith 1989a, 1989b, 1991). Two sets of variables can be distinguished (Skinner and Wood 2006:342; Robson and Wood 2008:401):

- **Life-history variables (LHV):** *gestation length, age at weaning, inter-birth interval, age of emergence of the first mandibular molar, age at sexual maturity, age at first birth, age at last birth, maximum potential life span or mean adult life span:* these are all ages or durations which define life history.
- **Life-history-related variables (LHRV):** *body mass adult and neonate, brain size adult and neonate, timing and sequence of dental formation and eruption:* these are second-order and morphological variables, either quantities or durations.

These variables are defined on extant primate species, principally our own. For extinct species, LHV and LHRV values have to be extrapolated from whatever information can be derived from teeth and fossilized bones. However, examination of dental microstructure allows accurate timing of dental formation and determination of age at death of subadult individuals, and studies of dental tissue and calculus and bone composition can elucidate environmental circumstances, pathology, and dietary content and changes, including possible weaning. Some values can be estimated, such as inter-birth intervals from ages at completion of weaning, but others, such as gestation length and ages at first and last reproduction (pregnancy), remain undetectable.

Life-history variables are based principally on female life history, because female capacity for reproduction and sustenance of offspring more closely defines the potential of the community for continuity and survival.

Life-history variables relating to females and infants are listed in Table 2.2, based upon Kuykendall's (2020:11) Table 31.2. The great ape data includes alternative values from different sources. Some of these are specifically identified here, they are supplemented by some further values from other widely cited sources, and columns for recent humans and Neanderthals are added. The chief interest is *Pan* and the two late species of *Homo*, but *Pongo* and *Gorilla* are retained to add perspective. The large discrepancies in values from different sources, e.g. body mass, are notable, as well as the large ranges observed in recent studies of female chimpanzee sexual maturity. Most but by no means all sexually maturing female chimpanzees *disperse* to other communities (~ female exogamy). Because these females tend to have later first reproduction than those who remain in the natal community, the range of this variable is extended (Walker et al. 2018:131,135).

Table 2.2: Some life-history variables of great apes, recent humans and Neanderthals

Trait	Pongo	Gorilla	Pan	Recent humans	Neanderthals
Female adult cranial capacity (cm ³)	338 (pygmaeus) 341 (abelii)	456 (gorilla) 480 (beringei)	350 (troglodytes) 326 (paniscus)	1250 ^{1,2} 1228 ²⁴	1230 ³
Female adult body mass (kg)	35.8 37.0 ¹ 36.0 ²⁰	71.5 93.0 ¹ 84.5 ²⁰	41.6 31.1 ¹ 35.0 ²⁰	40.1 ¹ 60 ⁴ 47.9 ²⁰ 55 ²⁴	66.1 ⁵ 60.4 ⁶
Neonatal body mass (kg)	-	1.82 ³⁰	1.45 ³⁰	3.2 ³⁰ 2.4–3.5 ³¹	-
Deciduous teeth first emergence (months)	-	-	3 ³³	6 ³²	-
Age at onset of weaning (months)	-	5–8 ³⁶	6–12 (Tai) ⁸ 6 (Mahale) ⁸	5–6 ¹² 5 ²³	9 ¹³ 7.5 ¹⁴ 3.8, 6.6, 5.3, >4.7 ¹⁵
Deciduous teeth fully emerged (months)	-	-	13 ³³	24–33 ³²	-
Age at cessation of suckling (y)	7.0, 6.0, 5.8–7.5 ³⁵	3.2, 3.4–4.7, 2.8, 2.0–6.2 ³⁵	5.0, 4.3–6.1, 4.1 4.4 (Tai) ⁸ 4.2–7.2 (Gombe) ⁸ 4.4–6.1 ²¹	2.4 ^{12,34} 3.0 ¹⁶ >2–5 ²² 2.5 but ≤5 ²³	2.5 ¹³ 1.2 ¹⁴ 4.0 ¹⁷
Inter-birth interval (y)	8.05 ²⁶	4.4 ²⁶	5.75 ¹² 5.46 ²⁶	3.7 ^{20,26} 2–3 ²²	-
First permanent molar emergence (y)	4.6	3.8	2.8–4.3 4.0 ⁷ ≤3.3 ⁸ 2.5–4.3 ²¹	4.74–7.05 ⁹ 5.8 ¹⁰ 6.2 ³⁹	6.7 ¹¹ <6 ¹⁸ <5.9 ¹⁹ <5.0 ¹⁹
Age at menarche (y)	-	-	11.5 (8.5–13.9) ²⁸	12.1–18.4 ²⁵ ~13 ²⁷	-
Age at completion of somatic growth (y)	-	Female 9.5, Male 12–15 ³⁸	Female 11–12, Male 12–13 ³⁸	17–22	-
Age at first birth (y)	15.7	10.1	14.3 14.9 (11.1–22.1) ²⁸	19 ¹⁶ 16.2–25.0 ²⁵	-
Age at menopause (y)	-	-	~45 ²⁶ 35–57 ²⁹	48.2–52.6 ²⁵	-
Typical lifespan (y)	43.0	20.6	29.7	70 ¹ 54.1 ³⁷	-
Data for <i>Pan</i>, <i>Gorilla</i>, <i>Pongo</i> from Kuykendall (2020:11), unless noted. His alternative values for their life events are from a number of studies cited in that publication. Some further values are added here. ¹ Harvey and Clutton-Brock (1985:566). ² Normalized to cranial capacity from MRI-scan brain volumes (Allen et al. 2002: 347), using 1330 cm³ (Holloway et al. 2004:301) as mean recent modern human cranial capacity across both sexes. CF = 1330 × AF / AA, where CF is female cranial capacity to be derived, AF is female mean MRI volume, and AA is average of female and male mean MRI volumes. ³ Mean of adults assigned female, Table E.4. ⁴ Bolter and Zihlman (2007:413). ⁵ Froehle and Churchill (2009:107). ⁶ Table H.2, from Will et al. (2017). ⁷ Zihlman et al. (2004, 2007); Kelley and Schwartz (2010, 2012). ⁸ T.M. Smith et al. (2013:2788–2789). ⁹ Liversidge (2003). ¹⁰ Kelley and Schwartz (2010:1037). ¹¹ Macchiarelli et al. (2006:750). ¹² Humphrey (2010). ¹³ T.M. Smith et al. (2018:5–6). ¹⁴ Austin et al. (2013). ¹⁵ Nava et al. (2020:3). ¹⁶ Bogin (1999). ¹⁷ Ogilvie et al. (1989:32). ¹⁸ T.M. Smith et al. (2007b). ¹⁹ T.M. Smith et al. (2010). ²⁰ Robson et al. (2006:22–29). ²¹ Machanda et al. (2015:140). ²² Konner (2005:22,35–36). ²³ Sellen (2006:186,189). ²⁴ Ross (2003:272). ²⁵ Kuzawa and Bragg (2012:S373). ²⁶ Robson et al. (2006:22–23,30). ²⁷ Cole (2000); Frisch (1994). ²⁸ Walker et al. (2018:131,135). ²⁹ Videan et al. (2006); Thompson et al. (2007); Lacreuse et al. (2008). ³⁰ Schultz (1969:152). ³¹ Eveleth (1978:274–375). ³² Dean and Liversidge (2015). ³³ Kuykendall et al. (1992:385). ³⁴ Sellen (2001:2707). ³⁵ Robbins and Robbins (2021:782). ³⁶ Dian Fossey Gorilla Fund 2020, https://gorillafund.org/uncategorized/gorilla-moms-and-dads-being-together/ retrieved 2023.11.28 ³⁷ Schwartz (2012:S399). ³⁸ Dean 2016. ³⁹ Gleiser and Hunt (1955), cited by Macchiarelli et al. (2006).					

2.4.2 Weaning and inter-birth interval

Weaning should preferably be represented by two life-history variables. It is not an event but a process lasting several years. Sellen (2006:158,195) distinguishes exclusive suckling, transitional feeding, and finally a weanling phase. Transitional feeding begins with *weaning onset*, when the infant is introduced to complementary foods such as soft fruit, relatively easy to ingest and requiring little or no chewing, and ends with *cessation of suckling* or *weaning completion* when the infant progresses to exclusively external foods.

Recent humans and chimpanzees

Weaning onset overlaps with or immediately follows the emergence of the first deciduous teeth, the upper central and lateral incisors, at ~6 months after birth in both chimpanzees and recent humans (Mahoney 2015:408; Sellen 2001). Chimpanzees begin to eat fruit at ~6 months but continue to be suckled with decreasing frequency until they are 4–7 years old (Schultz 1969; T.M. Smith et al. 2013). Cessation of suckling in human hunter-gatherer and subsistence-farming contexts occurs usually at 2.4–3 years (Humphrey 2010; 2006:189) but as late as 5 years (Konner 2005:21; Sellen 2006:186, citing Hartmann and Arthur 1986). While the age of weaning *onset* for chimpanzees and humans is similar, recent humans even in small-scale traditional societies have much earlier cessation of suckling than chimpanzees and the other great apes.

For chimpanzee mothers, late cessation of suckling promotes wide spacing between births, with a mean of 5.75 years (Humphrey 2010). Although the age of weaning completion in recent humans is early, it appears to be unconnected with timing of other life history milestones within the individual's lifetime such as puberty. However it does affect inter-birth interval and therefore the potential for greater lifetime production of offspring (Lee 1996, 2012). Long inter-birth intervals in great apes limit population growth and may further reduce viability of their communities already subject to restricted habitats (Kennedy 2005).

Lactation appears to induce the secretion of hormones which inhibit ovulation, so that the mother does not conceive while she is suckling an infant (Sellen 2006:173,188; Lee 1996:88; cf. Takada 2005:291). However, Skinner (1997a:690) observes that in small-scale human societies lactation does not always suppress ovulation, because the latter may resume after a few months of breast-feeding, and cessation of suckling itself may be precipitated by a new pregnancy. Frequent suckling day and night may tend more effectively to suppress ovulation (Konner 2005:35).

Table 2.3 lists ages of infants at completion of weaning and the inter-birth interval (IBI) for five widely separated recent forager groups. The span of weaning ages is ~2–3.5 years and IBI 3–4 years.

Table 2.3: Recent foragers, cessation of suckling and inter-birth interval

Society	Location	Cessation of suckling (mo)	Inter-birth interval (mo)
Ache	Paraguay	25	37
Aka	Centra Africa, Congo	42	48
Agta	Northern Philippines	27	36
Efe	Congo	30	38
Hadza	Tanzania	30	38
!Kung	Southern Africa	42	48
Data from Konner (2005:57).			

Neanderthals

It has been suggested that Neanderthals ceased suckling their infants late at 4 years, on the basis of a peak incidence of dental enamel hypoplasia around this age (Ogilvie et al. 1989). This would result in a probable inter-birth interval of ≥ 4 years, ~ 0.5 –1 year longer than often cited for recent foragers, although in recent humans cessation of suckling may be as late as 4–5 years and mean inter-birth interval of ~ 4 years has been observed (Table 2.3) (Robson et al. 2006:22–29; Takada 2005:291). If *Homo sapiens* ancestors did generally wean earlier, a Neanderthal IBI of ≥ 4 years would reduce, even if marginally, potential number of births per adult female lifetime, and therefore could contribute to lower reproductive fitness.

Stinespring et al. (2012:S278) report a peak of dental enamel hypoplasia in the Krapina Neanderthals at either 2.3–2.5 years, assuming a periodicity¹ of 7 days, or 2.6–2.8 years assuming a periodicity of 8 days. If hypoplasia is a signal of nutritional stress, here it may indicate cessation of suckling at the same ages as recent humans.

Weaning onset and completion are sometimes detectable from stable isotopes in teeth. Before birth barium/calcium ratio is low; during exclusive nursing barium/calcium ratio is high and strontium/calcium ratio is low: when complementary food is introduced, these ratios begin to be reversed, and the effect is more strongly expressed when nursing completely ceases (T.M. Smith et al. 2018). Further studies have shown that these effects are not universal in living humans or other primates, and may be masked or counteracted by inter-individual and seasonal variation in expression of the isotope ratios in teeth involving barium, strontium, calcium and zinc (T.M. Smith et al. 2022).

Using barium/calcium and strontium/calcium ratios, age at weaning onset 9 months and age at cessation of suckling 2.5 years were indicated in the dental individual Payre 6, while a second dental individual Payre 336 was still nursing at 2.5 years (T.M. Smith et al. 2018). Austin et al. (2013) determined that the Scladina juvenile experienced weaning onset at 7.5 months and “abruptly” ceased nursing at 1.2 years. This early age is unique to the Scladina individual, and the gradual decline of barium level characteristic of intentional weaning is not observed (T.M. Smith et al. 2018:4,6). It may be that the mother died or was incapacitated, but the child survived to 8 years (T.M. Smith et al. 2007b).

Nava et al. (2020) detected changes indicating introduction of complementary food in dental remains of two individuals: Fumane 1 at 3.8 months with a stronger signal at 6.6 months, and Broion 1 at 5.8 months. A third infant Nadale 1 was still being exclusively suckled at 4.7 months. For Fumane 1, Broion 1 and Nadale 1 there are no ages for nursing cessation.

From a study of enamel hypoplasia, Limmer et al. (2024) conclude that Upper Palaeolithic children had increasing incidence of defects at their dental stages² 1 (<1 y) and 2 (1–1.8y) and a peak shortly after their stage 3 (1.5–2.9y), i.e. in stage 4 (2.1–3.7y), while Neanderthals begin to show defects after stage 2 (0.65–1.53y), increasing to a peak at stage 6 (2.37–3.87y). Their Neanderthal stages 4 (1.47–2.75y), 5 (2.67–3.88y) and 6 (2.37–3.87y) overlap, and together include the age range 2.5–3.0y, which is the most common age for cessation of suckling among recent hunter-gatherers. By *ages*, their Neanderthal stages 5 and 6 correspond to stage 4 for the Upper Palaeolithic. It is not clear why the Neanderthal peak should be regarded as later than the Upper Palaeolithic peak when the ages are the same. The only anomaly, if it is one, is that the Neanderthal immatures appear to have been more advanced dentally at cessation of suckling than the *Homo sapiens* immatures.

¹ §3.4.2, §C.2, §C.3.

² The stages are defined by formation stages of a combination of teeth. However, according to the authors the stages translate to earlier ages in Neanderthals owing to accelerated dental development.

Buxton (1928:81) reports that the deciduous tooth crowns of the Gibraltar 2 child (4.6 years) were much worn, which indicates either or both of early weaning and a rough diet (Carbonell 1965:41).

On the evidence, limited though it is, Neanderthal weaning was neither early nor late but well within the range of modern human hunter-gatherers. The hypothesis of a longer inter-birth interval in Neanderthals is so far unsupported (Nava et al. 2020:8).

2.4.3 Menarche and menopause

It is difficult to assess ages of menarche and menopause in an extinct species. However, observation of chimpanzees has indicated the timing of these life history events among the nearest living species to our own.

Although clearly chimpanzees are earlier, for menarche the age range overlaps with living humans (Table 2.2). In countries affected by the positive secular trend (§2.6), ages at human menarche appear to have stabilized to a mode of ~13 years, just within chimpanzee range, while onset two years earlier is not uncommon (Eveleth and Tanner 1990:161–171; Cole 2003:161; Ellis 2004:921).

Menopause occurs because at birth the ovaries contain a finite number of oocytes. After menarche, oocytes are steadily lost through ovulatory cycling and atresia of ovarian follicles. Cycling ceases when the number of remaining ungrown follicles drops below a critical threshold. Menopause has rarely been noted in chimpanzees because lifespan is shorter than in humans, in captivity and more so in the wild. Chimpanzees begin to show signs of frailty and slowing mobility from the mid-30s, many die in their 40s, and maximum lifespan is thought to be ~60 years (Robson et al. 2006:24–25). Some researchers have suggested menopause may occur as early as 35–40 years (Videan et al. 2006), while other authors have observed chimpanzees continue menstruation into their 50s, with menopause rare and only near the end of the lifespan, in one case at ~2 years before death at 59 years (Lacreuse et al. 2008). At the Gombe and Kibale reserves in East Africa, females are known to have given birth to surviving offspring as late as 49.2 and 55.0 years of age respectively (Thompson et al. 2007). A recent survey of data for 1995–2016 at Kibale reports signs of menopause at ~50 years (Wood et al. 2023). For humans Kuzawa and Bragg (2012:S373) give a menopausal range centred on ~50 years, close to the median of 51.3 years reported by McKinlay et al. (1992:1,8).

Menopause, even more than menarche, appears therefore to occur at similar ages in chimpanzees and recent humans, indicating that timing of female reproductive life events may be conserved across these genera whereas the disparate lifespans are derived (Hawkes et al. 2003:215; Robson et al. 2006:43; Hawkes 2006:46,75; Lee 1993:79). If this is so, then females of other species of *Homo* should be expected to follow a similar pattern.

A major difference is the much longer lifespan of recent humans. Consequently, following menopause which is no later than in chimpanzees, there is for human females a post-reproductive stage of life lasting ~20 years assuming death at ~70 years. This development enables post-reproductive females, “grandmothers”, to contribute to caring for offspring of the younger generation of mothers. Thus human mothers can give up nursing their infants and are able to reproduce again at a younger age than among chimpanzees. A significantly shorter inter-birth interval leads to more offspring per lifetime.

2.4.4 First permanent molar emergence age

At first sight this parameter may appear to be an anomaly among such variables as age at weaning and age at sexual maturity. However, the case has been made that relatively faster development of the dentition (tooth formation and eruption) is correlated with more rapid growth to adulthood, as clearly observed in chimpanzees relative to humans. This observation has been generalized to the proposition that faster dental development in extinct hominins such as the australopithecines and early *Homo* (*H. habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*) and later non-sapiens species such as *H. heidelbergensis* and *H. neanderthalensis* is evidence of a “faster” life history in these hominins compared with modern humans. A faster life history means earlier attainment of life history events such as sexual maturity and adulthood, and thus a truncated subadult period, during which there would be significantly less time for neural reorganization in response to life experience, less time for learning survival and social skills and perhaps language, and, allegedly, the consequence of more weakly developed cognitive and affective capacities, relative to modern humans.

Specifically, analysis across a range of living primates by B.H. Smith (1989a, 1989b, 1991, 1992) determined that the age at which the mandibular permanent first molar (LM1) emerges through the gingiva is closely correlated with other life history and life history related variables such as body mass and brain size and with the pace of growth to adulthood. This finding is widely endorsed (e.g. Bermúdez de Castro et al. 1999, 2011; Macho 2001; Ramírez-Rozzi and Bermúdez de Castro 2004; Schwartz 2012; Kelley and Schwartz 2012; Modesto-Mata et al. 2020). Kelley and Schwartz (2012:1337) and Schwartz (2012:S395) emphasize that it is M1 emergence that is significant for life history and that there is no expectation that other aspects of dental development, such as anterior tooth formation time or eruption, be correlated with any life history variables.

Gorillas, gibbons and siamangs

Gorillas are conspicuously the largest-bodied primate. However, their average age at M1 emergence is similar to that of the much smaller-bodied chimpanzees (Kelley and Schwartz 2012). Gorillas are more folivorous than chimpanzees, and folivorous primates tend to have faster life histories (Foley and Lee 1991:224; Leigh 1994; Godfrey et al. 2001, 2003). The first permanent molars have to emerge in time to provide sufficient occlusal surface for a weaned gorilla infant to chew rough vegetable material, in contrast to the primarily frugivorous chimpanzees and orang-utans. Table 2.2 shows gorilla age at first birth earlier than chimpanzees, and lifespan shorter.

Whereas lowland gorillas (*Gorilla gorilla*) were known to eat some fruit, mountain gorillas (*Gorilla beringei*) were thought to be almost exclusively folivorous, as those inhabiting the Virunga region appear to be. A recent study within the Bwindi National Park in Uganda has shown that mountain gorillas there prefer fruit when it is available (Ostrowsky and Robbins 2020). Durations of fruit feeding observed for the Bwindi gorillas appear to be less than those for lowland gorillas, which in turn are less than those for chimpanzees or orang-utans, while at Bwindi the amount of time spent “travelling”, seeking food, is greater than that for the Virunga gorillas but less than that for chimpanzees or orang-utans (ibid.:13). In terms of activity Bwindi gorillas therefore appear to be intermediate rather than aligned with more fully frugivorous apes. The question arises whether there are observable differences in timing of life history events between the Bwindi and Virunga populations, although they may not have been separated long enough for such differences to develop. A possibility is raised that the distinction between folivory and frugivory and the connection between these diets and life history may be less clear cut than formerly thought.

The lesser apes, gibbons and siamangs, form a subfamily of two genera. Siamangs, being considerably larger-bodied, theoretically ought to have a slower life history than gibbons, but the reverse is the case. Again, the explanation may be the siamangs' folivorous diet.

Chimpanzees

Kelley and Schwartz (2010) argue that widely cited ages in the range 3.0–3.5 years for first molar emergence in chimpanzees (Table 2.2) (Kuykendall et al. 1992; Kuykendall and Conroy 1996), obtained from captive animals in zoos and research facilities, may be atypical of animals in the wild. Later ages derived from remains of wild-living chimpanzees have been put forward (Zihlman et al. 2004, 2007; Bolter and Zihlman 2007), raising the mean to 4.0 years (Kelley and Schwartz 2010; 2012; Schwartz 2012).

The revised ages have been criticized on the grounds that they were determined from deceased animals whose ages at death might be unreliable (TM. Smith et al. 2013). From study of living wild chimpanzees at Taï in West Africa, where M1s of five healthy infants emerged before 3.3 years, it appears that for both deciduous and permanent dentitions emergence ages lie broadly within the range of captive chimpanzees, but with the later-forming permanent teeth falling into the upper half of that range (*ibid.*:2787–2788; Hillson 2014:141). Subsequent studies of the East African wild Kanyawara community confirm that result, with late-developing canines in males, suggesting that later mineralizing teeth may be more affected by ecological conditions (Machanda et al. 2015).

Captive chimpanzees then appear to have only slightly earlier M1 emergence but potentially a more rapid ontogeny. Yet they do not suffer from high early mortality since there is no predation, and they are likely to receive medical care in the event of injury. One disadvantage in terms of individual survival may be elevated anxiety and stress because of the close proximity of conspecifics and inability to escape unwanted contact in a confined environment. However, the regular supply of food and the availability of adequate shelter and medical care ensure that captive chimpanzees do not suffer from the more pragmatic stresses of life in the wild: undernutrition from seasonal or local scarcity of food resources, chills resulting from rainy weather, or untreated injuries and disease.

The secular trend in recent human growth is discussed later (§2.6). A similar process may be occurring in captive ape communities. Earlier first molar emergence and possibly earlier attainment of other life history milestones in this case would represent developmental plasticity (Kuzawa and Bragg 2012:S371). Any advanced growth in this context is not due to natural selection, which has not had time to act and has largely been set aside by human agency.

Living humans

A wide range of mandibular permanent first molar mean emergence ages for samples of living human populations by country is presented by Liversidge (2003) (§3.4.7). The youngest listed mean age of only 4.74 years is supported by the next youngest mean 5.05 years, both for West African female samples.

It is clear that in several modern human geographical groups some individuals have M1 emerged well before their sixth birthday, and in some groups before their fifth. The later ages reported for chimpanzees in the wild, overall ranges for chimpanzees, and indeed the age reported for orang-utans approach the recent human range (Schwartz 2012:S389–S401; Dean and Liversidge 2015:417,423).

Cessation of suckling takes place at ~2.5–3 years in preindustrial modern human societies, but the first permanent molar does not emerge until ~5.8 years (Table 2.2), by which time the infant has been eating exclusively extrinsic food for half its life. The deciduous teeth alone serve the purpose of biting and chewing throughout the early childhood stage. Appearance of the deciduous dentition (Tables D.8 and D.9), beginning with emergence of the first incisors (di1), largely coincides with weaning onset, and completion of the deciduous dentition, with occlusal eruption of the second molars (dm2), largely coincides with cessation of nursing. The deciduous teeth suffice for approximately a further three years (Aiello et al. 1991:404–406), altogether twice as long as the duration in chimpanzees (cf. Schultz 1950:440). The permanent dentition is not required for modern human weaning. It would appear that in modern humans, and on present evidence Neanderthals, timing of M1 emergence has no causal or enabling effect on weaning.¹

Neanderthals

Neanderthal first molar emergence has a reported range of <5.0–6.7 years (§3.4.7 Table 3.15). This age range lies within the range for recent humans (Tables D.14 and D.15).

On the assumption of close correlation specifically between M1 emergence age and pace of life history, available evidence does not unequivocally indicate a more rapid life history for Neanderthals. However, in general their dental development was advanced by modern human standards (Chapter 3).

Correlation due to weaning or pleiotropic genes?

A connection between M1 emergence and weaning would explain the importance of M1 emergence as an indicator of life history, because weaning enables the infant to become nutritionally independent of its mother. This enabling potential of M1 emergence then is the putative factor that produces its effect on life history.

However, while M1 emergence is an event (strictly four almost coincident events), weaning is a process. In chimpanzees it takes ~4 years, lasting from *weaning onset* to *cessation of suckling*. M1s emerge part way through this period. Chimpanzees at Tai eat some solid food long before M1 emergence, suckle during the emergence period, and continue throughout the year after the M1s emerge (T.M. Smith et al. 2013:2787–2788). Among preindustrial modern humans, cessation of suckling takes place ~2.5–3.5 years before the M1s emerge. In terms of nutritional independence, it appears that in chimpanzees there is a temporally loose connection between M1 emergence and weaning (nutritional independence), but in modern humans there is a complete disconnection (Mahoney 2015:407). If the causative or enabling function of M1 emergence does not hold, then the significance of M1 emergence as an indicator of life history is called into question. Admittedly only in humans is there a clear disconnection.

An alternative possibility is to view pleiotropic genes which affect both dental and somatic development as governing internal systemic rhythms that determine the pace of life history (cf. Tanner 1962, 1989; Bromage et al. 2009, 2011, 2012). In this case, timing of M1 emergence would be one outcome of the systemic governing mechanism, and pace of bodily growth a separate outcome. If this is so, then not only in modern humans but also in other primates this pleiotropic developmental effect may be the phenomenon represented by correlations rather than a nutritional connection between M1 emergence and weaning.

¹ Contra Kelley and Schwartz (2012) and Schwartz (2012).

2.5 Demography, nutrition and pace of life history

2.5.1 Nutrition and young adult mortality

The risk of mortality in the end is one hundred per cent. For life history a significant factor is early or premature mortality: before and during the actively reproductive stages of life, i.e. within all stages except post-reproductive adulthood. The actively reproductive stages include mature or “prime” adulthood, young adulthood, and often adolescence. Young adult mortality has a particular significance for demography and community survival in a hunter-gatherer society, because individuals dying during this stage of life have received many years’ investment of energy by mothers and the community which potentially could result in more members for the next generation. Much of the investment is lost if the individual’s reproductive years are cut short early in that stage. In prolonged circumstances of high young adult mortality, natural selection is expected to promote earlier sexual maturity, reducing the risk of death before reproduction (Promislow and Harvey 1990; Migliano et al. 2007:20218).

Researchers have correlated human nutritional and mortality conditions with expected outcomes in terms of a set of life history variables and traits. Combinations of these conditions and outcomes are presented as distinct *profiles* in Table 2.4. The table is sourced from three papers, not all of which offer all outcomes and between which proposed outcomes may differ: e.g. Migliano and Guillon (2012) describe inhabitants of developed countries as maturing early (profile A2), rather than occupying a standard or intermediate position (profile A1). Outcomes *early*, *late*, *full* etc. for the other profiles B, C, D are with reference to the A profile.

Table 2.4: Modern human life history profiles

Profile	Conditions		Outcome			
	Nutrition	Premature mortality	Adult height	Cessation of growth	Life span	Fertility
A1	Abundant	Low	Full	Intermediate	Long	Intermediate
A2			Full	Early	-	-
B1	Abundant	High	Intermediate	Slightly early	Intermediate	High
C1	Poor	Low	Full	Delayed	Intermediate	Low
C2			Full	Delayed	-	-
D1	Poor	High	Reduced	Slightly delayed	Short	Intermediate
D2			Much reduced	Very early	Short	-
D3			Reduced	Early	-	-

Only Kuzawa and Bragg (2012) describe every type of outcome.
A1, B1, C1, D1 outcomes from Kuzawa and Bragg (2012).
A2, C2, D2 outcomes from Migliano and Guillon (2012) and Migliano et al. (2007).
D3 outcomes from Schwartz (2012:S401–S402).

Profiles A1/A2 are exemplified by the majority of people in developed countries. Profile B1 would include hunter-gatherers who consistently have access to game, in some cases supplemented by sea food, fruit or vegetables. In the absence of medical care, they would be subject to injuries and mortality risks from disease, injuries, and in some environments predation. Profiles C1/C2 would include such societies as some East African hunter-gatherers and pastoralists, among whom mortality risks are low and growth is slow but the period of growth extended (Migliano et al. 2007; Blurton Jones 2006:247–251). In their case adults may be tall owing to selection for the ectomorphic body form in a hot climate (Kuzawa and Bragg 2012:S374). Profiles D1/D2/D3 are exemplified by generally small-stature rainforest populations, among whom nutrition is limited and risk to life from disease and injury significant (Migliano et al. 2007; Migliano and Guillon 2012; Hochberg and Belsky 2013). Pygmies appear to occupy the “fast” segment of human life history strategies.

Of the profiles in Table 2.4, Neanderthals appear *prima facie* to fit the conditions, but not necessarily the expected outcomes, of either B or D profiles most closely.

2.5.2 Neanderthal nutrition abundant?

Evidence for profile B, requiring abundant nutrition, includes archaeological analyses which indicate that Neanderthals principally hunted large and intermediate-size herbivores such as aurochs, bison, horse, and deer (Bocherens et al. 1999, 2001; Richards et al. 2000; Gaudzinski and Roebroeks 2000; Richards and Schmitz 2008; Gaudzinski-Windheuser et al. 2014, 2018; Terlato et al. 2019; Wißing et al. 2019), and in the Last Interglacial elephant (*Palaeoloxodon*: Gaudzinski-Windheuser et al. 2023). They also consumed smaller animals such as rabbits and tortoises and plant material including tubers and nuts (Henry et al. 2011, 2014; Fiorenza et al. 2015; Weyrich et al. 2017, Carvalho et al. 2018; Power et al. 2018; Kabukcu et al. 2022), as well as birds (capercaillie, grouse and cormorant: Goffette et al. 2024). In coastal habitats they exploited marine animals including crustaceans, mussels and fish (Stringer et al. 2008; Cortés-Sanchez et al. 2011; Zilhão et al. 2010, 2020; Villa et al. 2020).

Their diet may have been very high in protein (Snodgrass and Leonard 2009) and their wide lower thorax and pelvic girdle may represent an adaptation for enlarged growth of the liver and kidneys to process an habitual diet of high animal protein and fat (Ben-Dor et al. 2016). However, they would have had to consume some plant foods to avoid protein toxicity in neonates and pregnant females (Fiorenza et al. 2015; Hardy et al. 2022), and there is evidence of plant food preparation and heating (Kabukcu et al. 2022). However, in a cold, arid, glacial period within MIS4, the La Quina H5 individual had a high-protein but plant-poor diet (Williams et al. 2022).

From age profiles of Neanderthal skeletal remains showing a dearth of older adults (above 30 years), it has been argued that they suffered very high young-adult mortality to a degree not matched in other archaeological or recent populations (Trinkaus 1995). Many Neanderthal skeletons show serious injuries, particularly to the upper body, indicating a hazardous life style. It has been proposed that these injuries largely resulted from the dangers of approaching large prey, especially at close quarters (Trinkaus and Zimmerman 1982; Ogilvie et al. 1989; Berger and Trinkaus 1995). However, the Neanderthal mortality and skeletal injury profile appears to be shared by Levantine Middle Palaeolithic and European Early Upper Palaeolithic *Homo sapiens* (Trinkaus 2011a, 2012; Beier et al. 2018).

Archaeological discoveries and upper-body anatomical analyses have provided evidence that Neanderthals and their ancestors used spears as projectiles (Villa et al. 2009; Soressi and Locht 2010; Rots 2013; Maki 2013; Berthaume 2014; Conard et al. 2015; Milks et al. 2019). These studies cast doubt on the hypothesis that close-quarter hunting was obligatory, although Spikins et al. (2019) suggest that to penetrate the hides of the very largest prey such as mammoth and woolly rhinoceros only close approach would have enabled sufficient thrust. Alternative explanations for observed injury patterns, including inter-personal violence, have been explored (Trinkaus 2012; Carrier and Morgan 2015).

2.5.3 Neanderthal nutrition poor?

Schwartz (2012) characterizes Neanderthals as having predominantly poor nutrition (condition D3). This conclusion is supported by a number of authors.

Ogilvie et al. (1989) studied a large sample of Neanderthal teeth from western and eastern Europe, Iraq and the Levant (1989:35). They state that Neanderthals exhibit very high

incidence of dental enamel hypoplasia (localized failure to form enamel matrix), indicating stress, nutritional or other, during ontogeny. Hypoplasia is less frequent in the youngest individuals. Only one, Pech de l'Azé, has hypoplasia in the deciduous dentition. In the sample there are two peak ages of incidence: ~4 years, attributed by the authors to cessation of suckling; and ~11.5 years, in the third molars (M3). This phenomenon during the years of M3 crown formation can be interpreted as due to nutritional stress, psychosocial stress, or participation in taxing physical activity and risk taking¹ by juveniles and adolescents. In support of the last explanation, adolescents accounted for the largest percentage of Neanderthal subadult deaths at 34.9%, followed by juveniles at 28.3% (Trinkaus 1995:133).

In Neanderthal teeth from Krapina (~130 ka), Hutchinson et al. (1997) assess incidence of hypoplasia and hypocalcification (disruption of mineralization), which suggest metabolic disruption of matrix secretion and maturation and may result from chronic physiological stress (1997:905). However, frequency and severity of dental hypoplasia and hypocalcification in Neanderthals was equalled and in some cases greatly exceeded by the incidence in recent prehistoric North American hunter-gatherer populations (Hutchinson et al. 1997:910–913). Linear enamel defects have been observed to a similar degree in the dentition of Neanderthals and recent Arctic hunter-gatherers, indicating episodes of stress, but these episodes appear to have been of shorter duration in the Neanderthal sample (Guatelli-Steinberg et al. 2004).

The Krapina Neanderthal assemblage exhibits a high incidence of dental enamel hypoplasia, taking the form of hypoplastic bands and also pits where enamel has failed to form (Molnar and Molnar 1985; Molnar et al. 1993). These authors note that ameloblasts are sensitive to metabolic depression which may be caused by nutritional deficiency or disease (cf. Hillson 2014:203). The sample of dental arches indicates at least 18 individuals, 10 of whom were under 16 years and the oldest 23 years, and in this young sample little dental attrition was observed (Molnar and Molnar 1985:541–542). Even so, the authors state that there was less hypoplasia in this sample than in a Mesolithic population, citing Brothwell (1963).

Another cause of hypoplasia could be vitamin D deficiency owing to lack of sunlight (Molnar and Molnar 1985:547). It would not be surprising if during glacial periods Neanderthal subadults from north of the Pyrenees and across central and eastern Europe were routinely bundled in furs and their bodies rarely exposed except on warmer days. In fact, Levels 4 and 5 of the Krapina site, bearing this sample, are dated to the last interglacial (Molnar and Molnar 1985:547). During the interglacial global temperatures became 1–2° C higher than in the early twentieth century, and tropical fauna such as hippopotamus are found in Europe (Burroughs 2005:82; Otto-Bliesner et al. 2013). However, a sharp rise in sea surface temperature by 3° C took place at ~125.6 ka (Obrecht et al. 2022), leaving the possibility that conditions on land were also slightly cooler in earlier millennia of the interglacial predating that rise. This earlier period seems to fit the dating of the Krapina hominin levels at ~130 ka (Rink et al. 1995; Mahoney et al. 2021).

Skinner (1996) compares Middle Palaeolithic (MP) and Upper Palaeolithic (UP) populations, but does not distinguish *Homo sapiens* (e.g. the Levantine group) from Neanderthals in the former. Previous studies of MP individuals, mostly adults, including Krapina (Ogilvie et al. 1989), discovered hypoplasia in the permanent dentition of ~57–78% of Neanderthals, but in only 3.9% of MP deciduous teeth, and there is no evidence of infectious disease in Neanderthal infants (Skinner 1996:834,847). In the MP, dental hypoplasia is concentrated at 3.5–5.0 years, with another peak at 11 years (hypoplasia in the third molar), while in the UP most stress seems to occur in early infancy, also with a higher infant death rate (Skinner 1996:834,847–848; cf. Limmer et al. 2024). A denser UP population in certain areas

¹ Self-restraint is reduced by pubertal hormone levels (Juraska and Willing 2017:92).

(Hayden 1993, 2012) may have created relative crowding and facilitated transmission of infectious disease (Skinner 1996:848). Localized hypoplasia of the deciduous canine and craniofacial osteopenia manifesting as thin bone is absent from the Middle Palaeolithic but very common among Upper Palaeolithic subadults; this may be due to low intake of vitamin A. While both populations subsisted on a similar high-meat-content diet, MP communities may have had access to pigmented vegetables and fresh meat, including liver, rich in vitamin A, but more organized UP communities may have stored dried meat, losing some of its nutritive value (Skinner 1996:845,848).

Evidence has been presented of cannibalism among Neanderthals, interpreted as a response to failure to obtain adequate nutrition from the environment because of unavailability of suitable prey and vegetable resources or inadequate numbers, strength and proficiency of active foragers. This represents obligatory nutritional cannibalism.

Antunes and Santinho Cunha (1992) refer to dental hypoplasia and apparent cut marks on a Neanderthal premolar at Figueira Brava, and infer nutritional deficiency and resulting cannibalism.¹ Defleur et al. (1991, 1993) discuss the Neanderthal sample at Moula Guercy, where human bones were defleshed. Rather than processing for secondary burial they infer cannibalism, because the bones show cut and percussion marks, were not in anatomical association, indicating dismemberment, and were broken and not treated with the care observed among recent ethnographic groups practising secondary burial. Rougier et al. (2016) identify what they regard as unambiguous cannibalism from signs of butchery on Neanderthal bones at Goyet in Belgium.

Defleur and Desclaux (2019) examine evidence from the Eemian interglacial, MIS5e, 128–114 ka, which included the warmest period of the last 400 ka. They state that for MIS5e there are only two occupation sites in France: Moula Guercy in the south and Caours in the north (2019:115). They infer that Neanderthals found hunting more difficult in the densely forested temperate environment than in the more open landscape of glacial periods, because woodland prey species, mainly medium-sized ungulates, were less numerous and more dispersed than the abundant large species including mammoth found on glacial steppe pastures (2019:119). As a result Neanderthals resorted to cannibalism. According to Slimak and Nicholson (2020), there were many more than two Neanderthal sites in France during MIS5e. This is disputed by Defleur and Desclaux (2020). A smaller number of sites would indicate a smaller population, and the explanation by Defleur and Desclaux (2019, 2020) seems cogent. However, studies cited above (§2.5.2 in discussion of Table 2.4 profile B) appear to show that in some locations Neanderthals consumed a diversity of food resources and hunted small animals successfully. It is not clear why they should have been unable to accomplish this sufficiently to survive in a forested interglacial environment while sustaining communities as numerous as those of glacial periods, unless perhaps disease reduced numbers early in that interglacial period, leaving communities small and sparsely distributed.

Cole (2017) determined that the nutritional value of human flesh is lower than that of typical prey fauna of which remains are often found with cut marks in Neanderthal deposits along with processed human remains. This suggests that, if non-human meat could be sourced, the motivation for cannibalism need not have been nutritional. Assemblages from Magdalenian deposits (~14.7 ka) at Gough's Cave include fragmentary human bones which had been butchered to remove flesh and extract marrow, with the further production of skull cups, which Bello et al. (2015) interpret as evidence of ritual cannibalism. While this case relates to modern humans, it raises the possibility of similar motivation in previous ages. Such a consideration weakens the argument for obligatory cannibalism in response to food scarcity.

¹ The other remains were a fractured phalanx and metacarpal, which did not display carnivore gnawing.

Underdown (2008) suggests that Neanderthals frequently consumed conspecifics' brain tissue and would have developed transmissible spongiform encephalopathy, and that this condition may have become a major factor in their numerical decline and extinction. Paşca and Nesse (2008) take issue with Underdown's inferences, noting that not all cannibalism involves consumption of brain tissue or results in encephalopathy, and that evidence of cannibalism exists also for *Homo sapiens* remains. Mead et al. (2003) discuss mortuary cannibalism including consumption of human brain tissue in Papua New Guinea in the twentieth century which resulted in an epidemic of encephalopathy (*kuru*). They report that individuals homozygous for a prion protein gene were eliminated by the disease, and interpret the widespread heterozygosity for this gene in modern humans generally as the outcome of natural selection in response to a widespread practice of cannibalism among *Homo sapiens* ancestors.

It seems clear that Neanderthals engaged in cannibalism, but ambiguous whether that was to a greater extent than *Homo sapiens* at various periods and whether their practice of it was always obligatory, i.e. nutritional.

2.5.4 Rapid growth on poor nutrition?

If Neanderthal immatures grew more quickly, the question arises how that was possible on poor nutrition. They grew to a small stature by 21st century western standards (§6.2 and Appendix H), but lean body weight, as for their predecessors *Homo heidelbergensis* and for Middle and Upper Palaeolithic *Homo sapiens*, appears to have been high by recent standards, at least for males: mean of females 60.4 kg, males 75.4 kg (Tables H.1 and H.2, and compare Tables H.3–H.22). To grow to 75 kg in possibly less than 18 years, as has been suggested (Chapter 7) would require a higher nutritional intake per unit time than growing to 65 kg in ~18–20 years.

Gorillas are the largest-bodied primate and heavier than all the extinct hominins, and reach maturity earlier than either orang-utans or chimpanzees. Yet for the most part they subsist on low-quality food consisting of plant shoots and leaves. On such a diet, rapid growth to their very large adult body size requires ingestion of a great quantity of this material and an extremely large gut to digest it. Gorillas are less active than chimpanzees except on occasions of conflict, and generally spend much of their day either eating or inactive while digestion takes place (Schultz 1969; Foley and Lee 1991:224). It is unlikely that Neanderthals could afford this way of life.

According to Heim (1982:159–162), the skeletons of Neanderthal adults and children show no trace of nutritional insufficiency and Neanderthals were as favoured by their nutritional environment as the best provisioned modern populations. He argues that they grew relatively rapidly, and that this was possible only because they had access to effective nutritional resources.

2.5.5 Archaeological evidence for subsistence and nutrition

Above I have cited archaeological reports of occupation sites, accepting the conclusions presented by the authors and using those as evidence of the success or otherwise of Neanderthal hunting and subsistence activities. However, palaeolithic archaeological deposits are rarely easy to interpret. A *palimpsest* or *time-averaged deposit* can be produced by more than one period of occupation combined with low rates of sedimentation and mixing by human and other animal activity (Bailey and Galanidou 2009). What may appear at first to be a rich living floor with large quantities of tools and butchered animal remains may represent multiple, much less

rich, occupations separated by weeks, years or centuries. It is to be expected that groups of hominins would revisit a previously occupied convenient site, perhaps having intentionally left tools and other materials such as hides there before making an expedition to another location and expecting to return. Even millennia later a cave or rock shelter would be an attractive place to stay for another band of hominins (ibid.).

Malinsky-Buller et al. (2011) distinguish a *living floor* as a thin layer representing a single occupation. A *rapid accumulation palimpsest* is rapidly buried or superimposed layers forming what may appear to be a single occupation. A *slow accumulation palimpsest* may be formed by long exposure of a surface combined with mixture from later and even previous layers and interference from biological and geological agencies. Sossa-Rios et al. (2024) discuss the problems of palimpsest deposits and propose *palimpsest dissection* to establish the temporal order of episodes identified in an archaeological unit.

These interpretative problems lie beyond the scope of the thesis. A more ambitious study might include more precise analysis of sources. Here, as with other specialized issues such as the reliability of body-mass estimation, the pragmatic approach has to be taken of accepting the results offered by archaeologists who analyse the topic of Neanderthal diet and subsistence. Issues arising from these sometimes conflicting results have been discussed in previous subsections.

2.5.6 Further considerations on Neanderthal nutrition and growth

To secure their probable high-protein diet, it appears that adult and adolescent Neanderthals engaged in extremely strenuous activity with higher daily energy expenditure (DEE) than recent humans,¹ and also in some periods had to cope with considerable cold stress (Froehle and Churchill 2009; Snodgrass and Leonard 2009; Weaver et al. 2009; García-Martínez et al. 2018). The wide lower rib cage characteristic of Neanderthals (García-Martínez et al. 2017) has been interpreted as an adaptation to accommodate either (a) a large liver and urinary system for processing a diet high in animal protein and fat (Ben-Dor et al. 2016) or (b) large lungs to deliver oxygen to the bloodstream in response to (b1) high demand from the musculature or (b2) cold climate, in the last case resembling some adaptations in modern human populations to cold or high-altitude environments (Franciscus and Churchill 2002; Churchill 2006; Weinstein 2008). As the above factors are well evidenced and not mutually exclusive, this feature of Neanderthal morphology may be the result of combined selective pressure.

On the B1, D1 or D2/D3 *outcomes* (Table 2.4), Neanderthals should have reached adult size slightly early, slightly delayed, or early, respectively, compared with recent humans. For an early outcome, those individuals bearing genes for early attainment of adulthood should have been favoured by selection, since more of their conspecifics with late-attainment genes would have succumbed before reaching reproductive age.

Such a population is expected to produce more offspring in a lifetime than a population meeting the A1 criteria of Table 2.4 (Promislow and Harvey 1990; Migliano et al. 2007). To enable this, early sexual maturation and early first reproduction are to be expected. Maintenance of a really high fertility rate would require stacking of offspring, enabled by early

¹ Froehle and Churchill (2009:106–107) estimated that in cold climates Neanderthal females may have averaged 3185 and males 4700 kilocalories per day, versus Upper Palaeolithic (UP) modern human females 3084 and males 4414. In temperate climates the values are: Neanderthal females 2409, males 3439; UP females 2256, males 3163. Heyes and MacDonald (2015) critique estimates of daily energy expenditure on the grounds that they depend upon body mass estimates with high standard errors.

cessation of suckling and the resulting short inter-birth interval combined with alloparenting, as seen in modern humans.

It would seem anomalous if Neanderthals experienced (a) persistently high young adult mortality, enjoyed (b) a sufficient high-protein diet, developed (c) early sexual maturation as part of the selective response to mortality risk, but failed to develop (d) early cessation of suckling allowing short inter-birth intervals. If all of b, c, d were in place, then their life history would be similar to that of modern people in developed industrial societies but possibly with some events at earlier ages. Without (d), if high mortality risk was sustained over generations, then their small communities of ~25 individuals (Hayden 2012:8,12) might frequently have found themselves close to extinction, unless other factors sometimes enabled survival of those at risk. Such other factors might include effective care of the wounded and sick, as argued by Spikins et al. (2018, 2019).

It seems unlikely that a population of communities spread over Europe and Central and Western Asia, each of which constantly suffered nutrition stress, generation after generation, and consequently hung perpetually on the verge of extinction, could have survived more than 200,000 years. What is more probable is that some communities regularly experienced high-quality and even abundant nutrition, and many others often enjoyed the same but from time to time underwent episodes, sometimes protracted, of poor nutrition. These suboptimal episodes might be due to such factors as global or localized changes in weather, dearth of expected prey animals from altered grazing and migration patterns, establishment of forest in place of open country or vice versa, inter-community conflict resulting from expansion of growing communities into the territory of others, or violence and accidents occasioning the loss of proficient adult hunters. Archaeological remains so far discovered represent only a subset of the populations which presumably existed, and generally give only a snapshot of a limited temporal period. Among others, the Krapina and Moula Guercy samples may represent communities undergoing nutritional stress.

2.6 Secular trends

For more than a century the secular trend of increasing human stature and lean body mass owing to better nutrition and healthier living conditions has been observed, beginning in North America in the late nineteenth century and extending by the mid twentieth century to Europe, Japan and increasingly beyond (Tanner 1966, 1989:131,156–162; Van Wieringen 1978; Eveleth and Tanner 1990:206–207; Hauspie et al. 1996, 1997). In comfortably off human populations with sufficient and reliable nutrition and reduced health risks, aspects of somatic growth are accelerated, with higher stature and weight at younger ages, an early adolescent growth spurt, and puberty and menarche occurring up to five years earlier than in previous centuries (Tanner 1962:152–155; Marshall 1978:167; Eveleth and Tanner 1990:217–219; Tobias 1985; Aksglaede et al. 2008). Life expectancy at birth has also increased dramatically in industrialized countries (Hawkes et al. 2003:210–213).

These changes in aspects of growth include considerable directional variation in some life-history variables (more rapid growth and earlier attainment). The circumstances and aetiology of these changes need to be considered in assessing life history of a closely related species of *Homo*.

2.6.1 Earlier sexual maturation

Eveleth and Tanner (1990:162–165) report ages at menarche for populations around the world, compiled from studies made from the 1950s onward. Some of these societies surveyed decades ago may enjoy different and in many cases more favourable conditions today. Ages range from 12.0 to 18.0 years. The latest ages are for small-scale societies in New Guinea and Rwanda. Other rural African societies have ages ~14–15 years, while well-off urban Africans and Europeans average ~13 years. The youngest ages of attainment, below 13 years, seem to occur in warm-climate societies with sufficiency if not affluence such as Mexico and among African Americans. As an example of secular change, Marshall (1978:168) illustrates a reduced age of menarche in Britain from 17 years in 1840 to 13 years in 1960.

It has been proposed that menarche is triggered by attainment of a certain body weight, specifically ~48 kg (Frisch and Revelle 1971; Frisch 1994), although this proposal has been rejected by others (e.g. Stark et al. 1989; Cole 2000 and his references). Rapid weight gain during infancy is associated with advanced puberty in both sexes, and a high body mass index is associated with early puberty in girls (Pereira et al. 2021). Also, obesity appears to be a causative or at least enabling factor in the trend to earlier menarche (Wagner et al. 2012). Obesity elevates concentration of the hormone leptin, which seems to play an enabling role in the initiation of puberty. If leptin is at very low levels, puberty does not occur. It has been suggested that the mechanism involving weight may have evolved to prevent pregnancy until the potential mother is sufficiently grown herself and has acquired sufficient energy stores in the form of fat to enable her to bring a fetus safely to term (Kaplowitz 2008). If there is an enabling weight and it is population-specific rather than proportionate to an individual's potential adult size, then a body growing faster toward a larger final size is likely to attain that weight at an earlier age than a body growing toward a smaller final size.

In the induction of earlier puberty some researchers have identified a role for toxins, specifically endocrine disruptive chemicals (EDC) found in the modern environment including food (discussion in Euling et al. 2008). However, authors who mention this explanation often do not argue in favour (e.g. Parent et al. 2003; Gluckman and Hanson 2006), and others reject any kind of pathological factor (Hochberg and Belsky 2013). The large body of evidence for a basis in improved nutrition and hygiene has been emphasized, often in a context of life-history theory (Tobias 1985; Hauspie et al. 1996, 1997; Cole 2000, 2003; Ellis 2004; Pereira et al. 2021).

2.6.2 Increase in stature and earlier attainment

Statural increase is established during infancy and is almost entirely due to greater leg length (Hauspie et al. 1996:8–9; Banik et al. 2017) achieved in the first two postnatal years (Cole 2000, 2003). The trend continues from generation to generation, but may have recently abated in some western countries, although this is not certain (Aksglaede et al. 2008) and in some countries it is ongoing (Holmgren et al. 2019). The twentieth-century secular trend has produced an earlier adolescent growth spurt and earlier sexual maturation, and these changes appear to have been accompanied by earlier completion of somatic growth.

In a high-altitude Peruvian population males and females grew in height to 22.3 years, which is interpreted as late completion of growth (Frisancho and Baker 1970). However, it appears that the cohort was examined only up to this age, so it is possible that some individuals continued to grow taller afterward. Among Hadza hunter-gatherers in Tanzania female growth ceased at the end of the teens, whereas males continued slow growth, particularly in weight, into the mid twenties (Blurton Jones 2006:247–251). Similarly slow but prolonged growth has been observed in Turkana and Karimojong peoples of Kenya and Uganda respectively (Little et al. 1993; Gray et al. 2004). These apparently late-growing populations exhibited only weak adolescent growth spurts. Communities in marginal environments such as these do not exhibit the secular changes observed in comfortably off social strata in the developed and developing worlds.

In the first decade of the twentieth century European men typically reached maximum height only at ~26 years, whereas in the 1960s this age for Europeans and North Americans had fallen to 18–19 years (Tanner 1966:527). Tanner cites Kiil (1939)¹ and Morant (1950). Morant had access to medical records for British military recruitment, providing successive dated samples each amounting to tens of thousands of males aged from 18 years to middle age. Before 1905 the greatest mean height was found in the oldest group, 25 years upward; in 1905–1913 the greatest mean was at 24 years in 7 out of 9 annual samples (1950:446). For the general population Morant (1950:448) reported that maximum height was attained at 26 years around 1880 and at 21.5 years around 1945. No increase was detected in maximum mean height, which remained at 5 feet 7.5 inches (171.5 cm) across all his samples (1950:449–451). On this evidence the secular trend in Britain prior to the Second World War delivered earlier growth but not greater final stature. From the late 1940s onward larger final stature has been attained in Britain and other industrial and industrializing countries.²

According to Tanner (1962:86), earlier dental development in the preadolescent years is accompanied not only by earlier menarche but also by earlier closure of tibial epiphyses, which should indicate earlier cessation of statural growth. For some European populations, Van Wieringen (1978:453) states that age at completion of somatic growth has decreased from 26 years to 18 years. Hermanussen et al. (2007) report that adult height has been attained earlier in Japan in 2003 than in the 1950s. If adult height is both greater and attained earlier, then overall growth rates must be much higher than in previous generations.

To this writer's knowledge, there are no detailed reports focusing specifically on earlier attainment of adult stature or earlier fusion of epiphyses. Van Wieringen (1978:453) proposes that males finish statural growth at a mean of 18 years. Given this mean, some would presumably finish considerably later, in the early 20s, and some considerably earlier, at 16 years or even younger. There is room to question such a claim. Earlier attainment in the year 2020 of height A, where A = mean adult height of a population in 1920, is not the same as

¹ Unavailable at the time of writing.

² References at beginning of §2.6.

earlier attainment of height B, where B = mean adult height of that population in 2020. If $B > A$, then attaining A in 2020 would be only a stage on the way to attaining B. This observation may be trite, but growth surveys in which the upper age limit is 17–18, as in school-based studies, and even surveys ending at 20 years, are missing potentially informative older individuals from the sample (cf. Gavan 1953:108; Taranger and Hägg 1980:65).

Graphs illustrating height growth and height velocity in Swedish boys and girls by Van Wieringen (1978:454–455, citing Ljung et al. 1974) are limited to 18 years. The girls' growth curve flattens at 17 years while the boys' curve is still increasing at 18; the girls' and boys' height velocities, diminishing after the peak, are plotted only to 15.5 and 16.5 years respectively and have not reached zero. Van Wieringen's (1978:456–457) graphs of Netherlands adolescent growth dated 1965 show girls' height increasing to at least 17.5 and boys' to at least 18.5 years, where the study ends. A study of British adult heights and weights (Rosenbaum et al. 1985:117) shows the mean heights of separate male and female five-year adult (i.e. ≥ 20 years) age cohorts (20–24, 25–29, ..., 60–64 years) increasing from older to younger adult cohorts, indicating a secular increase over four decades. However, the mean statures for male and female adolescent cohorts of 16–19 years are lower than means for the youngest four adult male and youngest five adult female cohorts respectively, suggesting that an average of at least 2 cm further growth had yet to take place in the subjects under 20 years.

While there may be scope for further clarification of age at cessation of statural growth, it is not doubted that in the twenty-first century in populations with adequate nutrition growth is generally complete by ~21 years, well before the mid twenties as recorded for some undernourished groups.

2.6.3 Positive and negative secular trends

The term “secular trend” is principally used to refer to the positive effects observed in developed countries as above, and is mostly so used here. Tobias (1985) points out that in different geographical regions secular trends have occurred, some with positive effects (increasing stature and accelerating growth) and others with negative effects (reducing stature and slowing growth). Negative trends as described by Tobias (1985:350–354) appear to have occurred when living conditions have deteriorated and a low standard prevails for several generations, owing to population increase, overcrowding, disease, or curtailment of a community's former range.

Adverse conditions for human growth became prevalent in exacerbated form in mediaeval England, owing to overcrowding, chronic poor nutrition and widespread and ready transmission of infectious disease (Shapland et al. 2015; Lewis et al. 2016a). Conditions may have reached their nadir during the Industrial Revolution in Britain, and in France and some other European countries, between ~1750 and ~1860, when working conditions were unregulated and child labour was commonplace in mills and factories, resulting in injuries, stunted growth and spinal deformities (Bogin 1999:32–35). Reduced adult stature became characteristic of urban and industrial communities as compared with rural communities in the same and preceding periods (Floud 2002). The small adult stature of working class Europeans in the mid nineteenth century should perhaps be viewed as a particularly severe outcome of deprivation, from which the growth of later generations slowly rebounded, beginning in the late nineteenth century as nutrition and health gradually improved following increases in wages and progressive regulation of working hours and conditions.

The positive secular trend observed in developed and developing countries can be interpreted as showing that sufficiency of nutrition enables genetic potential for large body size

and accelerated growth, latent in affected populations, to be actualized. In the late twentieth century and in the twenty-first century many populations around the world have attained a mean stature equivalent to that of Upper Palaeolithic Europeans and Middle Palaeolithic *Homo sapiens* of the Levant (Tables H.5–H.15). This change can be interpreted as recovery of statural growth potential which has been largely unachieved at a population-wide level since the end of the Mesolithic. Not only stature but also body weight has increased. In a survey of British adults in 1980 (Rosenbaum et al. 1985:117–118), postdating many decades of the secular trend but antedating the current era of widespread obesity, mean adult body weight was 73.6 kg (male) and 62.0 kg (female). These values are similar to means for the Upper Palaeolithic (Tables H.5 and H.6).

In contrast to the social equality characteristic of most hunter-gatherer communities,¹ during the Neolithic the adoption of agriculture led to the advent of larger and more sedentary populations living in close proximity, which exacerbated transmission of infectious disease and competition for land and resources, and promoted stratification of society into advantaged and disadvantaged classes (Tobias 1985:353–354). These circumstances led to reduction of stature, lean body mass and skeletal robusticity (Bednarik 2014). The prevalence of smaller human bodies during the Holocene appears to indicate that in this period reproduction was favoured in the trade-off between reproduction and individual growth.

2.6.4 Further considerations

Consensus is that the positive secular trend has produced greater adult stature, earlier attainment of adult stature, and earlier attainment of the reproductive milestones puberty and menarche, together with an earlier and more marked adolescent growth spurt. First reproduction is not necessarily earlier because it is constrained by social expectations whereas puberty and menarche are entirely physiological processes. On present evidence it seems that the following scenario cannot be completely ruled out. If puberty and menarche occur earlier by n years but mean age of attainment of adult height is earlier by m years, where $n > m$, then evidently some life-history variables may vary independently of others. In this way the variables representing reproductive capacity may become detached from those widely regarded as defining overall life history, such as age of first permanent molar emergence, third molar completion, and fusion of the epiphyses of bones contributing to stature

According to life history theory, high subadult and young adult mortality is expected to select for earlier sexual maturation so that an organism can reproduce before a probable early death (Walker et al. 2006b; Gurven and Walker 2006). It appears that the secular trend produces the same outcome for sexual maturation, and in this case the advantage for the organism is the longer reproductive lifespan from reproductive maturity to menopause and potentially a greater number of offspring (Ellis 2004:924; Hochberg and Belsky 2013:1). The secular trend appears to have occurred in response to sufficiency of nutrition with *low* subadult and young adult mortality owing to relatively safe living conditions and availability of medical care.

¹ It has been suggested that some Upper Palaeolithic groups in Europe were complex hunter-gatherers, with leaders or “big men”, like Native Americans of the North West Coast, while Neanderthals were generalized or simple hunter-gatherers (Hayden 1993, 2012:11,21). Complex hunter-gatherer societies are still relatively egalitarian compared with land-owning agricultural and urban societies.

2.7 Environmental conditions: nutrition, ecology and society

2.7.1 Factors other than nutrition influencing growth

In this chapter nutrition has been presented as a principal determinant of growth in subadult Neanderthals and as having enabled relatively high adult body mass. The biological importance of food is unquestionable, and starvation leads to growth inhibition (Hermanussen et al. 2018:1167). Reference is also made to partly genetically determined target body size and morphology (especially Chapter 6). The morphologies of living humans and Neanderthals are distinct, and primarily explicable by the considerable differences in the genome (Reich 2018).

Review of non-nutritional factors

Conditions in early life, intra-uterine and post-partum, can predispose human subjects to adult health problems (Wells et al. 2007). Low birth weight is associated with greater risk of disease. There appear to be critical periods in early ontogeny when the subject is highly sensitive to its environment and developmental plasticity modifies the expression of the phenotype. Early experiences can “program” later development of body composition, so that, e.g., excess fat deposition in response to circumstances leads to obesity and diabetes (ibid.). Childhood stress induced by traumatic events, peer pressure, and unhappiness however caused, is associated with adiposity (Vanaelst et al. 2014). The proximate cause of excess adiposity is often over-eating and sedentary lifestyle, e.g. consuming comfort food and reducing physical activity so as to avoid interacting with others (ibid.). However, there is evidence that unhappiness, stress and perceived insecurity can directly affect growth by interfering with secretion of pituitary and other hormones (Bogin 2021).

Additional factors known to affect growth and development have been foregrounded in recent publications, notably Bogin (2021), Hermanussen and colleagues (2018, 2019; Hermanussen 1997). These authors refer to surveys in low and middle income countries where undernutrition and stunting are common and where in some cases aid programmes providing food supplementation proved less effective than expected, indicating that other factors were in play (Hermanussen et al. 2018:1167). They also review German studies of child growth from the late nineteenth and early twentieth centuries when social inequality and war imposed austerity and starvation on numerous families. They conclude that undernutrition can cause stunting but that, because other kinds of deprivation can also impose it, stunting does not imply undernutrition (Hermanussen et al. 2019:2134; Bogin 2021:432).

Growth in stature and growth in body mass can become dissociated (Hermanussen et al. 2018:1171). Generally, catch-up growth produces recovery in height or length greater than in weight and ceases when the height deficit is corrected. After periods of starvation or severe undernutrition, refeeding typically enables catch-up growth, but when group-typical (see below) stature for age is reached increase of stature ceases, although body mass may continue to increase due to the laying down of fat deposits.

Hermanussen et al. (2019:2133) draw attention to a study by Koch (1935),¹ in which he states “nor does particular abundance of food appear to be a prerequisite for growth at all. Size recklessly increases even during marked undernutrition ... until the body has wasted its last depot.” During the Second World War, despite the reduction in food availability, height of lower class Germans “recklessly” increased (ibid.:2133). In South Africa more recently,

¹ Unavailable at time of writing.

Chidumwa et al. (2021:194) observe that stunted children suffering continued undernutrition may catabolize energy from protein stored in muscles, which can result in detrimental reduction of muscle mass. S. Tanner et al. (2014:93) suggest that stunted children have a reduced capacity to oxidize fat¹ and this may predispose them to increased body fat later in life.

Not all growth impairment can be attributed to nutritional deficit. Illness which reduces appetite or interferes with digestion clearly has an effect via nutrition, but additional factors such as inequality, low socioeconomic status and even political events and excessive exposure to violence can disrupt adolescent growth via psychoneurological effects (Hermanussen 1997:476). Bogin (2021:475,488–491) makes a case that, along with nutrition and basic health, favourable social, economic, political and emotional factors (SEPE) are necessary for growth and that SEPE factors participate in regulating expression of the genome.

Human growth factor (hGH), secreted by the pituitary, and insulin-like growth factor-1 (IGF-1), secreted primarily by the liver but also by other parts of the body, together are required for growth (Bogin 2021:66,376). These and other hormones can be influenced by nutritional status, infection and deprivation (ibid.:401–402,405). Absence of physical contact is known to inhibit growth, as evidenced most clearly by premature babies restricted to incubators, who thrive more when touched even for a few minutes per day, and the failure to thrive of Romanian orphans institutionalized during the 1965–1989 regime (ibid.:407,471).

Poverty, insecurity and perception of low status can lead to low self-esteem and depression which can inhibit growth (Bogin 2021:426). Among apes and humans, dominance, subordination, access to reproduction and other behaviours are affected by physical signals of which the most salient is body size, and for humans height (Hermanussen et al. 2019: 2132). Tallness is associated with prosperity, confidence and dominance in recent human society (Bogin 2021 411).

Group membership shapes identity and self-concept, and appears to have the physical effect of inducing growth in subadults toward a similar height among peers as if there is a group target height (Hermanussen et al. 2019:2133). In a Swiss study similar heights were observed within a local community with nearby communities more similar and more distant communities less similar (Bogin 2021:466). Those moving into an area even tend to grow toward the average of the host community (ibid.:467). Hermanussen et al. (2019:2133) propose that in times of major social transition such as a revolution lower-class adolescents tend to grow taller and are followed by upper-class adolescents who readjust height to compensate. This phenomenon is *strategic height adjustment*.

Applicability to Neanderthals

From time to time Palaeolithic hunter-gatherers such as Neanderthals will have experienced episodes of poor returns for their efforts and suffered undernutrition as a group. Hermanussen and colleagues (2018, 2019) highlight the only temporary effect of undernutrition in subadults provided that it is not prolonged, and the efficacy of catch-up growth, which prioritizes stature rather than weight. They also argue that growth in stature may continue even during prolonged periods of undernutrition, but this would require drawing upon fat reserves and even depleting muscle tissue. In archaeological remains the only evidence would be signs of undernutrition left on and within bone by resulting osteoporosis, rickets, deformities, stunting, and bone matrix decomposition (Kueper et al. 2015), not readily detectable in fossils. Claims by Ivanhoe (1970, 1983) to have identified rickets in subadult Neanderthals are disputed by Trinkaus (1983).

¹ Perhaps because they have exhausted accessible fat reserves already.

Non-nutritional factors affecting growth outlined by Hermanussen et al. (2018 2019) and Bogin (2021) are described as operating within recent societies, many of which around the world are highly stratified, with either an aristocratic or a technocratic ruling class, an intermediate professional or bourgeois class which in turn is internally stratified, and below that a working class or proletariat, itself internally stratified by trade and income. Individual status may be fluid up to a point. None of this can be expected in the Middle Palaeolithic.

Neanderthals most likely were simple hunter-gatherers, i.e. without chiefs (Hayden 1993, 2012:11,21). It is otherwise unknown what form of society characterized Neanderthals, but a comparable recent stone-age society may be that of Australian Aboriginals, among whom male elders were the principal decision-makers in each community.¹ There is no evidence that Neanderthal communities were large enough to support classes or factions which could persist over generations. Many political and socioeconomic factors which operate in complex recent societies and responses to them such as strategic height adjustment would appear not to apply. Similarly, comfort eating and avoidance of physical activity are likely unfeasible for subadults in a forager society. Stature and body mass in extinct hominins are difficult to estimate (§6.1, §H.1). Estimating body composition would be even more challenging (Ocobock et al. 2021).

What can be expected is not class rivalry but inter-community and intra-community competition and dominance, such as we observe among humans and chimpanzees. This could result in oppression by one community of another perhaps less numerous community, restricting their territory or physically fighting. Within a community competition could take the form of oppressing individuals or even a family group within a community of a few families, ostracization of individuals, and bullying and physical violence among adults and subadults. Subordination could lead to differential treatment by others, denial of otherwise shared food and other resources and denial of company, followed by depression and despair.

Any of these negative conditions could lead to growth impairment by deprivation of food if such deprivation was prolonged. But negative treatment by others could itself lead to depression and low self-esteem and may have directly influenced hormone production and reactions, disrupting the growth process (Bogin 2021:401–402,405).

How we might recognize sociobiological effects in subadult fossil remains is a matter for further research. Speculatively, there is a possibility that, besides the genome and proteome, molecular markers of ingested substances and of circulating hormones may be recovered from fossils, which would allow determination of cause of death and recent health status (cf. Hendy 2021). Otherwise, it is challenging to reconstruct the social environment of subadult Neanderthals from site archaeology and fragmentary fossils, which often represent a single individual from its time and place rather than a whole contemporary group.

Psychosocial conditions affecting growth are considered further in the next section.

2.7.2 Associations between environmental and social conditions and growth outcomes

Observations from twenty-two small-scale societies and hypotheses from life history theory are comprehensively analysed by Walker et al. (2006b:295–307). Table 2.5 lists associations found in that analysis, with additional comments. Some of the associations appear contradictory, e.g. 2 and 4, 6 and 7, 3 and 9, indicating that further conditions or factors are involved.

¹ Perhaps most extensively described by Spencer and Gillen (1898); Howitt (1904).

Table 2.5: Associations between environmental conditions and growth strategies

	Correlate 1 (condition or strategy)	Correlate 2 (condition or strategy)	Mechanism or Example	Other factor	Page reference
1	High risk of parasitic and infectious disease	Higher neonatal birth weight			296
2	High disease load often co-occurring with low calorie or low protein diet	Slow growth, later maturity	<i>Growth constrained by poor nutrition</i>		296
3	Attainment of larger size at earlier age	Higher survivorship	More robust immune system, less susceptible to disease and more resilience from fat stores?	<i>Possible only if growth of all body systems adequately supported by nutrition</i>	296,305
4	High subadult mortality	Faster growth, earlier maturity, smaller adult size	Selection for early reproduction		297
5	Smaller adult size (but not pygmy)	Slower growth, later completion of growth	E.g. Ju/'hoansi (southern Africa), New Guinea highlanders		301,307
6	Smallest stature	Faster growth, earlier maturity	E.g. African pygmies and some negrito populations		295,301
7	Larger and taller adults	Faster growth, earlier maturity	<i>Positive secular trend</i>		305
8	High subadult mortality		Selection for early reproduction		304
9	Faster growth	Higher mortality	Immune system compromised by trade-off with growth	<i>If growth too fast relative to nutrition?</i>	305
10	High subadult mortality	Less sibling competition for resources after infancy	<i>Elimination of weakest infants</i>		306
11	Slow growth	Minimize cost of provisioning for parents	<i>Growth constrained by poor nutrition, survival enabled by deferring growth</i>		306
12	Attainment of larger size at earlier age	Escape earlier from vulnerable small-body stage, better subadult survivorship	<i>Elimination of weakest infants</i>		306
13	Attainment of larger size at earlier age	Become productive for community earlier	<i>High provisioning cost to parents but over fewer years</i>	<i>If foraging consistently successful so plentiful nutrition</i>	
Correlations from Walker et al. 2006:296–307. Text in italics is additional comment by the present writer.					

Clearly there is no fixed association between a faster or slower growth strategy and single environmental conditions. Outcomes are determined by a complex of conditions, some of which may vary over time, within a lifetime or from generation to generation. Conditions include altitude, terrain, climate, flora, fauna, presence of parasites, prevalence of infectious or hereditary disease, foraging competence of community members, survival or otherwise of parents and alloparents during years of immature dependency, and genetic inheritance. Gurven and Walker (2006) emphasize that economizing body maintenance cost to the individual is the principal factor driving growth rates. Small final body size is one possible outcome of minimizing cost. Another is slow growth with later reproductive maturity, which minimizes cost per unit time.

With reference to other groups but principally to small-stature populations, Aeta, Agta and Batak (Philippines) and Aka, Biaka and Mbuti (Congo region), Migliano et al. (2007) argue that the pygmy phenotype is the product of a trade-off between the benefit of larger size for fertility and the risk of postponing reproductive maturation in conditions of high subadult mortality and restricted lifespan. Chance of survival to 15 years was 30–51% in the pygmy groups but 59–76% in full-stature forager and subsistence-agricultural societies. Life expectancy at 15 years was 20–32.5 years in the pygmies but 41–46.6 years in the others.

Female Aeta, Agta and Biaka attain adult size at ~13 years and Aeta have first reproduction at 15–16 years or earlier (Migliano et al. 2007:20217–20218).

In contrast, Hochberg et al. (2011:6) in a study of subsistence-based societies including two African pygmy groups, found no correlation between adult height, age of menarche and survivorship. The two pygmy groups in their study reached menarche at 14.5 and 15.5 years and first reproduction at 18.5 and 19 years, ages similar to those found in other full-stature peoples. Ramirez-Rozzi et al. (2015) made a longitudinal growth study of Baka pygmies of Cameroon, and contrast them with East African pygmies as described by other authors. While even newborns among the East African groups were small by the standard of full-size peoples, Baka newborns are within full-size range, but growth slows during the first two years of life and then proceeds at a rate comparable with full-size peoples and includes an adolescent growth spurt. Sexual maturation and first reproduction occur at ages expected for full-size peoples. The retardation in infancy accounts for the small adult stature.

It appears that even within the general pygmy phenotype alternative growth pathways have developed and multiple factors affect life history outcomes.

Walker et al. (2006b:297) hypothesize that variation in growth strategy maps onto both selection pressure and better nutrition. Combinations of these pressures and availability of resources produce the outcomes in growth strategy, affecting rapidity or slowness through subadult stages, timing of milestones including reproductive maturity, and final stature.

It is noticeable from Table 2.5 that (a) slow growth, (b) small adult stature, and (c) fast growth made possible by a trade-off of suboptimally developing the immune system and therefore increased mortality risk, are all associated with relatively poor nutrition. The worldwide positive secular trend discussed above suggests that, after a period of poor nutrition and unhygienic living conditions of any duration from a few generations to thousands of years, when eventually conditions for health are improved and better quality and quantity of nutrition is available, the human body grows larger and developmental milestones are reached earlier. Perhaps the hypothesis should be entertained that when the body *can* grow larger and faster it *does*. The proximate enabling factor is the intake of adequate nutrition.

Kuzawa and Bragg (2012:S371) define *developmental plasticity* as that subset of phenotypic responses that involve irreversible modifications to growth and development (cf. *reaction norms*, Stearns 1992:12). Nutrition, mortality, other environmental conditions and social circumstances can affect growth and attainment of stages of reproductive maturity. If certain conditions prevail during ontogeny, development or function of bodily components may be altered to cope with those conditions: e.g. children living continuously at high altitude will grow larger lungs than their low-altitude counterparts so as to increase oxygenation of the blood. When over generations individuals who do not develop adequate somatic responses to prevailing long-term conditions of life begin to be eliminated, the presence of these response traits will become fixed in the population genetically and continue to be maintained by natural selection.

In an individual subadult, some factors may not be extrinsic but perceptions or apprehensions by that individual, because the body can respond to a sense of well-being and security in supportive circumstances or a sense of unease and threat in unsupportive circumstances in the family or place of residence (Ellis 2004; Sheppard et al. 2015).

Table 2.6 outlines conditions and outcomes and suggests cases which may apply to Neanderthals as a population.

Table 2.6: Further conditions and growth/maturation outcomes

	Conditions	Subjects and timescale	Outcome	Mechanism	Example demographic or population	Neanderthal applicability
1	High premature mortality from predation or morbidity or high-risk subsistence practices	Community, long term	Faster growth, earlier reproductive maturation	Natural selection	<i>Homo erectus</i> ?	Neanderthals generally?
2	Unavailability of sufficient nutrition	Individual, infancy and childhood	Slower growth, later reproductive maturation	Developmental plasticity responding to nutritional intake	Some societies Neolithic onward, more intensely in parts of Europe during Industrial Revolution	Neanderthals when hunting unsuccessful?
3	Unavailability of sufficient nutrition combined with high premature mortality	Community, long term	Faster growth, earlier reproductive maturation	Natural selection	Some pygmies ²	
4	Availability of sufficient but not <i>abundant</i> nutrition	Community, long term	Slower growth, later reproductive maturation	Natural selection	Most societies Neolithic onward, some African foragers ³	
5	Perception of threat, while nutrition sufficient	Individual, infancy and childhood	Faster growth, earlier reproductive maturation	Developmental plasticity responding to psychological state	Recent children in unsupportive homes ¹	
6	Perception of security, while nutrition sufficient	Individual, infancy and childhood	Slower growth, later reproductive maturation	Developmental plasticity responding to psychological state	Recent children in supportive homes ¹	
7	Availability of abundant nutrition (relative to past generations)	Individual, infancy and childhood	Faster growth, earlier reproductive maturation	Developmental plasticity responding to nutritional intake	(a) Positive secular trend inception, (b) deprived children adopted into wealthier homes ⁵	
8	Availability of abundant nutrition (consistent high-energy diet)	Community, long term	Faster growth, earlier reproductive maturation, larger body size ⁶	Natural selection	(a) Positive secular trend, (b) Middle and Upper Palaeolithic <i>Homo sapiens</i> ⁴	Neanderthals when hunting successful?
9	Availability of abundant nutrition (consistent high-energy diet) combined with high premature mortality from morbidity or high-risk subsistence practices	Community, long term	Faster growth, earlier reproductive maturation, larger body size ⁶	Natural selection		Neanderthals generally?

¹ Ellis 2004; Hochberg and Belsky 2013; Sheppard et al. 2015.
² Walker et al. 2006b:295; Migliano et al. 2007.
³ Blurton Jones 2006:247–251; Gluckman and Hanson 2006:9.
⁴ Blurton Jones 2006:251–252; Gluckman and Hanson 2006:10.
⁵ Parent et al. 2002.
⁶ Antón et al. 2014.

The following two propositions appear to hold: *High mortality promotes faster growth* and *Abundant nutrition promotes faster growth*. Over generations, high subadult mortality eliminates the genes of individuals who grow too slowly to reproductive maturity. Independently, abundant nutrition enables the biological growth potential of the individual. If there is evidence that Neanderthals grew to adulthood more rapidly than modern humans, to deduce the proposition *Faster growth in Neanderthals is due to high mortality* is invalid, because in any given case faster growth could equally be due to abundant nutrition with low mortality, as it is in modern humans affected by the positive secular trend.

In humans, longer growth and larger female body size results in greater fertility and reduced infant mortality (Hochberg et al. 2011:4), so there should be selective pressure for late reproductive maturation. One somatic response to adverse conditions during infancy and childhood, whether inadequate nutrition, morbidity or perceived insecurity of circumstances, seems to be for the body to grow slowly, as if awaiting better times (Gluckman and Hanson

2006:9; Walker et al. 2006b:296,301,307). Health professionals used to call this response *failure to thrive*. Yet there is evidence that the response to insecurity in infancy and childhood is more often faster maturation, or at least faster reproductive maturation, unless the stress is severe (Ellis 2004; Hochberg and Belsky 2011, 2013; Sheppard et al. 2015). As indicated in Table 2.6, this severe stress may perhaps be identified as nutritional insufficiency acute enough to preclude rapid growth, since the other types of stress would not inherently inhibit growth.¹ In conditions of long-term poor nutrition, high morbidity, high premature mortality or insecurity owing to violence in a community, natural selection should favour faster growth, because those genetically disposed to late reproductive maturation would gradually be eliminated. Just as the outcome of faster growth can be produced by different conditions, it appears that similar conditions, e.g. combinations of opportunities or stress of various types, may produce different outcomes. Also, different outcomes may arise from application to (a) subadults as individuals experiencing either support or adversity during a period of their life and (b) subadults as members of a community in which either favourable or adverse conditions prevail long-term. In case (a) developmental plasticity is the presumed mechanism, in case (b) natural selection (Table 2.6).

Most recent hunter-gatherers have low body weight by comparison with mainstream populations, both urban and rural, in their own countries. Some, such as the Hadza of Tanzania, grow slowly to a tall stature comparable with urban and agricultural communities (Blurton Jones 2006:251). Others, such as negritos in South and East Asia and pygmies in Central Africa, are extremely small-bodied and grow quickly to their small adult stature (Walker et al. 2006b:307). Hunter-gatherers today tend to inhabit marginal environments such as desert and semi-desert or thick tropical forest, because pastoralist and agricultural peoples occupy the more productive land (Blurton Jones 2006:251–252). In these small scale societies the hunting of large animals often does not make the principal contribution to feeding the community, because even with bows and arrows success in hunting is not always achieved: although, when it is, meat is shared within and beyond the family. Instead, a regular and reliable supply of food is obtained by gathering vegetable matter including tubers and by capturing small animals (O’Connell et al. 1988; Hawkes et al. 2003:223–224).

Hunting societies focused on megafauna comparable with that of the European Middle and Upper Palaeolithic are no longer extant (F.H. Smith 1980:372). The Upper Pleistocene landscape of temperate and glacial Europe and Central Asia with its large-bodied bovids, equids and ungulates is not readily analogous even to East African savanna and forest with their abundant fauna, let alone the marginal habitats of tropical or southern hemisphere hunter-gatherers in recent centuries. However, recent foragers of the Arctic, North America and Siberia may offer a closer, though not exact, comparison to people of the northern hemisphere Palaeolithic.

The high lean body weights of Middle and Upper Palaeolithic hominins, whether Neanderthals or moderns (Appendix H), and the high volume of remains of large herbivores at their archaeological sites suggest that they were regularly successful at hunting such prey, and that intake of animal protein and fat was central to their diet. Blurton Jones (2006:252) infers that Upper Palaeolithic people, with abundant high-protein diet, may have reached reproductive maturity and attained adult stature earlier than recent populations. It has been proposed that Palaeolithic *Homo sapiens* females may have reached menarche within 7–13 years and progressed to “full reproductive competence” at 11–13 years (Gluckman and Hanson 2006:10). These ages would bring modern humans within or below the very early age (14 years) suggested by Thompson and Nelson (2011, 2016) for Neanderthals (§7.1). If Neanderthals did

¹ In a setting of perceived insecurity, a child may be reluctant to eat, so imposing nutritional insufficiency on itself.

mature earlier than recent humans, that phenomenon could be explained by the same factors as suggested for Palaeolithic *Homo sapiens*.¹

The possibility is raised that the skeletal robusticity and high lean body mass of *Homo heidelbergensis*, Neanderthals and early modern humans of the Middle and Upper Palaeolithic represent response to long-term consistent sufficiency or even abundance of nutrition with high-protein diet. In Neanderthals, unlike Palaeolithic *Homo sapiens*, this response evidently did not often result in high stature. Even so, in the sample of 19 Neanderthal adult males with computed statures, five were over 170 cm (5ft 7in) (Table H.1). As a comparison, *maximum* mean height for groups totalling 27,000 industrial workers measured in Britain in 1943 was 5ft 7½ in (Morant 1950:443).

As discussed earlier (§2.5.2), Neanderthal archaeology provides evidence for (a) abundant nutrition, but also evidence for (b) high mortality, and in some groups evidence from dental hypoplasia for (c) undernutrition and pathology during the immature years. However, it may be asked whether all three conditions could characterize the same communities at the same time. Rather than “typical” Neanderthal conditions, lifeways and traits to be found across their geographical and temporal range, it may be useful to think of communities in different places and at different times having different experiences, sometimes enjoying great success and sometimes enduring hardship.

Hypothetically, certain levels at some sites may represent a community experiencing regular foraging success and relatively good health while others represent a community under continual stress, undernourished, suffering infectious disease, and at risk of not surviving. The Krapina population may have been such a community at risk (Hutchison et al. 1997; Mahoney et al. 2021). On this hypothesis, comparison of archaeological levels at Neanderthal sites should in some cases be able to distinguish (a) communities enjoying hunting success as indicated by remains of animal butchery and experiencing low incidence of pathology, from (b) other communities where success is less evident from remains of prey and in which there is high incidence of pathology and perhaps evidence of cannibalism. Equally, for some Neanderthal groups poor nutrition may have been intermittent and irregular but fairly frequent, occasioned by fluctuations in the seasonal movements of the large prey animals which they favoured, adverse weather conditions, and the varying capability, strength, fitness and health of individual members of the community. The presence of a sufficient number of healthy, capable adult foragers to give leadership and provide for themselves and others must be an important factor in sustaining a viable community. In the event of debilitating or disabling injury or death of several such individuals, a community would be at risk unless they could be replaced by incomers from a neighbouring group or younger members could take up their role.

An earlier age of growth completion in Neanderthals than in modern humans could have been favoured by natural selection. Given probably small communities (Hayden 2012) enjoying successful hunting and gathering but with high young adult mortality, it would have been beneficial if the young contributed early to essential foraging activity that required considerable size and strength, since these are the principal attributes that make a forager effective (Bird and Bliege Bird 2005) (§2.8). If this were so, in Neanderthals sexual maturation might occur at ages comparable with living humans in developed societies, but completion of somatic growth would occur slightly earlier than in living humans, after a relatively short adolescence. On this scheme, while both are enabled by sufficiency of nutrition, sexual maturation and completion of somatic growth are subject to different selection pressures. This

¹ To my knowledge so far evidence has not been presented that such rapid growth to adulthood actually did occur in the Upper Palaeolithic. As the European UP subadult sample is even smaller than that of Neanderthals and few have reliable ages, it would be difficult to assess.

scenario is summarized in Table 2.6 (row 9), and can be seen as an adaptive life history strategy. Chapters 6 and 7 discuss the evidence of somatic growth in Neanderthal subadults, which appears *not* to demonstrate faster growth to puberty than in *Homo sapiens* but is ambiguous on the duration of adolescence.

Some populations of recent humans have accelerated growth to a degree even exceeding that suggested for Neanderthals. Among some Philippine small-stature forest dwellers, females finish somatic growth at ~13 years (Migliano et al. 2007:20217–20218), at least 4 years earlier than full-stature living peoples. In their case very small stature and light adult weight contrast with the Neanderthal physique, which, among living *Homo sapiens*, perhaps has its nearest counterpart among the Inuit (cf. Nelson and Thompson 2002; Thompson and Nelson 2011, 2016).

The stocky build of Inuit people appears to be attributable to a set of genes selected principally for their effect in counteracting health risks induced by their high-protein, high-fat diet based on marine mammals and fish, including a gene which guards against obesity by promoting increased energy expenditure (Fumagalli et al. 2015; cf. Harris and Elliott 2019). As certain of these alleles are shared with North American indigenous people but not with East Asians, it has been suggested that this dietary and genetic inheritance dates from a period of common ancestry in Beringia and may ultimately be derived from a late Palaeolithic diet rich in meat from land mammals (Fumagalli et al. 2015:1344,1346). A parallel with Neanderthals can readily be discerned, leading to the prediction that comparable sequences should be found within their genome. A variant haplotype associated with differentiation of adipose tissue and body fat distribution found at high frequency in Native Americans and especially in Greenland Inuit appears to have been derived from Denisovans rather than Neanderthals (Racimo et al. 2017): not a surprising result in view of the geography.

The concept of rapid growth as indicative of pathology, plesiomorphic physiology, or altogether an inferior life-history strategy may be mistaken (cf. Hochberg and Belsky 2013). As the positive secular trend shows, it can be seen primarily as a response to nutritional sufficiency or abundance, since without that sufficiency rapid growth to large body size simply does not take place.

2.8 Extended period of immaturity in humans

The Schultz-Bogin schema (Figure 2.1) illustrates the elongation of the modern human growth period relative to apes, partly by the intrusion of extra stages, *early childhood* and *adolescence*. On the basis of dental acceleration (Chapter 3), it has been argued that Neanderthals experienced more rapid somatic growth than modern humans (e.g. Nelson and Thompson 2002; Thompson and Nelson 2011, 2016), and that a curtailed subadult period must have limited learning time and so impaired their cognitive and social capacities, rendering them as a species competitively inferior to *Homo sapiens*.

A number of hypotheses have been proposed to explain the prolonged modern human subadult period (Leigh 2001:226–227; Deaner et al. 2003:241–260; van Schaik et al. 2006:139–150). One which is widely cited (Skill learning) and one which to the present writer seems very much the most cogent (Brain malnutrition) are discussed here.

Skill learning hypothesis

This hypothesis seeks to explain the long immature period of modern humans and the large size of the modern human brain functioning as the mechanism and repository of skill learning. However, its credibility has waned as recent studies have indicated that living hunter-gatherers do not need 18–20 years to learn skills for subsistence.

Adults tend to be more effective foragers than subadults of any age and older subadults are more effective than younger ones, principally because larger and stronger individuals can do more energetic work such as climbing and digging. Also, older individuals, e.g. in the teens and adulthood rather than pre-teen, are more likely to persist and less likely to be distracted during foraging activity. For example, among Hadza people of Tanzania, children who spent years at boarding school, where they did no foraging, became just as adept at foraging activities as those who stayed in the village. Men were as effective at extracting underground tubers as women, although women spent more time at this activity (Blurton Jones and Marlowe 2002). !Kung children (South Africa) did not begin to hunt until they reached 20 years, and among Ache (Paraguay) and Hadza their hunting skills improved during adulthood (Blurton Jones 2005:107). Among the Martu (Australia), for physical activity the forager's size and strength are more important than age (Bird and Bliege Bird 2005). Other scenarios leading to the conclusion that extended growth is not required for learning are presented in the cited works and by Bliege Bird and Bird (2002) and Blurton Jones (2006) for humans, and for non-human primates by Janson and van Schaik (1993:58–59,64–65).

In any case acquired skills can be improved and novel skills learned in adulthood, even until old age. Most athletes and most intellectual workers reach their peak in early to middle adulthood rather than in adolescence.

African pygmies, Philippine negritos and the Hiwi of Venezuela (Walker et al. 2006) grow more rapidly than most full-size populations, females in some groups reaching adult size at 13 years (Migliano et al. 2007:20217–20218). On the learning hypothesis, their shorter subadult life would imply that they have less to learn to be able to function as adult foragers in their society. However, evidence is lacking to imply that their modes of subsistence, social structures and language are less complex than those of full-size hunter-gatherers.

To take this consideration further, in the present writer's opinion it is very likely that a *Homo erectus* individual could function adequately in a recent forager society alongside modern human members. Such an individual might lack speech but might well be able to carry out all essential and typical subsistence tasks such as digging for tubers, collecting fruit, and

hunting for small animals, perhaps climbing trees and swimming, and might even be esteemed for physical strength. This is not to say that a group of exclusively *Homo erectus* individuals could have developed exactly such a way of life. However, it seems probable that material practices resembling that way of life, if not its cultural practices, could come about among *Homo erectus*.

Brain malnutrition hypothesis

The brain malnutrition hypothesis is favoured by Deaner et al. (2003) and has received qualified endorsement from Leigh (1996:471, 2001:233) and Leigh and Park (1998:346). Further evidence has emerged from neuroscience which strengthens its explanatory cogency. Here, therefore, I propose that the growth of our large brain, necessarily a slow process because of its high demand for energy, is responsible for the prolonged subadult period of modern humans.

Recent research (§4.3.2) indicates that throughout ontogeny the brain itself regulates somatic growth and prioritizes its own needs above the rest of the body, including even the dentition, which in turn is favoured over general somatic growth (Peters 2011; Kuzawa et al. 2014; Vandekar et al. 2019). This regulatory function of the brain, prioritizing itself, has its strongest effect during infancy, childhood and the juvenile stage, when components of the brain must grow in size and reorganize internally, and in these stages of ontogeny the rest of the body grows only slowly. At the end of the juvenile stage, when the brain's growth in gross volume and in specific late-maturing structures is nearing completion and its demand for metabolic resources is therefore reduced, more resources become available for somatic growth, which then proceeds at an increased rate for ~2 years within the first half of adolescence.

The brain malnutrition hypothesis has a parallel conceptually in the skill learning hypothesis. Learning and cognition are comprised in the internal psychological aspect of brain activity, and also have a cultural dimension. Growth and development of the brain are paralleled by the development of the cognitive faculties. But brain growth, unlike learning, is an essentially physiological process. The prolongation of human growth is a physiological phenomenon, and a physiological explanation avoids an appeal to the psychological or cultural domain. The brain malnutrition hypothesis is such an explanation. In any case the learning hypothesis as such seems to be unsupported.

As endocranial volumes of known Neanderthals lie entirely within the modern human range and are represented through lower and upper reaches of that range (§4.2, Appendix E), on a *prima facie* basis it should be expected that their brain growth was comparably extended, and that the principle of brain priority for growth over other tissues, including the dentition, applied to them.

2.9 Summary

Life history can be divided into phases of adult life (such as young adult, prime adult, and old age) and the stages of subadult life: infancy, (early) childhood, juvenility, and adolescence. Many Neanderthal subadult remains are sufficiently preserved to be assigned to one of these stages (Chapter 5).

Apes have a more rapid life history, i.e. progression through stages, and a shorter subadult period than recent humans. Consensus is that hominins other than *Homo sapiens* had a life history intermediate between those of living humans and chimpanzees: australopithecines almost indistinguishable from chimpanzees, and even *Homo ergaster/erectus* not much slower. Neanderthals fall somewhere on this putative spectrum. There has been a tendency to view a rapid life history in hominins as ape-like and as an inferior strategy for survival. In a trite sense it was inferior, since *Homo sapiens* is the only hominin species to have survived.

While the notion of a fast-slow continuum of life history may not account fully for the observed variation in schedules of growth and development, it is applicable at a gross level. A rapid life history delivers earlier attainment of milestones of sexual maturation and attainment of adult size than a slow life history.

Combinations of nutritional, social, health-related and demographic conditions are described and outcomes predicted based upon a number of studies, to assess which combinations may have applied to Neanderthals.

In populations which experience rapid growth in environments of low nutritional availability adults attain a small body size. Populations of industrialized countries and in other countries with unequal wealth distribution, frequent food shortages and famine have historically experienced relatively late attainment of sexual maturation milestones and slow growth to a small adult size. The positive secular trend, observed initially in industrialized nations and later worldwide, produces a more rapid life history in terms of sexual and statural maturation, with greater adult stature and body mass. These changes are principally a response of the human body to sufficiency of nutrition during growth, although other factors such as a sense of personal security contribute to steady growth.

In the Middle and Upper Palaeolithic, many human communities, both *Homo sapiens* and Neanderthals, appear to have subsisted on a high-protein, high-fat diet from the meat of large and small herbivores, and grew to large adult body mass. It is likely that their life history was as rapid as that of living humans whose development has been accelerated by the positive secular trend, and some authors have suggested that it could have been even more rapid.

The long duration of modern human ontogeny is explained by brain priority for energy allocation, which exerts its effect mainly through the infant, child, and juvenile stages. As their adult endocranial volumes are similar to those of *Homo sapiens*, Neanderthals would be predicted to have a similar long and slow ontogeny through those stages.

Further examination of the life history of Neanderthals depends on analysis of skeletal growth and development of the dentition, in particular enamel and dentine extension rates determining dental formation times, and ages for tooth eruption/emergence.

CHAPTER 3

DENTITION

3.1 Introduction

Teeth are the most numerous remains of fossil individuals. Dental development has long been used to determine age at death of fossil remains, and increasingly the dentition has been used to examine a subject's state of health, diet and local ecology and environment.

Aspects of Neanderthal dentition which have relevance to life history, state of maturation and age at death are covered here. The hypothesis of accelerated dental development in Neanderthals is supported. It is presented first by a review of the literature, and then detailed evidence from all aspects of dental formation and eruption is tabulated and discussed.

Appendix C offers background information on dentition and the calculation of chronological ages from counts of dental microstructure. Appendix D contains tables of dental data, mainly from modern humans.

Many dental abbreviations are used. These are listed in the Glossary.

3.2 Dental development and life history

Larger primates tend to have longer lives than smaller primates, as with mammals generally, so that individuals of larger-bodied taxa pass milestones, represented by life-history variables, such as emergence of the various tooth types, onset of puberty and menarche, and eventually first pregnancy, after longer intervals since their own birth, and remain in definable stages of life such as infancy for longer durations (Chapter 2). Life-history-related variables such as adult and neonatal body mass and adult and neonatal brain size are held to bear upon the timings and durations which define life history.

Following work by other scholars including Harvey and Clutton-Brock (1985), B.H. Smith (1989a, 1989b, 1991, 1992, 1994) used multiple regression to formalize correlations among these variables which are widely recognized to have strong primate-wide application. Significantly, the timing of events in development of the dentition appears to track the pace of life history: earlier or later dental formation and eruption, and in particular the life-history variable *age at clinical emergence of the permanent first mandibular molar* (§2.4.4).

Great apes have a shorter life span and a more rapid life history than living humans, and dental development stages are reached at younger ages. Australopithecines, early hominins from the Lower Pleistocene such as *Australopithecus afarensis*, *Au. africanus*, *Au. anamensis* (~4–2 Ma), have rounded human-like upper and lower dental arcades unlike chimpanzees, and their teeth, though large, resemble human teeth much more than those of chimpanzees (Le Gros Clark 1967:157–164). The first specimen to be found, an immature cranium from Taung, was assessed from the whole dentition to be at the stage expected at ~6 years in a modern human (Keith 1931:48).¹ Later analysis indicated an age of ~3.5 years (Conroy and Vannier 1991) or 3.73–3.93 years (Lacruz et al. 2005). The australopithecine dental development schedule was therefore closer to the chimpanzee schedule than the modern human one. Early true *Homo*, i.e. African *Homo erectus* (*s.l.*), also known as *Homo ergaster*, had a body size and shape similar to modern humans and significantly larger endocranial volumes than australopithecines. On the basis of B.H. Smith's regressions (1989a etc.), these hominins would be expected to have a more extended life history with later dental and somatic milestones. However, *Homo erectus s.l.* still evinces significantly more rapid dental development than recent humans (Dean et al. 2001; Dean 2009), and may have reached adulthood at an earlier age (§7.6).

The case has been made that Neanderthals also had faster dental development than *Homo sapiens*, whether recent or Palaeolithic. Because of the tight correlation implied by the results of B.H. Smith and colleagues, many authors have extrapolated from evidence of dental advancement to the contention that Neanderthals must therefore have had faster somatic growth and so a more rapid overall life history (e.g. Ramírez-Rozzi and Bermúdez de Castro 2004; T.M. Smith et al. 2007a, 2007b; Dean 2007; Bermúdez de Castro et al. 2010; Schwartz 2012).

It has been claimed that a shorter subadult period leaves less time to acquire cognitive, social, subsistence and survival skills and would lead to a Neanderthal community being less able to develop symbolic thinking and behaviour, competence and organization than a community of slow-growing *Homo sapiens*. Ethnographic evidence and varying development times in recent human populations indicate that earlier attainment of adulthood does not necessarily make individuals or a community less fit, i.e. disadvantaged or less competent in behaviours for survival (§2.8). The question of correlation of dental and somatic development is covered in Chapter 7, but it is necessary to assess the hypothesis of Neanderthal accelerated dental development itself.

¹ Keith (1931) did not assume Taung was 6 years old, but rather emphasized its cranial resemblance to apes.

The next section (§3.3) summarizes in temporal order key findings which have contributed to the case for and against this hypothesis, leading to the present consensus that it is broadly correct. The following section (§3.4) presents detailed comparative information on dental traits. This in my view supports the hypothesis.

3.3 Elaboration of the hypothesis of Neanderthal accelerated dental development

Examining dental remains from the Krapina site Wolpoff (1979, 1980a) observed that third permanent molar (M3) formation was advanced in relation to the other teeth in some immatures, leading to possible emergence of M3 at ~15 years instead of ~20 years as in recent humans.

The Gibraltar 2 Neanderthal child was aged 5 years by Buxton (1928). Dean et al. (1986) counted 119 perikymata on the upper permanent first incisor of this specimen representing 119 weeks of crown formation, assuming a periodicity of 7 days. Adding 6 months for cuspal enamel unrepresented by perikymata plus some time for the 1mm of root and a period between birth and crown initiation, they calculated that Gibraltar 2 was 3.1 years old at death.¹ The endocranial volume 1400 cm³ seemed large for the young age, and it was deduced that Neanderthal immatures must have grown very quickly and brain growth must be especially rapid.

B.H. Smith (1993) determined that dental development of the Nariokotome *Homo ergaster/erectus* child KNM-WT 15000 did not conform to either human or ape patterns. Further analysis by Dean et al. (2001) of KNM-WT 15000 and the Sangiran *Homo erectus* S7-37 concluded that in the Nariokotome child first permanent molar (M1) gingival emergence was at ~4 years, close to the expected mean for the species at 4.5 years on the basis of mean adult endocranial volume 826 cm³. For S7-37 emergence of M1 would have been at ~4.4 years and P4 and M2 at ~7.6 years. These ages are considerably lower than mean ages for recent humans, and the result makes it clear that in earlier species of the genus *Homo* dental growth patterns can differ considerably and are overall accelerated relative to recent humans.

Tompkins (1996a) compared three recent human populations and found that southern Africans² had advanced dental development relative to Native Americans and Europeans.³ Comparing living humans, Upper Palaeolithic *Homo sapiens*, and Neanderthals, Tompkins (1996b) reported that molar tooth development in both Palaeolithic populations was advanced over that of Native Americans and Europeans, though not clearly so over that of southern Africans. In both Palaeolithic samples the first incisor and first premolar are delayed with respect to molars. Tompkins observed that Neanderthal anterior teeth and premolars are larger than those of modern humans, which might suggest that they needed longer formation time, but this is not so for the Upper Palaeolithic population. An alternative interpretation is that the permanent molars are advanced in the Palaeolithic specimens, rather than premolars and incisors delayed. Earlier and more rapid molar development may be enabled by greater maxillary and mandibular length and depth (Merz et al. 1981:55–57), in which the Neanderthals and Palaeolithic *Homo sapiens* exceed southern Africans. Tompkins (1996b:114) acknowledges that without absolute timing of dental formation all these interpretations are speculative.

A study comparing anterior teeth of Neanderthals, Upper Palaeolithic and Mesolithic modern humans, *Homo heidelbergensis*, i.e. Sima de los Huesos (~430 ka) and *Homo antecessor* from Gran Dolina (~780 ka) reported that perikymata on the later developing cervical half, i.e. sixth to tenth deciles, of crowns were more widely spaced in the archaic hominins than in the modern humans (Ramírez-Rozzi and Bermúdez de Castro 2004). In living and early modern humans perikymata in the later deciles are more closely spaced, indicating

¹ Periodicity of Gibraltar 2 is 9 days rather than 7 as previously suggested. Recalculation, all else unchanged, gives an age at death of 3.73 years. See Appendix A and later this chapter for alternative ages assigned to this individual. Its endocranial volume is discussed in Chapter 4.

² Not including San, to my knowledge.

³ Confirmed by further studies, e.g. Esan et al. (2018) and their references. See also §7.3.2 and Appendix D.

extension at a lower daily rate, and generally more numerous, indicating prolonged duration. Of the four groups, Upper Palaeolithic and Mesolithic modern humans had the longest and Neanderthals had notably the shortest formation times, with perikymata more evenly spaced across all deciles, leading to completion of the dentition in 15% less time than modern humans. From these different *perikymata packing patterns* and their implications for extension and overall formation rates, the authors concluded that rapid dental formation in Neanderthals represents an evolutionary reversal from their unexpectedly more modern-like predecessors in Europe, and that correspondingly more rapid somatic growth might have brought them to adulthood at only ~15 years. Neanderthals thus appear not to conform to the expectation that life history, specifically length of the subadult period, is closely correlated with brain and body size (B.H. Smith 1989a etc.), but rapid growth might have been favoured by high young-adult mortality (Ramírez-Rozzi and Bermúdez de Castro 2004:938).

Again using anterior teeth, Guatelli-Steinberg and colleagues (2005, 2007; Guatelli-Steinberg and Reid 2008; Reid et al. 2008) compared Inuit, British, and southern Africans with Neanderthals. Lateral enamel formation times for Neanderthals appeared to be faster than Inuit, not faster than British, but slower than southern Africans. Periodicities were determined for the Inuit and British samples (2005:14198), but not for the Africans or Neanderthals. Reid and Ferrell (2005)¹ observed that enamel formation time appeared to be constrained by a negative correlation between periodicity and number of perikymata. A regression based on this relationship was used by Guatelli-Steinberg and colleagues to show that, on the hypothesis that Neanderthals had formation times 15% shorter than southern Africans, periodicity in Neanderthals would have to be less than 6 days. As 6–12 was the range known for apes and humans, the hypothesis could be rejected. The conclusion depends on the validity of the observation by Reid and Ferrell and was also limited by the absence of known periodicities for Neanderthals. Even so, Neanderthals exhibit a more even distribution of perikymata across cuspal and cervical halves, so that for them in the cervical half 58.4–62.4% of total perikymata appear while modern humans have 64.1–68.5% (Guatelli-Steinberg et al. 2007:72,78,83).

The work of Macchiarelli et al. (2006), using microtomography to explore internal short and long term incremental lines, showed that growth curves for a Neanderthal deciduous molar (Ldm2) and permanent first molar (LM1) from La Chaise followed the same pattern as modern humans. Periodicity was 8 days. Cuspal enamel formation times proved shorter in the Neanderthal M1: the protoconid, initiated 15 days before birth, took 1041 days to extend to the cervix and the metaconid 865 days, less than in a southern African sample at 1117±55 and 936±55 days respectively, which in turn are less than in Asians and Europeans. Root extension began slowly, with a late peak, in contrast to the modern human schedule (§3.4.6). This may be attributable to the taurodont character of the M1, where the root furcation below the expanded pulp chamber and surrounding dentine occurs at ~50% of the way between cervix and apices, whereas in a modern human it would be closer to 30% of that distance. Closure of the M1 root apex was calculated to be at 8.7 years, well within modern human range. Proportion of root formed to crown height at eruption is similar between apes and humans (Dean 2006:2802–2803). On this basis, gingival emergence was calculated to be at 6.7 years, which is within the upper range of modern human expectation: 4.74–7.05 years (Liversidge 2003) (§3.4.7). Macchiarelli et al. (2006) cite Gleiser and Hunt (1955) for their 6.2±0.8 years mean for recent human M1 emergence.² As, strictly, it is the age of M1 emergence that is held to be correlated with other life history variables (B.H. Smith 1989a), rather than other measures of dental development, this late emergence age is particularly notable, but also surprisingly late given the evidence from other sources for rapid dental formation in Neanderthals.

¹ The research was on recent human permanent canines.

² Kelley and Schwartz (2010:1037) give an inter-population mean 5.8 years. Also see Tables D.9–D.17.

The partial dentition of the Neanderthal child Obi-Rakhmat 1 was examined by T.M. Smith and Reid (2006). Although periodicity could not be determined, they found fewer perikymata than in a British sample on the cusps of most of the six crowns available and estimated shorter crown formation times, with some overlap with southern Africans. Age at death was likely 8.1 years, with 8.8 years maximum, while dental stages would suggest 9 years.

Whereas Tompkins (1996a, 1996b) had suggested Upper Palaeolithic *Homo sapiens* and Neanderthal dental development timings overlapped, a study of the much earlier *Homo sapiens* child Jebel Irhoud 3¹ using computed microtomography found close similarity with recent humans (T.M. Smith et al. 2007a). The Middle Palaeolithic Jebel Irhoud site had then been dated at ~160 ka, but later it was redated to roundly double that age, ~315 ka (Richter et al. 2017). Dental stages suggested an age at death 7.2–7.6 years, but periodicity was discovered to be 10 days, and microstructure counts from the canine crown and root assuming a modern human initiation age gave 7.78 years. If anything, this individual was dentally delayed in relation to recent humans. A possible explanation is that its teeth took a long time to form because the dentition of Jebel Irhoud 3 is megadont. For example, its canine height exceeds the means of not only recent and Palaeolithic *Homo sapiens* but also Neanderthals and even *Homo heidelbergensis* and *Homo antecessor* (T.M. Smith et al. 2007a:6130). The authors propose that the slow dental development of this individual is evidence of modern human life history with slow growth to adulthood (cf. Dean 2007).

T.M. Smith et al. (2007b) made a comparable study of the dentition of the Neanderthal child from Scladina. Its dental development was found to be rapid relative to modern humans. Periodicity was 8 days. For an upper M1, enamel formation time for the mesiolingual and mesiobuccal cusps was 2.35 and 2.22 years respectively, below modern human range. Molar cuspal enamel thickness was 60–90% of modern human mean. Daily secretion rates (DSR) are similar between modern humans and Neanderthals (Macchiarelli et al. 2006), so thinner enamel should take less time to form. Crown extension rates also appear to be faster than in modern humans, because in Neanderthals the angle made with the surface is steeper, i.e. more acute (angle CBC', Figure 3.4), so that a given DSR will produce greater extension (T.M. Smith et al. 2007b:20221). Age at death was calculated to be ~8.0 years, but attrition on cusps of the upper and lower M1s indicates that they had been in occlusion for >2 years. The lower M1 had reached apex closure and may have emerged before 6 years. The lower M2 had erupted almost level with the M1, which would be ≥2 years early for a modern human. M3 crown formation is also advanced. Given the estimates for M1 crown formation time, if M1 apex closure occurred just before death, root extension rate would be ≥6.6 µm/d, higher than the modern human average rate 6.1 µm/d or the La Chaise Neanderthal 6.0 µm/d. Altogether, Scladina is dentally less advanced than the Nariokotome *Homo ergaster* child, slightly more advanced than Obi-Rakhmat 1, much more advanced than Jebel Irhoud 3 (ibid.:20223), and evidently more advanced than La Chaise.² From this, Smith and colleagues infer that Neanderthals reached adulthood earlier than modern humans, thereby incurring putative cognitive and social disadvantages compared with modern humans (ibid.:20224).

Enamel thickness in molars was examined by Olejniczak et al. (2008) using both 2D and 3D imaging by microtomography. Neanderthal molar enamel was absolutely thinner than in modern humans (samples from Europe and North America) across most M1s, M2s and M3s, although the absolute quantity of enamel per tooth was similar because Neanderthal molars were larger. Neanderthal molars evinced a larger volume of dentine and somewhat larger pulp

¹ Jebel Irhoud 3 was one of Tompkins' (1996b:106) "archaic" sample with Neanderthals and Rabat 1. It was not then assigned to *Homo sapiens*. As it is even more delayed dentally than recent humans, the question arises whether its presence compromised the "archaic" sample.

² Scladina is further described later here and in Chapter 7.

chambers; hence a higher percentage of crown volume was dentine than in modern humans, ~60% versus ~50%. In Shanidar 3 maxillary M3 enamel thickness was within modern human limits (Olejniczak and Grine 2005). In ceboids, apes, and humans enamel thickness increases from M1 through M2 to M3 (Olejniczak et al. 2008:17). In modern humans later developing molars M2 and M3 have smaller crowns than M1 and M2 respectively but not proportionately smaller quantities of enamel. In Abri Suard S36 the mandibular M3 had thicker enamel than the M2, but this pattern was not observed across other individuals in the Neanderthal sample. The taurodontism seen in some Neanderthal molars may be linked to the relative excess of dentine (Olejniczak et al. 2008:21). Tooth size reduction within the *Homo sapiens* lineage could have reduced dentine without reducing enamel volume, leading to thick enamel. However, the megadont Jebel Irhoud molars have similar proportions of enamel and dentine to recent humans, which suggests that enamel as well as dentine has been reduced in the modern human lineage (Olejniczak et al. 2008:21), on the assumption that the Jebel Irhoud population is ancestral.

Bayle et al. (2009) analysed dental development in the infant Roc de Marsal, which has a complete set of deciduous teeth in occlusion and permanent tooth germs in the maxilla and mandible. Deciduous tooth roots are complete but apart from the LRd12, none have reached apex closed. The degree of development reached by the permanent crowns is in order from most to least developed: *M1 crc (crown complete)*, *I1*, *I2*, *C crown ½*, *P3 cusp outline complete*, *P4 cusp initiated*. The lower deciduous teeth have a sequence: *dm1 resorbing*, *di2 apex closed*, *di1 apex closing*, *dc* and *dm2 apex ½*. These permanent and deciduous sequences were found to have zero probability within a comparative sample of modern human dentitions, indicating different timing of development between tooth types in Neanderthals versus modern humans.

Guatelli-Steinberg (2009:11) notes Legoux's (1966) and Thoma's (1963) view that Neanderthal anterior teeth were more advanced relative to molars than in modern humans. Bayle et al. (2010:1339–1341) found that in Neanderthals and in the Upper Palaeolithic Lagar Velho child molars were advanced relative to incisors by recent human standards. Unless they refer to different specimens and therefore just express inter-individual variation, these propositions cannot both be true. The large dimensions of Neanderthal incisors may account for a relative delay versus molars. Bayle et al. (2009:73), citing T.M. Smith et al. (2007b), point out that the maxillary second incisors of *Sceladina* formed over a longer interval than the modern human mean, while the postcanine teeth formed more rapidly.

Dean (2009) compared tooth height increase of a *Paranthropus robustus* canine tooth SK63 against modern human canine height increase, measured along the EDJ and then CDJ, and found that SK63 fitted well within modern human range. Similarly, S7-37, a *Homo erectus* molar from Sangiran and the Neanderthal molar BD-J4-C9 from La Chaise (Bourgeois-Delaunay) both fitted within modern human distribution. S7-37 had an early spurt in growth and BD-J4-C9 a spurt late in the growth curve. Dean (2009:71) observes that in anterior teeth only ~50% of EDJ length, and in posterior teeth much less than 50%, is represented by striae of Retzius reaching the lateral surface as perikymata. Earlier forming cuspal enamel decussates and the striae do not outcrop as perikymata. For this reason perikymata counts alone may not demonstrate longer or shorter crown formation time.

T.M. Smith et al. (2009) examined a Neanderthal lower M3 from Lakonis by physical section. Principal findings confirmed by this study were that enamel thickness was 60–90% of that in modern humans. With similar enamel secretion rates (Macchiarelli et al. 2006), crown formation times were therefore shorter.

A comprehensive advance was made by the work of T.M. Smith et al. (2010) using synchrotron computed microtomography to examine dental microstructure in eight

Neanderthal and three early *Homo sapiens* immatures, with a large comparative modern sample. Ages at attainment of successive formation stages of individual teeth, e.g. crown initiation and completion, can often be determined from dental microstructure (T.M. Smith et al. 2007a, 2007b, 2010).

When compared with earlier taxa both *Homo sapiens* and Neanderthals are shown to have extended duration of dental formation, but it is significantly more prolonged in *Homo sapiens*, including the very early specimen Jebel Irhoud 3. By counts of short-period and long-period lines in enamel and dentine, secretion rates and crown and root formation times could be derived. Cuspal secretion rates are similar in the two species, but thinner enamel in Neanderthal teeth leads to earlier crown completion times. Mean periodicity in Neanderthals studied is 7.4 days, significantly shorter than the mean 8.3 days in recent humans but not significantly different from the mean 8.0 of Palaeolithic *Homo sapiens*. As a result of lower periodicity, although the total of long-period lines in comparable tissue regions is similar, formation time is again lower in Neanderthals. In addition, extension rates in Neanderthals are greater: that is, the rate of differentiation of ameloblasts along the enamel-dentine junction is greater. This phenomenon relates to the steeper (more acute) angle at which the ameloblast sheet moves away from the enamel-dentine junction (Figure 3.4). Thinner enamel, lower periodicities, faster extension rates and earlier initiation ages for some teeth must lead to shorter duration of formation and therefore earlier completion ages and presumably eruption ages (T.M. Smith et al. 2010).

Among the major results of the 2010 paper are new chronological ages at death for several Neanderthal and other fossil immatures (Table 3.1). These ages are used here throughout in preference to other estimates. Most, but not all, are younger than previous ages based on modern dental schedules.

Table 3.1: New ages at death, Palaeolithic immatures

Individual	Species	Previous age at death	2010 age at death
Engis 2	N	2–6	3.0
Gibraltar 2	N	3.1–5.8	4.6
La Quina H18	N	7	Not found
Krapina Maxilla B	N	6.5–8	5.9
Obi-Rakhmat 1	N	9–12	6.0–8.1
Scladina	N	8.5–12	8.0
Krapina Maxilla C	N	10–10.5	Not found
Le Moustier 1	N	12–20	11.6–12.1
Qafzeh 10	S	6	5.1
Qafzeh 15	S	9	Not found
Jebel Irhoud 3	S	7–8	7.8
Data from T.M. Smith et al. (2010:20925).			
Previous age at death as cited by those authors.			

Neanderthal dental development does not show variation by dating or geographical region, although Engis 2 (30–50 ka) and Scladina (80–127 ka), both from Belgium, seem especially rapid (T.M. Smith et al. 2010:20924).

Among the *Homo antecessor* remains from the Gran Dolina TD6.2 layer at Atapuerca was a juvenile mandible ATD6-112, representing individual H11, in which the permanent first molar had just emerged at an age calculated to be 5.3–6.6 years, so within modern range (Bermúdez de Castro et al. 2010:11739). In this mandible the authors detect a slowing of crown and root formation of the molar teeth relative to anterior teeth characteristic of modern humans and unlike chimpanzees. As M1 emergence age is held to be closely correlated with the other life history variables, they draw the conclusion that an early childhood stage (*sensu* Bogin) may

have been present in this population, which is dated 0.80–0.96 Ma (2010:11740,11742). If this is so, then it would be counterintuitive, though not impossible, that Neanderthals, probably descendants of the Gran Dolina hominins but much more recent and larger-brained, should not also exhibit this stage.

Citing Dean's (2009) work on extension rates, Guatelli-Steinberg et al. (2012) inferred that differences in overall tooth formation time are not necessarily due to differences in enamel extension rates. They contrasted (a) the perikymata packing pattern in modern human teeth whereby extension in the cervical half of the crown becomes slower and the perikymata shallower and more numerous than in the cuspal half, and (b) that in Neanderthals whereby extension ceases relatively abruptly rather than gradually slowing and the perikymata are less numerous, with a relative absence of the shallower late perikymata. Extension rates appear to be related to EDJ length (Shellis 1984): molars with a long EDJ tend to have higher initial extension rates than those with a shorter EDJ, and rates decline toward the cervical region. Extension stops when ameloblast differentiation is suppressed at the molecular level (Tummers and Thesleff 2003, 2008), and cessation has no direct connection with extension rates (Guatelli-Steinberg et al. 2012:484). This means that a short crown formation time as found in *Paranthropus robustus* could be due to earlier cessation of ameloblast differentiation rather than fast extension rates, and the same consideration could apply to Neanderthals, as already proposed by Ramírez-Rozzi (1996). Guatelli-Steinberg et al. (2012:476) contrast this explanation of shorter crown formation times in Neanderthals with the findings of T.M. Smith et al. (2010), who presented evidence of faster extension rates as an explanation. Both faster enamel extension rates and earlier cessation of ameloblast differentiation may characterize Neanderthal crown formation.

Shackelford et al. (2012:240–243) found that ages for dental formation stage fall within the modern human 95% confidence interval for all listed Neanderthal immatures except Scladina and Le Moustier 1. By stages Scladina would be aged 10–11 instead of 8.0. All permanent teeth in the Scladina maxilla and mandible are advanced with respect to modern human standards except the lower first incisors (I1s) and first molars (M1s). Just inside the early end of the distribution are the premolars, while the upper I2, canines, M2s and M3s lie outside. For the canine, stages *cuspal initiation* and *crown complete* fall within modern human age range, but *root apex ½* is beyond the early end. However, M1 *crown complete* is in the later half of modern human range and M1 *apex closed* is exactly in the middle. M2 *cuspal initiation* at 3.5 years and *crown complete* at 6.4 years were exactly “on target”, but the stage *root ½* at 8 years (death) is at the very advanced end. M3 *cuspal initiation* at 6.7 years is at the extreme early end of modern human range, while *crown complete* at 8 years is beyond it. These Scladina results indicate very early initiation of the third molar and for several teeth distinctly rapid root development following less remarkable crown completion times (Shackelford et al. 2012:243).

The Neanderthal juvenile El Sidrón J1 has been aged 7.7 years based on dental microstructure and described by Rosas et al. (2017). Its dentition is said to fall entirely within modern human distribution for its age, while its postcrania indicate a younger age.¹

Modesto-Mata et al. (2020) compared long-period and short-period striae of dental elements from Neanderthals and earlier hominins from Atapuerca: Sima del Elefante TE9 layer (1.3–1.1 Ma) and Sima de los Huesos (SH, ~430 ka). Among other results, perikymata counts were lower in the TE9 hominins than in modern humans, but even lower in the SH sample, which were similar to Neanderthals: i.e. the much older population is actually intermediate between (a) SH and Neanderthals and (b) modern humans. As the SH hominins are widely

¹ El Sidrón J1 is further described later and in Chapters 5, 6, 7.

regarded as direct ancestors of Neanderthals (Arsuaga et al. 2014; Appendix B), this appears to indicate more rapid dental development, with possible implications also for somatic growth, in the succeeding Neanderthal lineage than in very early European *Homo* (cf. Bermúdez de Castro et al. 2010): a counterintuitive result. The perikyma packing pattern, with more widely spaced perikymata in cervical halves of Neanderthal crown surfaces compared with modern humans, indicates greater secretion quantities within long-term periods, which themselves comprise fewer days, i.e. have lower periodicity (McGrath et al. 2021:4).

Mahoney et al. (2021) found high enamel and dentine secretion rates in Neanderthal deciduous teeth from Krapina, some above the uppermost range for modern humans. They deduce that Krapina infants grew rapidly overall. On their assumption that the slow growth of modern humans evolved in response to low (young-)adult mortality and to the need for time to develop the cognitive ability of a large brain (Mahoney et al. 2021:4,6), the deduced rapid growth of Neanderthals is taken to imply that they experienced high young-adult mortality and did not develop advanced cognitive ability.¹

Following developments to date, Schwartz (2012:S402) asserted that a convincing argument was mounting that Neanderthal dental development was accelerated. This view is current. Support for it is described in the next section.

¹ Of course this invites the question why natural selection permitted large brains to evolve if their possessors were unable to utilize their potential. The same question arises for East Asian contemporaries of Neanderthals (§B.2).

3.4 Evidence for the hypothesis of Neanderthal accelerated dental development

Neanderthals are held to exhibit the following traits supporting an hypothesis of accelerated dental development.

1. Earlier attainment for all teeth of stages of tooth formation¹
2. Lower periodicity
3. Shorter crown formation times
4. Thinner enamel
5. Higher enamel and dentine secretion rates
6. Higher enamel and dentine extension rates
7. Earlier eruption of posterior teeth, and specifically of the mandibular M1

Trait 1 and perhaps trait 7 may be explained by one or more of traits 2–6.

3.4.1 Earlier attainment of stages of tooth formation

As a reference for all Neanderthal immatures with sufficient dentition, formation stages for their tooth types are given in Table D.1.

Dental formation stages for individual teeth of immatures along with modern human standards for median and maximum stages by age from AlQahtani et al. (2010) are listed here in Table 3.2. The table includes immatures *Homo ergaster* KNM-WT 15000 and early *Homo sapiens* Jebel Irhoud 3 for comparison.

Apart from Krapina Maxilla B, the Krapina maxillae and mandibles have been aged by their dental stages, so it is not surprising that they fall within modern human ranges. More informative is the state of those specimens with chronological ages from counts of dental microstructure. Of those cases, Gibraltar 2 and El Sidrón J1 lie fully within modern limits, while the other Neanderthals have some teeth within modern limits and some more advanced (Shackelford et al. 2012). Contrastingly, the very early *Homo sapiens* juvenile Jebel Irhoud 3 appears dentally delayed.

Roc de Marsal, Engis 2, Obi-Rakhmat 1 (only if periodicity = 6), Scladina, Teshik-Tash and Le Moustier 1 have some teeth advanced (Table 3.2). Periodicity for Obi-Rakhmat 1 is unknown. If its periodicity is 6, 7, 8 or 9 then its age is 6.03, 6.72, 7.41 or 8.1 years respectively (T.M. Smith 2010 SI). The two lowest ages are shown in the table. For ages given by periodicities 7 upward the Obi-Rakhmat 1 dentition fits well within modern range.

The Scladina juvenile is the most advanced dentally for its age. Shackelford et al. (2012:242) produced density plots of modern human ages for tooth stages derived from the charts of Moorrees et al. (1963). They illustrated the position of the Scladina individual against these distributions. The outcomes are listed in Table 3.3. According to Shackelford et al. (2012:243) Neanderthal M1s are largely in step with modern humans, but the Scladina M3 is very advanced. Notably, Scladina matches KNM-WT 15000 for upper M3 and lower M2 formation stages (Tables 3.2 and 3.4).

¹ Stages as in §C.1.2 Figure C.1.

Table 3.2: Stages of permanent dentition: subadult Neanderthal, early Homo sapiens, Homo erectus, comparison with modern human standards

Age order	Species	Age (y)	UI1	UI2	UC	UP3	UP4	UM1	UM2	UM3	LI1	LI2	LC	LP3	LP4	LM1	LM2	LM3
Roc de Marsal ⁷	N	2.3?	cr ¾	cr ¾	cr ¾	coc	ci	crc	-	-	cr ¾	cr ¾	cr ¾	cr ½	-	crc	-	-
mh median	S	2.5	cr ¾	cr ½	cr ½	ci	-	cr ¾	ci	-	cr ¾	cr ¾	cr ½	cco	ci	cr ¾	ci	-
mh maximum	S		cr ¾	cr ¾	cr ½	cco	ci	cr ¾	ci	-	crc	crc	cr ½	cco	ci	crc	ci	-
Engis 2	N	3.0	crc	crc	cr ¾	cr ¾	-	ri	-	-	-	-	-	-	-	cli	-	-
mh median	S	3.5	cr ¾	cr ½	cr ½	coc	ci	crc	cco	-	crc	cr ¾	cr ½	cr ½	ci	ri	cco	-
mh maximum	S		ri	crc	cr ¾	cr ½	cco	r ¼	coc	-	ri	crc	crc	cr ½	coc	ri	coc	-
mh median	S	4.5	crc	cr ¾	cr ¾	cr ½	coc	r ¼	coc	-	ri	ri	cr ¾	cr ½	coc	r ¼	coc	-
mh maximum	S		ri	ri	ri	cr ¾	cr ¾	r ½	cr ½	-	r ¼	ri	ri	crc	cr ½	r ½	cr ½	-
Gibraltar 2	N	4.6	ri	ri	crc	crc	cr ¾	r ¼	-	-	ri	ri	crc	cr ¾	cr ½	r ¼	cr ½	-
mh median	S	5.5	ri	crc	crc	cr ¾	cr ½	r ¼	cr ½	-	r ¼	r ¼	crc	cr ¾	cr ¾	r ¼	cr ½	-
mh maximum	S		r ¼	ri	ri	crc	cr ¾	r ½	cr ¾	-	r ½	r ¼	ri	crc	cr ¾	r ½	cr ¾	-
Krapina Mandible A ⁵	N	5-6?	-	-	-	-	-	-	-	-	r ½	r ½	r ¼	ri	-	-	-	-
La Quina H18	N	5.7?	r ¼	ri	ri	ri	crc	r ¾	cr ¾	-	-	-	-	-	-	-	-	-
Krapina Maxilla B	N	5.86	r ¼	ri	ri	ri	crc	r ¾	crc	-	-	-	-	-	-	-	-	-
Obi-Rakhmat 1 ¹	N	6.03	-	r ¾	r ¼	r ¼	r ¼	-	r ¼	-	-	-	-	-	-	-	-	-
mh median	S	6.5	r ¼	ri	ri	crc	crc	r ½	cr ½	-	r ½	r ¼	ri	crc	crc	r ½	cr ½	
mh maximum	S		r ¾	r ½	r ¼	ri	crc	r ¾	crc	-	rc	r ¾	r ¼	ri	ri	r ¾	crc	
Obi-Rakhmat 1 ¹	N	6.72	-	r ¾	r ¼	r ¼	r ¼	-	r ¼	-	-	-	-	-	-	-	-	-
mh median	S	7.5	r ¾	r ½	r ¼	ri	crc	r ¾	cr ¾	-	rc	r ¾	r ¼	ri	crc	r ¾	cr ¾	-
mh maximum	S		rc	rc	r ½	r ¼	r ¼	a ½	r ¼	ci	a ½	a ½	r ¼	r ¼	r ¼	a ½	r ¼	ci
EI Sidrón J1 ²	N	7.7	rc	r ¼	r ¼	-	-	-	-	-	rc	r ¾	r ¼	r ¼	ri	rc	ri	crypt
Jebel Irhoud 3	S	7.8	-	-	-	-	-	-	-	-	r ¾	r ½	cli	cli	ri	rc	crc	-
KNM-WT 15000 ³	E	8.0	ac	rc	-	-	-	ac	-	cr ¾	-	ac	r ¾	r ¾	r ¾	ac	r ½	-
Scladina	N	8.0	-	ac	a ½	-	r ½	-	r ¼	cr ¾	ac	-	a ½	r ¾	r ½	ac	r ½	cr ¾
Teshik-Tash ⁶	N	8.2?	-	-	-	-	-	-	-	-	-	-	-	r ½	r ½	a ½	r ½	cr ¾
mh median	S	8.5	rc	r ¾	r ¼	ri	ri	rc	ri	ci	ac	a ½	r ¼	r ¼	ri	r ¾	ri	ci
mh maximum	S		a ½	rc	r ¾	r ½	r ½	ac	r ¼	coc	ac	ac	r ¾	r ½	r ¼	a ½	r ¼	cco
Krapina Mandible B ⁵	N	8-9?	-	-	-	-	-	-	-	-	-	r ¾	r ½	r ¼	r ¼	ac	-	
Krapina Maxilla C	N	9.3?	-	-	-	-	r ¼	ac	r ½	-	-	-	-	-	-	-	-	-
mh median	S	9.5	rc	rc	r ½	r ¼	r ¼	ac	r ¼	coc	ac	a ½	r ½	r ½	r ¼	a ½	r ¼	cco
mh maximum	S		a ½	a ½	r ¾	r ¾	r ¾	ac	r ½	cr ¾	ac	ac	r ¾	r ¾	r ¾	ac	r ½	cr ¾
mh median	S	10.5	a ½	a ½	r ¾	r ½	r ½	ac	r ½	coc	ac	ac	r ¾	r ½	r ½	ac	r ½	cco
mh maximum	S		ac	ac	r ¾	rc	rc	ac	r ½	cr ½	ac	ac	rc	rc	r ¾	ac	r ½	cr ½
Krapina Mandible C ⁵	N	11?										ac	-	-	r ½	ac	r ¾	crc
mh median	S	11.5	ac	ac	r ¾	r ¾	r ¾	ac	r ½	cr ½	ac	ac	r ¾	r ¾	r ¾	ac	r ½	coc
mh maximum	S		ac	ac	rc	a ½	rc	ac	rc	ri	ac	ac	a ½	a ½	a ½	ac	r ¾	r ¼
Le Moustier 1 ⁴	N	11.86	ac	ac	ac	ac	ac	ac	ac	r ¼	ac	ac	ac	ac	ac	ac	ac	r ¼
mh median	S	12.5	ac	ac	rc	rc	r ¾	ac	r ¾	cr ¾	ac	ac	a ½	rc	rc	ac	r ¾	cr ½
mh maximum	S		ac	ac	rc	a ½	a ½	ac	rc	r ¼	ac	ac	ac	ac	ac	ac	rc	r ¼

Fossil hominins in **bold**. Ages with ? are those not derived from counts of dental microstructure.

Stages in **italics** are accelerated beyond the nearest later age modern human maximum.

Modern human stages for ages from AlQahtani et al. (2010).

Fossil hominin stages from T.M. Smith et al. (2010 SI:26, Table S7), unless stated.

¹ Age 6.03 if periodicity=6, age 6.72 if periodicity=7.

² Rosas et al. (2017 SI:36, Table S6).

³ Dean et al. (2014:339,343-344); Dean and Smith (2009:107).

⁴ Thompson and Nelson (2005:214); Thompson and Illerhaus (2005:235-236).

⁵ Shackelford et al. (2012:249-251).

⁶ Gremyatski (1949).

⁷ Bayle et al. (2009).

Table 3.3: *Scladina* ages for stages against modern human distributions

		<i>Scladina</i>	Modern human	
Tooth	Stage	Age attained	Age range	Peak of distribution
UC	Crown initiated	~0.25	~0.0–1.0	~0.5
	Crown complete	~4.5	~3.0–5.0	~3.8
	Apex ½	8.0 (death)	~8.1–13.9	~10.7
M1	Crown complete	~2.5	~1.5–3.0	~2.0
	Apex closed	8.0 (death)	~6.0–11.0	~8.1
M2	Cusp initiated	~3.3	~2.5–5.0	~3.5
	Crown complete	~6.1	~4.2–9.0	~6.0
	Root ½	8.0 (death)	~7.0–13.5	~9.7
M3	Cusp initiated	5.9 ¹	~6.6–13.0	~9.2
	Crown ¾	8.0 (death)	~8.1–14.1	~11.5

Ages in years. Ages in *italics* are younger than modern human range.
Data from Shackelford et al. (2012:242): for *Scladina* citing histological ages for successive stages by T.M. Smith et al. (2010 SI), and for modern humans using plots generated from the charts of Moorrees et al. (1963)
¹ In their Figure 14D Shackelford et al. (2012:242) place the vertical line indicating initiation of the M3 at ~6.7y, whereas T.M. Smith et al. (2007b SI:9) give 2155 days (=5.9y) as initiation age for the M3.

Dean and Liversidge (2015) and Dean (2016) present density plots showing modern human distributions at stages of tooth formation for the second premolar and the three molars, and the position of *Homo erectus s.l.* specimens KNM-WT 15000 and Sangiran S7-37 along with the possibly early *Homo* individual StW 151. These are summarized in Table 3.4.

Some Neanderthals listed in Table 3.2 exhibit stages for the same teeth as the *Homo erectus* sample. These individuals are added to Table 3.4. It is not known at what age they entered those tooth stages. KNM-WT 15000 and Sangiran S7-37 fall in the earlier-attaining half of the modern human distribution, though sometimes below the 95% confidence interval (Dean 2016). The Neanderthals tend to be in the earlier-attaining half and some attainment ages of Roc de Marsal, Obi-Rakhmat 1 and Le Moustier 1 are younger than modern human range.

The sparse evidence so far is consistent with the proposition that some Neanderthals followed an advanced dental formation schedule not dissimilar to that of *Homo erectus* while others attained dental stages at ages within modern human range.

Table 3.4: Ages at attainment of dental formation stages of posterior teeth, comparison of Neanderthals with modern humans and early *Homo*

		Modern humans		<i>Australopithecus</i> or Early <i>Homo</i>	<i>Homo erectus</i> s.l.	Neanderthals									
Tooth	Stage	Peak	Range	StW 151	KNM-WT 15000	Sangiran S7-37	Roc de Marsal	La Quina H18	Krapina Maxilla B	El Sidrón J1	Scladina	Obi- Rakhmat	Krapina Maxilla C	Krapina Mandible C	Le Moustier 1
P4	Crc	6.47	4.17–10.00			5.2		5.7 ?	5.86			4.49–4.78			
	R ½	9.42	6.84–13.50			8.0					8.0				
	Rc	11.96	7.57–15.59												
	A½	12.66	9.81–18.50			10.7									
M1	Crc	3.08	2.47–6.50			2.47	2.3 ?				2.5	1.96–2.16			
	R ½	5.54	4.17–9.56			4.6									
	A ½	8.33	6.24–12.80			7.3					8.0				
M2	Crc	7.22	5.47–10.73	4.75											
	R ½	10.47	7.46–14.50		8.0						8.0		9.3 ?		
	R ¾	11.51	7.57–15.50												
	Rc	12.60	9.44–17.87												
M3	Crypt	8.26	4.85–12.96	4.75						7.7	5.9				
	C ¾	12.62	6.00–17.41		8.0						8.0				
	Crc	13.66	9.43–20.35											11.0 ?	8.64

Ages on entering given stage.

? indicates ages of fossil hominins *not* derived from dental microstructure.

Italics highlight early attainment ages below modern human range.

Data for modern humans and early *Homo* from Dean and Liversidge (2015) and Dean (2016). Age ranges approximated from their graphs.

Data for Neanderthals from T.M. Smith et al. (2007b, 2010 SI:9,28).

3.4.2 Periodicity

Periodicity¹ is constant across all teeth in one individual but varies from one individual to another (Hillson 2014:96). Living human populations can have different mean and modal periodicities: southern Africans mostly 9–10 and Europeans 8–9 (Reid and Dean 2006). If counts of long-period lines were approximately equal between populations, a lower periodicity in one population would tend to reduce total circadian lines and therefore intervals of crown and root development.

In recent human samples, Reid and Ferrell (2006) found an inverse correlation between periodicity and number of perikymata (long-period lines) on tooth surfaces (lower periodicity, more perikymata). Such a correlation would constrain the total of short-period lines (circadian cross-striations) within narrower limits. This correlation cannot be generalized to other primates (Hillson 2014:118–119) or to earlier *Homo*. In Neanderthals mean periodicity is lower than in modern humans (Table 3.5) and yet perikymata counts are lower rather than higher owing to a different *perikymata packing pattern* (Ramírez-Rozzi and Bermúdez de Castro 2004; Guatelli-Steinberg et al. 2007) (§3.3).

Periodicity has been determined for a number of individual Neanderthals and members of other fossil *Homo* species (Table 3.5).

Table 3.5: Periodicity, *Homo* species

Periodicity	Neanderthals	Early <i>Homo sapiens</i>	Recent <i>Homo sapiens</i>	Sima de los Huesos (430 ka) ²	<i>Homo antecessor?</i> (TE, >1 Ma; TD6, 0.8 Ma) ²	Asian <i>Homo erectus</i> ³	South and East African early <i>Homo</i>
6	Jonzac, Marillac	-	-	AT-827 (Hom XIX), AT-1942, AT-3192	ATD6-104	-	-
7	La Chaise BD-J4-C9, Krapina Maxilla B, Lakonis, Saint-Césaire 1	Hofmeyr, Qafzeh 15	-	AT-1475, AT-2135 (Hom XVIII), AT-6873, AT-6874	TE-1, ATD6-6, ATD6-92	S7-37 ³	DNH 35, DNH 100, KNM-ER 1482 ³
8	Engis 2, Le Moustier 1, Scladina, Tabun C1, Zafarraya ¹	Qafzeh 10, Skhul 2	-	AT-13 + AT-64 (Hom VII)	-	-	DNH 67/70/71, KNM-ER 809, KNM-ER 1802, KNM-ER 1805, UR-501 ³
9	Gibraltar 2	-	-	AT-43 (Hom II)	-	-	KNM-ER 3733 ³ , KNM-WT 15000 ⁴
10	-	Jebel Irhoud 3	-	-	-	-	-
Mean (range)	7.4 (6–9)	8.0 (7–10)	8.3 (6–12) ⁵	7 (6–9)	6.8 (6–7)	7 (7)	7.9 (7–9)

Data from T.M. Smith et al. (2010 SI:22) unless stated.

¹ Lacruz et al. (2008:154, citing Ramirez-Rozzi 1993).

² Modesto-Mata et al. (2020:6). Each specimen number denotes a single tooth. For the specimens dated at or before 0.8 Ma, each tooth represents one hominin. For Sima de los Huesos, some individuals are indicated by Hominin numbers (Roman numerals), but for other teeth it is not known how many individuals they represent.

³ Lacruz et al. (2008:152).

⁴ Estimate (Dean 2016:6).

⁵ Hillson (2014:96).

¹ The number of short-period (circadian) lines between long-period lines in dental tissue (§C.3).

Within the sample of Table 3.5, earlier dated hominins in Europe appear to have lower periodicity, most frequently 6 or 7, whereas among later dated hominins there are more at 8 or above, leading to the suggestion that periodicity increased during evolution of the genus *Homo*, peaking in recent *Homo sapiens* (Modesto-Mata et al. 2020:7). However, African early *Homo* exhibit higher mean periodicity than European early *Homo*, while the nine australopithecines examined all had periodicity 7 (Lacruz et al. 2008:152). The Neanderthal mean is significantly different from that of recent humans, but not from that of early *Homo sapiens* (T.M. Smith et al. 2010:20924).

A recent human comparative sample (n=10) utilized by Mahoney (2008) had periodicity range 6–9 days with a mode of 7 rather than 8 or 9: which illustrates that small random samples, such as there are for Neanderthals, may be unrepresentative of the population.

The earliest juvenile representative of *Homo sapiens*, Jebel Irhoud 3, has the highest periodicity of fossil *Homo*: so an hypothesis of increasing periodicity within the *Homo sapiens* lineage would be unsupported. Further, among australopithecines and African early *Homo* periodicities vary from 5 or 6 to 13 days, spanning the full range for living humans (Table 3.5), so that T.M. Smith et al. (2014, 2015) conclude that evidence is lacking for a trend of increasing periodicity within the hominin clade.¹

3.4.3 Crown formation times

Crown initiation and completion ages for the permanent dentition are listed in Table 3.6 and graphed in Figures 3.2 and 3.3. Not all columns of the table are shown in the graphs.

Scladina and Le Moustier 1 have both maxilla and mandible, Krapina Maxilla B and Obi-Rakhmat 1 only a maxilla, Jebel Irhoud 3 only a mandible. Initiation ages for Obi-Rakhmat 1, Le Moustier 1 and Krapina Maxilla B were not determined from histology but copied from Scladina, including a maxillary P3 value from the mandibular Scladina value (T.M. Smith et al. 2010 SI). Periodicity in Scladina is 7 days; in Irhoud 3, 10 days (ibid.). The periodicity of Obi-Rakhmat 1 could not be determined, so these authors give a range of times and durations dependent on periodicity, allowing four likely periodicities 6, 7, 8 and 9, of which 6 and 9 are shown in the graphs.

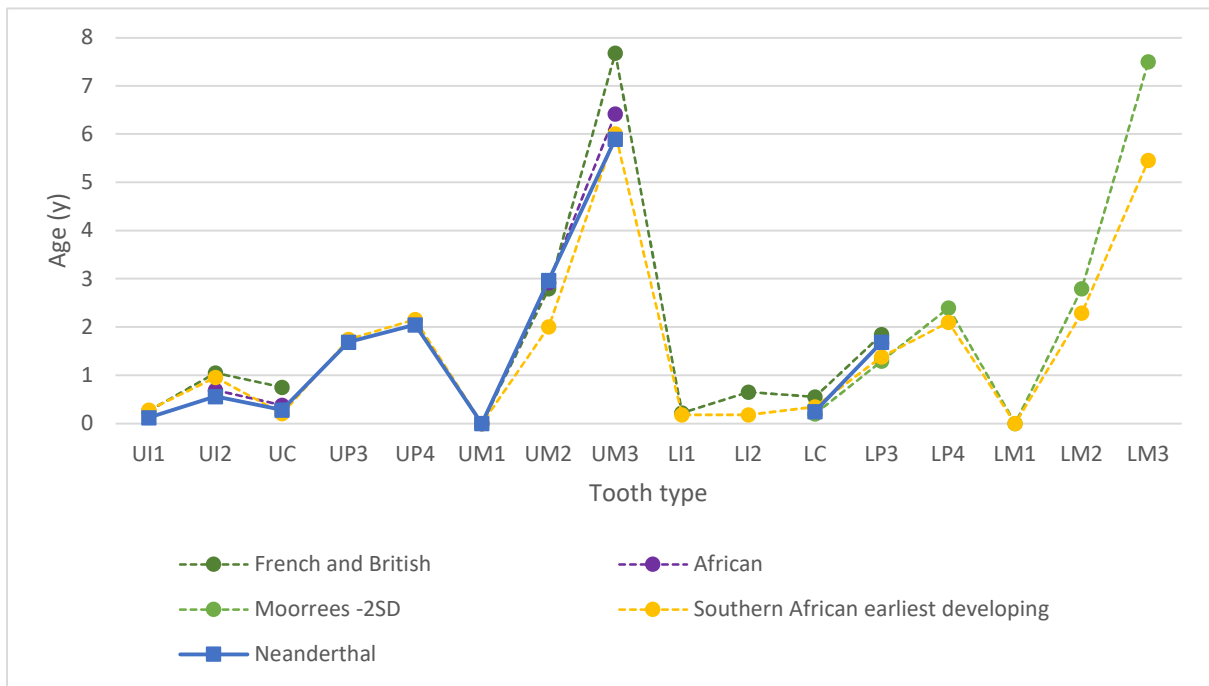
Reid and Guatelli-Steinberg (2017) provide new initiation ages for individuals forming a subset of an earlier Southern African sample (Reid and Dean 2006). The new ages are generally but not always younger, and using the new initiation ages the authors offer alternative mean crown completion ages also for the original data set. In Table 3.6 and Figures 3.2 and 3.3, “Southern African earliest developing” shows for crown initiation the youngest new ages and for crown completion the youngest ages whether new or original, for each tooth type. Neanderthal ages track these Southern African ages quite closely but in many cases are still younger. Even so, Reid and Guatelli-Steinberg (2017:828) observe that the new initiation ages have narrowed the differences between modern humans and earlier *Homo*.

Crown formation times are compared in Table 3.7. Neanderthal and *Homo erectus* durations are shorter, and Jebel Irhoud 3 durations much longer, than those of recent humans. Chimpanzee molar crown formation times overlap to some degree with modern and fossil human durations. Formation time of individual molars (to apex closed) overlaps between *Pan troglodytes* and living *Homo* (Dean 2010:3401, citing Liversidge 2009), with a mean 9.38 years for modern humans and range 6.47–10.75 years for chimpanzees (Kuykendall 1996:140).

¹ Of the two specimens of *Australopithecus anamensis* in their study one has double the periodicity of the other.

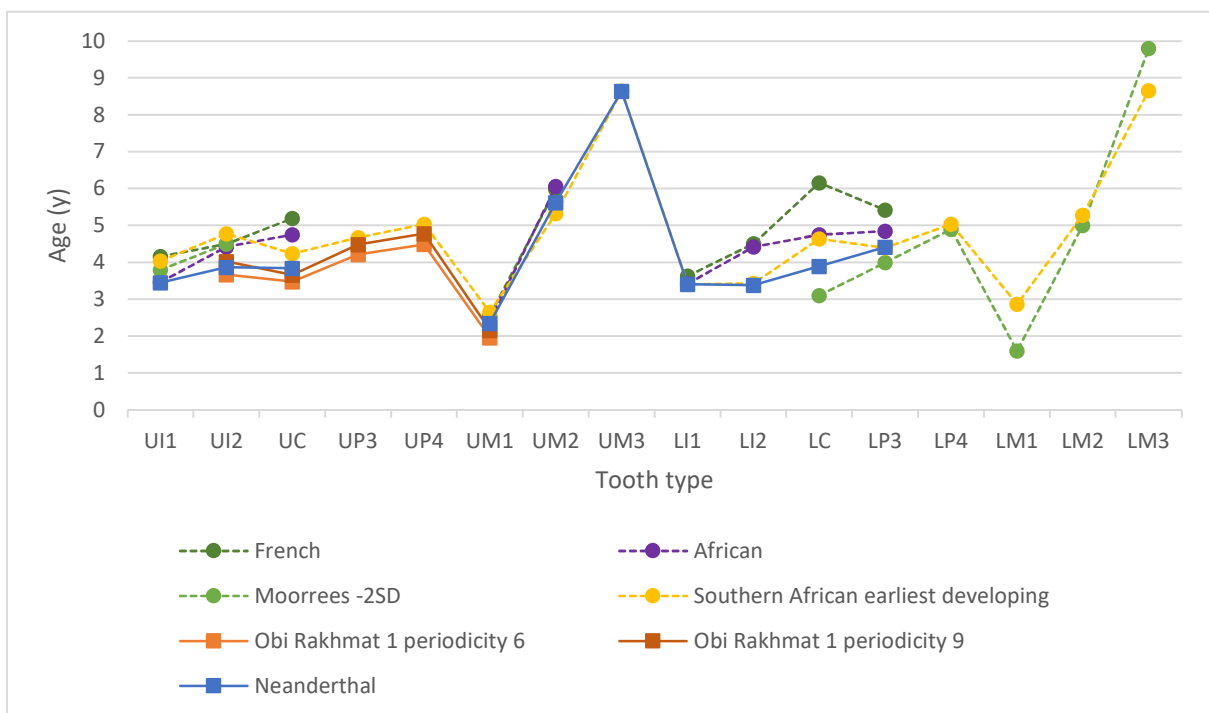
Table 3.6: Permanent dentition crown initiation and completion ages, Neanderthal and recent humans

	Tooth type	Neanderthal								Recent <i>Homo sapiens</i>								
		Krapina Maxilla B, 5.86y		Obi-Rakhmat 1, 6.0–8.1y ¹		Scladina, 8y		Le Moustier 1, 11.86y		Southern African earliest ⁵	African means		European means				Moorrees (±2SD ranges) ⁴	
		Days	Years	Days	Years	Days	Years	Days	Years	Years	Days	Years	Days	Years	Days	Years	Years	Years
Age at attainment of crown initiation (ci)	UI1	43	0.12	-	-	44 ³	0.12	-	-	0.28	-	-	-	-	96	0.26	-	-
	UI2	-	-	205 ²	0.56	205	0.56	-	-	0.96	253	0.69	383	1.05	447	1.22	-	-
	UC	102 ²	0.28	102 ²	0.28	102	0.28	-	-	0.21	138	0.38	274	0.75	199	0.55	-	-
	UP3	-	-	617 ²	1.69	-	-	-	-	1.75	-	-	-	-	-	-	-	-
	UP4	-	-	750	2.05	-	-	-	-	2.16	-	-	-	-	-	-	-	-
	UM1	-	-	-13 ²	0	-13	0.00	-	-	0	0	0	-18	0	35	0.10	-	-
	UM2	-	-	-	-	1084	2.97	-	-	2.01	1066	2.92	1022	2.80	-	-	-	-
	UM3	-	-	-	-	2155	5.90	2155 ²	5.90	6.01	2345	6.42	2803	7.68	-	-	-	-
	LI1	-	-	-	-	-	-	-	-	0.18	-	-	-	-	82	0.22	-	-
	LI2	-	-	-	-	-	-	-	-	0.18	-	-	-	-	137	0.65	-	-
	LC	-	-	-	-	93	0.25	-	-	0.35	138	0.38	201	0.55	98	0.27	0.5 (0.2–0.7)	0.5 (0.2–0.7)
	LP3	-	-	-	-	617	1.69	-	-	1.38	609	1.67	675	1.85	-	-	1.8 (1.5–2.5)	1.8 (1.3–2.4)
	LP4	-	-	-	-	-	-	-	-	2.10	-	-	-	-	-	-	3.0 (2.5–3.8)	3.0 (2.4–3.8)
	LM1	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	0 (0–0.4)	0 (0–0.3)
	LM2	-	-	-	-	-	-	-	-	2.29	-	-	-	-	-	-	3.7 (2.9–4.4)	3.5 (2.8–4.5)
LM3	-	-	-	-	-	-	-	-	5.46	-	-	-	-	-	-	9.3 (7.5–11.5)	9.6 (7.8–11.8)	
Age at attainment of crown completion (crc)	UI1	-	-	-	-	1259	3.45	-	-	4.04	1265	3.47	1518	4.16	-	-	5.4 (4.2–6.6)	4.9 (3.8–6.2)
	UI2	-	-	1339–1469	3.67–4.02	1411	3.87	-	-	4.78	1613	4.42	1643	4.50	-	-	5.9 (4.7–7.3)	5.7 (4.5–7.0)
	UC	1340	3.67	1271–1406	3.48–3.66	1403	3.84	-	-	4.24	1733	4.75	1894	5.19	-	-	-	-
	UP3buccal	-	-	1535–1634	4.21–4.48	-	-	-	-	4.67	-	-	-	-	-	-	-	-
	UP4buccal	-	-	1640–1746	4.49–4.78	-	-	-	-	5.04	-	-	-	-	-	-	-	-
	UM1mb	-	-	716–790	1.96–2.16	858	2.35	-	-	2.65	881	2.41	934	2.56	-	-	-	-
	UM2	-	-	-	-	2051	5.62	-	-	5.32	2211	6.06	2183	5.98	-	-	-	-
	UM3	-	-	-	-	-	-	3152	8.64	8.65	-	-	-	-	-	-	-	-
	LI1	-	-	-	-	1243	3.41	-	-	3.41	1250	3.42	1325	3.63	-	-	-	-
	LI2	-	-	-	-	1235	3.38	-	-	3.43	1613	4.42	1646	4.51	-	-	-	-
	LC	-	-	-	-	1419	3.89	-	-	4.64	1733	4.75	2248	6.16	-	-	4.0 (3.1–5.1)	3.9 (3.1–5.0)
	LP3	-	-	-	-	1611	4.41	-	-	4.40	1769	4.85	1978	5.42	-	-	5.2 (4.2–6.5)	5.0 (4.0–6.3)
	LP4	-	-	-	-	-	-	-	-	5.04	-	-	-	-	-	-	6.2 (5.0–7.7)	6.1 (4.9–7.6)
	LM1	-	-	-	-	-	-	-	-	2.87	-	-	-	-	-	-	2.2 (1.7–2.8)	2.3 (1.6–2.9)
	LM2	-	-	-	-	-	-	-	-	5.28	-	-	-	-	-	-	6.5 (5.2–8.0)	6.1 (5.0–7.8)
LM3	-	-	-	-	-	-	-	-	8.66	-	-	-	-	-	-	12.0 (9.8–14.8)	12.3 (10.0–15.1)	
Neanderthal ages in italics are earlier than all given modern human ranges. mb = mesiobuccal cusp. Negative numbers of days are days before birth. Table concept after Hillson (2014:254–255). Data from T.M. Smith et al. (2007a, 2007b, 2010 SI:9,28) unless stated. ¹ Obi-Rakhmat 1 periodicity not obtainable, hence age ranges. ² Copied by cited authors from Scladina individual, upper or lower. ³ Gibraltar 2 also 44 days. ⁴ Recent human means and ranges from charts of Moorrees et al. (1963). ⁵ Reid and Guatelli-Steinberg (2017).																		



Data from Table 3.6.

Figure 3.2: Crown initiation ages, recent humans and Neanderthals



Data from Table 3.6. Obi Rakhmat 1 is shown separately from other Neanderthals to show low and high possible periodicities.

Figure 3.3: Crown completion ages, recent humans and Neanderthals

Table 3.7: Permanent dentition crown formation times, *Neanderthal*, *Homo erectus* s.l., earliest *Homo sapiens*, recent humans and chimpanzees

Tooth	Neanderthal		<i>Homo erectus</i> s.l.			Early <i>Homo sapiens</i>	Recent <i>Homo sapiens</i>		Chimpanzee (only molars)
	Mean	Range	KNM-ER 820 (1.9–1.5 Ma)	KNM-WT 15000 (~1.47 Ma)	Sangiran 4 (~1 Ma?)	Jebel Irhoud 3 (315ka)	Southern African	Northern European	
UI1	3.34	3.21–3.47	-	2.6–3.2	-	-	3.5–3.7	4.1–4.5	-
UI2	3.11	2.98–3.24	-	2.7–3.2	-	-	3.5–3.8	3.7–4.3	-
UC	3.40	3.36–3.40	-	2.9–3.5	3.8–4.5	-	3.9–4.0	4.1–4.8	-
UP3 b	3.18	-	-	-	-	-	3.0–3.1	3.6–4.0	-
UP4 b	3.15	-	-	-	-	-	2.7–3.3	3.0–3.7	-
UM1 mb	2.28	2.22–2.35	-	-	-	-	2.3–2.9	2.6–2.9	2.1–2.9
UM1 ml	2.39	-	-	-	-	-	2.7–3.2	2.8–3.7	-
UM2 mb	2.90	2.59–3.22	-	-	-	-	2.8–3.4	2.6–3.1	2.9–3.2
UM2 ml	2.65	-	-	-	-	-	3.0–3.6	3.0–3.4	-
UM3 mb	2.73	-	-	-	-	-	2.7–3.1	2.5–3.1	2.2–2.7
LI1	-	-	-	2.6–3.1	-	-	-	-	-
LI2	-	-	2.9–3.5	2.5–3.0	-	5.1	-	-	-
LC	3.58	-	-	3.1–3.7	-	6.7	4.7	5.0–5.8	-
LP3 b	2.70	-	-	-	-	-	3.1–3.2	3.7–4.4	-
LP4 b	2.96	-	-	-	-	-	2.9–3.5	2.8–3.9	-
LM1 mb	2.58	2.26–2.85	-	-	-	4.0	3.0	2.9–3.2	2.0–3.0
LM1 ml	2.32	2.16–2.42	-	-	-	-	2.3–2.7	2.5–2.7	-
LM2 mb	2.55	-	-	-	-	-	3.0–3.2	2.9–3.3	2.2–3.8
LM3 db	2.69	-	-	-	-	-	-	3.2–4.0	2.7–4.0

Crown formation time (CFT) in years. Times in italics fall below modern human range.
Molar and premolar cusps: b = buccal, db = distobuccal, mb = mesiobuccal, ml = mesiolingual.
After Hillson (2014:256–257). Data for *Homo erectus* and chimpanzees from Hillson and his sources, including T.M. Smith et al. (2007c:209).
Data for Neanderthals and recent humans from T.M. Smith et al. (2010 SI).
Data for Jebel Irhoud 3 from T.M. Smith et al. (2007a).

3.4.4 Enamel thickness

Enamel thickness bears upon crown formation times because, if secretion and extension rates remain approximately constant across populations, thicker enamel in one population will take more time to form.

Among great apes and hominins, living humans are said to have the thickest molar enamel, gorillas the thinnest, while chimpanzees and orang-utans are intermediate (Kono 2004:121). T.M. Smith et al. (2012) found that chimpanzees have thinner enamel than gorillas, orang-utans or living humans. Humans and gorillas have proportionately thicker occlusal than lateral enamel and chimpanzees thinner occlusal enamel, perhaps attributable to their softer fruit diet. Even so, it seems that thick molar enamel is not a necessity for hard-object feeding (ibid.:407).

Although ape canine teeth are much larger than those of humans, even for canines modern humans have thicker cuspal enamel than chimpanzees and gorillas (Hillson 2014:147). Among hominins the thickest enamel is found in *Paranthropus* and modern humans. In recent humans thickness ranges from below 1mm to ~3mm. At unworn molar and premolar cusps enamel is generally thicker than at sulci between cusps.

Besides raw values, four measures have been devised to characterize enamel thickness: two-dimensional average and relative enamel thickness (2D AET and RET) based on physical or virtual 2D sections, and three-dimensional average and relative enamel thickness (3D AET and RET) based on volumes and areas calculated from computed tomography scans (Kono 2004; Grine 2005).¹ In all cases higher values indicate thicker enamel. Where dentine and pulp percentage of crown area (in section) or volume (in 3D CT scan) is high, relatively thinner enamel is indicated.

Neanderthals tend to have thinner enamel than modern humans (Table 3.8).

Table 3.8: Cuspal enamel thickness, Neanderthals, fossil and recent *Homo sapiens*

Tooth	Neanderthal		Fossil <i>Homo sapiens</i>	Recent <i>Homo sapiens</i>
	Mean	Range	Range	Range
UI1	737	690–836	900	750–960
UI2	800	750–894	625–965	700–900
UC	749	668–872	895–1300	750–1250
UP3 b	803	601–915	1175–1310	700–1200
UP4 b	1053	775–1250	1410–1485	650–1200
UM1 mb	755	455–1012	985	700–1300
UM1 ml	1027	860–1259	1155–1270	1100–2200
UM2 mb	1255	1055–1475	1535–1720	1000–1600
UM2 ml	1365	1075–1742	1855–2170	1400–2000
UM3 mb	1337	1105–1568	-	820–2350
LI1	610	-	625–940	520–800
LI2	695	-	570–790	550–695
LC	652	645–660	695–885	800–1175
LP3 b	760	690–830	1045–1210	600–1300
LP4 b	954	915–1032	1345–1595	950–1350
LM1 mb	834	612–1447	1080–1280	600–1600
LM1 ml	913	698–1263	800–1730	750–1600
LM2 mb	1115	1060–1185	1615–1845	1200–1700
LM2 ml	1112	965–1260	1485–1880	1000–1550
LM3 mb	1007	905–1097	~1400	950–2076
LM3 ml	954	783–1133	~1350	900–1800
LM3 db	1175	-	~1690	1680–2800
Thickness in μm . Values in italics fall below modern human range. Molar and premolar cusps: b = buccal, db = distobuccal, mb = mesiobuccal, ml = mesiolingual. Data for Neanderthals and recent humans from T.M. Smith et al. (2010 SI:20).				

In contrast, Olejniczak and Grine (2005:219) found that the relative enamel thickness of a third molar from Shanidar 3 exceeded the mean of a modern human sample of M3s.

¹ 2D AET and RET (Olejniczak et al. 2008:14; T.M. Smith et al. 2009:114):

$$2D \text{ AET} = \text{area of enamel cap} / \text{length of EDJ, in mm}$$

$$2D \text{ RET} = \text{AET} \times 100 / \text{square root of dentine area enclosed by enamel cap, dimensionless value}$$

3D AET and RET (Martín-Francés et al. (2020:9):

$$3D \text{ AET} = \text{volume of crown enamel} / \text{surface of EDJ, in mm}$$

$$3D \text{ RET} = \text{AET} \times 100 / \text{cube root of volume of dentine and pulp enclosed in crown, dimensionless value}$$

Olejniczak et al. (2008) tabulated measurements from their 3D data of 29 Neanderthal molar teeth from 10 sites ranging in date from ~130 ka to ~49 ka, summarized here in Table 3.9. While enamel volume is almost identical between the species, Neanderthal enamel thickness is lower by other measures. Contrastingly, four molar teeth (three LM1, one LM3) from the South African Middle Stone Age, contemporary with Neanderthals in Eurasia, have 3D enamel thickness closer to that of recent humans (Table 3.9), while their 2D AET and RET are within or slightly above the modern range (T.M. Smith et al. 2006:515).

Table 3.9: 3D Enamel thickness, molars, Neanderthal, African Middle Stone Age, and modern human

Population	Enamel volume (mm ³)	Dentine and pulp (mm ³)	Dentine only (mm ³)	Pulp only (mm ³)	EDJ surface area (mm ²)	AET (mm)	RET (no unit)	% Crown that is dentine
Neanderthal all molars, n=29, mean/range	225.47 154.04–302.07	345.65² 244.62–502.38	352.61² 229.52–496.04	15.39 6.33–31.63	211.60 129.33–284.64	1.08 0.82–1.63	15.55 11.61–24.02	60 54–69
Modern human mean	226.72	233.04	203.85	3.99	168.32	1.41	23.56	50
SA MSA LM1, n=3 ¹	271.7		349.3		204.6	1.33	18.86	
Modern human LM1 ¹	279.4		304.6		211.9	1.32	19.59	
SA MSA LM3, n=1 ¹	>169.5		189.5		148.3	>1.14	>19.91	
Modern human LM3 ¹	247.7		307.2		156.0	1.58	23.33	
Dentine volumes are within crowns, i.e. only as far as the enamel cervix. Neanderthal and modern human data from Olejniczak et al. (2008:16 and SI:Table 1). ¹ South African Middle Stone Age and further modern human data from T.M. Smith et al. (2006:515). ² Not all specimens represented in both columns.								

Further information on enamel thickness

Variation in enamel thickness across a number of fossil *Homo* populations and recent humans is analysed by T.M. Smith et al. (2012). An extract from their 2D results is given in Table D.2. Where available, possible ancestors of Neanderthals (*Homo heidelbergensis*) are shown. While the area of the enamel cap remains generally similar to that of recent humans, Neanderthals have consistently high enamel-dentine junction lengths and low average and relative enamel thickness.

Martín-Francés et al. (2020) examined molar teeth of Neanderthals, recent humans, Sima de los Huesos hominins (probable direct ancestors of Neanderthals), Atapuerca TD6 hominins (*Homo antecessor*), *Homo erectus*, and some other individuals. An extract of their results for 2D and 3D enamel thickness is given in Table D.3. The trait of thickest enamel in the third molars is evident. Neanderthals have consistently the thinnest enamel of the five populations.

Cuspal enamel formation time is closely correlated with thickness (Mahoney 2011:208), and this appears to be borne out by the contrast in formation times between Neanderthals and *Homo sapiens*. Greater volume of coronal dentine giving rise to a longer enamel-dentine junction in Neanderthal teeth, while the volume of enamel is similar to that of modern humans, seems to account for the difference in enamel thickness. However, enamel secretion rate varies independently of enamel thickness (Aris et al. 2020:155).

3.4.5 Secretion rates

Enamel secretion rates are often quoted as $\sim 4 \mu\text{m/d}$ (e.g. Nanci 2018:149); but they vary considerably between species, populations, individuals, teeth, and regions within a tooth. In modern humans, earlier *Homo* and australopithecines, secretion rates increase from the inner region close to the enamel-dentine junction toward the outer region near the tooth surface.

If secretion rates are higher in one population than in another, then, all else being equal (dimensions of tooth, quantity of enamel, etc.), teeth in that population will form more quickly.

Dean et al. (2001) plotted enamel thickness against formation times for permanent teeth using a sample of early *Homo erectus*, recent humans and one Neanderthal (Tabun C1). Table 3.10 lists some indicative daily secretion rates derived from their Figure 1. These values are means across the thickness of enamel examined. Tabun C1 fits within the faster end of the modern human distribution while rates of early *Homo* are higher still.

Table 3.10: Daily enamel secretion rates, permanent teeth: Neanderthal, early *Homo* and recent humans

Species	Thickness (μm)	Time (days)	Rate ($\mu\text{m/d}$)
Neanderthal	1250	350	3.57
Recent human fast	1250	340	3.68
Recent human slow	1250	420	2.98
Early <i>Homo</i> fast	1250	270	4.63
Early <i>Homo</i> slow	1250	300	4.17
Early <i>Homo</i>	1125	250	4.50
Recent human	2000	500	4.00
Data from Dean et al (2001:629).			

Enamel daily secretion rate (DSR) has been directly determined for several Neanderthal teeth (Tables 3.11 and 3.12). For deciduous teeth, Mahoney et al. (2021) observe that Krapina K11 cuspal DSR lies above modern human range and the lowermost range of DSR from the outer cuspal region of K16 and K21 extends above the uppermost range of modern humans. For teeth forming at birth, DSR drops at birth but recovers and continues to increase to a maximum well above the prenatal rate (Macchiarelli et al. 2006:749). Mahoney (2008:145) observes that DSR is similar across all four principal molar cusps so that data from one cusp can represent the rest.

Table 3.11: Enamel DSR, deciduous teeth: individual Neanderthals, recent humans and early *Homo sapiens*

Specimen	Tooth type	First 100 m from EDJ ($\mu\text{m/d}$)			Whole crown ($\mu\text{m/d}$)		
		Minimum	Median	Maximum	Minimum	Median	Maximum
Nadale 1	Ldm1	2.6	3.0	3.7	2.1	3.0	3.8
Recent human	Ldm1	2.9	3.5	4.3	2.5	3.8	4.9
Fumane 1	Ldm2	1.7	2.1	2.7	1.5	2.5	4.2
Recent human	Ldm2	3.4	3.7	4.2	2.1	3.7	5.0
Riparo Broion 1	Udc	1.9	2.4	3.1	1.9	2.7	4.1
Recent human	Udc	2.0	3.3	5.1	2.2	3.7	5.2
Fumane 2 UPal <i>Homo sapiens</i>	Ldi2	2.5	2.9	3.9	2.5	3.1	4.8
Recent human	Ldi2	2.4	3.4	4.4	2.5	3.7	4.8
Neanderthal data in bold.							
Data from Nava et al. (2020:3). Values are read off their Figure 2 B, C.							

Table 3.12: Enamel DSR: individual Neanderthals, recent humans and *Homo erectus*

Specimen	Tooth type	Cuspal ($\mu\text{m}/\text{d}$)		
		Inner	Mid	Outer
Tabun C1 ³	LM1 metaconid	3.57		
La Chaise ¹	LM1	~2.5–3.5	~4.0	~4.5–5.9
Recent human A ¹		~1.8–2.7	~3.8	~4.4–5.9
Recent human B ¹		~2.0–2.7	~4.4	~5.4–7.2
Lakonis ²	LM3	3.46	3.73	4.33
Recent human ²	hypoconid	2.99	3.74	4.11
Krapina K21 ⁴	Udi1	-	4.50	5.80
Recent human ⁴		2.00–4.37	4.50±0.67 and 4.76±0.46	4.96±0.63
Krapina K11 ⁴	Ldi2	4.50	-	-
Krapina K16 ⁴		-	5.22	6.20
Recent human ⁴		3.35±0.45	4.60±0.43	5.14±0.61
KNM-ER 3733 (<i>Homo erectus</i>) ⁵	P3 or P4	4.00±0.19	4.54±0.42	5.28±0.35
S7-37 (<i>Homo erectus</i>) ⁵	LM1	2.70±0.26	4.42±0.29	5.14±0.35

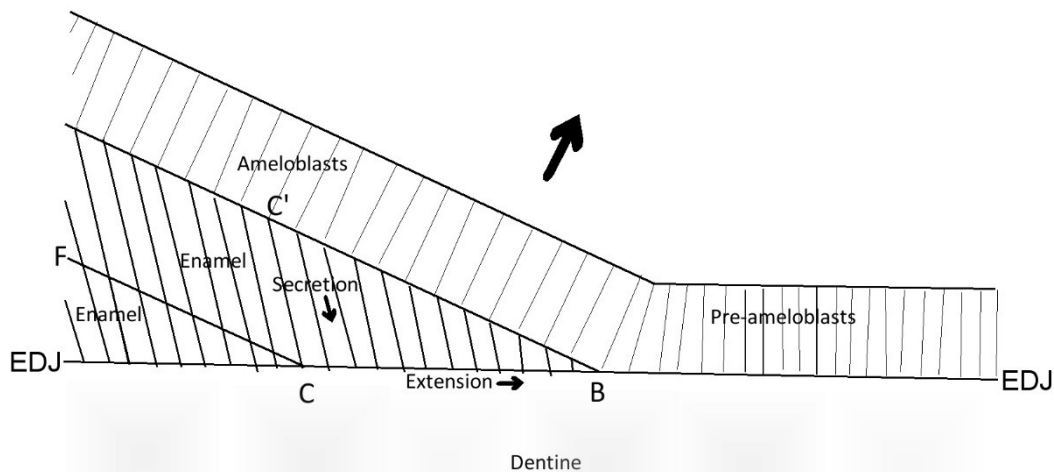
Neanderthal data in bold.
¹ Macchiarelli et al. (2006:749). Values are read off their Figure 3.
² T.M. Smith et al. (2009:116).
³ Dean et al. (2001:629).
⁴ Mahoney et al. (2021 Sl:26). Prenatal DSRs. For K21 only, "outer cuspal" is outer lateral: see source.
⁵ Lacruz et al. (2008:158).

Neanderthal teeth have large crown dentine volume, so that the enamel-dentine junction is longer and ameloblasts have to cover a larger surface. While secretion rates are similar, though in some cases higher, the thinner enamel in all Neanderthal teeth forms over a shorter duration (Mahoney et al. 2021:6).

3.4.6 Extension rates

Extension rate, quoted in micrometres per day, refers to growth of the crown, and eventually also root, away from the enamel-dentine junction (EDJ), which is the site of initial formation. Enamel extension terminates at the cervix, whereas dentine extension continues along the root surface, i.e. the cementum-dentine junction (CDJ). Extension can be measured directly by counting fluorescent markers or long-period lines along the EDJ or CDJ, or by methods of calculation based on daily secretion rate and the angle which the ameloblast or odontoblast sheet makes with the surface along which growth is measured (Shellis 1984; Dean 1985; T.M. Smith 2008:213–214).

Enamel extension along the EDJ is illustrated in Figure 3.4. Daily enamel secretion quantity C'C corresponds to extension quantity CB. If the angle CBC' is wider (less acute) extension will be less for the same secretion quantity, and all else being equal the enamel will be thicker; if the angle is more acute extension will be greater, and all else being equal the enamel will be thinner (Ramírez-Rozzi 1997; Dean 1998a:458–459). T.M. Smith (2008:214) cautions that effectively all else is not always equal: secretion rates decrease from the cuspal to the cervical region, and if even a wide angle is accompanied by a high secretion rate rapid extension can result.



Adapted from Shellis (1984).

Figure 3.4: Enamel secretion and extension

Neanderthal, recent human, and chimpanzee enamel extension rates are compared in Table 3.13.

Modern human enamel extension rates are higher near the cuspal area and slower toward the cervix. Guatelli-Steinberg et al. (2012:481) show declining extension rates by decile of tooth height. In their sample, extension rates in the first decile (nearest the occlusal surface) vary from ~3 to ~11 $\mu\text{m}/\text{day}$ with a mean of ~7.5 but outliers as high as ~16. The mean drops to ~6 $\mu\text{m}/\text{day}$ in the second decile and to ~5 in the fourth, then to ~4.5 in the ninth and ~4 in the tenth where the range is ~2–6. This phenomenon is related to the typical perikymata packing pattern whereby in the later forming deciles perikymata are more numerous because each represents secretion quantities reduced from those seen in earlier deciles.

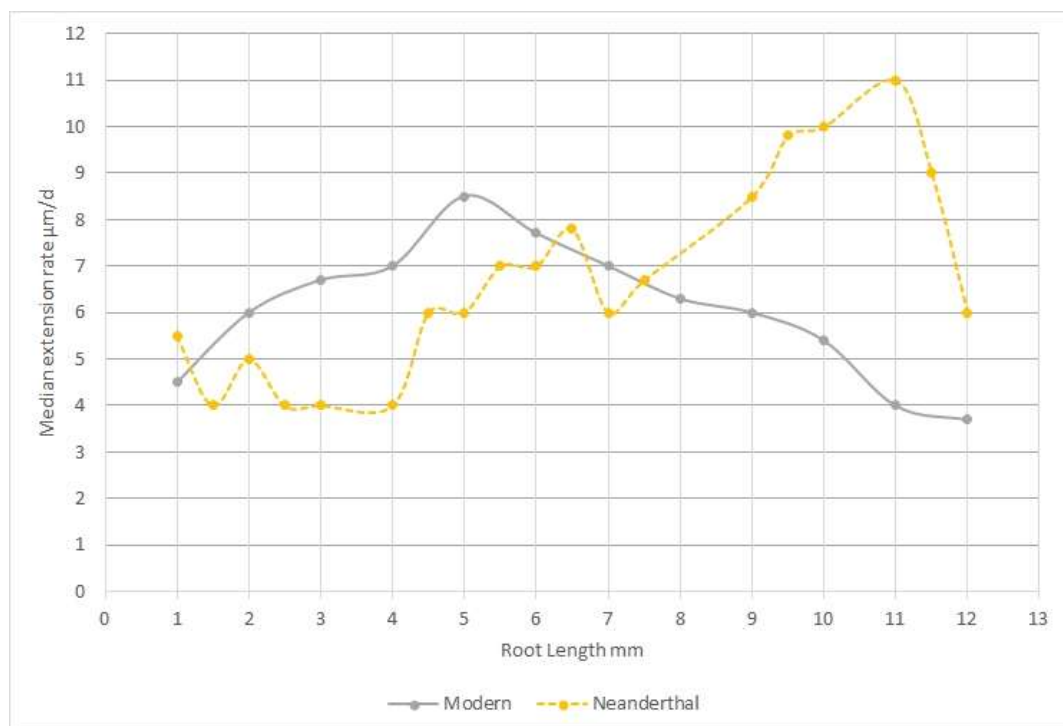
Root extension reflects the rate of differentiation of new odontoblasts at the CDJ; extension rates differ between tooth types and tend to increase overall but with a peak (*peak root velocity*) some time before completion (Dean and Cole 2013:4,13). Dean and Vesey (2008:265–266) document recent human rates. While the range of values at each root length is considerable and for incisors can reach ~15 $\mu\text{m}/\text{d}$, median incisor values begin at ~5 $\mu\text{m}/\text{d}$, plateau at ~10 $\mu\text{m}/\text{d}$ at 6 mm of root formed, and reach a peak of ~11 $\mu\text{m}/\text{d}$ at 9 mm formed; canines begin at ~4 $\mu\text{m}/\text{d}$, peak at ~8.5 at 9mm formed, and drop to ~7 at 10 mm formed; molars begin at ~3.45 $\mu\text{m}/\text{d}$, rise to ~7 at 7 mm formed, and decline to ~5 at 10 mm formed. A similar curve can be seen in Figure 3.5.

Much less work has been done on Neanderthal dentine than on enamel. However, Macchiarelli et al. (2006 SI:8) compared the varying rates of root extension in modern Southern Africans with the rates of BD-14-C9, the La Chaise lower M1. Figure 3.5 is a simplified version, showing only median values for the modern human sample, of their SI Figure 5. Both species show a spurt in root growth at about one third of root length, but the Neanderthal molar varies much more and exhibits a much higher spurt just before completion. Possibly this divergent curve is attributable to its taurodontism.

Table 3.13: Enamel extension rates: permanent teeth, Neanderthals, recent *Homo sapiens* and chimpanzees

Tooth	Neanderthal		Recent <i>Homo sapiens</i>		Chimpanzee (only molars)
	Mean	Range	Southern African	Northern European	Mean
UI1	10.42	9.95–10.89	6.36–7.48	7.23–8.84	-
UI2	9.86	8.87–10.84	5.04–6.27	6.02–7.94	-
UC	9.28	9.24–9.32	6.73–8.34	5.17–8.00	-
UP3 b	8.30	-	6.43–6.54	4.63–6.49	-
UP4 b	7.48	-	5.16–7.51	5.16–7.79	-
UM1 mb	8.32	8.32–8.33	4.99–8.07	5.71–7.44	6.71
UM1 ml	8.00	7.79–8.20	5.56–7.07	5.37–6.59	7.71
UM2 mb	6.11	5.66–6.45	4.76–6.54	5.89–7.87	5.54
UM2 ml	6.31	-	4.37–6.03	5.22–8.14	6.05
UM3 mb	5.20	-	4.51–6.94	5.11–6.51	5.91
LI1	-	-	-	-	-
LI2	-	-	-	-	-
LC	8.66	-	6.89	5.02–7.35	-
LP3 b	9.10	-	4.89–7.01	5.44–7.29	-
LP4 b	8.01	-	5.00–7.19	5.59–7.05	-
LM1 mb	8.73	7.70–10.04	-	6.71–7.72	7.94
LM1 ml	8.11	7.68–8.37	5.45–7.27	5.40–7.48	8.82
LM2 mb	8.28	-	5.52–6.12	5.27–7.29	6.61
LM3 db	5.63	-	-	3.72–4.79	5.10

Extension rate in $\mu\text{m}/\text{day}$.
Rates in italics are higher than modern human range.
Molar/premolar cusps: b = buccal, db = distobuccal, mb = mesiobuccal, ml = mesiolingual.
Data for Neanderthals and recent humans from T.M. Smith et al. (2010 SI:24); for *Pan troglodytes* from T.M. Smith et al. (2007c:210).



Data from Macchiarelli et al. (2006 SI: Figure 5)

Figure 3.5: M1 root extension rates: modern humans and La Chaise Neanderthal

3.4.7 Tooth eruption

Here *eruption* refers to tooth movement from the crypt into occlusion; *emergence* refers to the passing of the tooth through the gingiva, i.e. appearing in the oral cavity. Emergence ages for modern humans are given in Tables D.8–D.17.

Dental eruption is particularly significant in anthropology because it is explicitly referenced in life history theory (§2.4.1, §2.4.4). The age of emergence of the mandibular permanent first molar (LM1) is held to be a life history variable correlated with others such as weaning ages and reproductive milestones (B.H. Smith 1989a, 1989b, 1991, 1992).

In a living subject during the eruption process the incisal edge or one or more cusps of a tooth appear through the gingiva. This is (*gingival*) *emergence*. In archaeological material lacking soft tissue this stage is not directly identifiable. However, *alveolar eruption* is the stage when on the erupting tooth the incisal edge or cusp tips are level with the horizontal alveolar surface, and *partial eruption* is the stage when the incisal edge or cusp tips are level with the maximum bulbosity (approximately half way up the side of the crown) of an adjacent tooth (Liversidge and Molleson 2018:166). *Occlusal* or *full eruption* means that the tooth has assumed its functional position, normally level with adjacent teeth. Gingival emergence occurs at or before partial eruption and from a few months to a year or more after alveolar eruption (Hillson 2024:185)

During root formation, cementum forms on the outer surface of the dentine root, and the periodontal ligament forms outward of the thin cementum layer. The periodontal ligament attaches the tooth to surrounding alveolar bone, and it is remodelled by fibroblasts during eruptive movement to enable constant attachment despite changing position (Nanci 2018:220–222).

In modern humans, according to Grøn (1962, cited by Fanning and Moorrees 1969), gingival emergence occurs when roots are $\frac{1}{2}$ to $\frac{3}{4}$ complete. Liversidge and Molleson (2018:168–170) found the most common root stage at alveolar eruption was root $\frac{1}{4}$ and at partial eruption root $\frac{1}{2}$, while there were many teeth in their sample unerupted at root $\frac{1}{4}$ and many at full (occlusal) eruption at root $\frac{1}{2}$.¹ They conclude that, relative to tooth formation which takes several years, eruption is a rapid process. Their result also implies that root length at gingival emergence is expected to be between $\frac{1}{4}$ and $\frac{1}{2}$, although there will be exceptions.

Intuitively it seems that eruption must be related to root extension and the overall length of a tooth, and it is, in the sense that typically at least $\frac{1}{4}$ of root length has developed when the eruption process occurs. However, eruption has been observed even without any root formed and it appears that root extension is not the driving factor of eruptive movement (Nanci 2018:220–221; Dean and Vesey 2008:259).

Dean and Cole (2013:9–11) investigated the timing of *peak root velocity*² and eruption. In chimpanzees the mean age of peak root velocity coincides with mean age of the eruption process. For chimpanzees, M1 peak root velocity is at ~3.6 years, within range of gingival emergence, and in incisors a root spurt occurs at ~6.1 years with eruption at ~6 years. In *Homo erectus s.l.*, represented by KNM-WT 15000 and S7-37, molar emergence is estimated to have been at 4.5–5 years for M1, 7.6–9 years for M2, and 14.5 years for M3. Peak root velocity is then inferred to be at ~5–6 years (incisors), 7.6–8.9 years (canines), 4.5–5 years (M1), 7.6–8.9 years (M2), and ~14.5 years (M3).

¹ All deciduous tooth types were covered, but permanent incisors and first molars only, maxillary and mandibular.

² The stage of root formation when extension rate is highest.

All these ages are close to modern human ages of peak root velocity but earlier than modern human eruption ages. The authors conclude that timing of the *root spurt*¹ in modern humans is conserved from the condition in earlier *Homo*, while actual eruption has been delayed. In modern humans, canine and molar eruption ages, later than in earlier hominins, are not the result of slower dentine secretion or root extension rates. Dean and Cole (2013:11) suggest that selection may have delayed crown initiation times and the eruption process rather than acting upon formation, i.e. secretion and extension. This delay implies that in modern humans teeth erupt with more root formed than in earlier hominins (Dean and Cole 2013:10–12).²

Of all the Neanderthal immatures, the Scladina individual seems to be the most advanced dentally, with a dental age of 10.5 years, ~2.5 years above its chronological age (T.M. Smith et al. 2010 SI:26). In Table 3.2, its lower premolar formation stages are shown as beyond modern range by AlQahtani et al. (2010), but are just within range for Moorrees et al. (1963), especially if female. Scladina has been determined from DNA to be female (Peyrégne et al. 2019).

Toussaint and Pirson (2006:374) present a CT slice of the Scladina right hemimandible in their Figure 2b which shows a bicuspid crown with no more than $\frac{1}{2}$ root formed in its crypt immediately mesial to the erupted M1. No deciduous tooth appears above it. According to T.M. Smith et al. (2010 SI:26) the lower P3 is at root $\frac{3}{4}$ and the P4 at root $\frac{1}{2}$. If eruption is expected at root length between $\frac{1}{4}$ and $\frac{1}{2}$ (Liversidge and Molleson 2018:166), these teeth should be close to eruption or already erupted. Further discussion of the Scladina teeth reported to be present is in Appendix A.

For a selection of Neanderthal immatures, teeth observed at full, partial or alveolar eruption or still in their crypts are listed in Table 3.14. The specimens are mostly those which have ages obtained from counts of striae in dental microstructure. Given the dearth of older individuals, La Quina H18 and Teshik-Tash are also included although ages are not exact.

Most of the infants and early children seem unremarkable in terms of teeth *erupted*, whereas in some cases *formation* of the permanent teeth may be advanced. However, Dederiyeh 1 at ~18–21 months already has all teeth to dm2s in place, making it ≥ 4 months advanced (Table D.9) or at the early end of modern human range (Table D.8). La Quina H18 has its M1s emerged and worn, which may be early if it is 5.5 years old, though not if it is ≥ 6 years. Unless its M1s emerged before 4.7 years, it is within modern human range.

The juveniles attract more attention. Scladina at 8 years seems to be advanced by 2–3 years with the permanent canines and at least one premolar in occlusion, as well as the expected I1s, I2s and M1s (Tables D.9, D.12, D.13). The right upper and lower M2s are at partial eruption, again ~2–3 years advanced. In the fossil as recovered, the right upper and lower M1s and M2s were in their alveoli whereas the other teeth had fallen out (Otte et al. 1993).

¹ Peak root extension rate.

² To test whether this is so, one would have to find fossil jaws with teeth in course of eruption. As Liversidge and Molleson (2018) found stages $r\frac{1}{4}$ and $r\frac{1}{2}$ at eruption in recent humans, some erupting fossil teeth might be expected to begin eruption with less root than $\frac{1}{4}$.

Table 3.14: Teeth erupted and in crypts, Neanderthal immatures

Individual Age order	Age (y)	Deciduous observed in place	Permanent observed fully erupted	Permanent observed at alveolar eruption or partial eruption	Permanent observed unerupted
Dederiyeh 1 ³	1.5 or 1.7	URdi1, URdc, URdm1, URdm2, ULdi1, ULdm1, ULdm2, LRdi1, LRdi2, LRdc, LRdm1, LLdi1, LLdi2, LLdc, LLdm1, LLdm2 (rest could have been present in life)	None	None	URI1, URC, URM1, ULI1, ULC, ULM1, LRI1, LRI2, LRC, LLI1, LLI2, LLC, LLM1
Dederiyeh 2 ⁴	2.0	URdm1, URdm2, LRdi1, LRdi2, LRdc, LRdm1, LRdm2, LLdi2, LLdc, LLdm1, LLdm2 (rest could have been present in life)	None	None	URI1, URI2, URP3, LRI1, LRI2, LRC, LRM1, LLI1, LLI2, LLC
Roc de Marsal ⁸	2.3	URdi1, URdi2, URdc, URdm1, URdm2, ULdi1, ULdi2, ULdc, ULdm1, ULdm2, LRdi1, LRdi2, LRdc, LRdm1, LRdm2, LLdi1, LLdi2, LLdc, LLdm1, LLdm2	None	None	URI1, URI2, URC, URP3, URP4, URM1, ULI1, ULI2, ULC, ULP3, ULP4, ULM1, LRI1, LRI2, LRC, LRP3, LRM1, LLI1 LLC, LLP3, LLM1 (LRP4, LLI2, LLP4 not observed)
Engis 2 ⁵	3.0	URdi1, URdc, ULdi2, ULdc, Udm1, Udm2, Ldm1, Ldm2 (rest could have been present in life)	None	None	UI1, UI2, UC, UP3, UM1, LM1
Gibraltar 2 ⁶	4.6 male	URdm1, URdm2, LLdm1, LLdm2 (rest could have been present in life)	None	None	URI1, URI2, URC, URP3, URP4, URM1, LRI1, LRI2, LRC, LRP3, LRP4, LRM1, LRM2, LLI1, LLI2, LLC, LLP3, LLP4, LLM1
La Quina H18	5.5 ? female?	URdm1, URdm2, ULdm1, ULdm2 (anterior teeth could have been present in life)	URM1, ULM1	None	URI1, URI2, URC, URP3, URP4, URM2, ULI1, ULI2, ULC (rest probably present)
El Sidrón J1 ⁷	7.7 male	LRdc, LRdm1, LRdm2, LLdc, LLdm1, LLdm2 (rest could have been present in life)	LRM1, LLM1 (URM1 and ULM1 would have been present in life)	LRI2 alveolar	UI1, UI2, UC, LRI1, LRI2, LRC, LRP3, LRP4, LRM2, LLI1, LLI2, LLC, LLP3, LLP4, LLM2
Scladina ¹	8.0 female	URdm1, URdm2, LRdm2	URI1, URI2, URC, URM1, LRI1, LRI2, LRC, LRP3, LRM1, LLI2	URM2 partial, LRM2 partial	URP3, URP4, URM3, LRM3
Teshik-Tash	8.2 ? male?	URdm2, ULdm2, LRdc, LRdm1, LRdm2, LLdc, LLdm1, LLdm2	URI1, URI2, URM1, ULI1, ULI2, ULM1, LRI1, LRI2, LRM1, LLI1, LLI2, LLM1	None	URC, URP3, ULC, ULP3, LRC, LRP3, LRP4, LRM2, LRM3, LLC, LLP3, LLP4, LLM2, LLM3 (?)
Le Moustier 1 ²	11.86 male?	LLdc	All except M3s and LLC	None	URM3, ULM3, LRM3, LLM3

Ages in **bold** are from counts of microstructural striae. Some teeth are sided by authors, others not.
Permanent teeth are as listed by the authors referenced for each individual, supplemented by the list from T.M. Smith et al. (2010 SI:26), who used computed microtomography to scan erupted and unerupted permanent teeth.
¹ Toussaint et al. (1998:740, 2004:38). Scladina has right maxilla, right hemi-mandible and partial left hemi-mandible.
² Thompson and Illerhaus (2005:235–236). The LLC failed to erupt and the LLdc is retained.
³ Mizoguchi (2003:221).
⁴ Kondo and Ishida (2003b).
⁵ Tillier (1983:65–71).
⁶ Tillier (1982:138–142).
⁷ Rosas et al. (2017:2,3, SI:32,36)
⁸ Bayle et al. (2009:69–70).

Contrastingly, El Sidrón J1 at 7.7 years has only permanent incisors and M1s emerged, retaining deciduous canines and molars. It appears to be entirely within modern human range, as it is for tooth formation (Table 3.2). Teshik-Tash, probably not much older (8.0–8.5 years?), also has only permanent incisors and M1s emerged but has lost the upper deciduous canines and first molars ≥ 1 year early. P4, M2 and M3 formation is advanced (Table 3.2) and the LRM2 seems to be approaching alveolar eruption. A more precise age from dental histology is needed for this specimen. The adolescent Le Moustier 1 has all teeth erupted except M3s, not unusual at 11.86 years. M3 formation at root $\frac{1}{4}$ is clearly at the upper end of modern human range.

Overall, dental *formation* appears to be advanced in Neanderthals, somewhat for M1s, to a greater degree for M2s, and more for M3s. In three individuals, Scladina, Krapina Maxilla B and La Chaise, *emergence* of M1 has been estimated, spanning <5.0–6.7 years. These ages lie within modern human range. No precise estimates have been made for M2 and M3. Tentative ages for molar emergence are listed in Table 3.15 for comparison with other hominins.

Molar emergence is generally, but not invariably, earlier in Africans and Australasians than in Asians and Europeans (Table 3.15; Tables D.16–D.17). In Africans and Australasians, M1 emergence is ≥ 1 year ahead and the M3 can be ~ 4 years ahead. Small-stature people such as the Baka¹ may have clearly accelerated dental development (Ramírez-Rozzi 2016): their M1 emergence ages are among the earliest, but their M3 emergence ages are mixed, with females ~ 2 –3 years earlier than males. They provide an example of marked sexual dimorphism for M3 emergence.

Table 3.15: Molar emergence ages, Neanderthal, Homo erectus, Australopithecus, chimpanzees and modern humans

Population	Emergence age (y)		
	M1	M2	M3
Neanderthal	<5.0 ³ <5.9 ⁴ <6 ⁵ 6.7 ⁶ 4.8–6.7 ?	8.0 ⁵	15 ⁸
<i>Homo erectus</i> (Sangiran S7-37) ¹	4.4	7.6	-
<i>Homo erectus</i> (Dmanisi D2700/D2735) ¹⁰	3.8	7.2	10.6
<i>Homo erectus</i> estimates ¹¹	4.5	8.0	14.0
<i>Australopithecus africanus</i> (Taung)	3.73–3.93 ⁷	-	-
Chimpanzees ¹¹	3.2–4.0	6.0	11.0
Modern European	4.98–7.30 ²	10.25–13.58 ²	14–20+ ⁹
Modern African	4.74–6.67 ²	10.30–12.32 ²	13–24 ⁹
Modern East Asian	5.74–8.36 ²	10.83–14.49 ²	15–26 ⁹
Modern Australasian	5.1–5.8 ²	-	13–21 ⁹
¹ Dean et al. (2001:631). ² Liversidge (2003). ³ La Quina H18 (T.M. Smith et al. 2010). ⁴ Krapina Maxilla B (T.M. Smith et al. 2010). ⁵ Scladina (T.M. Smith et al. 2007b). ⁶ La Chaise (Macchiarelli et al. 2006). ⁷ Lacruz et al. (2005). ⁸ Krapina (Wolpoff 1979:79–80). ⁹ Table D.17. ¹⁰ Zollikofer et al. (2024:909–910). ¹¹ Dean and Lucas (2009:557); Dean (2010:3406).			

¹ §2.7, §7.4.7, Table D.17.

Early emergence ages of M1 are not always associated with early emergence of M3: e.g. the Kaiapit of New Guinea (Table D.17). Malcolm (1969a, 1969b) emphasizes the widespread undernourishment of New Guinea highlanders, exemplified most clearly by small stature, and suggests that even dental development may be slowed by chronic undernutrition, which might explain delayed or unaccelerated formation of M3.

Of the *Homo erectus s.l.* individuals listed, Sangiran S7-37 at ~1 Ma (Dean 2016:4) is much more recent than Dmanisi D2700/D2735 at 1.85–1.77 Ma (Zollikofer et al. 2024:906). Possibly emergence ages became delayed in later populations.

For Neanderthals, the age of 6.7 years is from a single lower left permanent M1, La Chaise BD-J4-C9, on which periodicity was identified as 7 and striae of Retzius were counted (Macchiarelli et al. 2006:750). This age practically coincides with the age of 6.6 years predicted for Neanderthals by regression on mean endocranial capacity (B.H. Smith 1991:163). The Scladina juvenile died just after reaching 8 years. Its M1 has apex closed and may have emerged before 6 years (T.M. Smith et al. 2007b). The Krapina Maxilla B subject died at 5.9 years and its M1 has slight wear facets, indicating that the molar had emerged (Smith et al. 2010). La Quina H18, which is said to be developmentally younger than Krapina Maxilla B, has extensive wear on both maxillary M1s and exposed dentine on the right M1 (ibid.). This subject has not been aged by counts on dental microstructure but is probably ~5.5 years old (Appendix A), so could have had the M1s emerged at or before 5.0 years. A definitive chronological age is needed.

From Table 3.15 (and Table D.17) it appears that some modern human populations have emergence ranges which include Neanderthal M1 calculated ages and even the 14–15 years estimated for M3. However, Neanderthal emergence ages, apart from the La Chaise M1, are at the earliest end of modern human range.

3.5 Further considerations

Hillson (2014:144) observes that often assumptions have been made in estimating extension rates and other quantities for analysis. Even in the most rigorous studies there is a degree of uncertainty. For example, in the research of T.M. Smith et al. (2010 SI:27,29), crown initiation ages were not obtainable for Le Moustier 1 and Obi-Rakhmat 1 and initiation ages from the Scladina individual had to be used in calculating age at death. For the Neanderthal specimens in the 2010 study enamel daily secretion rate (DSR) was not obtainable and mean DSR from the Lakonis Neanderthal M3 (3.84 $\mu\text{m}/\text{d}$) was used, but for the very early modern human Jebel Irhoud 3 recent human initiation ages were used (T.M. Smith et al. 2010:20926–20927). It was not possible to measure its enamel DSR so recent human rates were used in one method of deriving cuspal enamel formation time (thickness divided by mean DSR). Jebel Irhoud 3 formation times so derived exceeded the ranges of European and South African modern samples (T.M. Smith et al. 2007a:6130,6132).

Unlike Neanderthals and earlier *Homo*, Jebel Irhoud 3 is not dentally advanced relative to recent humans and it is cited as evidence that a modern human extended childhood with expected implications for learning, intellectual and social capabilities had already come into being for *Homo sapiens* by its era (T.M. Smith et al. 2007a:6132). However, Jebel Irhoud 3 is actually dentally delayed with respect to recent humans. If daily secretion rates and extension rates are similar to those of recent humans but crown and root formation times are greater, and emergence age therefore probably later, then the principal reason for this delay would be that its teeth are larger. If dental acceleration is an indication of rapid growth to adulthood, dental delay could be interpreted as an indicator of an even longer subadult period than is found among recent humans. It might be concluded that, all else being equal, a hominin with large teeth must have a longer childhood than a hominin with small teeth. However, Dean (2007:6094) comments that there is no evidence that larger crowns take longer to form.

Among the juveniles, there is a contrast between (a) Scladina and (b) Teshik-Tash and El Sidrón J1. Teshik-Tash is probably oldest and Scladina intermediate, but all three could be within 6 months of each other. Scladina is female, El Sidrón J1 male,¹ and Teshik-Tash is thought to be male. Among modern humans, females tend to have earlier dental formation and eruption of all permanent teeth by a few months, except M3 (Hillson 2024:188) (Table D.14). Adult body mass differs more between Neanderthal males and females than among recent or early modern humans (Tables H.1, H.2, H.5, H.6). The precocious dental development of Scladina relative to the other two juveniles may partly be due to sexual dimorphism.

There is no evidence that crown formation in anterior teeth is correlated with somatic growth (Guatelli-Steinberg 2009:13), whereas *emergence age of the permanent first molar* is claimed to have significant correlation with overall growth in primates (B.H. Smith 1989a, 1989b, 1991, 1992, 1994; Kelley and Schwartz 2012). Generally, among modern humans the emergence timing of M1, M2 and M3 together tends to be advanced or retarded between populations (Tables D.14–D.17).

Among modern humans advanced molar eruption in Australasians and southern Africans is observed relative to Asians and Europeans (Liversidge 2003, 2008) (Table D.17). The question arises whether advanced molar formation and eruption in some populations is an indicator of more rapid overall growth to adulthood in living humans. This issue and its implications for Neanderthals are discussed in Chapter 7.

¹ Both determined from DNA (Appendix A).

3.6 Summary

The subject of dental development in fossil *Homo* has been researched intensively since the 1980s. It has become possible not only to count perikymata on tooth surfaces, but also to count microstriae within enamel and dentine, to determine periodicity of dental microstructure for an individual hominin, and to detect inter-population differences. For example, perikymata packing patterns (frequency of perikymata within given deciles of tooth surface) and structure of the enamel-dentine junction have been shown to differ between modern humans and Neanderthals.

Researchers generally agree that in non-sapiens *Homo* dental development was accelerated versus modern humans. A possible exception is *Homo antecessor*, for which a modern pattern is asserted by Bermúdez de Castro et al. (2010). Even the Sima de los Huesos hominins appear to exhibit a slower rate of dental development than Neanderthals (Modesto-Mata et al. 2020). These results suggesting for Neanderthals a reversal of the slowing trend from australopithecines onward seem counterintuitive, but perhaps best represent the prevailing view.

Evidence has accumulated that Neanderthal dental *formation* was generally more rapid than in modern humans. This conclusion seems clear and incontrovertible. Cusp initiation and crown completion times are often earlier; enamel and dentine secretion and extension rates are often higher; lesser thickness of enamel should require less time to form; mean periodicity is lower while long-term striae are generally not more numerous. As a result, dental *eruption* may often be earlier. However, the overlap of the temporal variables with modern human ranges is extensive. Tooth formation and eruption of some Neanderthal immatures would fit within modern range but at the younger end, except in La Chaise and El Sidrón J1, which lie within the older end.

While some research has focused on anterior teeth or molars generally, strictly only the emergence age of the mandibular first molar (LM1) is claimed to be an indicator of life history (Kelley and Schwartz 2012:1337; Schwartz 2012:S395). Neanderthal M1 emergence has been estimated to occur at ages from below 5 years up to to 6.7 years (Table 3.15). These ages fit within modern human range, the youngest marginally (Table D.15), but all are early except the 6.7 years, which is conspicuously late. As always, more specimens are required to clarify the range.

CHAPTER 4

BRAIN AND NEUROCRANIUM

4.1 Introduction

The transition from Middle to Upper Palaeolithic in Europe and Western Asia, at or shortly before approximately 40 ka, coincides broadly with the disappearance of Neanderthals and appearance of modern *Homo sapiens*. The greater diversity of lithic and bone toolkits in the Upper Palaeolithic, behavioural modernity indicated by more numerous and differently organized living sites and apparent networks of communities, and symbolic behaviour exemplified by parietal painting in caves, figurines representing humans and animals, modified stone, bone and shell objects, and the increased prevalence of burial of the dead: these phenomena occurring more or less together have all been emphasized as constituting a “human revolution” (Mellars and Stringer 1989; Mellars 1996). Other researchers have disputed the alleged revolution by drawing attention to evidence of symbolic behaviour at much earlier periods, not only in Neanderthal contexts but in the eras of *Homo heidelbergensis* and *Homo erectus* (e.g. McBrearty and Brooks 2000; Bednarik 2014).

Concomitant with acceptance of a revolution in material and symbolic culture on the appearance of modern humans is the hypothesis that modern humans have a different mentality from their predecessors, a superior capacity which enables generation of novel ideas, more connected thought, and complex language (e.g. most authors in Mellars and Stringer 1989; Mithen 1996; Chase and Dibble 1987; Gargett 1989; Lieberman and Crelin 1971; Lieberman 1993). If such a comprehensive change in cognitive capability is real, it almost certainly must result from a substantial evolutionary change in brain structure and function (Zwir et al. 2021), which in turn implies differences in neural development during ontogeny.

In the course of the Palaeolithic, cultural complexity is broadly related to brain size: there is a gradual progression of more complex lithic and eventually other cultural remains and of increased endocranial volume from the australopithecines and habilines from before 2 Ma, through *Homo ergaster*, *Homo erectus* and *Homo heidelbergensis*, to the Middle Palaeolithic hominins *Homo sapiens* and *Homo neanderthalensis* (Rightmire 1985; Robson and Wood 2008:413). All known Neanderthal endocranial volumes fall within the range of modern humans, and they exemplify both low and high values within that range (§4.2), so size alone fails to distinguish the two species. Holloway (1985) argues that earlier attempts to present the structure of the Neanderthal brain as inferior have been unconvincing.

In recent decades more specific and persuasive evidence has been brought to light of significant differences in the structure of Neanderthal and modern human brains. Modern humans appear to exhibit a major apomorphy of the cranial base and the neurocranium generally, *globularization*, which manifests within the first year of postnatal life and may represent a change in brain organization (§4.5.1). It is not found in archaic humans such as *H. heidelbergensis* and *H. neanderthalensis* and their predecessors such as *H. erectus*. While all recent humans share it, among fossil populations commonly assigned to *Homo sapiens* it is absent from earlier groups such as Jebel Irhoud. Globularization is a specifically neurocranial apomorphy. In addition there has been reduction of viscerocranial dimensions and browridges. Evidence indicates that these apomorphies were acquired in stages after the divergence between *Homo sapiens* ancestors and the lineage leading to Neanderthals and Denisovans.

Owing to the limitations of evidence from fossils alone, Neanderthals often have to be considered by reference to our own species, so to assess Neanderthal brain and cranial ontogeny and its consequences it is necessary to cover some of the subject in respect of *Homo sapiens*.

Appendix E tabulates endocranial volumes of *Homo* species and Appendix F contains supplementary description and analysis. For reference modern human brain anatomy is illustrated in Figures 4.1 and 4.2.¹

¹ Images from Gray's Anatomy (1918).

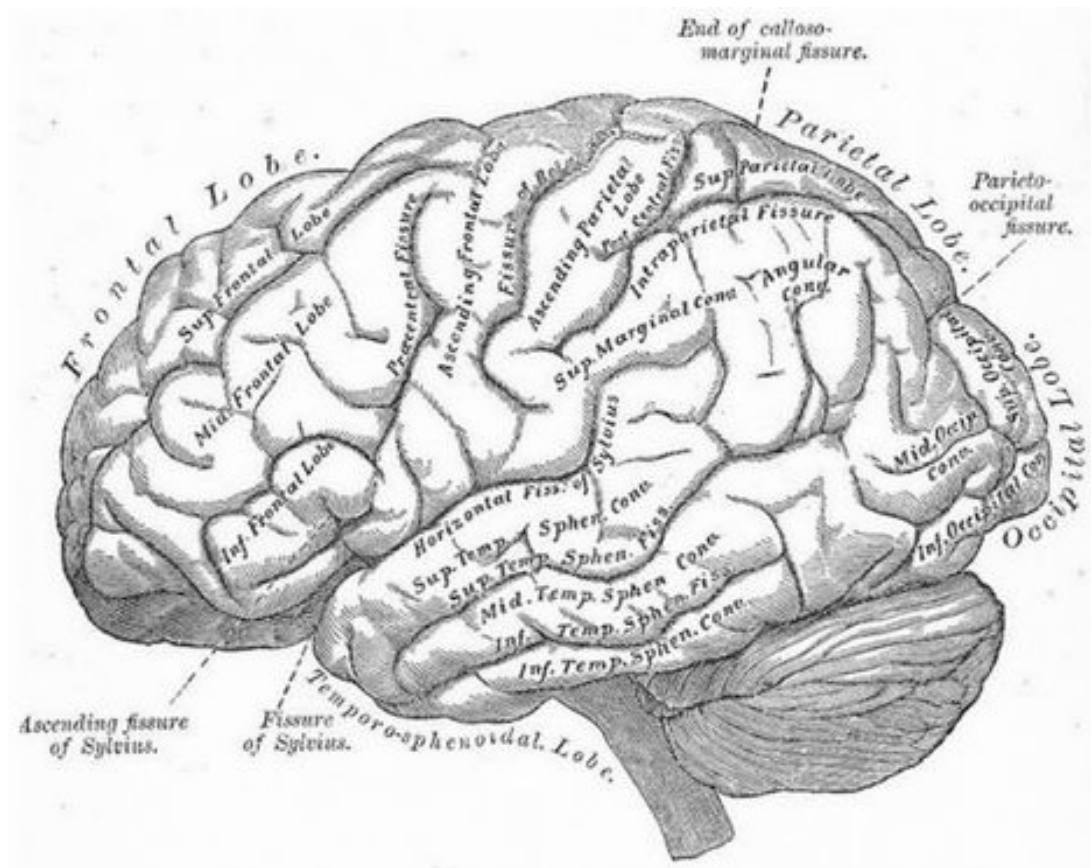


Figure 4.1: Human brain, lateral view, left hemisphere

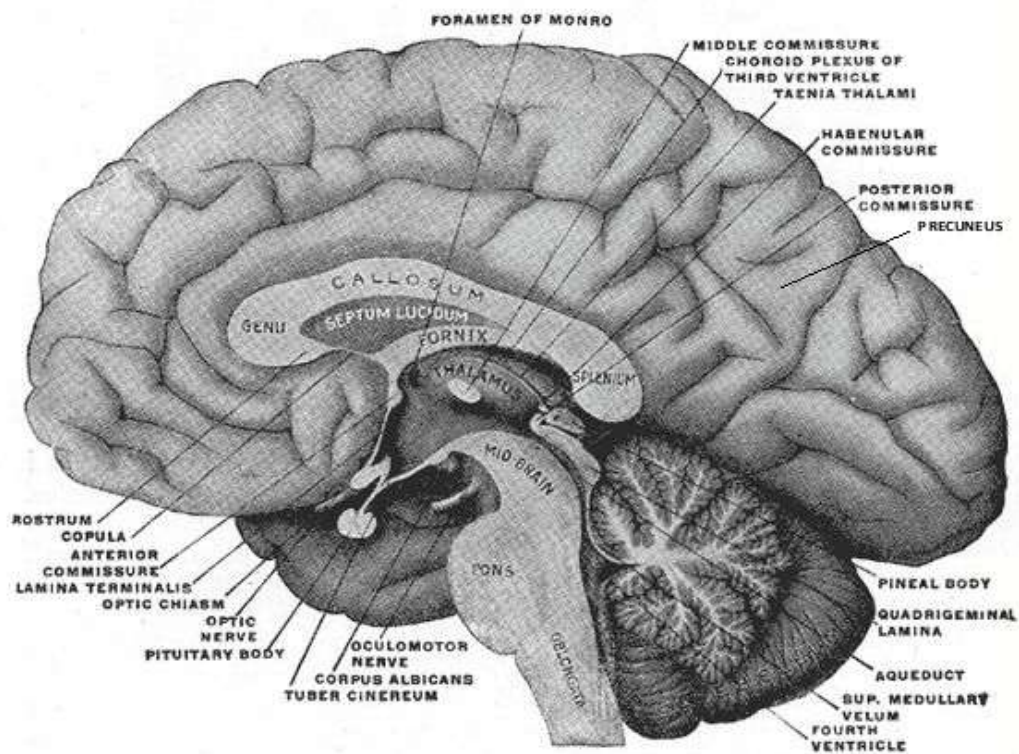


Figure 4.2: Human brain, medial/sagittal view, right hemisphere

4.2 Endocranial volumes of Lower, Middle, and Upper Pleistocene *Homo*

Recent human adult endocranial volumes (ECV) and brain volumes are found within the range of 1100–1700 cm³ and, including outliers or extremes, 790–2350 cm³ (Falk 2012). Notably, Falk’s inner range is matched by the known Neanderthal adult range 1065–1740 cm³ (Table E.2). Appendix E contains tables of endocranial volumes for species of *Homo*. Values are transcribed from several publications, illustrating the disparate results obtained by different researchers.

Most of the ECVs are presumed to have been obtained by traditional methods, either formulae or filling the endocranium with a measurable medium. The values from Neubauer et al. (2018) are from virtual endocasts, and seem higher than previous estimates for a number of specimens. Estimates of endocranial volumes by different authors are often widely discrepant for the same specimen. Some must be treated with caution. For example, Cro-Magnon 3 and Neanderthal (Feldhofer) lack the entire cranial base (Neubauer et al. 2018:4) and occipital fossae. Formulae such as those of Lee and Pearson (1901) and Olivier and Tissier (1975) use ectocranial dimensions (maximum length, maximum breadth, and basi-bregmatic or auricular or porionic height: Martin’s M1, M8, M17, M20; Howells’ GOL, XCB, BBH, AUH). They produce different results (Madre-Dupouy 1992:78; Coqueugniot 1994). Water displacement may be inaccurate owing to surface tension, because water may cling to a surface or run off it. The use of small seed to fill an endocranial cavity has been a traditional method (e.g. Freedman et al. 1991). Kubo et al. (2008) state that imaging from computed tomography generates more consistent and accurate results than the seed method, which they found to produce larger estimates. This is in contrast to the observation above regarding values from Neubauer et al. (2018). The discrepancy may not be large. Applied to the Minotagawa 1 skull, the results of Kubo et al. (2008) were 1335 cm³ from the virtual endocast and 1390 cm³ by the seed method.

Generally, australopithecines had ECVs similar to but often exceeding those of present-day chimpanzees and gorillas. From ~2.5 Ma, still within the Lower Pleistocene, ECVs increase with the appearance of the habilines, and continue to increase gradually in *Homo erectus sensu lato*, until some, in the 1 Ma–500 ka period, fall within the range of living humans. In the Middle Pleistocene, ~600–250 ka, *Homo heidelbergensis sensu lato* exhibits ECVs entirely within the range of living humans, albeit in the lower half, and subsequent pre-Neolithic *Homo sapiens* and *Homo neanderthalensis* exhibit almost the full upper range of recent human ECVs.

ECV in the modern human and Neanderthal lineages seems to have reached a maximum during the period 130–20 ka. Since the Mesolithic there has been a conspicuous decline in mean ECV (Henneberg 1988). This may be attributable in part to somatic gracilization leading to lower body mass, and comparable with the phenomenon of gracilization and concomitant brain size reduction observed in the domestication of animals, notably wolves to dogs (Cieri et al. 2014); but it is perhaps not yet satisfactorily explained (Bednarik 2014).

The range of ECV for each species by geographical and temporal populations is illustrated in Figure 4.3. Individual values are taken from Tables E.2–E.14. The preferred value for each specimen was taken from the leftmost column in which a value is assigned to it. Recent human ECVs are from Henneberg (1988:399), using his larger CCII male and female means and taking the mean of these.

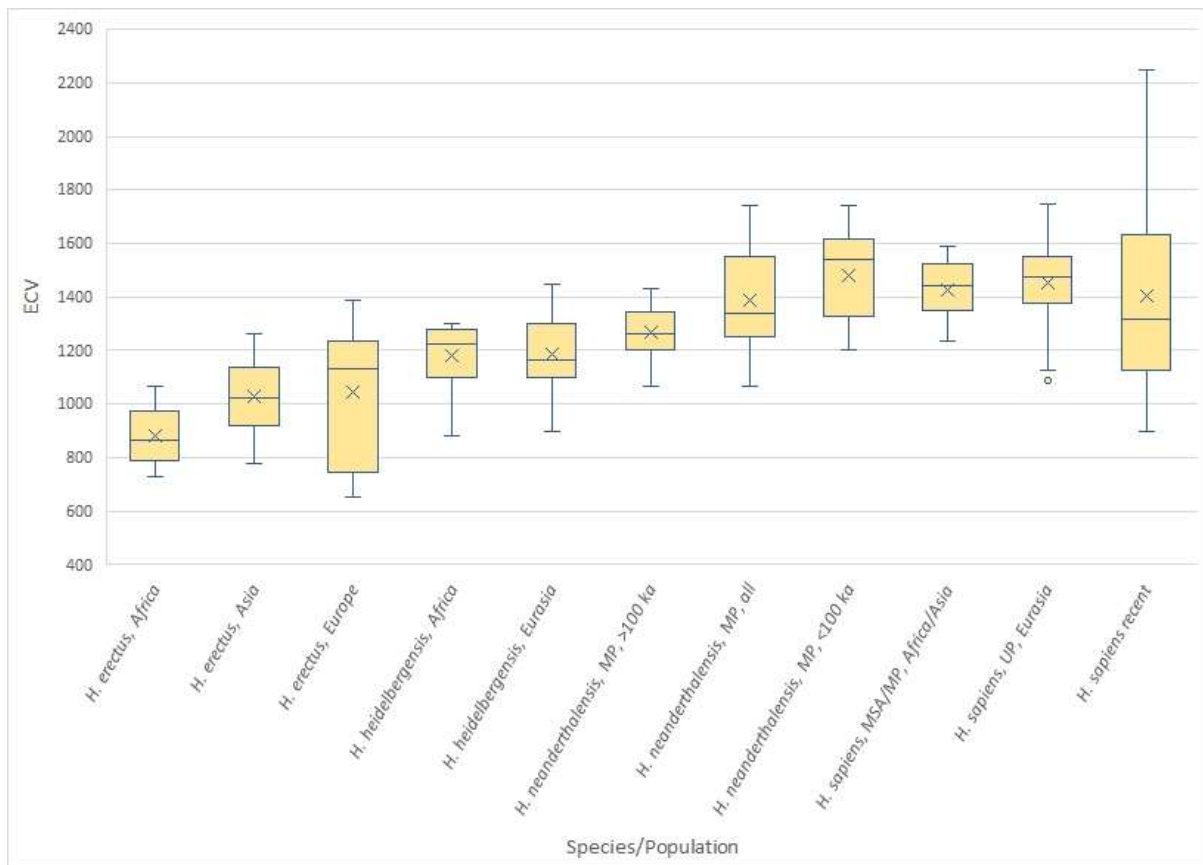


Figure 4.3: Homo endocranial volume by species and population

Endocranial volume, as a proxy for overall brain volume, is a potential indicator of cognitive ability (Deaner et al. 2007). However, differences in size and conformation of specific brain structures may represent differences in functionality. Surface areas of the cerebral and cerebellar lobes, but not their complete volumes, are broadly outlined on endocasts. Other brain structures of course lie within the interior and cannot be assessed from endocasts. To name only a few, the dimensions and form of the thalamus, which processes and relays signals via the brainstem to and from the rest of the body, basal ganglia, limbic system, corpus callosum, through which most interhemispheric communication takes place, and the lateral ventricles, around which neural stem cells proliferate and differentiate (Kaneko and Sawamoto 2018; Coletti et al. 2018) are not accessible.

Using Tables E.2, E.8 and E.9, Neanderthal mean adult ECV is 1385 cm³ (from individual consensus or compromise values); Middle Palaeolithic and Middle Stone Age *Homo sapiens* 1422–1461 cm³; Upper Palaeolithic *Homo sapiens* 1443 cm³ or 1547 cm³ using a smaller sample. Clearly, choice of specimens matters. For example, Holloway et al. (2004) give 1487 cm³ as a Neanderthal mean, but they include the Skhul fossils as Neanderthals instead of assigning them to anatomically modern *Homo sapiens*, which is currently more common practice. The Skhul group includes four males with ECVs 1450, 1554, 1520, and 1590 cm³, which enhance the mean of any population to which they are assigned.

A plot by dating, Figure 4.4, illuminates the history of Neanderthal ECV. The range of adult ECV is considerable, especially among only 23 specimens. Immature ECV should also be expected to show variation, as individuals of the same age will have had genetic potential for lower or higher adult ECV.

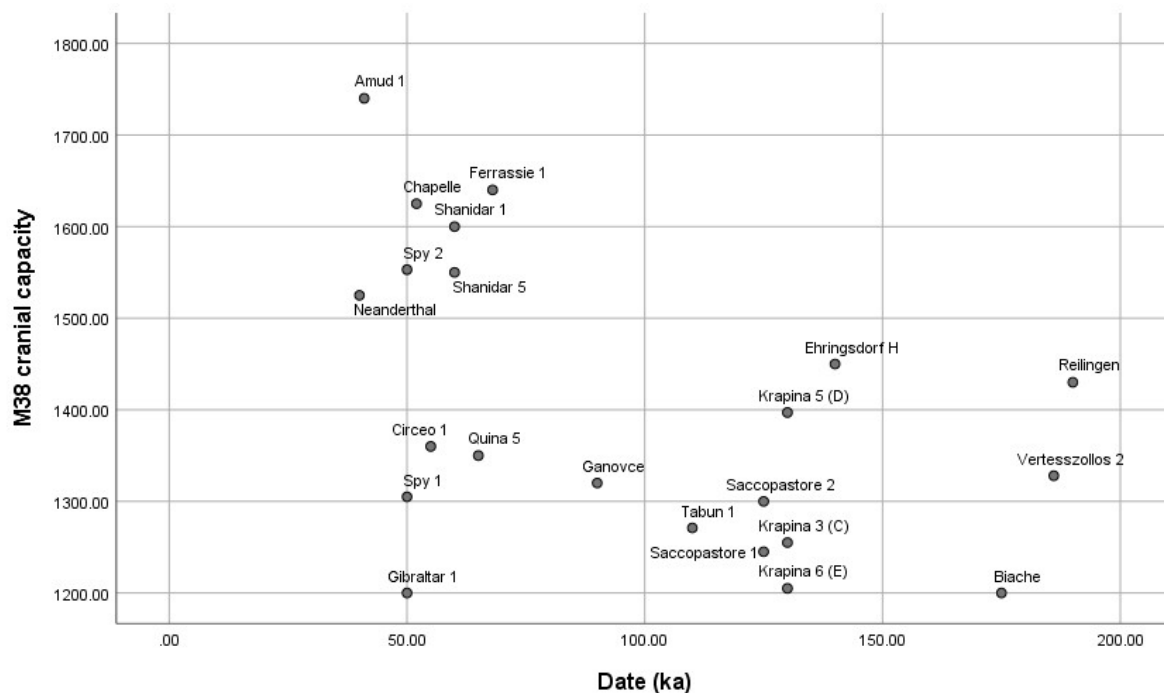


Figure 4.4: Neanderthal adult ECV over time

Many ECVs remain well below 1400 cm³ up to the time of extinction ~40 ka. Some may be female. Although there are two ECVs above 1400 cm³ in the period 200–130 ka, the ECVs above 1500 cm³ for which Neanderthals have been thought remarkable are not evident until after 100 ka or even 75 ka (cf. Pearce et al. 2013:4; Cofran et al. 2021:121). Individuals in this cluster are all regarded as male, while those from the same dates with lower ECV are regarded as female, with the possible exception of La Quina H5¹ and the likely exception of Monte Circeo 1. Tables E.2–E.7 list Neanderthal adult ECVs. It appears that selection was operating upon Neanderthals for larger endocranial volume over their span of existence and right up to extinction, although there may have been individuals with high ECVs in the earlier period as yet discovered.

The dating of this late cluster of high ECVs coincides with the Early Würm and also is close to the period when interbreeding between Neanderthals and modern humans occurred, probably in the Midde East and surrounding areas (Reich 2018). It is tempting to speculate whether interpersonal-intercultural contact had a stimulating effect on the cognitive development of one or both species, and whether exchange of genetic material manifested in brain enlargement through hybrid vigour.

¹ Trinkaus (2016) reclassifies La Quina H5 as male, as does Smith (1980).

4.3 Modern human brain growth

4.3.1 Prolonged brain growth

Bogin (2003:29) states that there is a very strong correlation between emergence of the first permanent molar and “cessation” of brain growth, citing B.H. Smith (1991), who presents a correlation across primates between these life-history variables and others such as gestation length (§1.4, §2.4). This assertion is often repeated (e.g. Neubauer et al. 2010:556).

It has also been stated (Thompson and Nelson 2016:82–83) that brain growth is 90% *complete* at the age of 5 years by volume, citing Robson and Wood (2008), and at the age of 7 years by weight, citing Bogin (2003:29); that brain growth is (100%) *complete* at 3–4 years (Robson et al. 2006:32–35), or 5–6 years (DeSilva and Lesnik 2008:1071, citing Leigh 2004) or 7 years (Jolicoeur et al. 1988; Bogin 1999:73,76); that the *majority* of brain growth is complete by 8–9 years but there are small increases until the late teens (Deaner et al. 2003:259); and that at 4 years brain weight has reached only 84.1% of adult weight, while in chimpanzees adult size is attained at 4 years (Foley and Lee 1991:226, citing Passingham 1982).

The claim of cessation of brain growth at ~5–7 years, the transition from early childhood to the juvenile stage, is not strictly supportable. Ninety per cent and 95% are not 100 per cent. Certainly a distinction has to be acknowledged between volume and weight, but brain weight, brain volume and endocranial dimensions are inevitably related at a gross level. The increase in brain weight after ~7 years largely represents growth of white matter with enhancement of projections between cortical areas (Caviness et al. 1996; Miller et al. 2012), not all of which need result in increase of overall brain volume, given that concurrently grey matter is slightly reduced in some areas (Huttenlocher 1990; Petanjek et al. 2011). However, many researchers have presented evidence that brain growth, in weight and volume, continues well into the second decade of life.

The contents of the endocranium include brain tissue comprising cerebral and cerebellar cortex, corpus callosum and the commissures connecting the hemispheres, central capsule, basal ganglia, amygdala, hippocampus and other subcortical structures, brainstem and medulla, ventricles containing cerebrospinal fluid, meninges, and blood vessels (cf. Pfefferbaum et al. 1994:876; Leigh 2006:105). When discussing encephalization, the gross measurement of endocranial volume is generally used, which does not distinguish brain tissue from all the other contents. For fossil specimens there is no other option, and it is perhaps not unreasonable to assume that the quantity of accessory tissues and fluids broadly scales with the quantity of brain tissue which these support, except in pathologies such as hydrocephalus.

The density of brain tissue is 1.036 g/cm³, so volume = weight / 1.036 (Navarrete et al. 2018:114). The weight and volume values are not identical but fairly comparable.

Boyd (1962) reports mean brain weights of North American children in 3-monthly, 6-monthly, and then annual increments up to 20 years. Table 4.1 lists weight values supplemented at each age by percentages of the adult value, taken to be that for ages 19–20 years.

Boyd’s data indicate that brain weight increases at least until the middle teens for females and late teens for males. In the table, at some ages the mean brain weight is less than the mean weight for one or more lower ages. The data are not from a longitudinal study, which is also true for the data set used by Robson and Wood (2008:401). However, if Boyd’s data are thereby held to be invalid and adult sizes were actually attained at 7 years, then it appears that the younger children in her sample were on course to be smaller-brained adults and the older children were on course to be larger-brained adults. From Boyd’s survey, 90% of adult weight

is attained at approximately 5 years in both boys and girls, in concordance with Robson and Wood (2008:402); 92% is attained in boys and 95% in girls at 7 years; and 100% attained at 19–20 years in boys and 14–15 years in girls. Maximum brain weight therefore appears to be attained earlier than, or at the lower end of, the expected age range for completion of dental and somatic growth (Cunningham, Scheuer and Black 2016).

Dekaban and Sadowski (1978) also report mean cranial volumes from neonates to adulthood. Table 4.2 presents their data supplemented at each age by percentages of the adult (21–39 years) mean. This study bears out Boyd’s (1962) results, showing brain weight increasing through adolescence.

Table 4.1: Brain weight (Boyd)

	Brain weight (grams)			
Age range	Male	% adult	Female	% adult
Neonate	353	24.7	347	26.8
0-3mo	435	30.4	411	31.8
3-6mo	600	42.0	534	41.3
6-12mo	877	61.3	726	56.1
1-2y	971	67.9	894	69.1
2-3y	1076	75.2	1012	78.2
3-4y	1179	82.4	1076	83.2
4-5y	1290	90.2	1156	89.3
5-6y	1275	89.2	1206	93.2
6-7y	1313	91.8	1225	94.7
7-8y	1338	93.6	1265	97.8
8-9y	<i>1294</i>	90.5	<i>1208</i>	93.4
9-10y	1360	95.1	1226	94.7
10-11y	1378	96.4	1247	96.4
11-12y	<i>1348</i>	94.3	1259	97.3
12-13y	1383	96.7	<i>1256</i>	97.1
13-14y	<i>1382</i>	96.6	<i>1243</i>	96.1
14-15y	<i>1356</i>	94.8	1318	101.9
15-16y	1407	98.4	<i>1271</i>	98.2
16-17y	1419	99.2	1300	100.5
17-18y	<i>1409</i>	98.5	<i>1254</i>	96.9
18-19y	1426	99.7	1312	101.4
19-20y	1430	100.0	<i>1294</i>	100.0
Bold = maximum, italic = decrease from younger age Means from Boyd (1962).				

Table 4.2: Brain weight (Dekaban and Sadowsky)

	Brain weight (grams)			
Age range	Male	% adult	Female	% adult
0-10d	380	26.2	360	27.9
4-8mo	640	44.1	580	45.0
9-18mo	970	66.9	940	72.9
19-30mo	1120	77.2	1040	80.6
31-43mo	1270	87.6	1090	84.5
4-5y	1300	89.7	1150	89.1
6-7y	1330	91.7	1210	93.8
8-9y	1370	94.5	<i>1180</i>	91.5
10-12y	1440	99.3	1260	97.7
13-15y	<i>1410</i>	97.2	1280	99.2
16-18y	1440	99.3	1340	103.9
19-21y	1450	100.0	<i>1310</i>	101.6
22-30y	<i>1440</i>	99.3	<i>1300</i>	100.8
31-40y	1440	99.3	<i>1290</i>	100.0
Adult 21-39y mean	1450	100.0	1290	100.0
Bold = maximum, italic = decrease from younger age. Means from Dekaban and Sadowsky (1978).				

Figure 4.5 illustrates the data from Boyd (1962) and Dekaban and Sadowsky (1978) on increase in brain weight.

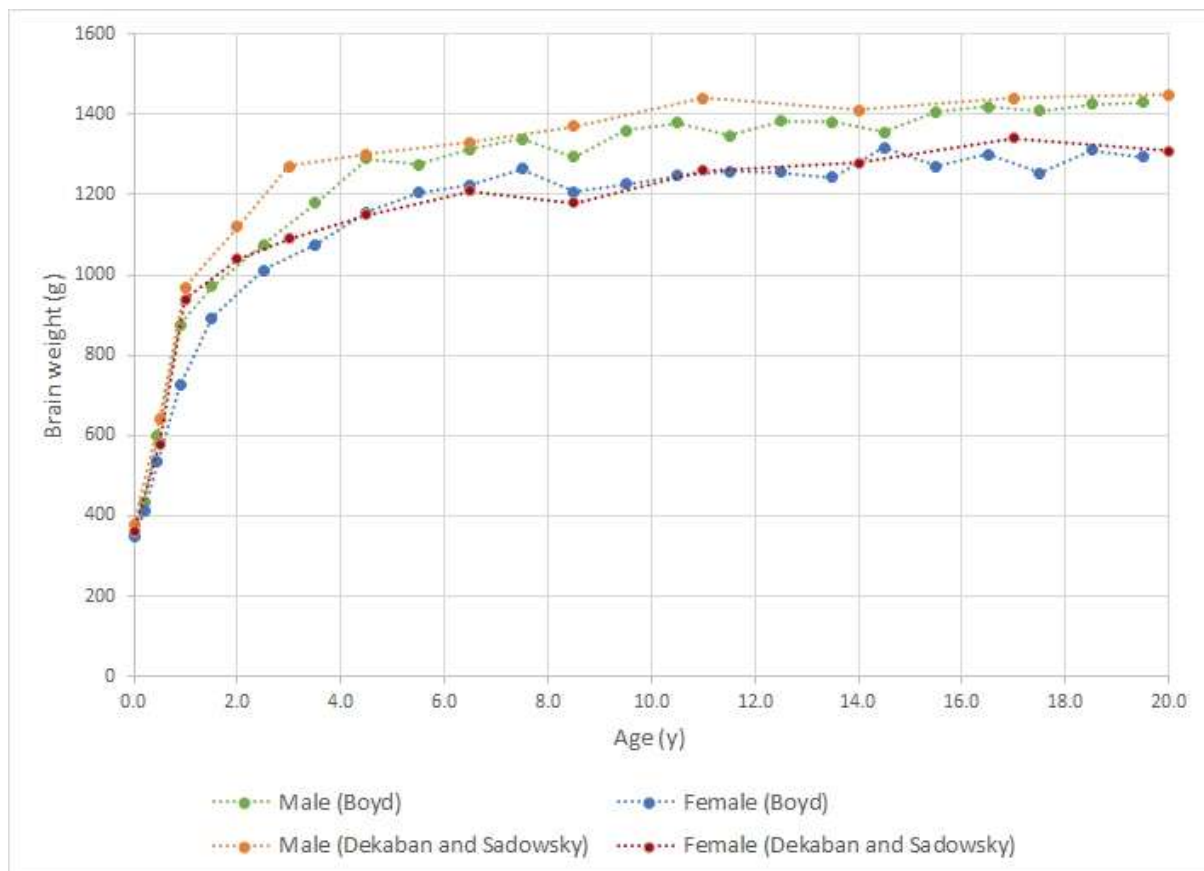


Figure 4.5: Recent human brain weight from birth to adulthood

Dekaban (1977) surveys brain volumes from neonates to young adults, revealing a similar progressive increase in volumes, shown in Table 4.3. The data are supplemented here by percentages of adult volume. In this study the adult mean endocranial volume is ~100 units higher than the corresponding weights in Tables 4.1 and 4.2, and the percentage sizes attained are lower in middle childhood.

Table 4.3: Brain volume (Dekaban)

Age range	Brain volume (cm ³)			
	Male	% adult	Female	% adult
7d	410	26.5	398	27.9
1mo	522	33.7	510	35.8
2mo	609	39.3	529	37.1
4mo	766	49.5	721	50.6
6mo	847	54.7	748	52.5
9mo	896	57.9	845	59.3
1y	1010	65.2	913	64.1
1.5y	1078	69.6	1012	71.0
2y	1129	72.9	1033	72.5
3y	1206	77.9	1148	80.6
4y	1267	81.8	1180	82.8
5y	1281	82.8	1198	84.1
6y	1309	84.6	1218	85.5
7-8y	1354	87.5	1260	88.4
9-10y	1384	89.4	1310	91.9
11-12y	1424	92.0	1339	94.0
13-14y	1480	95.6	1371	96.2
15-16y	1492	96.4	1386	97.3
17-18y	1533	99.0	1402	98.4
19-20y (adult)	1548	100.0	1425	100.0
Bold = maximum. Means from Dekaban (1977).				

The cranial vault expands in response to the growth of the brain: in infancy and to a lesser extent in childhood the endocranial aspects of cranial squamae are resorptive, the ectocranial aspects depository, and the expanding brain imposes tensile strain on sutures, mediated by the dura mater (Henderson et al. 2004; Liebermann 2011). As a result, head circumference is an indicator of endocranial volume, found to be highly reliable at least up to 6 years and an adequate predictor thereafter through childhood and adolescence (Bartholomeusz et al. 2002). Head circumference can be expected to increase slightly during adulthood beyond the value for 18 years, owing to growth of the bony cranium (Roche 1992: 165). World Health Organization standards of child head circumference for age are exceeded by the means of some living populations in widely separate geographical regions (Natale et al. 2014), while other groups fall below the standards owing to suspected undernutrition and unhygienic environment (Aslam et al. 2019; Pomeroy et al. 2012).

Nellhaus (1968) provides data on head circumference from neonates to 18 years. Table 4.4 is derived from his graphs. His data are supplemented here by percentages of “adult” circumference, taken to be at 18 years. For medical purposes, head circumference is measured over the eyebrows (not above), above the ears and over the most posterior part of the occiput,¹ although Cameron (1978:65–66) states that measurement can be above or on glabella. This means that, particularly in adolescence, some of the increase is due to bony enlargement of the supraorbital region. From the fact that the mean female circumference remains ~0.9 cm less than the male at all ages, even up to 18 years (Nellhaus 1968:107), it appears that the supraorbital contribution in recent humans, males as well as females, is slight. This would not be the case for archaic hominins or many Palaeolithic *Homo sapiens* examples. Even so, it is clear that the increase in circumference does not cease at 6–8 years but continues from birth to virtually the end of adolescence in both sexes. This result is confirmed by the study of Eichorn and Bailey (1962), whose values for male and female head circumference continue increasing slightly up to the age of 21 (Table 4.5). Percentages for circumference are close to those for brain weight and volume at corresponding ages.

Table 4.4: Head circumference (Nellhaus)

Age range	Head circumference (mm)			
	Male	% adult	Female	% adult
Neonate	350	62.5	340	61.8
3mo	410	73.2	395	71.8
6mo	440	78.6	429	78.0
9mo	460	82.1	448	81.5
1y	470	83.9	458	83.3
2y	495	88.4	480	87.3
3y	505	90.2	494	89.8
4y	510	91.1	500	90.9
5y	514	91.8	506	92.0
6y	517	92.3	508	92.4
7y	520	92.9	514	93.5
8y	524	93.6	517	94.0
9y	527	94.1	519	94.4
10y	530	94.6	521	94.7
11y	535	95.5	526	95.6
12y	538	96.1	530	96.4
13y	541	96.6	536	97.5
14y	547	97.7	540	98.2
15y	550	98.2	543	98.7
16y	554	98.9	545	99.1
17y	558	99.6	548	99.6
18y (adult)	560	100.0	550	100.0
Means from Nellhaus (1968).				

Table 4.5: Head circumference (Eichorn and Bayley)

Age range	Head circumference (mm)			
	Male	% adult	Female	% adult
Neonate	357	62.3	345	61.5
3mo	414	72.3	401	71.6
6mo	448	78.3	433	77.3
9mo	471	82.4	453	80.8
1y	484	84.5	466	83.1
2y	505	88.3	490	87.3
3y	514	89.8	495	88.2
4y	522	91.3	507	90.4
5y	530	92.6	515	91.8
6y	534	93.4	520	92.7
7y	539	94.1	525	93.6
8y	541	94.7	529	94.4
9y	543	95.0	532	94.8
10y	549	95.9	536	95.5
11y	552	96.4	540	96.3
12y	555	97.1	547	97.6
13y	558	97.5	551	98.2
14y	561	98.1	554	98.8
15y	566	98.9	556	99.1
16y	570	99.6	559	99.6
17y	571	99.8	559	99.6
18y	572	100.0	558	99.6
21y (adult)	572	100.0	561	100.0
Means from Eichorn and Bayley (1962).				

¹ Growth charts, Pfizer Australia Pty Ltd. Their standards are taken from Nellhaus (1968).

In modern humans the brain doubles in volume during the first 6–9 postnatal months, and grows rapidly for the first two years after birth (Dobbing and Sands 1973:758; Martin 1983:27; Martini et al. 2018:3–4). Growth rate remains high but slows through infancy. Throughout the period up to ~4–6 years there is substantive increase in grey matter at the outer level of the neocortex, where the development of the cerebral convolutions continues, and cell proliferation and synaptogenesis establish connections throughout the cortical areas (Huttenlocher 1990; Pfefferbaum 1994:884–885). About 40–50 per cent more connections are made during these early years than will be sustained later in ontogeny (Caviness et al. 1996:733).

From ~4–6 years onward the growth of cortical grey matter volume is reversed, as the brain commences elimination of superfluous synaptic connections, hitherto only increasing (Huttenlocher 1990:524; Jernigan et al. 1991:2044; Pfefferbaum 1994:878,885). The process is not merely pruning but reorganization (Petanjek et al. 2011:13284). In parallel, from early childhood onward, white matter, located throughout the brain but much of it underlying the grey matter in the neocortex, accounts for most of the small but continuing increase in brain volume, as axonal connections continue to grow and myelinate (Paus 2010; Miller et al. 2012; Pfefferbaum et al. 1994:878). Networks within the brain are remodelled as nodes establish efficient long-distance connections by myelination of axons (Hagmann et al. 2010). Prefrontal cortex is one of the latest regions both to begin and to complete this process, during adolescence and throughout the third decade of life (Thomas and Johnson 2008; Petanjek et al. 2011). The volume of white matter continues to increase up to 17–20 years, then remains stable (Caviness et al. 1996:729; Pfefferbaum 1994:881,885; Miller et al. 2012). The ratio of grey matter to white matter declines from ~2.3 at 3 years to ~1.1–1.4 in adulthood (Jernigan and Tallal 1990:303).

These processes of synaptic elimination and axonal growth and myelination do not occur uniformly, as some parts of the brain are affected earlier than others (Lenroot et al. 2007:1068–1071; Miller et al. 2012:16481). At the same time, subcortical grey matter, e.g. amygdala, hippocampus, caudate and putamen, along with diencephalic structures, continues to increase in volume. Despite the pruning of cortical grey matter, peak cortical surface area is attained at ~10–12 years (Brown 2017:2).

Generally, phylogenetically older parts of the brain such as the brainstem mature earlier than later evolved parts such as the neocortex; and within the neocortex sensory and motor areas attain adult structural appearance earlier than associative areas. Temporal and frontal poles mature relatively early. The latest maturing area is the posterior end of the superior temporal gyrus, which is thought to be a higher association area (Gogtay et al. 2004; cf. Lenroot et al. 2007; Brown 2017).

From a longitudinal study, Giedd et al. (1999) report the volume of white matter increasing by 12.4% between age 4 and 22 years. Lindhout et al. (2024:601,603) state that brain weight increase is known up to 22 years and refinement of neural circuits, including synaptic pruning in the prefrontal cortex, up to 30 years.

Ages for peak volumes are given in Table 4.6.

Ages and quantities reported differ between studies according to sample and methods, but the research represented by the works cited above demonstrates that during the second decade of life the modern human brain is engaged in critical reorganization and some of its components are still significantly increasing in volume and weight. Caution is therefore appropriate regarding conclusions drawn from an assumption that brain growth is “complete” at ~5–7 years and that this putative event is approximately coincident with the emergence of the mandibular first molar.

Table 4.6: Age of peak volume attainment by brain structure

Structure	Sex	Age of peak volume attainment (years)	Source
White matter		17–20	Caviness et al. (1996:729); Pfefferbaum (1994:881,885); Miller et al. (2012)
Frontal lobe grey matter	F	11	Giedd et al. (1999)
	M	12.1	
Parietal lobe grey matter	F	10.2	
	M	11.8	
Temporal lobe grey matter	F	16.5	
	M	16.7	
Occipital lobe grey matter		20 (still increasing)	
Cerebrum (whole)	F	10	Lenroot et al. (2007)
	M	14.5	
Frontal lobe grey matter	F	8.5	
	M	10.5	
Temporal lobe grey matter	F	10	
	M	11	
Caudate nucleus	F	10.5	Tiemeier et al. (2010)
	M	15	
Cerebrum (whole)	F	12	
	M	18	
Cerebellum (whole)	F	11.8	
	M	18.5	
Superior posterior lobe of cerebellum	F	15.8	
	M	18.2	
Corpus medullare of cerebellum	F	17.2	Brown (2017)
	M	24 (still increasing)	
Cortical surface area		10–12	
Left hippocampus		13	
Right thalamus		14	

4.3.2 Brain growth priority

The adult human brain makes up only 2% of body mass but accounts for 20% or more of the body's metabolic energy consumption (Vandekar et al. 2019), in contrast to 9% in chimpanzee adults (van Schaik et al. 2006:149) and 3–5% in non-primate mammals (Leonard et al. 2003:5). In infancy the growing brain consumes even more of available energy, exceeding the requirements of other major organs such as the liver (Holliday 1978:126,131), but reducing from a peak of ~80% of resting metabolic rate in neonates to ~60% during the first postnatal year and to ~40% by the sixth year (Leonard et al. 2003:12). These values for energy can be compared with values for human cerebral oxygen consumption as a percentage of total body consumption: 60% in neonates, 19.6% in adults (Kuzawa 1998:186).

A developing human brain is vulnerable to shortage of energy resources. While other tissues can catabolize lipids, proteins and carbohydrates, the brain is unable to catabolize its own substance for energy production, being dependent on glucose and ketones (Cohen 1987). Although some degree of recovery from malnutrition is possible (Levitsky and Strupp 1995), if energy remains scarce a subadult brain can suffer irreversible damage to growing structures, with resulting behavioural abnormality (Winick 1976; Levitsky and Strupp 1995; Moran and Lowe 2017).

Peters (2011) and Harris et al. (2012:769) propose that the brain actively demands energy from the body. Astrocytes induce endothelial cells of the brain capillaries to extract nutrient, which the astrocytes then transfer to their neighbouring neurons (Nortley and Attwell 2017; Allen and Eroglu 2017). This “brain-pull” mechanism appears to impose a priority over the demands of other structures of the body (Peters 2011; Kuzawa et al. 2014; Vandekar et al. 2019).

Kuzawa et al. (2014) argue that brain growth imposes compensatory slowing of body growth rate. At ~5.2 years the brain’s uptake of glucose substrate peaks at almost double (1.82–1.88 times) the stable uptake in adulthood, although the body is only one third of adult volume. This peak coincides with the attainment of ~90% adult brain weight, and occurs ~2 years after weaning in pre-industrial societies, not in infancy but in childhood at an age when body fat stores are at their lowest level in life and when the body shows the lowest rate of weight gain (2014:13011–13014). Substantial increase in somatic growth is necessarily deferred to an age when glucose uptake by the brain will be sufficiently reduced as its growth and reorganization slow down.

Widdowson (1967) observed that the brain is relatively unaffected by undernutrition and illness compared with the rest of the body, whereas the dentition may be affected, as shown by enamel hypoplasia (May et al. 1993:37). Dental development is less retarded than somatic growth by undernutrition and illness (Eveleth and Tanner 1990:146,156–158; Konigsberg and Holman 1999:270–271; Liversidge 2003:73; Roberts and Lucas 2009:152). If during ontogeny energy requirements of the brain are prioritized over those of the rest of the body, then this implies that development of the dentition comes second and development of the skeleton, musculature, bodily organs and all other tissues comes third.

If available energy from food is high, then there will be a greater remainder after brain growth has consumed its share. In such a case somatic growth can become more rapid (Deaner et al. 2003:255–257). However, for small children the quantity of food that can be ingested and digested is limited by the size of the gut, so that even as members of a group enjoying abundance of nutrition their somatic growth will not speed up dramatically.

The long childhood and juvenile period noted for *Homo sapiens* in contrast to chimpanzees and other apes (Schultz 1960; Bogin 1999; Bogin and Smith 2012), when somatic growth is relatively slow even through puberty up to onset of the adolescent growth spurt, is therefore to be expected if the brain is still consuming substantial energy resources throughout that period. As the human brain approaches its full size in the second decade of life, continuing to reorganize and mature but adding less year by year to its volume and weight, more energy should become available for somatic growth. Timing of the adolescent growth spurt may be explained by the gradual release of the constraint imposed by brain priority (Kuzawa et al. 2014:13010; Harrington et al. 2019:161–162).

4.4 Neurocranial evolution in the genus *Homo*

Overall, the modern human brain is ~3 times the volume of the chimpanzee brain (Allen et al. 2004:248). Clearly, absolute size is the most significant difference, but there is evidence of reorganization and increased levels of connectivity within human versus ape brains (Holloway 2002; Allen et al. 2004; Allen 2009). Australopithecine endocrania were not much larger than those of chimpanzees, but a notable expansion is seen with the appearance of early *Homo*, i.e. *H. habilis/rudolfensis* and *H. erectus s.l.* (Table E.14).

Lobes of the neocortex do not precisely match the squamae of the calvarial bones: e.g. the central sulcus which divides the motor cortex of the frontal lobe from the somatosensory cortex of the parietal lobe lies some millimetres posterior to the coronal suture, and the occipital lobe typically extends slightly anterosuperiorly past the lambdoid suture (Bruner et al. 2015a:271; Albessard et al. 2016:2). Even so, endocranial capacity and markings represent the young adult condition at the completion of brain growth, and sometimes these markings allow delineation of lobar surfaces (Balzeau et al. 2012:697). There are indications that the relations of lobes to the coronal and occipital sutures in *H. sapiens* are shared by *H. erectus* and *H. neanderthalensis* (Albessard et al. 2016:10–11).

In living great apes and humans, the proportions of each hemispheric volume formed by the four lobes vary within a small range: frontal 36–43%, temporal 19–24%, parietal 21–28%, occipital 7–12% (Allen et al. 2004:248,250; cf. Semendeferi and Damasio 2000; Semendeferi et al. 2001). It is reasonable to expect extinct *Homo* species to conform to these ranges.

During the transition from australopithecines to *Homo erectus (s.l.)* the temporal and parietal lobes became wider; while the transition from *H. erectus* through *H. heidelbergensis* to *H. sapiens* and *H. neanderthalensis* produced wider frontal lobes. Maximum cranial width in *H. erectus* and *H. heidelbergensis* is low on the temporal bone, whereas in *H. sapiens* and *H. neanderthalensis* it is on the temporal-parietal boundary or above, indicating also parietal expansion (Bruner and Holloway 2010:138,143–144). Whereas *H. erectus* and even *H. heidelbergensis* skulls, including the Sima de los Huesos specimens, are often angular, keeled in the sagittal line and “tent-shaped” in coronal profile, Neanderthal and modern human skulls look filled out, owing to parietal lobe expansion (Bruner et al. 2003:15537).

Neanderthal neurocrania viewed posteriorly are transversely oval or “en bombe”, while modern human vaults tend to high, sometimes almost vertical and parallel temporoparietal profiles, the latter owing to further superolateral parietal expansion coupled with narrowing of the cranial base (Bruner et al. 2015a:274).

Of all *Homo* species from *H. erectus s.l.* onward, Asian *H. erectus* have the smallest temporoparietal lobes but have larger occipital lobes than African and Georgian *H. erectus*. The latter have the smallest frontal lobes. Neanderthals have relatively larger frontal and occipital lobes and smaller temporoparietal lobes than modern humans (Balzeau et al. 2012). The relative increase in size of temporoparietal lobes is a modern human autapomorphy.

4.5 Divergent neurocranial apomorphies of *H. sapiens* and *H. neanderthalensis*

Both modern humans and Neanderthals exhibit increased endocranial volume over that of Middle Pleistocene *Homo heidelbergensis* (*s.l.*) populations, some of which presumably were our common ancestors (Tables E.2, E.10, E.11). As body weights remained at Middle Pleistocene levels or even slightly declined in the successor species, Neanderthals and *Homo sapiens* are more encephalized than *Homo heidelbergensis*.

In the 21st century evidence has emerged that the modern human lineage after ~315 ka and before ~35 ka underwent cranial and neural developments which distinguish *Homo sapiens* from all archaic humans including Neanderthals and Middle Pleistocene hominins. The resultant apomorphies, described below, centre mainly on two related developments, flexion of the cranial base and globularization of the brain, which occur early in ontogenesis, but also include changes in relative dimensions of the lobes. In the last 35–10 ka, further developments include gracilization of the skull, with reduction in facial dimensions of 10–30% and since ~20–15 ka a reduction in average endocranial volume of ~10% (Lieberman 2011:556).

Neanderthals exhibit cranial apomorphies which distinguish them also from their presumed Middle Pleistocene ancestors, though to a lesser degree, and they differ from *Homo sapiens* by lacking the modern apomorphies and retaining the plesiomorphic *Homo* cranial form, modified by greater encephalization. As is often the case, the Neanderthal condition has partly to be described by contrast with modern humans.

Two major neurocranial apomorphies are covered in this chapter: globularization, which occurs in modern humans but not Neanderthals (§4.5.1), and the occipital bun or chignon, which is more defined in Neanderthals and may be associated with late brain growth (§4.5.2). Further apomorphic growth of the neurocranium is covered in Appendix F, where the function and morphology of frontal, parietal, temporal and occipital lobes and bones are discussed in some detail.

4.5.1 Globularization

In comparison with Neanderthals and earlier hominins, modern humans have higher and more rounded neurocrania. Antón and Leigh (2003) observe that the Mojokerto *Homo erectus* immature calvaria (4–6 years) resembles adult modern human neurocrania more than adult *Homo erectus* specimens do, and attribute modern human morphology to paedomorphosis. Among other possible selective factors, they suggest that the retention of subadult cranial morphology to adulthood in modern humans could be linked with retention of structure and developmental plasticity characteristic of the subadult brain, which may have given a cognitive advantage (Antón and Leigh 2003:238–240): this may perhaps include continued inquisitiveness and openness to ideas.

Globularization phase after birth

Evidence has been presented that between birth and emergence of the deciduous dentition by 1.5 years (Nanci 2018:233), the brains of modern human infants experience a *globularization phase* which renders the brain higher and shorter, and so more rounded, and that this process is unique to anatomically modern humans (Gunz et al. 2010, 2012; Neubauer et al. 2010, 2018; Liebermann 2011; Balzeau et al. 2012; Tilot et al. 2019). The globularization phase coincides with the period of the brain's highest growth rate postnatally and therefore can be assumed to be driven by the brain itself (Neubauer et al. 2010:563; Neubauer et al. 2018). Brain globularization would appear to be a neural counterpart of osseous basicranial flexion. This

neurocranial apomorphy appears to be a genuine evolutionary development which may be expected to have an effect on brain function.

Modern human and Neanderthal neonates, the latter represented by Le Moustier 2 and Mezmaiskaya 1, have neurocrania of similar dimensions and elongated anteroposteriorly; Neanderthal neonate brains are only slightly more elongated than those of modern humans (Gunz et al. 2010:R921). While *Homo sapiens* crania begin to diverge dramatically in shape during the first postnatal months, the globularization phase is absent from Neanderthals and all earlier hominins. Neanderthals retained the plesiomorphic morphology, becoming, at least outwardly, a further encephalized *Homo heidelbergensis*.

A more spherical brain should shorten pathways between outlying cortical regions, such as prefrontal and superior parietal areas, and central structures including the thalamus and brainstem. If there is an intrinsic tendency for neural tissue to pull together so as to reduce axon lengths, that would lead overall to greater sphericity. Shorter distances between lobes of the cortex and between subcortical structures and cortical centres should enable faster responses, so that a greater number of cerebral activities can be completed in a given period (Ross and Henneberg 1995:588; Lieberman et al. 2000b:137; Allen 2009:83; cf. Wynn et al. 2016:204), thus providing a selective advantage.¹

A further consequence of increased sphericity of the neurocranium may be that vault bones can become thinner, owing to the greater structural strength of a spherical rather than cylindrical form (Demes 1985, cited by Ross and Henneberg 1995:588). However, selection for thick calvarial walls appears to have abated only at the end of the Mesolithic; in this respect Palaeolithic *Homo sapiens* did not consistently differ from Neanderthals (Lieberman 1996).

A study by Tilot et al. (2019) finds that living humans with homozygous Neanderthal alleles located on chromosomes 1 and 16, influencing brain growth, show more elongated, less globular crania; in heterozygous cases there is an intermediate effect.

Globularization postnatal phase questioned

In contrast to the studies by Gunz, Neubauer and colleagues cited above, Ponce de León and Zollikofer (2001, 2016) propose that Neanderthal and *Homo sapiens* crania differ at birth but follow the same developmental trajectory from birth onward. Their research does not find a distinct globularization phase. All hominoids share a broadly common pattern of cranial development (Scott et al. 2014). According to Gunz et al. (2010, 2012), the modern human trajectory is the same as that of Neanderthals, but only after a globularization phase.

Zollikofer et al. (2017) emphasize effects of viscerocranial growth on the neurocranium, mainly via the cranial base, and also propose that posture and locomotion influence cranial shape. They find, in early postnatal life, expansion of the posterior cranial fossae, the temporal poles of the middle cranial fossae, and the orbitofrontal region of the anterior cranial fossae: developments which they suggest correspond to globularization (ibid.:94). Specifically modern human globularity is the product of a large neurocranium combined with a small face (ibid.:85). The expansions listed above are found in gorillas and orang-utans but not in chimpanzees and bonobos (ibid.:86). Whether these expansions constitute a modern human apomorphy is not yet determined (ibid.:86,94). The question here is clearly wider than a distinction between modern humans and Neanderthals.

¹ In an electronic parallel, the late Seymour Cray in the 1960s–1970s designed mainframe supercomputers on an innovative cylindrical rather than linear layout to reduce length of pathways between units within the processor and memory complex.

It is not disputed that modern humans have more globular neurocrania than archaic hominins. Either modern humans are born with globular neurocrania or globularization takes place postnatally. Neanderthal neonates are acknowledged to differ in cranial morphology from modern humans (Gunz et al. 2012:303; Ponce de León and Zollikofer 2016). The results of Ponce de León and Zollikofer (2016) imply that modern human neonatal neurocrania are sufficiently globular at birth (cf. El-Showk 2019) to have the same developmental trajectory as Neanderthals, who began life with and retained more elongated neurocrania. The results of Gunz, Neubauer and colleagues imply that modern human neonatal neurocrania are not sufficiently globular to have the same trajectory from birth.

One factor in the discrepancy may be the Neanderthal samples. Gunz et al. (2010) used Le Moustier 2 as the neonate versus Pech de l’Azé as the ~2-year-old. Gunz et al. (2012) added Mezmaiskaya 1 as a second neonate. Ponce de León and Zollikofer (2001) used Amud 7, taken to be aged 0.5 years, as an early infant versus Pech de l’Azé as the 2-year-old. Ponce de León and Zollikofer (2016) used Mezmaiskaya 1 versus Dederiyeh 1 (1.5 years) and Dederiyeh 2 (2 years). Bruner (2019) candidly remarks on the discrepancy, suggesting that sample differences, problems with fossil reconstruction, and differences in landmark configuration and algorithms used may be responsible.

Evolution of globularization

Globularization is not a result of encephalization and did not feature in the earliest *Homo sapiens*. Neubauer et al. (2018) distinguish three stages among the African, Levantine and European representatives.

(i) The Jebel Irhoud fossils, dated to $\sim 315 \pm 34$ ka (Richter et al. 2017), are among the earliest assigned to *Homo sapiens* (T.M. Smith et al. 2007a). Facial size is reduced from Middle Pleistocene dimensions and endocranial volume is within modern range (Jebel Irhoud 1 and 2, 1375 and 1467 cm³ respectively), but the neurocrania are low and elongated (cf. Tilot et al. 2019:121; Bruner and Pearson 2012). The more fragmentary fossils Omo 1 and 2 dated to ~ 195 ka are also in group (i).

(ii) Transition to the second group involves relative expansion in lateral parietotemporal areas and the cerebellum. The former relatively enlarges the posterior endocranium superolaterally and the latter enlarges it superoinferiorly, thus introducing globularity (cf. Bruner and Pearson 2012). Group (ii) is represented by Ngaloba (LH18) dated to ~ 120 ka and the Skhul and Qafzeh specimens dated to ~ 115 ka. Another specimen which may fit with this group is Singa, dated to 131–135 ka (Stringer 2016:5–6), which additionally displays a modern expansion of the middle cranial fossae (Bastir et al. 2008:137).

(iii) Transition to the third group is characterized by further size increase in the cerebellum and the occipital area. Into this group fall the European Upper Palaeolithic skulls including Hofmeyr (~ 36 ka) and the Mladeč fossils (~ 35 ka). The Manot 1 skull from a Levantine Middle Palaeolithic context dated to 54.7 ka already exhibits high, subparallel parietals as part of a cranial configuration aligning it with the Upper Palaeolithic Europeans (Grimaud-Hervé et al. 2020). The final transition to modern human endocranial shape therefore should have taken place between ~ 115 ka and ~ 55 ka. Throughout the process from (i) to (iii), the frontal area gradually becomes taller, the superior parietals more bulging, the occipital rounder and less prominent, and the temporal poles more anteriorly positioned (Bruner et al. 2017b; Pereira-Pedro et al. 2017:956).¹

¹ Stages of craniofacial morphological change in Africa, not focused only on the endocranium, have been surveyed from the Bodo fossil (~ 600 ka) onward by Rightmire (2009, 2012).

In contrast to the above processes in *Homo sapiens* over the last 315 ka, during that timescale Neanderthals became further encephalized by expanding the cerebrum overall above the cranial base (Bruner et al. 2003:15535,15537; Neubauer et al. 2018:2). Though large-brained like modern humans, Neanderthals therefore followed the allometric trajectory shared with all other forms of archaic *Homo*, including the common ancestor with *Homo sapiens*.

4.5.2 Late brain growth and the occipital chignon

Some scholars have mooted relatively late brain growth in Neanderthals. Weidenreich (1945:155) noted the endocranial volume of Teshik-Tash, 1490 cm³ (reported by Debetz in 1940 and republished in Gremyatskii 1949), and anticipated that in adulthood the volume would have become 1600 cm³, an increase of ~7%. Weidenreich took the age to be 8–9 years. As the child was probably ~8 years old (Appendix A), such an increase is within expectation for modern humans (§4.3.1). On the same basis, Le Moustier 1, with an ECV of 1540–1565 cm³ at 12 years, could have reached 1600 cm³ with an increase of ~4%, compatibly with modern standards. Occipital remains of the juvenile El Sidrón J1, aged 7.7 years, preserve the interparietal part and most of the supraoccipital: the endocranial surface shows some resorptive fields in several areas including both cerebral fossae, suggesting that brain growth was continuing (Rosas et al. 2017:1287).

A feature commonly found in adult Neanderthal skulls is a prominent posterior convexity of the occipital bone, known as a bun or chignon.¹ This affects only the interparietal squama, where the cerebral fossae accommodate the poles of the occipital lobes. By no means all Neanderthal adults have occipital buns. For example, El Sidrón SD-1219, a young adult male with vault sutures unfused, has a distinct occipital bun, whereas SD-1149, also a young adult, has no bun but has a well defined occipital torus (Bastir et al. 2010:71).²

The cranial base reaches adult dimensions before the vault, lengthening at the synchondroses into the second postnatal decade (Lieberman et al. 2000b:123–124,129). On the cranial vault the major sutures fuse in the following order: metopic in early infancy, then sagittal, coronal, lambdoid in adulthood: for the latter three the process of closure can begin during an individual's late twenties or thirties but generally is not complete until the sixties or seventies (Todd and Lyon 1924; Key et al. 1994; Meindl and Lovejoy 1985). During ontogeny the brain is constrained inferiorly and to some degree laterally by the cranial base, including the petrous temporals, and anteriorly by the orbits and also in archaic humans by the developing supraorbital torus, so that the available directions of growth are superior and posterior (cf. Lieberman et al. 2000a:292–293). In relation to the vault the insula moves posteroinferiorly during childhood (Trinkaus and LeMay 1982:30), confirming posterior extension.

The occipital cerebral fossae are resorptive for the first ~6 years of life, and then the endocranial surface becomes mostly depository, although small resorptive fields may continue into adulthood. The cerebellar fossae, which do not contribute to bunning, may remain resorptive up to adulthood (Kranioti et al. 2009:1764,1766,1768–1769).

The growing brain exerts pressure on the dura, which in turn promotes osteoblast activity at the sutures (Henderson et al. 2004:279; Lieberman et al. 2000a:308; Gunz and Harvati 2007:271). When the interparietal squama is displaced posteriorly, new bone growth

¹ The term originated with Marcellin Boule in his description of La Chapelle aux Saints (Trinkaus and LeMay 1982:27).

² The SD-1149 occipital is listed as a young adult (Rosas et al. 2006:19267–19268). It is robust but smaller than the adult male SD-1219 occipital, and, unlike SD-1219, has neither a chignon nor a suprainiac fossa (Bastir et al. 2010:68, 77).

will form a more horizontal curvature at the lambdoid suture, defining the external profile of the chignon against the surrounding parietal curvature.

Occipital buns occur in recent humans but are more common in Upper Palaeolithic skulls and have their greatest incidence in Neanderthals (Trinkaus and LeMay 1982:28; Trinkaus 2007). The high incidence among these groups is attributed to the combination of a large brain relative to the cranial base (Lieberman et al. 2000a:307) or a large brain and relatively narrow vault (Gunz and Harvati 2007:263). In Neanderthals the occipital region is relatively inclined superoposteriorly to the rest of the cranium. It is more elevated and located further posteriorly with respect to the biasterionic axis than in modern humans, in whom inion lies at the same level as the biasterionic axis (Bastir et al. 2010:70). This orientation of the occipital, contrasting with the condition in recent humans, whereby the occipital lobes are tucked under the parietal lobes in a more globular neurocranium, may conduce to the development of a bun (Gunz and Harvati 2007:271).

Lieberman et al. (2000a:308) observe that the buns or “hemibuns” of Upper Palaeolithic skulls tend to be less concave endocranially than Neanderthal examples. The bone is thicker in the Upper Palaeolithic cases, giving rise to external convexity, but the occipital lobes within are less projecting. Trinkaus and LeMay (1982:42; Trinkaus 2007) and Gunz and Harvati (2007:272) regard Neanderthal and Upper Palaeolithic buns as homologous.

Wormian bones are more often present at the lambdoid suture than in other regions of the vault, and indicate posteriorly directed brain growth (Trinkaus and LeMay 1982:31). In living humans these are explained by dural strain on the suture, and can be caused by premature sutural closure, artificial deformation, or incomplete ossification owing to metabolic bone disease (Bellary et al. 2013).

It has been suggested that occipital buns and hemibuns are produced by late brain growth (Trinkaus and LeMay 1982:41–42), or subtle differences in timing of brain and vault growth (Gunz and Harvati 2007:271–272), or, in modern humans, can develop in a long, low neurocranium, specifically with elongated parietal and frontal bones (Karban 2020). In modern humans, the major sutures do not close until the third or fourth decade of life, and both vault and facial skeleton continue to increase very slightly in all dimensions during adulthood, although this increase has been attributed to bony structure, e.g. extension of the frontal sinuses, rather than brain growth (Thompson and Kendrick 1964; Kendrick and Risinger 1967; Israel 1973; Ruff 1980).

Neanderthal immatures such as Engis 2 (3 years, formerly assessed as 5–6 years), Krapina B (5–6 years), Teshik-Tash (~8 years) and Le Moustier 1 (12 years) have buns (Trinkaus and LeMay 1982:28). However, according to Thompson and Billsborough (2005:82,87–88), Le Moustier 1 has no distinct bun. When buns are present on immatures, they are less prominent than on adults such as La Ferrassie 1 (Heim 1970), La Chapelle-aux-Saints (Heim 1989), Monte Circeo 1 (Trinkaus and LeMay 1982:29), or Spy 1 and 2 (Thoma 1975).

By definition, in the case of very young individuals *late* brain growth is not responsible. Engis 2 has a bun as illustrated by Fraipont (1936), but the neurocranium was reconstructed to be extremely long, 176 mm or even 188 mm (§5.2). Cuozzo (2005:107) measured it¹ at 164 mm. Tillier (1983) states that it has a chignon, but her photographs show the neurocranium much shorter and the occipital without the extreme projection shown by Fraipont.

Heim (1982:131) notes that the mendosal suture and intraoccipital synchondroses are closed in La Ferrassie 8 aged 23 months,² in contrast to an expectation of 4 years in living

¹ This was circa 1979.

² Aged 1.37 years by Shackelford et al. (2015:237).

humans, and suggests on the basis of this and height of the occipital squama that ossification was precocious in Neanderthals. However, according to Cunningham, Scheuer and Black (2016:65), the mendosal suture starts to close from ~4 months after birth and is normally closed but not always obliterated by 1 year; the posterior intraoccipital sutures or synchondroses (joining left and right lateral parts with the supraoccipital part) fuse between 1 and 4 years, while the anterior intraoccipital sutures (joining left and right lateral parts with the basilar part) may begin to close from 3 years.

The transverse oval shape, “en bombe”, of the Neanderthal neurocranium is present in both adults and young individuals, notably Gibraltar 2. It contrasts with the more vertical sides exhibited by modern humans, which form a parietal boss or eminence where the vault curves superomedially. In addition to the superior parietal eminence, less clearly expressed than in modern humans, Richards et al. (2021:219, 2022b:584) identify in late Neanderthals a secondary posteroinferior parietal eminence which contributes to the “en bombe” morphology.¹ They attribute this eminence to dorsocaudal expansion of the parietal and occipital lobes. Increase in biasterionic breadth with age may be a related indicator (§6.4).

A study of the Saccopastore 1 and 2 and Monte Circeo 1 adult skulls by Manzi et al. (1996) concludes that occipital and lateral regions exhibit hypostosis resulting from the combination of plesiomorphic platycephaly with the synapomorphic trend of encephalization in later *Homo*. The possibility is raised that in Neanderthals growth of the platycephalic vault in response to the large brain in some individuals may have introduced a degree of structural instability, manifesting in additional centres of ossification, particularly at the lambdoid area. That is, in the Neanderthals archaic neurocranial morphology reached its dimensional limit. It is further suggested that the more globular neurocranium of later *Homo sapiens* may be the result of positive selection on a morphology which overcame the structural limitations of the archaic form (Bruner et al. 2003:15339, 2014:9–11, 2015a:274–275; cf. Antón and Leigh 2003:240–241).

What is witnessed in Neanderthal immatures with developing chignons is perhaps early posterior direction of brain growth. This condition may be associated with the genetically determined target dimensions of relatively large adult Neanderthal occipital lobes compared with those of modern humans. It neither confirms nor precludes further, i.e. late, gradual brain growth during the second decade of life, which is itself consistent with modern human development.

¹ Among the earlier Neanderthals at Krapina, it is present only in Krapina 2 (B) (Minugh-Purvis et al. 2000:417).

4.6 Neanderthal brain growth rate

As Neanderthals formed a parallel lineage and shared the same range of endocranial volumes as ourselves, it is a reasonable null hypothesis that their brains experienced changes in grey and white matter volumes, synaptic reorganization, and extended growth similar to those of living *Homo sapiens*. Such an hypothesis is already falsified in part by the differential development of the neurocranium and the neocortical lobes and cerebellum (§4.5). However, for brain processes and for unobservable structures, from the brain stem through the cerebral peduncles, the internal capsule, the basal ganglia and limbic system, to the white matter tracts below the superficial grey matter, i.e. most of the brain, there is no available model except our own species.

4.6.1 Subadult endocranial volumes

Endocranial volumes for Neanderthal immatures from neonates to the adolescent, showing estimates from a number of authors are listed in Table E.1. Using consensus or compromise values (Appendix E), growth of the brain is illustrated here in Figure 4.6. The spread of ECVs is considerable from infancy onward. Some individuals come into adult range early, but continued growth is indicated by older individuals.

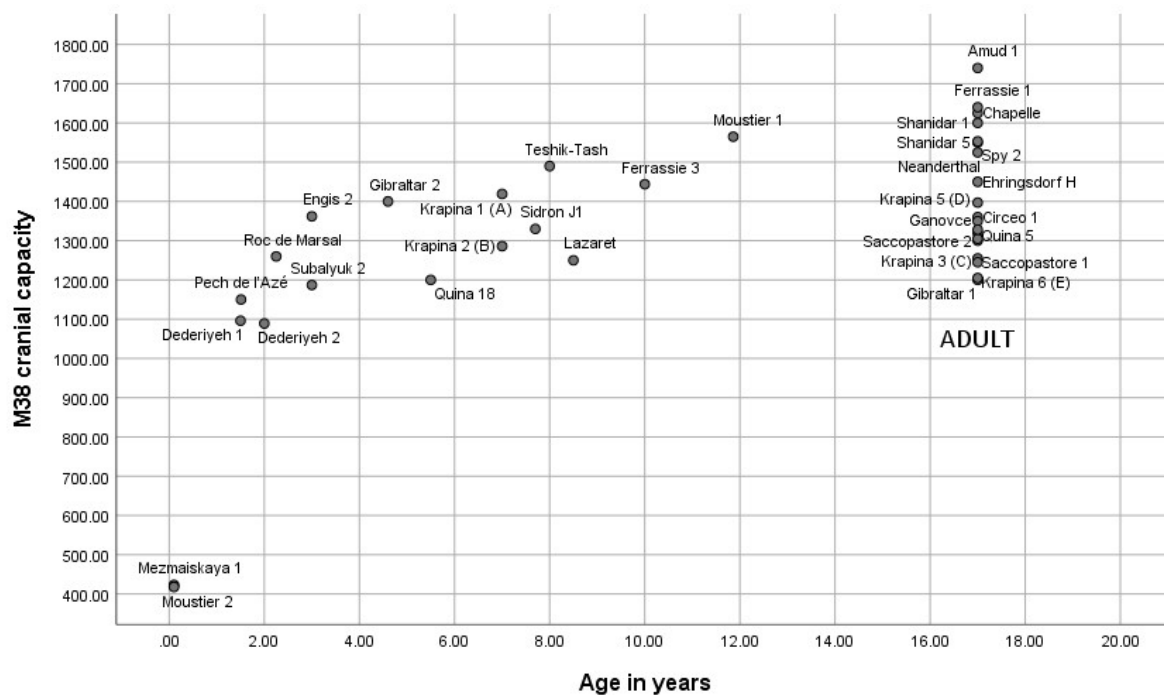


Figure 4.6: Neanderthal ECV increase by age, neonates to adults

The growth curve (Figure 4.7) is steep in the first year, slowing and gradually levelling out into the second decade of life, much as expected in modern humans (cf. Figure 4.5).

At any age there seem to be specimens distinctly larger or smaller. For example, Dederiyeh 2 is thought to be ~0.5 years older than Dederiyeh 1 but has a lower ECV. By splitting the subadult specimens into larger-ECV and smaller-ECV series, it is possible to find separate trend lines (Figure 4.8) which fit the data more closely than the single line. Each series would then join the upper or lower half of the adult distribution, at ~1500 or ~1300 cm³.

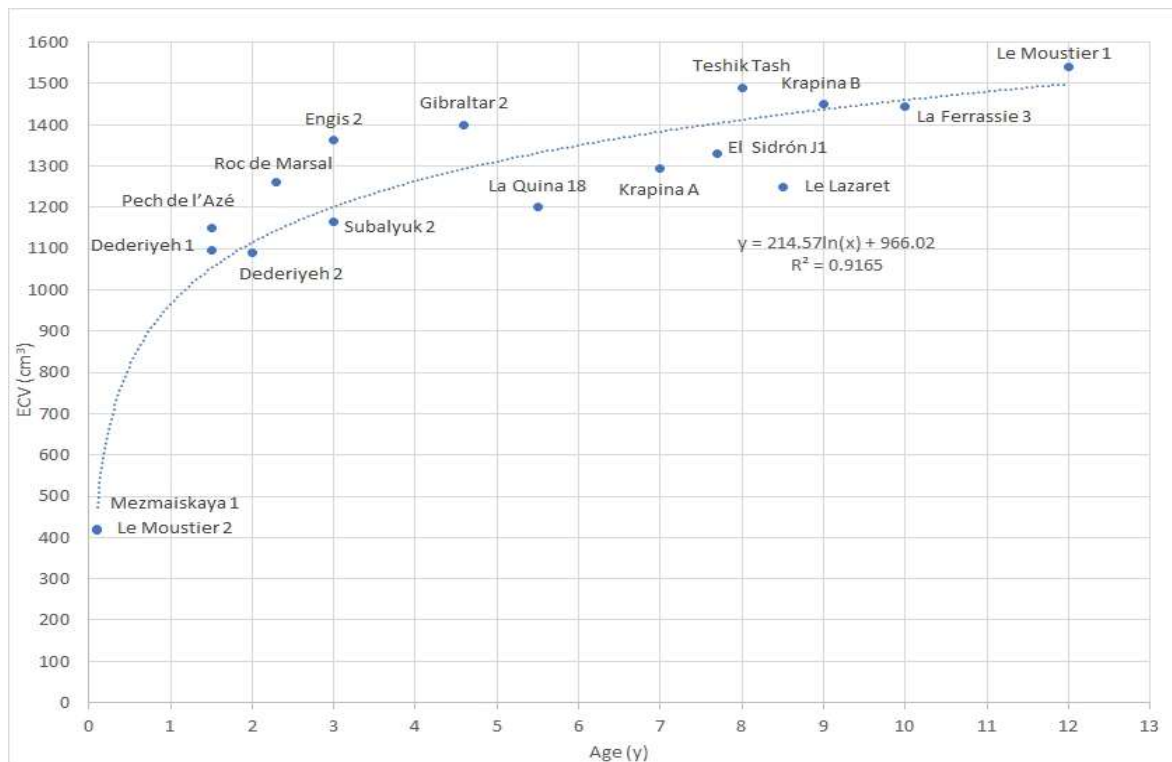


Figure 4.7: Neanderthal ECV increase by age, neonates to adolescent

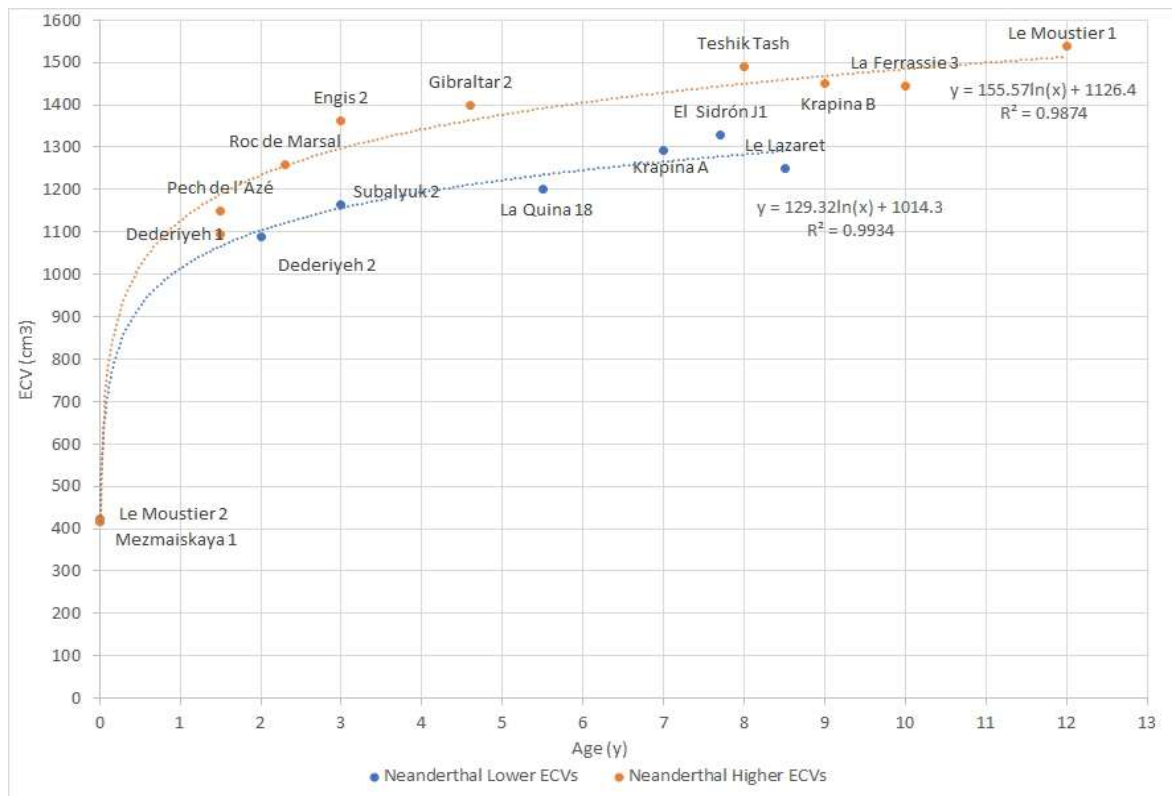


Figure 4.8: Neanderthal ECV increase by age, lower and higher trajectories

Subadults which for their age seem to fit the lower-ECV and higher-ECV series are listed in Table 4.7.

Table 4.7: Neanderthal immatures, higher and lower ECV for age

Age (y)	ECV (cm ²)	Lower	Higher
0	418	? ←	Le Moustier 2
0	422	? ←	Mezmaiskaya 1
1.5	1096		Dederiyeh 1
1.5	1150		Pech de l'Azé
2	1089	Dederiyeh 2	
2.25	1250		Roc de Marsal
3	1187	Subalyuk 2	
3	1362		Engis 2
4.6	1400		Gibraltar 2
5.5	1200	La Quina H18	
6–8	1419		Krapina 1 (A)
6–8	1280	Krapina 2 (B)	
7.7	1330	El Sidron J1	→ ?
8.2	1490		Teshik-Tash
8.5	1250	Le Lazaret	
10	1444		La Ferrassie 3
12	1540		Le Moustier 1

4.6.2 Rapid brain growth?

The case of Gibraltar 2

Rapid brain growth in infant Neanderthals was postulated by Dean et al. (1986) from a study of the Gibraltar 2 immature partial cranium, on the basis of its large vault dimensions in relation to an age at death of 3.1 years. Age was determined from a count of perikymata (with unknown periodicity) on the upper permanent first incisor, which is unerupted but exposed.

If brain growth more rapid than in recent humans was experienced not only *post partum* but also *in utero*, then Neanderthals could have given birth to neonates with larger neurocrania than recent humans without extending the gestation period (Dean et al. 1986:307; Ponce de León et al. 2008:13766). However, such a scenario would lead to risk of cephalopelvic disproportion (§G.5).

A new age at death of Gibraltar 2 obtained by computed microtomography of dental microstructure with known periodicity is 4.6 years (T.M. Smith et al. 2010:20925), close to the ~5 years first assigned by Buxton (1928:61) and on comparison with other Neanderthal immatures by Tillier (1982, 1988:258). With reversion to a higher age, 50% older than that proposed by Dean et al. (1986), the argument for rapid brain growth becomes much less cogent.

There are several Neanderthal immatures older than Gibraltar 2 which have lower ECVs (Table 4.7, Figure 4.8). Gibraltar 2 has relatively high ECV, the highest known below 7 years. Its nearest age peer is La Quina H18, ~1 year older but with 200 cm³ lower ECV. There is considerable variation in ECV among Neanderthal immatures and adults, just as among modern humans (Tillier 1995). Therefore, even if Gibraltar 2 had been 3.1 rather than 4.6 years old, it would be unwarranted to treat it as typical and use it to argue that Neanderthals in general had faster brain growth than modern humans (Tillier 1988: 261).

Comparison with recent humans - 1

Zollikofer and Ponce de León (2013) are among scholars who propose that Neanderthal brain growth was faster than in modern humans. They take both Neanderthal and modern human brain volume to be $\sim 400 \text{ cm}^3$ at birth. The Neanderthal value is derived from the neonates or near-neonates Le Moustier 2 with $408\text{--}428 \text{ cm}^3$ (Gunz et al. 2012) and Mezmaiskaya 1 with $414\text{--}423 \text{ cm}^3$ (Gunz et al. 2012) or $422\text{--}436 \text{ cm}^3$ (Ponce de León et al. 2008). For the modern human 400 cm^3 the common source cited in this and several other recent papers is Huppi et al. (1998:227), who used MRI to obtain values from a Massachusetts sample.

Alternative sources present modern human neonatal brain size considerably lower (§4.3.1). Table 4.8 compares percentage growth against the neonatal value and adult value using means from Tables 4.1 and 4.3 and from Zollikofer and Ponce de León (2013). Some of the Neanderthal ECVs and percentages attained at 1 year, 1.5 years and adulthood are lower than in the modern human samples. The neonatal and intermediate values selected for modern humans largely determine the outcome.

Table 4.8: Brain growth, percentages of neonatal and adult values

Study and weight or volume	Species/sex	Neonate		1 year			1.5 years			Adult	
		ECV	% adult	ECV	% neonate	% adult	ECV	% neonate	% adult	ECV	% neonate
Boyd (1962), g	Modern male	353	25	877	248	61	971	275	68	1430	405
Boyd (1962), g	Modern female	347	27	726	209	56	894	258	69	1294	373
Dekaban (1977), cm^3	Modern male	383	25	1010	264	65	1078	281	70	1548	404
Dekaban (1977), cm^3	Modern female	361	25	913	253	64	1012	280	71	1425	395
Zollikofer and Ponce de León (2013), cm^3	Modern	400	30	850	213	63				1350	338
Zollikofer and Ponce de León (2013), cm^3	Neanderthal	400	27	900	225	60	1092 ¹	273	73	1500	375

¹ Dederiyeh 1.

Comparison with recent humans - 2

ECV growth trajectories of male and female modern humans and of Neanderthals with higher and lower ECVs are compared in Figure 4.9. Neanderthal adult mean values are from Tables E.6 and E.7. Modern human brain volumes are from Dekaban (1977) as listed in Table 4.3. Dekaban's (1977) values for modern humans are rather high than low, as discussed earlier. Percentages of adult size are plotted in Figure 4.10. Alternative graphs Figures 4.11 and 4.12 use modern human brain weights from Dekaban and Sadowsky (1978) as listed in Table 4.2. These weight values are lower than the 1977 volumes.

The Neanderthal lower-ECV group are closely comparable with modern human females, although at 2 years a Neanderthal lower-ECV individual, Dederiyeh 2, lies slightly above the modern female data point. In percentage of adult ECV attained the lower-ECV group run ahead of the higher-ECV group and the modern humans. At 1.5 years a Neanderthal higher-ECV individual, Dederiyeh 1, coincides with the modern human male data point. At the same age (though it may be 2.0 years rather than 1.5), Pech de l'Azé has a slightly greater ECV than Dederiyeh 1. From then up to 12 years, the maximum subadult age available, the Neanderthal higher-ECV group exceeds the mean values for modern males.

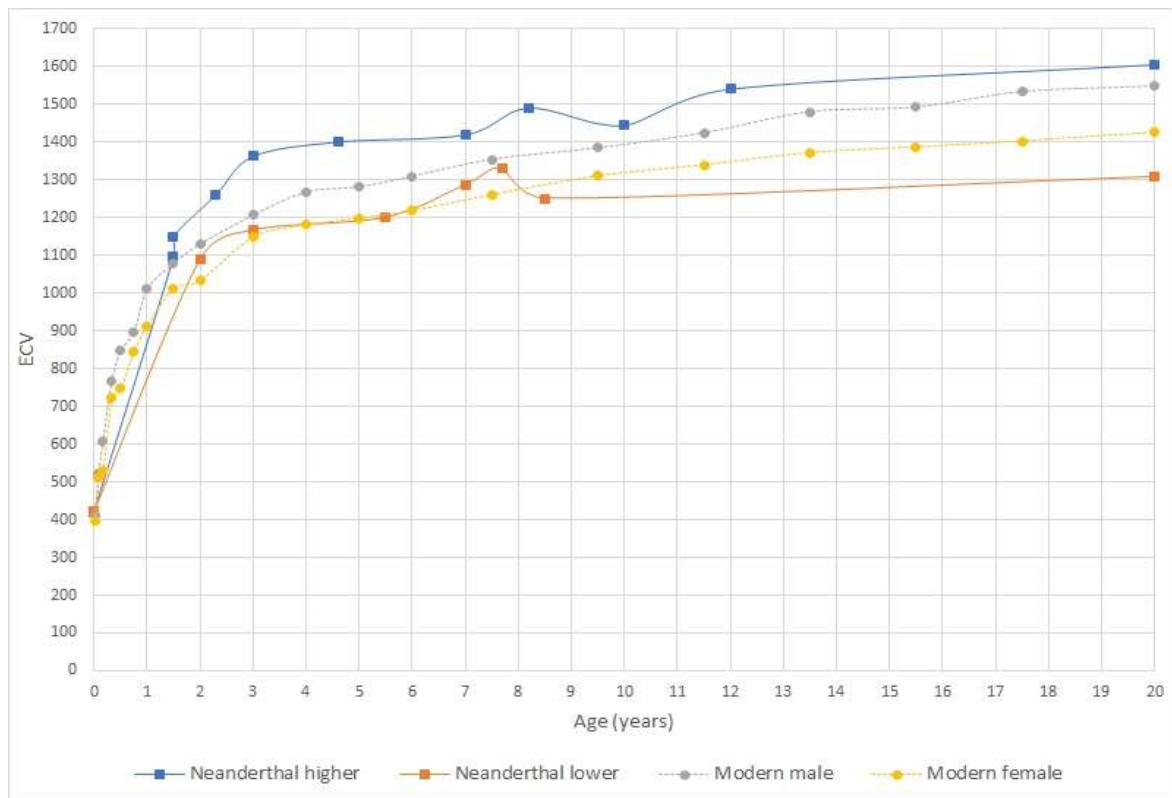


Figure 4.9: Subadult ECV, Neanderthal higher and lower with modern human data from Dekaban (1977)

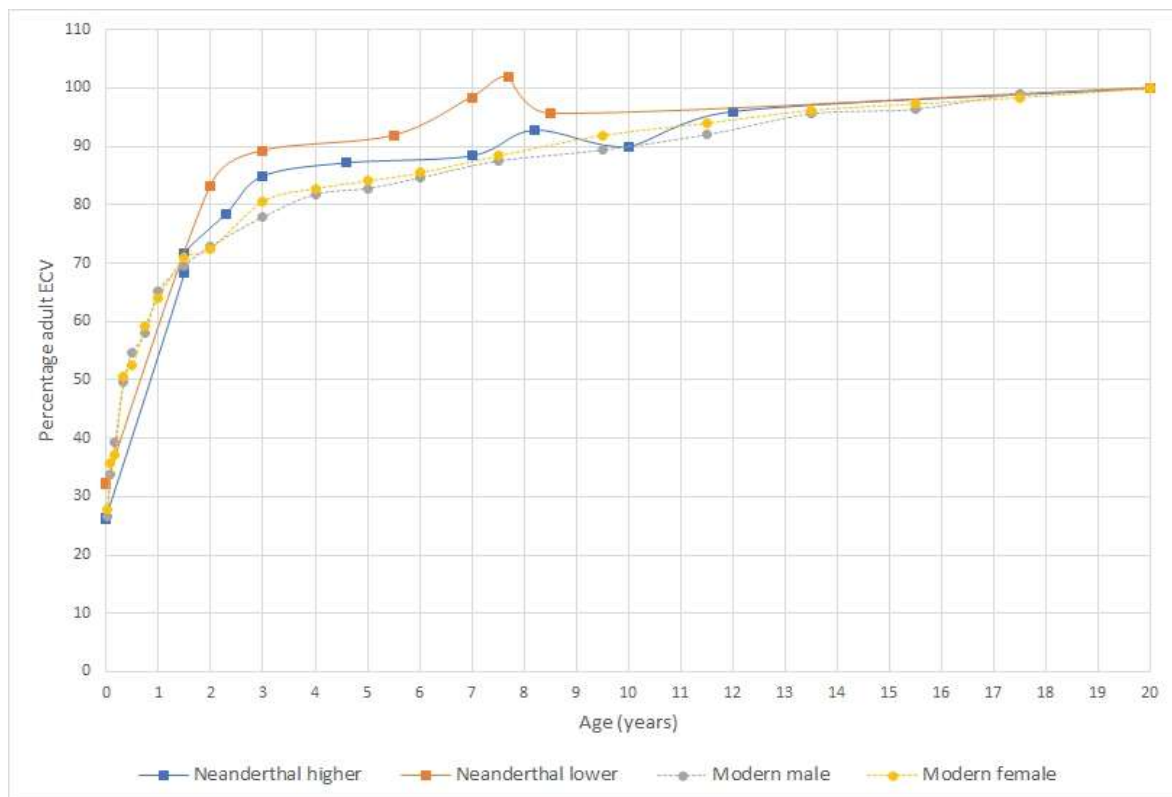


Figure 4.10: Percentage of adult ECV attained, Neanderthals with modern human data from Dekaban (1977)

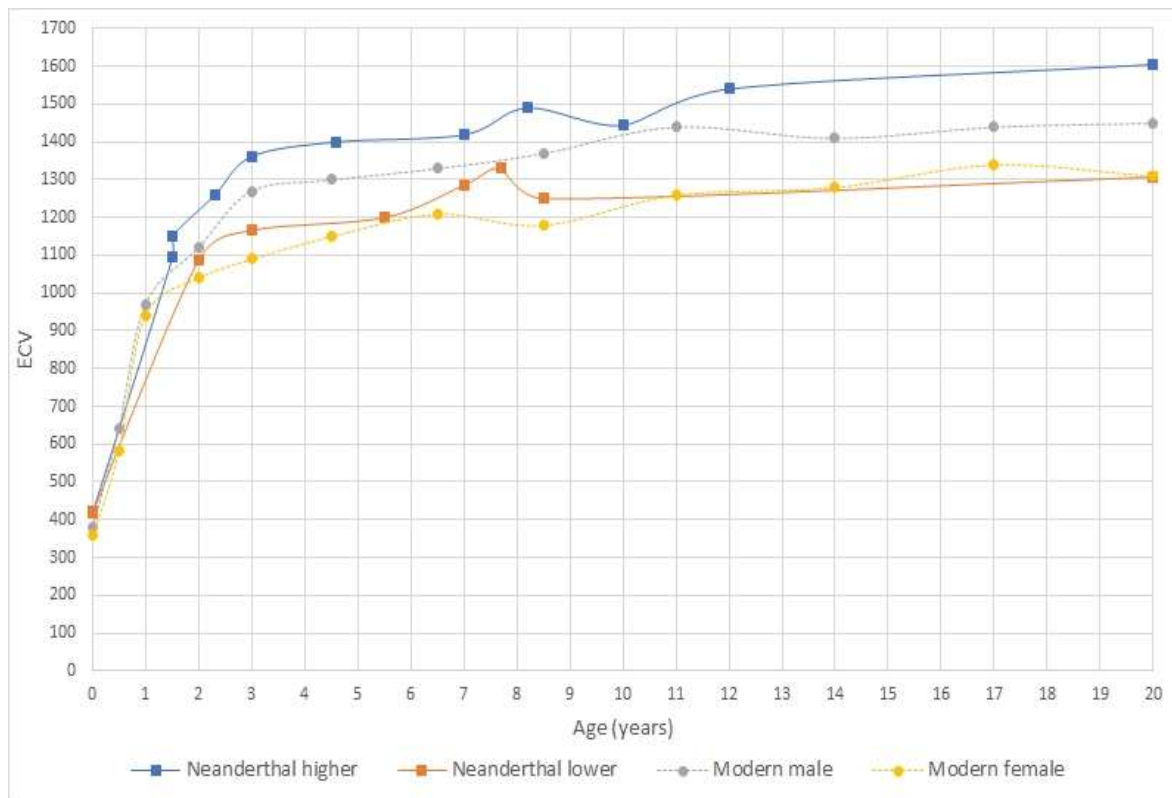


Figure 4.11: Subadult Neanderthal ECV with modern human brain weight from Dekaban and Sadowsky 1978

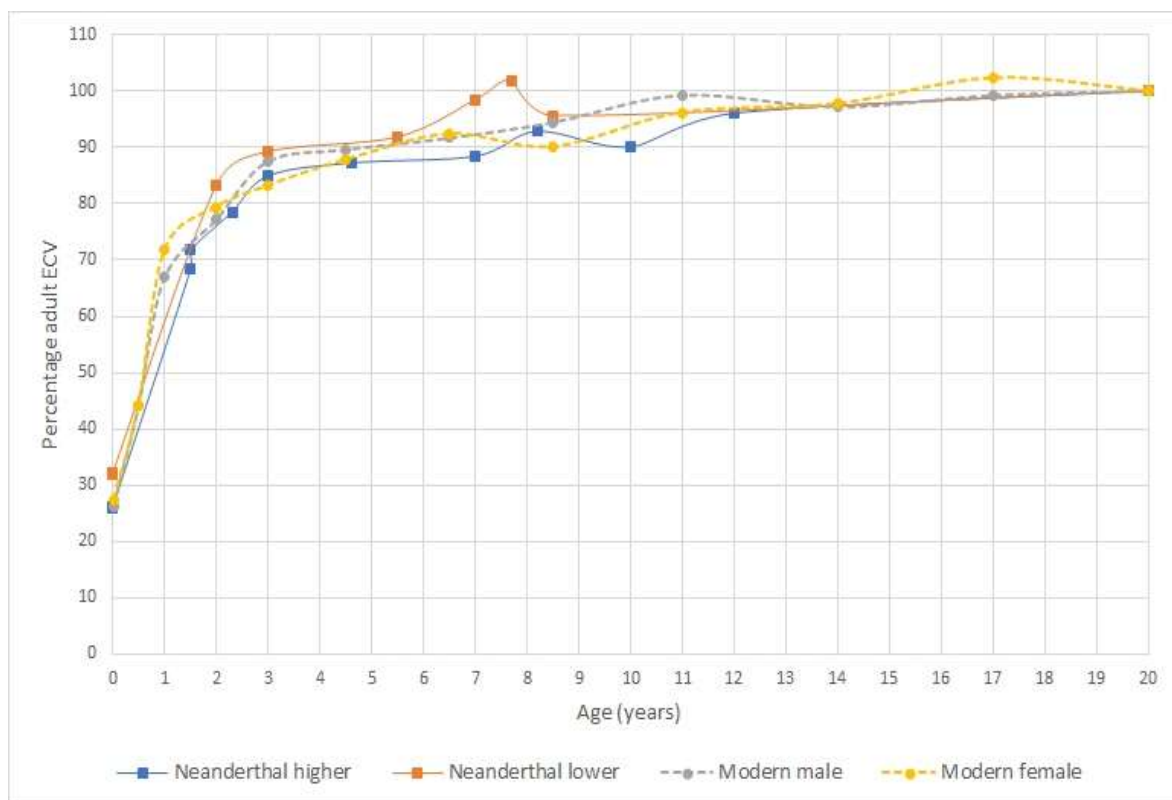


Figure 4.12: Percentage of adult size attained, Neanderthal ECV with modern human brain weight from Dekaban and Sadowsky 1978

In both absolute and percentage terms, up to 1.5–2 years the Neanderthal infants are comparable with or slightly ahead of the modern humans, but from that age onward the higher-ECV group exceed the rest in absolute terms and the lower-ECV group exceed the rest in percentage growth. The dearth of younger infants with well preserved neurocrania resulting in absence of Neanderthal data points below ~1.5 years leaves it ambiguous whether their brains grew faster than modern humans from birth through that period of early infancy. However, for the higher-ECV group there is indication of continued growth after the first 1.5–2 years exceeding the rate of the modern humans.

Here ECVs from Table E.1 and chronological ages from Appendix A are used. If anything, the revised usually younger ages should make Neanderthal growth appear even more rapid. The mean of all Neanderthal adult ECVs used for the present survey is 1384.8 cm³ (Table E.2).

Table 4.9 lists the immatures and percentage of mean adult ECV attained by each. Some of the immature ECVs exceed 100% of an adult mean, as also occurs in the analysis of Coqueugniot and Hublin (2007). It is unknown what adult ECV would have been attained by any of the immatures had they lived. The variation of ECV at similar ages indicates that some may have been on course toward markedly lower or higher adult ECVs. Coqueugniot and Hublin (2007) reject the hypothesis of sexual dimorphism among the subadult ECVs, citing Tillier (1999:164,169,173), who, referring to the Qafzeh and Skhul hominins, especially subadults, cautions that sex attribution is problematic.

Table 4.9: Immature Neanderthal ECV as percentage of adult means

Specimen	Age (y)	ECV (cm ³)	% Male adult mean	% Female adult mean	% All adult mean
Le Moustier 2	0	418	28.0	34.0	30.2
Mezmaiskaya 1	0	422	28.3	34.3	30.5
Pech de l'Azé	1.5	1150	77.1	93.5	83.0
Dederiyeh 1	1.5	1096	73.4	89.1	79.1
Dederiyeh 2	2	1089	73.0	88.6	78.6
Roc de Marsal	2.25	1260	84.4	102.5	91.0
Subalyuk 2	3	1187	79.5	96.5	85.7
Engis 2	3	1362	91.3	110.8	98.4
Gibraltar 2	4.6	1400	93.8	113.9	101.1
La Quina H18	5.5	1200	80.4	97.6	86.7
Krapina A	7	1419	95.1	115.4	102.5
Krapina B	7	1286	86.2	104.6	92.9
El Sidrón J1	7.7	1330	89.1	108.2	96.0
Teshik-Tash	8	1490	99.9	121.2	107.6
Le Lazaret	8.5	1250	83.8	101.7	90.3
La Ferrassie 3	10	1444	96.8	117.4	104.3
Le Moustier 1	12	1540	103.2	125.2	111.2
Adult mean			1492.2	1229.6	1384.8
Ages from Appendix A. ECV data from Tables E.1–E.4.					

However, an exploration may be informative. Figure 4.4 shows a cluster of high adult ECVs toward the end of the Neanderthal period, while there were contemporary adult specimens with lower ECVs. As the high ECVs appear late and most of the available immatures are also late, in the following analysis adult specimens earlier than 100 ka are omitted. Then means of the lower-ECV adults and higher-ECV adults respectively are 1307.0 and 1604.9 cm³ (Tables E.6 and E.7).

Percentages of adult value attained by individuals of the two subadult series are shown in Table 4.10. Each series begins with the same two neonates, although both neonates fit more naturally in the higher-ECV series. Values for recent human immature ECV and percentage adult ECV at comparable ages to the Neanderthal immatures are attached to the table for comparison. These come from Dekaban (1977) and are selected rows from Table 4.3. Compare also Figures 4.9–4.12.

The attainment for age resembles that of modern humans. For example, the youngest specimens other than neonates, which are Dederiyeh 1 and Pech de l’Azé at ~1.5 years, have attained 68.3% and 71.7% of high-ECV adult mean volume. In Dekaban’s (1977) series the expectation for males is 69.6%. Not in the first year and a half but from 2 years upward some of the Neanderthal infants seem to forge ahead. This observation raises the possibility that, after the initial fetal-like rapid growth in the first year known for recent humans and evidently shared by Neanderthals, some of the latter may have experienced for some duration a continued elevated rate of growth, not fetal-like but higher than expected in modern humans.

On the basis of Table 4.9, Le Moustier 1 at 12 years is on the verge of adult ECV. However, there are several Neanderthal adult males with larger ECVs than this individual. Some of the higher-ECV immatures may have had the potential to reach 1600 cm³, as Weidenreich (1945:155) anticipated for Teshik-Tash.

It could be argued that some immature individuals belong in the opposite series: e.g. El Sidrón J1 could be higher-ECV. The genetically enabled potential adult ECV for each Neanderthal subject is plainly unknown. That consideration of course applies to all immature hominin specimens from archaeological and medical collections. At any age among Neanderthals, Middle and Upper Palaeolithic *Homo sapiens*, and the rest, there would have been a spread of ECVs, but for most ages the hypodigm offers only single random data points. Only more specimens with accurately determined ages at death and accurate ECVs will refine the trajectory or trajectories involved.

Comparison with Upper Palaeolithic immatures

Minugh-Purvis (1988:263–264) observes that neurocranial dimensions of the Upper Palaeolithic *Homo sapiens* infant Předmost 6, at 2–2.5 years, are larger than those of Gibraltar 2 and all the other Upper and Middle Palaeolithic infants and early children of either species, and therefore, by the logic applied to Gibraltar 2, could be used to argue that Palaeolithic *Homo sapiens* experienced rapid brain maturation. Předmost 22 is also large, but dimensions of the Předmost 6 infant are only comparable with Neanderthal or *Homo sapiens* immatures at least twice its age (Table 4.11, Figures 4.13 and 4.14).

Tillier (1995:66) shows that Upper Palaeolithic immatures exceed recent humans in maximum frontal breadth and maximum cranial breadth to no less a degree than Neanderthals.¹ Coqueugniot (1994:248) and Tillier (1999:169) calculated endocranial volumes of recent human and Palaeolithic immatures using the same equations. Neanderthals were Pech de l’Azé, Engis 2, La Quina H18 and Teshik-Tash. Tillier adds Roc de Marsal. In a comparison by age classes, only Teshik-Tash and possibly Sungir 3 exceeded modern range at 2 standard deviations. Those immatures which have had ages revised since those studies still fit in range.

¹ Neurocranial dimensions are also discussed in §6.4.

Table 4.10: Higher and lower subadult ECV as percentage of Neanderthal adult means, and comparison with modern humans at similar ages

Neanderthal subadults higher ECVs with adult mean higher ECV				Neanderthal subadults lower ECVs with adult mean lower ECV				Modern human, comparable ages				
Specimen	Age (y)	ECV (cm ³)	% adult	Specimen	Age (y)	ECV (cm ³)	% adult	Age (y)	Male ECV (cm ³)	Male % adult	Female ECV (cm ³)	Female % adult
Le Moustier 2	0	418	26.0	Le Moustier 2	0	418	32.0	(1 week)	410	26.5	398	27.9
Mezmaiskaya 1	0	422	26.3	Mezmaiskaya 1	0	422	32.3					
Dederiyeh 1	1.5	1096	68.3					1.5	1078	69.6	1012	71.0
Pech de l'Azé	1.5	1150	71.7									
Roc de Marsal	2.3	1260	78.5	Dederiyeh 2	2	1089	83.3	2	1129	72.9	1033	72.5
Engis 2	3	1362	84.9	Subalyuk 2	3	1166	89.2	3	1206	77.9	1148	80.6
Gibraltar 2	4.6	1400	87.2	La Quina H18	5.5	1200	91.8	5	1281	92.8	1198	84.1
Krapina 1 (A)	7	1419	88.4	Krapina 2 (B)	7	1286	98.4	7.5	1354	87.5	1260	88.4
Teshik Tash	8.2 ?	1490	92.8	El Sidrón J1	7.7	1330	101.8	9.5	1384	89.4	1310	91.9
La Ferrassie 3	10	1444	90.0	Le Lazaret	8.5	1250	95.6	11.5	1424	92.0	1339	94.0
Le Moustier 1	12	1540	96.0					13.5	1480	95.6	1371	96.2
Adult mean after 100 ka		1604.9	100.0	Adult mean after 100 ka		1307.0	100.0	Adult	1548	100	1425	100
Neanderthal data from Tables E.1, E.2, E.6, E.7. Modern human data from Dekaban (1977) (from Table 4.3).												

Table 4.11: Cranial vault comparison of some European Upper Palaeolithic and Neanderthal immatures

	UP <i>Homo sapiens</i>			Neanderthal										
<i>Dimensions in mm</i>	Maldeč 3	Předmost 6	Předmost 22	La Ferrassie 8	Pech de l'Azé	Roc de Marsal	Subalyuk 2	Engis 2	Gibraltar 2	La Quina H18	Carigüela 2	Krapina 1	Teshik- Tash	Le Moustier 1
Age (y)	2.0–2.5	2.0–2.5	8–9	1.4	1.5	2.3	2.5	3.0	4.6	5.5	6	6–8	8	12
M23 Cranial circumference (over supraorbital)		520	499		482	502 ²	470			510			530	534
M26 Sagittal arc nasion–bregma	115	119	129		(104)	115 ²	115	118	117	103.5	100	111	120	122
M27 Sagittal arc bregma–lambda		138	124			106 ²	118.5	112	110	106			110	124
M28 Sagittal arc lambda–opisthion	100	121	113	92		118 ²	110	110					125	125
M25 Total sagittal arc nasion–opisthion		378	366			339 ²	343.5	340 332 ¹					355 356 ¹	371
Data from Minugh-Purvis (1988) unless otherwise stated. Neanderthal ages from Appendix A. ¹ Tillier (1983:53). ² Madre-Dupouy (1992:74,259).														

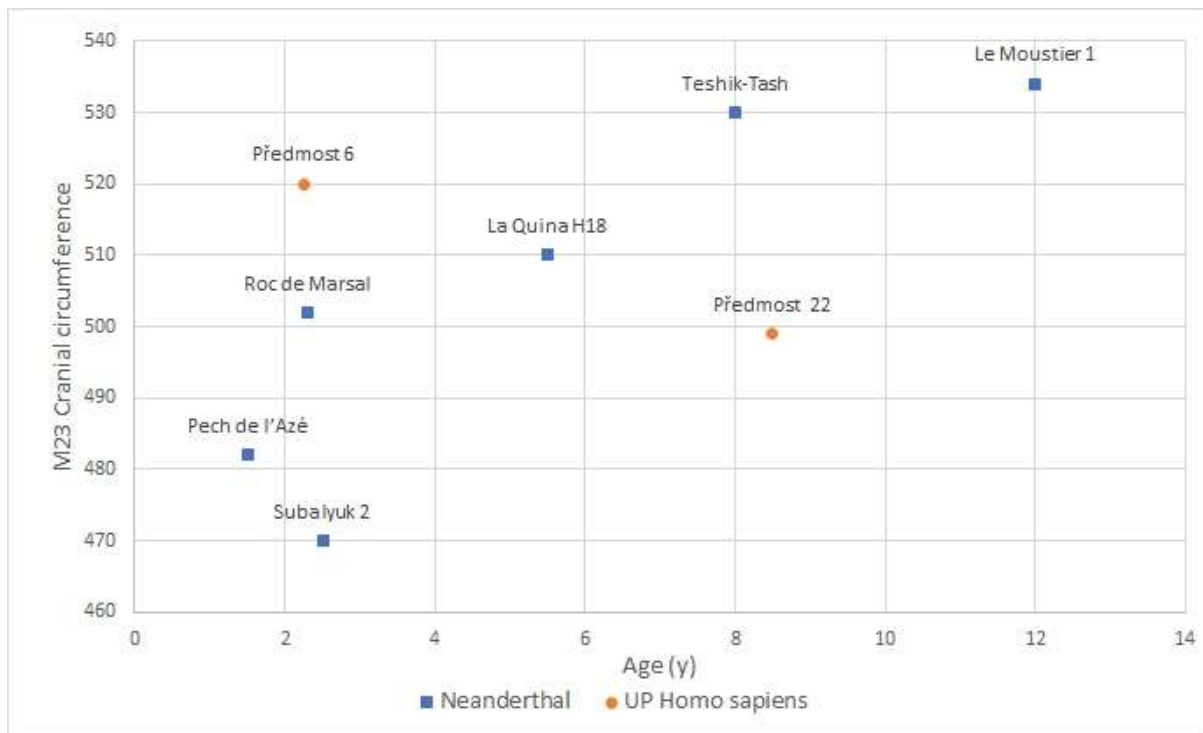


Figure 4.13: Cranial circumference, Předmost (Upper Palaeolithic) and Neanderthal immatures

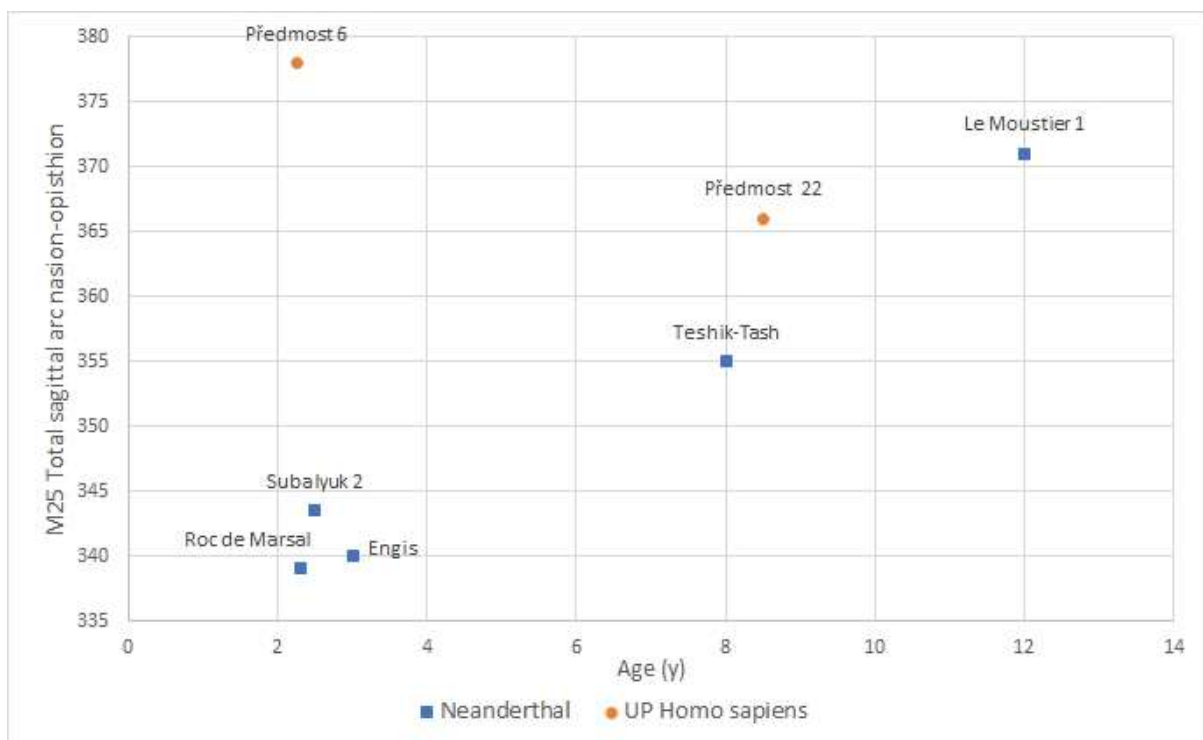


Figure 4.14: Total sagittal arc, Předmost (Upper Palaeolithic) and Neanderthal immatures

Comparison with Middle Palaeolithic *Homo sapiens* and suggestion of autism

Another framework for this topic is provided by Coqueugniot and Hublin (2007). The authors argue that Neanderthal immatures experienced more rapid brain growth than recent humans or Middle Palaeolithic Levantine *Homo sapiens*. The result is obtained by recalculating immature ECVs and examining percentage of adult endocranial volume achieved at given ages. From this result they extrapolate to an implication of rapid life history with relative deficiency in secondary altriciality at birth and earlier attainment of adulthood. They also raise the possibility of social and cognitive impairment, since abnormally fast brain growth in the first postnatal year has been associated with autism (ibid.:380).

Coqueugniot and Hublin (2007) determined percentage adult ECV attained by two Middle Palaeolithic *Homo sapiens* immatures, Skhul 1 at 4–4.5 years and Qafzeh 10 at 6 years, and presented their attainment as lying below percentages attained by Neanderthals, to indicate slower brain growth in Middle Palaeolithic *Homo sapiens* than in Neanderthals.

Skhul 1 and Qafzeh 10 are compared with modern humans in Table 4.12 using data from Tables 4.1–4.3. Both subjects have lower percentages attained than even the recent humans at comparable ages. This is because the Middle Palaeolithic *Homo sapiens* adult ECV used in the 2007 study, 1545 cm³, is the mean of five presumed male crania Skhul 4, 5, 9 and Qafzeh 6 and 9, which have ECVs 1554, 1518, 1590, 1568 and 1531 cm³ respectively. As Skhul 1 and Qafzeh 10 do not have ECVs above the mean ECV or brain weight values for recent human males at comparable ages, and sex attribution is problematic (Tillier 1999), there is no reason to believe that they would have grown to be large males with an ECV as high as 1545 cm³. They may have had that potential. It is just unknown. Choosing a lower adult target ECV, such as the 1300 cm³ of Skhul 2, results in higher percentages attained, more in line with recent human percentages; and a combined male and female Skhul and Qafzeh mean 1422.5 cm³ is also provided for comparison, which fits more closely with recent human values (Table 4.12 and Figure 4.15).¹

The suggestion of autism (Coqueugniot and Hublin 2007:380) is worth consideration. Courchesne et al. (2003) find that high percentages of children diagnosed as autistic experienced rapid increase of head circumference between birth and 2–3 years. However, such children began with a *smaller than average* neonatal head circumference, growing from the 25th percentile to the 84th percentile in 6–14 months (Courchesne et al. 2003). They reached the same neurocranial dimensions as healthy children but ~8 years too early. As brain growth slows during childhood the condition stabilizes, but the affected children have missed the opportunity for much interaction during the formative time of early postnatal brain growth (ibid.:337,340–341).²

¹ In Figure 4.15 the most noticeable feature is the large increase between Skhul 1 at 4.25 years and Qafzeh 10 at 6 years. If we did not recognize that these are two unrelated individuals from different cave deposits, we might infer that brain growth was extremely rapid between the ages of 4 and 6 years in Middle Palaeolithic *Homo sapiens*.

² Autism as interpreted today comprehends a wide variety of symptoms and is thought to have highly diverse aetiology including genetic and environmental factors as well as maternal health and others, as reviewed by Wang et al. (2025).

Table 4.12: Skhul and Qafzeh and recent human subadults, percentage of adult ECV or brain weight

Middle Palaeolithic <i>Homo sapiens</i>						Recent humans, comparable ages												
							Dekaban 1977				Boyd 1962				Dekaban and Sadowsky 1978			
Subadults			Adult ECV Mean of Skhul 4, 5, 9 and Qafzeh 6, 9	Alternative adult ECV Skhul 2	Alternative adult ECV <i>mean of male and female</i>		Male		Female		Male		Female		Male		Female	
Specimen	Age (y)	ECV (cm ³)	% adult	% adult	% adult	Age (y)	ECV (cm ³)	% adult	ECV (cm ³)	% adult	Brain weight (g)	% adult	Brain weight (g)	% adult	Brain weight (g)	% adult	Brain weight (g)	% adult
Skhul 1	4–4.5	1141	73.9	87.8	80.2	4	1267	81.8	1180	82.8								
						4.5					1290	90.2	1156	89.3	1300	89.7	1150	89.1
						5	1281	82.8	1198	84.1								
						5.5					1290	90.2	1206	93.2				
Qafzeh 10	6	1268	82.1	97.5	89.1	6	1309	84.6	1218	85.5								
						6.5					1313	91.8	1225	94.7	1330	91.7	1210	93.8
Adult ECV			1545	1300	1422.5	Adult	1548	100	1425	100	1430	100	1294	100	1450	100	1290	100
Data from Coquegniot and Hublin (2007), Tables 1–3 this chapter, and Table E.9. <i>Mean of male and female</i> = mean(Skhul 2, mean(Skhul 4, Skhul 5, Skhul 9, Qafzeh 6, Qafzeh 9)).																		

On this basis Neanderthal evidence is inconsistent with a diagnosis of autistic tendency. What we see in the higher-ECV series is a neonatal ECV not small but at least as great as the modern human mean, rapid growth in the first two years, in percentage terms not abnormal by recent human standards, and possibly prolonged growth thereafter to reach a high target adult ECV. In the lower-ECV series, less well represented, we appear to see brain size and growth comparable with recent humans.

Identification of high and low ECV series among Neanderthals is intriguing but not all-important. With future discoveries of intermediates, such distinction as there is may become less evident. However, a distinction explains the large spread of adult ECV in the small late Neanderthal sample. It possibly represents sexual dimorphism, which would be consistent with the ~15 kg difference in mean body mass between males and females (Tables H.1–H.4). It also serves here to illustrate that immatures and adults with smaller or larger ECVs can be compared like with like when envisioning target adult ECVs of given immatures.

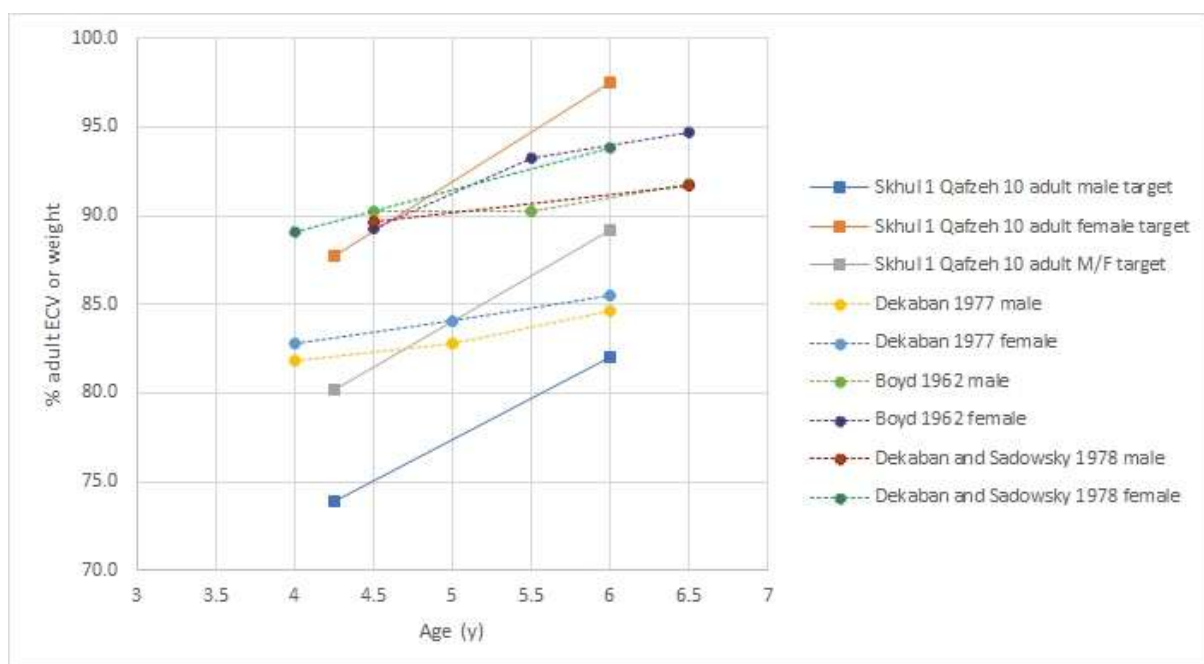


Figure 4.15: Skhul 1 and Qafzeh 10 percentage ECV/brain weight growth using different adult target values, comparison with modern humans at similar ages

4.7 Further considerations on apomorphies

In *Homo sapiens* the length of the cranial vault is reduced and the crown raised in comparison with the parent *H. heidelbergensis* and the sister Neanderthal species, and the cranial base is more flexed. In the compact modern human neurocranium the occipital lobes become tucked under the parietal lobes instead of projecting posteriorly, and increasingly press upon posterior gyri of the temporal lobe. This competition for space may force the temporal lobes to grow laterally and anteriorly. Such a process would result in widening the temporal fossae and, to accommodate the temporal poles, extending them as closely as possible behind the orbit, more anteriorly than in earlier species, as is observed (§F.4).

A distinctive attribute of Neanderthals is the width and transverse roundness of the cranial vault, giving rise to the “en bombe” appearance from behind. Whereas in living *Homo sapiens* the sides of the vault may be almost vertical, with prominence of the superior parietal regions, in Neanderthals the temporals and inferior parietals seem to bulge, and mean maximum cranial breadth is absolutely greater. Was the cortex transversely deeper in Neanderthals, with more white matter tracts in these regions? Were the lateral ventricles larger?

If globularization can be viewed as the result of a large brain combined with a small face (Zollikofer et al. 2017; cf. Pereira-Pedro et al. 2017), two questions arise which have been posed and given different answers by different research groups and cannot be resolved here. (1) Is the cranial base flexed in response to tension generated by the growing and globularizing brain, or is it flexed to accommodate a smaller face? How much of the reconfiguration of the neurocranium in *Homo sapiens* is due to relative expansion of specific lobes, lobules, the cerebellum and other structures in response to selection based on cognitive demands, and how much to craniofacial integration, itself changing under selection based on mechanical and architectural demands? (2) Does the brain contained in a globular neurocranium more effectively perform its functions of managing the organism and enabling the organism to carry out tasks for self-preservation and living in a society, than a brain of comparable volume contained in an elongated platycephalic neurocranium? When in the laboratory a wet human brain is laid on a tray base downward it tends to spread under its own weight, assuming a longer, wider, lower profile. Would it have been less capable of carrying out its functions if it had assumed that extended, quasi-archaic shape in life?

The arguments for (a) improved cognitive function resulting from brain globularization and (b) recruitment of the cerebellum to higher cognitive function would seem to follow conflicting logic. Globularization potentially shortens pathways within the cerebrum. In contrast, the cerebellum is remote from the cerebral cortex, and especially from prefrontal areas, where the highest cognitive functions, including decision-making, are generally agreed to take place (Allen 2009). The cerebellum is attached to the posterior aspect of the brain stem by the cerebellar peduncles, through which bundles of afferent and efferent fibres pass. These communicate via the pons and olive with the forebrain rostrally and with the spinal column caudally. The distance to be travelled by signals between the cerebellum and the prefrontal area is much longer than distances within the cerebrum. From the cerebellum signals have to pass through the thalamus to reach the cerebral cortex, whereas within the neocortex there are direct connections: for example, the temporal lobe is connected to prefrontal areas by the uncinate fasciculus (Vanderah and Gould 2021:65,489,519–520). Brainstem pathways and the cerebellar peduncles would appear *prima facie* to be a potential bottleneck for the transmission of signals. However, presumably a selective advantage must have accrued to those hominins in which some cognitive functions, such as language and thought enabled by linguistic structuring, of which the homologues in earlier hominins were perhaps carried out wholly by the cortex, were outsourced to the cerebellum; or even if from the outset, when these cognitive

functions were new and distinctive, they recruited the fast parallel processing capabilities of the cerebellum.

In most studies, such as the ones cited above, the calculated relative volume of one brain structure to another, or to the whole brain, has been the basis of interpretation. Yet absolute brain volume appears to be the best predictor of cognitive capacity (Deaner et al. 2007; Schoenemann 2010; cf. Hofman 2014). Clearly, if a community of chimpanzees were found in which the proportions of cerebellar and cerebral lobes were exactly the same as living humans, one would not expect those chimpanzees to have the same cognitive abilities as living humans, because all their brain structures would be only approximately one-third of human volume (cf. Schoenemann 2010:37–41). Some calculated Neanderthal cerebellar volumes are absolutely larger than the volumes of some *Homo sapiens* individuals and higher than the recent human mean (Table F.4). This could be interpreted as showing that some Neanderthals should have had at least equal capabilities associated with cerebellar function.

Caution is perhaps advisable in divining the consequences of differences in brain structure between populations, especially when one is represented only by fossils whose endocranial markings may be ambiguous, when samples may be insufficiently representative of variation within a group,¹ and when the effects of diverse and successive analytic techniques may distance results from the physical evidence, as acknowledged and explained by Bruner (2019:1754).

¹ E.g. the almost invariable use of the more complete Skhul 5 instead of the more typical Skhul 4 or 9 to represent this population of *Homo sapiens* from the Levantine Middle Palaeolithic (cf. Corrucini 1992).

4.8 Summary

Endocranial volumes of Neanderthals were similar to those of *Homo sapiens* contemporary with them. Both populations exceeded the ECVs of their ancestral groups within *Homo heidelbergensis s.l.* To have developed such large brains at comparably high metabolic cost, it is reasonable to assume that Neanderthals needed and made use of the cognitive processing power so provided to carry out the activities of their lives. The largest adult endocranial volumes appeared late, after ~100 ka.

Between ~150 ka and 60 ka, *Homo sapiens* neurocrania became more rounded, and this effect was produced by a globularization phase occurring before the end of the first postnatal year. Neanderthal infants did not develop this phase, and throughout life their neurocrania remained long, wide and low. The configuration of Neanderthal brains was therefore not identical with that of recent *Homo sapiens* or even those *Homo sapiens* contemporary with late Neanderthals. Faster processing enabled by a more globular brain may have been a factor giving *Homo sapiens* a cognitive advantage, although it is not clear in what way.

Although the spatial relation of brain lobes and the squamae of the cranial vault may have differed between species, it appears that in *Homo sapiens* temporal and parietal lobes are relatively larger, so that in Neanderthals frontal and especially occipital lobes must be relatively larger. In absolute sizes, ranges overlap. As the frontal lobe is regarded as the focus of executive function, it is not clear whether differences in behaviour would have resulted from smaller or larger relative size, but volume and composition of afferents to the frontal lobe from differently sized temporal and parietal structures would presumably have affected frontal-lobe processing. The larger occipital lobes in Neanderthals (§F.5) may have subserved more precise vision combined with greater sensitivity in low lighting situations, emphasizing visual sense and perhaps graphic memory, sense of place, and visualization abilities. Their sense of smell, as indicated by the smaller cribriform plate (§F.2) and presumably smaller olfactory bulbs, may have been less acute than ours. Most of the brain volume of course lies beneath the lobar surfaces, and it is not possible with any confidence to determine from fossil endocrania the configuration of subsurface or deep brain structures, such as the limbic system, concerned with emotion and the assignment of significance and value to experience.

Apart from globularization, Neanderthal subadult brain growth followed a trajectory similar to that of recent *Homo sapiens*, with very rapid growth in the first year, continuing at pace until the juvenile stage of life and thereafter with much slower enlargement into the second postnatal decade. Some key individuals have endocranial volumes in the higher end of modern human ranges for their age: the two neonates Mezmaiskaya 1 and Le Moustier 2, one of the early children Gibraltar 2, one of the juveniles Teshik-Tash, and the single early adolescent Le Moustier 1. So much growth of brain tissue would demand high levels of nutrition (§2.5–§2.7). Prioritization of brain growth over the rest of the body may account for the small stature of the Neanderthal juveniles and adolescent.

Arguments have been made that the brains of Neanderthal immatures grew more quickly than those of modern humans. Some of these arguments have been discussed in this chapter and are found unconvincing. One by Dean et al. (1986) depends upon an early age at death of 3.1 years for Gibraltar 2, which has a high endocranial volume for a child of that age. Later research delivered a 50% older age at death of 4.6 years from more precise counts of dental microstructure (T.M. Smith et al. 2010), rendering the high endocranial volume less remarkable. Another argument, by Coqueugniot and Hublin (2007), depends upon percentages of adult ECV attained by immatures of the Skhul/Qafzeh early *Homo sapiens* population alleged to be less than percentages attained by Neanderthal immatures. The choice of the mean of five large males as Skhul/Qafzeh adult ECV biases the result. Also, some Upper Palaeolithic

Homo sapiens infants have large external neurocranial dimensions only equalled by much older Neanderthal immatures, which could be construed as evidence for more rapid brain growth in the Upper Palaeolithic.

There are many uncertainties about attribution of cognitive functions to specific areas of the brain and caution is warranted in drawing conclusions about cognitive differences between *Homo sapiens* and Neanderthals. That there were differences seems certain but their exact nature, magnitude and consequences await elucidation.

CHAPTER 5

DEVELOPMENT: INFANT, CHILD, JUVENILE, ADOLESCENT STAGES

5.1 Introduction

Here characteristics of Neanderthals at each stage of postnatal life up to and including adolescence are summarized. Observations are made about some of the more complete and informative specimens including those most referenced in the thesis. Pathological and developmental features and problems with certain reconstructions are highlighted.

Specimens are assigned to stages of the Schultz-Bogin schema (§2.3.1) using assessed chronological age. Some ages may be different, usually younger, than previously reported.

Assigned purely by age, none of the immature individuals up to and including the oldest stand out by size or state of development as being assigned inappropriately. This means that up to puberty at 11–12 years the stages for ages correspond to those of modern humans. The adolescent stage is problematic, mainly because only one reasonably complete skeleton exists. Further research on the more fragmentary crania and postcrania assigned as adolescent may help to illuminate this stage of development.

Drawings of crania of some of the immatures, along with adults, are in Appendix J. They are marked here with *.*.

5.2 Infant stage

Infants (from neonates to 3.0 years) are listed by age in Table 5.1.

Table 5.1: Infants

<i>Specimen</i>	<i>Age (years)</i>
Sesselfels 1	0
Le Moustier 2	0
Mezmaiskaya 1	0–0.1
La Ferrassie 4bis	0–0.2
Hortus I	0–0.5
Kiik-Koba 2	0.5
Kebara KMH 1	0.7
Shanidar 7	0.75
Amud 7	0.8
Shanidar 9	1
Krapina Skull G	0.5–1.5
La Ferrassie 8	1.37
Pech de l'Azé	1.5
Spy 6	1.5
Dederiyeh 1	1.5
Dederiyeh 2	2
Krapina Skull F	2
Mezmaiskaya 2	1–2
Shanidar 10	1–2
Krapina Temporal 4	1–2.5
Palomas 49	1.5–2.5
Roc de Marsal	2.25
Lozoya	2.5
Palomas 88	2–3
Archi	2.4–3.5
Barakai	3
Combe Grenal 31	2–4
Petit-Puymoyen 5	2–4
Ages from Appendix A.	

Modern human newborns have elongated neurocrania relative to modern human adults. Neanderthal neonatal neurocrania, represented by Le Moustier 2 and Mezmaiskaya 1, are more elongated than those of modern humans (Gunz 2010:R921). For both these neonates endocranial capacity is above 400 cm³, at the high end of expectation among modern humans (§4.3).

Within the first year and a half of postnatal life, the brain and cranial vault of modern human babies undergo a globularization phase, leading to a rounder, higher neurocranium (but see Ponce de León et al. 2016). This phase is absent from archaic *Homo* such as Neanderthals and *Homo heidelbergensis* and from the earliest *Homo sapiens* (those before ~150ka). Instead, Neanderthals underwent a general expansion of the cerebrum to modern-human volume while retaining the elongated shape throughout life (§4.5.1).

The infant neurocranium already exhibits distinctive Neanderthal apomorphies: the “en bombe” transverse oval shape as viewed posteriorly, the suprainiac fossa and incipient bilateral occipital (nuchal) torus (Tillier 2000:112; Dodo et al. 2003:101–107; Ishida and Kondo 2003:274). Rak et al. (1996) add the elongated foramen magnum as an apomorphy, conspicuous in Amud 7, while Tillier (2000:112–114) argues that its presence in immatures is an infantile feature found among recent humans and is not perpetuated in adult Neanderthals such as La Ferrassie 1.

The frontal squama, as seen in Pech de l’Azé, Dederiyeh 2 and Roc de Marsal, already differs from modern humans (Bulygina 2007:195). It is bulbous as in modern humans (Tillier 1991), but superolaterally lacks the prominent frontal bosses or eminences of modern foreheads, instead having an even curvature. However, the squama remains roundly vertical and not receding. On the lower region of the infant forehead, up to Roc de Marsal at 2.3 years, there is no clear sign foreshadowing the adult browridge (Tillier 1986:211, 1991) (§6.5.2). The most striking features of the neonates and infants are the high, round orbits.

The nasomaxillary region of the Neanderthal neonatal face is distinctively larger and more projecting (Gunz et al. 2012:303). According to Schuh et al. (2025:1,6,14), Neanderthal midfacial projection is already present at birth, but becomes fully accentuated during infancy and continues expansion into adolescence (cf. Krovitz 2003:334).

The mandible is retracted and small in the Dederiyeh infants and Pech de l’Azé (Ishida and Kondo 2001, 2004; Cuzzo 2005). Morphologically, infant and early child mandibles such as Archi 1, Barakai, Châteauneuf 1, Pech de l’Azé and Roc de Marsal resemble each other closely (Mallegni and Trinkaus 1997).

The wide and anteroposteriorly deep ribcage, in the adult indicating copious lung capacity (Churchill 2006; Weinstein 2008) or digestive capacity (Ben-Dor et al. 2016) or both, is seen in the neonates Le Moustier 2 and Mezmaiskaya (Weaver et al. 2016:6472) and infants Dederiyeh 1 and Roc de Marsal (García-Martínez et al. 2020). Notably, while the thorax is anteroposteriorly larger than the mean of modern humans, its width is less in the neonates and comparable in the infants (García-Martínez et al. 2020:3).

The characteristic mediolaterally elongated pubic bone (§B.3) is evident from birth (Tillier 2003; Weaver et al. 2016:6472). Bowed long bones, indicative of strong musculature, are evident in the neonates (Weaver et al. 2016:6474) and in the Dederiyeh infants (Kondo and Ishida 2001, 2003).

Dederiyeh 1 (1.5 years) **

Dental stage is said to be earlier than in Pech de l’Azé (Akazawa et al. 1999:139). If this is the case, Dederiyeh 1 should be under 2 years old.

Fukase et al. (2015) argue that the mandible of Dederiyeh 1 has elements of the modern chin, including an incipient mental trigone. In the slightly older Dederiyeh 2, the deciduous incisor roots are thicker and the crypts of the permanent incisors are larger, distending the surface of the anterior corpus: this is said to preclude potential chin features appearing at the symphysis. A critique of alleged incipient chin features in non-sapiens fossils, not specifically concerning Dederiyeh, is given by Tattersall and Schwartz (2008) and Schwartz (2016:67–69), who argue that the true chin is a *Homo sapiens* autapomorphy.

Dederiyeh 2 (2 years)

Although this individual is dentally slightly older than Dederiyeh 1, it is smaller in all respects, including endocranial volume and stature, evidencing a degree of individual variation in Neanderthal infants (Ishida and Kondo 2001; Kondo and Ishida 2001, 2003; Ishida et al. 2004).

Kiik-Koba 2 (6 months)

The long bones of this infant already show the short distal segments of upper and lower limbs characteristic of Neanderthals (Trinkaus 2016).

Pech de l'Azé (1.5 years) **

Patte (1957) reconstructed the cranium. He stated that the skull was distorted by post-mortem deformation, and that when the dentition was placed in occlusion the mandibular condyles did not articulate with the cranium. Clearly this could not have been the condition in life. While the temporal squamae are present on both sides, the zygomatic arches and the ethmoid and sphenoid are missing, so that the maxillae are connected to the neurocranium only via the orbital margins. From Patte's photographs of the reconstruction, it appears that the maxilla is positioned too far anteriorly, with the posterior edge of the palate positioned too far inferiorly. Thus the occlusal plane becomes angled horizontally instead of rising posteriorly, as would be necessary to allow the vertically short mandibular rami to reach the temporomandibular joint (Figure J.2). The case of Roc de Marsal is similar.

Ivanhoe (1970; 1983) claims that many Neanderthal specimens, in particular all the immatures that he examined, show signs of severe rickets. This includes Pech de l'Azé, of which he also states that the dentition is grossly maloccluded, without explaining what form the alleged malocclusion takes. It is presumably related to the prognathic positioning of the maxilla, which, if the condyles were articulated in the glenoid fossae, would prevent the mandibular and maxillary dentition from meeting at all, let alone correctly. It is not clear whether Ivanhoe examined the remains as reconstructed by Patte, which would have had the defects which he lists, or, less probably, the 1962 version by Vlček. Ivanhoe's general contentions regarding rickets in Neanderthals are disputed and dismissed by Trinkaus (1983).

The effect of a reconstruction which arguably places the maxilla and mandible too far anteroinferiorly is to create a more prognathic, less modern, less child-like profile. Given the limited preservation of the facial skeleton of this specimen, it would seem necessary to take guidance in locating the maxillary elements from the position assumed by the mandible when each condyle rests in the corresponding glenoid fossa (cf. Tillier 1984:9).

Vlček made a completely new reconstruction in 1962 (Stewart 1972). According to Vlček (1970), Patte's earlier reconstruction was distorted by post-mortem deformation and poor preservation of the facial skeleton. His photographs show a neurocranium not superficially different from Patte's version, but in the 1962 reconstruction the maxilla is angled superoposteriorly instead of being pulled anteriorly perpendicular to the plane of the orbital apertures. This more natural rearrangement is evidently what enables Vlček to show the mandible in articulation with the basicranium in his drawing of the cranium in *norma lateralis*. The drawing shows the dentition in normal occlusion, i.e. with a moderate and modern-looking maxillary overjet. However, none of his photographs illustrate the mandible in position.

It is not stated by either Patte (1957) or Vlček (1970) what the effect of the post-depositional deformation was, e.g. skewing, or what caused it, e.g. compression on one side.

In later photographs of the calvaria as reconstructed by Vlček it presents a symmetrical, natural-looking conformation.

Cuozzo (2005:113–115) described and photographed the Pech de l’Azé infant, having positioned the mandible with condyles in the glenoid fossae, which enables the upper and lower dentition to assume normal occlusion and the whole skull to assume a natural configuration (Figure J.3). As the neurocranium and facial parts are assembled in one piece, the reconstruction examined by Cuozzo in the late 1970s appears to be the one by Vlček. Cuozzo comments on the smallness of the mandible for its age, taken at the time to be 2–2.5 years.

The area of bregma is wide open, forming an anterior fontanelle, and the metopic suture is patent (Vlček 1970). The bregmatic lacuna is discussed by Trinkaus (2018 SI:15–16). While there has been post-mortem loss of bone (cf. Trinkaus 1970), he states that the bregmatic fontanelle was not much reduced from its maximum dimensions. Trinkaus (2018) cites ages at death from a number of sources using dental developmental criteria, and offers a modal age of 2.5 years. He does not mention the estimate of 1.51 years from a recent study (Shackelford et al. 2015). The patent metopic suture is not itself anomalous for an age of 1.5 or 2.5 years. Pindrik et al. (2016) report closure of the metopic suture by age 9 months in 100% of a large sample of normal modern children, but instances of delayed closure are not uncommon in recent humans and Middle and Upper Palaeolithic infants older than Pech de l’Azé (Trinkaus 2018, SI:15). While the bregmatic fontanelle may represent ontogenetic delay (Trinkaus 2018 SI:16), it would appear less anomalous the younger the specimen’s age.

The mastoid processes differ in superoinferior dimension (Vlček 1970). Trinkaus (2018, SI:16) also describes the asymmetry of the mastoid processes. Typically smaller in Neanderthals than in modern humans, in Pech de l’Azé the heights of the processes are 10.5 mm (right) and 14.5 mm (left), a degree of asymmetry which, he emphasizes, is exceptional for recent and Palaeolithic populations.

Roc de Marsal (2.25 years) **

Madre-Dupouy (1992:85) observes that when the maxillary and mandibular teeth are in occlusion there is a gap of 13 mm between the condyle of the right mandible and the temporomandibular fossa. Clearly this could not be the condition in life and must be due to either injury (of which no evidence has been presented), post-depositional distortion, or a faulty reconstruction. In the photograph (1992:86), the mandibular and maxillary dentitions are in occlusion and the gap is largely horizontal.

It seems highly probable that the maxilla was reconstructed¹ too far forward, and therefore to place the dentition in occlusion the mandible had to be positioned so far anteriorly that articulation at the glenoid fossa was impossible. If so, the case is similar to Pech de l’Azé. In such cases where the reconstruction gives rise to impossible articulations, little confidence can be placed in conclusions drawn from quantitative analyses of measurements. Lengths such as basion–prosthion and any other measurements connecting points on the maxilla or mandible to points on the neurocranium would be erroneous. In both cases a presumption of exaggerated prognathism appears to have guided the reconstruction.

Bayle et al. (2008, 2009) describe the dentition. In comparison with modern humans, there is a larger volume of pulp and dentine in proportion to enamel. The anterior permanent teeth took longer to form whereas development of the postcanine teeth was advanced: this is the opposite conclusion to that of Faerman et al. (1994:414) regarding Barakai.

¹ Not by Madre-Dupouy.

5.3 Early childhood stage

Early children (from 3.0 to 7.0 years) are listed by age in Table 5.2.

Table 5.2: Early childhood specimens

<i>Specimen</i>	<i>Age (years)</i>
Engis 2	≥3
Subalyuk 2	3–4
Châteauneuf 1	3–4
Palomas 7	3.5–4.5
Moula-Guercy 4	3–5
Krapina Temporal 3	3.5–5.5
Montmaurin Coupe-Gorge 3	3.9–5
La Chaise S15/16	3–6
La Ferrassie 6	3–7
Palomas 7	3.5–4.5
Gibraltar 2	4.6
Cova Negra	5–8
Châteauneuf 2	5–6
La Chaise 13	5–6
La Chaise 14	5–6
Krapina Mandible A	5–6
Krapina Maxilla B	5.9
Carigüela	6
Krapina Maxilla A	6–7
La Quina H18	5–8
Combe Grenal I	4.5–9
Ages from Appendix A.	

Carigüela (6 years)

Jiménez-Arenas et al. (2019) made a virtual reconstruction of the partial cranium, obtaining a virtual endocast. There is a wide nasal bridge by modern human standards, as expected in Neanderthals. Bregma is missing and the coronal suture is present only at lower, i.e. lateral, extremities. The frontal lobes would have been longer and wider but lower than in a modern human child of this age; the frontal areas are said to be not “reduced” compared with modern children.

La Chaise (Suard) 15 and 16, aka S15 and S16 (3–6 years)

Coqueugniot et al. (1996) note a “hypertension intracrânienne” possibly due to hydrocephalus. Intracranial markings of blood vessels are well defined. Frontal sinuses are minimally extended, so the individual has been aged under 6 years.

Engis 2 (3 years) **

Fraipont (1936:33), in a table, lists cranial length (glabella–opisthocranium) as 188 mm. Measuring from his declared half-size Figure 12 (1936:30), the maximum breadth 65 mm can be doubled to give 130 mm. In the table the maximum breadth is listed as 131 mm. Similarly from Figure 12 the half-size cranial length 86 mm can be doubled to give 172 mm. From the half-size 89 mm in Figure 16 (ibid.:32) the length should be 178 mm. Tillier (1983a:53) gives 176 mm, as does Minugh-Purvis (1988:204). Thompson and Illerhaus (2005:229) measured 171 mm. Cuzzo (2005:107) measured 164 mm. At the time of writing I am not aware of a new reconstruction having been made between the times when Tillier and Cuzzo (in the late 1970s) examined the cranium. Fraipont's exaggerated length appears only in the table and 188 is conceivably a misprint, perhaps for 178.¹

Engis 2 exhibits the expanded maxillary sinuses and the medially oriented excrescence into the nasal cavity observed in some Neanderthal adults (Schwartz and Tattersall 1996).

La Ferrassie 6

Distal limb shortening, an immature trait as well as a trait of cold-adapted populations, is present (Tillier 2000:115–116).

Gibraltar 2 (4.6 years) **

The partial calvaria is large and wide, but the vault bones are extremely thin. The occipital and entire cranial base are missing. There are two upper and two lower deciduous molars, which are taurodont. The unerupted anterior mandibular dentition is said to exhibit some anomalies (Buxton 1928:61,80–82). B.H. Smith (1989a:83,91) notes that Gibraltar 2 resembles modern humans in having no permanent teeth erupted in line with its age, then assumed to be ~4 years (Buxton had aged it at ~5 years), and the canine is advanced relative to the first molar, as in modern humans and unlike australopithecines and early *Homo*.

Palomas 7 (3.5–4.5 years)

The Palomas 7 mandible exhibits a rounded flange of bone on the external basilar margin, a feature unknown in Middle or Upper Palaeolithic hominins except at this site (Trinkaus 2018:15). In Palomas 7 it may represent the early stage of a development seen in more pronounced form in the adult mandibles Palomas 6 and 23. Particularly in Palomas 23 this strip of bone gives the appearance of having ossified separately and then fused to the corpus (Walker et al. 2010:264; Trinkaus 2018 SI:14).

Subalyuk 2 (3–4 years)

Thoma (1963) describes supraorbital relief more marked than on a modern child, metopic suture clearly visible as in some other Neanderthal infants, and deciduous molars moderately taurodont. Pap et al. (1996) describe the remains and note an unusual depression behind bregma attributed to ante-mortem deformation.

¹ There are other misprints in Fraipont (1936). On page 51, point 2 refers to “Le crâne n° 1” as Cro-Magnon, and then point 3 states that “Le crâne n° 1” (again) is incontestably Neanderthal. Point 3 should read “Le crane n° 2”. This is additional to typographical errors such as “linge” for “ligne” (ibid.:35).

5.4 Juvenile stage

Juveniles (from 7.0 to 11.0 years) are listed by age in Table 5.3.

Table 5.3: Juveniles

<i>Specimen</i>	<i>Age (years)</i>
Palomas 97	Juvenile or child
Krapina Frontal 3 aka 24	Juvenile or child
Krapina Skull A aka 1	6–8
Obi-Rakhmat 1	6–8.1
El Sidrón J1	7.7 (7.61–7.78)
Scladina (Sclayn)	8
Teshik-Tash	8.2 (7.5–10)
Hortus II/III	6.48–8.17
Le Lazaret	8–9
Krapina Mandible B	8–9.5
Fate 2	8–10
Okladnikov 2	8–10
Šipka	9–10
Marillac 25	9–10
Macassargues radius	10
Ehringsdorf G	10–12
Krapina Maxilla C	10–12
Krapina Skull B	Juvenile
La Ferrassie 3	10–12
Moula-Guercy 3	10–12
Krapina Mandible C	11
Malarnaud	11
Palomas 80	11–12
Ages from Appendix A.	

Ehringsdorf 7 aka G (10–12 years)

This mandible has marked alveolar prognathism, unusual for Neanderthals (Wolpoff 1980a:272).

Fate 2 (8–10 years)

While the retreating frontal profile would indicate progressive maturation leading to development of a supraorbital torus, the cranial and mandibular elements appear to be smaller than similar-aged Neanderthal immatures, leading to the suggestion that there existed a relatively gracile Mediterranean Neanderthal population (De Lumley and Giacobini 2013). The Palomas individuals (e.g. Palomas 97) from southeastern Spain are also said to be small (Walker et al. 2011b; 2012).

La Ferrassie 3

This is the only Neanderthal subadult to have all three inner ear ossicles, malleus, incus and stapes, preserved apart from the neonate Le Moustier 2. Incudes are preserved in the infant Amud 7 and the adolescent Le Moustier 1. The ossicles of La Ferrassie 3 confirm the distinctiveness of Neanderthal morphology (Quam et al. 2013; §F.4.3).

Hortus II and III (6–8 years)

This is one individual. The sockets of the anterior mandibular deciduous teeth are vacant, but the permanent canines and premolars are in their crypts with roots up to ½ complete. In life the deciduous molars 1 and 2 and permanent M1 would have been in occlusion. The maxillary M2 is crown complete (De Lumley 1972:379–381). In dental development the Hortus II-III individual seems to be at the same stage as Teshik-Tash.

Krapina Skull A aka Krapina 1 (6–8 years)

The calvaria in its more complete state appears to be undistorted, contrary to early publications. The bregmatic fontanelle is closed but the metopic suture is open, the frontal moieties separated by matrix and glue 3.4 mm across (Minugh-Purvis et al. 2000). Cranial capacity is given as 1293 cm³ (Coqueugniot and Hublin 2007:381). Bone erosion centred on the left temporal may have resulted from otitis media and subsequent mastoiditis and possibly meningitis, which may have been the cause of death (Minugh-Purvis et al. 2000:418).

Krapina Frontal 3 aka Krapina 24 (6 years?)

This frontal has a thinner squama but more robust lateral browridge than Krapina 1 (Minugh-Purvis et al. 2000:404).

Malarnaud (11 years)

On this mandible, the alveolar rim is open above the third molar crypt. The two mesial incisors are absent owing to agenesis (Granat and Heim 2003:185).

Marillac 25 (9–10 years)

Dimensions of this femoral diaphysis resemble those of Teshik-Tash, although some are slightly smaller (Garralda et al. 2014:103–107). Since Neanderthal immatures have generally been assigned younger ages when it is possible to determine age more precisely from dental microstructure, it is possible that Marillac 25 and Teshik-Tash may be nearer 8 years than 9–10.

Obi-Rakhmat 1 (6.0–8.1 years)

Teeth are stated to have Neanderthal affinity, while the parietal fragments have some resemblance to the Skhul-Qafzeh material (Glantz et al. 2008:231), which is assigned to early *Homo sapiens* with a date of ~100 ka. Similar phylogenetic considerations have been thought to apply to the other major Uzbekistan discovery, Teshik-Tash.

Okladnikov 2 (8–10 years)

A study of carbon and nitrogen isotope ratios in the Okladnikov skeletal material confirmed reliance of the Neanderthals at this site on a high-protein diet sourced from large herbivores. These Neanderthals were more often affected by dietary stress than average anatomically modern humans. However, the duration of dietary-stress episodes was on average half that among recent forager populations, and young children were relatively unaffected – deciduous teeth showing very low levels of linear enamel hypoplasia compared with the permanent teeth – in contrast to the pattern observed among recent foragers (Dobrovolskaya and Tiunov 2013:80–81).

Scladina (8 years)

The dentition appears only lightly worn. Development of permanent molar roots would indicate an age of 12–13 in a modern human child, but deciduous molars are still in place, leading to an estimate of 10 years (Toussaint et al. (1998, 2001:27). Periodicity of long-period lines in enamel (perikymata and striae of Retzius) was determined from an upper first molar, and the duration of crown formation and root development was calculated to produce an age at death of 8 years (T.M. Smith et al. 2007b:20220–20221).

Scladina is female (Peyrégne et al. 2019:2). Mitochondrial DNA was retrieved from one of the teeth, and indicates greater genetic diversity at this period (>100 ka) than among later Neanderthals (Orlando et al. 2006).

Collagen analysis indicated a high-protein “carnivore” diet (Toussaint et al. 1998), as for the Spy adults (Toussaint and Pirson 2006).

El Sidrón Juvenile 1 (7.7 years) **

Rosas et al. (2017) report that skeletal elements were as expected for the calculated dental age, except that the atlas and mid-thoracic vertebrae remained at a stage corresponding to ~5.6 years. This is therefore one of several Neanderthal immatures in which some or all of the postcrania – in this case only some – appear underdeveloped for an absolute chronological age as determined by dental microtomography. Many vertebrae have unfused posterior or neurocentral synchondroses which in a modern human would be expected to have fused by ~7.7 years; but earlier fusing (in modern humans) vertebrae have fused and later fusing vertebrae remain unfused, so the individual appears to be following the modern human sequence (Rosas et al. 2017 SI:56–60). The femur is short at 250 mm, but the individual is said to fall well within the modern human range of variation for this age (Rosas et al. 2017 SI:23,73–74).

At ~7.7 years El Sidrón J1 already exhibits specific Neanderthal traits including an occipital torus, suprainiac fossa, chignon, and taurodont molars with mid-trigonid crest on the M1, as well as postcranial features, some observed on other subadult Neanderthals (Rosas et al. 2017 SI:21).

Rosas et al. (2017) estimate endocranial capacity as 1330.57 cm³. Endocranial volume as a percentage of mean adult volume (Appendix E) is low, suggesting that brain growth was not complete. This appears to be confirmed by the presence of resorptive bone on the surfaces of the occipital fossae. DeSilva (2018) disputes the conclusion of incomplete brain growth on the grounds that the target adult mean volume used was too high. Rosas et al. (2018) defend their conclusion using several methods of estimation.

Teshik-Tash (8.2 years?) **

In a study of mitochondrial DNA extracted from the left femur, Krause et al. (2007) determined that Teshik-Tash aligned with Neanderthals from Western Asia and Europe and not with early or recent modern humans. In the same study the juvenile Okladnikov 2 was also found to be Neanderthal. The Teshik-Tash mtDNA seems to be more closely related to the mtDNA obtained from the Scladina juvenile from Belgium than to that of the geographically closer Okladnikov specimen.

Some of the morphological analyses made by Glantz et al. (2009) align Teshik-Tash with Upper Palaeolithic modern humans in respect of the cranium and with recent humans in respect of the mandible. In other tests the Neanderthal attribution is confirmed. The question arises whether Teshik-Tash (and the juvenile Obi-Rakhmat 1) may be Central Asian examples of a Middle Palaeolithic population represented in the Levant by the Skhul and Qafzeh fossils, which were once considered Neanderthaloid (McCown and Keith 1939) but are today considered to be early anatomically modern humans. This hypothesis was first put forward by Weidenreich (1945).

Weidenreich (1945:155–157) draws attention to the basi-bregmatic height (BBH, M17) of the Teshik-Tash skull, which he takes to be 132 mm, greater than in the Neanderthal adults (his mean 125 mm, range 115–131 mm). In his view, this and other features are evidence that the subject may not have been a Neanderthal but more closely related to the Skhul hominins: for example, the contour of the lower frontal squama, more inclined than in a modern child, could represent an immature stage leading to a supraorbital torus either of Neanderthal form or as seen in the Skhul adults. The BBH value 132 mm comes from Gremyatskii (1949:146,181). Later authors have presented lower values. Madre-Dupouy (1992:67) measured 129 mm on a cast. Tillier (1983:53) gives 129 mm. Minugh-Purvis (1988:216) gives 128 mm. Thompson and Illerhaus (2005:329) give 124 mm. Lower values, if correct, reduce the cogency of a *Homo sapiens* attribution.

The interorbital index¹ is the focus of further examination (Weidenreich 1945:159). The index is stated to vary little during growth despite the enlargement of components of the upper face, and therefore indicates population affinity. In Teshik-Tash, the interorbital index 23.7 and interorbital breadth 22.5 mm, indicating a broad nasal root, along with the shovel-shaped incisors, are suggested to indicate affinity with the Skhul population and possibly “Mongoloid” modern humans. However, a study of local hospital skeletal material in Maharashtra, India, found a range of interorbital breadths from 14 mm up to 27.6 mm (Gosavi et al. 2014), rendering the measurement of Teshik-Tash unexceptional. According to Weidenreich (1945:159), the interorbital index of Teshik-Tash exactly equals that of Le Moustier 1, which would appear to align it with Neanderthals.

Minugh-Purvis and Lewandowski (1994) find anatomically modern, Neanderthal and intermediate features in the cranium of this subject, and suggest the possibility of biological continuity between archaic and modern humans in Asia.

The study of interorbital breadth is reprised by Coqueugniot et al. (1996), who plot interorbital breadth against age and find that Teshik-Tash, assumed to be aged 9 years, fits almost exactly on the regression line of modern human children, while the Neanderthal immatures shown, all much younger, have interorbital breadth above the 95% confidence interval. Recent calculations of chronological age of Neanderthal immatures using computed tomography of dental microstructure (e.g. T.M. Smith et al. 2010) have in most cases produced younger ages than those derived from modern dental standards. A younger age should probably

¹ M50 interorbital breadth / M44 biorbital breadth.

therefore be expected for Teshik-Tash. In the absence so far of direct measurement on dental microstructure, the reduced age of 7.5 years proposed by Granat and Heim (2003:186) could be accepted, or an intermediate age of ~8.0–8.2 years may be an appropriate compromise. Using the age of 7.5 years, Teshik-Tash would fall just above the 95% confidence interval for modern human interorbital breadth given by Coqueugniot et al. (1996); using 8 years the subject would fall within the 95% CI but in the upper range. The Le Moustier 1 youth is not included in their study. His interorbital breadth is 26.2 mm (Thompson and Illerhaus 1998:658), which places him also a little above the 95% confidence interval at the revised age of 12 years, although he would fall within it at 14 years. These similarities of placement depending on age would seem to align Teshik-Tash with Le Moustier 1.

A geometric morphometric comparison of the frontal bone with modern humans, recent and Upper Palaeolithic, and extrapolation of growth trajectories to adulthood based on modern humans and on Neanderthals, concluded that Teshik-Tash was a Neanderthal (Gunz and Stansfield 2012). According to Bulygina (2007:251) the zygomatic bones are swept back, which is a Neanderthal apomorphy.

On a *Gestalt* basis (cf. Tattersall 1995; Tattersall and Schwartz 2008), with its long, wide neurocranium Teshik-Tash as a juvenile (*sensu stricto* Bogin) is a credible intermediary between (a) the group of infants and early children such as Pech de l’Azé, Dederiyeh 1 and 2, Gibraltar 2, Engis 2, La Quina H18, and (b) the early adolescent Le Moustier 1, all of which are generally accepted as Neanderthals. See also Appendix J.

As summarized above, the genetic evidence presented by Krause et al. (2007), would seem to be definitive in assigning Teshik-Tash to the Neanderthal hypodigm, unless further genetic research were to uncover closer affinity with a population of early modern *Homo sapiens* such as Skhul.

Teshik-Tash has weak browridge development. It is more of a “bulbing” than a defined torus. Only the supranasal region of the squama is pneumatized and the frontal sinuses have not invaded the developing torus (Tillier 1986:211) (§6.5.2).

5.5 Adolescent stage

Adolescents (from 11.0 to 16–20 years) are listed by age in Table 5.4.

Table 5.4: Adolescents

<i>Specimen</i>	<i>Age (years)</i>
Le Moustier 1	11.86
Vindija Frontals Vi-224 and Vi-229	12 ?
Petit-Puymoyen 1/2	9–14
Petit-Puymoyen 3/4	Adolescent
El Sidrón Adolescent 3	Adolescent
Fontéchevade 1 ¹	Adolescent
Malarnaud 1	11–14
Montgaudier	12.5–14.5
Combe Grenal III	13–14
Külna	14
Krapina Maxilla D	14.5
Combe Grenal IV	14–15
Hortus IV	14–17
Krapina Mandible D	15–17
Krapina Mandible E	15–17
Montmaurin La Niche	15.5–18
Petit-Puymoyen 7	Late adolescent
Hohlenstein Stedels	Late adolescent
Ages from Appendix A.	
¹ This specimen may be an adult <i>Homo sapiens</i> (Appendix A).	

Hortus IV (14–17 years)

This mandible with left and right corpora and left ramus has both M2s but no M3 erupted. It may represent an adolescent at a similar or slightly later stage than the more complete Le Moustier 1.

Montgaudier (12.5–14.5 years)

This mandibular corpus is probably female, small and without a chin but with multiple mental foramina, as commonly found in Neanderthals.

Montmaurin La Niche (15.5–18 years)

Dating (190–240 ka, Vialet et al. 2018) indicates that this specimen is pre-Neanderthal or early Neanderthal.

Vallois (1956) states that the mandible is smaller than a Neanderthal (adult) mandible and less voluminous than in a fossil or modern human, but very thick and robust. He does not state that it is immature.

On the basis of dimensions Vialet et al. (2018) regard the specimen as female. They relate the molar dentition to both Neanderthals and the Sima de los Huesos hominins. In the mandible itself they do not identify a full suite of Neanderthal apomorphies and find that it clusters with European Middle Pleistocene hominins other than the Sima de los Huesos group, and with African and Asian contemporaries.

Bilaterally all three molars are erupted but there is no retromolar gap and the molars look remarkably little worn. This mandible therefore seems to represent one of the few Neanderthal adolescents. If the individual had survived, probably the mandible would have become further elongated anteriorly (§6.5.4).

Le Moustier 1 (12 years) **

Ahern and Smith (2005:128) state that no other Neanderthal adolescent has a dentition associated with a supraorbital region. More than this, Le Moustier 1 is the only putative adolescent Neanderthal skeleton complete enough to yield coherent information about dental, cranial and postcranial development at this stage of ontogeny.

The dentition by modern human dental schedules indicates an age of 15–16 years, and the specimen was treated as such by most workers through the twentieth century. A thorough investigation by many researchers of all the remains (Ullrich 2005a) and finally a new age at death derived from counts of striae in dental microstructure (T.M. Smith et al. 2010) have concluded that this individual was 11.86 (roundly ~12) years old, with the postcrania indicating a younger age, ~10.5 years (§7.5). Given the small stature, 138.5 cm (§6.2.1), and young chronological and skeletal ages, the question arises whether the subject was only at the juvenile stage.

Methods have been proposed to distinguish substages of adolescence from a number of criteria utilizing sites in the skeleton of the living individual via radiography (Chertkow 1980; Coutinho et al. 1993) and on the dry skeleton (Shapland and Lewis 2013; Lewis et al. 2016b).¹ The dental (canine) criterion can be checked on Le Moustier 1. The permanent canines are all in occlusion except for the left mandibular canine, which is impacted below the deciduous canine, a stump of which remained in the alveolus until death. However, the permanent canines are fully formed (Bilsborough and Thompson 2005). As they are beyond the root $\frac{3}{4}$ or *prepuberty* stage of Lewis et al. (2016b:51), the subject would be placed at the next stage: *acceleration of the growth spurt*. On this basis Le Moustier 1 has recently begun adolescence, as would be expected of a 12-year-old male today. It cannot just be assumed that Neanderthals followed a modern human correlation of canine formation and puberty, but no evidence has been brought forward that makes the assumption untenable or improbable, so it seems reasonable to accept this inference.

Other criteria for attainment of puberty have been described by the above researchers: development of the hamate hook, fusion in phalanges and distal radius, iliac crest development, and cervical vertebrae maturation (Lewis et al. 2016b). These require access to well preserved postcrania, but the incompleteness and damaged state of the surviving Le Moustier 1 postcrania offer little scope. Although some small hand bones were mentioned in publications from 1909 by the discoverer Hauser and the anatomist Klaatsch (cited in Ullrich 2005a), none have been preserved and none were reproduced as casts (Thompson and Nelson 2005b:280). The “left forearm” and right radius were allegedly recovered, but only the right radius was cast, with

¹ Lewis and colleagues refer to adolescence as “puberty”, whereas Tanner (1962), Bogin (1999, 2003, 2016:52–55,84–85), Hochberg and Belsky (2013:2), and perhaps the majority of researchers distinguish puberty as the endocrine-initiated process of a few months’ duration which introduces the stage of adolescence.

distal and proximal ends reconstructed (Ullrich 2005a). None of the long bones had begun to fuse (Thompson and Nelson 2000:479; Thompson et al. 2002:58). Some fragments of the ilium and other pelvic elements have been preserved, but not superior parts of the ilium (Ullrich 2005a). The ischium and pubic ramus had not fused. Fusion normally occurs by 9 years, but occasionally is delayed in normal subjects (Thompson and Nelson 2005a:216). Some vertebrae were discovered in 1909, but of these the lumbar vertebrae turned to dust on being unearthed and the rest were poorly preserved; they have not been seen since 1945 (Ullrich 2005a).

The cranium has undergone at least four physical reconstructions (Ullrich 2005b), the first by Klaatsch, which is illustrated by Boule and Vallois (1957:205) and described by them as a “caricature”. A later one by Weinert (1925) remained the reference for several decades, but was dismantled. More recently, virtual reconstructions have been made (Thompson and Illerhaus 1998; Zollikofer and Ponce de León 1999), which diverge in the positioning of certain elements, including the foramen magnum, and result in different dimensions (§6.5.3).

The lower left deciduous canine remained in place, and the permanent canine, fully developed but impacted, lies inferior to it within the corpus at an almost horizontal angle (Thompson and Bilsborough 2005:88; Thompson and Illerhaus 2005:231,235). A similar condition is exhibited by El Sidrón Adolescent 3 (below) and the adult individual El Sidrón 2 (§6.5.4).

In some photographs of the Le Moustier 1 skull, the third molars are shown as if they are in process of erupting. At the time of writing, available photographs are usually of reconstructions dating before the Second World War. The earliest reports attest that the third molars (M3s) were not erupting but still enclosed within the alveolar bone (Klaatsch 1909, cited by Bilsborough and Thompson 2005:183). In the process of computed tomography and virtual reconstruction, it was found that the developing M3s, which are at stage root $\frac{1}{4}$, could readily be accommodated within their crypts, and they have been so positioned in the virtual reconstructions by Thompson and Illerhaus (1998; 2005:236–240) and Ponce de León and Zollikofer (1999; 2005:248,255). According to Cuzzo (2005:115–116) the mandibular third molars would have been impacted and there is insufficient space for the maxillary third molars to erupt.

Le Moustier 1 suffered injury to the left mandibular condyle, caused by a blow to the head or a fall, but the injury healed (Ullrich 2005c:299; Ponce de León and Zollikofer 1999:488, 2005:258). The cause of death may have been several blows to the crown and front of the head, which displaced sections of the outer table (Ullrich 2005a:18, 2005c:296,299,303–304), and exposed the left frontal sinus (Weinert 1925:325).¹

Thompson and Illerhaus (1998; 2005:228–230) argue that older reconstructions incorporated post-depositional deformation preventing natural articulation of the mandible with the basicranium. Cuzzo (2005) finds no compressive deformation and argues against it on the grounds that fine features such as the patent foramen caecum at the junction of frontal and ethmoid would not have remained undistorted. He discusses faults of reconstruction, including the join of the two halves of the frontal out of alignment vertically by 1 mm at the metopic suture.

Cuzzo (2005:115–116) also comments on misplacement of the mandible anteriorly with respect to the basicranium. In his assessment the state of the dentition in life was an orthodontic Class I (i.e. normal) occlusion, as seen in his photographs. The infant crania Pech de l’Azé and Roc de Marsal (§5.2) were also originally reconstructed with projecting maxillae,

¹ The Middle Palaeolithic *Homo sapiens* adolescent Qafzeh 11, aged ~13 years, also suffered trauma to the right frontal, but lived long enough for the healing process to begin (Tillier 1999:138,155,174–175).

so that the mandible could not simultaneously articulate with both the glenoid fossae and the maxillary dentition.

Petit-Puymoyen 1 and 2 (9–14 years)

This is one individual. Petit-Puymoyen 1 is said to be the only Neanderthal mandible that possesses the four components of the chin: tuber symphyseos, tubercula lateralia, fossae mentales, incurvatio interior mandibulae (Tillier and Genet-Varcin 1984). The P4 is in occlusion and the M3 between root $\frac{3}{4}$ and root complete. This specimen and Petit-Puymoyen 3 appear to have a more modest degree of mid-facial prognathism than most Neanderthals (Quam et al. 2011:98–100).

El Sidrón Adolescent 3 (12–13 years)

A deciduous canine root remains within the alveolus mesial to the LLP3 but the crown has broken off. An isolated and incompletely formed lower left permanent canine has been identified as belonging to Adolescent 3 on the basis of shared hypoplastic banding. It has been suggested that the permanent canine failed to erupt normally, with retention of the deciduous canine (Trinkaus 2018 SI). El Sidrón Adult 2 also exhibits retention of a deciduous canine, but in this adult the unerupted permanent canine lies horizontally within the mandibular corpus below the M2 and M3, as if left behind by anterior growth of the alveolar portion of the mandible (§6.5.4). Mitochondrial DNA indicates a close relationship between Adult 2 and Adolescent 3, so their dental condition may be hereditary (Dean et al. 2013; Trinkaus 2018 SI). A similar condition, also affecting the lower left canine, is exhibited by Le Moustier 1, but there the unerupted canine remains below the deciduous one.

Vindija Vi-224 and Vi-229 (12 years?)

These two isolated frontals with their incipient browridges are reported to be at a similar state of development to that of the more complete Le Moustier 1 (Ahern and Smith 2005).

CHAPTER 6

GROWTH TO ADULTHOOD

6.1 Introduction

Here growth – strictly ontogenetic difference with age – of the Neanderthal skeleton is described with measurements and comparisons. Stature and body mass are tabulated and evaluated against recent human growth standards. Detailed description of postcrania is not attempted. For the neurocranium and viscerocranium, apart from the most salient dimensions, discussion concentrates on distinctive Neanderthal features, e.g. midfacial projection.

Neurocranial growth in relation to the growing brain, including growth of the cranial base, is also covered in Chapter 4. Growth of the supraorbital torus, although it is comprised in the frontal bone, is treated here under viscerocranial growth, since it is the growth of the midface and orbital region that induces its development.

At the time of writing, only some Neanderthal immatures have chronological ages at death by counts from dental microtomography, a method which allows greater confidence to be placed in assessments of their stages of development. The ages of others have been derived by dental formation or eruption schedules or from dimensions and morphology.

For convenient reference, cranial and mandibular measurements are identified where possible by traditional numbers, e.g. M17 = cranial height (Martin 1914; Martin and Saller 1957).

Measurements often differ between publications. Generally, measurements from later publications are favoured here in graphs and discussion. Graphs illustrate growth in cranial and postcranial dimensions from ~1.5 years (Dederiyeh 1 and Pech de l’Azé) to putative adulthood, i.e. attainment of adult stature, here usually taken to be at 17 years (rather than 19 or 20 years), on the widely held assumption that Neanderthals may have reached adulthood earlier than modern humans. Whether they did is taken by the present writer to be possible but not certain, and by acknowledging the consensus confusion should be minimized.

Particular attention is paid to the most complete single adolescent and two juveniles. Le Moustier 1 is the only adolescent Neanderthal available of any degree of completeness, and is a male only beginning the process of adolescence. Teshik-Tash, fairly complete, is a juvenile and probably male. The other relatively complete juvenile, El Sidrón J1, also assessed as male, has recently been comprehensively described (Rosas et al. 2017). In the absence of female specimens of these older age groups, male development has to be emphasized, which, as with modern humans, is expected to involve larger changes skeletally.

Whereas measurements such as femoral length and maximum cranial breadth can be made directly on fossils, estimates of stature and body mass of individual hominins are derived measures and cannot be precise. Methods of derivation and the uncertainty of estimates are discussed in the introduction to Appendix H.

It is beyond the scope of the present work to critique or compare adult estimates. For the present purpose, stature and body mass estimates for individual Palaeolithic *Homo* adults in Chapter 6 and the tables of Appendix H are taken from the comprehensive study by Will et al. (2017). For Neanderthal and other subadults, values presented in this chapter are taken from the cited descriptive papers or studies estimating stature or body mass of specific immatures.

6.2 Stature

6.2.1 Neanderthal subadults

At equivalent dental ages Neanderthal immatures are absolutely smaller postcranially than recent humans (Nelson and Thompson 2002:444). When chronological age is substituted for dental age the observation holds. A study of the Cova Negra femur and remains of other immature Neanderthals by Arsuaga et al. (2007) concludes that they had considerably lower stature than modern humans at any given age, confirmed by Martín-González et al. (2012).

Some of the younger immatures have sufficient postcrania to estimate stature. Kondo et al. (2000), Martín-González et al. (2012) and Vlček (1973) calculate values for a number of them, giving a range taking account of variation due to sex and using either only lower limb bones or the lower limb plus vertebrae. These are given below, along with the juveniles El Sidrón J1 and Teshik-Tash and adolescent Le Moustier 1 (Table 6.1, Figure 6.1).¹ Mezmaiskaya 1 and La Ferrassie 4bis give identical results (Martín-González et al. 2012).

Table 6.1: Stature, Neanderthal immatures

	Age (years)	Stature (cm)
Le Moustier 2	0	50.4 (49.1–51.6) ¹
Mezmaiskaya	0–0.1	52.2 (51.0–53.4) ¹
La Ferrassie 4bis	0–0.2	52.2 (51.0–53.4) ¹
Kiik-Koba	0.5	64 ²
Shanidar 10	1–2	79.6 (79.5–79.6) ¹
Dederiyeh 1	1.5	82.3 (81.15–83.48) ³
Dederiyeh 2	2.0	75.4 ¹
Roc de Marsal	2.25	82.4 (81.93–82.78) ³
La Ferrassie 6	3	82.5 (81.73–83.34) ³
Cova Negra (Femur I)	5–6	93.6 (93.1–94.0) ¹
El Sidrón J1	7.7	110.6 (104.98–120.00) ⁴
Teshik-Tash	8	112.9 ⁵
Le Moustier 1	12	138.5 ⁵
Neanderthal mean	Adult	162.8 ⁵
Ages from entries in Appendix A. ¹ Martín-González et al. (2012:142). ² Vlček (1973:540). ³ Kondo et al. (2000:468). ⁴ Rosas et al. (2017 SI:23). ⁵ Nelson and Thompson (1999:96–97). Adult mean both sexes in Table H.4 is 162.7 cm.		

¹ Martín-González et al. (2012) used equations for modern human children from Ruff (2007), based on femoral length except for Shanidar 10, for which the tibia had to be used. As Neanderthals have distal limb shortening, they acknowledge that femur-based estimates may be slightly high and the tibia-based estimate low. Kondo et al. (2000), in addition to estimates from femora, made a physical reconstruction from casts of the entire skeleton of Dederiyeh 1 allowing for shrinkage of the casts, and measured that. The value for Kiik Koba is a compromise of estimates from the femur using a variety of methods by Vlček (1973:539–540). Rosas et al. (2017:23) used published regressions to estimate stature from the femur and also the humerus, radius and ulna. Nelson and Thompson (1999) made estimations from femoral length using the methods of Feldesman (1992) and Feldesman et al. (1990).

The statures of four of the five infants aged 1.5–3 years are almost identical, despite the youngest age proposed for La Ferrassie 6 (range 3–7 years) being twice that of Dederiyeh 1. On the basis of Tanner’s (1989:180–181) modern human standards for infants, Shanidar 10 is on the 50th centile if female and just below if male; Dederiyeh 1 is just above the male 50th centile and above the female 50th centile; Dederiyeh 2 is below the 3rd centile for males and females; Roc de Marsal is below the male 50th centile but well within the distribution and not much below the female 50th centile; while La Ferrassie 6 is at or below the male 3rd centile and below the female 10th centile.

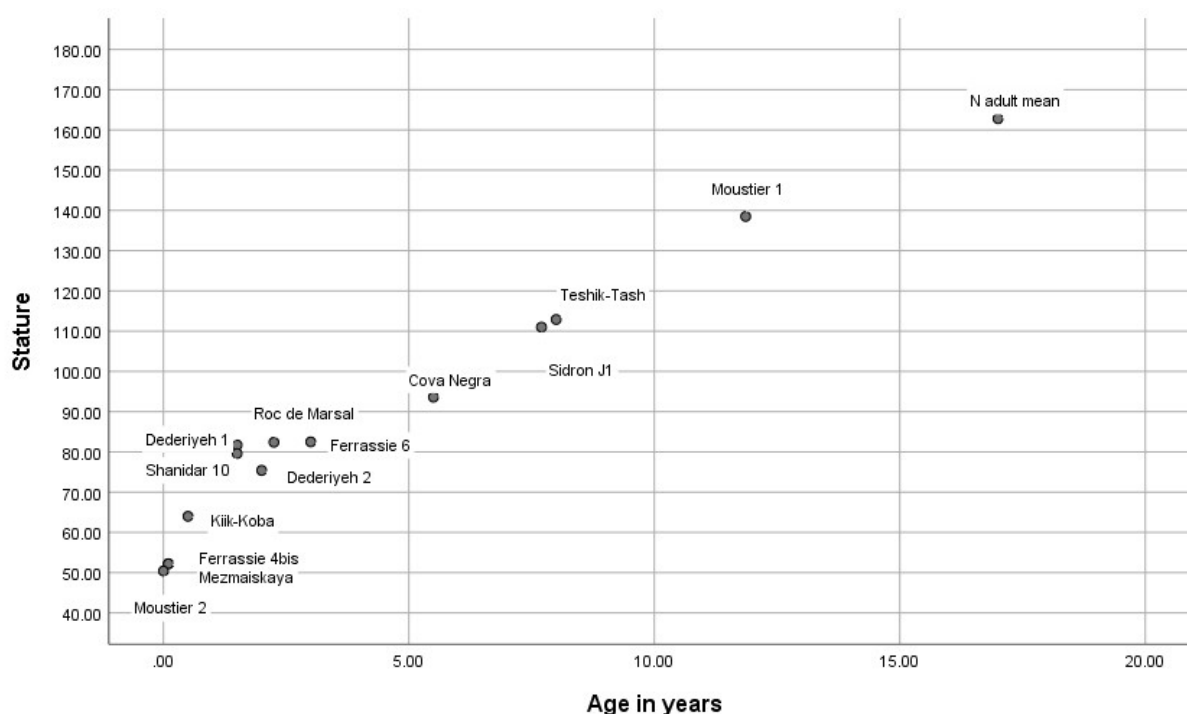


Figure 6.1: Stature, Neanderthal immatures with mean adult stature (cm)

Arsuaga et al. (2007:52) state that Roc de Marsal and la Ferrassie 6 (using the same statures cited here) fall below modern human range, but they take La Ferrassie 6 to be 3–5 years and Roc de Marsal presumably to be above 3 years, although that is not stated.

If the infant group at 1.5–3.0 years form one end of a growth trajectory and the adults form the other end, then the ~8-year-olds are at one-third of the way and the ~12-year-old two-thirds, indicating that considerable growth in height takes place during the late juvenile phase and in the adolescent years: ~25 cm in each phase.

With a sample of 1 at age 3, 2 at age ~8 and 1 at age 12, a tentative rate of growth per year can be derived (Table 6.2). The rate in adolescence does not indicate a growth spurt. As samples are so small, crudely derived values such as these are indicative only.

Table 6.2: Growth per year, Neanderthal infant–adult

Stage	Age interval	Growth (cm)	Growth per year (cm)
Early Child	3 – 7/8	30.4	6.08
Juvenile	7/8 – 12	25.6	6.4
Adolescent	12 – 17 (adult)	24.3	4.86

Percentage of adult stature

Nelson and Thompson (1999) give a mean 162.8 cm for a sample of male adult Neanderthals. Martín-González et al. (2012) give 160.6 cm for both sexes, contrasting with early modern humans at 177.4 cm and recent modern humans at 170 cm.¹ From the comprehensive data of Will et al. (2017), mean adult stature for all Neanderthals having informative fossils can be obtained as shown in Tables H.1–H.4. Mean male stature 166.2 cm is higher than previous estimates.²

Table 6.3: Neanderthal juvenile and adolescent stature, percentage of adult males

	Age (years)	Stature (cm)	El Sidrón J1 % adult stature	Teshik-Tash % adult stature	Le Moustier 1 % adult stature
El Sidrón J1	7.7	110.6			
Teshik-Tash	8 ?	112.9			
Le Moustier 1	12	138.5			
La Quina H5	Adult	161.0	68.70	70.12	86.02
La Chapelle aux Saints	Adult	162.5	68.06	69.48	85.23
Neanderthal (Feldhofer)	Adult	165.6	66.79	68.18	83.64
La Ferrassie 1	Adult	171.6	64.45	65.79	80.71
Mean adult males (Nelson and Thompson 1999)		162.8	67.94	69.35	85.07
Mean of 4 adult males this table		165.2	66.95	68.34	83.84
Mean adult males, Table H.1.		166.2	66.55	67.93	83.33
Expected % of adult height at 7.5–8.5 and 11.5–12.5 years, modern UK males ¹			69.1–75.3		82.7–86.6
Expected % of adult height at 7.5–8.5 and 11.5–12.5 years, modern US males ²			70.0–74.0		82.0–85.0
Neanderthal data from Nelson and Thompson (1999), Rosas et al. (2017), Will et al. (2017 SI). See text.					
¹ Using 3 rd and 97 th centiles from Tanner (1989:180).					
² Buschang et al. (1983:377).					

Table 6.3 lists the statures of the best preserved two juvenile and one adolescent Neanderthals, all believed to be male, and four adult male Neanderthals of low, intermediate and high stature from western Europe, whose mean height is 165.2 cm. The percentage height attained by each subadult is given against each of the various adult heights, individual and mean.

Calculated stature for El Sidrón J1 is from Rosas et al. (2017) and statures for the other two immatures are from Nelson and Thompson (1999:96–97); values for individual adults are taken from Will et al. (2017 SI). These authors list La Quina H5 as a female, but it is assumed here to be male, following Trinkaus (2016). It represents the smaller end of the adult male distribution.

El Sidrón J1 and Teshik-Tash are very similar. The heights 110.6 cm for El Sidrón J1 and 112.9 cm for Teshik-Tash place them below the 3rd centile for 8-year-old modern British boys but just above it for 7-year-olds (Tanner 1989:20). The mean heights of twentieth-century

¹ Coon (1939) made an extensive survey of the modern inhabitants of Europe. He gives a stature of 164 cm for the Neanderthal adult male La Chapelle-aux-Saints from Corrèze in South-West France, which he observes is half an inch taller than French men living there in the 1930s (Coon 1962:548). Carretero et al. (2012:251) state that Neanderthals were not short by the standards of Southern Europeans in the late twentieth century.

² Gallagher (2013:558) estimates mean male stature 169.2 cm and female mean 156.4 or 154.2 cm, indicating considerable dimorphism in Neanderthal adult stature.

European males by country at age 7.0 range from 114.2 to 126.1 cm and at age 8.0 range from 120.9 to 130.5 cm (Eveleth and Tanner 1976:277). Low means are from rural populations in Greece, Poland and Sardinia, and some individuals in these populations would have lower stature than the country mean by a few centimetres.

In percentage of adult height attained the juvenile Neanderthals lie below modern expectation, though slightly, while the adolescent meets but does not exceed modern expectation.

Growth required to bring the two juveniles and adolescent to adult height is presented in Table 6.4.

Table 6.4: Neanderthal juveniles and adolescent, statural growth remaining to adulthood

	Age (y)	Height (cm)	% adult height using alternative adult means (previous table)	Growth to reach adult height	
				(cm)	(inches)
El Sidrón J1	7.7	110.6	64.5–68.7	50.4–61.0	20–24
Teshik-Tash	8.2 ?	112.9	65.8–70.1	48.1–58.7	19–23
Le Moustier 1	12	138.5	80.7–86.0	22.5–33.1	9–13

6.2.2 Comparison with recent humans

The height 138.5 cm of Le Moustier 1 fits the 10th centile for a 12-year-old modern British boy (Tanner 1989:20). The heights of European modern human males at age 12 range from 139.0 to 150.6 cm (Eveleth and Tanner 1976:277). The smallest mean height, 139.0 cm, is from Sardinia, where the mean young adult male height, also the smallest listed, is 164.4 cm (Eveleth and Tanner 1976:285). Thus a Sardinian boy at 139 cm reaches 84.5% of adult height, within the percentage range of Le Moustier 1 as shown in Table 6.3.

Le Moustier 1 was taller than the mean for 12-year-old Netherlands boys in 1865 (128 cm) and lower-class Utrecht boys in 1905 (133 cm), and almost matched lower-class Amsterdam boys in 1916 (140 cm) (Van Wieringen 1978:456). These early surveys predate full development in Europe of the secular trend for increasing stature (§2.6).

The low values above, raw and percentage, confirm that Le Moustier 1 is not a middle adolescent equivalent to a modern 15-year-old but very much at the beginning of adolescence. Teshik-Tash and El Sidrón J1 are clearly far from even beginning adolescence.

Ontogenetic variation in Neanderthal stature is compared with that of recent Africans and Europeans in Figures 6.2 and 6.4. Values for the Neanderthal individuals are taken from Table 6.1. Modern human measurements are from Eveleth and Tanner (1990:226–229, 266–269, 274). They provide means (or sometimes medians) for each age group centred on age 1 year, 2 years, ..., 18 years, from studies in several countries of each continent or region. The lowest means and the highest means for each age are graphed here to make two series, which are used to represent the range of means for each age.¹ As well as the actual values, percentages of adult height at each age are graphed in Figures 6.3 and 6.5.

¹ Mean adult height for Neanderthals is 162.7 cm for both sexes (Table H.4, from the data of Will et al. (2017 SI)). This practically matches the 162.8 cm from Nelson and Thompson (1999) used in the subsection above. Male and female data have been combined for recent humans. African values exclude the specifically small-stature (pygmy) populations and are taken only from data for African countries, omitting the diaspora in the Americas and Europe. Percentages are of adult height for each group. Eveleth and Tanner (1990:274) give adult heights for African groups. Of these, omitting small-stature populations, the lowest and highest are used as adult

In view of the period during which the modern human data were collected, prior to 1990, it is likely that some of the communities represented by the lower-stature African group suffered a degree of undernutrition, since they contrast with the European lower-stature groups in subsequent figures.

In Figure 6.2, the Neanderthal immatures seem to track the African lower-stature group, except that the two Neanderthal infants at 1.5 years are closer to the higher-stature group, and the adolescent at 11.86 years lies in the middle of the distribution for that age. In Figure 6.3, showing the percentage of adult stature attained, the Neanderthals at 1.5 years align with or above the higher-stature group, while those between 2.0 and 8.2 years lie below the lower-stature group. Again, the adolescent lies mid way in the distribution. The position of the infants at 1.5 years versus those at 2 and 3 years may suggest rapid growth in length during early infancy which decreases during the second and subsequent years, as in recent humans (Tanner 1989:13–14).

In comparison with European immatures, the younger Neanderthal infants at ~1.5 years fit within the distribution, but from then on all the Neanderthals fall below the lower-stature moderns (Figure 6.4). In percentage of adult height attained, after 1.5 years the Neanderthals again fall below modern European levels, except that the adolescent meets the lowest mean (Figure 6.5).

Evidence presented here, particularly the percentage of adult size attained for age, does not support an hypothesis that Neanderthal immatures were growing more rapidly than recent African or European humans. Even if the data point representing Neanderthal adult size were moved to a younger age, e.g. 16 years instead of 20, that might indicate a rapid adolescence but would not affect the curve up to 12 years, where the oldest subadult is placed.

Rosas et al. (2017 SI:74–75) determined that statural growth in Neanderthals was slower than that of children in northern Spain from the 1990s onward, but similar to that of twentieth century disadvantaged children in the Portuguese cities of Lisbon and Coimbra (§2.5.3, §7.5.1).

means for the lower-stature and higher-stature groups. For Europeans, in the absence of separate adult values, the tallest of the lower-stature group (age 18) and the tallest of the higher-stature group (age 17) are used as adult means for those respective groups. In the absence of adult values for those groups, it is possible that these tallest adolescent statures may be below the target adult stature for their groups, so that the apparent percentage attained may be slightly too high.

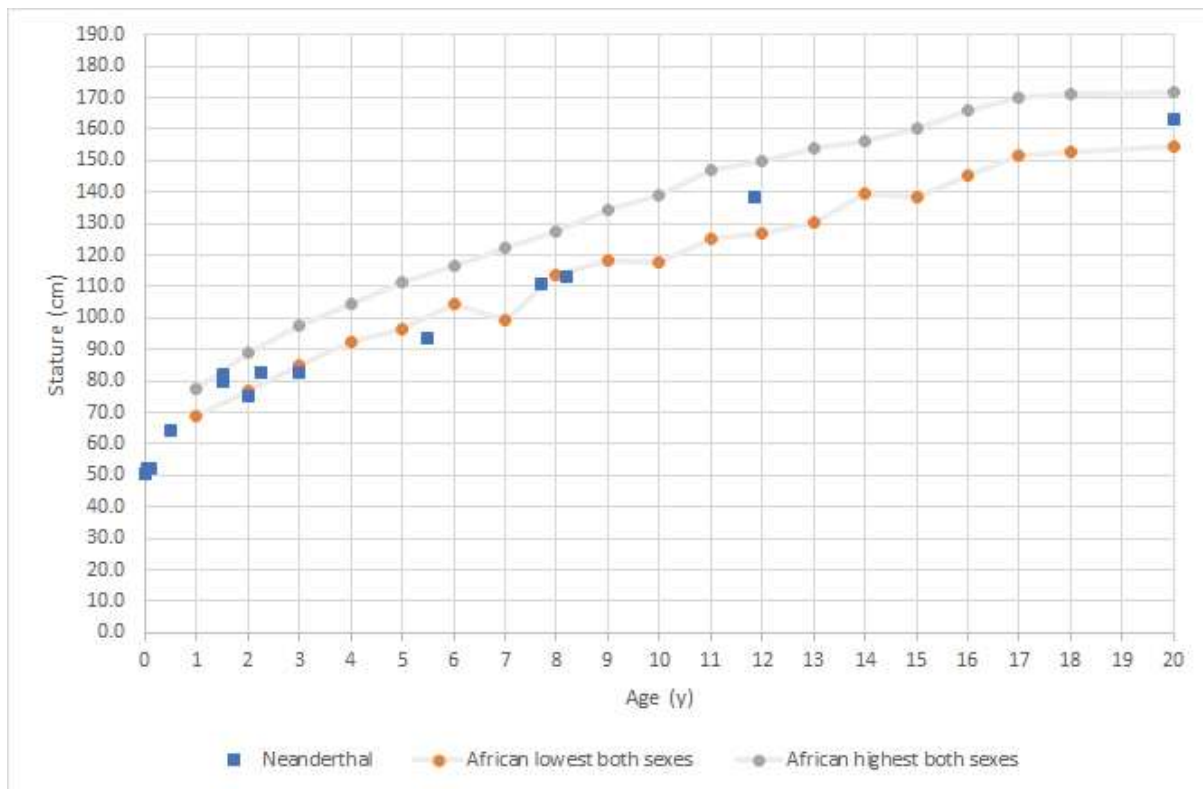


Figure 6.2: Stature, Neanderthal immatures, comparison with African populations

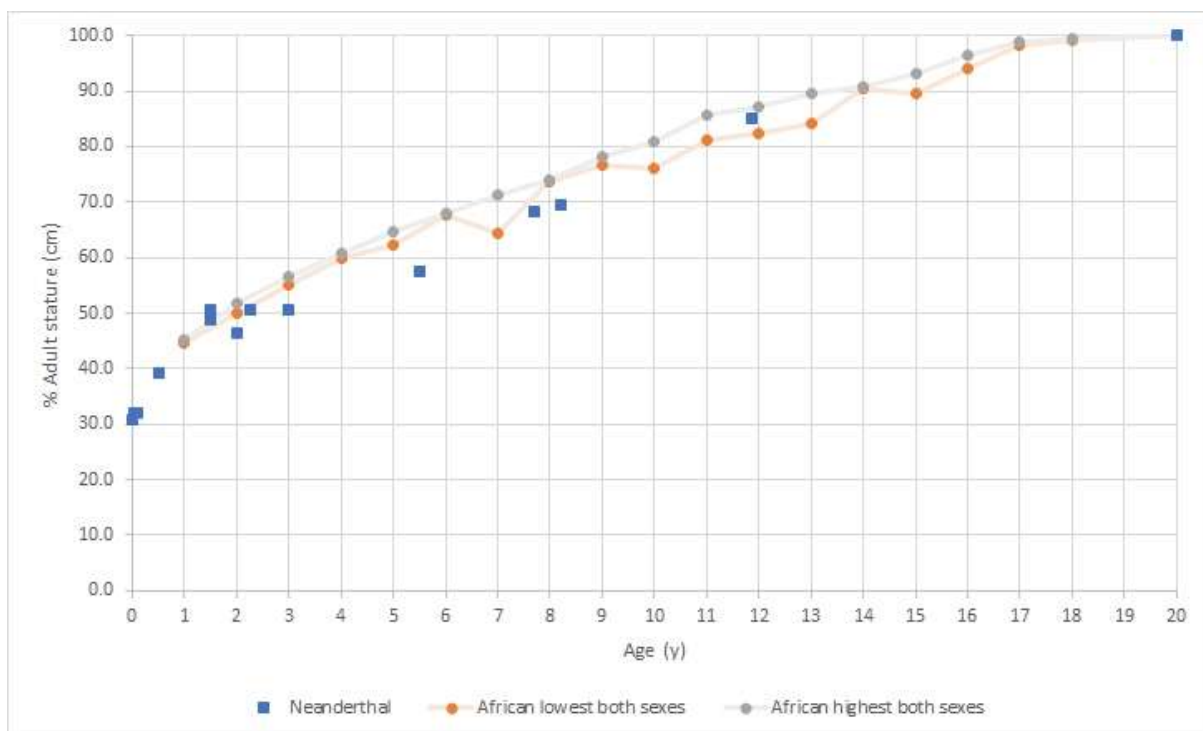


Figure 6.3: Percentage of adult stature, Neanderthal immatures, comparison with African populations

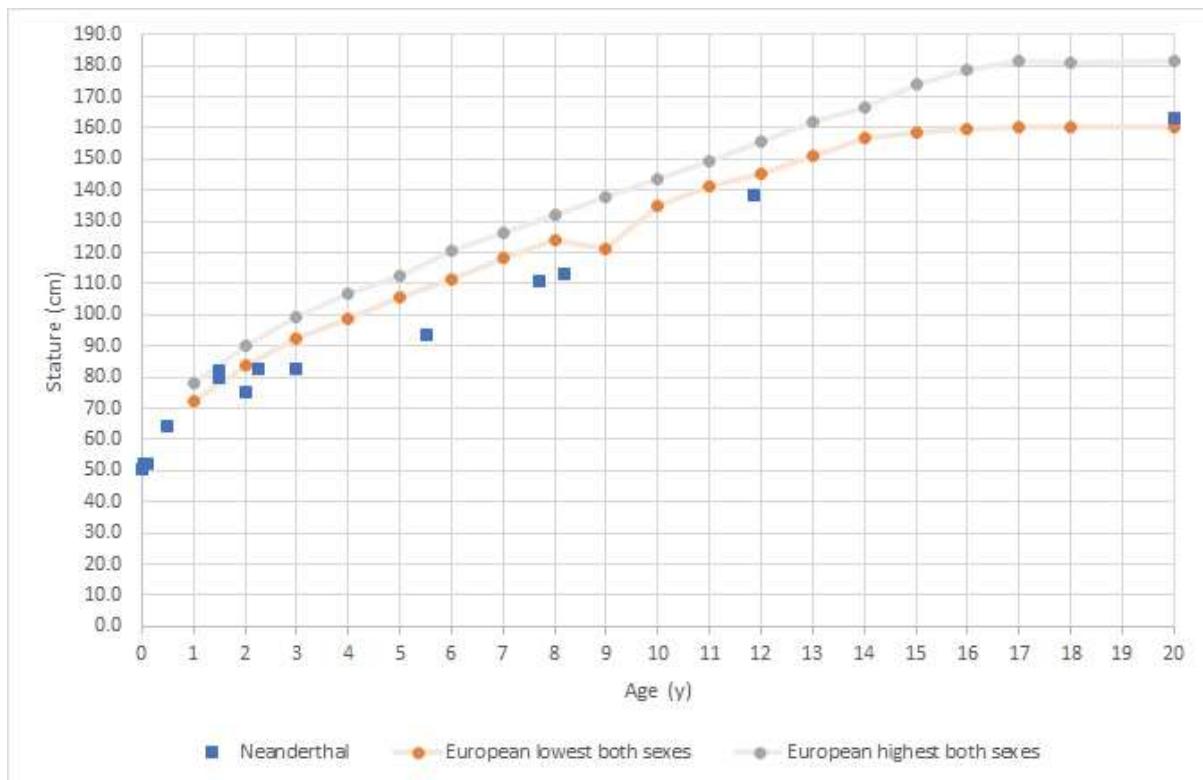


Figure 6.4: Stature, Neanderthal immatures, comparison with European populations

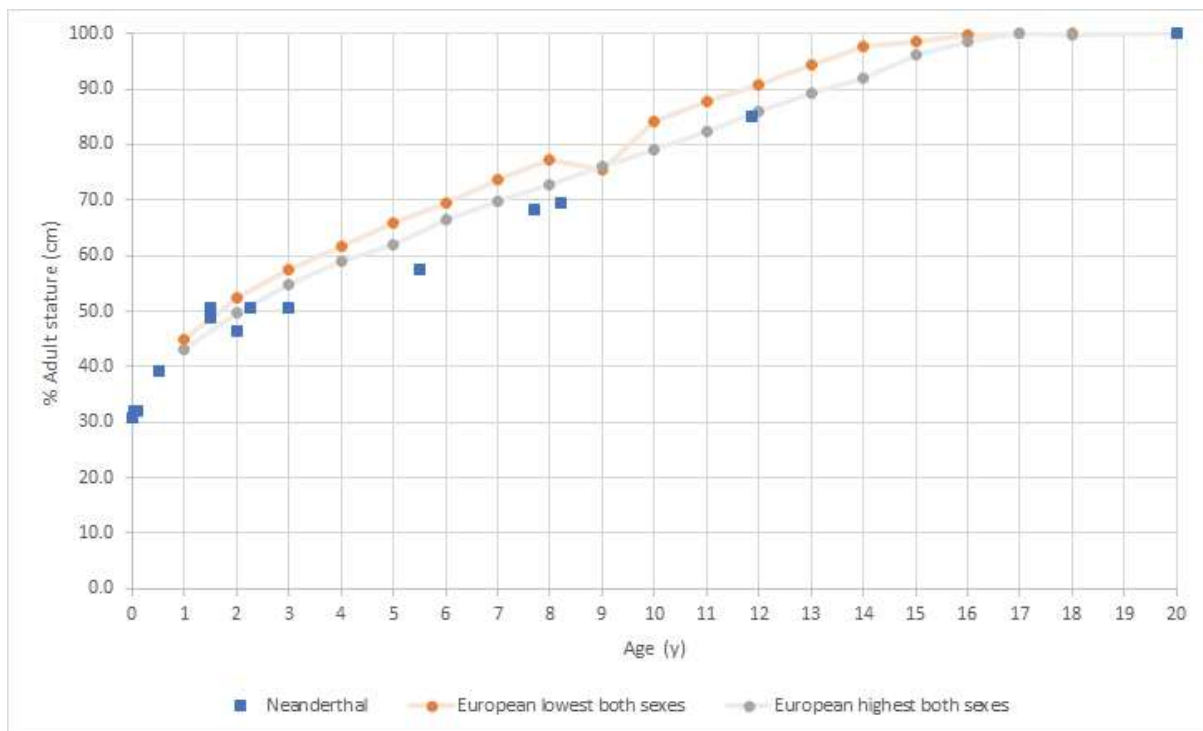


Figure 6.5: Percentage of adult stature, Neanderthal immatures, comparison with European populations

6.3 Body mass

Mateos et al. (2014) use stature information from Martín-González et al. (2012) and weights of circumpolar peoples to derive lean body mass for Neanderthal infants and young children, with ranges to take account of error in ages. Main results are shown in Table 6.5, with modern human weight ranges for comparison.

Table 6.5: Body mass, Neanderthal immatures by age range

Neanderthal				Modern human		
Age range (y)	Weight (kg)	Weight range (kg)	Weight gain (g/day)	Age (y)	Weight range (kg) African	Weight range (kg) European
1–2	11.92	11.62–12.23	6.22	1+	7.4–10.5	9.2–10.9
2–3	13.41	13.10–13.72	4.04	2+	9.3–12.5	11.6–13.4
3–4	14.54	14.23–14.85	3.10	3+	10.1–14.8	13.6–16.1
4–5	15.50	15.18–15.92	2.62	4+	12.7–16.8	15.4–18.0
5–6	16.37	16.05–16.70	2.37	5+	13.4–19.8	17.2–20.0
				6+	14.4–20.8	19.0–22.7
Neanderthal data from Mateos et al. (2014:171).						
Modern human data from Eveleth and Tanner (1990:230–233,270–273).						

The estimated weights of Neanderthal infants are high at first compared with living African and European populations, but then begin to fall behind. Mateos et al. (2014:171) note that weight gain decreases with age, in contrast to modern human groups from Spain and Siberia, in which gain is said to be stable during the studied period up to 6 years.

According to Arsuaga et al. (2007) the individual represented by the Cova Negra femur had body mass 12.4–13.5 kg, more typical of a modern 2-year-old than a 5-year-old. Body mass was derived by regression from the metaphyseal mediolateral breadth of the distal femur. This surprising result raises the questions whether the regression is fully applicable to Neanderthals and whether the estimated age at death is too high (ibid.:51–52). Yet in terms of stature in relation to the infant and juvenile specimens, Cova Negra falls credibly into place at ~5 years. Table 6.5 shows that the upper estimate for the weight of Cova Negra fits into the low end of the modern African range. A revised weight for Cova Negra from Mateos et al. (2014) shown in Table 6.6 turns out higher than in Arsuaga et al. (2007) and fits within the African ranges for both 5+ and 6+ years in Table 6.5 while remaining outside the modern European ranges.

Mateos et al. (2014:171) selected their *circumpolar set* of modern-human data as a proxy for Neanderthals. Using their regression equation¹ for that population, the weights of individual Neanderthal infants and young children are derived in Table 6.6. The equation is not intended for juveniles and above, but weights for the two juveniles and adolescent are extrapolated here for illustration. Altogether, the Neanderthal immatures seem to keep pace with living European populations up to 2 years, then drop below that expectation. At 12 years, with the extrapolated weight, Le Moustier 1 would rejoin the modern European cohort.

Body mass of El Sidrón J1 has been assessed at 25.9 (24.31–27.54) kg (Rosas et al. 2017 SI:23–24). This places El Sidrón J1 within the upper end of modern European range.

¹ $\log_e(W) = -5.933E-8 \times h^4 + 2.845E-5 \times h^3 - 0.004939 \times h^2 + 0.3857 \times h - 8.892$, where W = weight in kg and h = height in cm (Mateos et al. 2014:171).

Table 6.6: *Body mass, Neanderthal immature individuals*

Neanderthal						Modern human, comparable ages ²	
Specimen	Age (y)	Stature (cm) from Mateos et al. 2014	Alternative stature (cm) ¹	Body mass (kg) using Mateos et al. 2014	Alternative body mass (kg)	Age (y)	Weight European (kg)
Le Moustier 2	0	49.1	50.4 (49.1–51.6)	3.20	-	0	3.32 – 3.53
Mezmaiskaya 1	0–0.1	53.4	52.2 (51.0–53.4)	4.35	-	0.1	3.75 – 4.50
La Ferrassie 4bis	0–0.2	53.4	52.2 (51.0–53.4)	4.35	-		
Kiik-Koba	0.5	64.0	64	7.58	-	0.5	7.00 – 8.50
Shanidar 10	1–2	79.6	79.6 (79.5–79.6)	11.97	-	1.0	9.46–10.90
Dederiyeh 1	1.5	81.7	82.3 (81.15–83.48)	12.48	-	1.5	10.85 – 12.40
Dederiyeh 2	2.0	76.0	75.4	11.06	-	2+	11.6–13.4
Roc de Marsal	2.25	83.6	82.4 (81.93–82.78)	12.92	-	-	-
La Ferrassie 6	3	85.3	82.5 (81.73–83.34)	13.30	-	3+	13.6–16.1
Cova Negra (Femur I)	5–6	97.9	93.6 (93.1–94.0)	16.05	12.4–13.5 ⁷	5+	17.2–20.0
El Sidrón J1	7.7	-	110.6 (104.98–120.00)	19.36 ³	25.9 ⁴ (24.31–27.54)	7+	21.3 – 26.4
Teshik-Tash	8	-	112.9	19.81 ³	25.9 ⁸	8+	22.4 – 29.0
Le Moustier 1	12	-	138.5	34.45 ³	72.4 (60.0–80.0) ⁵ 81.2 (56.1–117.6) ⁶	11+	30.1 – 40.0
-	-	-	-	-	-	12+	32.6 – 44.3
Ages from Appendix A. ¹ Column 4 alternative stature from Table 6.1 and sources there. ² Columns 7–8 European age/weight ranges from Eveleth and Tanner (1990:230–235). ³ Body mass also calculated for juveniles using method of Mateos et al. (2014).				⁴ Rosas et al. (2017 SI:23–24), from J1 skeleton. ⁵ Arsuaga et al. (2015 SI: section 2.2), from femoral head size. ⁶ Kappelman (1995:254), cited range is 95% CI. ⁷ Arsuaga et al. (2007). ⁸ Copied from similar-age El Sidrón J1.			

The body mass of Le Moustier 1 is calculated to be 72.4 kg by Arsuaga et al. (2015 SI).¹ This is just above their combined-sex mean for adult Neanderthals of 72.1 kg. Kappelman (1995) assigns this subject a span of estimates centred on 81.2 kg. Values for other individuals in his 1995 paper tend to be high compared with other studies. Bearing in mind that Le Moustier 1 is ~15% shorter than mean stature for adult male Neanderthals, even 72.4 kg seems very high. It is double the expectation for modern human children at his age and almost three times the body mass of El Sidrón J1 (Table 6.6), only four years younger.

Left femoral head diameter of Le Moustier 1 is 48 mm, just below the mean (49.3±4.2 mm) for European Neanderthal adults (Thompson and Nelson (2005b:275). Neanderthals have more robust femoral and tibial diaphyses in relation to articular sizes than modern humans and a higher percentage of cortical area in cross-section of the midshaft (Ruff et al. 1993a). This trait also applies to the immatures La Ferrassie 6 and Teshik-Tash (Ruff et al. 1994). Possibly such traits rendered Neanderthals heavier than modern humans at equivalent age and height. Yet examination of the Le Moustier 1 skeleton shows that it had not yet developed the full

¹ With 95% confidence interval in table. Body mass = 2.268 × FHD - 36.5: formula by Grine, cited by Ruff et al. (1997:175). Ruff et al. cite alternative formulae deriving body mass from stature and bi-iliac breadth, but insufficient pelvic material has survived (Ullrich 2005b).

muscular hypertrophy typical of Neanderthal adults (Thompson and Nelson 2005b:280). This factor and the small stature make a body mass in the middle of adult range appear excessive.¹

Weight is a less reliable indicator of growth than stature (Tanner 1989:197), because body mass incorporates the entire range of tissues together with blood and other fluids. However, it is informative to compare the weights of specific Neanderthal immature specimens with modern humans at the same ages. Table 6.7 lists the Neanderthal immatures from Table 6.6 excluding the neonates, and gives the percentage attained of male and female Neanderthal mean adult body mass. On the right side are modern human weights at the same ages as the Neanderthals, taken from growth charts for British children (Tanner 1989:196–197), together with their percentages of modern human adult weight, assumed here to be at 19 years.²

While the male modern humans are slightly heavier in infancy than the females, females begin to outweigh males in the juvenile stage. Sex of most Neanderthal immatures is unknown, although El Sidrón J1 is male and the other juvenile and the adolescent are thought to be male. On the assessed ages and weights, the pre-adolescent Neanderthals generally keep pace with the modern humans in absolute weight, male and female. In percentages of adult female weight, they almost keep pace. However, they are consistently behind the modern humans in percentages of adult male weight. This result may reflect slow progression to achieve the greater adult sexual dimorphism in mean body mass in Neanderthals (difference ~15 kg versus ~7 kg for recent humans), as presented in Tables H.1 and H.2.

The adolescent appears anomalous, especially with the weight 72.4 kg. The value 34.45 kg, not provided by Mateos et al. (2014) but obtained by extrapolating using their method, matches the modern human male mean at this age. However, an intermediate value somewhat higher may be closer to the truth. For illustration, using the expectation of 57.3% of adult weight for a modern human male at 12 years (Tanner 1989:196–197), with Neanderthal mean adult male weight at 75.4 kg Le Moustier 1 should weigh ~43 kg (Table 6.7). Of course the assumption of 57.3% of adult weight at 12 years may be unwarranted for Neanderthals, although some credibility is given by the stature of this individual fitting the expected percentage (~84%) of adult stature for his age.

Growth in body mass of the Neanderthals is graphed in Figure 6.6, along with low and high modern human series. These are weights from the 3rd centile males (lower than females at preadolescent ages) and 97th centile females (higher than males), together with the adult male and female data points for these centiles, taken from Tanner (1989:196–197). From Tanner's charts data points for modern humans are chosen matching the ages of the Neanderthal individuals. At no point do the Neanderthal infants, early children or juveniles exceed or fall below modern human limits. The relative stasis between ~2 and ~4 years is shared by all three groups.

From these comparisons evidence is lacking that Neanderthal immatures were growing more rapidly than modern humans at any age, unless one accepts the high body mass estimates for the adolescent, which seem disproportionate relative to its stature, the body mass of the younger individuals, and the adult mean body mass.

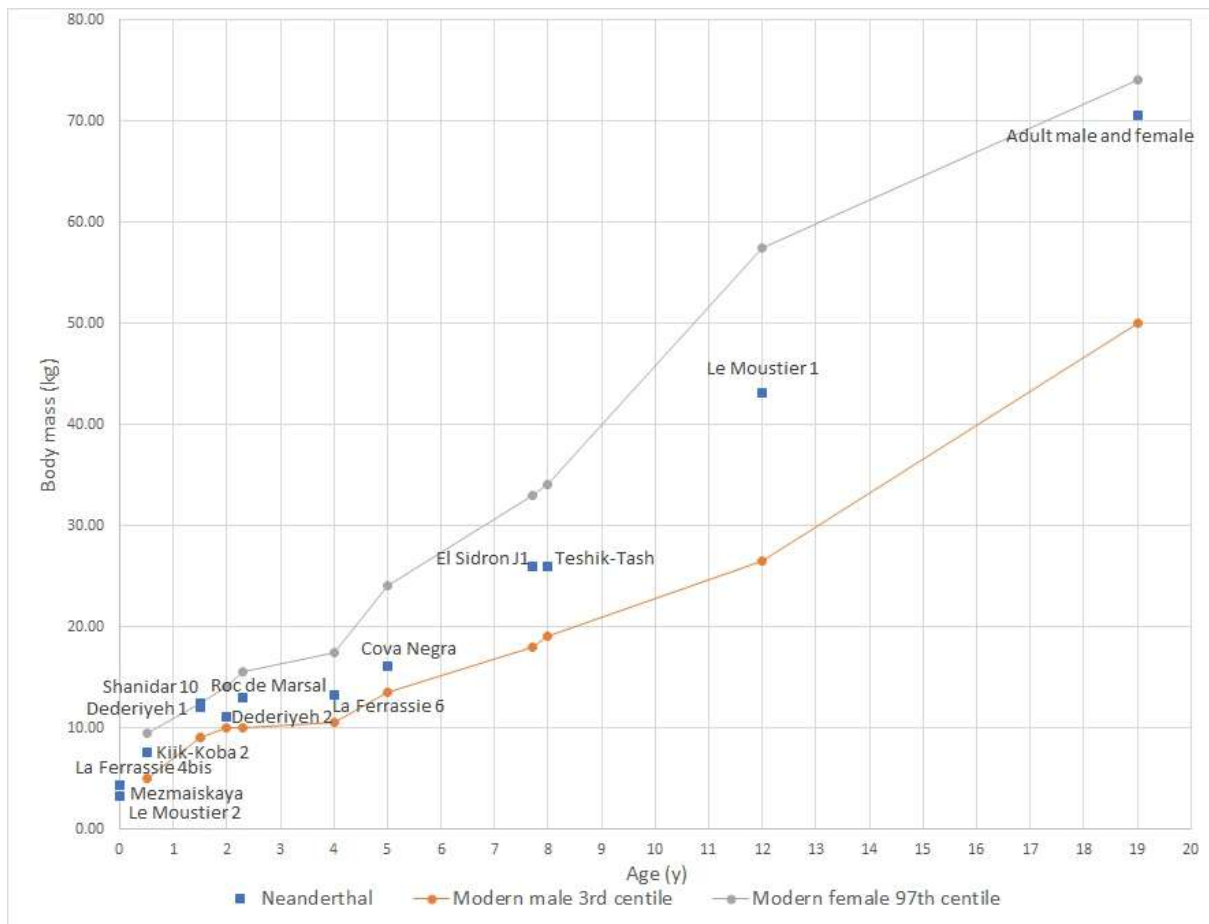
The uncertainties of chronological ages, of deriving weight from height, of deriving body mass from femoral head diameter, and of cross-species comparison require results to be treated with caution (cf. R.J. Smith 1996).

¹ The body mass index of a modern child 138.5 cm tall but weighing 72.4 kg is ~38, excessively obese. Healthy range is 15–21. The Le Moustier 1 femur is well short of adult size (§7.6 Table 7.11) but the femoral head appears to be maturing faster than the length of the whole bone (Thompson and Nelson 2005:274–275).

² To justify use of these British values from Tanner: (1) they are readily accessible, (2) they date from a period before the current epidemic of obesity, (3) Neanderthals lived in temperate as well as cold climates.

Table 6.7: Percentage of adult body mass at given ages of Neanderthal immatures, compared with modern humans at same ages

Neanderthals				Age (y)	Modern humans							
Specimen	Body mass (kg)	% adult male mean	% adult female mean		Male 50th centile % adult male mean	Female 50th centile % adult female mean	Male body mass (kg)			Female body mass (kg)		
							50th centile	3rd centile	97th centile	50th centile	3rd centile	97th centile
Kiik Koba	7.58	10.05	12.55	0.5	11.3	12.7	7.0	5.0	9.5	7.0	5.0	9.5
Shanidar 10	11.97	15.88	19.82	1.5	17.7	19.1	11.0	9.0	14.0	10.5	9.0	12.5
Dederiyeh 1	12.48	16.55	20.66	1.5	17.7	19.1	11.0	9.0	14.0	10.5	9.0	12.5
Dederiyeh 2	11.06	14.67	18.31	2.0	19.4	20.9	12.0	10.0	15.0	11.5	9.5	14.0
Roc de Marsal	12.92	17.14	21.39	2.3	19.8	21.8	12.3	10.0	16.0	12.0	10.0	15.5
La Ferrassie 6	13.30	17.64	22.02	3.0	22.6	24.5	14.0	10.5	18.0	13.5	10.5	17.5
Cova Negra	16.05	21.29	26.57	5.5	30.6	34.5	19.0	13.5	23.5	19.0	14.0	24.0
El Sidrón J1	25.90	34.35	42.88	7.7	37.1	41.8	23.0	18.0	32.0	23.0	18.5	33.0
Teshik-Tash (using El Sidrón J1)	25.90	34.35	42.88	8.0	38.7	43.6	24.0	19.0	33.0	24.0	19.5	34.0
Le Moustier 1	34.45 ¹	45.69	57.04	12.0	57.3	71.8	35.5	26.5	51.0	39.5	29.0	57.0
	72.40 ² 60.0 ²	96.05 79.60	119.87 99.34									
	43.17 ⁴	57.30	68.53									
Adult female mean	60.40 ³									55.0	44.0	74
Adult male mean	75.38 ³						62.0	50.0	81.0			
Modern human weights from Tanner (1989:196–197). Neanderthal immature data from Table 6.6, but see further notes. ¹ Calculated using method of Mateos et al. (2014). ² Arsuaga et al. (2014 SI:61; 2015 SI: Section 2.2). 60 kg is the lower limit of the 95% CI. ³ Tables H.1 and H.2, calculated from values for individuals in Will et al. (2017 SI), using only specimens assigned male or female by those authors. ⁴ Derived from Neanderthal adult male mean assuming modern human percentage at this age (57.3%).												



Data from Table 6.7

Figure 6.6: Body mass, Neanderthal immatures, comparison with modern humans

6.4 Neurocranium

Neurocranial dimensions of subadults together with European adult Neanderthals are listed in Table 6.8. In the graphs following, Neanderthal adult means are from Minugh-Purvis (1988).

Spy 1 and 2 are both robust, but Spy1 is considered female (Toussaint and Pirson 2006:378). La Quina H5 has usually been considered female, but according to Trinkaus (2016) its robusticity indicates that it may be male.

Figure 6.7 shows maximum cranial length from glabella to opisthocranium. Most of this length is accounted for by the endocranium, so the measurement is large even in younger immatures. However, some of the length is due to thicker bone, especially at glabella, which forms the medial portion of the supraorbital torus. On the measurement of Thompson and Illerhaus (2005) graphed here, Le Moustier 1 at 12 years already lies above the best-fit line leading to “adult” size at 17 years. Even so, this individual appears to have 3 mm additional growth to accomplish to equal La Quina H5, and up to 13 mm to equal La Chapelle. On the alternative measurement (Table 6.8) of Ponce de León and Zollikofer (2005), not graphed here, Le Moustier 1 has already exceeded La Quina H5, almost equalling Circeo 1.

Growth of cranial breadth is shown in Figure 6.8, cranial height in Figures 6.11 and 6.12. In Figure 6.11 the lower measurements of Teshik-Tash and Le Moustier 1 are taken from Thompson and Illerhaus (2005). In Figure 6.12 the higher Teshik-Tash value is from Minugh-Purvis (1988) and the higher Le Moustier 1 value from Ponce de León and Zollikofer (2005).¹

Maximum frontal breadth (Figure 6.9), measured on the coronal suture and indicating the lateral extent of the frontal lobes, varies greatly between individuals, masking any degree of growth with age. The wide range of adult dimensions, however, leaves the possibility that subadults with smaller and larger breadths may have been on course to become adults with breadths respectively in the lower and upper reaches of the distribution.

In contrast, biasterionic breadth (Figure 6.10) increases during the juvenile stage, as observed by Heim (1982:42,130–131,159) for the Neanderthal immatures and by Minugh-Purvis (1988:viii,248–249,251,266) for both Neanderthals and Middle and Upper Palaeolithic *Homo sapiens*, but not for recent humans. She attributes this development to continuing posteriorly directed growth of the brain (i.e. occipital lobe and posterior regions of the parietal and temporal lobes) in both Palaeolithic populations.

Cranial circumference (Figure 6.13) and total sagittal arc from nasion over the frontal, parietal and occipital bones to the posterior margin of the foramen magnum (Figure 6.14) both appear to show clear increase with age (cf. §4.6.2, Table 4.9).

¹ The large cranial breadths (M8) of some adult Neanderthals are much exceeded by those of some crania from northern China. Xujiayao 6 (dated 160–200 ka) is long and low and has an endocranial volume (ECV) ~1700 cm³ and M8 175 mm (Wu X.-J. et al. 2022). Xuchang 1 (105–125 ka) with ECV ~1800 cm³ has M8 173.5 mm (Li et al. 2016 SI: 61).

Table 6.8: Neurocranial dimensions, immatures and adults (mm)

Specimen	Age (y)	M1 glabella–opisthocranion length	M8 maximum cranial breadth	M10 maximum frontal breadth	M12 biasterionic breadth	M17 basion–bregma height	M23 horizontal cranial perimeter	M25 total sagittal arc nasion–opisthion
Pech de l’Azé	1.5	169	126.5 130 ^{1,12}	112 ¹ 109 ⁵	101 ⁵	110 118 ¹ 113 ¹²	482 ¹	
La Ferrassie 8	1.5				95 ¹			
Roc de Marsal	2.3	174 ¹	130 ¹	118 ^{1,5}	109 ¹	118 ¹	502 ¹	339 ¹
Subalyuk 2	2.5			112 ⁵	100 ⁵		470 ^{1,5}	343.5 ¹
Engis 2	3.0	171 176 ^{1,10} 164 ¹³ 188 ¹⁴	130	113.6 ¹ 115 ⁵	105 ¹ 106 ⁵	112 115 ¹		332 ⁵
Gibraltar 2	4.6	184 ³	140 ⁴ 150 ³ 145 ¹⁰	125 ^{1,5,10}				
La Quina H18 ¹	5.5	172	131	106 ^{1,10} 108 ⁵	102.8 ⁵	120	510 ^{1,5}	
Carigüela	6			120 ¹¹				
Krapina 1	6–8			121 ¹¹				
Le Lazaret	8–9		132 ⁹					
Teshik-Tash	8.0	185	143 145 ¹⁰	120 ^{1,5,10}	118 ¹ 116 ⁵	124 129 ^{1,7} 128 ⁵ 132 ⁶	530 ^{1,5}	355 ¹
Le Moustier 1	11.86	197 202.4 ² 196 ⁸	146.7 152.4 ² 150 ⁸	115 ⁵	120 ¹ 124 ⁵	120.9 127.4 ² 128.5 ⁸	534 ^{1,5}	371 ¹
La Chapelle-aux-Saints	Adult	210	156		130.5 ¹	128	600 ¹	357 ¹
Circeo 1	Adult	203.5	152		124 ¹	123	590 ¹	
La Ferrassie 1	Adult	207	158.5		125 ¹	135	592 ¹	367 ¹
Neanderthal 1 (Feldhofer) ¹	Adult	199	146.7				578 ¹	
La Quina H5	Adult	200	139		109.3 ¹		558 ¹	
Spy 1	Adult	200.4 ¹	144.3 ¹		121.2 ¹		589 ¹	
Spy 2	Adult	200 ¹	153.2 ¹		131.2 ¹			
Gibraltar 1	Adult		144					
Mean	Adult	200 (179–209) ⁵ 203.1 ¹⁰	149.4 (138–158.5) ⁵ 150.2 ¹⁰	120.7 (108–127) ⁵ 123.6 ¹⁰	120.3 (108.5–129.9) ⁵	126.2 (111–135) ⁵	576.3 (522–610) ⁵	
Ages from Appendix A. Dimensions from Thompson and Illerhaus (2005) unless otherwise stated. ¹ Madre-Dupouy (1992). ² Ponce de León and Zollikofer (1999, 2005). ³ Estimate by Buxton (1928). ⁴ Thompson and Illerhaus (1998). ⁵ Minugh-Purvis (1988). ⁶ Gremyatskii (1949:146,181). ⁷ Tillier (1983:53). ⁸ Weinert 1925, cited by Thompson and Illerhaus (2005:229). ⁹ De Lumley (1973:70). ¹⁰ Tillier (1988:262). ¹¹ Minugh-Purvis et al. (2000:402). ¹² Tillier (1996:115). ¹³ Cuzzo (2005:107). ¹⁴ Fraipont (1936:33).								

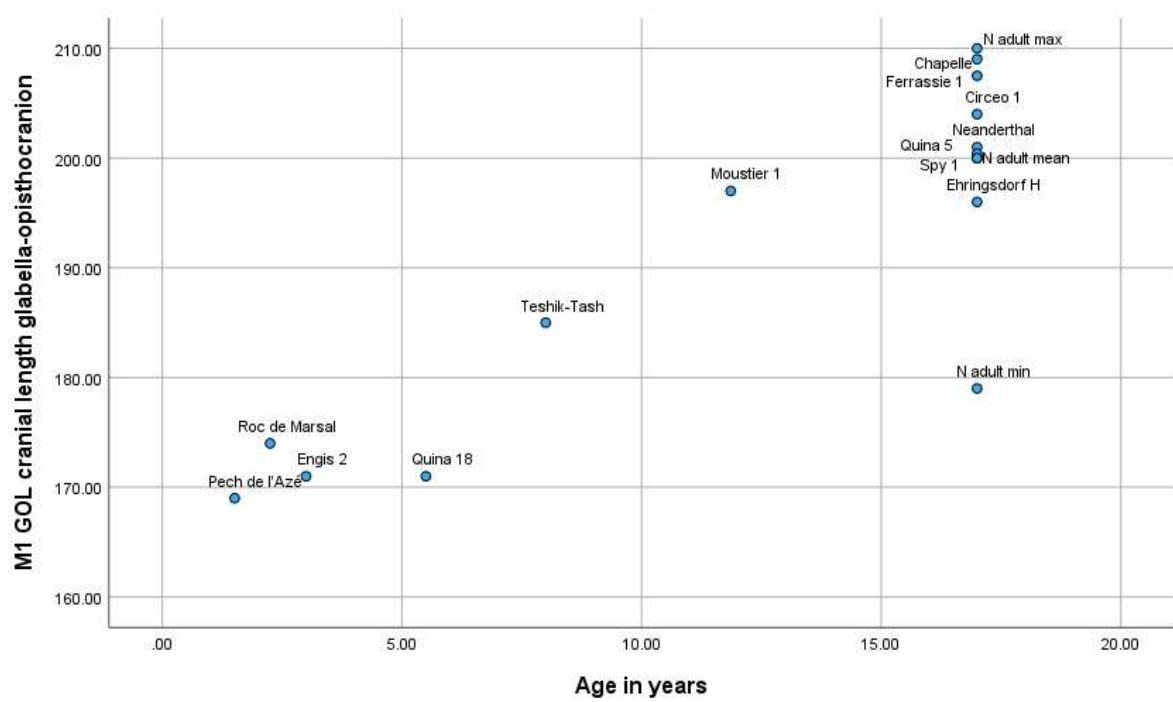


Figure 6.7: Maximum cranial length (mm), Neanderthal immatures

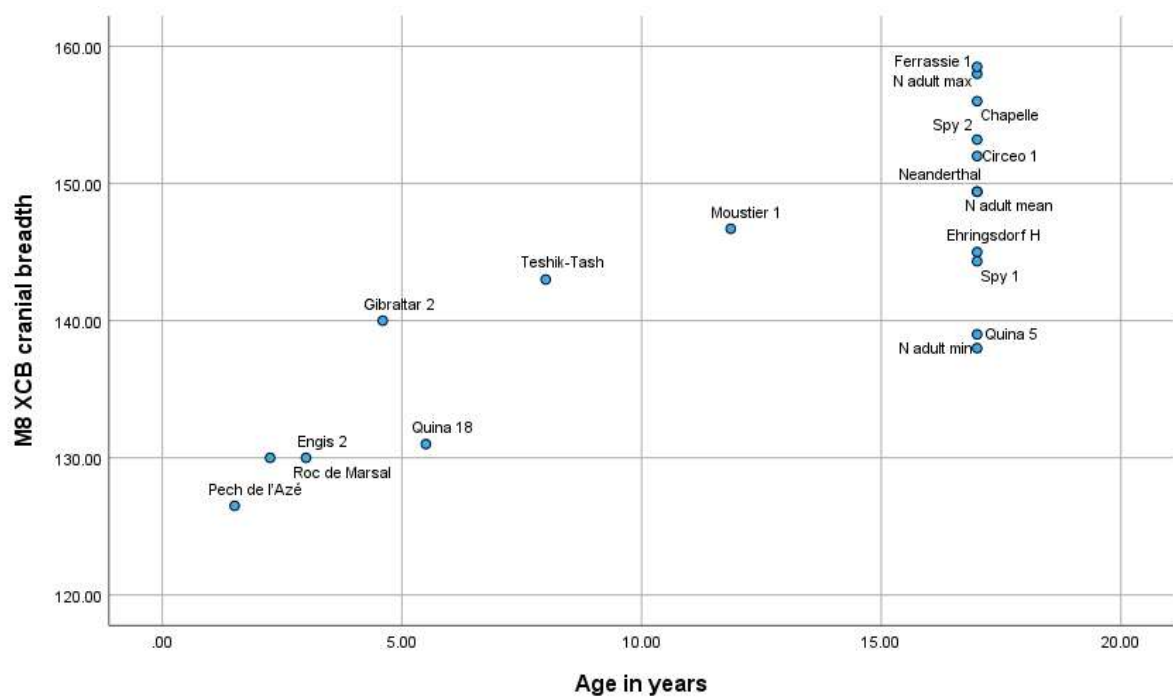


Figure 6.8: Maximum cranial breadth (mm), Neanderthal immatures

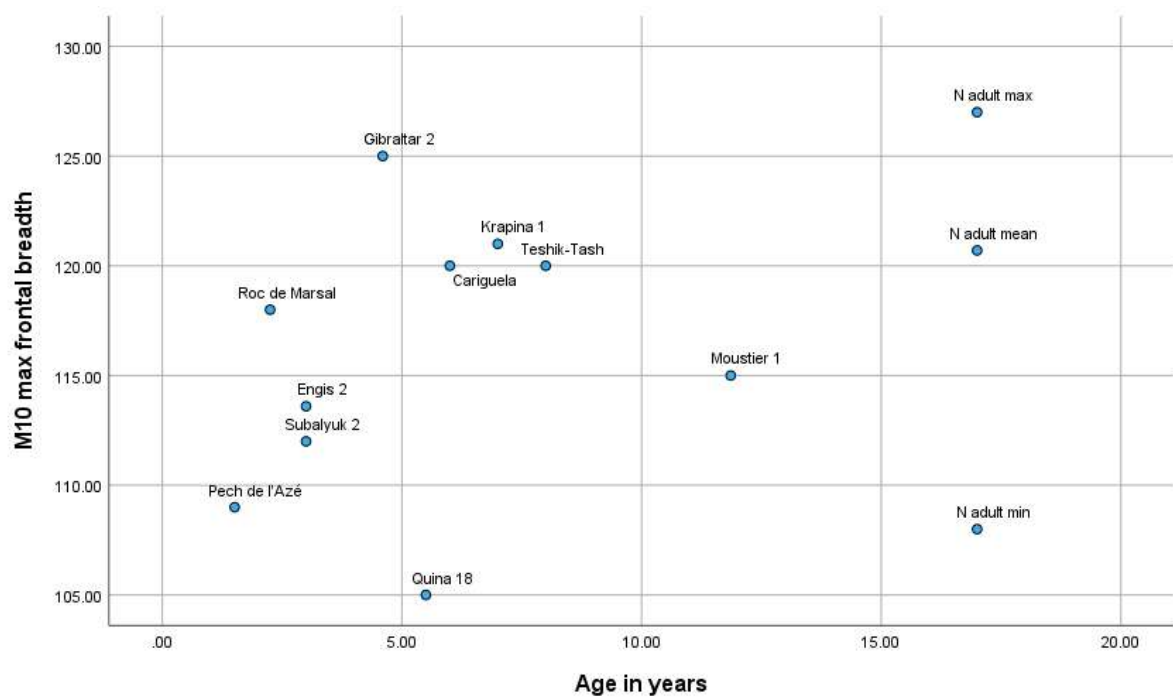


Figure 6.9: Maximum frontal breadth (mm), Neanderthal immatures

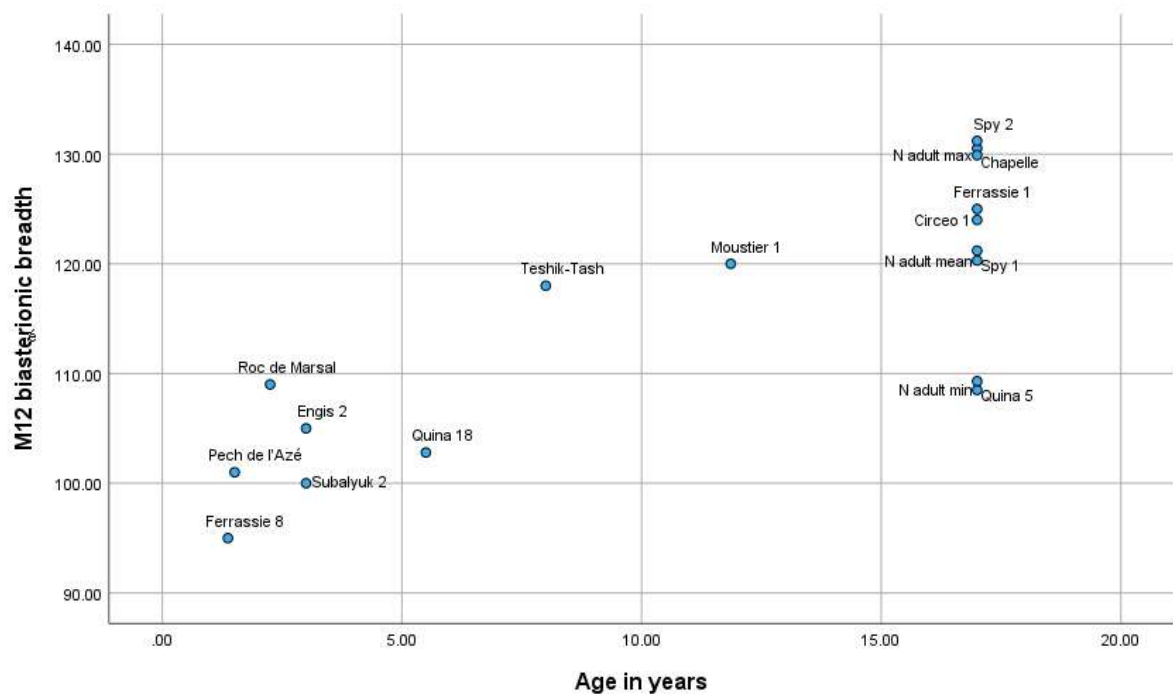


Figure 6.10: Biasterionic breadth (mm), Neanderthal immatures

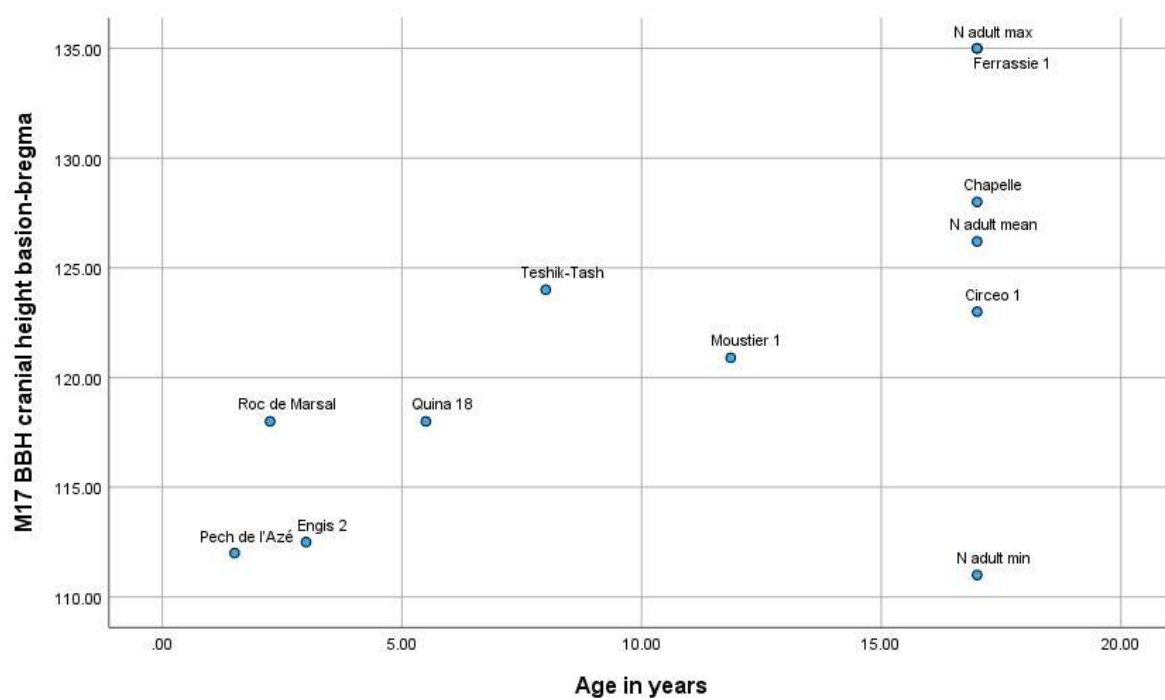


Figure 6.11: Cranial height basion–bregma (mm), lower estimates for Teshik-Tash and Le Moustier 1

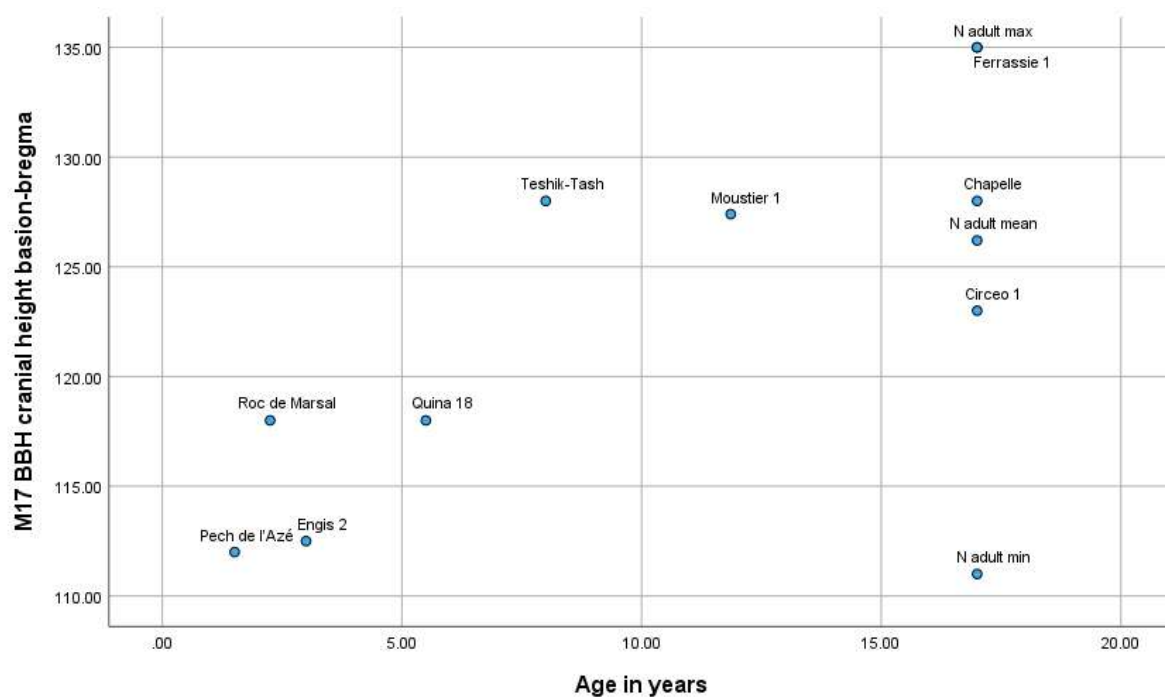


Figure 6.12: Cranial height basion–bregma (mm), higher estimates for Teshik-Tash and Le Moustier 1

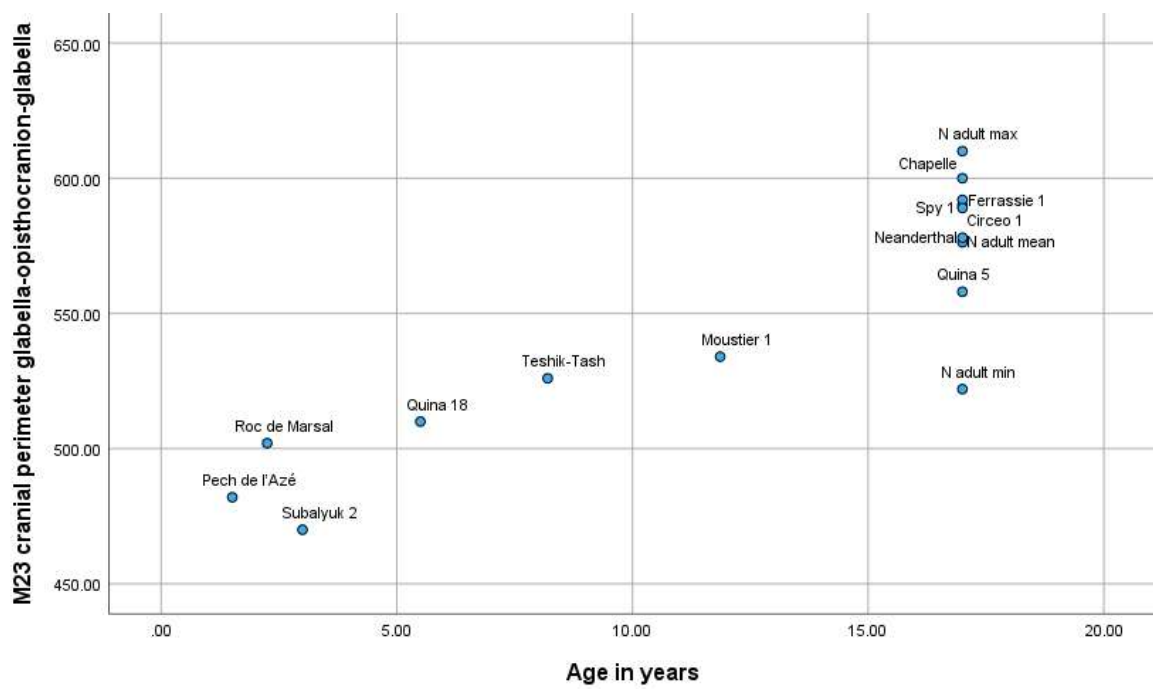


Figure 6.13: Cranial circumference (mm), Neanderthal immatures

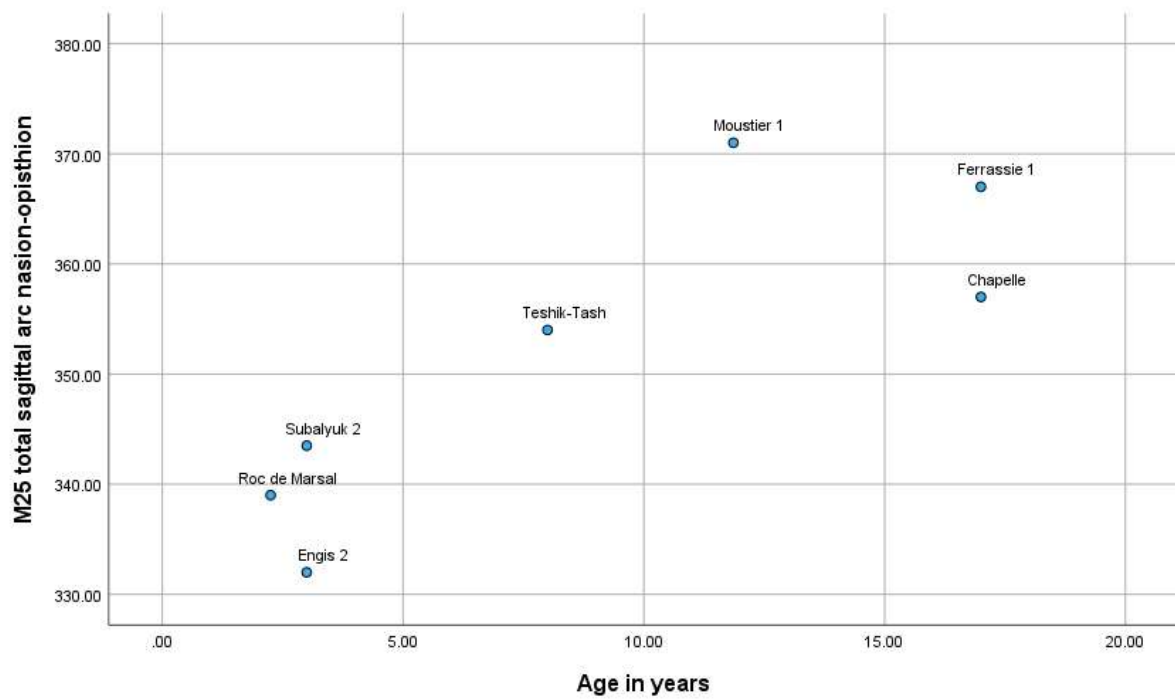


Figure 6.14: Total sagittal arc (mm), Neanderthal immatures

6.5 Viscerocranium

6.5.1 Upper face: orbits and nose

Basic measurements of the orbital and nasal areas are listed in Table 6.9,¹ and graphed in Figures 6.15–6.21.

Table 6.9: Orbital and nasal measurements (mm)

	Age (y)	M44 Biorbital breadth internal	Biorbital breadth external	M50 Interorbital breadth	M51 orbital breadth	M52 orbital height	M54 nasal breadth	M55 nasal height nasion–nasospinale
Pech de l'Azé	1.5	75	86.2 ⁷	19 23.6 ⁷	32.5 (R34, L31) 33 ³ 30 ⁵	33.5 (R33, L34) 33.4 ³ 38 ⁵	19.5	36.5
Roc de Marsal	2.25	90	97 ⁷	24.5 23 ⁵	34.5 L34, R35)	35	21.8	42.6
Engis 2	3		90 ⁷	24.5 ¹	30.2 ³			
Subalyuk 2	3		85.8 ⁷	10.7 ⁷	38.4 ³		23	
La Chaise Suard 15	3–6			24				
Gibraltar 2	4.6		102.6 ⁷	24.5 ¹	35 ³			
La Quina H18 ¹	5.5	82	89.6 ⁷	14	32 35 ³ 34.5 (R32, L37) ⁵	34 36.5 ³ 36.5 (R39, L34) ⁵	22.5	45.4
Carigüela	6	99 ³		29.5 ^{3,5} 26.5 ⁴	(35) ⁵	(31) ⁵		
Teshik-Tash	8	83	105.4 ⁷	24.5 22.5 ¹ 25 ⁵	37.5 38 ^{3,5}	33 33 ^{3,5}	29	46
Fate 1&2	9	100 ³		26 ^{1,3}				
Le Moustier 1	12			26.2 ²	45 (R47, L43) 42 ³	41.5 (R41, L42) 42 ³	28	
Gibraltar 1	Adult		117.4 ⁷	23 ⁶				
Galilee	Adult			28 ⁶				
Krapina C	Adult		122.2 ⁷	29 ⁶				
La Chapelle-aux-Saints	Adult		110.4 ⁷	29 ⁶	47 (R47.5, L46.5)	38.5 (R39, L38)	34	61
Neanderthal 1 (Feldhofer)	Adult			30 ⁶				
Sala	Adult			30 ⁶				
Spy 1	Adult		122 ⁷	32 ⁶				
Tabun 1	Adult		115.5 ⁷	32 ⁶				
La Ferrassie 1	Adult		126.2 ⁷	32 ⁶	41.5 (R43, L40)	36.5 (R36, L37)	34	62
La Quina H5	Adult		106.5 ⁷			38		
Circeo 1	Adult		124.1 ⁷		49	37	36	66
Mean (Range)	Adult	110.1 (98.5–118) ³		29.9 (23.1–36.6) ³	44.4 (39–49) ³	37.9 (36.1–43) ³	34.5 (32.3–38) ³	62.6 (58–67) ³
Data from Madre-Dupouy (1992) unless otherwise stated. Left and right orbital measurements are given if available. Adult means are from Minugh-Purvis (1988:223,228) and may not coincide with means of specimens listed here. ¹ Coqueugniot et al. (1996). ² Thompson and Illerhaus (1998). ³ Minugh-Purvis (1988). ⁴ Tillier (1982). ⁵ De Lumley (1973:284,287). From the Carigüela frontal De Lumley estimates orbital breadth and height. ⁶ Trinkaus (1973). ⁷ Williams and Cofran (2016 SI). These authors measured biorbital breadth to the outer borders of the orbits (~frontomale temporale), giving an upper facial breadth.								

¹ Madre-Dupouy's (1992:112,265) Tables 21 and 55 appear to have the orbital breadths under M51 (breadth) but labelled "hauteur" or "longueur" and orbital heights under M52 (height) but labelled "largeur". For the youngest specimens the breadth and height are similar but for adults they differ considerably. Accordingly, here the values given by Madre-Dupouy under M51 and M52 are taken to be breadth and height respectively, except for Roc de Marsal, which was directly measured by that author. If transposed, some adult values would lie outside the minimum and maximum given by Minugh-Purvis (1988).

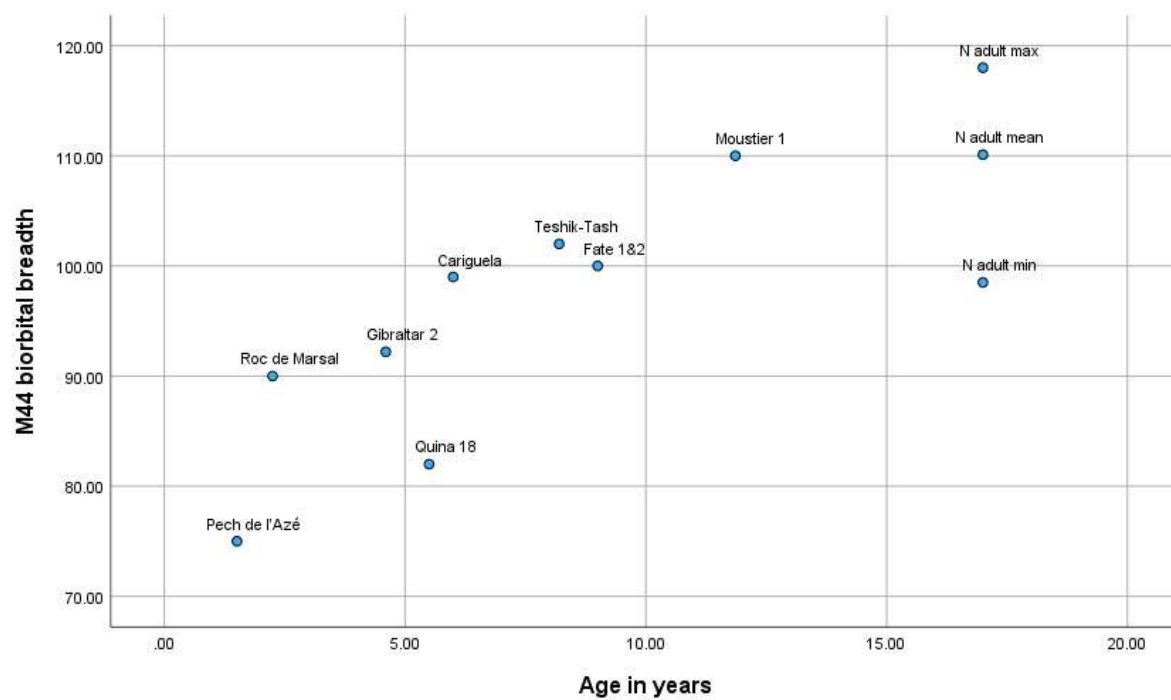


Figure 6.15: Biorbital breadth (mm), Neanderthal immatures

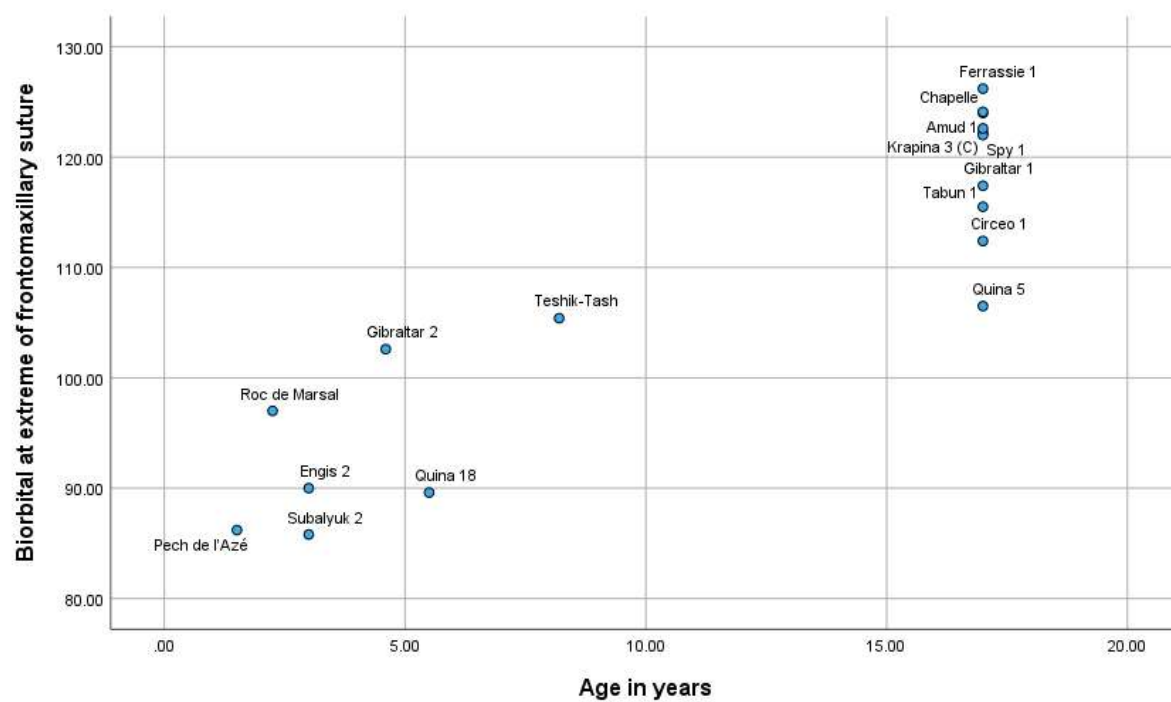


Figure 6.16: Biorbital external breadth, Neanderthal immatures

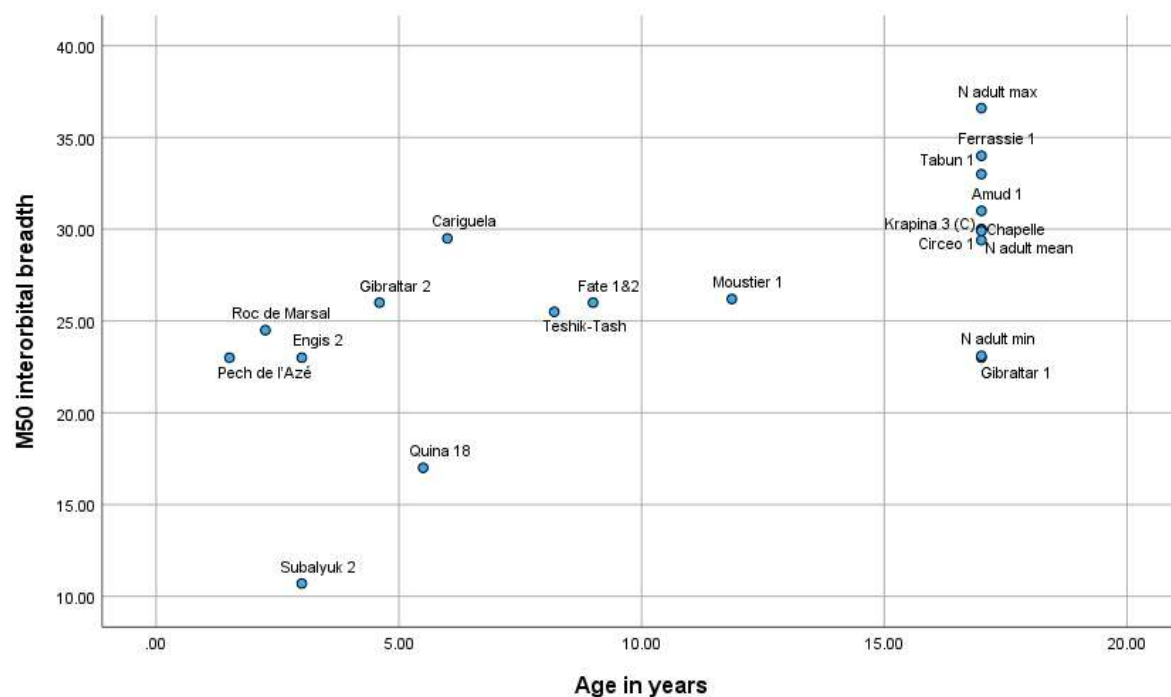


Figure 6.17: Interorbital breadth (mm), Neanderthal immatures

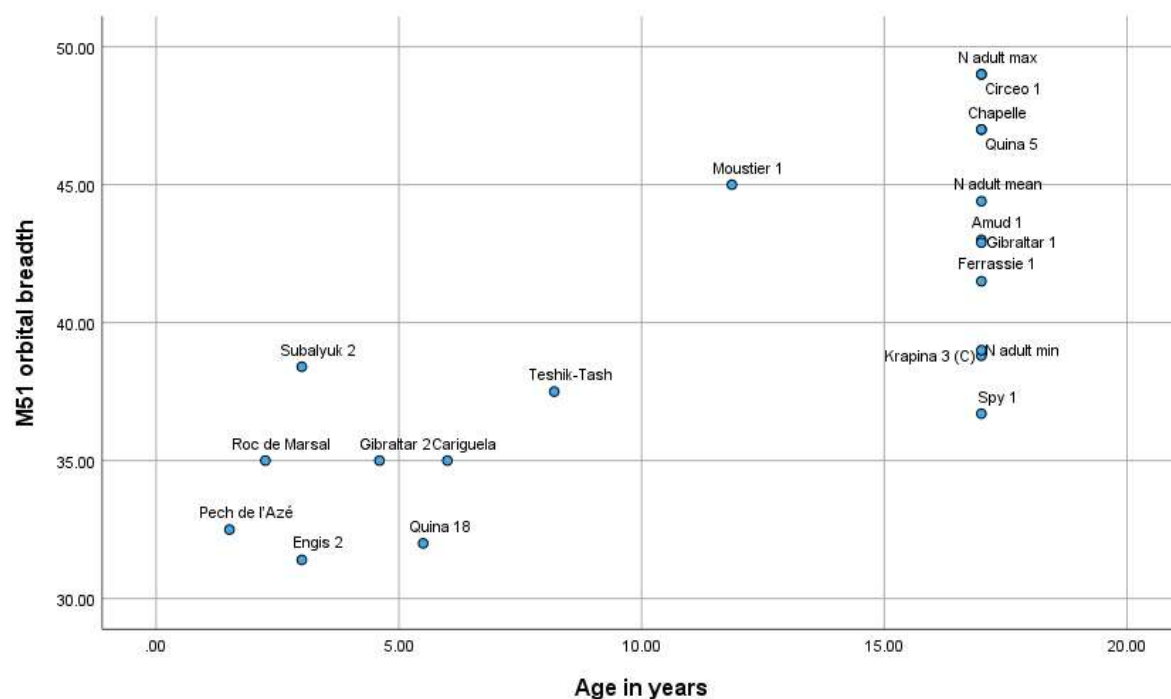


Figure 6.18: Orbital breadth (mm), Neanderthal immatures

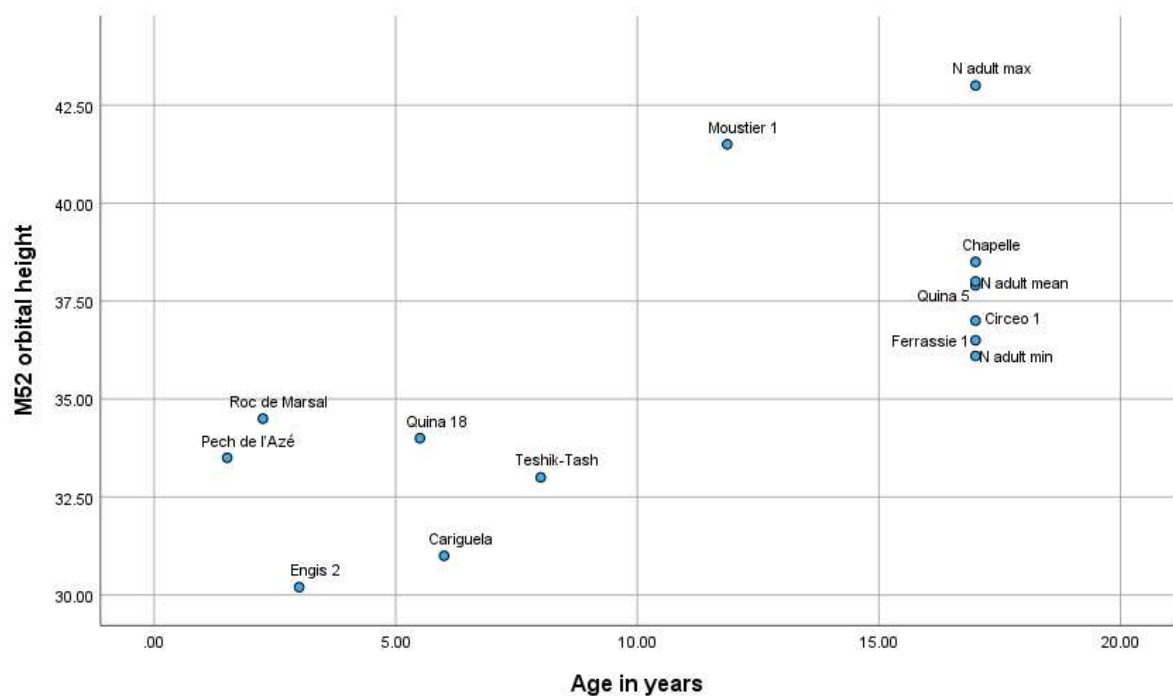


Figure 6.19: Orbital height (mm), Neanderthal immatures

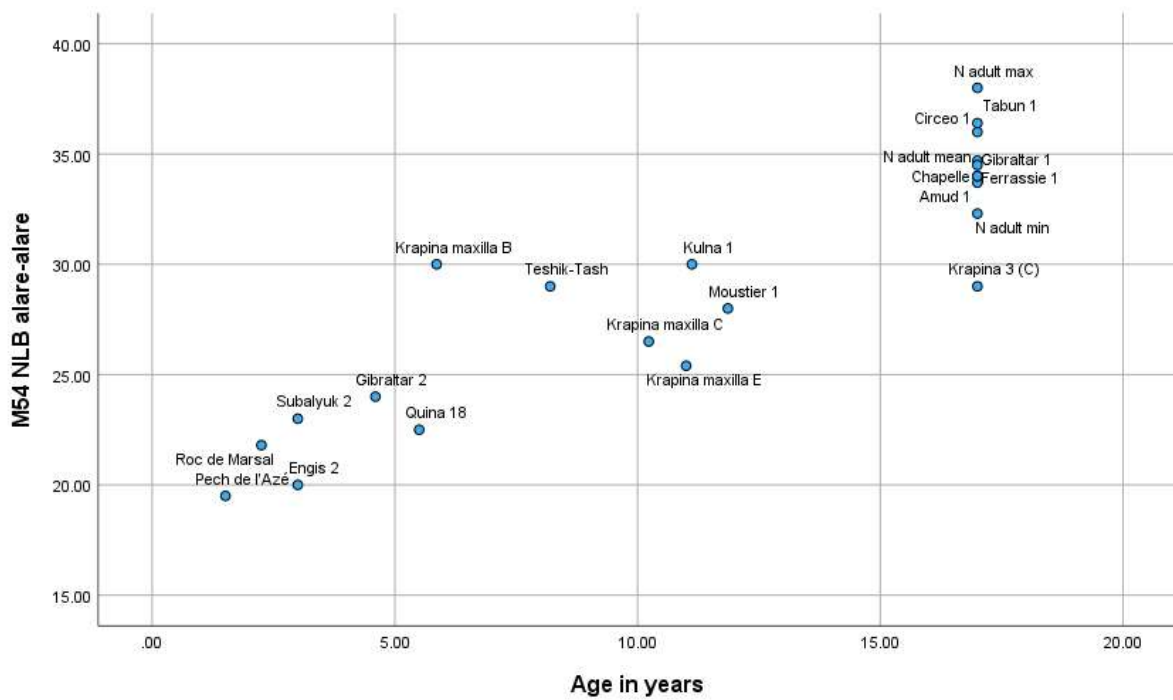


Figure 6.20: Nasal breadth (mm), Neanderthal immatures

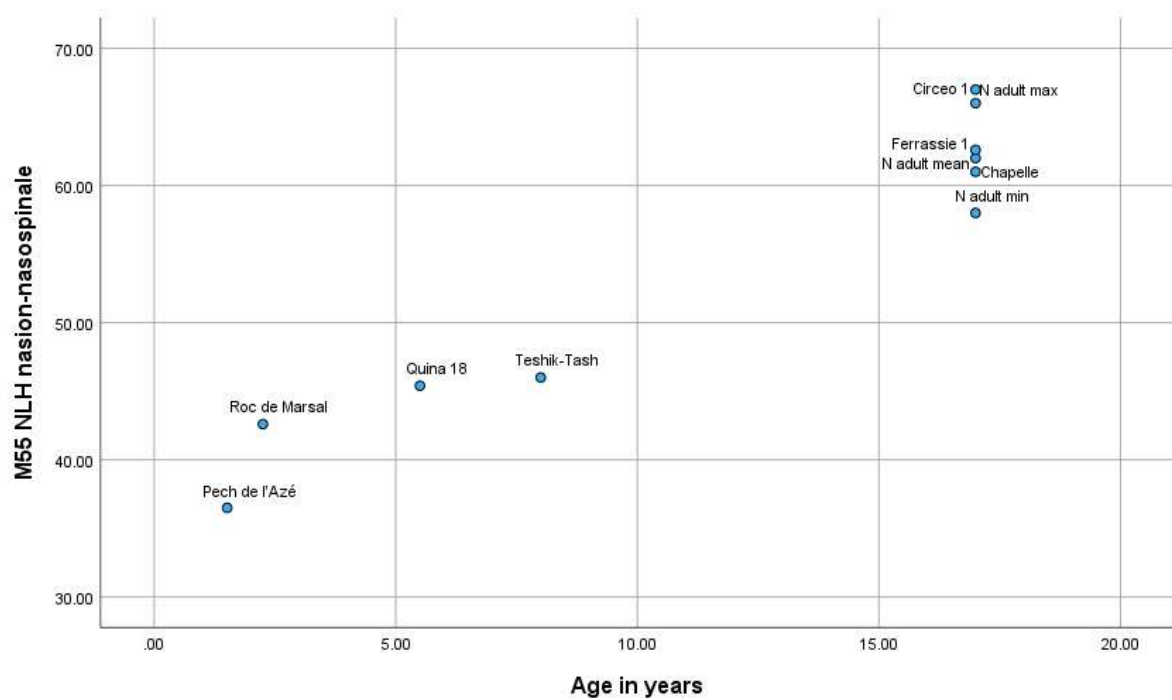


Figure 6.21: Nasal height (mm), Neanderthal immatures

While biorbital breadth increases steadily from infants to adults, interorbital breadth, still rising with age, is more similar across the subadults. Orbital breadth and height are almost equal in the youngest specimens but in adults orbital breadth is generally larger than height. Neanderthal infants and children have much larger orbital apertures than recent humans owing to greater orbital height, but anteroposterior depth of the orbit may be less in Neanderthal subadults than in recent humans (Table 6.10).

Table 6.10: Orbital dimensions, Neanderthal subadults, comparison with recent humans

	Modern French			Neanderthal	
	Orbital breadth (mm)	Orbital height (mm)	Anteroposterior depth of orbit (mm)		
4 years	32	29	35		
6 years	38	31	39	33	Carigüela, ~6 years
8 years	39	32	37	31.5	Teshik-Tash, ~8 years
Data from De Lumley (1973).					

6.5.2 Frontal bone morphology, sinuses, supraorbital torus, and recession

The most striking feature of the Neanderthal face in popular culture¹ is the distinctive browridge or supraorbital torus, a plesiomorphic inheritance shared with all previous populations of *Homo* and even early *Homo sapiens*, especially Skhul (~100 ka), but largely lost among *Homo sapiens* since the early Upper Palaeolithic.

Aetiology and function of the supraorbital torus are considered in Appendix I.

Morphology

In Neanderthals the torus forms a continuous bony bar extending across the inferior region of the frontal bone and incorporating the superior orbital margins. It forms an arch above each orbit. Medially it incorporates glabella and laterally it incorporates the orbital trigone (trigonum supraorbitale) at the superior portion of the zygomatic process of the frontal (F.H. Smith and Ranyard 1980:591; Bulygina 2007:222). While in *Homo erectus* glabella is as prominent as the lateral parts, in Neanderthals the supraorbital and lateral components are more prominent and there is a depression at glabella separating the two arches (Athreya 2009:797,799).

In modern humans the trigone at the inferolateral corner of the frontal squama is normally undistinguished and flat with no projection; and projection of the lower frontal region is not continuous but divided into oval supraciliary eminences on either side of glabella with a faint supraorbital component inferolateral to these along the superior orbital margin. In living humans the largest supraorbital structures, sometimes forming a true continuous torus, but with distinct supraciliary and supraorbital components, are found in Australian Aboriginals, although other populations such as New Guineans and even Fuegians have shown considerable development at lower incidences (Larnach and Mackintosh 1970). Some, but not all, *Homo sapiens* crania from the European Early Upper Palaeolithic such as those recovered at Mladeč, Předmost and Brno (Brünn) have continuous tori (Bulygina 2007; F.H. Smith and Ranyard 1980).

Earlier *Homo sapiens* from the Middle Palaeolithic in the Levant (~110 ka) and from Morocco (~315 ka) have continuous tori. In *Homo heidelbergensis/rhodesiensis* from the Middle Pleistocene the torus is similar to that of Neanderthals but often much larger, and in Asian *Homo erectus* the torus takes on a more rectilinear form without arching (Aherne 2015:172).

Frontal sinuses

The frontal sinuses have relevance to supraorbital morphology, because in most extinct forms of *Homo* the greater part of their volume is found in the interior of the torus. In modern humans there appears to be a correlation between sinus development and supraciliary arch development (Minugh-Purvis et al. 2000:400; Trinkaus 1973:28). For archaic *Homo* arguments have been made that the sinus and torus are independent (Tillier 1977:187–188,311). Tillier (1977:183–184) observes that frontal sinuses in Australian Aboriginals are no larger than in modern French, despite the greater osseous supraorbital development in the former.

In modern humans, according to Enlow (1990:112–113), when enlargement of the frontal lobe is much slowed during the juvenile phase, the inner table of the frontal bone ceases to relocate anteriorly while the outer table continues its anterior drift, carried by the expanding nasomaxillary complex (cf. Moss and Young 1960). The resulting space within the diploë

¹ E.g. the movie *William* (2019).

between outer and inner tables allows the frontal sinuses to develop (cf. Bulygina 2007:69). Sinus development begins in the nasofrontal region, i.e. between the orbits and anterosuperior to the ethmoid, extending from the air pockets of the ethmoid (Tillier 1977:177; Aiello and Dean 2002:40; Lieberman 2000:101). Tillier (1977:177) states that true frontal sinuses reach the level of the superior orbital rim, expected at 8–9 years in modern humans (cf. Björk 1955:201). According to Vlček (1967:183), frontal sinuses develop around the time of the emergence of the permanent canines, i.e. 9.2–11.2 years (Hillson 2014:234).

In modern human adults, the frontal sinuses, though anteroposteriorly narrow, may extend superiorly into the frontal squama (Björk 1955:201; Tillier 1977), while in Neanderthals anterolateral extension of the sinuses pneumatizes the supraorbital torus itself rather than the squama posterosuperior to it (Tillier 1977). Within the torus the sinuses generally reach only as far laterally as the midpoint of each orbit (Tappen 1978:4). However, in individuals with large tori, such as La Ferrassie 1, Spy 1 and La Quina H5, they reach beyond the orbital midpoint within the torus, at least unilaterally, and in these cases they also invade the frontal squama or at least the region posterior to the supratrochlear sulcus (Vlček 1967; Tillier 1977). In Neanderthals the supratrochlear sulcus arguably corresponds to the squamal region immediately superior to the supraciliary eminences in recent *Homo sapiens*.

Neanderthal tori contrast with those of *Homo erectus*, which may be pneumatized but are often solid bone (Tillier 1977; Aiello and Dean 2002:203). The largest and most pneumatized supraorbital tori are found in Middle Pleistocene hominins assigned to *Homo heidelbergensis/rhodesiensis*, of which the large males Kabwe and Petralona are the most extreme examples (Tillier 1977; Stringer 1983; Rightmire 2012). Their large, projecting tori are almost entirely occupied by extensive sinuses which pass beyond the orbital midpoints almost to the lateral trigones and also extend superiorly into the squama (Seidler et al. 1997; Tillier 1977). The Neanderthal adult condition is a reduced development of the *Homo heidelbergensis* pattern. In contrast, modern human sinuses do not typically manifest the anteroposterior expansion with age seen in archaic hominins (Prossinger et al. 2005:145).

Vlček (1967:182–183) examined frontal sinus development in immature as well as adult Neanderthals. His observations and others are summarized in Table 6.11, with revised ages taken from Appendix A. According to the ages listed here, transformative and rapid frontal sinus development takes place during the later juvenile years as the Neanderthal individual approaches puberty. While frontal morphology already differs from that of modern humans at young ages and is very different in adults, there is no indication from this small sample that ages for sinus stages in Neanderthals differ from those of recent humans.

Contrasting with the child and juvenile Neanderthals, the immature *Homo ergaster* from Nariokotome KNM-15000 also ~8 years old (Dean et al. 2014), already manifests frontal sinuses extending into the developing browridges, and other cranial sinuses were also expanded beyond modern human expectation even for its initially determined age 11–12 years (Walker and Leakey 1993:65). In the Nariokotome *Homo ergaster* population, dating at least ~1.3 million years (Brown and McDougall 1993) earlier than the Neanderthals, adolescence may have begun at a younger age than in Neanderthals or *Homo sapiens*.

Table 6.11: Frontal sinus development by age, Neanderthals

Specimen	Age (y)	Volume of sinus (cm ³)	Development
Pech de l'Azé	1.5	-	Inner and outer tables not separated, no trace of pneumatization of the frontal bone. (Metopic suture unfused.)
Dederiyeh 2	2.0	-	No development. ⁶
Subalyuk 2	3–4	0.064 ⁵	-
Gibraltar 2	4.6	-	Bone still uniformly flat in glabellar area, no sinus.
La Chaise Suard S15	3–6	-	Ethmoid cellules present but do not yet occupy all the medial region. ³
La Quina H18	5.5	-	Small cavity a few millimetres across, in nasofrontal region.
Carigüela	5–7	-	Small cavity limited to area inferior to glabella. ¹
Teshik-Tash	8.2	-	Four small cavities like the one cavity of La Quina H18, in nasofrontal region.
Le Moustier 1	11.86	5.3 ⁵	Frontal sinuses resemble those of adults in dimensions and shape (Vlček). Break in outer table of left browridge exposes hollow interior. Sinuses occupy medial portions of developing browridges, but not to midpoints of orbits, and do not extend into squama. ²
Krapina 23, Vindija 224	Adol.		Sinuses well developed. ⁴
Krapina C	Adult	9.34 ⁵	-
Circeo 1	Adult	9.09 ⁵	-
Data from Vlček (1967) unless noted. Ages from Appendix A.			⁴ F.H. Smith and Ranyard (1980:594).
¹ Tillier (1977:303).			⁵ Prossinger et al. (2005:135).
² Thompson and Illerhaus (1998:660–661).			⁶ Ishida and Kondo (2003:271).
³ Coquegniot et al. (1996:13,15).			

Development of the supraorbital torus

Growth with some degree of projection of the supraorbital region takes place in modern humans to the end of adolescence (Fiscella and Smith 2006). For *Homo ergaster/erectus*, with reference to KNM-WT15000, Antón (2002:369) maintains that the supraorbital torus is the last cranial structure to reach adult form. Evidence below suggests this also for Neanderthals.

Inner frontal tables maintain the same sagittal contour from early Middle Pleistocene hominins onward, beginning with Ceprano at ~600 ka and continuing through Neanderthals and *Homo sapiens* despite the extensive differences in contour of the outer table in adults (Bookstein et al. 1999; Schaeffer et al. 2005). Analysis of the outer frontal contour shows from *Homo heidelbergensis* (*sensu lato*) through Neanderthals to recent humans a reduction in frontal bone thickness, taking the form of retraction or posterior repositioning of the outer table toward the inner table (Schaeffer et al. 2005). Three immatures were included in that study: a recent human female aged ~2 years and the Neanderthals Subalyuk 2 and Le Moustier 1. All three immatures and all recent human adults show much less frontal space than all the archaic adults, while recent human adults have less than Le Moustier 1. Surprisingly, Subalyuk 2 has less than the recent human child (Schaeffer et al. 2005:152–153). Even if, as the authors suggest, Subalyuk 2 may be younger than 3 years, it is unlikely to be less than 2 years old. These results confirm that Neanderthal infants have smooth frontals and that major torus enlargement occurs later in ontogeny.

Some supraorbital torus measurements are given in Table 6.12. Projection is measured from the anteriormost point on the endocranial surface of the frontal bone to the corresponding anteriormost point on the toral surface. Thickness is superoinferior diameter. ¹ Reliable ages are

¹ Measurements of projection require access to the endocranium either in the laboratory or by means of radiography or 3D scans. An alternative *supraorbital torus length* defined by Weidenreich is measured anteroposteriorly from the anteriormost point on the torus to the anterior face of the frontal squama (Wolpoff

not available for the Vindija subadult fragments, but they are assessed as adolescent (Ahern and Smith 2004).

Medial thickness in Le Moustier 1 equals the maximum of the adult sample yet the torus lacks the final growth and remodelling to adult form (Bulygina 2007:237). This anomalous result calls into question the significance of *thickness* as a browridge measurement. Some of the adult sample, especially those from Vindija, have well defined projecting browridges which superoinferiorly are quite thin (F.H. Smith and Ranyard 1980). The browridge of Le Moustier 1 has not yet clearly separated (*séparé*) from the squama (Tillier 1983:61, 1995:66) and does not have the well defined supratotal sulcus found above the adult browridge (F.H. Smith and Ranyard 1980:593). At the lateral trigones it is separating (Table 6.12), already to a degree rarely seen in modern humans, but the medial region, centred on glabella, only forms a moderate curve out from the squama in profile.

Table 6.12: Supraorbital torus projection and thickness, adolescent and adult Neanderthals and adult Upper Palaeolithic and Middle Pleistocene hominins

Specimen		Projection (mm)			Thickness (mm)		
		Lateral	Midorbit	Medial	Lateral	Midorbit	Medial
Vi 279	Adolescent	16.0	13.0	11.0	7.6	7.0	15.1
Vi 224	Adolescent	19.5	17.5	17.0	9.1	9.7	15.5
Kr 23	Subadult	-	-	17.5	-	-	-
Le Moustier 1 ¹	12 years M	21.0	15.0	13.0	10.7	9.9	21.9
Guercy 1 ⁴	16 years F	22.8	-	-	7.5	-	-
Gibraltar 1	Adult F	-	20.5 L, 21.5 R ⁵	-	-	-	-
Vindija, Krapina and Šala	Adult	23.3 (19.5–27.0)	21.7 (16.0–26.0)	18.3 (17.5–23.0)	11.5 (10.0–16.0)	9.8 (7.0–14.3)	16.0 (15.0–22.0)
Neanderthals ²	Adult	24.2 (23.3–25.1)	22.6 (21.5–23.7)	-	12.2 (11.6–12.8)	10.6 (10.0–11.2)	-
Upper Palaeolithic ²	Adult	19.8 (17.8–21.8)	15.7 (13.0–18.2)	-	8.6 (7.7–9.4)	6.1 (5.5–6.7)	-
Bilzingsleben ³	Adult	-	30.9	25.0	-	-	-
Steinheim ³	Adult	-	20.7	19.5	-	-	-
Data from F.H. Smith and Ranyard (1980:610) unless noted.		³ Middle Pleistocene <i>Homo heidelbergensis</i> (Wolpoff 1980b:348).					
¹ Ahern and Smith (2004:7).		⁴ Richards et al. (2021:208,210).					
² Ahern et al. (2004:37).		⁵ Pers. obs. on virtual 3D model.					

In the absence of readily available measurements for the younger specimens, Table 6.13 presents the state of development by age qualitatively.

Browridges of fossil *Homo* exhibit *vermicular bone*, with tiny grooves and whorls visible to the naked eye, different from the surface of the rest of the skull and postcrania (Tappen 1973, 1978). According to Oyen et al. (1979:85) it is non-lamellar fine cancellous bone. It appears on the anterior and superior surface of the torus from the lateral trigones extending medially and in large browridges as far as glabella (F.H. Smith and Ranyard 1980:593). Tappen (1973, 1978) found it extensively developed on the robust crania La Chapelle and Spy 1, and on all other adult Neanderthal skulls that he examined except two: Gibraltar 1 and Krapina br. 373 (a fragment). It ceases at the orbital margin and tends to be confined to the frontal at the junction with the zygomatic, but on La Quina H5, which has a robust browridge, it extends onto the zygomatic (Oyen et al. 1979:84). Tappen also found it on

1980b) and is therefore not comparable. Such a measurement would scarcely be meaningful on most recent humans.

Skhul 9 (*Homo sapiens*) and Kabwe (*Homo rhodesiensis*), on both of which it extends into the supratotal sulcus and in Kabwe also onto the zygomatic (Oyen et al. 1979:84).¹

Table 6.13: Supraorbital torus development by age

Specimen	Age (y)	Development
Pech de l'Azé	1.5	Slight inflation medially as on modern children, no relief otherwise ¹
Dederiyeh 2	2	Slight inflation of supraorbital region ⁴
Engis 2	3	Inflation limited to medial half of each orbital contour ¹
Subalyuk 2	3–4	Slight inflation medially as on modern children ¹ Supraorbital ridge relief ²
Gibraltar 2	4.6	Inflation medially and extended laterally forming continuous relief ¹
La Quina H18	5.5	More accentuated relief ¹ (than Engis 2 and Subalyuk 2)
Carigüela	5–7	Inflation medially and extended laterally forming continuous relief ¹
Krapina 1 (A)	7	Inflation limited to medial half of each orbital contour ¹ Squama less vertical than modern children ²
Teshik-Tash	8.2	More accentuated relief ¹ (than Engis 2 and Subalyuk 2)
Le Moustier 1	11.86	Torus development well advanced in projection, especially laterally, and in thickness, but separation and further projection still to take place; supratotal sulcus not defined. ³
Ages from Appendix A.		³ Bulygina (2007:237); Tillier (1983:61, 1995:66).
¹ Tillier (1983:61, 1986:211).		⁴ Ishida and Kondo (2003:285–286).
² Williams and Cofran (2016:395).		

Tappen (1978:101) did not detect vermicular bone on any of the immatures La Quina H18, Pech de l'Azé, Krapina 1, Krapina br. 24, or Gibraltar 2. Oyen et al. (1979:84) found it on Gibraltar 2 along the anterior aspect of the superior orbital margin. There is a patch which may be vermicular bone on the right lateral area medial to the trigone (pers. obs.). Vermicular bone is identified by F.H. Smith and Ranyard (1980:596,599) on two Neanderthal subadults Krapina 1 (A) and Vindija Vi227. They find it inextensive in younger children and limited to the lateral segment (i.e. trigonal area). In older immatures (juveniles *sensu* Bogin) it extends onto the lateral aspect of the orbital segment, whereas in adults it covers the whole torus except where sinus walls are very thin.

F.H. Smith and Ranyard (1980:596,599) conclude that it is the deposition of vermicular bone that transforms the subadult form into the adult torus, and the torus begins to separate from the squama at their *second stage* (i.e. juvenile). Infants and early children lack browridges and manifest little or no vermicular bone. It seems that the developing torus takes definition, i.e. separates from the squama, beginning from the lateral ends, since the trigones become projecting first, and that is where vermicular bone is seen at younger ages.

¹ Tappen (1973, 1978) also discovered patches of vermicular bone on the brows of some recent human skulls from a variety of populations: Arabs, East Indians, French, Australian Aborigines, Japanese, and Native Americans.

Frontal recession (flattening)

Dimensions indicating increasing recession of the frontal squama are given in Table 6.14 and graphed in following figures. The frontal index chord/arc is an indicator of frontal curvature: the higher the value the more flattened is the frontal bone. De Lumley (1973:253–257) measured the sagittal angle formed by the tangent glabella–metopion with the Frankfort plane (porion–orbitale bilaterally). Her results are graphed in Figure 6.24 and again, to compare with modern French, in Figure 6.25. Inter-individual variation is high, and there is a dearth of adolescent subjects.

Table 6.14: Frontal squama, recession

Specimen	Age (y)	M26 Frontal arc nasion–bregma (mm)	M29 Frontal chord nasion–bregma (mm)	Frontal sagittal index M29/M26	M32a frontal angle of Schwalbe (degrees)	Angle of tangent glabella–metopion with Frankfort plane orbitale–porion (degrees)
Pech de l'Azé	1.5	103 ²	90 ²	87.4 ²		99 ¹
Roc de Marsal	2.3	115 ²	101 ²	87.8 ²	90	
Engis 2	3.0	115 ²	98.5 ²	85.6 ²	88	
Subalyuk 2	3.0	95 ²	78 ²	82.1 ²		
La Chaise (Suard) 15	3–6	105 ²	94 ²	89.5 ²		
Gibraltar 2	4.6	116.5 ²	101 ²	86.7 ²		70 ³
La Quina H18	5.5	105 ²	94 ²	89.5 ²		75 ¹
Carigüela	6	100 ⁴	88.1 ⁴	88.1 ⁴		75 ¹
Krapina 1	6–8	111 ⁴	94.5 ⁴	88.2 ⁴		
Teshik-Tash	8.0	121 ²	106 ²	87.6 ²	82	74 ¹
Le Moustier 1	11.86				69	
Neanderthal (Feldhofer)	Adult				72	
La Chapelle- aux-Saints	Adult				65	58 ¹
Circeo 1	Adult				62	
La Ferrassie 1	Adult				66	
Gibraltar 1	Adult					55 ¹
La Quina H5	Adult				57	45 ³
Spy 1	Adult				57.5	
Spy 2	Adult				67	
Galilee	Adult					62.5 ¹
Tabun 1	Adult					65 ¹
Mean	Adult	122.2 (106.8–135.0) ⁵	109.1 (100.6–121.9) ⁵	90 (86.7–92.7) ⁵		
Ages from Appendix A. Values from Madre-Dupouy (1992) unless stated. ¹ De Lumley (1973). ² Tillier (1983:55).				³ Measured from drawings in De Lumley (1973: 256–257). ⁴ Minugh-Purvis et al. (2000:402). ⁵ Minugh-Purvis (1988).		

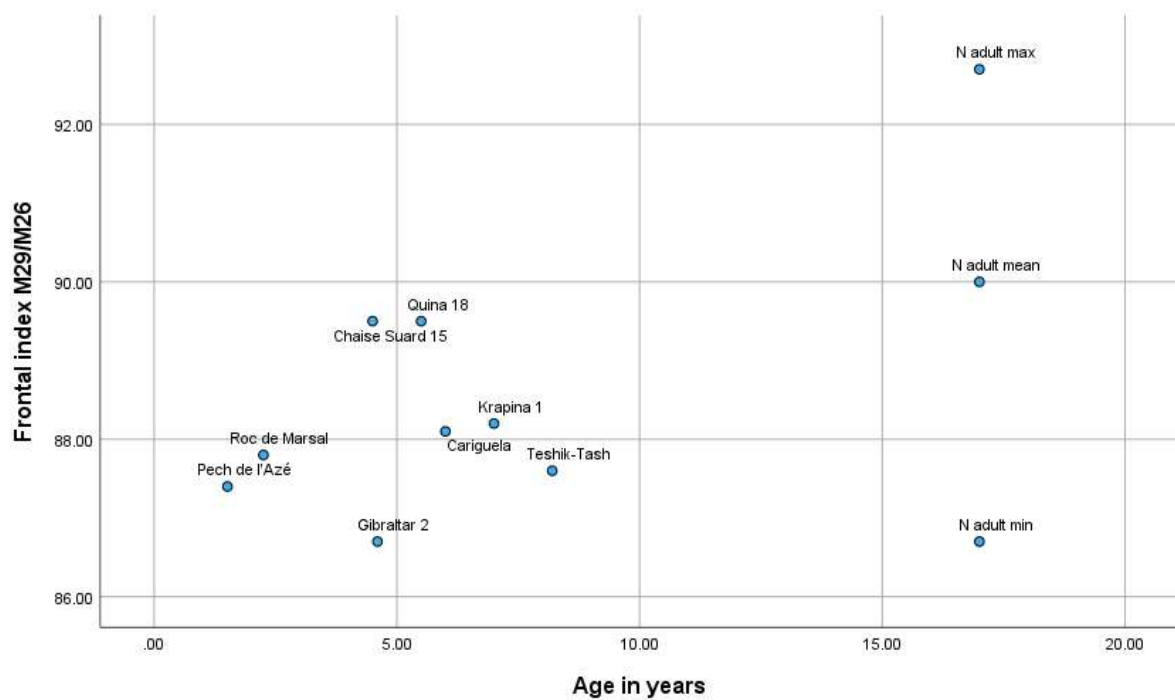


Figure 6.22: Frontal sagittal index chord/arc, Neanderthal immatures

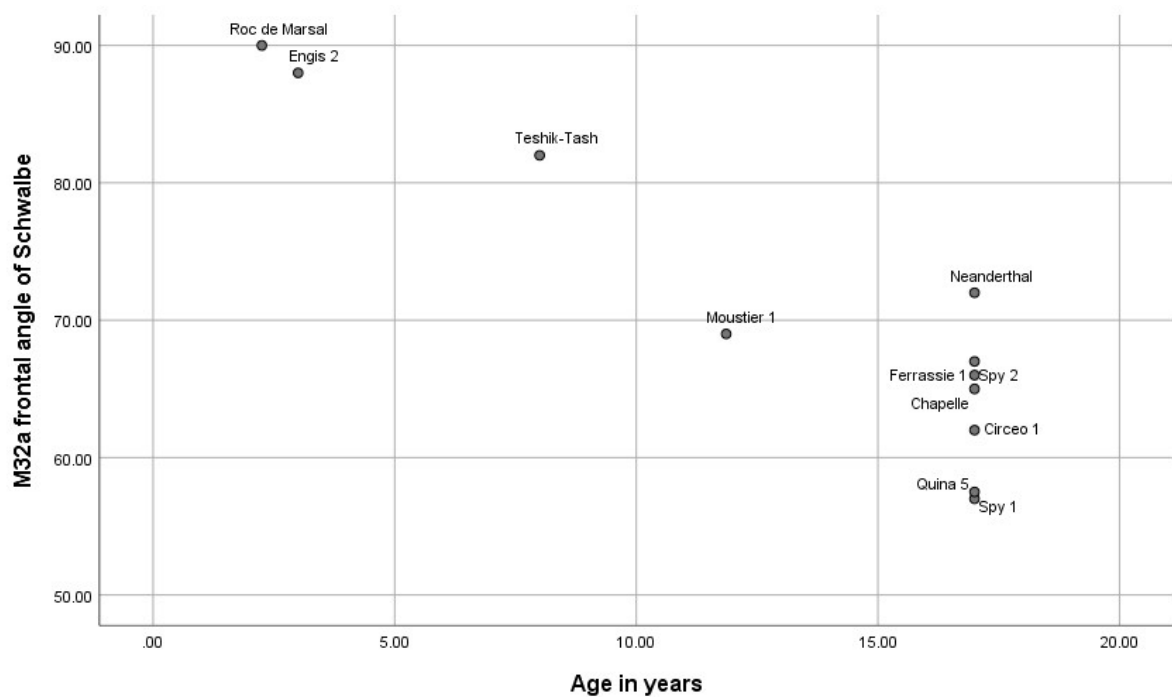


Figure 6.23: Frontal angle of Schwalbe (degrees), recession of frontal, Neanderthal immatures

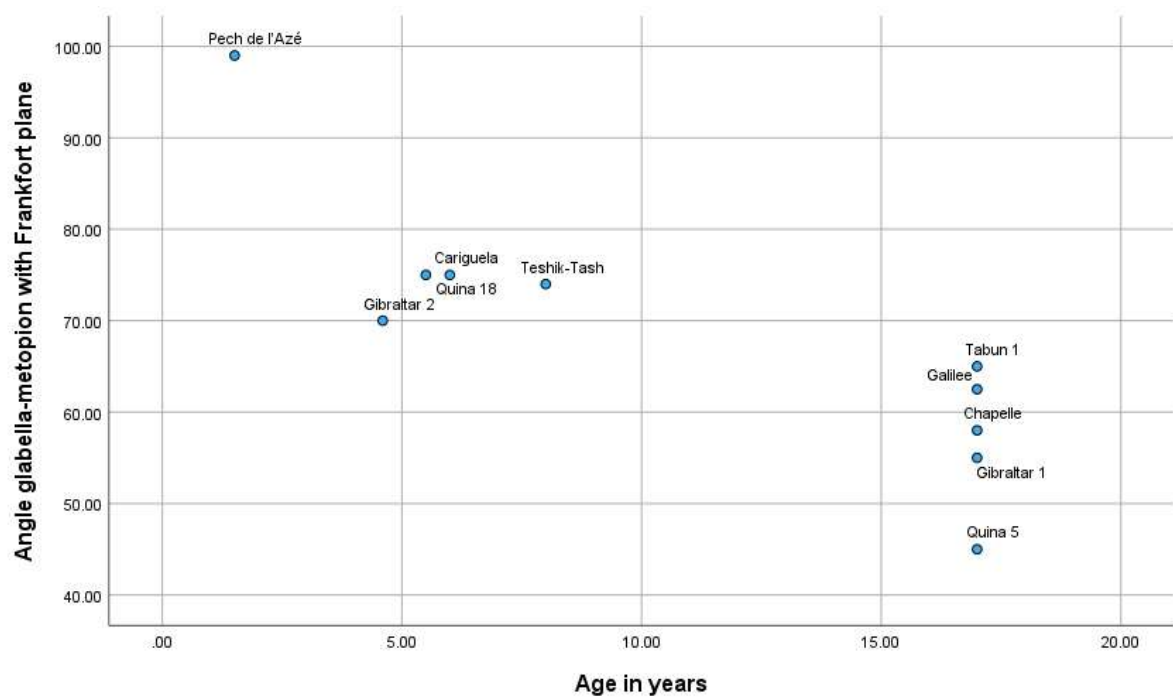
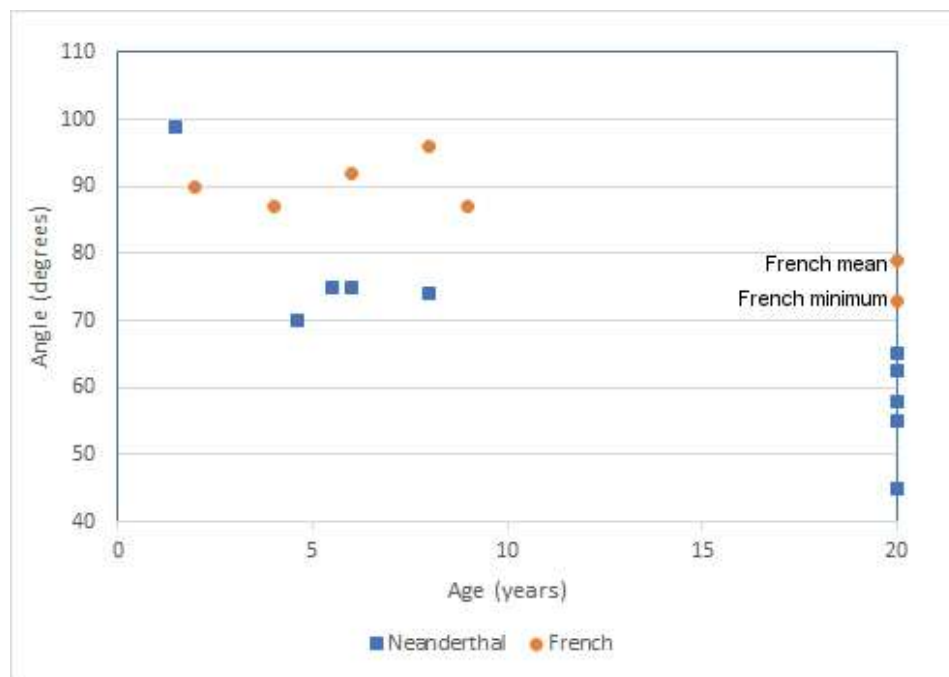


Figure 6.24: Angle tangent glabella–metopion with Frankfort plane, Neanderthal immatures



Data from De Lumley (1973), 20 years = Adult

Figure 6.25: Angle tangent glabella–metopion with Frankfort plane, comparison with modern French

6.5.3 Facial height and projection

Table 6.15 lists measurements which express facial growth. Dimensions from basion anteriorly measure facial projection. Dimensions from nasion inferiorly measure growth in facial height.

Table 6.15: Facial growth and projection

Specimen	Age (y)	M5 basion–nasion	M40 basion–prosthion	M47 nasion–gnathion	M48 nasion–prosthion
Pech de l'Azé ¹	1.5	87	75	79	50
Roc de Marsal ¹	2.5	90	88	86.5	58.5
Engis 2 ¹	3.0	91.5			
La Quina H18 ¹	5.5	96			57
Teshik-Tash	8.0	96	95	107	63
Le Moustier 1	11.86	106.7 106.2 ²	98.6 109.6 ²	123.7	81.7 79.6 ²
La Chapelle-aux-Saints	Adult	120	122.5	131 ¹	84.5
Circeo 1	Adult	115	120		85
La Ferrassie 1	Adult	119	124	137 ¹	87
La Quina H5	Adult				86 ¹
Ages from Appendix A. Measurements from Thompson and Illerhaus (2005) unless otherwise stated. ¹ Madre-Dupouy (1992). ² Ponce de León and Zollikofer (1999, 2005).					

Growth in upper facial height is shown in Figure 6.26, and full facial height (i.e. including the mandible) in Figure 6.27. Increase of linear distances on the facial skeleton is greater per year than in modern humans (Krovitz 2003:332), as the target adult size is larger.

In modern humans there is often a growth spurt in facial dimensions, including vertical length, some months after peak height velocity has been passed in adolescence, which in males is expected at ~14.0 years (Tanner 1962:16; Marshall 1978:145; Mellion et al. 2013). Figures 6.26 and 6.27 are ambiguous regarding a spurt in facial height. The sole Neanderthal adolescent has almost attained the adult dimensions for facial height but is probably only at the beginning of adolescence (§5.5, §7.5). One could claim a growth spurt between ~8 years (Teshik-Tash) and 12 years (Le Moustier 1), but Teshik-Tash is a small juvenile and Le Moustier 1 has still 15% of statural growth to achieve before reaching adulthood. This percentage is characteristic of an early adolescent in which the growth spurt in stature is at most only beginning.

Figure 6.28 shows growth in upper facial projection using the diameter basion–nasion. To reach adult size at 17 years, growth in this dimension has to be more rapid after the age of 12 years. If cessation of growth occurs later, then of course the slope of the upper segment can be flatter. If cessation of growth was at ~20 years, then growth could have continued from 12 to 20 years at the relatively slow rate of younger immatures. If growth ceased at ~17 years as shown, or earlier, then growth would have been accelerated, indicating a possible adolescent spurt.

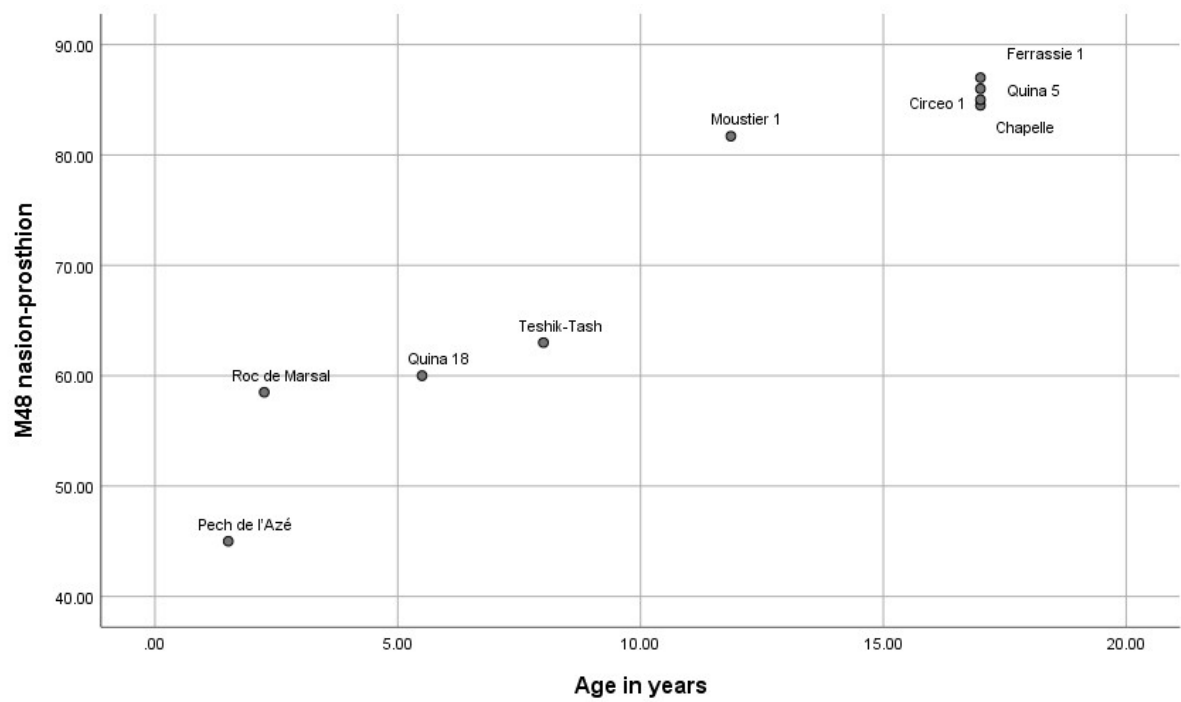


Figure 6.26: Upper facial height nasion–prosthion (mm), Neanderthal immatures

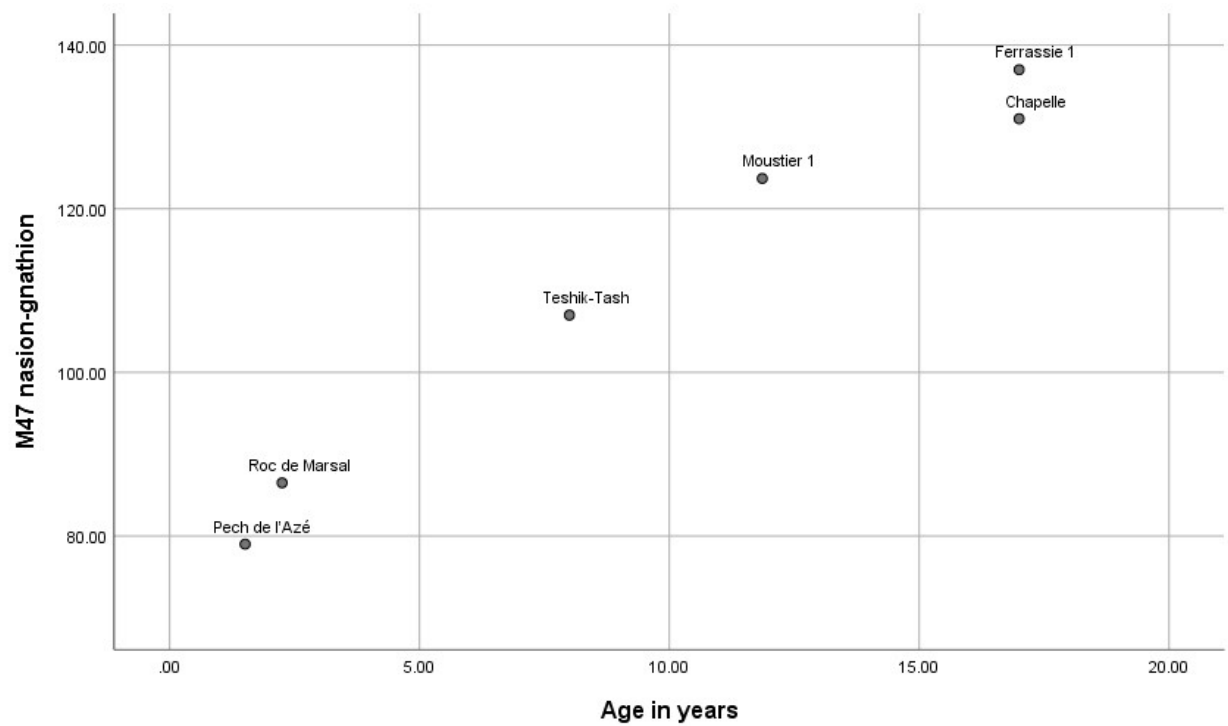


Figure 6.27: Full facial height nasion–gnathion (mm), Neanderthal immatures

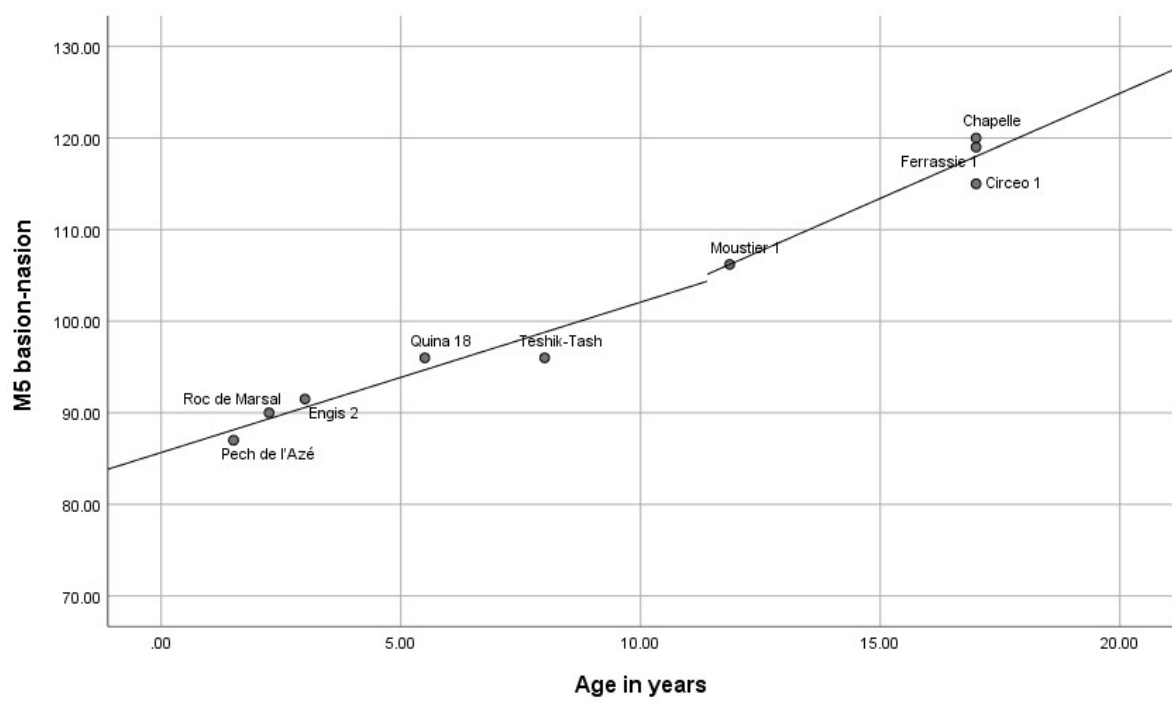


Figure 6.28: Cranial base length and upper facial projection, basion–nasion (mm), Neanderthal immatures

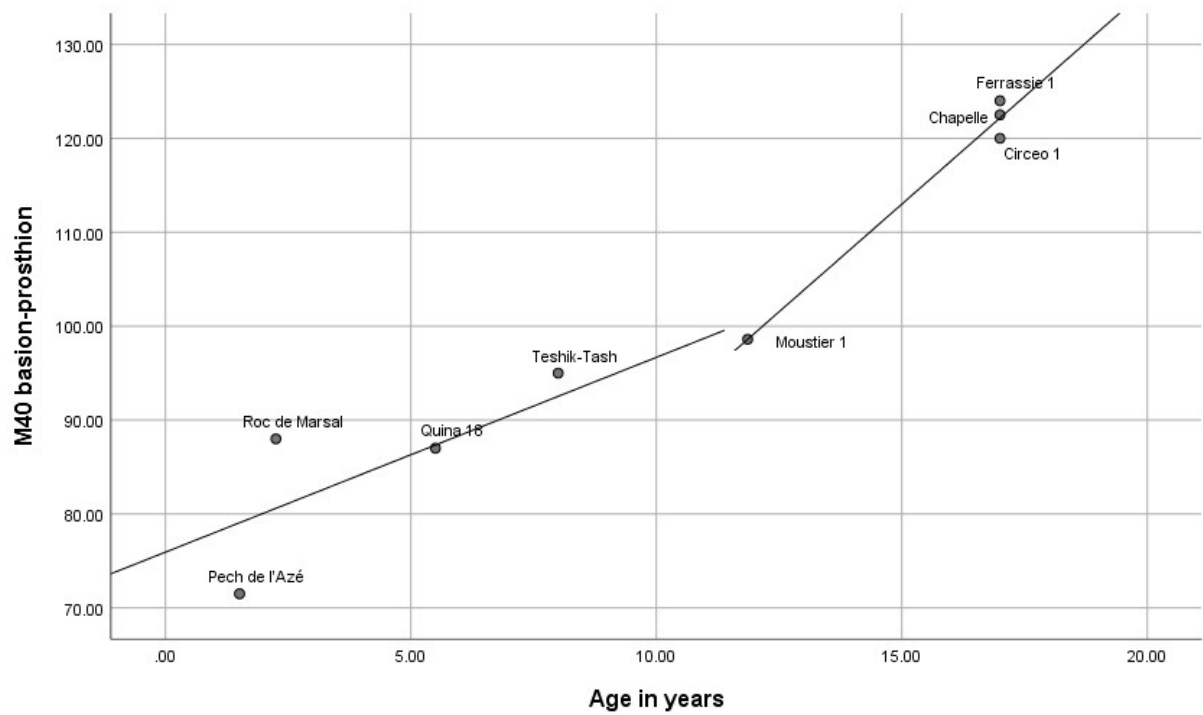


Figure 6.29: Lower facial projection, Neanderthal immatures, Le Moustier 1 basion–prosthion 98.6 mm

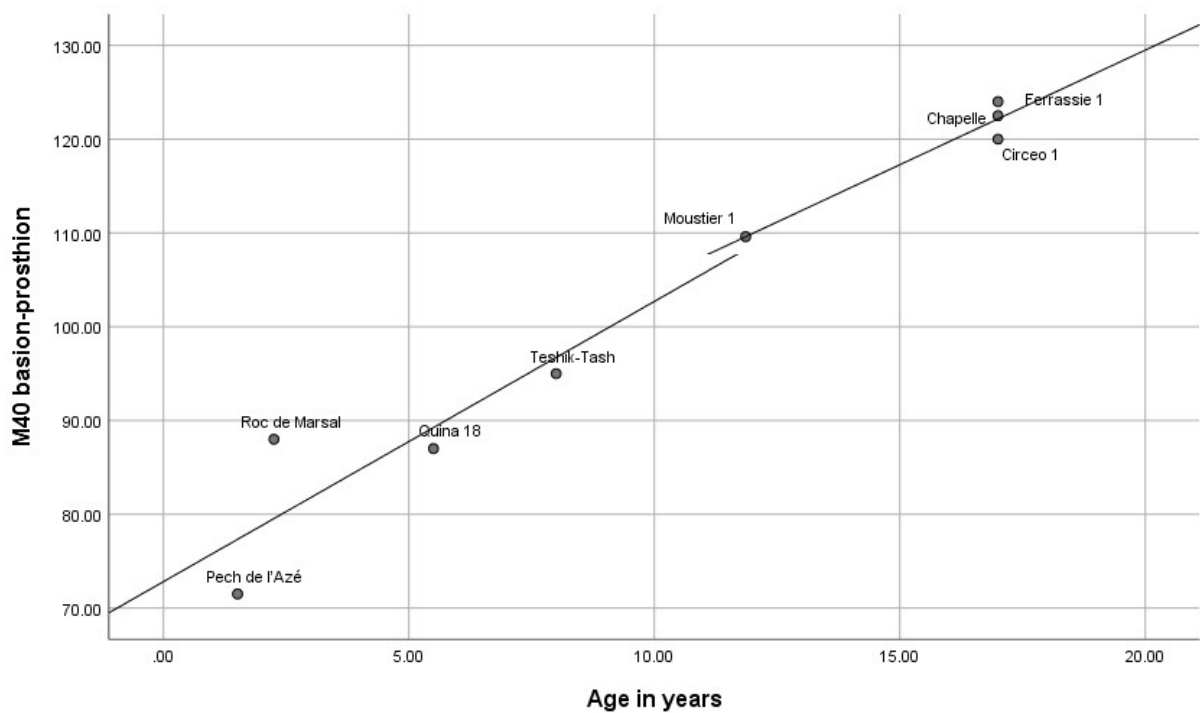


Figure 6.30: Lower facial projection (mm), Neanderthal immatures, Le Moustier 1 basion–prosthion 109.6 mm

Increase in lower facial projection with age, using alternative reconstructions of Le Moustier 1, is illustrated by Figures 6.29 and 6.30.

Figure 6.29 uses the basion–prosthion measurement 98.6 mm from Thompson and Illerhaus (1998, 2005:229). These authors made a virtual reconstruction of the cranium from constituent fragments and located the foramen magnum in a more anterior position than in the reconstruction by Weinert (1925). The latter, which has been referred to extensively in the past, gives basion–prosthion length 125 mm. This value is already at the top of the adult range, because the Weinert reconstruction has the foramen magnum very posteriorly positioned. According to Thompson and Illerhaus (1998, 2005:228–230), older reconstructions did not correct post-depositional distortion and failed to secure natural articulation of the mandible with the basicranium (§5.5). In their reconstruction, the basion–prosthion measurement of Le Moustier 1 is little greater than that of Teshik-Tash (Figure 6.29), whereas considerable vertical growth has taken place, represented by upper facial height nasion–prosthion (Figure 6.26) and full facial height nasion–gnathion (Figure 6.27).

Figure 6.29 indicates that considerable anteriorly directed lower facial growth, i.e. of the maxilla and mandible, is to be expected during adolescence. An increase of ~20 mm would allow the mandibular third molars to come into occlusion and open the retromolar gap. Such rapid growth in five years (age 12–17) may indicate an adolescent growth spurt.

In contrast, Figure 6.30 uses the basion–prosthion measurement from the alternative virtual reconstruction by Ponce de León and Zollikofer (1999, 2005). These authors (2005:251–253) also place the foramen magnum more anteriorly than in Weinert's reconstruction, though not so far, so that the distance basion–prosthion becomes 109.6 mm and the distance basion–nasion becomes 106.7 mm. Their measurement of basion–nasion differs by only 0.5 mm from that of Thompson and Illerhaus, so there appears to be close agreement on the anterior dimensions of the neurocranium. However, the two values for basion–prosthion

are widely discrepant and must relate to a more posterior positioning of the foramen magnum by Ponce de León and Zollikofer (2005) versus Thompson and Illerhaus (2005) or a different relative location of the glenoid fossae. The measurements also produce different results regarding growth trajectory, as illustrated.

If the starting point is a basion–prosthion distance of 109.6 mm, then growth could continue at a pre-adolescent rate between 12 and 17 years to result in adult lower facial dimensions, as shown in Figure 6.30. Even this case requires anteroposterior maxillary growth of ~10–13 mm to reach adult dimensions.

6.5.4 Mandibular and maxillary growth, prognathism, mid-facial projection

Neanderthals are orthognathous with respect to apes and monkeys but prognathous with respect to most modern humans (Picq 1994:61–62). Neanderthal adults have conspicuously projecting maxillae and large mandibles.

Since the Krapina remains were first examined it has been noted that Neanderthal mandibles often have the mental foramina doubled and that the foramina lie in what appears to be a more posterior position than in modern humans. Using a sample of Neanderthal immatures up to early adolescence, Coqueugniot and Minugh-Purvis (2003) find that the mental foramen seems to migrate posteriorly during ontogeny. In the earliest age group, the modal position of the foramen is below the deciduous first molar (dm1), with some below dm1–dm2 (i.e. between), none more posterior; and in the oldest group the modal position is below and between the premolars P3–P4, few more anterior, but many below P4 and some below P4–M1. Hublin and Tillier (1988:239) observe that in the juvenile mandibles Zaskalnaya VI (Zsk VI-72) and Fate 2¹ the mental foramen lies under dm2 but in adults it is found beneath M1 (cf. Tillier 1986:213–214). This pattern of migration is not observed among the Skhul-Qafzeh hominins, the Eurasian Upper Palaeolithic sample, or recent humans. Neanderthal premolars are mesiodistally shorter than the deciduous molars which they replace, but this factor is insufficient to explain the apparently rearward repositioning of the mental foramen: which implies that there must be growth which carries the dentition anteriorly.

Williams and Krovitz (2004) find that adult Neanderthals sometimes have the mental foramen below M1, while in modern humans the usual position is below P3, P3–P4 or P4, as in the immature Neanderthals. Rosas (2001) draws attention to the marginal tubercle which occurs below and slightly anterior to the mental foramen, so that they are repositioned together. These markers are accompanied by the retromolar gap, as part of a complex of features associated with excess mandibular length in relation to length of the dental arcade. This complex, as it affects the external or buccal face of the mandible, is shared with the Middle Pleistocene population from Sima de los Huesos, which is most probably ancestral to Neanderthals, but is not found in the African, Asian or earlier European Middle Pleistocene hominins (Franciscus and Trinkaus 1995:586). In some cases the Sima de los Huesos hominins are more extreme than Neanderthals, eight out of twelve adults having a retromolar gap of more than 10 mm, three more than 15 mm, and one 18.5 mm. Certain features reflecting muscle attachment on the internal face of the mandibular corpus in Neanderthals are not manifested in the Sima de los Huesos hominins, indicating that further apomorphic development took place in the evolving population (Rosas 2001).

The mandibular foramen is not posteriorly placed within the mandibular corpus but only relative to the tooth row (Williams and Krovitz 2004). As the mandible, including the

¹ Zsk VI-72 and Fate 2 are aged 10–12 and 8–12 years respectively (Appendix A).

dental arcade, increases in size during ontogeny, in modern humans the dental arch increases in length relative to mandibular length, whereas in Neanderthals the proportion remains the same. The described effect would bring the postcanine teeth proportionately and absolutely further forward in Neanderthals than in modern humans, in relation to a posterior reference point such as gonion or condylion (Bastir et al. 2007:1128–1129). It can perhaps be explained by anterior growth principally at alveolar level, which would carry the dentition mesially in relation to the corpus.

The posterior dentition is reduced in Neanderthals compared with Middle Pleistocene hominins, an effect probably attributable to new practices in food preparation – pounding, grinding and cooking – leading to less need for heavy chewing (Franciscus and Trinkaus 1995:577). The mandibular ramus is anteroposteriorly shorter than in the Middle Pleistocene hominins, but the anterior dentition remains large, although the dental arcade is relatively flattened anteriorly (ibid.:592). These anteroposterior reductions in component structures take place on a mandible whose overall length remains largely unreduced (Williams and Cofran 2016:406), so retaining the retromolar gap.

The isolated mandible from Montmaurin La Niche belonged to an early Neanderthal provisionally dated to MIS7, possibly female, aged ~15.5 years, though previously estimated at ~18 years, so apparently a late adolescent (Violet et al. 2018). It possesses all three permanent molars bilaterally. All are scarcely worn, even the M1s. Each side has two mental foramina, one, larger, more anterior below the alveolus for P4, and the second below M1. However, it has no retromolar gap (Violet et al. 2018). Possibly, if the subject had lived, there would have been further anterior growth by a few millimetres.

The maxilla growing anteriorly, as the main component of the projecting Neanderthal mid-face, carries the upper dentition forward, and this has to be matched by anterior growth in the mandible so as to maintain effective occlusion (Wolpoff 1980a:285). Rather than the basal region of the corpus it is the alveolar component that must match the maxillary counterpart (Arat et al. 2001:358), as an intermediary tissue between teeth and skeleton (Ten Cate and Mills 1972; Ten Cate 1997). This would explain the finding by Williams and Krovitz (2004) that the mandibular foramen is posteriorly placed only relative to the tooth row, not to the corpus as a whole. Thus the anterior position of the alveolar arcades, maxillary and mandibular, with concomitant features such as the retromolar gap and posterior location of the mental foramen and marginal tubercle, may be a consequence of the distinctive Neanderthal mid-facial projection.

The aetiology of mid-facial projection itself is not clear: e.g. selective benefit or genetic drift. However, this feature has a long history, since it is found developing in the Sima de los Huesos hominins at ~430 ka (Rosas 2001). It has been attributed to a need for a large nasal cavity to warm air in cold climates (Coon 1962; Wolpoff 1980a). This explanation does not fully convince: in part because, before and after the period of the Sima de los Huesos hominins, the ancestors of Neanderthals lived not only through glacial periods but also through interglacials, when prevailing climate was often warmer than the present day. Coon (1962) attributes not only the Neanderthal but also the modern human “Mongoloid” (East Asian) facial structure to cold adaptation, although to the present writer the latter appears to be almost the antithesis of the Neanderthal configuration (cf. F.H. Smith 1983:152). Tillier (1977a:178) contrasts the degree of pneumatization of Neanderthal crania, particularly maxillary sinuses, with the minimal development of sinuses in modern cold-climate populations (cf. Viðarsdóttir 1999:215).

In modern human children the viscerocranium grows predominantly inferiorly, and the anterior face of the maxillary bone where there is bone activity displays resorptive fields, as

confirmed by a sample aged between 10 months and 17 years (Lacruz et al. 2015). These include the subnasal area, which recedes in modern humans but is inflated in archaics. Neanderthal immatures exhibit fewer resorptive areas on the maxillary surface than modern human children of comparable age, and growth of the maxilla continues into adolescence (Schuh et al. 2025). In the Neanderthal early children Gibraltar 2 (4.6 years) and La Quina H18 (~5.5 years) the whole anterior face of the maxilla bears predominantly depository fields (Lacruz et al. 2015). Continued deposition is consistent with the substantial anterior growth leading to midfacial prognathism. Similar extensive depository fields were found in immatures of the Sima de los Huesos hominins, in whom midfacial prognathism exists to a lesser degree. They and Neanderthals are plesiomorphic in this regard, while the condition in *Homo sapiens* is a significant apomorphy (Lacruz et al. 2015). The Neanderthal form of midfacial prognathism, with the more parasagittal orientation of the lateral maxillae, is itself apomorphic with respect to *Homo heidelbergensis s.l.*

The incisive or premaxillary suture in young infants traverses the palate at a level between the second incisors and the canines, dividing the premaxilla from the postmaxilla. Before birth these develop from separate ossification centres. According to Maureille and Houët (1993), in modern human children the incisive suture is synostosed on the nasal aspect but may remain open for some years on the palatal surface. In four Neanderthal infants – Roc de Marsal, Engis 2, Pech de l’Azé and Subalyuk 2 – the suture is open inferiorly and also on the nasal floor, while in La Quina H18 it is open at least on the palatal surface.¹ Whereas Maureille and Bar (1999) suggest that in Neanderthals the suture may synostose after age 6 years, they also report Vlček’s (1970) opinion that the suture synostoses late in these immatures, at ~9 years. As the incisive suture is an area of osteogenesis, if it remains open for its full vertical extent between the nasal and oral cavities it may contribute significantly to development of mid-facial projection and maxillary prognathism during the stages of infancy and early childhood, and perhaps also in the early juvenile stage. However, because an open incisive suture has not been observed in Neanderthal adults or immatures over 9 years, this specifically premaxillary growth presumably does not contribute to the further anterior extension of the maxilla during the late juvenile or adolescent stages.

Williams and Cofran (2016:403–406) assign the majority of mandibular growth leading to the distinctive adult Neanderthal size and conformation, including lengthening of the corpus and broadening of the ramus, to the stage of adolescence, after emergence of the second molars. They also note that the juvenile Teshik-Tash has a broad nasal aperture in relation to height, more so than the younger Neanderthal immatures, and suggest that such midfacial morphology may have been a feature of Neanderthal juveniles before a final increase of facial height during adolescence. However, they acknowledge that its appearance in Teshik-Tash may be due to an ethnic difference between this Central Asian individual and the European Neanderthal immatures. Maureille and Houët (1993) attribute the absolutely wide nasal aperture of Neanderthals to the potential for growth afforded by the premaxillary suture remaining open up to the juvenile stage. Late closure may contribute to the much greater growth in width of the anterior maxilla from infancy in Neanderthals relative to modern children highlighted by Viðarsdóttir (1999:340).

Le Moustier 1, El Sidrón Adolescent 3 and the associated El Sidrón Adult 2 exhibit anomalies of the left mandibular canine. In all three individuals the deciduous canine was retained in place, although in the El Sidrón adolescent only the root remains. In El Sidrón Adult 2, the deciduous canine is of abnormal form and the unerupted permanent canine was left horizontally orientated in a cyst low within the corpus, not below the deciduous canine but with

¹ On Subalyuk 2, Pap et al. (1996:256) only state that the suture is open on the palatal surface.

its crown lying below the normally erupted second and third molars and with the root apex protruding lingually from the corpus through a fenestration aligned beneath the anterior edge of the ascending ramus (Dean et al. 2013; Trinkaus 2018, SI). Since the failed eruption, it appears to have been left behind by mandibular growth incorporating anterior displacement of the alveolar arcade with respect to the base of the corpus. In Le Moustier 1 an unerupted left permanent canine remains in its crypt beneath the retained deciduous canine, with its crown protruding buccally through the wall of the corpus below the permanent lateral incisor (Thompson and Bilsborough 2005:88; Bilsborough and Thompson 2004:158,172; Thompson and Illerhaus 2005:231,235). Its apparently original location below the deciduous predecessor, contrasted with the case of El Sidrón Adult 2, suggests that full anterior migration of the alveolar arcade had yet to take place.

The infant Pech de l'Azé and early adolescent Le Moustier 1 dentitions appear to exhibit normal or orthodontic Class I occlusion (Cuzzo 2005:115–116; Ponce de León and Zollikofer 2005:248,252,255,258). In this condition, the mesiobuccal cusp of the upper first molar fits into the buccal groove of the lower first molar, so that the lower molar lies partly anterior to the upper but the upper incisors project forward of the lower incisors (overjet) and slightly overlap them vertically (overbite). This is regarded as normal for living humans, immature and adult, and is the ideal in orthodontics (Broadbent et al. 1975; Kelly and Harvey 1977:3). In contrast, adult Neanderthals, along with adult Palaeolithic *Homo sapiens* and earlier hominins, generally display an edge-to-edge bite at the upper and lower incisors while simultaneously the molars are held in occlusion, which would require matching anteroposterior growth of mandible and maxilla during ontogeny. In most adult living humans the mandibular corpus, or at least the alveolar arcade, would have to be lengthened anteriorly by at least ~2–5 millimetres (Corrucini 1991:301) to achieve an edge-to-edge bite. In the above-mentioned Neanderthal immatures, even their minimal overbite associated with normal occlusion, if it persisted, would obstruct such anterior positioning of the lower incisors.

The anterior dentition in Neanderthals is often worn down to the dentine, a condition which, according to the *anterior dental loading hypothesis*, is ascribed to habitual practice of using the teeth for paramasticatory activity, specifically to hold material while working on it with both hands, e.g. scraping hides (F.H. Smith 1983; F.H. Smith and Paquette 1989). Ponce de León and Zollikofer (2005:257) suggest that, during the later adolescence of Le Moustier 1, had he lived, paramasticatory wear would have levelled the tips of the upper and lower anterior teeth, so enabling mandibular anterior growth and edge-to-edge anterior occlusion. It seems counterintuitive that such mandibular development, almost universal among adult Palaeolithic hominins and presumably under genetic control, would depend upon a cultural activity believed to occur principally among Neanderthals. The paramasticatory anterior dental loading hypothesis has been disputed (Wallace 1975; Clement et al. 2012). In Schuchhardt's (1912:6) illustration of the first reconstruction of the Le Moustier 1 skull, the tips of the upper incisors are positioned anterior to the lower incisors but do not appear to overlap vertically, and in 1930 Hrdlička illustrated Le Moustier 1 with this vertically non-overlapping overjet (Nesturkh 1967:269). Similarly, Teshik-Tash was reconstructed by Gerasimov with the tips of the upper incisors just anterior to the lower incisors but not overlapping vertically (Gremyatskii 1949:145–146; Nesturkh 1967:280,283).

In modern human children the angle sella–nasion–subspinale¹ indicates position of the maxilla relative to the anterior cranial base. This angle slightly decreases up to the age of 10

¹ Subspinale (A-point in orthodontics) is the most posterior or recessed point on the nasoalveolar clivus, i.e. the anterior surface of the maxilla in the sagittal plane between the anterior nasal spine and alveolare (Broadbent et al. 1975:47,135). In recent humans the anterior face of the maxilla retreats posteriorly above the incisors and below the anterior nasal spine.

years while the face grows inferiorly, then increases as the maxilla begins to grow more anteriorly during adolescence (Roche 1992:175). The face of Neanderthal immatures is already growing anteriorly as well as inferiorly during infancy (Lacruz et al. 2015), as seen in Figures 6.29 and 6.30, but a continued emphasis on anterior maxillary growth would explain the prognathism seen in Neanderthal adults.

In modern human males and females during later adolescence, i.e. after peak height velocity has been passed and even up to the age of 20 years, there is anterior growth of the mandible exceeding that of the maxilla (Tanner 1989:67–68; Love et al. 1990; Foley and Mamandras 1992). While facial projection is incomplete in Le Moustier 1 as indicated by the browridge, mandibular length is already within adult range.¹

Growth of the mandible from the youngest available subject to the adult range is documented by Table 6.16 and Figures 6.31–6.35. Because partial and occasionally complete mandibles are relatively well represented among archaeological remains, many individuals appear in the table and graphs.

As the neurocranium of Le Moustier 1 is large, with endocranial volume well above 1500 cm³ (Table E.1), it is reasonable to conjecture that this subject would have become one of the cranially larger males with comparable facial development. He might therefore have come to resemble La Ferrassie 1 or La Chapelle rather than Regourdou or La Quina 9, in maxillary and mandibular dimensions. This would entail anteroposterior extension of the mandible by 7–11 mm, approximately matching expectation for the maxilla discussed above. In the reconstruction by Ponce de León and Zollikofer (2005:258), to match the profile of La Ferrassie 1 the maxilla of Le Moustier 1 would require more than 1 cm anteroposterior extension and the mandible almost 2 cm.

In modern humans mandibular length gonion–pogonion increases throughout adolescence (Marshall 1978:145; Love et al. 1990:200–202; Arat et al. 2001:257). Only a continuation of the trajectory so far, not accelerated growth, is required during adolescence for Le Moustier 1 to achieve the mandibular length of the larger adults (Table 6.16, Figure 6.33). Comparing Figures 6.28–6.30 with Figure 6.33 makes it clear that mandibular length is only one factor that contributes to facial projection, the principal factor being anterior growth in the whole facial skeleton forward of the cranial base.

¹ Rosas et al. (2017 SI:65) list mandibular lengths for a set of adult Neanderthal specimens. However, their values, most of which appear to have been measured specifically for the 2017 study, are 10–26 mm larger than the values reported by other researchers such as Franciscus and Trinkaus (1995). For example, La Quina 9 is given as 137.8 mm (Rosas et al.) versus 112 mm (Franciscus and Trinkaus), Amud 1 136.3 versus 111, La Ferrassie 1 142.6 versus 122 (while other authors have 126 for La Ferrassie 1). It is often unclear how lengths were measured: e.g. taken sagittally, pogonion–gonion (Martin’s M68) or pogonion–condylion (M68/1). Williams and Cofran (2016) measure mandibular length gnathion–gonion, and their values tend to be lower, since gnathion on the inferior surface of the symphysis is posteroinferior to pogonion, so their measurements for this variable are not cited here.

Table 6.16: Mandibular dimensions

Specimen	Age (y)	M65 bicondylar breadth (mm)	M66 bigonial breadth (mm)	M68 corpus length (mm)	M69 symphyseal height (mm)	M70 ramus height (mm)
Amud 7	0.5		63.2 ⁸		16.4 ⁸	26.2 ⁸
Pech de l'Azé	1.5	89 ¹ 85 ²	76 ⁸	62 67 ¹	17 ¹ 18.3 ⁸	26.4 ¹
Roc de Marsal	2.25	95 94 ¹	72 70.7 ⁸	70 71 ¹	20.4 ¹	32.4 ¹ 33.2 ⁸
Archi	3		58.2 ⁸		22.5 ¹	
Barakai	3			55.9	24.1	36.2
Châteauneuf 1	3.5				20.5 ¹	
La Chaise 13	3.75				22.5 ¹	
Gibraltar 2	4.6			72	21.2 22.4 ¹	43.3 42.1 ¹ 40.9 ⁸
Teshik-Tash	8	119 ¹ 128 ² 122 ⁵	83 ² 80.2 ⁸	95 106.8 ¹	26 27 ¹	50 49.9 ¹ 49.2 ⁸
Hortus II/III	8				23.6 ¹ 24.7 ⁶	
Scladina	8		80.4 ⁸		27.3 ⁸	47.1 ⁸
Fate 1&2	9	115 ⁵				45
Krapina Mandible B	9.5				27 ¹	
Sipka 1	9–10				28.4 ¹ 30.8 ⁸	
Krapina Mandible C	11				23.7 ¹	
Ehringsdorf 7	12				28.3 ¹	
Le Moustier 1	12	118 125.4 ² 133 ³	88	115 103.2 ¹	30 ¹	42.5 ¹
Malarnaud	11–14		81.8 ⁸		25.1 ⁸	48.5 ⁸
Montgaudier	13.5				18.5	
Zaskalnaya VI.1	14	111 ¹ 109 ⁵		95.8 ¹	30 ¹	54.4 ¹
Hortus 4	14	116	108	108	34.8	65
Petit Puymoyen 1	14				28.1	
Krapina Mandible E	15				34.5 ¹	
La Naulette	Adult				31	
Tabun 1	Adult		92.1 ⁸	102 ⁴	30.9 ⁸	58.6 ⁸
Bañolas	Adult			105 ⁴	26 ⁶	
Zafarraya	Adult			107 106.5 ⁴		
Regourdou	Adult	127		108 100 ⁴	35 ⁶	55
La Quina 9	Adult			112 ⁴		
La Quina H5	Adult				31.2 ⁸	66 58.5 ⁸
Shanidar 2	Adult			112 ⁴		
Shanidar 4	Adult			110 ⁴		
Circeo 3	Adult	128	96 91 ⁸		35.2 ⁸	55 66 ⁸
La Ferrassie 1	Adult	136 130 ²	99 94.1 ⁸	126 122 ⁴	33	67
La Chapelle- aux-Saints	Adult	136 142 ²	80 84.7 ⁸	122	36 34.5 ⁸	67
Spy 1	Adult		96.9 ⁸	125	36	
Amud 1	Adult		102 ⁸		39.8 ⁸	67.2 ⁸
Mean	Adult	136 ⁷				
Immature ages from Appendix A. Measurements from Madre-Dupouy (1992) unless otherwise stated. ¹ Minugh-Purvis (1988:174). ² Thompson and Illerhaus (2005:229). ³ Weinert (1925). ⁴ Franciscus and Trinkaus (1995:583). ⁵ Hublin and Tillier (1988). ⁶ De Lumley (1973). ⁷ Tillier (1988:262). ⁸ Williams and Cofran (2016 SI).						

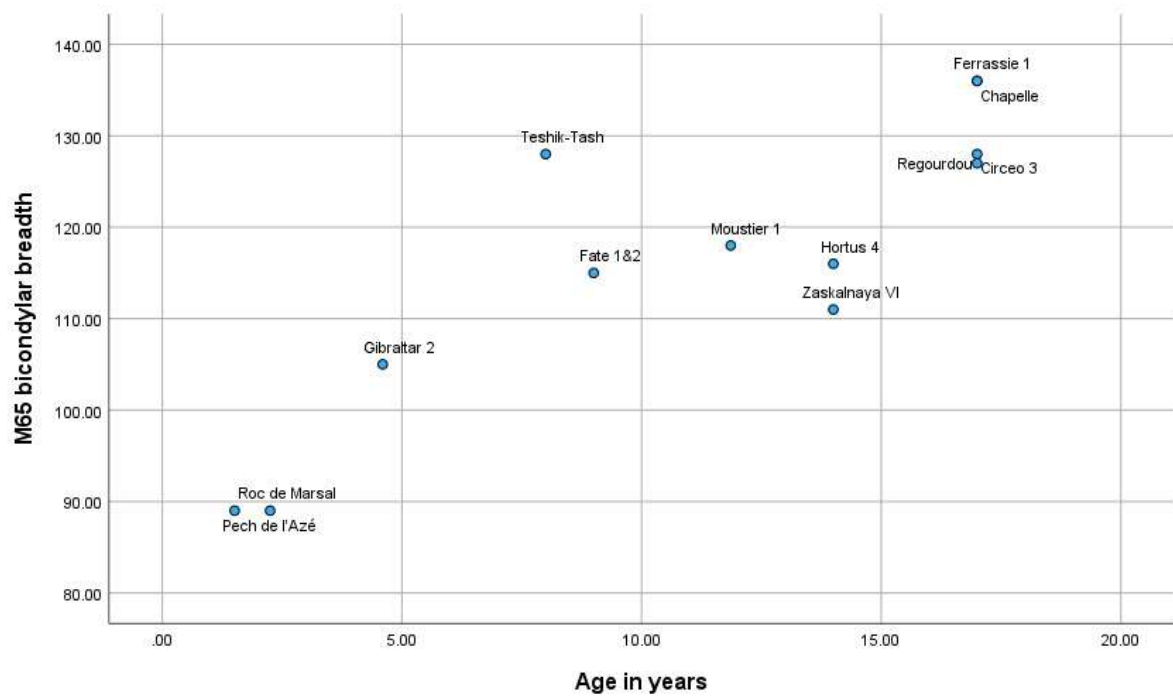


Figure 6.31: Bicondylar breadth (mm), Neanderthal immatures

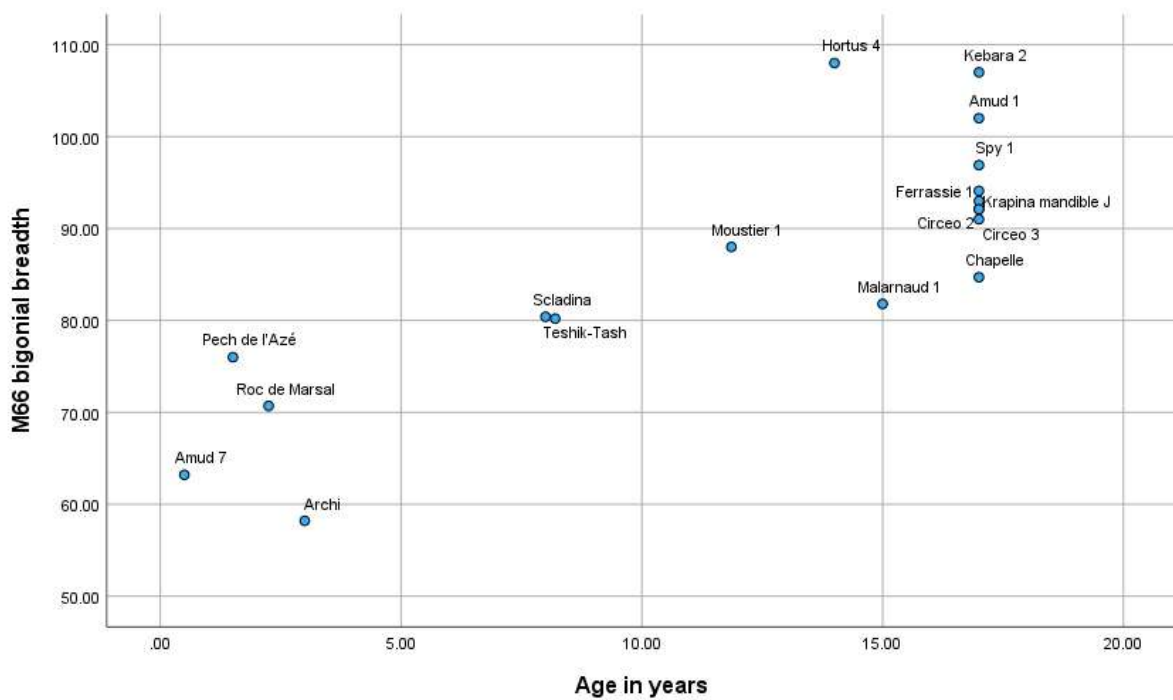


Figure 6.32: Bigonial breadth (mm), Neanderthal immatures

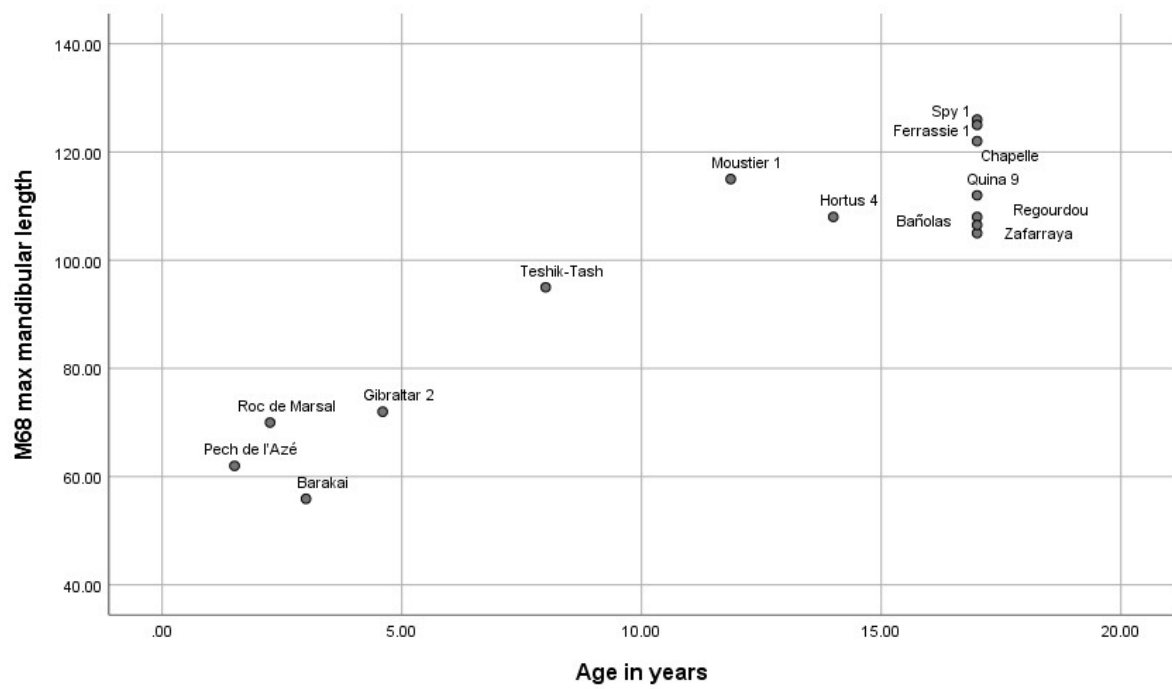


Figure 6.33: Mandibular length (mm), Neanderthal immatures

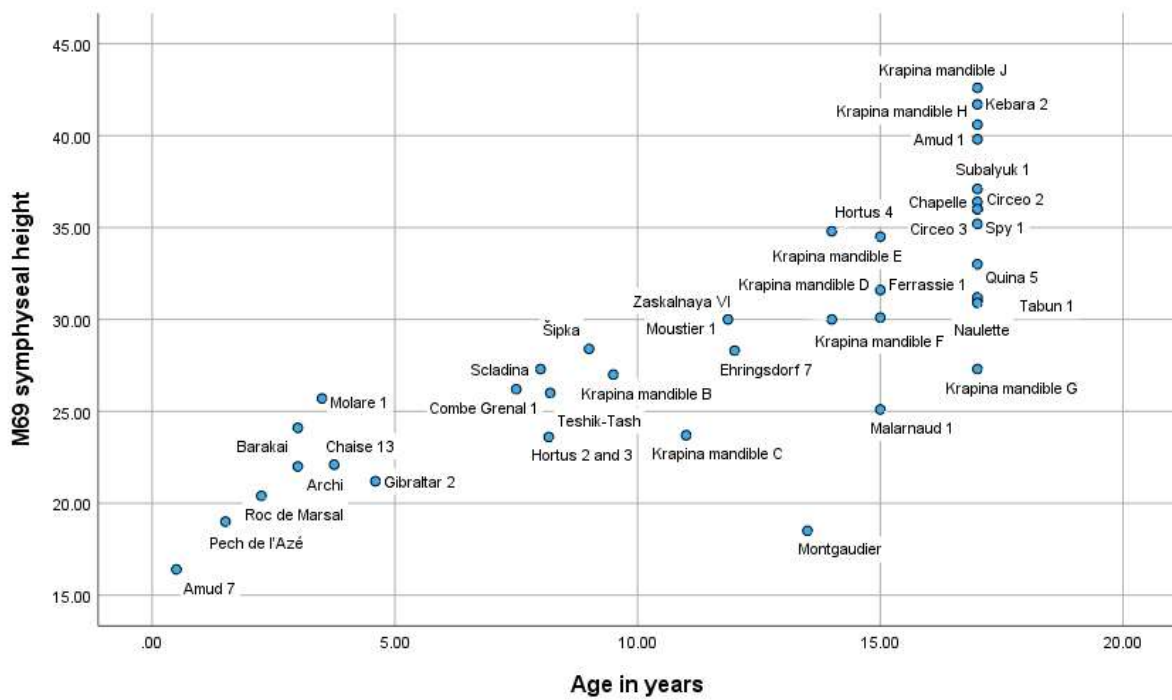


Figure 6.34: Mandibular symphyseal height (mm), Neanderthal immatures

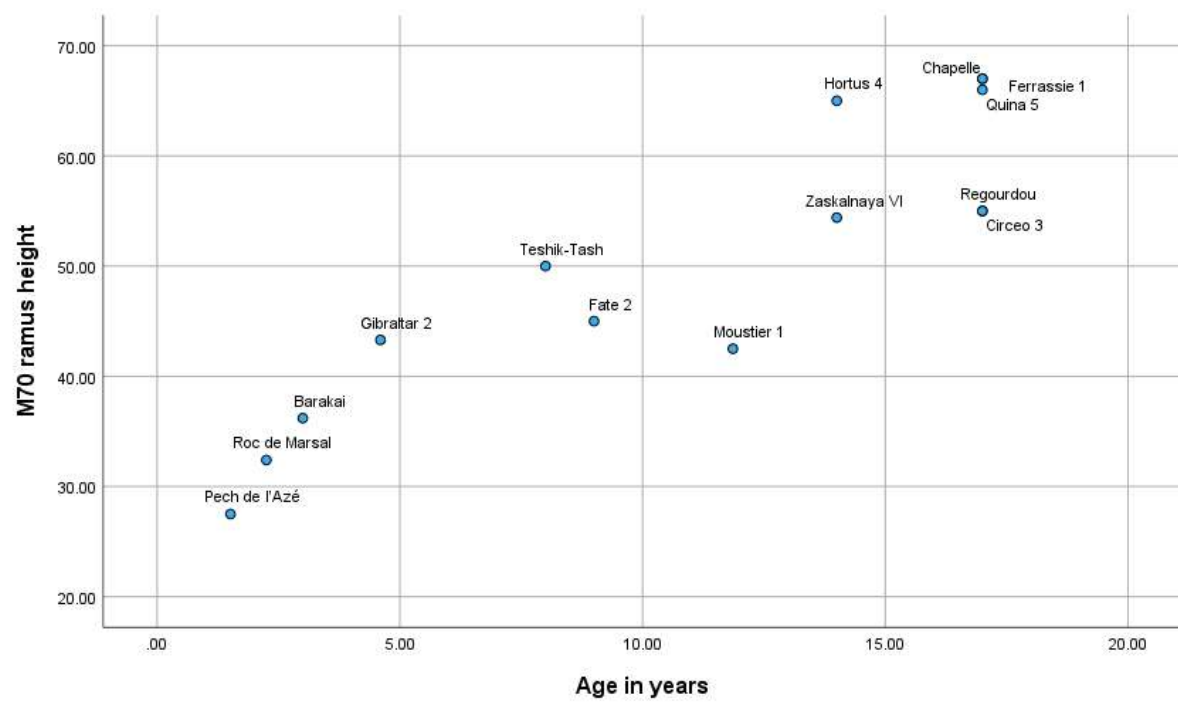


Figure 6.35: Mandibular ramal height (mm), Neanderthal immatures

6.6 Growth to target adult morphology

On the basis of Le Moustier 2 and Mezmaiskaya 1, the Neanderthal neonate is similar to a modern human with a similar endocranial volume, but with a larger midface, larger orbits, and more elongated neurocranium. Compared with modern humans, the typical Neanderthal adult cranium is larger in length and breadth overall and in facial height and breadth, and has much more salient bony superstructure such as general viscerocranial and especially midfacial projection, expansion of the nasal area, browridges, and thickening of the nuchal region. Postcranially, the Neanderthal adult is not taller than the modern human adult, but has generally more robust morphology of the vertebral column, rib cage, pelvis and limbs.

Thompson and Nelson (2001) state that in absolute terms Neanderthal subadults appear to be advanced in cranial growth, but that taking into account the difference in adult cranial size and robusticity the trajectories seem similar between them and modern humans. This is so because, from a similar starting point as a neonate, a Neanderthal child has to achieve more cranial growth and also, in robusticity rather than length, more postcranial growth than a modern human child.

Tillier (1995:66) observes that Neanderthal apomorphies become more intensified with age. Many of these involve robusticity. If completion of growth is to be achieved within the same period as for recent human children, ~20 years, then greater changes in both shape and dimensions must take place in each year of life for the immature Neanderthal. Consequently, at any age the Neanderthal child should appear more adult-like compared with the relatively neotenous modern human child and adult, as indeed it does (Bastir et al. 2007:1130). However in percentage of its own species' adult dimensions achieved, the Neanderthal immature is not advanced for its age. If the span of subadulthood is abbreviated, then of course the rate of change must be even greater.

6.7 Summary

Ages determined from counts of dental microstructure are taken to be reliable, whereas those derived from modern human dental or skeletal schedules are provisional and apt to be misleading when applied to an extinct species, when we know that growth schedules may differ considerably, as demonstrated by the Nariokotome *Homo ergaster* skeleton. Some cases of apparent slow growth may be the result of undernutrition (cf. §2.5.3, §2.5.6, §7.5.2).

Some measurements differ widely between authors. Discrepancies can arise because of different physical and virtual reconstructions of the fossils, especially crania, and also occasionally from faulty recording or transcription (Chapter 5 and Appendix A). In some measurements increase seems to be linear. Examples are stature from 2 years upward, cranial length, and even frontal angle of Schwalbe. However, infants and younger children show much variation. Linearity is surely an illusion created by the absence of infants between neonates and those ~1.5 years old, and at the later end the presence of only two juveniles and one adolescent only beginning adolescence. Increase in other measurements shows no linearity at all: e.g. nasal breadth, frontal sagittal index.

Growth in stature is similar to modern human growth up to 2 years. Thereafter, in absolute dimensions Neanderthals keep pace with lower-stature recent African groups and fall behind higher-stature Africans and lower-stature and higher-stature Europeans. In percentage of adult height Neanderthals follow the modern samples more closely but fall below during early childhood and juvenile stages. There are no indications that Neanderthal subadults are growing more rapidly than modern humans.

Body mass is more problematical to estimate. Apart from the very high, perhaps anomalous, estimate 72.5 kg for Le Moustier 1 (12 years), the Neanderthal immatures fit within modern human distribution. There is no indication that the Neanderthal subadults are advanced in percentage of adult weight attained at their ages.

The morphological distinctiveness of the cranium between Neanderthals and modern humans makes comparison of growth problematical, since the neonatal morphology already differs and the adult form is even more different and larger. The considerable increase of dimensions and distinctive growth of the midface and corresponding lengthening of the mandible are described. It appears that full development of the Neanderthal browridge does not occur before 12 years and therefore must be deferred to adolescence. Samples with reliable ages between 12 years and adulthood are lacking.

At any age Neanderthal immatures appear advanced in robusticity relative to recent human children, but are not advanced in relation to their target adult morphology.

CHAPTER 7

THE ARGUMENT FOR AND AGAINST RAPID GROWTH IN NEANDERTHALS

7.1 Introduction

Over several decades the hypothesis has been presented that Neanderthals had a faster dental formation and eruption schedule and grew to adulthood more quickly than modern humans (e.g. Dean et al. 1986; Ramírez-Rossi and Bermúdez de Castro 2004; T.M. Smith et al. 2007b, 2009; Thompson and Nelson 2011, 2016).

The core argument for rapid ontogeny as it concerns Neanderthals is adapted from Thompson and Nelson (2011, 2016), and can be formalized as follows.

Premises

1. Neanderthals had an accelerated dental formation and eruption schedule compared with both early modern (e.g. Upper Palaeolithic) and recent humans.
2. Revised ages at death from computed microtomography of the dentition of Neanderthal immatures are in most cases younger than previous ages derived from modern human dental standards, confirming the hypothesis of rapid dental development.
3. Development of third molars is advanced (equivalent to modern humans at 15.5 years) in a key Neanderthal adolescent, Le Moustier 1, relative to chronological age (12 years), so this individual had only 2–3 years of growth left before the third molars complete formation.
4. For apes and humans, dental growth and skeletal growth cease at approximately the same time, when the third molars complete formation and the later epiphyses fuse.

Conclusions

5. So, if Neanderthal third molars complete formation at ~14–15 years, skeletal growth should also be completed at ~14–15 years.
6. Completion of growth at ~14–15 years rather than at 18–20 years means an attenuated adolescence and overall duration of growth to adulthood ~25% shorter than in modern humans.

Premises 1 and 2 are well supported (Chapter 3) but premises 3 and 4 are not unequivocally supported. There is evidence that the time interval between the dental stage of Le Moustier 1 and completion of the dentition may be twice as long as suggested, and that the age of completion of skeletal growth, and bodily growth in general, may be later than the age of completion of the dentition. The discussion following therefore analyses evidence concerning premises 3 and 4 and includes further observations.

The hypothesis of rapid ontogeny has wider scope, in that it has been argued that all hominins prior to *Homo sapiens* experienced faster dental development, eruption schedules and skeletal growth than modern humans (B.H. Smith 1993; T.M. Smith et al. 2007b, 2010). In these respects ontogeny in australopithecines was similar to that of chimpanzees, and in *Homo erectus* (*s.l.*) intermediate, more prolonged than in australopithecines but much more rapid than in modern humans (Graves et al. 2010; Cunningham et al. 2018). In Neanderthals *prima facie* it should be slower still, but it is suggested that they grew to adulthood more rapidly than *Homo sapiens* (Nelson and Thompson 2005; Thompson and Nelson 2016).

As will be discussed later, *Homo erectus s.l.* has accelerated dental development and correspondingly accelerated skeletal development, but such a correspondence is not found in Neanderthals. Skeletal growth appears to be delayed across the subadult Neanderthal hypodigm (§6.2, §6.3). A dissociation between dental and skeletal development is therefore discussed here.

Frequent reference will be made to three Neanderthal immature individuals: Teshik-Tash and El Sidrón J1, which are juveniles, and particularly Le Moustier 1, which is most probably an early adolescent, in terms of the growth stages proposed by Bogin and colleagues (Bogin 1999, 2003; Bogin et al. 2016, 2018). Other Neanderthal potential juveniles and adolescents have been recovered but are much less complete, lacking either dentition or measurable postcrania (Chapter 5 and Appendix A). So for the juvenile stage the sample size is 2 and for the adolescent stage 1. It is not unreasonable to treat these subjects as if they are typically developing Neanderthal immatures, but it is appropriate to be cautious in generalizing to a whole population from such limited data.

7.2 Age at death

El Sidrón J1, Teshik-Tash and Le Moustier 1 are relatively complete older subadults. They can exemplify the phenotype a substantial way along their species' ontogenetic trajectory.

El Sidrón J1 is aged 8 years (Rosas et al. 2017). Age estimates for Teshik-Tash have been given as 9 years (Gremyatskii 1949:142), or dental age 7–10 years with skeletal age 6–7 years (Thompson and Nelson 2011:262). On modern human dental schedules, the Le Moustier 1 individual was assessed to be 15–16 years old (Schuchhardt 1912:10). Thompson and colleagues (Thompson and Illerhaus 1998; Thompson et al. 2002; Thompson and Nelson 2005a) have drawn attention to the striking contrast between the dental age which they arrived at, 15.5 years, and the much less mature state of the postcranial skeleton, which indicates an age of 10.5 years.

Given the discrepancy between somatic and dental development, several possibilities are open, two extreme: (a) if the skeletal age 10.5 years is correct, then Neanderthal dental development was much more rapid than that of modern humans, so that they might be close to adulthood at early-teen ages; or (b) if the dental age 15.5 years is correct, Neanderthal somatic development was much slower and adulthood might not be attained until ages well into the third decade of life. One to argue for (b) has been Cuozzo (2005). A third possibility (c) is that, relative to modern humans, Neanderthals followed an ontogenetic schedule of advanced dental development but delayed somatic development up to adolescence.

A revised age at death for several Neanderthal immatures including Le Moustier 1 was presented by T.M. Smith et al. (2010, especially SI:27), based on dental computed microtomography (Table 3.1). The ages of fossil individuals were calculated from daily growth cross-striations and longer-term lines (striae of Retzius) within tooth crown enamel and enamel surface waves (perikymata), as the sum of initiation age, crown formation time, and root formation time. For Le Moustier 1, root formation time was in turn based on the length of the root (3.8 mm, 25% formed) divided by alternative root extension rates, rapid (modern African) 3.5 mm per day and slower (modern European) 3.0 mm per day, given that root extension rates for Neanderthals themselves were unknown. The result was 11.61–12.11 years.

Thompson and Nelson (2011, 2016) adjust this value downward to 11.0 years, as a consensus value using the skeletal age ~10.5 years and on the basis that modern human dental development schedules overestimate Neanderthal ages. The latter has been true of previous estimates for Neanderthal specimens based on modern human dental eruption or dental formation schedules (Table 3.1). However, the method used by T.M. Smith et al. (2010) is based entirely on incremental growth lines in the dental microstructure, apart from the root extension rates. This method is intended to yield not a relative age derived from the Neanderthal dental stage compared with recent modern human schedules but an *absolute chronological age at death* (Le Cabec et al. 2015:13–16; Liversidge 2016:175). A relative or consensus age from modern human dental and skeletal standards is no longer appropriate when an independently derived chronological age is available. Instead, both dental status and skeletal status of an individual have to be assessed in the context of chronological age, which will reveal any advancement or delay in either status.

The estimate of 11.61–12.11 years should therefore not be adjusted. For this reason it seems appropriate to settle upon the mean of the unadjusted range given by T.M. Smith et al. (2010), which is 11.86 years – roundly 12 years, given that 12.0 is within their estimated range. As if presciently, Thompson and Nelson (2005a:218) stated earlier that a chronological age of 11–12 years was indicated by the skeletal growth achieved, ~85.1% of adult height (cf. Table 6.3).

7.3 Third molars and completion of permanent dentition

7.3.1 Starting point of the argument

Chapter 3 covered the evidence of advanced dental development in Neanderthals. This chapter takes up the topic again, focusing primarily on the age of completion of the permanent dentition, i.e. when third molars reach apex complete, and the question whether age of completion of the permanent dentition coincides with age of completion of skeletal/somatic growth.

The starting point is that the oldest subadult Le Moustier 1 exhibits all four third molars at formation stage root $\frac{1}{4}$ (Thompson et al. 2002:58; Thompson and Illerhaus 2005:235–236). Completion of dental development is defined by closure of the M3 root apices. Thompson and Nelson (2011, 2016) suggest that from this stage to root apex closure in modern humans takes 2–3 years. Adding this to their estimate of 11 years at death, they get 13–14 years for dental (and skeletal) maturity.

The chronological age for this individual by dental microtomography is ~12 (11.86) years. Adding 2–3 years, the age of dental maturity becomes 13.86–14.86 years. Even this is somewhat earlier than Wolpoff (1979) proposed, because he predicted M3 emergence at ~15 years and emergence occurs well before closure of the root apex. If completion of dental growth at apex closure coincides with completion of skeletal growth, this means that a Neanderthal individual would have completed growth to adulthood in the mid-teens.

Modern human ages for M3 development are reviewed below, to compare ages at the M3 root $\frac{1}{4}$ stage and to compare intervals from that stage to M3 apex complete. Molar root $\frac{1}{4}$ is equivalent to Demirjian stage E (Demirjian et al. 1973; Demirjian and Goldstein 1976).

7.3.2 Advanced dental development in some living human populations

Advanced dental development, particularly of M3, has been reported in several living human populations in Africa and Australasia (Tanner 1962:71; Eveleth and Tanner 1976:210,427–428; Gillett 1998; Liversidge 2003) (§D.3). While the possibility of differences of method between observers is always present, consensus is that the variation is genuine and considerable.

Chagula (1960) reports from a survey in Uganda that East African males erupt their third molars earlier than Caucasians, and some have the M3 emerging through the gingiva at 13 years. He acknowledges that there may be some inaccuracy in reported ages, since parents sometimes present children as younger than they are for secondary school admission after age 13. Fanning (1962) finds Chagula's (1960) African children up to 2.5 years in advance of Boston children in the early-middle teens, but only 1.25 years advanced in the later teens. The study by Hassanali (1985) finds that Kenyan Africans have their third molars emerged almost two years earlier than Kenyan Asians. A small number of his African subjects have one or more M3s emerged from 13 years, but a smaller proportion than Chagula (1960). For the African subjects, M3 emergence becomes more frequent at 16 years, and median ages for each of the four M3s are 17.85–18.89, while for Asians the median ages are 19.89–20.65 (Hassanali 1985:518–519). In Nigeria, Odusanya and Abayomi (1991) found M3 emergence in males beginning at 15 years and in females at 13 years, with all emerged by 19 years. Chertkow (1980), comparing permanent canine apical closure times with hand-wrist maturation, found

that most of the African children in the age group studied had already attained apical closure, while most of the European children had not.

Fanning and Moorrees (1969) report from their sample that formation of M1 and M2 is entirely comparable between Australian Aborigines and Caucasians but M3 formation is delayed in Caucasians. Crypt formation and crown mineralization of M3 had begun in the Australians when M2 was only at crown $\frac{1}{2}$; in Caucasians the M3 crypt did not form until M2 was at root $\frac{1}{4}$. This delay represents three dental stages on the schedule of Moorrees et al. (1963), and translates to an interval between population means of 4.3 years.

Liversidge (2008a:308) states that South African Black children erupt and complete maturation of the mandibular third molar significantly earlier than other groups in the study, namely Cape Coloured in Cape Town and Bangladeshi and White children in London. Specifically, the mean ages on entering stages root $\frac{1}{4}$ and apex $\frac{1}{2}$ among the African males are 14.59 and 19.31 years.¹ The minimum age of children within stage root $\frac{1}{4}$ in the whole study was a Cape Coloured subject at 9.85 years, presumably an outlier, since the mean in Cape Coloureds was 15.51. Mean age for M3 root $\frac{1}{4}$ in the Bangladeshi group was the highest in the survey at 15.76 years, but the minimum was early at 11.72 years.

German, Southern African and Japanese populations have been compared for attainment of Demirjian formation stages D–H in third molars (Olze et al. 2004) and eruption of third molars (Olze et al. 2007). Southern African subjects attained Demirjian stages D–E in males and E–G in females 1–2 years earlier than Germans and 1–4 years earlier than Japanese. However, the reported differences are greater at the earlier stages (D = crown complete) than the later (G = root complete). The study defines four stages of eruption from enclosed crypt through resorption of overlying alveolar bone and gingival emergence to full occlusion. Southern African females reached stages a mean 1.6–1.8 years earlier than German females, who in turn were 0.9–3.3 years earlier than Japanese. Southern African males attained each stage 3.0–3.2 years earlier than Germans and 3.1–4.2 years earlier than Japanese. Olze et al. (2007:447–448) attribute the differences to palatal dimensions, East Asians being generally the smallest. As with the previous study, the differences between populations appear greater at earlier stages.

Duration of M3 formation derived from ages listed by Liversidge (2008a:298–300,306,308) for four ethnic groups is listed in Table 7.1. Although the African mean ages are younger than those of other groups by 1–2 years at the early stages, the later stages are attained at similar ages by all groups. The African group reaches M3 crown initiated almost 2 years ahead of the White group, but the White group reaches apex $\frac{1}{2}$ marginally before the African group. The whole process of crown plus root formation appears to take ~1.0–1.5 years longer in Africans, with an earlier inception but simultaneous finish. As the study is cross-sectional, this conclusion can be criticized. Here it serves to illustrate the possibility that tooth formation which begins earlier may not be bound to complete correspondingly earlier.

¹ Mean age on entering a stage is age at which 50% of the children from an age group have entered that stage (Liversidge 2008a:299).

Table 7.1: Mean ages on entering M3 stage and resulting intervals, modern humans

	Mean ages on entering stage							
	Male				Female			
M3 stages	African	Cape Coloured	Bangladeshi	White	African	Cape Coloured	Bangladeshi	White
Crypt formed	7.33	9.26	8.22	8.8	6.99	8.81	8.26	9.31
Cusp initiated (ci)	7.92	9.89	8.92	9.69	7.88	9.54	8.95	9.78
Crown complete (cc)	13.38	13.95	13.77	14.23	12.65	13.61	13.42	14.21
Root ¼ (r¼)	14.59	15.19	15.16	15.38	14.14	15.37	15.55	15.62
Apex closure (ac)	19.31	20.06	19.53	19.26	19.17	21.31	20.07	20.88
<i>Interval crypt to ci</i>	<i>0.59</i>	<i>0.63</i>	<i>0.7</i>	<i>0.89</i>	<i>0.89</i>	<i>0.73</i>	<i>0.69</i>	<i>0.47</i>
<i>Interval ci to cc</i>	<i>5.46</i>	<i>4.06</i>	<i>4.85</i>	<i>4.54</i>	<i>4.77</i>	<i>4.07</i>	<i>4.47</i>	<i>4.43</i>
<i>Interval ci to r¼</i>	<i>6.67</i>	<i>5.3</i>	<i>6.24</i>	<i>5.69</i>	<i>6.26</i>	<i>5.83</i>	<i>6.6</i>	<i>5.84</i>
<i>Interval ci to ac</i>	<i>11.39</i>	<i>10.17</i>	<i>10.61</i>	<i>9.57</i>	<i>11.29</i>	<i>11.77</i>	<i>11.12</i>	<i>11.1</i>
<i>Interval r¼ to ac</i>	<i>4.72</i>	<i>4.87</i>	<i>4.37</i>	<i>3.88</i>	<i>5.03</i>	<i>5.94</i>	<i>4.52</i>	<i>5.26</i>
Ages and intervals in years. Values in italics calculated from given values. Data from Liversidge (2008a:298–300).								

7.3.3 M3 root development time

The duration of the interval from M3 root ¼ to apex complete in Neanderthals is unknown. Together with Table 7.1, Table 7.2 provides a modern human reference set with which to assess possible development time for an individual such as Le Moustier 1 to reach completion of the dentition.

Table 7.2: Modern human male M3 formation stages, ages and resulting intervals, and predicted age at apical closure for Le Moustier 1

	Anderson et al. (1976) mean	Moorrees et al. (1963) earliest	Moorrees et al. (1963) and B.H. Smith (1991) mean	Liversidge (2008a:304) African male earliest	Liversidge and Marsden (2010) mean	Liversidge and Marsden (2010) earliest (95% CI)	Al Qahtani et al. (2010) median	Al Qahtani et al. (2010) earliest	Jung and Cho (2014) earliest
Age at root ¼	15.5	11.9	14.5	12.5	15.23	11.68	15.0	11.5	12.0
Age at apex ½	-	-	-	16.72	18.79	15.89	21.5	19.5	-
Age at apex closed	18.2–18.5	16.5	20	-	-	-	23.5	21.5	17.0
<i>Interval r¼ to a½</i>	-	-	-	<i>4.22</i>	<i>3.56</i>	<i>4.21</i>	<i>6.5</i>	<i>8.0</i>	-
<i>Interval a½ to ac</i>	0.25	-	-	<i>0.25</i>	<i>0.25</i>	<i>0.25</i>	-	<i>2.0</i>	-
<i>Interval r¼ to ac</i>	2.7–3.0	4.6	5.5	<i>4.47</i>	<i>3.81</i>	<i>4.46</i>	8.5	10.0	5.0
<i>Subject 11.86y at r¼, predicted age at ac</i>	14.56–14.86	16.46	17.36	16.33	15.67	16.32	20.36	21.5	16.86
Ages and intervals in years Values in italics are calculated or extrapolated from values in cited sources.									

The studies referenced in Table 7.2 are cross-sectional, so the time intervals between means do not represent individuals, but together may serve to illustrate the variation of intervals occurring between tooth stages.

Using mean ages for males of living populations in Anderson et al. (1976:193–194), M3 root ¼ occurs at 15.5 years and apical closure at 18.2–18.5, so the interval from root ¼ to completion of dental development would be 2.7–3.0 years. In Le Moustier 1, adding this growth interval places completion of dental development between 14.5 and 15.0 years. If the Neanderthal root extension rate was faster, then completion might occur even earlier. Contrastingly, for mandibular M3s, B.H. Smith (1991:160) provides the age 14.5 years for root

¼ and 20 years for apical closure. These values give a much longer interval from root ¼ to completion, 5.5 years, which would bring the subject to 17.36 years at completion. Liversidge and Marsden (2010:4), using data from three ethnic groups, give mean age for M3 root ¼ as 15.23 years with apex ½ at 18.79 (apex closed is not listed), an interval of at least 3.56 years.

According to Anderson et al. (1976), the interval from apex ½ to closure is 0.2–0.3 years, while according to AlQahtani et al. (2010:489) it can be >1 year. In the Liversidge and Marsden (2010) study, minimum ages listed for root ¼ and apex ½ in males are 11.68 years and 15.89 years respectively, producing an interval of at least 4.21 years if these were to represent the same individual. It is notable that this minimum-age subject at root ¼ is marginally younger than Le Moustier 1.

Moorrees et al. (1963:1496–1497) show dental formation ranges for males with the earliest M3 distal (later completing) root ¼ occurring just below 12 years and the earliest apical closure of the distal root at 16.5 years. Jung and Cho (2014) in a Korean study found the earliest mandibular or maxillary M3 root ¼ at 12 years, with mean 16.25, and earliest M3 apical closure (Demirjian stage H) at 17 years, with mean 21.96 years. This was not a longitudinal study, but the interval of 5–5.71 years between root ¼ and apex complete is notable.

AlQahtani et al. (2010) document attainments per year group. This study presents long development intervals and late completions. In it the age groups 14–15 and 15–16¹ years both have median attainment M3 root ¼: so I have listed 15.0 as median age for root ¼. Similarly, the first and only group to show apex closure as median stage is 23.5 years. The earliest group to exhibit apex closure is 21.5 years. These ages, from radiographs, are the latest in available literature, and produce the longest interval from root ¼ to completion, up to 8.5 years. The youngest age group exhibiting root ¼ is 11–12 years, but root ¼ remains the most advanced stage reached in each of the three succeeding year groups up to 14.5 years, indicating that the youngest subjects are probably outliers.

In the core argument earlier, the interval from M3 root ¼ to apex closure was proposed as 2–3 years. Yet from all studies in Table 7.2 apart from Anderson et al. (1976), the interval is substantially longer at 3.81–10 years, leading to predicted ages at apex closure of 15.67–21.5 years. The studies listed are not longitudinal. It cannot be inferred that Neanderthals must have taken as long as 3.81–5.5 years, let alone 8.5 or 10 years, and if dental formation rates were faster they might have taken less time. Root extension rates in Neanderthals are found to be distinctly faster than in modern humans (§3.4.6), which probably renders these very long intervals to apex closure inapplicable.

Even so, the possibility has to be entertained that this interval for Neanderthals was longer than the 2.7–3.0 years mooted earlier. If age of M3 apex closure coincides with age of completion of skeletal growth, time has to be allowed for skeletal growth to take place. The two similarly aged juveniles and the adolescent have attained only ~67% and ~84%, respectively, of adult stature and have not developed adult cranial morphology (§6.5.2). If they are typical, it cannot just be assumed that their somatic growth would suddenly have accelerated to reach full adulthood by the end of their fourteenth, fifteenth or sixteenth year.

The development of third molars in recent humans is much more variable than that of the earlier appearing teeth (Garn et al. 1962; Moorrees et al. 1963; Anderson et al. 1976; Liversidge 2008a). The above examples indicate that it is variable enough to include Le Moustier 1 within modern human ranges, but certainly at the early end of the distribution.

¹ Upper limits are just under 15 and 16 years respectively.

7.3.4 Molar development, maxillary and mandibular growth

Anteroposterior growth of the maxilla and mandible, creating space at the distal end of the dental arch, appears to enable formation and eruption of the molar teeth (Forsberg et al. 1989; Randhawa et al. 2022; Gao et al. 2024).¹ This proposal receives support from the finding that, in an archaeological Sudanese sample, each of the three molars erupts successively at a consistent distance from the temporo-mandibular joint, as part of a process which maintains optimal effectiveness of the masticatory musculature (Spencer and Schwartz 2008:199). In modern Europeans a mandibular third molar may erupt to alveolar level at an angle and appear impacted, but roots are often curved inferoposteriorly and sometimes the tooth realigns on a curved path and comes upright into occlusion as the jaw lengthens and space becomes available (Richardson 1992; Hattab 1997).² Length is not the only factor: a positive correlation has been found between vertical height of the mandibular corpus and degree of formation and eruption of the posterior dentition (Takeshima et al. 2004).

In African and Australasian populations the generally greater length of the dental arch achieved by early adolescence (Keith 1925; Broadbent et al. 1975; Brown 1978; Liversidge 2008a; Sardi and Ramírez-Rozzi 2012) may be the factor that permits M3s to emerge within a shorter interval following M2 emergence, and so at earlier ages, than in South Asians, East Asians and Europeans, and also reduces the incidence of M3 agenesis (Chagula 1960; Fanning 1962; Fanning and Moorrees 1969:1000; Brown 1978; Merz et al. 1981; Tompkins 1996a:95; Olze et al. 2004, 2007; Liversidge 2008a:317). M3 agenesis can be interpreted as the extreme case of a range of reduced or delayed development (Roche 1992:144; Tompkins 1996b:111).

The Bolton Standards for orthodontics present optimal dentitions for each year from 1 to 18 years, each from radiographs of an actual child subject. The jaws of these optimal subjects had grown sufficiently to permit eruption without malocclusion or crowding. Broadbent et al. (1975:138) discovered that consequently the standards imply eruption of each tooth at a slightly later age (by months) than expected from earlier studies.

If this principle applies to Neanderthals, then, as their alveolar arches are large from infancy onward, development of all three molars may be expected to be precocious by the standard of many recent human populations.

7.3.5 Further dental comparisons: modern humans, Neanderthal juveniles and adolescent

The juvenile Neanderthal specimen from Teshik-Tash is the next younger relatively complete individual below Le Moustier 1. At the time of writing, the age at death of Teshik-Tash is not known to have been assessed from the dentition by counts of dental microstructure.

Gremyatskii (1949) shows that Teshik-Tash retains its deciduous canines and molars, but the permanent M1s are in occlusion. In the right mandible, the M1 is approximately at apex $\frac{1}{2}$ or apex closed, the unerupted M2 is at root $\frac{1}{2}$, and the M3 in its crypt partially behind the ramus is at crown $\frac{3}{4}$. The unerupted P3 and P4 are approximately at root $\frac{1}{2}$ and in position to replace the deciduous molars, of which the roots are resorbing. Mean and earliest ages for the observed formation stages of these teeth from Moorrees et al. (1963:1496–1497) are given in Table 7.3.

¹ An equivalent hypothesis is rejected in the case of *Pan* and *Papio* by Boughner and Dean (2004). Ramírez-Rozzi and Bermúdez de Castro (2004:938) also reject it for the Neanderthals, on the grounds that Neanderthals had faster enamel secretion rates. But the two explanatory factors could be complementary, not mutually exclusive.

² The present writer experienced exactly this with his right mandibular M3.

Table 7.3: Mean and earliest modern human ages for stages of Teshik Tash mandibular permanent teeth

Teshik-Tash	Modern human	
	Mean age (years)	Earliest age (years)
P3 root ½	9	7.1
P4 root ½	8	7.7
M1 apex ½ ¹	7.5	6.2
M1 apex closed ¹	9.5	7.7
M2 root ½	10	8.2
M3 crown ¾	11.5	9.5
Modern human ages from Moorrees et al. (1963).		
¹ Distal (later completing) root.		

Proposed ages at death have ranged up to 10 years with 9 preferred (Gremyatskii 1949:142) but as low as 7.5 years (Granat and Heim 2003). A compromise young age, ~8.2 years, places this individual within the early end of the modern range, apart from the M3 development, which appears advanced. In some recent human populations the M3 can be more advanced relative to the M2 (Brown 1978). In an Australian Aboriginal sample, of 18 subjects with the mandibular M2 at root ½, 10 had M3 at crown ½, although none were more advanced (Fanning and Moorrees 1969:1004).

Table 7.4 compares the juvenile and adolescent with modern human age peers. Teshik-Tash has M2 advanced by ~1 year and M3 even more advanced. Le Moustier 1 is within the upper range for M3 development.

Table 7.4: Comparison of Neanderthal dental development with modern human age peers, mandibular permanent teeth

Teshik-Tash	Modern human 7–8 y		Modern human 8–9 y	
	Median	Maximum	Median	Maximum
P3 root ½	root initiated	root ¼	root ¼	root ½
P4 root ½	crown complete	root ¼	root initiated	root ¼
M1 apex ½	root ¾	apex ½	root ¾	apex ½
M2 root ½	crown ¾	root ¼	root initiated	root ¼
M3 crown ¾	none	cusps initiated	cusps initiated	coalescence of cusps (cco)
Le Moustier 1	Modern human 11–12 y		Modern human 12–13 y	
	Median	Maximum	Median	Maximum
M3 root ¼	cusp outline complete (coc)	root ¼	crown ½	root ¼
Modern human data from AIQahtani et al. (2010:488).				

In contrast, El Sidrón J1 is not dentally advanced. This juvenile has an age at death 7.7 years (7.61–7.78 years) obtained by counts from dental microstructure (Roses et al. 2017 SI:31–33). Table 7.5 gives the stages of the mandibular dentition with corresponding ages for modern humans.

El Sidrón J1 is older than the mean ages for its dental development by the standards of Moorrees (1963). Initially, Rosas et al. (2012) assessed its age as 6 years. Rosas et al. (2017) use their own large modern human samples to show that this individual is within modern range for each tooth, and conclude that it can no longer be assumed that all Neanderthals were dentally advanced.

Table 7.5: Modern human mean, earliest and latest ages for stages of El Sidrón J1 mandibular permanent teeth

El Sidrón J1	Modern human		
	Mean age (years)	Earliest age (years)	Latest age (years)
I1 root complete	6.5	5.5	8.5
I2 root $\frac{3}{4}$	6.7	5.5	8.3
C root $\frac{1}{4}$	6	4.5	7.3
P3 root $\frac{1}{4}$	7	5.5	8.6
P4 root initiated	7	5.5	8.5
M1 root complete	5.8–6.3	~5	8
M2 root initiated	7	5.7	8.8
M3 crypt present	<7	<9	<11.5
El Sidrón J1 dental stages from Rosas et al. (2017). Ages from Moorrees et al. (1963)			

Comparison with *Homo ergaster*

The Neanderthal juveniles and the *Homo ergaster* individual KNM-WT 15000 are of a similar age. Age for Teshik-Tash is less certain than for the others. Teshik-Tash is advanced over El Sidrón J1, Scladina is advanced over Teshik-Tash, and KNM-WT 15000 is only slightly advanced over Scladina (Table 7.6). In this small sample, one Neanderthal is not advanced over recent humans, another is almost as advanced as *Homo ergaster*, and the third appears to be intermediate. Scladina has the earliest date (127–80 ka) and El Sidrón J1 (~49 ka) probably the latest (Appendix A). Given that KNM-WT 15000 is dated ~1.5 Ma, it seems unlikely that the dating of Scladina, more than a million years later, has any bearing on its dental precocity.

Table 7.6: Comparison of mandibular dentition at ~8 years, Neanderthal and *Homo ergaster/erectus*

Tooth type	Neanderthal			<i>Homo ergaster/erectus</i>
	El Sidrón J1, 7.7y	Teshik-Tash, 8.2y?	Scladina, 8.0 y	KNM-WT 15000, 7.6–8.8y
I1	root complete	-	apex complete	-
I2	root $\frac{3}{4}$	-	-	-
C	root $\frac{1}{4}$	-	apex $\frac{1}{2}$	root $\frac{3}{4}$
P3	root $\frac{1}{4}$	root $\frac{1}{2}$	root $\frac{3}{4}$	root $\frac{3}{4}$
P4	root initiated	root $\frac{1}{2}$	root $\frac{1}{2}$	root $\frac{3}{4}$
M1	root complete	root complete	apex complete	-
M2	root initiated	root $\frac{1}{2}$	root $\frac{1}{2}$	root $\frac{1}{2}$
M3	crypt present	crown $\frac{3}{4}$	crown $\frac{3}{4}$	mandibular M3 absent, maxillary M3 crown $\frac{3}{4}$
Neanderthal data from previous tables and Chapter 3. KNM-WT 15000 data from Dean et al. (2014:339,343–344).				

Stature and body mass of KNM-WT 15000 and the Neanderthal immatures are compared later (§7.6).

7.4 Correlation of somatic growth with dental development

7.4.1 Central premise of the argument

A crucial premise in the argument for shorter Neanderthal ontogeny is that general growth of the body is closely correlated with dental development, and specifically that the completion of dental growth, marked by apex closure of the third molars, coincides with the completion of skeletal growth, marked by the fusion of those epiphyses which have remained unfused or only partially fused until this time. If the end of adolescence, including somatic growth generally, is signalled by M3 apical closure, then Neanderthal males would have been fully grown by 14.56–17.36 years (§7.3.2), or even earlier if their dental formation rate was faster.

In support of this specific premise Thompson and Nelson (2011:264; 2016:94) cite Tanner 1990,¹ Anemone et al. (1996), Kuykendall and Conroy (1996), Leigh and Shea (1996), and Simpson et al. (1996).²

7.4.2 Degree of correlation

Many researchers have stated that dental and somatic growth are tightly correlated (e.g. Dean et al. 2001:628; Schwartz 2012:S397), citing the work of B.H. Smith (1989a, 1989b, 1991, 1992). This claim unqualified may be an overstatement. In these publications Smith does not claim that the development of the whole dentition is correlated with skeletal or somatic growth. Her argument concerns only a correlation, across a large range of primates, between the age of emergence of the mandibular first molar (M1) and a set of life-history and life-history-related variables (cf. Macho 2001): gestation length, age at weaning, age at female sexual maturity, lifespan, body weight and brain size. Generally, the larger-bodied and larger-brained the primate, the larger the age or interval, e.g. lifespan, represented by those variables becomes, and the later the mandibular M1 emerges. The highest correlation, $r=0.98$, is between brain size and mandibular M1 emergence.

One influential outcome of the analysis of brain and body size versus M1 emergence has been the implication that australopithecines, with endocranial capacity and body weight similar to those of chimpanzees, would have had a more rapid life history than modern humans. They would have experienced early M1 emergence, around 3.2 years like chimpanzees (B.H. Smith 1992:138), in agreement with earlier proposals of Bromage and Dean (1985) from their examination of australopithecine dentition. In turn, early *Homo erectus s.l.*, with mean endocranial capacity below 1000 cm³, would be expected to have an intermediate status in terms of dental development and life history. Neanderthals, however, with estimated body weight and endocranial capacity comparable with or possibly slightly exceeding those of modern humans, would be expected to emerge M1 at a relatively late age of 6.6 years, grow

¹ US edition 1990; UK edition 1989 listed in References.

² In his book *Foetus into Man* Tanner does not discuss completion of dental growth versus skeletal growth. The four papers are from the same issue, Vol. 99(1), of the *American Journal of Physical Anthropology*. Anemone et al. (1996) and Kuykendall and Conroy (1996) discuss chimpanzee dental development but make no mention of skeletal growth; Leigh and Shea (1996) discuss body size variation in apes but make no mention of dental development; Simpson et al. (1996) use dental stages to normalize skeletal growth trajectories between their chimpanzee series and modern humans, given that human ontogeny is of longer duration, but do not present any argument for a correlation between completion of the dentition and completion of skeletal growth. However, as discussed later in this chapter, information from Webb and Suchey (1985) and Cunningham, Scheuer and Black (2016) shows that there is a broad timescale within which M3 completion and fusion of epiphyses contributing to stature take place (§7.4.6).

up more slowly, and enjoy a potential lifespan slightly longer (B.H. Smith 1991:163). This implication has not found favour among palaeoanthropologists.

Later studies have found more variability than previously expected in chimpanzee and australopithecine dental formation and eruption times, with chimpanzee M1 emergence as late as 4.1 years, and suggest greater overlap between modern human and extinct hominin schedules (Kelley and Schwartz 2012; T.M. Smith 2013; T.M. Smith et al. 2013, 2014; Le Cabec et al. 2015).

Undoubtedly during ontogeny there is a correlation between dental development and skeletal development. All parts of the body are constrained to grow in such a way as to maintain the viability and functionality of the organism at any time: e.g. legs have to be of equal length for effective mobility, jaws and teeth have to occlude effectively for biting and chewing food for sustenance (Bogin 1999:79–81). It has been suggested that the human body demonstrates a harmony of growth (Widdowson 1970).

B.H. Smith (1989b:63,66–67) argues that, as the dentition processes food, essential for survival of the organism, its development must be correlated with the maturation of muscles of mastication and somatic growth in general. Clearly, development of the dentition must be synchronized with that of surrounding and supporting cranial bones and muscles of mastication so that they function adequately. However, it is not clear that somatic growth in general need be highly correlated with dental development. The variation in living human stature and in robusticity and muscularity of the torso and limbs, regardless of maxillary, mandibular and dental dimensions, in immatures and adults, is itself evidence that during ontogeny the former somatic characteristics develop with a high degree of independence from dental development. As B.H. Smith (1989b:66–67) states, dental development is more resistant to environmental circumstances than skeletal maturation. The latter points positively entail that there be scope during ontogeny for general somatic development to diverge from synchronization with dental development.

7.4.3 Environmental influence

Somatic systems and their development are subject to both genetic control and environmental influence (Tanner 1962:77–85; Eveleth and Tanner 1990:176–179; Bogin 1999:339–340) (§2.7).

When the body is deprived of adequate nourishment to sustain all aspects of growth in the organism, growth faltering occurs (Bogin 1999:378–380). However, dental development proceeds and may be relatively unaffected (Eveleth and Tanner 1976:207,210, 1990:146,156–158; Konigsberg and Holman 1999:270–271; Liversidge 2003:73). This factor alone leads to the possibility that among Palaeolithic forager populations dental development for many individuals could be completed several years before the body would attain its full potential stature and lean mass. This is because such communities surviving in suboptimal environments may often have been subject to nutrition stress, coupled with infection as it often is in recent societies (Proos and Gustafsson 2012:1792), and attainment would have depended on catch-up growth, possibly extending over a number of years, following the period of undernutrition (Tanner 1962:123; Prader et al. 1963; Eveleth and Tanner 1990:192–196).

Some anthropological studies have drawn attention to widespread undernutrition among Australian Aboriginal children, especially in rural missions and farm stations, in periods when these studies were carried out, leading to abeyance of growth or slowing of the rate of growth (Klekamp et al. 1987:203–205; 1989:85–86; Riedel 1994:538). However, in the survey by Klekamp et al. (1989) the mean age at death, body height and body mass for both male and

female adults scarcely differed between Aboriginal and Caucasian subjects, except that Aboriginal males were 3 cm taller than Caucasians. It is possible that adult subjects in the above studies themselves suffered undernutrition in early childhood but in later years achieved their potential stature through catch-up growth.

Even if the dentition itself were to be compromised in cases of severe and prolonged lack of nutrition, dental microstructures (e.g. in enamel, cross-striations within the striae of Retzius) will continue to record daily growth, though presumably by less secretion and extension per day, so that a correct age at death is still in principle recoverable.

7.4.4 Survey of correlation studies

Tanner (1962:77–85) reports that measures of skeletal and sexual maturity are more highly correlated with each other than with dental development. Dental formation is less variable for age than somatic maturation, according to studies by Lewis and Garn (1960). Noting the only slight correlation of M3 development with tibial union and hand-wrist union, Garn et al. (1962) express “no great enthusiasm for the rather low relationships” between dental and somatic development.

Orthodontists seek to determine when the adolescent growth spurt is taking place and what stage a patient has reached, so as to time treatment to take advantage of facial growth. Hägg and Taranger (1982) compare timing of dental emergence stages, hand-wrist bone development, menarche and voice changes to identify stages of the adolescent growth spurt. Their correlations of pubertal growth events with dental emergence were weak for both sexes, with values in the range $r=0.01$ – 0.32 . Bielicki et al. (1984) evaluate somatic markers of the adolescent growth spurt and statural attainment versus dental development; but on the basis of correlations at $r=0.07$ – 0.32 conclude that, while linear growth and sexual and skeletal maturation are sufficiently interrelated to indicate a shared general somatic maturation factor, this is distinct from the process governing dental development. Demirjian et al. (1985) also observe strong correlation among markers of skeletal, somatic and sexual maturity, but not of these with dental development. They attribute this difference to independence of controlling mechanisms: the somatic-skeletal system, derived from mesodermal tissue and regulated by pituitary and gonadal secretions, and the dental system arising from ectomesenchymal tissue. The dentition and alveolar bone have a common origin distinct from that of the surrounding mandibular and facial bone (Ten Cate and Mills 1972; Ten Cate 1997).

In contrast, Kumar et al. (2012) find high correlations, $r=0.854$ – 0.866 , between Demirjian (1973) stages of the mandibular second molar and stages of cervical vertebrae maturation. Similarly, Sachan et al. (2011) report high correlations, $r=0.635$ – 0.891 , between formation stages of the maxillary and mandibular right canines and maturation stages of cervical vertebrae.

Among Caucasian early adolescents the timing of dental development, particularly involving exfoliation of deciduous molars and eruption of permanent molars and premolars, has been reported to vary between communities in two US states by as much as 1.5 years, while hand-wrist x-rays disclosed no difference. This result was attributed to essential independence of the dental and osseous tissue systems (Mappes et al. 1992).

The discrepancies among studies of human dental-skeletal correlation are striking, and probably have to be attributed to selection and classification of data and the statistical methods chosen. Referencing previous human studies, Brimacombe et al. (2015b) discuss how data can be grouped or classified and the use of different statistical techniques, in their study of chimpanzee dental and skeletal maturity indicators. That study concludes that chimpanzees

exhibit higher correlations than humans, perhaps because of the greater opportunity for variation afforded by the extended human ontogenetic timescale, ~20 rather than ~12 years.

7.4.5 Correlation of dental advancement with skeletal advancement, modern humans

If somatic growth is tightly correlated with dental development, then a population which is dentally advanced should be expected to be skeletally advanced. As discussed (§7.3.1), it is widely accepted that African groups experience earlier dental development than Caucasians, typically by 1–2 years during infancy and early childhood. Several studies have indicated advanced skeletal development, though not consistently.

On the basis of hand-wrist bone development, Massé and Hunt (1963) report that West African children experienced precocious growth up to 30 months, then by European standards became delayed. Marshall et al. (1970), also using hand-wrist radiographs, found Jamaican children advanced over (White) British from birth to 2.5 years, similar in middle childhood, then from 13 years delayed.

Garn et al. (1973) show that Black American children were generally advanced by up to 0.5 years in dental development compared with White children of the same socioeconomic status. Garn et al. (1972) report advancement of both hand-wrist ossification and stature in Black American children compared with White children. Importantly, the Black children were all from low-income families and all the Whites from a more advantaged background. The difference appears to narrow slightly after 3 years (Garn et al. 1972:967 Table I), but the authors stress that the African American children were still well ahead up to 7 years, the limit of the sample.

Owen et al. (1974:628–629), reporting on children in the United States in similar socioeconomic circumstances, show Black children marginally taller and heavier than White between birth and 6 years. Roche et al. (1975) compared United States children in varied socioeconomic circumstances: in general, Black children were skeletally advanced by a few months but not consistently. A study by Languerrand and Harding (2010) found that Black African and Caribbean infants in the United States had lower birth weights but grew faster than White children to 5 years, and at 6 years were taller and heavier. Malina and Little (1981) found that Black and White children in Philadelphia kept pace until 6–9 years, after which the Black children became taller and heavier.

In contrast, Owings (1981), examining late-fusing epiphyses, anterior iliac crest and medial clavicle, in a sample of Americans of African, European, Latino and East Asian origin, did not find any major distinctions in timing between ethnic groups or between males and females.

Eveleth's (1986:229) assessment is that African children grow more rapidly in the early stages but at a slower rate later in ontogeny. Some of the studies above outline a pattern of skeletal growth slightly advanced for age in children of African descent during the period from birth to ~2–3 years, after which in comfortable socioeconomic circumstances the advancement continues in height and weight, while in less developed environments the advancement is lost and may turn to delay. It is tempting to attribute the change to weaning (Tanner 1989:144), with the transition, in pre-industrial societies, to a possibly plant-based diet which may provide insufficient calories to sustain optimal growth (cf. Bogin 1999:175,274). Either way, a genetic potential for advanced growth seems to be indicated, which in disadvantageous environments is frustrated after infancy. Advancement in growth, when observed, seems to amount to no more than 1–2 years during childhood. Moreover, degree of advancement does not increase with age.

In the teenage years the variable timing of the adolescent growth spurt may mask differences between populations, but these appear to be slight compared with inter-individual variation. It is evident that results of surveys may be compromised by differing socioeconomic circumstances between samples.

7.4.6 Epiphyseal fusion

The argument for early attainment of adulthood by Neanderthals requires that completion of dental development be closely correlated temporally with cessation of skeletal growth, or even coincide with it. Completion of the dentition is represented by the four third molars all reaching apical closure, which occurs some time after eruption to occlusal level. In modern humans the age of attainment varies considerably (§7.3.1, §7.3.2).

Fusion of epiphyses is the principal indicator of completion of growth in the skeleton. Fusion occurs at the various epiphyseal sites at different times through juvenile, adolescent, and young adult years. Stevenson (1924:88) lists the order of epiphyseal fusion events in the skeleton as a whole, and states that the nineteenth year is the most intense period of epiphyseal activity (*ibid.*:92). Some epiphyses and other skeletal elements fuse very late: the medial clavicle at 16–30 years, the pubic symphyseal rim 23–34 years, the jugular growth plate of the occipital 22–34 years (Cunningham, Scheuer and Black 2016); and the anterior iliac crest may be still only partially fused up to 23 years (Webb and Suchey 1985).

The attainment of adulthood in a biological sense, let alone in a social sense, is a process rather than an event, and the end point of skeletal development, the closure of final epiphyses, is unobservable without radiography. However, attainment of adult stature is observable, at least retrospectively, and could be taken to be the indicator of skeletal adulthood or maturity. This permits leaving most of the later-fusing sites out of account and focusing on the axial skeleton and the lower limb.

A list of fusion sites which contribute to stature, with ranges of ages when the fusion process has been observed under way, is given in Table 7.7. Femoral trochanters are omitted. The age ranges reported by Cunningham, Scheuer and Black (2016) are merged from several sources, so that in some cases the ranges are ~1 year wider than in any of the source studies. Cunningham, Scheuer and Black (2016) include the two recent studies by Coqueugniot and Weaver (2007) and Cardoso (2008), each of which examines different samples of Portuguese subjects. The Coqueugniot and Weaver (2007) study produces upper ages for fusion periods which in some cases are ~1 year later than Cardoso (2008) and most earlier surveys.

Table 7.7: Ages of epiphyseal fusion at sites contributing to stature, modern human male

	Fusion period, dry bone (ages in years)
Vertebral column: annular rings, sacral elements	Early 20s, column complete by 25+
Triradiate complex of pelvis	11–20
Proximal femur (head)	15–24
Distal femur	16–21
Proximal tibia	16–21
Distal tibia	15–20
Proximal fibula	16–21
Distal fibula	15–21
Data from Cunningham, Scheuer and Black (2016)	

The termination of epiphyseal fusion at sites contributing to stature could be said to be broadly aligned with M3 eruption and the later stages of M3 formation; but since the temporal

spread is so large for both the dental and the skeletal processes in question, some degree of coincidence is inevitable.¹ Detailed intra-population data seem to be lacking to show whether individual early or late dental developers are generally early or late skeletal developers respectively, which would indicate more precisely how closely the processes are related.

It has been hypothesized (Tanner 1962, 1989) that a central somatic growth programme may control all aspects of growth in the body, including the dentition, skeleton, musculature, organs and other tissues. As part of this schema, catch-up growth would be initiated by a systemic control function to bring the body back to its individually predetermined growth path after a period of stress when growth had wholly or partially stalled. Such a systemic function might be expected to induce correlation between all aspects of development, including the dental and skeletal.

Other mechanisms have been proposed, on the basis that epiphyseal fusion follows rather than causes the cessation of growth (Parfitt 2002:337). Skeletal growth rates are high in infancy and progressively decline with age, apart from the limited duration of the adolescent growth spurt. Growth-plate senescence, a terminal decline in growth rate, supervenes when the lifetime capacity for chondrocyte proliferation in each growth plate eventually becomes exhausted (Parfitt 2002; Nilsson and Baron 2004; Finkelstein et al. 2013). This explanation in terms of localized capacity receives confirmation from the observation that transplanted growth plates in laboratory animals continue to grow at a rate appropriate to the age of the donor organism, not the recipient, as would have been expected if growth were controlled by a central function (Nilsson and Baron 2004:371; Finkelstein et al. 2013).

The potential for locally controlled growth in parts of the body would tend to permit asynchronous growth among units of the body not closely related functionally, such as the dentition and parts of the postcranial skeleton. Where somatic units must match size and shape to function coherently together – for example, at a gross level left and right limbs, and at a more specific level epiphyses of bones meeting at the same joint, e.g. the knee or elbow – natural selection would eliminate those organisms in which too great a degree of asynchronization compromised viability.

From the information in Webb and Suchey (1985) and Cunningham, Scheuer and Black (2016) it appears that there is a period of ~6–8 years in recent humans centred on age ~19–20 years within which occur both (a) third molar emergence and, later, apex closure and (b) fusion of most remaining epiphyses, including those of long bones. While some epiphyses may remain partially fused beyond this period, notably the anterior iliac crest and the medial clavicle, they are few and do not contribute to stature. In a broad sense, then, completion of the third molars overlaps with or even follows rather than precedes completion of statural growth.

For *Pan troglodytes* and *Pan paniscus*, Brimacombe et al. (2015a, 2015b, 2018) assess dental maturity from all maxillary and mandibular teeth, using Demirjian stages (Demirjian et al. 1973) translated to numerical values 0–8 for each tooth type per quadrant. They find that completion of the dentition (dental maturation score 64) precedes epiphyseal fusion at many skeletal sites, in contrast to their expectation for humans. If this apparent disjunction between chimpanzees and humans in the pattern of epiphyseal fusion versus dental completion is sustained, the question arises whether the chimpanzee or modern human pattern, or neither, is characteristic or plesiomorphic within the hominin clade. The variability exhibited by both dental and skeletal developmental processes in living hominoid species is perhaps sufficiently

¹ For example, if it could be shown specifically that completed fusion of the right and left femoral heads occurred almost invariably within two months of right and left mandibular M3 apical closure, that would be a convincing indicator that dental and skeletal growth were “tightly” correlated. Correlations naturally become less convincing the less specific they are.

high that extinct hominins, australopithecines, *Homo erectus*, or more recent ones, should not necessarily be expected to conform to the pattern of either *Homo sapiens* or *Pan*.

7.4.7 Recent assessments of relation between dental and somatic development

Kelley and Schwartz (2012) discuss estimates of age at M1 emergence in chimpanzees, gorillas and orang-utans, and compare those with *Australopithecus* and *Paranthropus*. Revised estimates have resulted from recent study of live subjects in the wild, and from study of dental microstructure in australopithecine fossils. They conclude (ibid.:1336,1347,1357) that age at M1 emergence is a reliable proxy for the general pace of life-history, which includes weaning, inter-birth interval, and other measures. They state (ibid.:1339): “in extant anthropoid primates cranial capacity strongly correlates with age at M1 emergence.” However, they also state (ibid.:1357): “in extant great apes and humans, cranial capacity is neither a particularly precise nor accurate predictor of age at M1 emergence, nor is it strongly concordant with the timing of key life-history attributes” and (ibid.:1347): “cranial capacity is poorly correlated with the life-history attributes most closely linked to lifetime reproductive output.”¹

On the basis of cranial capacity, Kelley and Schwartz (2012:1339) and Schwartz (2012) would predict a mean age for M1 emergence in modern humans of 7.1 years, and suggest that a partial dissociation has been forced between cranial capacity and M1 emergence because otherwise M1 emergence would be delayed beyond a point where the dentition would be fully compatible with weaning. As cessation of suckling in pre-industrial modern human societies takes place at a mean age of 2.5–3 years (Bogin 1999:173–174; Houghton 2010), ~3 years before M1 emergence, it would seem that in modern humans any connection of M1 emergence with weaning has already been completely lost (§2.4).

Schwartz (2012:S403) and Kelley and Schwartz (2012:1347,1349), while asserting the significance of M1 emergence for life history as opposed to other aspects of dental development, suggest that in monkeys, apes and hominins there may be dissociation between life history variables, such that natural selection can operate in a modular pattern on aspects of dentition, reproductive development and general growth.

Šešelj (2013) finds much variation and at most only moderate correlation between dental development and skeletal growth. In her survey from three recent human populations, individuals who were dentally delayed were always skeletally delayed, and those who were skeletally delayed were also delayed dentally but to a lesser extent. She cautions that it may be misleading to use one developmental system, i.e. dental or skeletal, as a proxy for the other, in modern humans and especially in extinct hominins (cf. Šešelj 2017:534).

As part of a wide-ranging survey, Dean and Liversidge (2015:427) implicitly withdraw earlier claims (e.g. Dean et al. 2001) when they explicitly conclude that dental and skeletal development are “not in lockstep” and caution against the assumption that dental versus

¹ The statements at pages 1339 and 1357 are strictly contradictory, since great apes and humans are anthropoid primates. The statements at pages 1347 and 1357 explicitly contradict the propositions that there is tight correlation between cranial capacity and age at M1 emergence and that these define a primate’s life history. In all cases known to me these propositions can be traced back to Smith (1989a, 1989b, 1991, 1992) and have been extensively repeated since (e.g. Bogin 1999:182–183; Bermúdez de Castro et al. 1999; Ramírez-Rozzi and Bermúdez de Castro 2004; Schwartz 2012:S400; Modesto-Mata et al. 2020:7). In some cases they are implicitly contradicted later in the same publication (e.g. Modesto-Mata et al. 2020:8; and the Kelley and Schwartz 2012 cases above). In the species whose life history has been most studied, i.e. great apes and humans, the correlation appears not to hold tightly.

skeletal development in earlier hominins should conform to patterns which apply to modern humans.¹

The Baka pygmies of Cameroon are reported to have the earliest emergence of the mandibular M1 of all human populations, at ~4.95 years in females (Ramírez-Rozzi 2016) (cf. Tables D.15 and D.16), rather than ~6 years. However, their small stature seems to be mainly due to slow growth in the first two years of life, and otherwise ontogeny resembles that of full-size Bantu people and includes an adolescent growth spurt. The Nariokotome *Homo ergaster* youth² aged ~8 years is thought to have had M1 emergence at ~4.5 years, skeletally resembles a modern human of 14–16 years, and therefore appears to have accelerated life history (Dean and Lucas 2009). Ramírez-Rozzi (2016:7 and SI) suggests that if the reasoning applied to Nariokotome is applied to the Baka, then they would be expected to have a life history more like that of *Homo ergaster* than some other *Homo sapiens* populations. However, they reach adulthood at ~20 years and girls reach menarche at ~14.5 years, later than in many full-stature African groups. He proposes that variation within *Homo sapiens* allows adaptation to environmental conditions, and that one such adaptation could be a dissociation between dental development and life-history variables, contrary to correlations observed at higher taxonomic levels. Notably, for Nariokotome somatic advancement inferred from the dentition is actually observed in its postcrania, whereas for the Baka somatic advancement is observed not to occur.

Modesto-Mata et al. (2020:7–8) suggest that advanced dental development observed in fossil hominins may not have been accompanied by faster skeletal growth. It has been proposed that the relationship between dental and somatic growth expressed by the primate-wide regressions of B.H. Smith may not apply at lower taxonomic levels, such as within species or between closely related species, e.g. within the hominin clade (R.J. Smith et al. 1995; B.H. Smith and Tompkins (1995); Guatelli-Steinberg 2009:17; T.M. Smith et al. 2010:20295, 2015:12; Kelley and Schwartz 2012:1336,1347; Schwartz 2012:S403).

As early as 1995, B.H. Smith and colleagues revisited the initial argument of 1989 and 1991, both the data and the statistical procedures, and advised that applicability of the results is more constrained than initially proposed. While a broad correlation between means of cranial capacity and M1 emergence age across primates is supported, M1 emergence age and other maturation milestones “are not perfectly correlated”, confidence intervals are large, and prediction of values for individual organisms and sets of life-history variables in extinct species may not be valid (R.J. Smith, P.J. Gannon, and B.H. Smith 1995:164–165).

The same authors provide new equations to predict emergence ages for M1 from endocranial volume, for generalized anthropoid primates as in the earlier work, and with adjustments incorporating residuals for chimpanzees and modern humans. Australopithecines are considered to be chimpanzee-like, while some other hominins may be more human-like (R.J. Smith et al. 1995). Table 7.8 illustrates a wide range of predicted ages for M1 emergence generated from the huge range of ECV among hominins. Even so, for ECVs 1100–2350 cm³, the *human-like* equation produces M1 emergence ages within documented recent human range. Whether M1 emergence ages correlate with ECVs in this way among recent humans has not been demonstrated.

R.J. Smith et al. (1995:159–160) use African mean values 1292 cm³ and 5.4 years as mean ECV and M1 emergence age for living *Homo sapiens*. Other commonly used means for M1 emergence include 5.8 years and 6.2 years (Table 2.2).

¹ Dean and Liversidge (2015) bring together much evidence and analysis and, in effect, contradict the arguments repeatedly cited for 30 years.

² Nariokotome (KNM-WT 15000) is discussed later in this chapter.

Table 7.8: M1 emergence age predicted from ECV

Species	Adult ECV	Predicted M1 emergence age		
		Anthropoid-like	Chimpanzee-like	Human-like
<i>Australopithecus africanus</i>	440 ¹	3.12	3.40	2.87
<i>Homo habilis</i>	610 ¹	3.77	4.12	3.48
Lowest recent human	790 ²	4.38	4.78	4.04
<i>Homo erectus</i>	826 ¹	4.50	4.91	4.15
<i>Homo erectus</i>	983 ¹	4.98	5.43	4.59
Low recent human	1100 ²	5.32	5.80	4.90
	1200	5.59	6.10	5.15
	1300	5.86	6.39	5.40
Neanderthal adult mean	1385 ³	6.08	6.63	5.60
	1400	6.12	6.67	5.64
	1500	6.37	6.95	5.87
	1600	6.61	7.21	6.09
High recent human	1700 ²	6.85	7.47	6.31
Highest recent human	2350 ²	8.27	9.02	7.62
Ages from equations of R.J. Smith, Gannon, and B.H. Smith (1995:161–162). Italics and shading indicate ages outside recent human range (Tables D.9, D.12, D.13, D.15). ¹ R.J. Smith et al. (1995:162). ² Falk (2012). ³ Table E.2.				

The correlations which have been highlighted are among means of quantities, whether ages, durations or sizes such as age at first reproduction, potential lifespan or endocranial volume. The meaning of correlation of *means* of these variables is unclear when the *ranges* of values of some variables are so extensive among recent humans. Additionally, there is an enormous difference in mean endocranial volume (ECV) between living great apes, with means 379–484 cm³ (Kelley and Schwartz 2012:1338), and living humans, with a range 1100–1700 cm³ or even 790–2350 cm³ including extremes (Falk 2012), which in absolute terms sets humans apart from the apes, let alone the smaller anthropoids.

A modern human with an adult ECV of 1700 cm³ is not expected to take longer to reach adulthood or to live significantly longer by any proportion than a modern human with an ECV of 1100 cm³. Even if these were not individual values but means of separate modern human populations, we would probably not expect life history to be accelerated in the 1100 cm³ group and prolonged in the 1700 cm³ group on the basis of ECV alone.

The range of known adult Neanderthal ECV 1065–1740 cm³ is almost identical to Falk’s inner range for recent humans. Therefore Neanderthal mean age of M1 emergence should be similar to that of recent humans and similarity of the other life history variables should follow M1 emergence age. However, as with age at cessation of suckling (§2.4.2, §2.4.4), actual Neanderthal values for these other variables must be discovered independently.

7.5 Neanderthal skeletal growth delayed

7.5.1 Developmental disjunction

The Neanderthal juveniles El Sidrón J1 and Teshik-Tash appear to exhibit the same developmental disjunction as Le Moustier 1 (Table 7.9).

Table 7.9: Pattern of assessed ages of Neanderthal juveniles and adolescent

	El Sidrón J1 ²	Teshik-Tash ¹	Le Moustier 1 ¹
Actual (dental microtomography)	7.7	Not available (8.2 ?)	12
Dental (modern human standard)	7.7 ?	8–10	15–16
Skeletal (modern human standard)	5–7 overall 4–6 years (vertebral fusion status)	6–7	10.5
Ages in years. ¹ Thompson and Nelson (2011). ² Rosas et al. (2017).			

Fusion of major long bones had not begun in either Teshik-Tash or Le Moustier 1 (Thompson and Nelson 2000:479). Even on the basis of a chronological (as opposed to dental) age at death of 12 years, Le Moustier 1 is still skeletally less developed than expected. And even when Teshik-Tash is assigned a low age, ~8 years rather than 9, taking into account accelerated dental development in Neanderthals (Granat and Heim 2003), this individual remains slightly skeletally delayed (Thompson and Nelson 2011:262). El Sidrón J1 falls within modern human limits for skeletal maturation generally at its known age, while having some vertebral attributes at a stage characteristic of a child up to 2 years younger (Rosas et al. 2017).

As Thompson and Nelson (2000, 2001, 2005a, 2011, 2016) have pointed out, by the standard of modern humans Le Moustier 1 exhibits a disconnect between dental development and skeletal development. So do the juveniles and, to a lesser degree, younger Neanderthal subadults up to ~6 years (Mateos et al. 2014:175). If such a disconnect were found in a modern human sample, it would be natural to consider growth faltering.

7.5.2 Growth faltering

Le Moustier 1 has signs of pathology. The individual bears the scars of serious injury to the left temporomandibular joint and mandibular condyle, from which he apparently recovered (MacGregor 1964; Ponce de León and Zollikofer 2005:258–259; Bilsborough and Thompson 2005:184; Ullrich 2005b:299). The injury could have been caused by a blow to the face inflicted by a companion or by a fall onto a hard surface. He also suffered severe perimortem impacts to the cranial vault (Ullrich 2005b). Ramsey et al. (2005:286–288) note considerable osteon remodelling in the humerus. They state that, while systemic bone disease cannot be ruled out, it is unlikely because the effect is limited to the humerus and there is no evidence of it in the lower limb bones. They attribute the high rate of humeral osteon remodelling to biomechanical strain from strenuous use of the upper limbs.

Bilsborough and Thompson (2005:184) note widespread enamel hypoplasia in the dentition, some or all of which they assign to the age of 3–4 years and attribute to weaning (cf. Thompson and Nelson 2000:488). Any hypoplasia at later ages may be evidence of stress, nutritional or traumatic. The severe fracture of the left mandibular condyle would have been traumatically painful. Ponce de León and Zollikofer (2005:258, citing Dimitroulis 1997) note

that the temporomandibular joint is typically immobilized during the healing process after injury. Thus the trauma and subsequent remodelling, together with pain, may well have prevented normal biting and chewing for a long period, perhaps leading to undernutrition.

General growth faltering does not manifest lesions, so the only evidence of it may be lower stature and more limited bone development than expected for age. It may be compensated by catch-up growth when nutritional status improves or health recovers following disease (Prader et al. 1963; Prader 1978; Williams 1981; Boersma and Wit 1997; Bogin 1999:9–10,81–82). It has been suggested that at early adolescence catch-up growth would already have taken place (Thompson and Nelson 2000:488). However, this may have been prevented by repeated or prolonged periods of undernutrition. At any stage prior to adulthood and before catch-up growth has succeeded in fully reinstating the individual's potential attainment, the skeleton will exhibit shorter stature than expected (Tanner 1962:123–124; 1989:166–167; Eveleth and Tanner 1976:244–245; Saunders and Hoppa 1993:147; Bogin 1999:89–90).

Le Moustier 1 most probably died not from disease or undernutrition but from serious head injury: violent impacts to the left frontal and parietal and the right frontal, either resulting from a fall or inflicted by another member of the community (Ullrich 2005a, 2005b). The probability of interpersonal violence does not necessarily invalidate the hypothesis that he was affected by growth faltering, because that condition might have made him weak and less able to fight off an attacker.

Thompson and Nelson (2000:488) argue that the apparently slow growth of Le Moustier 1 might appear to be explicable by undernutrition, but that this explanation does not hold, on the grounds that prolonged undernutrition would retard development of internal organs and other soft tissue, including the brain. They draw attention to the relatively high cranial capacities of Teshik-Tash and Le Moustier 1, quoting 1440 and 1540 cm³ respectively, which suggest that there was no stunting of brain development.

Recent research (§4.3.2) provides evidence that during ontogeny the brain uses mechanisms to ensure its own energy uptake from the blood with priority over all other body tissues including the dentition, skeleton, and other organs such as the heart, lungs and liver, musculature, skin and connective tissue. Among tissues other than the central nervous system, dentition appears to have its own priority. This effect continues until brain growth slows down toward the end of the juvenile stage. The result is that skeletal growth and growth of all other organs and tissues may be delayed by undernutrition while the brain continues to grow. The bones of the neurocranium must grow to accommodate the brain. If the brain imposes these regulatory priorities, then any signs of undernutrition in a fossil human, manifesting at a gross level as small linear dimensions, would not be seen in the neurocranium but only in the rest of the skeleton. Such an effect explains why the endocranial capacities of Teshik-Tash and Le Moustier 1 can be high, and their dentition advanced, while their skeletal growth appears to be retarded. It therefore remains possible that they could be suffering from growth faltering.

Further, Le Moustier 1, Teshik-Tash and El Sidrón J1, being individuals who did not survive to adulthood, may have been weaker than the norm in their communities, as cases of mortality bias (Wood et al. 1992; Saunders and Hoppa 1993). It is unknown whether either of them, or indeed any of the other immature specimens from this species, represents a “normal” or healthy Neanderthal child. If El Sidrón J1, Teshik-Tash and Le Moustier 1 were cases of growth faltering to different degrees, El Sidrón J1 not so severe, they may be distorting our perception of normal childhood development in this species. On the other hand, the concept of a normal or typical healthy child may not be readily applicable in a community where subadults probably were variably healthy from season to season and year to year, depending on prevailing climate, transitory weather conditions, and the community's hunting and gathering success.

7.5.3 Ages and proportions

The skeletal age of Le Moustier 1 is 10.5 years (Thompson and Nelson 2005a:208, 218). On the basis of osteon fragment counts in the humerus the age is 10.02–10.47 years and on gross morphology 10–12 years, the individual being “clearly juvenile” (Ramsay et al. 2005:285–286). The actual age at death from computed microtomography is 11.86 (~12) years.

Height is 138.5 cm (4 feet 6½ inches), which places him at 85.1% of mean height for adult male Neanderthals, given as 162.8 cm. This percentage is characteristic of a modern human male 11–12 years old (Thompson and Nelson 2005a:208,217). Using a higher adult male Neanderthal mean stature calculated from Will et al. (2017) the percentage attained is slightly less at 83.33% (§6.2.1, Appendix H). While it can be argued that the apparently small stature of Le Moustier 1 is attributable to growth faltering, it may perhaps equally be explicable by normal variation.

The dental age, on the basis particularly of M2 and M3 development, is calculated to be 15.5 years. This represents 84.5% of adult dental development. An average modern human male at this dental stage, indicating ~15.5 years, would be in the middle of adolescence and have achieved ~96.7% of adult stature (Thompson and Nelson 2005a:208,217–218).

At a chronological age of 12 years, Le Moustier 1 has the dentition of a modern human adolescent 15.5 years old. Therefore, if dental development is tightly correlated with somatic growth, as a Neanderthal at 12 years he ought to be well into adolescence and have attained somatic development comparable to that of a modern human 15.5 years old, including ~96.7% of adult stature, or at least a value in the range 88.2–98.7% (Table 7.10).

A faster-growth schema implies that all life-history milestones should be reached sooner in Neanderthals than in modern humans. The only known ratio is the Neanderthal age of 12 years at M3 root ¼ corresponding to 15.5 years for recent humans. Taking recent human ages for some life history events and adjusting them downward for Neanderthals the result is shown in Figure 7.1.

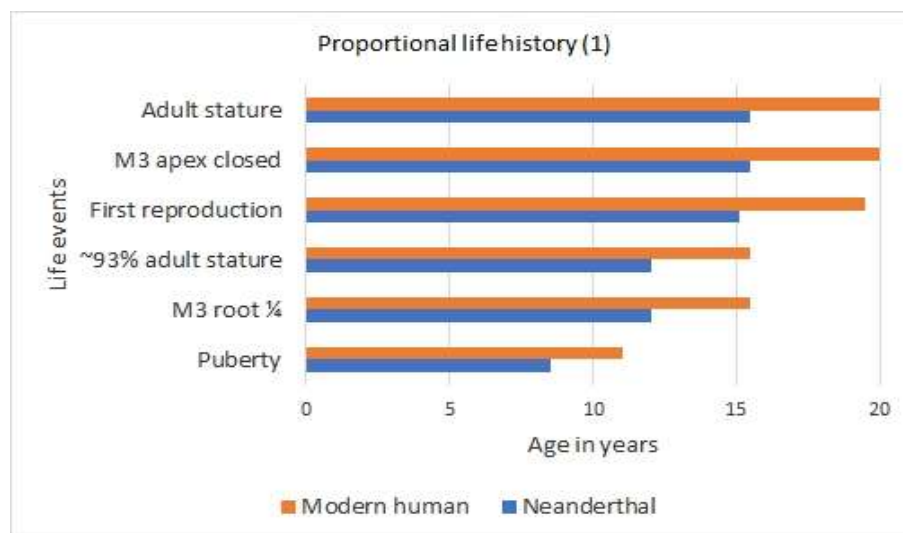


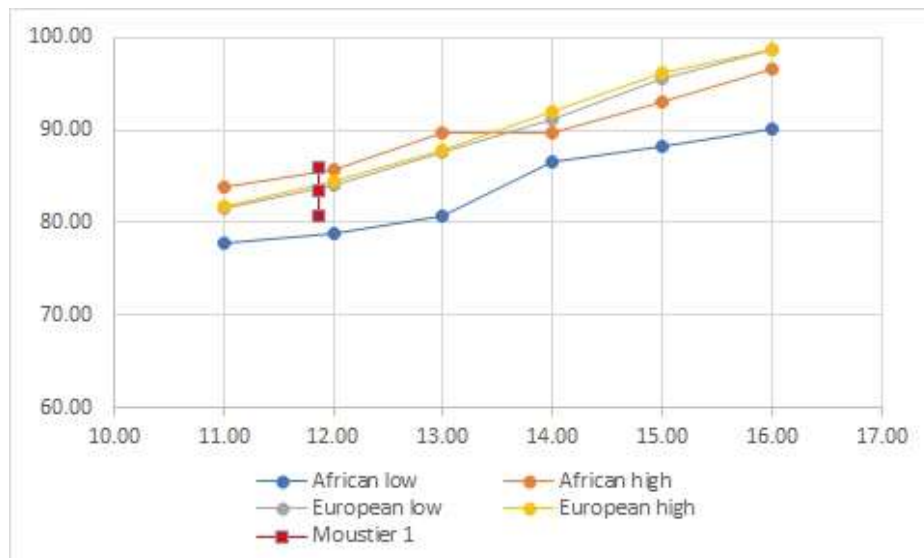
Figure 7.1: Neanderthal proportional life history (1)

Actual attainments in stature are shown in Table 7.10 and Figure 7.2. Percentage of adult stature attained by the Neanderthal is that of a modern human aged 11–12 years, not 15–16.

Table 7.10: Percentage of male adult stature by age

Neanderthal Le Moustier 1	Age (y)	Modern humans			
		African low %	African high %	European low %	European high %
	11	77.8	83.8	81.6	81.7
83.33 (80.71–86.02)	12	78.8	85.8	84.1	84.5
	13	80.7	89.6	87.6	87.8
	14	86.6	89.6	91.1	91.9
	15	88.2	93.1	95.5	96.1
	16	90.1	96.6	98.7	98.7

Modern human data from Eveleth and Tanner (1976).
Neanderthal data from §6.2.1 Table 6.3.
83.33 is percentage of mean adult male Neanderthal stature from Table H.1 sourced from Will et al. (2017), likely to be the most accurate value.
The range includes percentages using other means and individual adult males (Table 6.3).



Le Moustier 1 percentage range from Table 7.10

Figure 7.2: Percentage of male adult stature by age, Le Moustier 1

On the assumption of dental and somatic correlation, severe growth faltering probably has to be invoked to explain the discrepancy. Yet the skeletal robusticity and remarkably high body mass calculated by some researchers (§6.3) would be unlikely if the subject were chronically undernourished.

The subject at 12 (11.86) years is skeletally equivalent to a modern human at 12 years or less in terms of percentage of adult stature attained and degree of bone development (Tables 7.9 and 7.10). It could be that the result is peculiar to this individual. An as yet undiscovered Neanderthal adolescent might display conspicuously accelerated skeletal growth. Until such a discovery is made, it is legitimate to consider the implications if Le Moustier 1 were to be typical.

As is becoming clear, this individual is not in mid adolescence equivalent to an age of 15.5 years but early adolescence, and is undergoing this process at the same age as modern humans. A legitimate view is that Le Moustier 1 is dentally advanced comparably with the earliest dental developers in modern human populations (§3.4.1), is skeletally developing at the later end of modern human standards, but is beginning adolescence at the expected age and has the expected degree of somatic growth yet to achieve, including ~15% of stature (§6.2.1).

Adolescence at a gross level and in terms of functional outcome is a primarily somatic and social rather than dental process. It turns a small subadult, already functioning as a communicating and contributing member of its community, into a full-size adult. As discussed above (§7.4), somatic maturation and dental development are interdependent, but to a lesser degree than the component developments of somatic maturation are with each other, such as skeletal growth and growth of musculature and internal organs. The facial skeleton and the facial soft tissues must remain compatible with and match the growth of the dentition, and the rest of the mandible and maxilla must grow around the developing alveolar bone, in such a way that the organism can successfully ingest food, while also being able to breathe effectively, maintain vision, speak (if applicable) and the rest (cf. Tanner 1989:35; Bogin 1999:81–82). However, there is no clear demand in terms of biological fitness that dental and overall somatic, especially postcranial, development should synchronize identically in every individual or population.

An alternative summary of life history, removing the constraint that end of growth must occur at the same time as M3 completion, is offered in Figure 7.3 as an update to Figure 7.1. There is no evidence for or against earlier puberty than recent humans. The ages for completion of M3, end of growth, and first reproduction are simply not known, but are suggested as earlier for Neanderthals, while allowing more time for the considerable somatic growth necessary to turn a subadult such as Le Moustier 1 into an adult.

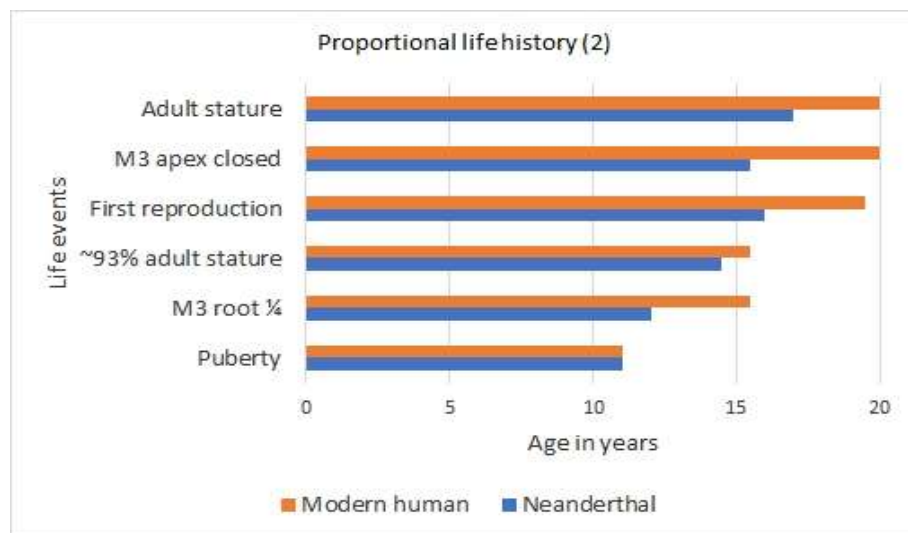


Figure 7.3: Neanderthal proportional life history (2)

7.6 Comparison of subadult Neanderthals with *Homo ergaster*

Not only Neanderthals appear to follow a different developmental trajectory from that of modern humans. Immature *Homo ergaster* is represented most completely by the Nariokotome skeleton KNM-WT 15000 dated to ~1.5 Ma (Brown and McDougall 1993).

This youth exhibits advanced dental and somatic development over modern humans (Walker and Leakey 1993; Hublin 2005; Dean and Smith 2009), and is described as following a developmental pattern more like that of chimpanzees than living humans, but not the same as either, reaching adulthood at ~13 years (Graves et al. 2010; Cunningham et al. 2018). Even so, KNM-WT 15000 is morphologically and in skeletal dimensions more like a modern human than an australopithecine, let alone a chimpanzee. By modern human dental formation and eruption schedules, the age is 10–12 years but by skeletal development 13–16 years (Table 7.11). In modern human children it is unusual for dental and skeletal ages to differ by more than 2 years in either direction (S.L. Smith 2004:111,119). In Smith's modern human sample it was difficult to find individuals who matched the divergent dental and skeletal stages exhibited by KNM-WT 15000, and no subject approached those stages at a chronological age as young as ~8 years. KNM-WT 15000 has been aged by study of dental microstructure to 7.6–8.8 years (Dean and Smith 2009; Dean and Lucas 2009). Yet in terms of skeletal development this individual is already adolescent (Hublin 2005:5), with a physiological age equivalent to a modern human aged 14–16 years or a chimpanzee aged 7.5–9 years (Cunningham et al. 2018:122; Dean et al. 2014:345).

Table 7.11 compares KNM-WT 15000 with the Neanderthal juveniles and adolescent.

Table 7.11: Comparison of Homo ergaster and Neanderthal subjects

	<i>Homo ergaster</i>	<i>Homo neanderthalensis</i>		
	KNM-WT 15000	El Sidrón J1 ¹	Teshik-Tash ²	Le Moustier 1
Chronological age (years) from dental microstructure	7.6–8.8 ³ 7.89–8.8 ¹⁴	7.7	Not available (8.2 ?)	11.86 (11.61–12.11) ⁶
Age (years) by modern human dental standards	10 ⁴ 10.4–12.0 ⁵	~7.7	9–10	15.5 ⁷
Age (years) by modern human skeletal standards	13–14 (epiphyses) ¹³ 13.0–13.5 (epiphyses) ⁴ 14–16 ¹¹	5–7 overall, 4–6 (vertebral fusion status)	6–7	9–14 (epiphyses), 10.5 (bone length) ⁷ 10.02–10.47 (bone remodelling), 10–12 (gross morphology) ⁸
Femoral length, diaphyseal	400 ¹⁹	250	270 ¹⁸	350 ¹⁹
Femoral length, epiphyseal	432 ¹⁸	-	-	380 ¹⁸
Stature (cm)	≤160 ⁴ 154 ⁹ 159±7 ¹⁶ 157 ¹⁷	111.0	112.9	138.5 ⁷
Body mass (kg)	48 ⁴ 52.4 ¹¹ 49.2±10 ¹⁶ 50–53 ¹⁷	25.9 ¹²	-	72.50 ? ¹⁰ 34.45 ? ¹⁵ 43.17 ? ¹⁵
¹ Rosas et al. (2017 and SI:23). ² Thompson and Nelson (2011). ³ Dean and Smith (2009). ⁴ Ruff and Walker (1993b:254); Hublin et al. (2015). ⁵ B.H. Smith (1993). ⁶ T.M. Smith et al. (2010). ⁷ Nelson and Thompson (2005); Thompson and Nelson (2005a). ⁸ Ramsay et al. (2005). ⁹ Graves et al. (2010); Cunningham et al. (2018). ¹⁰ Arsuaga et al. (2015 SI: section 2.2).		¹¹ Cunningham et al. (2018:121). ¹² Rosas et al. (2017 SI:23–24). ¹³ Dean and Lucas (2009); Dean (2010). ¹⁴ Dean et al. (2014). ¹⁵ §6.3. ¹⁶ Dean (2016:7). ¹⁷ Ruff and Burgess (2015). ¹⁸ Thompson and Nelson (2000:478). ¹⁹ Šešelj (2017:533).		

Most authors argue that both *Homo ergaster* and *Homo neanderthalensis* grew to adulthood more rapidly than modern humans (e.g. Hublin et al. 2015 and their references). Both species show differences from *Homo sapiens* in the form of discrepancies among chronological ages (from counts of striae in dental microstructure), dental ages (formation and eruption) and skeletal ages (formation and fusion) by modern human standards.

While El Sidrón J1 falls within modern human dental schedules (Rosas et al. 2017), KNM-WT 15000, Teshik-Tash and Le Moustier 1 are all advanced by modern dental schedules for their respective ages. All four subjects exhibit developmental discrepancies (Figure 7.4).

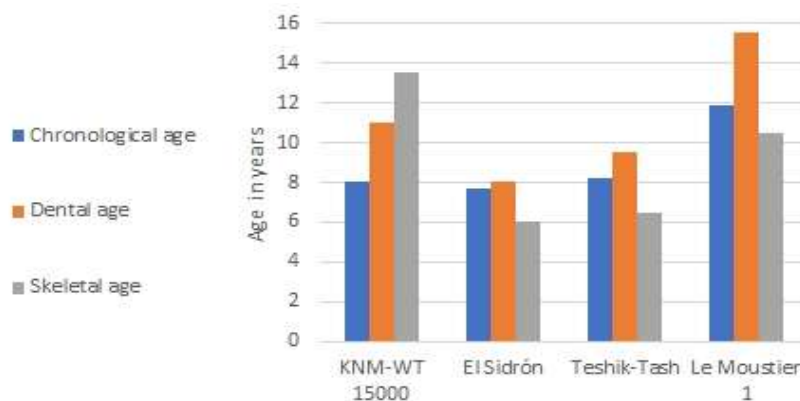


Figure 7.4: *Homo ergaster* and *Neanderthal* growth

- KNM-WT 15000 is advanced dentally by ~3 years and advanced skeletally by ≥ 5 years for its chronological age and advanced skeletally by ~2 years for its modern human dental stage.
- El Sidrón J1 is not advanced dentally but is delayed skeletally by ≥ 1.5 years for its chronological age and modern human dental stage.
- Teshik-Tash is advanced dentally by ~1 year but delayed skeletally by ≥ 1 year for its probable chronological age and delayed skeletally by ≥ 2 years for its modern human dental stage.
- Le Moustier 1 is advanced dentally by ~3.5 years but delayed skeletally by ~1.5 years for its chronological age and delayed skeletally by ~5.0 years for its modern human dental stage.

KNM-WT 15000 epitomizes the type of a “more ape-like” early human, advanced dentally and skeletally. The three Neanderthals do not conform to this type.

KNM-WT 15000 is tall for its chronological age; the Neanderthals are short. Femoral length of KNM-WT 15000 considerably exceeds that of the Neanderthals of similar age and of Le Moustier 1, which is almost four years older. Relating femoral length, dental stage and chronological age, Šešelj (2017:531) observes that while KNM-WT 15000 is dentally advanced for its age, it almost exactly matches dental stage predictions when femoral length is included as a predictive variable along with chronological age. Clearly this is because its skeletal growth is advanced comparably with its dental development. When femoral length is included as a predictor for Le Moustier 1, its later developing posterior teeth P4, M2 and M3 are still underestimated, i.e. advanced, by several stages (Šešelj 2017:535). This is because its skeletal and dental development are not in expected synchronization.

KNM-WT 15000 is approximately the same age as the two Neanderthal juveniles, but the different polarities of their developmental trajectories are striking. As Bogin (1999:203) has pointed out, the dental versus skeletal discrepancies of Le Moustier 1 are *completely the reverse* of those of KNM-WT 15000. The Neanderthal juveniles exhibit discrepancies with the same polarity as Le Moustier 1 but to a lesser degree, as should perhaps be expected when they have not progressed so far along their species' growth trajectory (Tillier 2000:114). If the discrepancies of KNM-WT 15000 are evidence for more rapid somatic growth than *Homo sapiens*, then the discrepancies of El Sidrón J1, Teshik-Tash and Le Moustier 1 could be interpreted as *prima facie* evidence for slower somatic growth, unless other explanatory factors are invoked.

7.7 Adolescence

Comparing KNM-WT 15000 upper facial and mandibular dimensions with those of adult *Homo erectus s.l.*, Antón (2002) and Antón and Leigh (2003) concluded that this individual had considerable growth remaining before adulthood, even on the then current assessment of its age at ~11 years. Captive chimpanzees attain adult body length at 12–13 years but thereafter exhibit extended growth in the radius, ulna and wrist (Cunningham et al. 2018, citing Hamada and Udono 2002). Cunningham et al. (2018) raise the possibility that *Homo erectus s.l.* males also experienced hormonally induced cranial growth after attainment of adult body length, as observed in male gorillas and orang-utans (Balolia et al. 2013; cf. Bolter et al. 2007).

Either of these forms of continued male growth after reaching adult stature, evincing a degree of bimaturation, may conceivably apply to Neanderthals. The dentally most advanced juvenile, Scladina, is female (Peyrégne et al. 2019) but lacks postcrania, which could have been informative. However, the fact that the Neanderthal male juveniles and adolescent are skeletally delayed, rather than advanced like KNM-WT 15000, emphasizes that they have not only arm and wrist or facial and mandibular growth remaining, but also considerable growth to achieve over the entire skeleton.

Graphs in Chapter 6 illustrate Neanderthal growth assuming adult size attained at 17 years, and on that basis neither cranial nor postcranial elements appear to require a growth spurt, i.e. more rapid growth than in the preceding juvenile stage. For individuals so much retarded skeletally in relation to their dental stage – by as much as 5 years in the case of Le Moustier 1 – the attainment of adult body size at the same time as completion (apex closure) of M3 development, i.e. at 15 years, as suggested by some authors, rather than 17 years, would almost certainly require an adolescent growth spurt (Thompson and Nelson 2011:265, 2016:94–95).

Based on analysis of KNM-WT 15000, B.H. Smith and Tompkins (1995:273) proposed:

- (a) If a growth spurt **is not present** in Neanderthals, then discordance between dental and skeletal development will be patterned: preadolescents will seem tall for skeletal age and tall relative to known adult heights, whereas older adolescents will seem to be of more ordinary size;
- (b) If a growth spurt **is present** in Neanderthals, then juveniles will show concordance or random discordance between dental development and stature.

El Sidrón J1, Teshik-Tash and Le Moustier 1 are not tall for their skeletal age or in relation to adult height, so (a) is not fulfilled. All three show discordance, with the same polarity, between dental development and stature, so (b) is nominally fulfilled. This would indicate a growth spurt, according to the above. In fact, the two juveniles are marginally small for their age, falling below 70% of Neanderthal mean adult height (Table 6.3). However, although bone development is retarded, Le Moustier 1 at ~80–85% of mean adult height shows concordance between stature and chronological age.

If the ages assigned to the two juveniles (~8 years) and adolescent (~12 years) are accurate and these individuals are typical for their age, then the small stature of the two juveniles and adolescent, absolute and relative to adults of their species, and the incomplete statural and viscerocranial development in the adolescent are evidence that Neanderthals were progressing through the infant, child and juvenile stages no more rapidly than modern humans (Thompson and Nelson 2011:268, 2016:92). Without older adolescents of sufficient completeness to be diagnostic, somatic evidence is lacking for either more rapid or slower progress from puberty through adolescence to adulthood. The earlier formation of third molars

may be an indication that adolescence should be of shorter duration, on the basis that dental and skeletal development are correlated. However, this possibility remains hypothetical until more adolescent individuals with associated dentition and postcrania are found.

On the above basis, it appears that Neanderthal subadults were dentally advanced but either kept pace with or lagged behind present-day modern humans in somatic growth up to the age of ~12 years. For adolescent growth there is insufficient evidence.

The reason why KNM-WT 15000 at ~8 years appears to be already adolescent (Hublin 2005:5) may be that as *Homo erectus s.l.* its genetically determined target brain size was lower than that of *Homo sapiens* or Neanderthals, and therefore brain growth slowed significantly at a younger age than in the later species, releasing more energy from nutrition to be expended on somatic growth (§4.3.2).

Zihlman et al. (2004:10541) report from field studies that chimpanzees in the wild appear to take up to three years longer to finish growth than captive animals. They also report that males do not adopt fully adult behaviour until ~16 years, several years after completion of somatic growth at ~13 years (ibid.:10543). This delay, which represents continuing social adolescence after attainment of adult body length, is perhaps discernible in recent humans, in whom the timescales of late adolescence are more extended and more variable than in chimpanzees. If so, such a delay may have been replicated in extinct species of *Homo*.

For chimpanzees, completion of growth in length is reached at 13–14 years according to Pusey (1978). Hamada et al. (1996:286–287) give 13.4 years for females and 15.0 years for males, but Hamada and Usono (2002:271–272) give 12.5 years for both sexes. Bolter et al. (2007) find wild chimpanzees finish somatic growth at ~11–13 years, males later than females. While female gorillas finish growth in length at ~9.5 years, males continue until 12–15 years (Dean 2016:1). Brimacombe (2017:328) indicates female chimpanzee growth in length up to 12.5 years, males to almost 15 years, taking into account these earlier references.

Proposed ages for *Homo erectus s.l.* M3 emergence are 10.6 years and ~14 years (Table 3.15). If somatic growth ends ~2 years after M3 emergence, then *Homo erectus s.l.* would have completed somatic growth not much later than the mean for male chimpanzees. This seems unlikely given the much more human-like ECV and body size of *Homo erectus s.l.*

As discussed (§7.1), an argument has been made that in Neanderthals M3 emergence was at ~13–15 years, with closure of the M3 apices only 2–3 years later, in which case a similar early completion of somatic growth, at ~15–16 years, would theoretically have applied to them. Skeletal evidence from the two juveniles and the adolescent appears to conflict with this proposition.

Brimacombe and colleagues (2015a; Brimacombe 2017) make the observation that in chimpanzees apex closure of all four third molars may occur before the fusion of many epiphyses. According to Simpson et al. (1996:70), the duration of epiphyseal growth in recent humans is ~1.2–1.6 times as long as in chimpanzees, but dental development is ~1.8–1.9 times as long. The different scales of prolongation may explain why in recent humans there is overlap and even reversal (in relation to chimpanzees) of the timing of dental and skeletal maturation. It seems likely that such an extreme delay in dental development is an autapomorphy of *Homo sapiens*. It would appear to be already present in the Jebel Irhoud 3 juvenile at 315 ka (Table 3.2).

It has been proposed (Antón 2002, 2003:160–161; S.L. Smith 2004) that in *Homo erectus s.l.* there was continued cranial growth after adolescence, i.e. possibly after completion of the dentition, bringing the cranial superstructures such as supraorbital and nuchal tori to adult form. The possibility arises that such continued skeletal growth after completion of the

dentition occurred in some of its descendant species including Neanderthals, but not in *Homo sapiens*, and that such growth may not have been limited to the viscerocranium but extended to the postcrania.

Relative to recent humans, it is clear that the Nariokotome subadult was much advanced dentally and skeletally, while Neanderthal subadults appear to be dentally either comparable (El Sidrón J1) or, more often, advanced (Le Moustier 1), but skeletally delayed. No pertinent information seems to be available about subadults of other species of *Homo*, e.g. *Homo heidelbergensis*.

An hypothesis to account for dental/skeletal disjunction

The reader is invited to consider the following outline hypothesis regarding the disjunction between dental and somatic development in Neanderthals.

Homo heidelbergensis s.l. exemplifies a morph expected of a more encephalized *Homo erectus s.l.*; and, apart from the shorter, stocky build, Neanderthals appear to be, very broadly, a further encephalized *Homo heidelbergensis*. In contrast, *Homo sapiens*, with its globularized neurocranium (§4.5.1) and gracile, neotenous skeletal morphology (S.L. Smith 2004:160), presents a clear departure from the plesiomorphic mainstream of earlier *Homo*.

The dental and skeletal developmental discrepancy observed in the older Neanderthal subadults may be produced by the coupling of (a) a plesiomorphic dental formation and eruption schedule, somewhat less advanced than in earlier *Homo*, with (b) slow skeletal growth emulating that of recent humans. Skeletal growth in Neanderthals would be constrained through the preadolescent years by the nutritional demands of growing a significantly larger brain than their predecessors. Dental growth would not be so much constrained. The result is that, relative to *Homo erectus s.l.* (and, it should be predicted, *Homo heidelbergensis*), Neanderthals are only moderately dentally delayed but distinctly skeletally delayed. Similarly, owing to the demands of growing a large brain, recent humans are distinctly skeletally delayed, but for reasons as yet unclear also distinctly dentally delayed relative to their predecessors. In this case the slow dental formation and eruption schedule of recent humans is an autapomorphy. It is not so much the Neanderthal condition that requires explanation but rather why modern humans have evolved such prolonged dental development. Gracility may be a separate issue.

While dental secretion and extension rates are largely conserved in *Homo*, crown initiation times in recent *Homo sapiens* are late relative to *Homo erectus* and Neanderthals, and the eruption process begins some time after the occurrence of peak root (extension) velocity, whereas in *Homo erectus* peak root velocity and eruption coincide (Dean and Cole 2013) (§3.4.7). Postponement of formation and eruption processes must contribute to the evolution of prolonged dental development. If this is a *Homo sapiens* autapomorphy, then in Neanderthals eruption can be predicted to be more closely timed with peak root velocity.¹ It is already clear that Neanderthal initiation times were generally accelerated (§3.4.1, §3.4.3).

This hypothesis is offered for consideration rather than fully argued for here, because there is not scope for more detailed analysis. It is consistent with the phenomena of Neanderthal growth described here and in Chapter 6. However, it conflicts with the hypothesis of “tight correlation” between dental and somatic growth as discussed earlier, and with the assertion of extended sapiens-like somatic growth in the relatively small-brained *Homo antecessor* (Bermúdez de Castro et al. 1999), which is based upon dental development and so far not verified from postcrania. The hypothesis of prolonged skeletal growth in Neanderthals can be

¹ To my knowledge this has yet to be demonstrated.

tested, if not by the present sample, by new discoveries of individuals at late adolescent ages (§7.8.2).

Three graphs of *proportional life history* have been presented in this chapter. Figure 7.1, with skeletal growth ending at ~15 years, makes adolescence probably too rapid for the somatic growth required, if Le Moustier 1 is typical of its age. Figure 7.3 accommodates that requirement more adequately. In Figure 7.5 the full interpretation of the hypothesis to account for dental/skeletal disjunction suggests that, owing to brain size, late Neanderthal somatic growth must have been prolonged as in *Homo sapiens* fossil and recent. The largest Neanderthal endocranial volumes are not found until well after 100 ka (§4.2, Figures 4.3 and 4.4), which on this hypothesis implies that early Neanderthals would have exhibited less prolonged subadulthood than their late successors, though longer than *Homo heidelbergensis*.

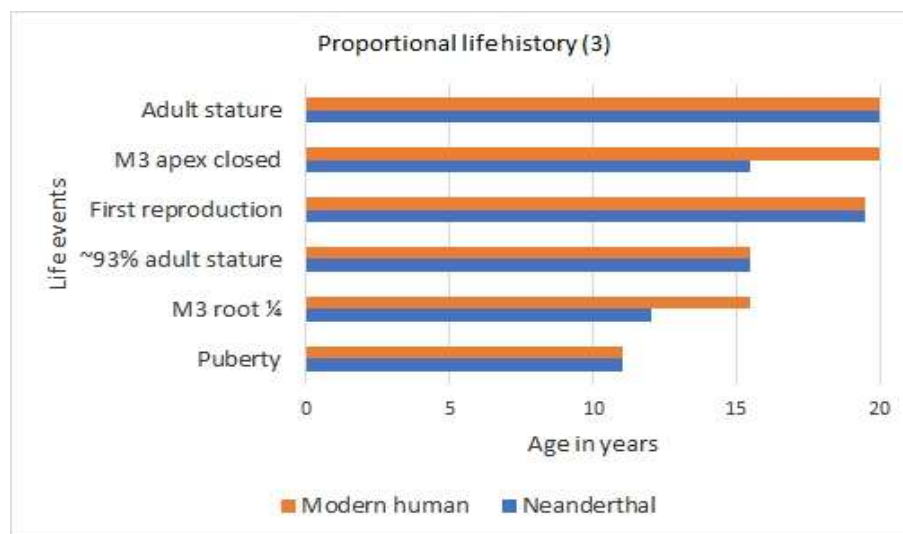


Figure 7.5: Neanderthal proportional life history (3)

7.8 Rapid growth and life history

7.8.1 Rapid somatic growth

Neanderthals became extinct. To explain this, studies of their morphology, ontogeny, genetics, and the archaeology of lithic technology, layout of campsites, intentional structures and marks on cave walls, have all been used to identify areas of apparent inferiority in Neanderthal physiology, adaptation, life history, subsistence strategy, skills, social organization, and cognition, which would explain why they did not survive. In the case of growth and development, a more rapid pace would show similarity with earlier species such as *Homo erectus* and therefore a primitive level of attainment in all spheres of life relative to *Homo sapiens*. From the Jebel Irhoud hominins at 315 ka onward, *Homo sapiens* is asserted to have had a prolonged subadulthood like recent humans (T.M. Smith et al. 2007a; Dean 2007). It has been proposed on dental evidence that even *Homo antecessor* at 800 ka may have had an essentially modern human life cycle, and included speech in its repertoire (Bermúdez de Castro et al. 1999, 2010:11743).

Abbreviated ontogeny is interpreted as a response to chronic stress on the community, in particular high young adult mortality (§2.5.1, §2.7). Stress and high premature mortality could be symptoms of a less effective adaptation to environment. Reaching adulthood at an earlier age, as alleged for Neanderthals, may appear to imply that less time is available for the immature hominin to learn skills for life: hunting and gathering, observation of seasonal prey animal movements, tool making, food preparation, hide preparation, use of complex language, social skills, cooperation, identity and allegiances to community and perhaps tribe, and ability to forge alliances with other groups.

It is clear that Neanderthal dental formation and eruption is generally advanced compared with modern human schedules (Chapter 3). In fossils somatic growth can be indicated by skeletal evidence almost exclusively.¹

There are thus two aspects to the question of rapid growth.

- Does skeletal evidence indicate rapid somatic growth?
- Would rapid somatic growth prevent adequate acquisition of life skills?

7.8.2 Does skeletal evidence indicate rapid somatic growth?

The rapid growth hypothesis predicts from dental acceleration observed in some archaic species of *Homo* that immatures of such species will show signs of accelerated skeletal growth. Predictions need to be tested against fossil evidence, consisting of subadult remains with sufficient dentition for ageing by dental microstructure and sufficient postcrania developed enough to exhibit skeletal growth status: whether accelerated, normal or delayed by modern human standards.

In the case of *Homo erectus* there is only one such subadult. This is the Nariokotome individual which appears to be adolescent at 8 years and shows distinctly accelerated skeletal growth, confirming the hypothesis for its species so far. For Neanderthals there are two juveniles and one adolescent, old enough to exhibit clearly whether growth is accelerated. They

¹ Cerrito et al. (2022) have derived ages of menarche, menopause and other life events from dental cementum microstructure.

show delayed skeletal growth (§7.6). These three could be interpreted as falsifying the hypothesis unless other factors can account for their lack of advancement.

High young adult mortality is a factor given prominence in life history, and for Neanderthals has been suggested as promoting rapid ontogeny through natural selection. Young adult mortality and child mortality are themselves products not only of physiological and cognitive factors relating to size and morphology of the body and brain but also of external circumstances such as the diet obtainable, habitat, climate, disease, parasites, predators, injury risk during both regular and one-off activities, presence or absence of fully proficient foragers in the community, and even prevalence of favourable and unfavourable choices made by members of the community regarding locations for settlement and timing and direction of foraging expeditions. In *Homo* the latter highly variable circumstances of everyday life, including choices and decisions made by individuals, must become more prominent, whereas in lower primates activity is governed more by instinct than choice. It would be difficult to quantify such varied circumstances, especially since some are likely to change over time, between generations and even within a lifetime. The *generally prevailing* circumstances can be ascertained from archaeological and anthropological evidence, but when envisioning communities of extinct *Homo* the advantageous or disadvantageous effects of *unique* actions and decisions of individual community members should perhaps be allowed for.

One application of this approach is to reconsider the suggestion that Neanderthals sometimes, frequently or even chronically suffered from undernutrition. The question has already been raised (§2.5, §7.5.2). It is barely credible that the population with recognizable Neanderthal morphology could survive more than 200,000 years with almost every member chronically undernourished yet with every calculated adult lean body mass in the range of healthy living human adults (Appendix H).¹ Applied to a population, the claim of chronic undernutrition should probably be set aside. However, there are individuals showing slow skeletal growth relative to living humans. The three older subadults whose characteristics have been most discussed in this work are such cases. They died young. The proximate cause of death has been identified for Le Moustier 1 (§5.5), but not yet for the others. Even if, for example, a parasitic infection were to be identified as cause of death in one of them, still undernutrition, compromised immune system, and general weakness could be contributory conditions. If they were undernourished, the reasons for that will lie in their own personal history: e.g. early death or disability of a caregiver, injury which for a long period prevented normal ingestion of food (again Le Moustier 1), infection leading to prolonged diarrhoea, allergies, or an inherited or acquired disability.

Evidence from extant subadult remains does not support the proposition that Neanderthals grew up rapidly. However, some, many, or most of the subadults who did grow up, and whose remains are therefore not extant in subadult form, may have grown up rapidly. Propositions of generally rapid or slow growth are testable, perhaps not with the present hypodigm but with discoveries yet to be made. For example:

- **Rapid growth** would be supported by finding an adolescent, aged below ~16 years by dental microstructure, whose third molars were at root complete or apex ½ (i.e. still not complete, to enable precise ageing) but who had reached adult stature, with fully adult size maxilla and mandible and close to fully adult browridge;
- **Prolonged growth** would be supported by finding an adolescent, aged above ~15 years by dental microstructure, regardless of modern-schedule dental age, who had clearly not reached adult stature or viscerocranial maturity.

¹ Estimates in Appendix H are generally means with large possible ranges: this applies to all species represented.

While skeletal evidence at present does not favour a more rapid Neanderthal subadulthood, it remains a possibility. Just as there is variation in the age of attainment of adulthood in living humans, if the typical Neanderthal subadult period was 16 years, some individuals would attain adulthood at 14–18 years, depending on such factors as adequate nutrition and absence of disease. Those epiphyses which close very late in *Homo sapiens* (§7.4.6) would most likely close late in Neanderthals, taking them also over 20 years.

In any case, a rapid ontogeny enabled by abundant nutrition may be viewed as an adaptive strategy to allow young individuals to become productive earlier (§2.7, §2.8).

7.8.3 Would rapid somatic growth prevent adequate acquisition of life skills?

As an explanation for the prolonged subadult period of modern humans, the *learning hypothesis* has been discussed (§2.8). Attention was drawn to studies of forager societies which concluded that many years of childhood were not necessary to acquire skills for successful adult hunting and gathering.

A case could perhaps be made that learning *social*, rather than subsistence, skills needs many years, but such an hypothesis seems to the present writer equally unsupported. Human society in developed countries, with copious bodies of law and regulation, political and professional organizations, access to local and foreign cultures, a great body of knowledge and skills required for each trade or profession, a great body of knowledge and skills to be acquired in formal education, and above all a great variety of unequal social and professional ranks and competing roles imposing different expectations of conduct, would appear to be much more demanding of an individual's capacity for learning to cope with human interaction than a subsistence-level society. Yet the span of subadulthood is not known to have increased since the Neolithic or to differ between subsistence-level societies and developed ones. Further, in richer countries the recent secular trend has seen *earlier* attainment of somatic growth milestones (§2.6).

If a *Homo sapiens* individual reached adulthood¹ at, say, 16 years rather than 20 years, would that individual be just as able to cope with subsistence activity or social interaction in a complex modern society? I suggest yes, and *a fortiori* in a forager society. If a Neanderthal individual reached adulthood at 16 years, I suggest that individual would be just as able to cope with subsistence activity or social interaction in a modern human forager society, though perhaps not in a complex modern society. Speculatively, the reason for not being able to cope with a complex modern society, even if the individual had grown up in that society, might be cognitive and linguistic differences arising from apomorphies of brain structure, not the abbreviated subadulthood.²

There is correlation between somatic growth and dental development, but it is at least questionable to assume a tight correlation leading to attempts to use dental evidence alone to infer stages of somatic growth in various systems, whether skeleton, musculature, internal organs, or brain, in modern humans or earlier species of *Homo*, and then make further inferences about life history, subsistence competencies and social structure.

¹ Third molar apex complete and closure of major epiphyses could count as reaching adulthood.

² This is of course a major subject, which deserves much fuller discussion than is possible here.

7.8.4 Stages of life, revised

The Schultz-Bogin schema of stages of life from Chapter 2 is amended in Figure 7.6 to include Neanderthals and, even more speculatively, *Homo heidelbergensis*.

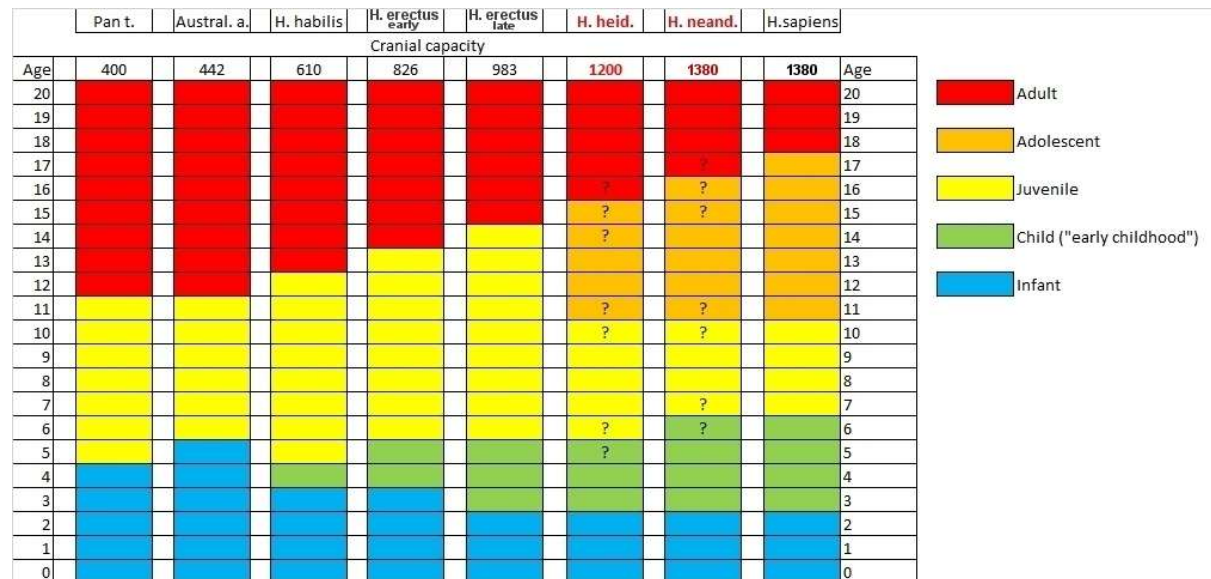


Figure 7.6: Ages and stages of hominid growth, amended

7.9 Summary

Dental development has been held to be tightly correlated with somatic development. Although the principal primate-wide correlation is between first molar (M1) emergence and a set of life-history and life-history-related variables (§1.4, §2.4.1), some authors have also predicted completion of the permanent dentition (third molar apex complete) to coincide with the end of somatic growth. If M3 completion occurs not long after emergence in Neanderthals, estimated to be at ~15 years, then Neanderthals would finish somatic growth in the middle-late teens, several years younger than living humans.

It seems indisputable that Neanderthal dental development is generally accelerated with respect to living human populations, probably including those African and Australasian groups advanced relative to others.

The variability of dental development, including eruption ages, among living humans has been demonstrated in Chapter 3 and further discussed here, with emphasis on the M3. Some degree of overlap is found between Neanderthals and living humans, even in Moorrees stages of M3 formation.

The coincidence of M3 completion and completion of skeletal growth is questioned. Numerous authors detect a degree of dissociation in modern humans at population level between dental and skeletal development, sometimes considerable. If brain growth is prioritized over dental, and dental growth is prioritized over growth of the rest of the body, then such dissociation must be expected at population and individual level.

Growth status for age, principally stature but also body mass and degree of robusticity, of two Neanderthal juveniles and one adolescent does not indicate acceleration of skeletal growth but the reverse in all three. One juvenile is not dentally advanced for its chronological age but is slightly delayed skeletally. No reliable chronological age is available for the older juvenile, but it is skeletally delayed for its dental age and probable chronological age. The adolescent is the most advanced dentally and the most delayed skeletally for its chronological age. On this basis, a pattern is exhibited of advanced dental development but delayed skeletal development, so that the dental and skeletal gaps of opposite polarities between Neanderthals and modern humans increase with age at least up to 12 years.

The possibility of undernutrition as the cause of delay cannot be excluded, because brain growth priority explains the large neurocranial development of these individuals, and dental priority over somatic growth would explain their undelayed dental attainment, leaving only the rest of the body delayed.

Besides undernutrition, the hypothesis of brain priority offers an explanation for slow somatic growth up to adolescence in Neanderthals. In living humans, early in the second postnatal decade brain growth is much slowed (§4.3) leaving more energy to be allocated to somatic growth. Conceivably, after slow somatic growth to the age of ~12 years, Neanderthal adolescents, fortified by a customary high-protein diet (§2.5.2), rushed through adolescence and attained adult stature at 14–16 years. On the other hand, if dental and skeletal growth were further dissociated, adolescence may have lasted a few years longer so that age at attainment of adult stature would fall within recent human range.

A comparison of Neanderthal juveniles with the Nariokotome *Homo ergaster* youth is instructive. The Nariokotome specimen is much advanced both dentally and skeletally for its chronological age, being apparently adolescent at ~8 years, while the Neanderthals, despite being dentally advanced, are skeletally delayed. Slow growth to 12 years would not apply to *Homo ergaster* because its target brain size was smaller.

Examination of a different sample of Neanderthal specimens might lead to modified conclusions, but other relatively complete skeletons are currently limited to infants, which would not be diagnostic of the juvenile and adolescent stages of life when differences from modern humans should be more pronounced.

In the meantime, evidence does not support rapid somatic growth through the stages before adolescence. The adolescent specimen is only at the beginning of that stage, and in percentage of adult stature at chronological age fits or slightly falls below recent human standards, as do the two juveniles. If there is a difference in the duration of subadulthood between Neanderthals and living humans, it appears that the difference must be largely confined to adolescence.

Rapid growth after puberty producing a short adolescence is possible. However, if life history in non-*sapiens* species of *Homo* may diverge from both the ape-like and human-like patterns, as has been suggested for *Homo erectus s.l.*, then Neanderthals may demonstrate advanced dental development but delayed skeletal growth leading to a prolonged subadulthood.

Evidence from ethnography indicates that a long childhood is not necessary to develop subsistence and social skills. Even if subadulthood was abbreviated in Neanderthals, that would not of itself compromise their competence as hunter-gatherers.

CHAPTER 8

CONCLUSIONS

8.1 Review

This thesis attempts to describe Neanderthal ontogeny using developmental milestones and age ranges derived from modern human growth studies. Conclusions are as follows.

1. The immatures of this species seem to fit comfortably the modern human stages and ages of the Schultz-Bogin schema up to early adolescence (Chapters 2, 5, 6, 7).
2. Rapid skeletal/somatic growth is enabled and promoted by sufficiency of nutrition and is not necessarily a sign of plesiomorphic physiology on a “fast-slow continuum” (Chapter 2).
3. Dental development in most, but not all, subadults is advanced with respect to recent humans, and advancement becomes more distinct with increasing age (Chapter 3).
4. Neurocranial differences have been identified between (a) recent and Upper Palaeolithic (and possibly African Middle Stone Age) humans and (b) Neanderthals. These include globularization and perhaps increased cerebellar dimensions in modern humans and smaller and slightly differently configured temporal labyrinths in Neanderthals (Chapter 4).
5. It has been asserted that development of the neurocranium and therefore the brain is accelerated, but evidence presented in several studies appears to be an artifact of sample selection and of an early age estimate which recently has been revised upward (Chapter 4).
6. There are indications of a high rate of neurocranial growth after 1.5 years in larger-brained infants and continued posterior neurocranial growth in juveniles (Chapter 4).
7. Brain growth priority can explain the rate and timing of somatic growth (Chapter 4).
8. Growth in stature and body mass are not accelerated with respect to modern humans, at least not for subadults between ~1.5 and ~12 years old; in fact, Neanderthal immatures are small for their age (Chapter 6).
9. Change of the postcrania, cranium and mandible at any age appears more advanced than in modern humans because the target adult morphology is more robust (Chapters 5, 6).
10. At all ages, and most evidently in the juveniles and early adolescent, dental growth is advanced and somatic growth delayed by recent human standards. This dissociation increases with age. It differs from the condition in *Homo ergaster*, in which dental and skeletal development are both advanced. The questions (a) whether the dissociation is apomorphic or shared with some recent and Palaeolithic modern human groups and (b) whether delay is due to undernutrition in individuals are unresolved (Chapter 7).
11. It remains unclear whether Neanderthal adolescence and hence overall subadulthood were prolonged as in recent humans (Chapter 7).
12. It is unlikely that a shorter subadulthood would have caused much, if any, disadvantage to hunter-gatherer communities in terms of subsistence or social skills (Chapters 2, 7).

8.2 Limitations and further research needs

The Neanderthal fossils yielding measurements such as ECV, stature, etc. did not form a *population* that ever existed as a biological entity comparable with a regional population in the twentieth century (Tillier 2000:110). Remains are a random collection temporally from ~250 ka to ~40 ka and geographically from Gibraltar to Central Asia (Heim 1982:158). In an evolving population across such a span, variation is to be expected.

For modern humans the wide variation of gross development observed among normal healthy juveniles and adolescents of the same chronological age – in stature, muscularity and degree of sexual maturation, from child-like to adult-like – is repeatedly emphasized by Tanner (1962, 1989) and Marshall and Tanner (1970). Among Neanderthals there may have been early and late developers as there are among recent humans. Known individuals cannot be assumed to be typical.

While the use of mean values for skeletal dimensions in analyses of fossil populations is inevitable for convenience when specimens are as numerous as they are for Neanderthals, their remains are numerous only in relation to other archaic *Homo*. The available sample is not comparable with the thousands of recent human children in the surveys of Eveleth and Tanner (1976, 1990) and others in the human growth literature. For any single measurement, the number of Neanderthal individuals is generally limited to fewer than twenty across the entire hypodigm, frequently much fewer as can be seen in the tables and graphs of Chapter 6. Information is lost when only a mean is considered and not the range of observed values.¹

The present work attempts to be comprehensive and offer an account of the subject as it stands, in the process coming to an interim conclusion about the question of rapid growth. While the thesis is already lengthy and has covered brain development to a greater degree than most texts, some avenues of inquiry have been omitted. Among problems worthy of further attention are the following, both large-scale and more specific.

1. To elucidate Neanderthal ontogeny, the greatest need is to recover more fossil individuals, especially those complete enough to combine dentition, so that dental and chronological ages can be derived, with postcrania, particularly lower limb bones, so that stature and body mass can be estimated. Age groups which are currently unrepresented are early infants between neonates and ~1.5 years and adolescents between ~12 years and adulthood. As the mean age of attaining adulthood is unclear and disputed, a set of individuals of ~13–18 years chronological age and including both sexes would be greatly informative.
2. Another necessity is to derive chronological ages from dental microstructure wherever possible for all Neanderthal and other fossil subadults, e.g. Upper Palaeolithic *Homo sapiens*. To my knowledge, no new project comparable with that of T.M. Smith et al. (2010) has been conducted.
3. It is still not entirely clear whether Neanderthal dental development was so accelerated that it does not fall within recent human range. One individual, Scladina, has dental formation advanced beyond recent human schedules; another, El Sidrón, is fully within expected range. Does the very advanced individual represent normal attainment for Neanderthal early developers or is it an outlier?
4. On the hypothesis that advanced molar formation and earlier emergence of the mandibular M1 imply more rapid somatic growth, Sub-Saharan Africans and Australasians should generally exhibit more rapid somatic growth. Some twentieth century surveys may be compromised by a high incidence of undernutrition in these populations. In the twenty-first

¹ Wherever possible ranges or confidence intervals have been given in this work.

century countries such as Nigeria and South Africa have a growing indigenous middle class. The opportunity is available to clarify with a large-scale targeted survey whether somatic growth is rapid in these communities.

5. Tompkins (1996a, 1996b) highlighted advanced molar development relative to Asians and Europeans in (a) recent southern Africans, (b) Upper Palaeolithic *Homo sapiens*, and (c) Neanderthals together with other “archaics”. Omitting Rabat 1, which is not a Neanderthal, the archaic group became less distinguishable from the Upper Palaeolithic group. The study used earlier forming teeth as a reference to assess relative development of permanent molars. On this assessment the Upper Palaeolithic specimens appeared closer to Neanderthals than to most recent humans. The question then arises whether dentally advanced Upper Palaeolithic individuals were also skeletally advanced or exhibited the dissociation observed in Neanderthal subadults. Further work would have to use chronological ages instead of relative development.

8.3 Neanderthal and *Homo sapiens* contemporaries

This thesis does not attempt to address why Neanderthals became extinct, but some findings may have a bearing on the interaction between them and modern humans entering South West Asia and then Europe.

8.3.1 Implications of results

As discussed earlier (§1.4), a rapid ontogeny is widely held to have characterized Neanderthals and to represent a life history strategy inferior to that of *Homo sapiens*. Here I have argued (§7.5–§7.8) that Neanderthal ontogeny may have been approximately as prolonged as that of *Homo sapiens*. The causal factor for a hominin with body size and brain size comparable to those of *Homo sapiens*, with all values within modern human range, would have been the need to devote comparable energy and time to growing such brains along with such bodies (§4.3.2).

Conceivably, if Neanderthals regularly consumed prodigious amounts of highly nutritious food, they would have been able to grow both body and brain faster. Such a life history does not seem inferior, since young group members would become large enough to be independent and fully productive earlier (§2.7.2). However, evidence from calculated stature, body mass and endocranial volumes does not support a proposition that ontogeny was more rapid (§4.6, §6.2, §6.3, §7.8).

If Neanderthals and modern humans shared a prolonged subadulthood, that attribute may have facilitated acceptance of one species by the other as fellow humans and as potential mates. On the other hand, simple hunter-gatherers may have estimated maturity of offspring by size rather than by counting years of life.

Dental development was more rapid than in modern humans (§3.3, §3.4). I have suggested that the Neanderthal dental schedule is a plesiomorphic retention, whereas somatic growth was necessarily lengthened during evolution of the Neanderthal clade to accommodate larger brain growth (§7.8).

The widely held view that dental development, and specifically age of emergence of the mandibular first molar, is “tightly correlated” with life history (§7.4) is potentially called into question by the claim that Neanderthal ontogeny was as lengthy as that of *Homo sapiens*. It is not clear whether emergence of LM1 in Neanderthals was significantly earlier than in *Homo sapiens* generally, since the range of ages found in Neanderthals is included within recent human range (§3.4.7; Tables D.15–D.17). Even omitting the highest age, 6.7 years for La Chaise, the lower ages are readily found among African and Australasian groups.

A number of researchers (§7.4.7) have proposed that the model expressing correlation between dental and somatic development schedules (B.H. Smith 1989, etc.), which appears to hold at family and subfamily levels, may not apply at the lowest taxonomic levels: genus, species and geographical populations (e.g. among living humans and between them and sister species such as Neanderthals).

In addition, there may be scope to review the ranges of ages of first molar emergence and other life-history milestones among short-lived monkeys and prosimians which contribute data upon which the model is based. The resolution of ages and stages offered when lifespan is only a few years is much less precise than for *Gorilla*, *Pan* and *Pongo*, where lifespan runs into decades and field observation is much easier.

8.3.2 Differences between Neanderthals and *Homo sapiens*

“Neanderthals appear 350,000 years ago and disappear 30,000 years ago.... The stone tools that they make at the beginning of their history and at the end of their history are pretty much identical. Modern humans appear, say, 100,000 years ago. And I think we agree ... that technology today is different from 100,000 years ago.”¹

This statement, by one of the most renowned scholars of this century, is largely true but elides the temporal dimension. The lineages of *Homo sapiens* and Neanderthals, while they were contemporary, had existed for exactly the same duration since their last common ancestor, whatever species they and their immediate ancestors may be assigned to. After Neanderthal extinction (~40–45 ka), *Homo sapiens* spent another 30,000 years, and in many geographical areas a further 10,000 years, exclusively as hunter-gatherers, before, at first very slowly and later more rapidly, developing the social organization, written language, world outlook, empirical science, mathematical techniques, and complex technology that makes twenty-first century society possible. If the Jebel Irhoud hominins (~315 ka) are *Homo sapiens*, then *Homo sapiens* in one continent coexisted with the immediate ancestors of Neanderthals and then Neanderthals themselves in another continent for ~275,000 years up to Neanderthal extinction, and for almost all of that period subsisted at a similar level of material culture.

A practically identical Mousterian lithic technology accompanied by hearths and apparent burials seems to have been shared in the Levant by early *Homo sapiens* at Skhul and Qafzeh (~130–100 ka) and Neanderthals at Tabun earlier and Kebara later down to 50 ka (Tattersall 1995:245), a period of ~70,000 years. A uniform lithic, hunting and social culture including intentional burial appears to have been practised by *Homo sapiens* and “Neanderthal-like” hominins living alongside each other at 130–80 ka in the Levant (Zaidner et al. 2025). If *Homo sapiens* already enjoyed a modern human life history and Neanderthals did not, the apparent similarities of culture are remarkable (Hillson 2014:156) and indicate that any putative differences of ontogeny were not disadvantageous.

As Tattersall (2005:212) strikingly observes, the stocky form of Neanderthals with their wide shoulders, thorax and pelvis and possibly different gait, and the more ectomorphic, long-legged form of early modern humans entering Asia would have presented “enormous *Gestalt* differences” and we might expect the two species to have appeared to each other as “very different figures on the ancient landscape”. Yet evidently some individuals were able to view members of the other species as potential mates, because interbreeding took place (Green et al. 2010; Reich 2018), beginning perhaps during the period of these Levantine cave occupations at ~130–50 ka (Higham 2021). Mating would have been unlikely had the phenotype and society of the other seemed wholly alien to individuals of either group. In more northerly or high-altitude regions of Asia, the two types of hominin on the landscape may have resembled each other more closely, because they would almost certainly have covered their bodies with furs tied with coarse ligaments and would all have been, like recent cold-climate hunters, unwashed, with straggling hair, and infested with lice (cf. Rasmussen 1908).

Hermanussen et al. (2018, 2019) and Bogin (2021) draw attention to socioeconomic and emotional factors influencing human growth. Large stature indicates dominance among humans and can induce those of lesser stature to see themselves as subordinate or even oppressed. The difference in mean adult stature between Upper Palaeolithic humans and Neanderthals of either sex is roundly ~10 cm (Tables H.1–H.8). When modern humans entered Neanderthal territory during the last glacial, if the pioneers were indeed taller than Neanderthals and both species recognized each other as humans, then it is possible that modern

¹ Svante Pääbo, lecture from 2014, <https://www.youtube.com/watch?v=JcyGIwJXGLw> retrieved 2025.06.10.

humans saw themselves as dominant and equally that Neanderthals saw themselves as subordinate. In areas where groups of both species lived in proximity, negative self-evaluation might result in depressive tendencies and failure to thrive among Neanderthal young (§2.7.1). On the other hand, if Neanderthals were more strongly built and valued such attributes, despite any statural advantage of the modern humans, then Neanderthals may have regarded themselves as superior. Either way, perceptions and reactions based partly on size difference would have played a part in future relationships between species groups.

It was suggested earlier (§7.8.3) that members of extinct *Homo* would not struggle to cope in a recent human forager society but might struggle in a complex modern developed society. The most extraordinary feature of *Homo* is our large brains. Mean endocranial volume reached its maximum probably in the Upper Palaeolithic (Table E.8). During the development of increasingly organized and specialized society during the last 10,000 years since the Mesolithic, through agriculture, cities, literacy and empires, endocranial volume did not increase, rather the reverse (§4.2). Evolution has endowed us with hunter-gatherer brains which can conceive philosophical abstractions and make logical deductions, solve problems using calculus, devise and program computers, construct and operate land, sea, air and space vehicles, and function in societies with online banking and social media. We do not need 20 years to learn to hunt and gather (§2.8), but most of us do need 20 years or more to acquire the education which enables these more intellectual competencies. Recent children from subsistence-level societies who go to school (Blurton-Jones and Marlowe 2002) are making a transition to complex modern society and have no counterpart in the Palaeolithic. The fact that they can make such a transition is evidence that they and we generally have cognitive abilities which exceed the demands of everyday life.

The subject of the cognitive and affective capacities of *Homo sapiens* ancestors and their Neanderthal contemporaries deserves much more attention than can be given here. That Upper Palaeolithic people had capacities similar to those of living people has seemed likely to many researchers on the grounds of their anatomical similarity (e.g. Mellars and Stringer 1989). It is unknown whether Neanderthals, and perhaps Denisovans, may have shared at least some or many of those capacities. What is most intriguing is the possibility that complex brains with the capacity to function in a complex modern society may have existed 30,000 or more years ago when *prima facie* there was no requirement for such complex brains to evolve.

Final caveat

With Neanderthal immatures it is largely unknown whether the individual examined was typical or atypical, one who died by accident, was killed by a conspecific, was bitten by an animal, contracted an illness that became fatal, was an orphan at risk, was neglected or a poorly nourished member of its group, or became a casualty at a particularly stressful time for the local community. There never was an average *Homo sapiens* or Neanderthal adult or child. There have only ever been individual organisms, or people, who lived and died. The individual, existential aspect of hominin life is generally set aside in anthropology, but may be worth remembering from time to time, to avoid abstraction disconnecting us from the reality of ancient lives.

APPENDIX A

CATALOGUE OF NEANDERTHAL IMMATURE REMAINS

Archaeology has been bringing Neanderthal remains to light since 1829, beginning with the Engis fossils from Belgium, and a considerable hypodigm has accumulated. Neanderthals are better represented than any other of the hominin species or types which can be distinguished from anatomically modern humans in the approximately seven million years since our lineage diverged from that of the chimpanzees. There are a number of almost complete skeletons, and even more almost complete crania. Even so, as with the other extinct hominins, remains are often very fragmentary, consisting sometimes of only teeth or a partial mandible, some small parts of a cranium or unconnected fragments of the postcranial skeleton.

This catalogue documents a large cohort of the known immature Neanderthal individuals, from fetuses to adolescents. Determination of Neanderthal affinity is guided by the most recent literature. Excluded are: (1) non-Neanderthal fossil remains, e.g. the Skhul material; (2) adult, i.e. fully grown, Neanderthals; (3) remains which are too fragmentary to be diagnostic of the developmental status or specific affinity of the individual; and also usually excluded are (4) isolated small elements such as individual teeth or phalanges. Even after these exclusions, the number of fossils of Neanderthal immatures is considerable, and a few for which descriptions were unavailable or lacking useful details have been omitted. However, all the relatively complete individuals and many fragmentary and rarely cited pieces are listed.

Entries are presented in the same format but information varies according to availability and completeness of sources.

The specimens are listed in alphabetical order of the designations by which they are commonly known. These designations are typically the name of the archaeological site, with a specimen number in cases where remains of more than one individual were recovered or where isolated skeletal parts were assigned an identifier. Alphabetical order here ignores the definite article *Le*, *La*, *Les*, *El* found in some French and Spanish site names. The names of countries are as at the time of writing, which may differ from those at the time of discovery, e.g. the former Yugoslavia.

Amud III, IV, 5, 8, 10, 11, 12, 15, 16, 18

Remains:

Amud III: Right temporal, possible frontal, fragment of maxilla, lower right deciduous second molar

Amud IV: Right temporal

Amud 5: Humerus, tibia, radius

Amud 8: Upper right deciduous molar

Amud 10: Radius

Amud 11: Upper deciduous canine

Amud 12: Distal radius

Amud 15: Radius

Amud 16: Femur

Amud 18: Humerus

Provenance: Amud Cave, Galilee, Israel: Amud I–IV excavated 1961; Amud 5–18 excavated 1991–1992.

Dating: 50–60 ka by thermoluminescence (Rak et al. 1994:314; Hovers et al. 1995:54).

Age at death: by size comparison with modern humans or by dental development (Rak et al. 1994:314; Hovers et al. 1995:50).

Amud III: 4 years.

Amud IV: 3 years.

Amud 5: 6–9 months

Amud 8: 8 years

Amud 10: Infant

Amud 11: 7 years

Amud 12: Infant

Amud 15: Infant

Amud 16: 18 months

Amud 18: Infant.

Observations:

The much more complete infant skeleton Amud 7 is listed separately below.

Amud I is the complete adult male skeleton found in the 1961 excavation (Suzuki and Takai 1970). Amud II, 9, 13, 14, and 17 are fragmentary adult remains. The Amud 6 neonatal skeleton is a modern human intrusive burial dated to 1250 BP (Rak et al. 1994:314; Hovers et al. 1995:50).

Amud 7

Remains: Partial skeleton consisting of calvaria (frontal, partial sphenoid, temporals, parietals and occipital, incomplete basicranium), maxilla and mandible with deciduous dentition, and postcranial elements: clavicle, scapula, first to twelfth ribs, fragments of all seven cervical vertebrae, eight thoracic vertebrae, three lumbar vertebrae, fragments of ilium; humerus, radius, ulna, metacarpal bone, phalanx; tibia, metatarsals and phalanx; plus isolated petrous bone and distal fibula.

Provenance: Amud Cave, Galilee, Israel, excavated 1991–1992; one of the petrous temporals was found in the 1960s excavation by Suzuki and Takai (1970).

Dating: 50–60 ka by thermoluminescence (Rak et al. 1994:314).

Age at death: 10 months by dental development (Rak et al. 1994:314; Been and Rak 2012).

Observations:

An isolated petrous temporal found by Suzuki and Takai in the 1960s has been identified as the second petrous of Amud 7. Only a cast is now available. A fragmentary distal fibula was recovered in the 1990s, which may also belong to the Amud 7 individual (Been and Rak 2012).

Archi

Remains: Mandibular left and right corpora with some of the dentition, missing rami.

Provenance: Archi, Reggio di Calabria, Italy, 6 September 1970.

Dating: Würm; >40 ka by U/Th dating on mollusc remains, MIS4–MIS3 (Arnaud 2015).

Age at death: 2.5–3.3 years (Mallegni and Trinkaus 1997); 2 years 6 months (Granat and Heim 2003:186); 2.4–3.5 years by dental microtomography (Bernardini et al. 2013); 3 years (Arnaud 2015).

Arcy-sur-Cure aka Grotte du Renne

Remains: Isolated immature temporal, including petrous, tympanic and mastoid portions.

Provenance: Grotte du Renne, Arcy-sur-Cure, south east of Auxerre, France, excavation directed by A. Leroi-Gourhan 1958–1962.

Dating: Châtelperronian Layer Xb, 33.8 ka by ^{14}C (Hublin et al. 1996), ≥ 39 ka ^{14}C Cal. (Hublin et al. 2013:227).

Age at death: ~1 year (Hublin et al. 1996).

Observations:

Identified as Neanderthal from the low position of the posterior semicircular canal.

Barakai

Remains: Mandible, complete except for left ramus.

Provenance: Barakai Cave, Western Caucasus, Russia; excavation 1977–1980.

Dating: Würm II.

Age at death: 3 years (Faerman et al. 1994).

Carigüela aka Carihuela

Remains: Frontal bone, two fragments.

Provenance: Carigüela Cave, north east of Granada, Spain, 4 May and 22 May 1955.

Dating: Würm II.

Age at death: 6 (4–8) years, male (De Lumley and Garcia-Sanchez 1971; De Lumley 1973:252); 4–6 years (Jiménez-Arenas et al. 2019:96).

La Chaise (Bourgeois-Delaunay) 17

Remains: Parts of several individuals, including an incomplete calotte and a mandibular M1.

Provenance: Abri Bourgeois-Delaunay, La Chaise de Vouthon, Charente, France, excavated by David 1952 onward and from the 1970s Debénath.

Dating: 152±16 ka (Schwarcz and Debénath 1979, cited by Cook et al. 1982); 116–127 ka (Zanolli et al. 2020).

Age at death: Adult or adolescent (Cook et al. 1982:39).

Observations:

Although the remains were assigned one designation, ~3–4 individuals are represented (Cook et al. 1982:39). Remains from Abri Bourgeois-Delaunay have been designated with BD numbers, e.g. BD9. The partial calotte is described, along with the rest of the more complete remains, by Condemi (2001).

La Chaise (Suard) 13 and 14, aka S13 and S14

Remains: Mandible, isolated deciduous teeth of two individuals of the same age.

Provenance: Abri Suard, La Chaise de Vouthon, Charente, France, 1950 and 1951.

Dating: Riss III, OIS 6, $\sim 126 \pm 15$ ka (Schvoerer et al. 1977, cited by Tillier and Genet-Varcin 1980:197); 185 ± 30 ka or 101 ± 7 ka (Arnaud 2015:45).

Age at death: 5–6 years (Tillier and Genet-Varcin 1980); 4.5 years (Minugh-Purvis 1988:283).

La Chaise (Suard) 15 and 16, aka S15 and S16

Remains: Frontal and parietal of one or more immature individuals.

Provenance: Abri Suard, La Chaise de Vouthon, Charente, France, excavated by David, 1952.

Dating: OIS 6 (Coqueugniot et al. 1996:10).

Age at death: 3–6 years by comparison with other immatures (Coqueugniot et al. 1996:15).

Observations:

According to Minugh-Purvis (1988:281), La Chaise 15 is a parietal and 16 is a frontal. According to Coqueugniot et al. (1996), La Chaise 15 is a frontal, and they do not mention 16.

La Chaise (Suard) occipital

Remains: Two-thirds of an occipital squama.

Provenance: Abri Suard, La Chaise de Vouthon, Charente, France, excavated by Debénath, 1975.

Dating: Riss III, 126 ± 15 ka (Hublin 1980:669); OIS 6 (Coqueugniot et al. 1996:10).

Age at death: Very young infant (Hublin 1980:669).

Châteauneuf 1

Remains: Fragment of mandible.

Provenance: La Grotte à Melon, Châteauneuf-sur-Charente, France, excavated by Chauvet, 1908.

Dating: Mousterian layers.

Age at death: 3–4 years (Tillier 1979).

Châteauneuf 2

Remains: Maxilla with deciduous teeth and two permanent crowns, right mandibular ramus.

Provenance: Abri Hauteroche, Châteauneuf-sur-Charente, France, excavated by Cauvin and Debénath, 1968.

Dating: Mousterian layers.

Age at death: 5–6 years (Tillier 1979); 5.75 years (Shackelford et al. 2015:237).

Circeo 4 aka Fossellone 3

Remains: Fragment of mandible with exfoliated second premolar and first and second molars, belonging to one individual.

Provenance: Grotta Fossellone, Monte Circeo, Latium, Italy, excavated by Blanc, 1953–1954.

Dating: MIS3 (Rolfo et al. 2023:10, citing Blanc 1954).

Age at death: 9 years (Mallegni 1992:21).

Observations:

Mallegni (1992) states that this individual may be a female or gracile male.

Combe Grenal I

Remains: Fragment of right anterior mandibular corpus with 5 teeth.

Provenance: Bed 25, Grotte de Combe Grenal, near Domme, Dordogne, France, excavated by Bordes, 10 July 1954.

Dating: Würm (Vallois 1960:130–131); 65–75 ka (Garraalda and Vandermeersch 2000:215).

Age at death: 5–9 years (Garraalda and Vandermeersch 2000:227); 4 years 6 months (Granat and Heim 2003).

Combe Grenal III

Remains: Fragment of left mandibular ramus.

Provenance: Bed 25, Grotte de Combe Grenal, near Domme, Dordogne, France, excavated by Bordes, 1953–1955.

Dating: 65–75 ka (Garraalda and Vandermeersch 2000:215,250).

Age at death: 13–14 years (Garraalda and Vandermeersch 2000:227).

Observations:

There are possible intentional cut marks on the ramus (Le Mort 1989:82–83; Garraalda and Vandermeersch 2000:247–248).

Combe Grenal IV

Remains: Superior fragment of left mandibular corpus with P4 and M1.

Provenance: Bed 25, Grotte de Combe Grenal, near Domme, Dordogne, France, excavated by Bordes, 1953–1955.

Dating: 65–75 ka (Garralda and Vandermeersch 2000:215,250).

Age at death: 14–15 years (Garralda and Vandermeersch 2000:227).

Observations:

There are possible intentional cut marks on the corpus (Le Mort 1989:82–83).

Combe Grenal 31

Remains: Single deciduous lower right incisor.

Provenance: Bed 60, Grotte de Combe Grenal, near Domme, Dordogne, France, excavated by Bordes, 1954–1955, identified among the existing collection by S. Madeleine, 2009.

Dating: MIS 6, ~130 ka (Maureille et al. 2011).

Age at death: 2–4 years (Maureille et al. 2011).

Observations:

Dated much earlier than the other Combe Grenal immatures.

Cova Negra

Remains: Possibly 4 immature individuals: adolescent right parietal, immature left frontal, four left parietal fragments, occipital fragments, right mandibular fragment, isolated deciduous and permanent teeth, right radius, two right metatarsals, distal and proximal parts of a right femur, adolescent right distal femoral diaphysis, distal fibula.

Provenance: Cova Negra, Valencia region, Spain, excavated by Viñez 1928–1933, Jordà 1950–1957, and Villaverde 1981–1991.

Dating: Würm I-II, II, and II-III: OIS 5b, OIS 5a dated by TL to 96–107 ka; OIS 4, OIS3 dated by TL to 50–53 ka (Arsuaga et al. 2007).

Ages at death: (Arsuaga et al. 2007)

CN42174 right parietal: 2 years.

Parietal II: adolescent.

Other cranial remains: 5–8 years.

CN42165 radial diaphysis: 5–6 years.

CN42166 and CN42167 metatarsals: 5–8 years.

CN42168 and CN42169 Femur I: 5–6 years.

Observations:

The remains were recovered from several layers at the site, are fragmentary, and belong to different individuals. Most complete are the radius and femur. Immatures under 10 years account for 4 of the 7 minimum number of individuals.

La Crouzade

Remains: Partial gracile left humeral diaphysis (La Crouzade I), and three manual phalanges (II, III, IV).

Provenance: Mousterian Bed 8, Grotte de la Crouzade, Commune de Gruissan (Aude), south of Narbonne, France, excavated by Th. and Ph. Hélène, Genson and Albaille before 1946.

Dating: Würm II (M.A. De Lumley 1973:569–570).

Age at death: La Crouzade I ~20 years (M.A. De Lumley 1973:569–570).

Observations:

The distal end of the humerus is broken and the humeral head is missing, not having fused, indicating a young subject. The phalanges may belong to separate individuals.

Dederiyeh 1

Remains: Almost complete skeleton including cranio-dental remains missing much of the facial skeleton; and postcranial elements; all twelve ribs are present and there are hand and foot phalanges.

Provenance: Layer 11, Cave in Wadi Dederiyeh, Afrin Valley, Syria, excavated 29 August 1993.

Dating: Mousterian Tabun B lithic industry (Akazawa et al. 1995); >54 ka by ¹⁴C (Fukase et al. 2015:483); OIS 3 (Arnaud 2015:45).

Age at death: ≤2.0 years (Akazawa et al. 1995:80); 1.5–3 years (Kondo et al. 2000); 1.3–2.5 years (Kondo and Ishida 2003a); 1.5 or 1.7 years by counts of striae on sectioned tooth (Sasaki et al. 2003); 1.5 years (Fukase et al. 2015:483).

Observations:

The infant was lying on its back with legs flexed, and is said to have been deliberately buried (Akazawa et al. 1995:79–81).

Dederiyeh 2

Remains: Partial skeleton including cranio-dental remains with virtually complete facial skeleton; and postcranial elements from the axial skeleton and limbs.

Provenance: Layer 3, Cave in Wadi Dederiyeh, Afrin Valley, Syria, excavated 1997 and 1998.

Dating: Mousterian Tabun B lithic industry (Akazawa et al. 1995); 48–54 ka by ¹⁴C (Fukase et al. 2015:483).

Age at death: ≤2.0 years (Akazawa et al. 1999:138); 2.15 (1.2–2.5) years (Kondo and Ishida 2003); 2.0 years (Fukase et al. 2015:483).

Observations:

From the Middle Palaeolithic layers at Dederiyeh remains of fifteen individuals have been recovered, more than half of which are young children (Akazawa et al. 1999:141).

Ehringsdorf 7 aka G (and 8)

Remains: Mandible with dentition.

Provenance: Kämpfe quarry, Ehringsdorf, near Weimar, Germany, 8 May 1914.

Dating: Riss-Würm (MacCurdy 1915); 200–350 ka by U-series (Blackwell and Schwarcz 1986); 230 ka (Arnaud 2015:45).

Age at death: 10 years (Keith 1925:195); adolescent (Wolpoff 1980a:272); 12 years (Minugh-Purvis 1988:299).

Observations:

Minugh-Purvis notes that there is additionally a fragment of mandible with a lower deciduous molar, designated Ehringsdorf 8.

Engis 2

Remains: Almost complete and undeformed calotte including frontal, left and right parietals, occipital and right temporal. Missing left temporal, basicranial and facial bones and mandible. No postcrania.

Provenance: Cave at Engis near Liège, Belgium, discovered by Schmerling, 1829.

Dating: 30–50 ka (quoted by T.M. Smith et al. 2010:20925).

Age at death: 5 years (Fraipont 1936), 6–7 years (Hublin 1980:670); 5–6 years (Tillier 1983a); 3.0 years by dental microtomography (T.M. Smith et al. 2010:20925).

Observations:

Engis 2 represents the historically earliest discovery of Neanderthal remains, in 1829. With their resemblance to the immature La Quina H18 (q.v.), found in association with the adult La Quina H5, the Engis 2 remains came to be recognized as another immature representative of this population (Fraipont 1936).

Engis 1¹ also described by Fraipont (1936), is a *Homo sapiens* skeleton interpreted as an intrusive burial from overlying levels. It has been dated to 4.59–4.92 ka (Toussaint and Pirson 2006).

Fate 1 and 2

Remains:

Fate 1a: Frontal fragment including supraorbital.

Fate 1b, 1c, 1d: Fragments of frontal squama.

Fate 2: Left hemimandible with postcanine permanent dentition, some unerupted, and two isolated deciduous molars.

Provenance: Caverna delle Fate, Finale Ligure, Savona, Italy: 1887–1888, excavated by Amerano; 1983–1987, excavated by Franco-Italian collaboration.

Dating: MIS 5a, 72–74 ka by ESR, 76–82 ka by gamma spectrometry (De Lumley and Giacobini 2013:277).

¹ Tattersall (1995:78–79) Figure 55 shows a page from Lyell's *Antiquity of Man* (1863) illustrating Engis 1, but the 1995 caption identifies it as Engis 2.

Age at death: 3.5 years (Giacobini and De Lumley 1988, cited by De Lumley and Giacobini 2013:278 as an error); 8–10 years (De Lumley and Giacobini 2013:273, 275–276).

Observations:

The first immature frontal fragment and hemimandible, along with a mandibular fragment of an adult, were identified in 1981 among the faunal remains from the early excavation. Subsequent renewed excavation uncovered further adult and immature remains. The immature elements Fate 1 and 2 are all attributed to the same juvenile.

La Ferrassie 3

Remains: Cranial and postcranial fragments, including left parietal, occipital squama, petrous parts of 2 temporals, from one of which the auditory ossicles were retrieved, left side of sphenoid, left and right ulnae and radii, left and right hand bones, 1 talus.

Provenance: Rock shelter at La Ferrassie, Savignac de Miremont, Dordogne, France. Retrieved from a pit, adjacent to (south of) the pit containing immature La Ferrassie 4bis (q.v.), located 4 metres east of the adult male skeleton La Ferrassie 1. Excavated by Peyrony and Capitan, 8 August 1912.

Dating: MIS 3, 54–40 ka by OSL and ¹⁴C (Guérin et al. 2015).

Age at death: 10–12 years (Heim 1982).

Observations:

Discovered in a pit sunk into a living floor alongside several other individuals in separate pits, hence possible burial.

The ossicular chain from the petrous temporal of this specimen has recently been restudied (Quam et al. 2013).

“La Ferrassie 4” (Le Moustier 2)

Remains: Right femur and humerus.

Provenance: Allegedly from rock shelter at La Ferrassie, Savignac de Miremont, Dordogne, France. Allegedly retrieved from a pit shared with La Ferrassie 4 bis (q.v.).

Dating: MIS 3, 54–40 ka by OSL and ¹⁴C (Guérin et al. 2015).

Age at death: Fetus at term, a little over 8 months (Heim 1982).

Observations:

The femur and humerus have been reassigned to Le Moustier 2 (q.v.), on the grounds that they had adhering deposit and state of fossilization identical to that of the other known Le Moustier 2 remains, which had been lost but in 1996 were identified in the museum at Les Eyzies de Tayac. The femur and humerus may have been sent by Peyrony, who excavated both La Ferrassie and Le Moustier, to M. Boule at Paris and there confused with the La Ferrassie remains (Maureille 2002).

While La Ferrassie 4bis represents a genuine La Ferrassie individual, it would appear that there is no object correctly denoted by “La Ferrassie 4”,

La Ferrassie 4bis

Remains: Partial cranial and postcranial skeleton, including part of left frontal, left petrous temporal, 2 deciduous molars, 7 vertebral centra and 14 neural arches, 10 left ribs, 11 right ribs, left clavicle and right scapula, 2 humeri, right radius and ulna, left and right ilia, left and right femora, tibiae and fibulae.

Provenance: Rock shelter at La Ferrassie, Savignac de Miremont, Dordogne, France. Retrieved from a pit adjacent to (north of) the pit containing La Ferrassie 3 (q.v.), located 4 metres east of the adult male skeleton La Ferrassie 1. Excavated by Peyrony and Capitan, 10 August 1912.

Dating: MIS 3, 54–40 ka by OSL and ^{14}C (Guérin et al. 2015).

Age at death: Neonate, about 15 days (Heim 1982); 3 months (Granat and Heim 2003:186).

Observations:

Discovered in a pit sunk into a living floor, hence possible burial, as with La Ferrassie 3 (q.v.). It was thought that this individual La Ferrassie 4bis shared the pit with the neonate humerus and femur La Ferrassie 4 (q.v.). This would have been the only instance of a double burial among Neanderthals. However, the La Ferrassie 4 femur and humerus have been identified as belonging to Le Moustier 2 (q.v.), so that there is no longer a second individual with La Ferrassie 4bis. La Ferrassie 4bis, not La Ferrassie 4, is therefore the genuine La Ferrassie specimen.

La Ferrassie 5

Remains: Some remains of cranial vault including frontal and parietal fragments and right temporal; The postcrania are represented by 1 neural arch.

Provenance: Rock shelter at La Ferrassie, Savignac de Miremont, Dordogne, France. Retrieved from a small pit, the northernmost of nine in a formation north-south in the interior of the rock shelter. Excavated by Peyrony and Capitan, 26 April 1920.

Dating: MIS 3, 54–40 ka by OSL and ^{14}C (Guérin et al. 2015).

Age at death: Fetus, 7 months (Heim 1982).

Observations:

Discovered in a pit sunk into a living floor, with a mound of fill above, hence possible burial, as with La Ferrassie 3 (q.v.).

La Ferrassie 6

Remains: Postcranial skeleton very well preserved; cranium, located apart from postcrania, completely crushed.

Provenance: Rock shelter at La Ferrassie, Savignac de Miremont, Dordogne, France. Retrieved from a pit in the rear of the rock shelter. Excavated by Peyrony and Capitan, 1 June 1921.

Dating: MIS 3, 54–40 ka by OSL and ^{14}C (Guérin et al. 2015).

Age at death: 6–7 years (MacCurdy 1922); 3 years (Heim 1982).

Observations:

The remains were discovered in a pit which in plan assumes a triangular shape, sunk into a living floor with fill above, hence probable burial. A triangular flat stone block with 12 cupules gouged out on the underside lay over the pit, apparently placed centrally, i.e. symmetrically. The postcrania lay at the bottom of the pit at the western apex of the triangle, while the cranial remains, reduced almost to dust, lay at the southern corner (MacCurdy 1922; Heim 1982). The meaning of prehistoric cupules such as these is unclear (Bednarik 2016).

La Ferrassie 8

Remains: Fragmentary cranial remains including occipital squama and right parietal, small fragment possibly of facial bone, some deciduous teeth; 12 vertebrae including 12 centra and 13 neural arches, 1 manual phalanx, 11 identifiable ribs, left and right ilia and pubes and left ischium. Further remains identified in the 21st century: significant portions of cranium (occipital pars basilaris and partes laterales, left temporal including petrous with stapes, 3 parietal fragments), mandible, further vertebrae, and fragmentary manual and costal remains.

Provenance: Rock shelter at La Ferrassie, Savignac de Miremont, Dordogne, France. Retrieved just north of the location of La Ferrassie 5 (q.v.), near the north wall of the rock shelter; excavated by Delporte and colleagues, 1970 and September 1973.

Dating: MIS 3, 54–40 ka by OSL and ^{14}C (Guérin et al. 2015), 41.7–40.8 ka (Balzeau et al. 2020:1,4).

Age at death: A little under 2 years (Heim 1982); 1 year 6 months (Granat and Heim 2003:181–182, 186); 1.37 years (Shackelford et al. 2015:237).

Observations:

Discovered semi-flexed below a living floor, possible burial but with no outline of an intentional pit (Heim 1982). Additional fragments from the 1968–1973 excavation have recently been identified in the collection and have been described by Gomez-Olivencia et al. (2015), who also provide an inventory to date (2015:109). Further analysis including taphonomy and confirmation of intentional burial is presented by Balzeau et al. (2020).

Figueira Brava

Remains: Fragment of frontal bone including glabella; left first metacarpal, right first phalanx from digit 3; upper left premolar.

Provenance: Bed 2, Gruta de Figueira Brava, on Atlantic coast south west of Portinho, Portugal.

Dating: 30930±700 BP ^{14}C , 30561+10726/-11759 BP U-series (Antunes and Santinho Cunha 1992:683).

Age at death: Adolescent, 16–17 years (Antunes and Santinho Cunha 1992:688,691).

Observations:

The teeth exhibit hypoplastic pitting and have been scraped with stone implements. The hand bone epiphyses are missing. Antunes and Santinho Cunha (1992) deduce cannibalism.

Fontéchevade 1

Remains: Fragment of frontal bone including glabella.

Provenance: Bed E, Cave of Fontéchevade, Charente, France, excavated by Henri-Martin, 1947.

Dating: Riss-Würm (Trinkaus 1973:25); OIS3, ~33 ka or >57 ka (Chase et al. 2007).

Age at death: Adolescent ≥ 10 years (Trinkaus 1973); adolescent or young adult (Tillier 1983b; Chase et al. 2007).

Observations:

Recovered at a depth of 2.4–2.6 metres, near the Fontéchevade 2 adult calotte (depth 2.6–2.8 metres), the frontal was initially assigned to the Riss-Würm Interglacial (Trinkaus 1973:25), OIS5a (Chase et al. 2007). Fontéchevade 1 shows no clear sign of browridges. Earlier in the twentieth century it was interpreted, along with Fontéchevade 2 and Swanscombe, as evidence for the presence of “presapiens”, i.e. ancestral *Homo sapiens*, contemporary with Neanderthals in Europe (Boule and Vallois 1957:188–190). Otherwise it could be identified as an immature Neanderthal with incomplete development of the supraorbital torus, although attribution remains ambiguous (Wolpoff 1971; Trinkaus 1973). Later excavation at the site has resulted in redating of Fontéchevade 1 and 2, which can be assigned to OIS3 (Chase et al. 2007:219). During OIS3 *Homo sapiens* entered Europe. Chase et al. (2007:220) therefore suggest that the Fontéchevade specimens, which they regard as relatively gracile, need not be identified as Neanderthal. However, the identification as a young Neanderthal remains possible on the basis of the analysis by Trinkaus (1973), so this specimen is included here.

Gibraltar 2 (and 3?), aka Devil’s Tower

Remains: Calvaria including frontal, left parietal, right temporal; right maxilla; mandible; deciduous molars two upper right and two lower left, developing permanent dentition in crypts. No postcrania.

Provenance: Devil’s Tower cave, Gibraltar; excavated by D. Garrod, 1926.

Dating: 28–32 ka by AMS on charcoal from hearths in Gorham’s Cave, i.e. not from Devil’s Tower itself (Finlayson et al. 2006); 30–50 ka (quoted by T.M. Smith et al. 2010:20925); >39 ka (Arnaud 2015:45).

Age at death:

Gibraltar 2: 5 years, male, by craniodental development (Buxton in Garrod et al. 1928); 5 years (Tillier 1982); 4.3–5.8 (Skinner and Sperber 1982, cited by Skinner 1997b); 3.1 years by perikymata (Dean et al. 1986); 4.5–5.0 years (Minugh-Purvis 1988); 4 years by dental stages (B.H. Smith and Tompkins 1995:268); 4.6 years by count of striae using microtomography (T.M. Smith et al. 2010:20925); male by DNA (Bokelmann et al. 2019).

Gibraltar 3 (putative), the temporal bone only: 3 years (Tillier 1982; 1988).

Observations:

Buxton (in Garrod et al. 1928) attributed all the remains to one individual aged ~5 years. Tillier (1982) argued that, as the tympanic ring remains unfused, the single temporal bone is too immature and must belong to a second individual which could not be more than 3 years old. If the new calculation derived from dental microstructure had reduced the age at death of this specimen to ~3 years or below, it might have resolved the apparent discrepancy. However, the

age from counts of striae by microtomography, 4.6 years, remarkably confirming Buxton's assessment, leaves it unresolved. Consensus is that there is only one individual.

In the maxilla and mandible only deciduous teeth had erupted, many lost. Of permanent teeth, one maxillary and two mandibular first molars and the crown of a mandibular second molar were in their crypts (Carbonell 1965). The mandibular left M1 has roots at $\frac{1}{4}$ or $\frac{1}{2}$, well within modern human range for 4.6 years.

Guercy: See *Moula Guercy*

Hohlenstein Stadels

Remains: Nearly complete right femoral diaphysis.

Provenance: Near the entrance to the Stadelhöhle des Hohlensteins in the Lonetal, Baden-Württemberg, during a survey (sondage), 26 July 1937.

Dating: 60–120 ka (Kunter and Wahl 1992:113), Eemian or early Würm (Street et al. 2006:559).

Age at death: Adolescent, male (Street et al. 2006:559); ≥ 20 years, male (Kunter and Wahl 1992:117).

Hortus

Remains: Many fragmentary remains. Three identified immature individuals, and the remainder of isolated immature elements, have separate entries below.

Provenance: Hortus Cave, near Montpellier, Languedoc, France, excavated under direction of H. de Lumley, 1960–1964.

Dating: Wurm II, 55–35 ka (De Lumley 1972)

Age at death: subadults only (De Lumley 1973:322):

0–1 year: Hortus I, I bis, XVII (2 individuals)

1–5 years: Hortus XV (1 individual)

5–15 years: Hortus II and III, XX, XXIII–XXVIII, XXXIX, XLIII, XLIV (2–5 individuals)

15–30 years: Hortus IV (adolescent) and others

Observations:

The Hortus cave yielded remains of 20–30 individuals, of which 75% were “adult” aged over 15 years (De Lumley 1973:322). The unexpectedly low proportion of immatures may indicate that those inhabiting the cave did not represent a complete community (De Lumley 1972). On the other hand, the high proportion of “young adults” aged 15–30 years, 40% of total, may represent elevated mortality in this age group.

Hortus I and I bis

Remains:

Hortus I: Left parietal

Hortus I bis: Right parietal.

Age at death: 0–7 months (De Lumley (1973).

Hortus II and III aka Hortus 2 + Hortus XX, XXIII–XXVIII, XLIII, XLIV

Remains: These elements are attributed to one child (De Lumley 1973:532).

Hortus II: Anterior mandibular corpus and associated teeth

Hortus III: Maxillary teeth

Hortus XX: Right clavicle

Hortus XXIII–XXVIII: Right manual phalanges

Hortus XLIII: Right proximal radial diaphysis

Hortus XLIV: Right proximal radial epiphysis

Age at death: 9 years (De Lumley 1972, 1973); 6.48–7.86 years (Ramirez-Rozzi 2005); 8.17 years (Shackelford et al. 2012:237).

Hortus IV

Remains: Mandible comprising left and right corpora and left ascending ramus, with incomplete dentition.

Age at death: ≥17 years (De Lumley 1972:382–383); adolescent (De Lumley 1973:375); 14 years (Wolpoff 1980a:300).

Observations:

The anterior alveolar area is damaged and part of the bone missing, as are the anterior teeth, but the basal part of the symphysis is intact. Photographs (De Lumley 1972:382–383; Wolpoff 1980a:301) show what appear to be the permanent right canine, PM1, M1 and M2 in place, with P4 missing, and on the left M1 and M2 in place. De Lumley attributes this specimen to a subject aged at least 17 years, and states that it has a retromolar gap (De Lumley 1972:384), although the third molars have not erupted. Wolpoff (1980a:300) in agreement with the photographs states that it has “an anterior position for the ramus relative to the teeth”. The photographs in the two cited publications indicate that the same mandible is under discussion.

Hortus, other immature remains

Remains:

Hortus XV: Maxillary fragment

Hortus XVII: Fragment of mandibular corpus

Hortus XXXIX: Distal femur

Hortus XL: Distal fibular epiphysis

Age at death: (M.A. De Lumley 1973)

Hortus XV: 3–4 years.

Hortus XVII: Neonate.

Hortus XXXIX: Neonate.

Hortus XL: 16–17 years.

Kalamakia

Remains: Isolated upper di1 and di2 and lumbar vertebra.

Provenance: Kalamakia cave, Mani Peninsula, Southern Greece, excavated 1998–2006.

Dating: 100–39 ka (Harvati et al. 2013).

Age at death: Deciduous incisors ~6 years, L3 or L4 vertebra 6–18 years (neural arch and body fused, epiphyses unfused) (Harvati et al. 2013).

Observations:

There are isolated permanent teeth and a cranial, possibly occipital, fragment.

Kebara aka KMH 1

Remains: fragmentary skeleton of an infant.

Provenance: Kebara Cave, Mount Carmel, Israel, excavated by M. Stekelis, 1965.

Dating: 48–64 ka (Bar-Yosef et al. 1992:532).

Age at death: 7–9 months (Tillier et al. 2003:36).

Observations:

KMH = Kebara Mousterian Hominid.

Tillier et al. (2003:58) make the case that KMH 1 was a deliberate burial and that the adult KMH 2 was the subject of secondary mortuary practice, in this case removal of the head after decay of cervical ligaments.

Kebara aka KMH 3, 4, 5, 7, 8, 12, 13, 14, 15, 16, 30

Remains (immatures only):

KMH 3: Upper right first deciduous molar

KMH 4: Upper and lower deciduous teeth and germ of one first permanent molar.

KMH 5: Fragment of mandibular symphysis missing dentition

KMH 7: Lower right deciduous incisor

KMH 8: Upper left deciduous lateral incisor

KMH 12: Upper right deciduous second molar

KMH 13: Upper left germ of deciduous first molar

KMH 14: Lower left permanent second molar

KMH 15: Upper right deciduous central incisor

KMH 16: Lower left deciduous central incisor

KMH 30: Upper deciduous first molar

Provenance: Kebara Cave, Mount Carmel, Israel: KMH 3–8, excavated by M. Stekelis, 1957–1965; KMH 12–30 excavated 1986–1987.

Dating: 48–64 ka (Bar-Yosef et al. 1992:532).

Age at death:

KMH 3: 8–10 years (Tillier et al. 2003:36).

KMH 4: 9–12 months (Tillier et al. 2003:36).

KMH 5: 2 years (Tillier et al. 2003:37).

Kiik-Koba 2

Remains: Infant humerus, ulna, radius, femur, fibula, tibia, left ilium, right scapula, isolated phalanges of fingers and toes, some vertebral centra and arches, and fragments of ribs.

Provenance: Layer IV, Kiik-Koba Cave, near Simferopol, Crimea, Ukraine, excavated by Bonch-Osmolovsky, 1924–1926.

Dating: 35–37 ka ¹⁴C cal. (Majkić et al. 2018).

Age at death: 5–7 months (Vlček 1973), 4–6 months (Trinkaus 2016).

Observations:

The carbon dating, calibrated from a raw date 32.3 ka as cited by Majkić et al. (2018), still seems late in relation to the revised dating of many European sites (Higham et al. (2014).

The infant skeleton was found close by that of an adult, Kiik-Koba 1. Each was reported by the excavator to have been buried in a pit, but the infant skull had been crushed to powder by overlying sediment (Vlček 1973).

Kozarnika

Remains: Two fragments of a single infant radial diaphysis.

Provenance: Layer 10b, Kozarnika Cave, Bashovishka Bara Valley, near Oreshets, Dimovo, Bulgaria, excavated 2003 and identified in 2013.

Dating: 128±13–183 14 ka by OSL, OIS6 (Tillier et al. 2017).

Age at death: <6 months (Tillier et al. 2017).

Krapina

Remains: This rock shelter site has yielded the single largest assemblage of Neanderthal skeletal and dental material, much of it subadult. Individual entries are listed below.

Provenance: Various levels, Hušnjakovo rock shelter, Krapina, Croatia, excavated by Gorjanović-Kramberger, 1899–1905.

Dating: Würm I–II (Minugh-Purvis 1988:337); 130±10 ka, OIS 5e/6 (Rink et al. 1995).

Observations:

Although Krapina 1 was previously thought to date from the last glacial, all the Krapina hominin remains are now dated to ~130 ka as above.

Owing to the preponderance of subadult remains and the prevalence of developmental anomalies attributable to sickness or undernutrition, Wolpoff (1980a:273) proposed that the Krapina cave was not the normal habitation of a complete mixed-age community but a place of safety where children were kept, while active adults used open-air sites as hunting camps.

Krapina Skull A aka Krapina 1

Remains: Partial calvaria, consisting of almost complete frontal, left temporal and parietal, partial right parietal; no facial bones, occiput or cranial base except the left petrous.

Provenance: Level 8.

Age at death: 6–8 years (De Lumley 1971, cited by Madre-Dupouy 1992; Minugh-Purvis et al. 2000; Rosas et al. 2013 SI).

Observations:

The partial Skull A, consisting then of the frontal and anterior parts of the left and right parietals, was described by Gorjanović-Kramberger (1906). Since 1981 the calvaria has been rendered more complete with further vault components identified in the Krapina collections (Minugh-Purvis et al. 2000; Cofran et al. 2021).

Krapina Skull B aka Krapina 2

Remains: Partial calvaria, consisting of nearly complete occipital, damaged at the margins of the foramen magnum, and two parietals.

Provenance: Level 4.

Age at death: 5–6 years (Trinkaus and LeMay 1982:71); juvenile (Minugh-Purvis 1988:339).

Krapina Skull F aka Parietal 2 + Temporal 28

Remains: Isolated parietal and temporal identified as belonging to the same individual.

Provenance: Level 3.

Age at death: 2 years (Minugh-Purvis 1988:341); younger than Krapina 1 (q.v.) (Minugh-Purvis et al. 2000).

Krapina Skull G aka Temporal 41 + unnumbered frontal + fragment

Remains: Isolated temporal, frontal and vault fragment belonging to the same individual.

Provenance: Level 4.

Age at death: 0.5–1.5 years (Minugh-Purvis 1988:342).

Krapina Frontal 3 aka Krapina 24

Remains: Isolated frontal bone.

Provenance: Level unknown.

Age at death: Younger than Krapina 1 (q.v.) (Minugh-Purvis et al. 2000).

Krapina Temporal 3 aka Krapina 39.2

Remains: Isolated temporal squama.

Provenance: Level unknown.

Age at death: 3.5–5.5 years (Minugh-Purvis 1988).

Krapina Temporal 4 aka Krapina 39.3

Remains: Isolated left temporal squama.

Provenance: Level unknown.

Age at death: 1–2.5 years (Minugh-Purvis 1988:345).

Observations:

The tympanic ring is fully formed. This temporal may belong to Skull F (Minugh-Purvis 1988:345).

Krapina Temporal 11 aka Krapina 38.4

Remains: Isolated right temporal.

Provenance: Level unknown.

Age at death: Juvenile (Minugh-Purvis 1988:346); if part of Skull A then 6–8 years (Minugh-Purvis et al. 2000).

Observations:

This temporal may belong to Skull A (Minugh-Purvis 1988:345).

Krapina Maxilla A aka Krapina 45

Remains: Fragment of left alveolar process with partial mixed dentition.

Provenance: Level unknown.

Age at death: 6–7 years (Minugh-Purvis 1988:346).

Krapina Maxilla B aka Krapina 46

Remains: Maxilla including complete palate, corner of nasal aperture, and small portion of zygomatic process, with almost full deciduous dentition and permanent M1s erupted.

Provenance: Level 7.

Age at death: 8 years (Wolpoff 1979:77); 6.5 years (Minugh-Purvis 1988:347); 5.9 years by dental microtomography (T.M. Smith et al. 2010:20925).

Krapina Maxilla C

Remains: Maxilla with alveolus and part of palate including margin of nasal aperture, with partial mixed dentition.

Provenance: Level 5.

Age at death: 10–10.5 years (Wolpoff 1979:80); 11.5–12 years (Minugh-Purvis 1988:348); age by dental microtomography attempted but not obtained (T.M. Smith et al. 2010:20925).

Krapina Maxilla D

Remains: Fragment of left inferior maxilla with partial dentition.

Provenance: Level 4.

Age at death: 14.5 years (Minugh-Purvis 1988:349).

Krapina Mandible A aka Krapina 51

Remains: Symphysis and partial left corpus with partial dentition.

Provenance: Level unknown.

Age at death: 6 years (Wolpoff 1979:77); 5–5.5 years (Minugh-Purvis 1988:350).

Krapina Mandible B aka Krapina 52

Remains: Partial symphysis with portions of left and right corpora, with partial dentition.

Provenance: Level 5.

Age at death: 8 years (Wolpoff 1979:77); 9.5 years (Minugh-Purvis 1988:350).

Observations:

This mandible may represent the same individual as Maxilla A (Wolpoff, cited by Minugh-Purvis 1988:350).

Krapina Mandible C aka Krapina 53

Remains: Mandibular symphysis, right corpus, and ramus lacking only condylar process, with partial dentition.

Provenance: Level 7.

Age at death: 11 years (Wolpoff 1979:78; Minugh-Purvis 1988:351).

Krapina Mandible D aka Krapina 54

Remains: Mandibular symphysis and right corpus with partial dentition.

Provenance: Level 5.

Age at death: 15–17 years (Wolpoff 1979:78–79).

Krapina Mandible E aka Krapina 55

Remains: Mandibular symphysis with left corpus and partial dentition.

Provenance: Level 5.

Age at death: 15–17 years (Wolpoff 1979:78–79; Minugh-Purvis 1988:352).

Kůlna

Remains: Partial right maxilla with canine, both premolars, and first molar.

Provenance: Kůlna Cave, Moravian Karst, Czech Republic, excavated 30 July 1965.

Dating: End of Würm I (Jelínek 2012:147).

Age at death: 14 years (Jelínek 2012:165).

Le Lazaret

Remains: Right parietal.

Provenance: Grotte du Lazaret, Mont-Boron, near Nice, France, excavated 1964 by Octobon.

Dating: Riss III (M.A. De Lumley 1973); MIS6, 190–120 ka (Michel et al. 2011).

Age at death: 8–9 years (M.A. De Lumley 1973:70; Tillier 1982).

Observations:

Two isolated teeth were also recovered at the site: an adult canine and a deciduous first incisor.

Lozoya

Remains: Six teeth and a mandible, all of which may belong to one infant.

Provenance: Des-Cubierto Cave, Calvero de la Higuera, Pinilla del Valle, Comunidad de Madrid, Spain; first excavated spring 2009.

Dating: 38–42 ka by ¹⁴C (Baquedano et al. 2017:41).

Age at death: female, 2.5 years (Baquedano et al. 2017:41).

Macassargues

Remains: (1) Lower second permanent molar, (2) proximal third of a right radius, epiphysis not fully fused, (3) distal humerus missing epiphysis.

Provenance: Grotte de la Verrerie, Macassargues, Montmirat, Gard, France, excavated 1947 by Gagnière and Hugues.

Dating: Mousterian levels, bed 5.

Age at death: (1) 13–15 years, (2) 10 years (Hugues et al. 1951:15); (2 and 3) 13–14 years (De Lumley 1973:559–562).

Malarnaud 1

Remains: Mandible with right first permanent molar in place; left M3 crown almost complete, in crypt.

Provenance: Grotte de Malarnaud, Ariège, France, excavated by Regnault and Bourret, 1888.

Dating: Mousterian level; MIS5–3b (Trinkaus 2018 SI:25).

Age at death: 11 years 2 months (Granat and Heim 2003:185–186), adolescent <14–15 years (Trinkaus 2018 SI:26).

Marillac 25

Remains: Immature diaphysis of right femur.

Provenance: Marillac (Les Pradelles), near Marillac-le-franc, Charente, France, excavated by Vandermeersch, 1967–1980.

Dating: Thermoluminescence dated to MIS 4, 57.6±4.6 ka (Garraalda et al. 2014:99).

Age at death: 9–10 years like Teshik-Tash (Garraalda et al. 2014:103).

Mezmaiskaya 1

Remains: Almost complete neonatal skeleton, well preserved.

Provenance: Mezmaiskaya Cave, Northern Caucasus, Russia; excavation 1993.

Dating: 29.195 ka, by ¹⁴C direct dating on hominin fossil rib (reported in Barriel and Tillier 2002 and Pinhasi et al. 2011:8612); 57–68 ka (suggested by Pinhasi et al. 2011:8613).

Age at death: Fetus ≥7 months or infant ≤2 months (Golovanova et al. 1999:81); not fetus (Barriel and Tillier 2002:166); neonate ≤2 weeks (Ponce de León et al. 2008:13765,SI:2).

Observations:

The skeleton was recovered in anatomical position in the lowermost Middle Palaeolithic layer at the site. As the Memaiskaya 2 individual (q.v.) from an upper level of the Middle Palaeolithic deposit has been directly dated at ~40 ka, Pinhasi et al. (2011:8613) argue that Mezmaiskaya 1 from the lowest layer cannot be as late as the ~29 ka previously reported; they attribute the late age to likely contamination of the carbon sample, and suggest that the ESR dating of the lower layers, 57–68 ka, should be adopted.

Mezmaiskaya 2

Remains: 24 cranial fragments.

Provenance: Mezmaiskaya Cave, Northern Caucasus, Russia; excavation 1993.

Dating: 39.65–42.62 ka, based on ESR late uptake and ultrafiltration carbon AMS direct dating on fossil hominin (Pinhasi et al. 2011).

Age at death: 1–2 years (Pinhasi et al. 2011:8612)

Observations:

The remains were recovered from a pit dug down from the uppermost Middle Palaeolithic layer at the site. Whereas the Mezmaiskaya 1 skeleton from the lowest level was previously dated to

29 ka, suggesting very late survival of Neanderthals in the Caucasus, Mezmaiskaya 2 as the stratigraphically later fossil is more likely to represent the latest surviving Neanderthal population in the area, which would therefore be unknown after ~40 ka.

Molare 1

Remains: Mandible with incomplete deciduous dentition, lacking left ramus and distal corpus and much of right ramus.

Provenance: Molare Shelter, Cilento Coast, Italy, excavated 1985.

Dating: OIS5 (Giacobini and Manzi 2005, cited by Tuniz et al. 2012:180)

Age at death: 2.5–3 years (Tuniz et al. 2012:180).

Observations:

Microtomography revealed nine unerupted permanent teeth in addition to the four erupted deciduous molars (Tuniz et al. 2012:180).

Montgaudier

Remains: Mandibular anterior corpus with left lateral incisor, canine and first molar.

Provenance: Grotte de Montgaudier, Montbrun, Charente, France, excavated by Duport, 1974.

Dating: Late Riss, unless the fossil slid down from the Abri Lartet above, in which case it would be later; end of the Middle Pleistocene or the beginning of the Upper Pleistocene (Mann and Vandermeersch 1997); 130 ka (Arnaud 2015:45).

Age at death: 12.5–14.5 years, female (Mann and Vandermeersch 1997).

Montmaurin Coupe-Gorge 3

Remains: Mandibular symphysis and isolated teeth.

Provenance: Grotte de Coupe-Gorge, Montmaurin, Haute-Garonne, France, excavated by Méroc, 1946–1961 (Billy 1985:223).

Dating: Würm I (Billy 1985:224); 125–150 ka (Riss) (Granat and Heim 2003:178).

Age at death: 4–5 years (Billy 1985:226); 3 years 10 months (Granat and Heim 2003:179, 186).

Montmaurin La Niche

Remains: Mandible with all six molars, rest of dentition absent.

Provenance: Grotte de La Niche, Montmaurin, Haute-Garonne, France, discovered by R. Cammas, 18 June 1949.

Dating: Riss-Würm or Mindel-Riss (Vallois 1956); MIS 7, 190–240 ka “last third of the Middle Pleistocene” (Violet et al. 2018).

Age at death: 18 years (Billy and Vallois 1977); 15 years 6 months (Granat and Heim 2003:185–186).

Moula-Guercy cranial and mandibular remains

Remains: Cranial and mandibular fragments and teeth of three immatures plus unassigned fragments and teeth.

1. Guercy 1: Conjoining fragments frontal M-D1-74, frontal and parietals M-G2-463, left parietal M-G1-98 + M-S-16 + M-I2-136 + M-I2-135 + M-S-9 + M-G2-69, right parietal M-G1-117 + M-G2-435 + M-S-9. A partial mandible M-G2-419 with all three molars can be associated with the cranial components.
2. Guercy 3: Partial right maxilla with dm2 and M1 and unerupted I2 and P4.
3. Occipital M-S-41 + M-S-61.

Provenance: Level XV, Baume Moula-Guercy, Soyons, Ardèche, France, excavated by Defleur and colleagues 1992–1998.

Dating: Eemian interglacial, 100–120 ka, MIS5e (Richards et al. 2021:202).

Age at death:

1. Guercy 1: 15–16 years, female (Defleur et al. 1999; Richards et al. 2021, 2024).
2. Guercy 3: 7.0 years (Richards et al. 2023:2487, age reduced from modern human standard by method of Granat and Heim 2003).
3. Occipital: 6–8 years (Richards et al. 2022a, 2022b).

Observations:

Cranial remains are assigned to Guercy 1–6 (Richards et al. 2021 SI:2). Guercy 2 is a young adult female, Guercy 4 comprised of cranial and mandibular fragments is a large adult male. Guercy 5 (~10–11.0 years) and Guercy 6 (~5 years) are dental individuals. Guercy 5 and 6 could correspond to postcranial Individuals 3 and 4 respectively, listed in the next entry (Richards et al. 2021 SI:35).

Moula-Guercy postcrania

Remains: Postcrania of two immatures.

Individual 3: anterior portion of axis, right clavicle missing ends, left ischium with acetabulum, right femur proximal diaphyseal fragment, right tibia anterior diaphyseal fragment.

Individual 4: left fibula diaphyseal fragment.

Provenance: Level XV, Baume Moula-Guercy, Soyons, Ardèche, France, excavated by Defleur and colleagues 1992–1998.

Dating: Eemian interglacial, 100–120 ka, or by biostratigraphy and thermoluminescence dating on an ash layer to 72 ka (Mersey et al. 2013).

Age at death: Individual 3: 10–12 years; Individual 4: 3–5 years (Mersey et al. 2013).

Observations:

Individuals 1 and 2 are adults. The later cited report (Mersey et al. 2013:531) explicitly supersedes previous descriptions by this team of researchers, e.g. Defleur et al. (1999). Further information is given by Richards et al. (2021 SI:2,35), who assign postcranial individuals 3 and 4 to Guercy 5 and 6 respectively.

Defleur et al. (1999) and Mersey et al. (2013) infer cannibalism at this site from comparative analysis of hominid and ungulate bone spatial distributions, modifications by stone tools, and skeletal part representations. The recourse to cannibalism is explained by lesser availability of prey biomass in the altered floral and faunal environment brought about by warm climate.

Le Moustier 1

Remains: Almost complete skeleton at time of discovery, including complete cranium with mandible and dentition. Postcrania currently extant are: fragment of first left rib; fragments of ilium and ischial ramus; incomplete right and left femoral diaphyses; incomplete left tibial diaphysis; fragment of right scapula; fragments of right humeral and ulnar diaphyses.

Provenance: Lower rock shelter at Le Moustier, Dordogne, France, excavated by Hauser, 10 April 1908.

Dating: 40–42 ka by ESR and thermoluminescence (Mellars and Grun 1991); 40–45 ka by carbon AMS (Higham et al. 2014).

Age at death: 15–16 years by dental development (Schuchhardt 1912:10); 13 years (Wolpoff 1980a:288); 16.5 years by dental formation (Minugh-Purvis 1988); 15.5 years by dental formation but 10.5 years by postcranial development (Thompson and Nelson 2005:218); 10–12 years from bone histology (Weaver et al. 2005:288); 11 years by “consensus of the skeletal growth age, the dental advancement hypothesis [more rapid dental eruption schedule in Neanderthals], as well as histomorphometric analysis” (Thompson and Nelson 2011:262–263); 11.86 (11.6–12.1) years by dental microtomography (T.M. Smith et al. 2010:20925).

Observations:

Shortly after excavation the remains were removed from France to Berlin. Before and during the Second World War; some elements were lost and others damaged (Ullrich 2005a; 2005b). While the skull escaped destruction, it has suffered damage and loss of substance in the course of several physical reconstructions made before the war (Ullrich 2005a:11). The last of these, by Weinert, was dismantled and the parts have remained isolated (Thompson et al. 2002:56). Two virtual reconstructions using computed tomography have been made, one by Thompson and Illerhaus (1998, 2005) and the other by Ponce de León and Zollikofer (1999, 2005). The incomplete postcrania were badly damaged by fire following bombing of Berlin in 1945, suffering shrinkage and distortion; and some parts previously recorded as present were not recovered from the débris (Ullrich 2005a:11; Thompson et al. 2002:58; Thompson and Nelson 2005b:265).

Some further bones besides those listed above are represented by casts, and a few others were reported by the discoverer Hauser and the anatomist Klaatsch in 1909. Original parts extant, the casts, and the rest are listed by Ullrich (2005b). Daumas et al. (2021) report that two further sets of casts from the early 20th century have recently been found in Belgium. Measurements of these match existing bones and casts held elsewhere. No additional parts are represented by these casts.

Ullrich (2005b, 2005c, 2005d) reviews and disputes the claims, made at the time of recovery, that Le Moustier 1 represented an intentional burial of the complete skull and postcrania, concluding that the skeleton was never seen complete when discovered. He offers an alternative explanation of the state of the remains: the individual died by violence and the bones were subject to defleshing and then intentional disposal of the skull and certain postcranial elements together under the rock shelter “according to customary rites”.

Le Moustier 2

Remains: Almost complete skeleton, missing scapulae and pubis.

Provenance: Lower rock shelter at Le Moustier, Dordogne, France, excavated by Peyrony, 1914.

Dating: MIS 3 (Maureille and Partiot 2019:157).

Age at death: neonate, <4 months (Maureille 2002).

Observations:

A lost right humerus and right femur have been restored to the Le Moustier 2 skeleton, rendering it almost complete. Maureille (2002) documents that when these remains were sent to Paris by the excavator, they were set aside and later wrongly identified as coming from La Ferrassie and numbered “La Ferrassie 4” (q.v.). They were believed to form part of a unique double burial of this child with La Ferrassie 4bis. Subsequently they were found to be encrusted with sediment identical to that from Le Moustier and identified as belonging to the neonate.

Obi-Rakhmat 1

Remains: Cranial fragments numbering 121, reconstructed to form parietals and temporals of a partial calvaria, preserving petrous parts including all inner-ear structures, and six isolated maxillary teeth, from a single subadult.

Provenance: Middle Palaeolithic context, Obi-Rakhmat Grotto, 100 km north of Tashkent, Uzbekistan.

Dating: 60–90 ka based on dates 70–100 ka by U-series and 57–73 ka by ESR linear uptake (Glantz et al. 2008).

Age at death: 9 years by modern human developmental standards, but more probably 8.1, maximum 8.8 years (T.M. Smith and Reid 2006); 9–12 years (Glantz et al. 2008:233); 6.0–8.1 years by dental microtomography (T.M. Smith et al. 2010:20925).

Okladnikov 2

Remains: Distal halves of an immature humerus and femur; loose teeth found in association.

Provenance: Okladnikov Cave, Soloneshensky District, Altai Krai, southern Siberia, Russia.

Dating: 37.75–43.7 ka, direct dating on teeth; 29.99–37.8 ka, direct dating on humerus: uncalibrated ¹⁴C (reported in Krause et al. 2007:902).

Age at death: Subadult (Krause et al. 2007:902); 8–10 years (Dobrovolskaya and Tiunov 2013:82).

Observations:

For many years the cave of Teshik-Tash (q.v.) in Uzbekistan was believed to be the eastern limit of the Neanderthal habitation range. Now that range is known to have extended to Okladnikov and Denisova in the Altai region of southern Siberia.

As well as the immature remains, there are an adult middle phalanx and a distal humerus, designated Okladnikov 1. Mitochondrial DNA did not distinguish these as Neanderthal, and the adult humerus was directly dated to 24 ka, considerably younger than the immature material (Krause et al. 2007:902).

Palomas 7, 49, 80, 88

Remains:

Palomas 7: Partial left mandibular corpus.

Palomas 49: Anterior left and right mandibular corpus.

Palomas 80: Left corpus and partial ramus.

Palomas 88: Small lateral fragment of corpus.

Provenance: Sima de las Palomas del Cabezo Gordo, south-eastern Spain, discovered ex situ in material discarded by 19th-century miners.

Dating: 40 ka or 50–60 ka, dates of two deposits bearing other Neanderthal remains (Walker et al. 2010:263); Late Middle Palaeolithic, MIS 3 (Trinkaus 2018).

Age at death: (Walker et al. 2010:262)

Palomas 7: 3.5–4.5 years.

Palomas 49: 1.5–2.5 years.

Palomas 80: 11–12 years.

Palomas 88: 2–3 years.

Palomas 97

Remains: Partial skeleton

Provenance: Sima de las Palomas del Cabezo Gordo, south-eastern Spain, excavated from Conglomerate A deposit, 2008.

Dating: 50–60 ka (Walker et al. 2011a:10087).

Age at death: Juvenile or child (Walker et al. 2012:15).

Observations:

Palomas 97 was found underlying the young adult female skeleton Palomas 96, which is the most complete individual, and alongside another adult skeleton Palomas 92. Since all three are articulated, it is suggested that these individuals were intentionally deposited, though not literally buried, in the cave (Walker et al. 2012). As the specimens are encrusted with a marble breccia, it is taking years in the laboratory to extract them from the matrix (Trinkaus and Walker 2017).

The Palomas individuals are said to be small by more northern Neanderthal standards (Walker et al. 2011b; 2012), a condition in line with previous suggestions of a gracile southern or Mediterranean population, e.g. at Fate in Italy (q.v.).

Payre

Remains: Isolated teeth and a fragment of left parietal.

Level Gb: Payre 731: LRI1 or I2

Level Gb: (a) Payre 6, 250, 237: LLM1 or M2, LRI1, LRI2

Level Ga: (b) Payre 254, 127, 344, 654, 633: LRP3, LLP4, LLP1, ULM1 or M2, LRC

Level Ga: (c) Payre 335: fragment of left parietal reaching asterion

Level F: (d) Payre 717, 482: URP3, URC

Level F: Payre 336: LRM1

Level E: Payre 29: LLP4

(a), (b), (c), (d) are assigned to individuals; (b) teeth and (c) parietal may be the same individual.

Provenance: Entrance to collapsed cave on terrace above Payre river, off Rhone Valley, near Valence, south-eastern France; excavated 1994–2002.

Dating: Dates by ESR and U/Th (Moncel and Condemi 2007)

Levels Gb, Ga, F: MIS 7 (243–191 ka).

Levels E, D: MIS 5 (130–71 ka).

Age at death: (Moncel and Condemi 2007)

(a) Child aged 7 years.

(b) Child aged 12 years.

(c) Young individual.

(d) Young child.

Observations:

The Payre 15 partial mandible discovered in 2010 is adult (Verna et al. 2020)..

Pech de l’Azé

Remains: Almost complete cranium and mandible. No postcrania.

Provenance: Pech de l’Azé, Carsac-Aillac, Dordogne, France; excavated by Peyrony, 1909.

Dating: MIS 3 (Maureille and Soressi 2000); 43–51 ka (Soressi et al. 2007).

Age at death: less than 2.5 years (Patte 1957); 2 years (Vlček 1970; Tillier 1996); 1.5 years (Granat and Heim 2003); 1.51 years (Shackelford et al. 2012:237).

Observations:

Maureille and Soressi (2000) reassign this specimen to an upper layer of the site and suggest that it may be one of the most recent Neanderthals in France.

Petit-Puymoyen 1 and 2

Remains:

Petit-Puymoyen 1: Symphysis and left mandibular corpus with dentition.

Petit-Puymoyen 2: Left maxillary fragment with some dentition and loose maxillary teeth.

Provenance: Rock shelter at Petit-Puymoyen, Charente, France, excavated by Favraud, 1907.

Dating: OIS 3 (Arnaud 2015:45).

Age at death: Adolescent (Tillier and Genet-Varcin 1984); 14 years 4 months (Granat and Heim 2003:186); 9–14 years (Quam et al. 2011:96).

Observations:

Quam et al. (2011:100) assign to the same individual the maxilla and teeth comprised in Petit-Puymoyen 2 and the Petit-Puymoyen 1 mandible, because of similar wear status.

Petit-Puymoyen 3 and 4

Remains:

Petit-Puymoyen 3: Symphysis and partial right mandibular corpus with dentition, lower half of corpus mostly missing.

Petit-Puymoyen 4: Isolated right molars M2 and M3.

Provenance: Rock shelter at Petit-Puymoyen, Charente, France, excavated by Favraud, 1907.

Dating: OIS 3 like Petit-Puymoyen 1?

Age at death: Adolescent?

Observations:

Quam et al. (2011:100) associate the loose molar teeth comprised in Petit-Puymoyen 4 with the mandible Petit-Puymoyen 3, following Siffre (1908). M2 is in occlusion. The apex is open on the M3 distal root. The right P3 has a distal root with one tip and a mesial root with two root tips, a primitive condition rarely found in *Homo* (Quam et al. 2011:99).

Petit-Puymoyen 5

Remains: Temporal bone.

Provenance: Cave at Petit-Puymoyen, Charente, France; identified by Boeuf (1969), among faunal remains recovered from the interior (not the rock shelter).

Dating: Würm II or earlier (Elyaqine 1997).

Age at death: 2–4 years (Elyaqine 1997).

Petit-Puymoyen 7

Remains: Partial occipital squama including lambda and medial portions of the lambdatic suture.

Provenance: Cave at Petit-Puymoyen, Charente, France; identified by Boeuf (1969), among faunal remains recovered from the interior (not the rock shelter).

Dating: OIS 3 like Petit-Puymoyen 1?

Age at death: Late adolescent/young adult (Quam et al. 2011).

Observations:

This fragment was referenced in archives in 1975 but is first described by Quam et al. (2011), who assign the specimen number 7. It is small but relatively thick.

La Quina H18

Remains: Almost complete cranium. Missing mandible. No associated postcrania.

Provenance: La Quina rock shelter, near Les Gardes de Pontaroux, Charente, France, excavated by Henri-Martin, 1915.

Dating: 45–60 ka (quoted by T.M. Smith et al. 2010:20925)

Age at death: 8 years by Henri-Martin (MacCurdy 1922) or 5 years by P. Legoux (Henri-Martin and Legoux both cited in Piveteau 1965); 7 years (quoted as “previous age” by T.M. Smith et al. 2010:20925); 5 years (Granat and Heim 2003:186); 5.5 years (Shackelford et al. 2015:237).

Roc de Marsal

Remains: Almost complete infant skeleton: neurocranium with facial skeleton and mandible, postcrania including vertebrae and fragmentary pelvis, ribs, scapulae, clavicles, humeri, radii, ulnae, metacarpals, phalanges, femur, tibia, fibula, metatarsals.

Provenance: Roc de Marsal Cave, Campagne-du-Bugue, near Les Eyzies-de-Tayac, Dordogne, France, excavated by Lafille, 15 August 1961.

Dating: OIS4, 60–70 ka by TL and OSL on quartz and flint (Guerin et al. 2012), previously dated OIS5e (Bayle et al. 2005:67).

Age at death: 2.5–3 years by dental development (Legoux 1965, cited by Madre-Dupouy (1992:17); 2.5–4 years (Madre-Dupouy 1992:267)); 2 years 5 months (Granat and Heim 2003:186); 2.5–3 years by dental development (Bayle et al. 2009); ~2.3 years (Shackelford et al. 2015:237).

Observations:

Additional fragments of the right clavicle, right radius and a manual phalanx were identified in the museum collection in 2019, along with some other small fragments which possibly belong to this individual (Gómez-Olivencia and García-Martínez 2019).

Turq (1989) describes the excavation and states that sedimentological data neither confirm nor disprove intentional burial. Gómez-Olivencia and García-Martínez (2019:167–168) discuss this question in the light of other recent studies, the additional material, and new work at the site, leaving it unresolved.

Les Rois Mandible B

Remains: Partial right mandibular corpus bearing first and second premolars, with loose canine and second incisor.

Provenance: Unit A2, Aurignacian layer, Les Rois cave, south of Mouthier-sur-Boëme, Charente, France, excavated by Mouton and Joffroy 1948–1952.

Dating: 28–30 ka (Ramirez-Rozzi et al. 2009).

Age at death: Juvenile, 11 years (Vallois 1958:143,155).

Observations:

Also from Unit A2, the fragmentary Mandible A (10–11 years, Vallois 1958:141), was recovered, along with other loose teeth belonging to up to four other individuals besides the

mandibles. According to Vallois (1958), both mandibles have primitive features. Mandible A is said to be anatomically modern human, while Mandible B is identified as Neanderthal from the configuration of the tooth row, dental dimensions and perikymata packing pattern (Ramirez-Rozzi et al. 2009). Mandible B bears cut marks characteristic of defleshing (Vallois 1958:141; Ramirez-Rozzi et al. 2009:170–172), which the latter authors attribute to cannibalism with possible ritual use of the Neanderthal juvenile by modern humans.

Sarstedt I, II, III

Remains:

Sarstedt I: Almost complete temporal bone

Sarstedt II: Occipital fragment

Sarstedt III: Left parietal fragment

Provenance: Surface finds from gravel pits, Leine Valley, Sarstedt, Hildesheim, Germany, on 2 January and 30 October 1999.

Dating: Sarstedt I: >58 ka, possibly >115 ka (Czarnetski et al. 2001); 25–117 ka (Street et al. 2006:559).

Age at death: Sarstedt I: 2–4 years, female (Czarnetski et al. 2001).

Observations:

It is not stated whether the three bones belong to the same individual.

Scladina aka Sclayn

Remains: Right maxilla, right and left hemi-mandibles, missing left ramus, with dentition, some elements in place, others found isolated: upper right dm1, dm2, I1, I2, C, M1 and M2; upper left I2 and C; lower right I2 and C; lower left M3.

Provenance: Scladina Cave, Sclayn, Belgium; excavated 1993.

Dating: 70–75 ka (Otte et al. 1993); 127+46/-32 ka by gamma-ray spectrometry directly on mandible (Toussaint et al. 1998; Toussaint and Pirson 2006); 95–105 ka (Toussaint et al. 2004:38); 80–127 ka (quoted by T.M. Smith et al. 2007b:20220).

Age at death: 10–11 years (Otte et al. 1993); 10 years (Toussaint et al. 1998; 2004:27); 8.5–12 years (Toussaint and Pirson 2006:382–383); 8.0 years by dental microtomography (T.M. Smith et al. 2007b; T.M. Smith et al. 2010:20925). Female by DNA analysis (Peyrégne et al. 2019).

Observations:

The M2s are almost level with the M1s in occlusion, which would indicate an age of ≥ 12 years, but the deciduous molars are still in place, which would suggest ≤ 10 years (Toussaint et al. 1998:740; Toussaint and Pirson 2006:382–383).

There is some ambiguity in reports of the dental elements present, as follows.

- Otte et al. (1993:329) state that the right maxilla as recovered contained only the URP4 in its socket and the other permanent teeth had fallen out. In the hemi-mandible the LRM1 and LRM2 (erupted) and LRP4 and LRM3 (unerupted) remained, while the LRC, LRP3 and LRdm2 had fallen out (but therefore had erupted).

- Toussaint et al. (1998:740) give this inventory: a fragment of maxilla, a right hemi-mandible, a mandibular symphysis and left corpus; and teeth: URdm1, URdm2, URM1, URM2, LRP3, LM3. They state that the URM1 and URdm1 and URdm2 insert perfectly into the alveoli of the right maxilla; the URM1 and URdm2 articulate perfectly with the LRM1, which remained in the mandible; the URM2 fits harmoniously behind the URM1, and the LRP3 fits into the corresponding alveolus of the right hemi-mandible. This seems to imply that the teeth in occlusion included the *URdm1*, *URdm2*, URM1, *LRP3*, LRM1 and LRM2, the last two having remained secure in the mandible. So the maxilla had the two deciduous molars retained but the mandible had at least the first permanent premolar emerged.
- Toussaint et al. (2004:38) present a photograph showing what appear to be URdm1, URdm2, URM1, URM2, LLM1 erupted, and LLM2 erupting.
- The inventory given by Semal et al. (2005:35) lists a right maxilla, right hemi-mandible and left hemi-mandible; and the teeth listed are: URI1, URI2, URC, URdm1, URdm2, URM1, URM2, ULI2, ULC, LRI2, LRC, LLM3.
- Toussaint and Pirson (2006:383) refer to persistence of the deciduous molars. They present a CT scan slice of the right hemi-mandible in their Figure 2b (2006:374) which shows a bicuspid crown with no more than ½ root formed in its crypt immediately mesial to the erupted M1. No deciduous tooth appears above it. As a slice it may not have captured a tooth out of the slice alignment.
- The teeth analysed by T.M. Smith et al. (2010 SI:26) are listed (without siding) as UI2, UC, UP4, UM2, UM3, LI1, LC, LP3, LP4, LM1, LM2, LM3, i.e. only permanent.
- At some point¹ the maxilla and mandible were restored with a full set of teeth which fit in the sockets. The permanent teeth emerged appear to be URI1, URI2, URC, URdm1, URdm2 and URM1, with URM2 at alveolar eruption; LLI2, LLP3, LLP4, LRI1, LRI2, LRC, LRP3, LRdm2 and LRM1, with LRM2 at partial eruption, i.e. beyond gingival emergence. This interpretation avoids conflict with the 1993 description, by which the upper P4 was unerupted and the dm2 had fallen out, and with the 2005 inventory, in which there is no mention of upper P3 or P4 but rather deciduous molars. The URM2 seems to have been glued onto the end of the broken alveolar bone.

Sesselfels 1

Remains: Partial fetal skeleton: left frontal squama, left mandibular corpus, one thoracic vertebra, with further postcrania, all right side: ribs 1, 2, 4 and two lower ribs, diaphysis and distal humerus, diaphysis and proximal ulna, diaphysis and proximal femur, fibular diaphysis.

Provenance: Sesselfelsgrötte rock shelter, lower valley of Altmühl river, Bavaria, Germany, excavated 1964–1977 by Institut für Ur- und Frühgeschichte der Universität Erlangen-Nürnberg.

Dating: Mousterian layer G5, 48 ka (Rots 2009:38; Rathgeber 2006); 57–47 ka (Street et al. 2006:560).

Age at death: Fetus at term (Rathgeber 2006; Rots 2009); fetus or neonate (Street et al. 2006:559).

Observations:

Humerus and femur resemble neonate Le Moustier 2 but appear less developed (Rathgeber 2006).

¹ Photographs dated 2016: <https://www.scladina.be/> retrieved 2024.11.02.

Shanidar 7

Remains: Cranial vault fragments, 15 deciduous teeth and 1 permanent M1, some postcranial fragments.

Provenance: Shanidar Cave, Kurdistan, Iraq, excavated by R. Solecki, 1953.

Dating: .70 ka (Stewart 1977:122); 60–70 ka (Pomeroy et al. 2020:22).

Age at death: ≤9 months, female (Şenyürek 1957a:50); 0.75 year (Stringer and Trinkaus 1981:130).

Observations:

This specimen was first denoted by “Infant” without a number. The dentition is described by Şenyürek (1957a, 1957b).

Shanidar 9

Remains: Infant vertebrae.

Provenance: Shanidar Cave, Kurdistan, Iraq, excavated by R. Solecki, 1960.

Dating: .70 ka (Stewart 1977:122); 60–70 ka (Pomeroy et al. 2020:22).

Age at death: 1.0 year (Stringer and Trinkaus 1981:130).

Shanidar 10

Remains: Distal tibia, fibula, first metatarsal, and two tarsals.

Provenance: Shanidar Cave, Kurdistan, Iraq, excavated by R. Solecki, 1957 (1953, Pomeroy 2025, pers. comm.), identified among faunal collection by M.A. Zeder, 2006.

Dating: .OIS4–6 (Cowgill et al. 2007).

Age at death: 1–2 years (Cowgill et al. 2007).

Observations:

The level from which the stored remains were excavated is 1 metre below the oldest of the previous specimens (Shanidar 9), hence the early date.

Shukbah

Remains: Zygomatic root and a temporal fragment.

Provenance: Shukbah Cave, Wadi en-Nauf, near Jerusalem, excavated by D. Garrod, beginning 1928 (Buck and Stringer 2015:327).

Dating: Level D (Mousterian).

Age at death: Immature.

Observations:

Other remains in Level D are believed to be intrusive from the overlying Natufian Level B (Buck and Stringer 2015:327).

El Sidrón

Remains: This karstic cave has yielded Neanderthal remains of all ages from infant to adult. Individuals are listed below.

Provenance: El Sidrón, Asturias, Spain.

Dating: 49 ka (Rosas et al. 2007).

El Sidrón Adolescent 1

Remains: Small maxillary fragment (SD-917) and 13 teeth (upper left C, P3, P4, M1, right C, P4, M1; lower left M1, right I1, I2, P3, P4, M2).

Age at death: Adolescent male 11–12 years (Rosas et al. 2013:285).

El Sidrón Adolescent 2

Remains: Small mandibular fragment (SD-1510) and small maxillary fragment (SD-331a, SD-331b) and 20 teeth (upper left I1, P4, M1, M2, M3, right I1, I2, P3, P4, M1, M2, M3; lower left P3, M1, M2, M3, right I2, C, M1, M3).

Age at death: Adolescent (Rosas et al. 2013:285).

El Sidrón Adolescent 3

Remains: Fragment (SD-912) of left mandibular alveolar bone containing the left P3 with vacant socket for the P4, and isolated teeth (upper left I1, I2, C, P3, P4 and crowns of M2 and M3, lower right P4 and left P4).

Age at death: Adolescent (Dean et al. 2013); male 12–13 years (Rosas et al. 2013:285).

El Sidrón Infant 1

Remains: Distal fragment of right tibia, right hallux and fifth metatarsal.

Age at death: 1.5–3 years by skeletal development (Rosas et al. 2013:285,289).

El Sidrón Juvenile 1 (J1)

Remains: Partial skeleton including cranio-dental and postcranial elements.

Age at death: male, 6 years by dental development (Rosas et al. 2012); 7.5 years (Rosas et al. 2013:289); 7.7 (7.61–7.78) years by dental microtomography (Rosas et al. 2017).

Observations:

The mandible of this juvenile, missing the left condyle, is SD-1660 (Rosas et al. 2012).

El Sidrón Juvenile 2

Remains: Ulna, radius and right fifth metacarpal.

Age at death: 9–10 years by skeletal development (Rosas et al. 2013:285, 289).

El Sidrón SD-2300

Remains: Occipital with attached fragment of left parietal.

Age at death: 7.7 years (García-Tabernero et al. 2018:39).

Šipka

Remains: Anterior mandibular corpus with dentition.

Provenance: Šipka Cave near Štramberk, Moravia, Czech Republic, excavated by Maška, 26 August 1880.

Dating: Interstadial within Würm glacial (T.M. Smith et al. 2015:63).

Age at death: 9–10 years (Vlček 1996:52); 8–10 years (T.M. Smith et al. 2015:63).

Observations:

The partial mandible was recovered in one piece with erupted and unerupted teeth in place. The specimen was lost at the end of the Second World War (Vlček 1958).

Spy III aka 26C

Remains: Immature tibial diaphysis.

Provenance: Bèche-aux-Roches Cave, Spy, Jemeppe-sur-Sambre, Belgium; excavated by Twiesselman 1952–1954.

Dating: 44200–40600 ka (Devièse et al. 2021: see under Spy VI below).

Age at death: 5.5–7.5 years (Cowgill 2014).

Observations:

Two teeth were at first assigned to Spy III, but according to Rougier et al. (2004:183,185–186) they cannot be attributed to a child. Cowgill (2014) assesses the tibia as modern and most probably an intrusion from an overlying Neolithic deposit. If so, there is no Neanderthal subadult individual Spy III.

Spy VI

Remains: Left and right fragments of mandibular corpus with teeth Udi1, Ldi1, Ldi2, Ldc.

Provenance: Bèche-aux-Roches Cave, Spy, Jemeppe-sur-Sambre, Belgium; excavated by Twiesselman 1952–1954; remains recovered 2004–2006 from stored assemblage.

Dating: 36.87–41.07 ka Cal ¹⁴C directly dated on dentine (Crevecoeur et al. 2010); 44.2–40.6 ka (Devièse et al. 2021).

Age at death: 1.5 years (Crevecoeur et al. 2010).

Observations:

Dates are close to the ~36 ka determined (Semal et al. 2009) by direct dating on the adult remains Spy I and Spy II discovered in 1886. However, Devièse et al. (2021) argue that late dates have likely been produced by contamination from collagen in bovid-based glue on the specimens. They have obtained new dates from seven other uncontaminated elements (bones and teeth) in the Spy collection, and make the case that Neanderthals at the site date no later than 44.2–40.6 ka.

Subalyuk 2

Remains: Partial neurocranium consisting of frontal, partial sphenoid, temporals, parietals and occipital, basicranium incomplete; maxillae with palate and left nasal bone; maxillary dentition consisting of both right deciduous incisors, both deciduous canines and all four upper deciduous molars, with an isolated deciduous second molar; also four vertebral centra, two cervical and two thoracic.

Provenance: Subalyuk Cave, near Cserépfal, Hungary, excavated by Kadic, 1932.

Dating: Late Mousterian, early Würm (Thoma 1963).

Age at death: 3–4 years, female (Thoma 1963); 3 years (Tillier 1988); 3–4 years (Vlček 1996:56); 3 years (Pap et al. 1996).

Observations:

The immature remains were discovered along with many parts of an adult skeleton Subalyuk 1 (Szabo 1935). Dentally, Subalyuk 2 is at the same stage as Engis 2.

Teshik-Tash

Remains: Almost complete cranium and mandible; postcrania including cervical, thoracic and lumbar vertebral fragments, left and right clavicles, complete and fragmentary ribs, left humeral diaphysis, pelvic fragments, diaphyses of right femur and tibia, and fragmentary fibular diaphysis: altogether comprising 150 pieces.

Provenance: Teshik-Tash Cave, near Baisun, south of Samarkand, Uzbekistan, excavated by Okladnikov, 24 July 1938.

Dating: Early Würm by faunal analysis (Movius 1953, cited by Glantz et al. 2009); “late interpleniglacial”, i.e. 24–57 ka (Vishnyatsky 1999, cited by Glantz et al. 2009); 24–57 ka (Arnaud 2015:45).

Age at death: 8–10 years, male¹ (Gremyatskii 1949); 9 years (Ullrich 1958; Coqueugniot et al. 1996); 7 years 6 months (Granat and Heim 2003:186).

Vindija Vi-224 and Vi-229

Remains: frontal bones only, of two individuals.

Provenance: Vindija Cave, Croatia.

Dating: 29–42 ka, possibly >42 ka (Wild et al. 2001).

Age at death: Adolescent, approximately same age as Le Moustier 1 (Ahern and Smith 2005), i.e. 11.61–12.11 years (T.M. Smith et al. 2010).

Observations:

Two other Neanderthal bones Vi-207 and Vi-208 from this site were directly dated to 28–29 ka, apparently indicating late survival of Neanderthals in a Croatian refugium during glacial conditions (F.H. Smith et al. 1999). Subsequently, the same bones were directly dated to 32.4

¹ Uzbekistan tourist websites state that Teshik-Tash was thought to be male but is female. However, I have not found any academic publication giving this conclusion. One book chapter cites Krause et al. 2007, which does not suggest anywhere that the subject is female. The large and robust dimensions of the skull, including the high cranial capacity of 1490 cm³, have from the 1940s onward been taken to indicate that Teshik-Tash is male.

ka (Higham et al. 2005). More recently a sample of six bones, again including Vi-207 and Vi-208 (but not including the Vi-224 and Vi-229 immature mandibles), have been directly dated by AMS ^{14}C using further filtration techniques, this time yielding dates 42.7–46.2 ka, which are believed to be more accurate (Devièse et al. 2017). The hypothesis of late survival at this site is no longer readily sustainable.

Zaskalnaya VI Mandible Zsk VI-72

Remains: Partial mandible with three teeth in place, including two dm2s, and fourteen isolated teeth.

Provenance: Layer III, at Zaskalnaya VI (aka Kolosovskaya), a collapsed rock shelter, near Vishennoye, Belogorsk District, in the Krasnaya gully, right bank of the Biyuk-Karasu river, Crimea, excavated 1972.

Dating: 38.1–42.9ka by ^{14}C cal. (Majkić et al. 2017:7–8).

Age at death: 10–12 years (Majkić et al. 2017:8; Stepanchuk et al. 2017:142).

Zaskalnaya VI Mandible Zsk VI-78

Remains: Fragment of right mandible with 3 permanent teeth in place.

Provenance: Layer III, at Zaskalnaya VI (aka Kolosovskaya), a collapsed rock shelter, near Vishennoye, Belogorsk District, in the Krasnaya gully, right bank of the Biyuk-Karasu river, Crimea, excavated 1978.

Dating: 38.1–42.9ka by ^{14}C cal. (Majkić et al. 2017:7–8).

Age at death: 14–15 years (Majkić et al. 2017:8; Stepanchuk et al. 2017:142).

Zaskalnaya VI Other immature remains (postcrania)

Remains: This site has yielded a large quantity of isolated and fragmentary immature remains, besides the mandibles Zsk VI-72 and Zsk VI-78 listed above.

Item	Age at death, years (Stepanchuk et al. 2017:142)
1. Hand phalanx, medial	14–15
2. Hand phalanges, proximal	14–15
3. Right hand phalanx, carpal, metacarpal	2–3
4. Right tibia	1
5. Thoracic vertebral centrum	1–4
6. Lumbar vertebra	2–4
7. Vertebral arch	2–3
8. Thoracic vertebral arch	1–5
9. Fragments of vertebral arches	1–5
10. Lumbar vertebra	1–5
11. Lower sacral vertebrae	1–5
12. Talus	1
13. Calcaneus	1
14. Foot phalanges, distal	1
15. Foot phalanges, distal	2–3
16. Metatarsal, talus, tarsus, capitata	2–3

17. Hand phalanges, distal	5–6
18. Hand phalanges, proximal	2
19. Hand phalanges, medial and distal	14–15
20. Ribs	1
21. Ischial, iliac, pubic fragments	1
22. Ischial fragment	2–3
23. Right radius	1–2
24. Right clavicle	1.5–2
25. Left? Clavicle	2–3
26. Left femur	2–3
27. Right femur	2–3
28. Left humerus	5–12
29. Right tibia	2–3
30. Vertebra	?
31. Radius	?
32. Right humerus	<1

Provenance: Layers II, III, IIIa, at Zaskalnaya VI (aka Kolosovskaya), a collapsed rock shelter, near Vishennoye, Belogorsk District, in the Krasnaya gully, right bank of the Biyuk-Karasu river, Crimea, excavated 1972 (Items 1–2 above), 1973 (Items 3–27), 1978 (Items 28–31), 2005 (Item 32).

Dating: Layer II: 33.0–36.0 ka, Layer III: 38.1–42.9 ka, Layer IIIa: 33.6–46.5 ka, by ^{14}C cal. (Majkić et al. 2017:8).

Age at death: See above under **Remains**.

APPENDIX B

PHYLOGENY AND MORPHOLOGY

B.1 Introduction

Over the last hundred years Neanderthals have been classified as either *Homo neanderthalensis*, a separate species, or as *Homo sapiens neanderthalensis*, a subspecies, in which case modern humans become *Homo sapiens sapiens*. Most commonly, at the time of writing, they are treated as a separate species. Here usual current practice is followed, so the term “*Homo sapiens*” is used to refer only to anatomically modern humans, whether recent or fossil. Figure B.1 illustrates species, major sites, geography and timescale.

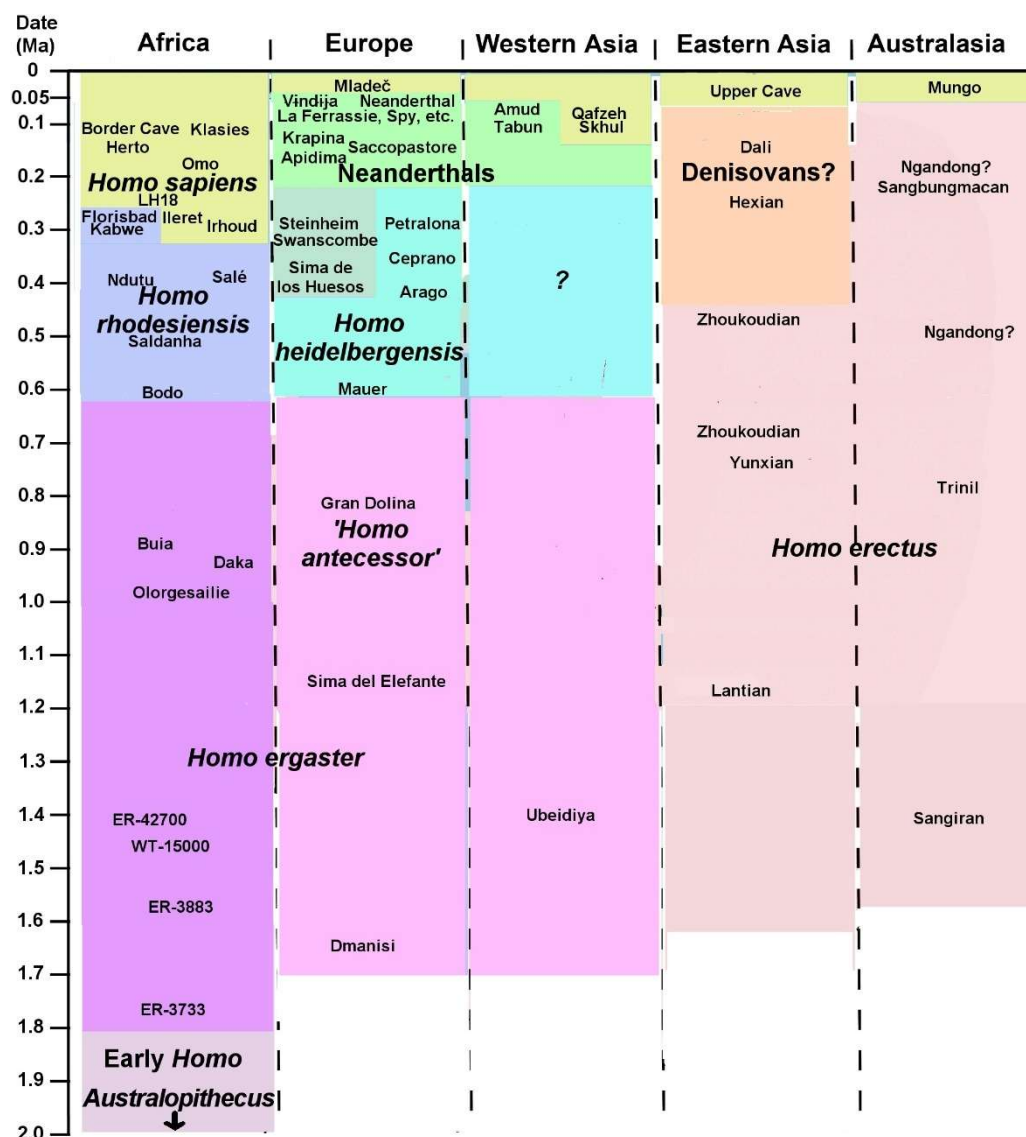


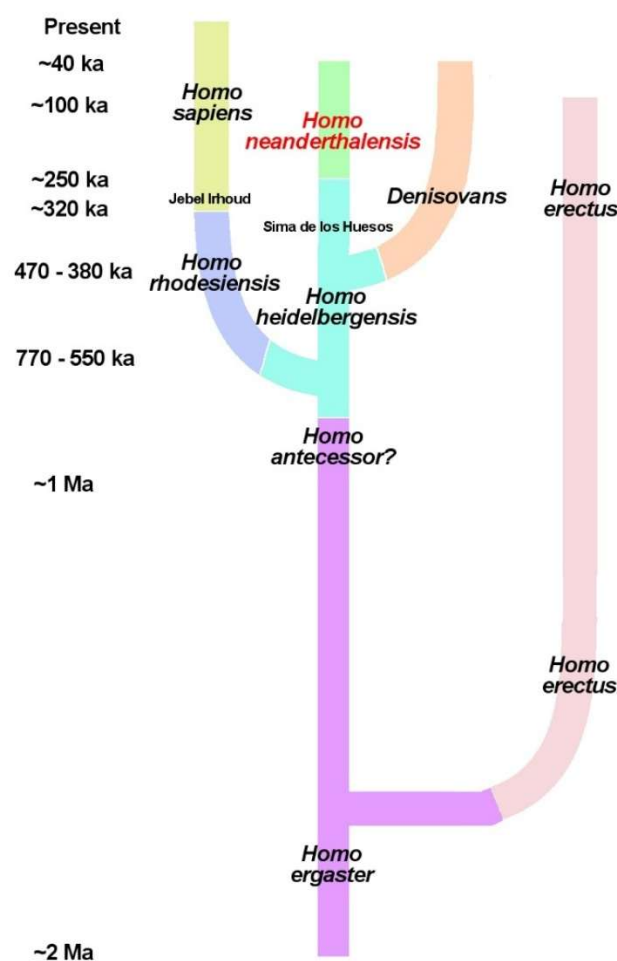
Figure based upon Figure 21 in Bräuer et al. (2020:1389).

Figure B.1: Species and populations of *Homo* by geography and date

B.2 Phylogeny

In the Upper Pleistocene for a duration of ~500,000 years until only ~40 ka the two lineages ending in *Homo sapiens* and Neanderthals were contemporaries in different parts of the world. Modern humans are thought to have evolved in south, east and north-west regions of Africa (Hublin et al. 2017), and to have made excursions out of East Africa into South West Asia several times beginning by ~130 ka (Bae et al. 2017; Zaidner et al. 2025). Neanderthals occupied Europe and parts of Western and Central Asia; their maximum eastward extent was the Altai region north of Tibet. Eastward from there, contemporaries of Neanderthals, named Denisovans from the Altai cave where remains were first found, occupied East Asia.

Populations of *Homo* by date and geography since ~2 Ma are indicated in Figure B.1, and an outline evolutionary tree of *Homo* species is presented in Figure B.2. As the purpose of this appendix is only to place Neanderthals in context, these figures do not attempt to express the complexity of morphs, lineages and interbreeding as currently understood.



Dates of separation of *Homo sapiens*, Neanderthal and Denisovan lineages from Reich (2018:55).

Figure B.2: *Homo* species since ~2 Ma

The three parallel species *Homo sapiens*, Neanderthals and Denisovans, are presumably descended from Middle Pleistocene hominins dating from 700–500 ka and exemplified by fossils from Africa and western Eurasia, which are typically more robust skeletally and smaller-brained, but with endocranial volumes still within modern human range. These are referred to as *Homo heidelbergensis sensu lato (s.l.)*. The type specimen is the Mauer mandible. Other European examples include Ceprano, Petralona and Arago. *Homo heidelbergensis s.l.* is widely regarded as the stem group for Neanderthals and *Homo sapiens* (Stringer 2012).

African representatives, among which are expected to be the ancestors of modern humans, are sometimes distinguished as *Homo rhodesiensis*, leaving the European group to be *Homo heidelbergensis sensu stricto (s.s.)*, as discussed by Rightmire (2008). The very robust Kabwe (Broken Hill) skull, which is the type specimen of *Homo rhodesiensis*, has recently been dated to ~299 ka (Grün et al. 2020). This is later than the ~315 ka date of the less archaic Jebel Irhoud hominins, which are claimed to be the earliest *Homo sapiens* (Hublin et al. 2017). If the dating is correct then it appears that at least two lineages, including one more robust and one less so, coexisted in Africa during the period when *Homo sapiens* was emerging, and possibly more than one lineage contributed to producing the more clearly sapient later (160–195 ka) hominins such as Herto and Omo (Grün et al. 2020).

Among the European Middle Pleistocene groups, the hominins recovered from Sima de los Huesos (~430 ka) at Atapuerca exhibit incipient Neanderthal features contributing to midfacial projection which are not found in other contemporary European or African specimens. The proposal on the basis of morphology that they are direct ancestors of the Neanderthals (Rosas 2001; Arsuaga et al. 2014) is confirmed by similarities of nuclear DNA (Meyer et al. 2016). An early (172±15 – 130.1±1.9 ka) Neanderthal cranium from Altamura retains certain features of the Sima hominins (Profico et al. 2023).

Some authors would exclude the Sima de los Huesos population from *Homo heidelbergensis (s.s.)* (Arsuaga et al. 2014:1362). Some define the African hominins as *Homo rhodesiensis*; others include all in *Homo heidelbergensis* (discussed by White et al. 2022). Tattersall (2005:207) would place the Sima group in a clade with *Homo neanderthalensis*, while Rightmire (2008:19–20) notes that the Sima hominins share some characteristics with Petralona and thus with *Homo heidelbergensis* generally.

In East Asia, particularly China, hominin remains contemporary with *Homo heidelbergensis* and later with Neanderthals have been found which share many *heidelbergensis* features but have characteristics of their own. They have often been referred to as Archaic *Homo sapiens*. This designation is problematic if true *Homo sapiens*, i.e. the ancestors of living humans, originated in Africa and spread to East Asia only some time after ~120 ka.

Living Australasians (Oceanians) carry Denisovan DNA at 3–6% as well as Neanderthal DNA at ~2% (Reich 2018). This is explained if *Homo sapiens* pioneers, ultimately from Africa, migrating east, encountered Denisovans in East or South East Asia and interbred. Two or three genetically divergent populations of Denisovans existed (Reich 2018; Higham 2021).¹ The traces of interbreeding are evidence that the Denisovan population was fairly numerous and prevalent in the areas traversed by the modern human migrants.

Remains of Middle and Upper Pleistocene Homo in East Asia exhibit considerable morphological diversity with evidence of local evolution within lineages, especially following a major climate shift at ~300 ka (Curnoe et al. 2012; Bae et al. 2017; Wu, Liu et al. 2022; Wu,

¹ Siberian Denisovans as at Denisova Cave, and one or two populations of Australo-Denisovans in South East Asia.

Xiu-Jie et al. 2022; Bae and Wu 2024). The Harbin cranium with a very wide face and endocranial volume 1420 cm³, dated 146 ka, has been assigned to a new species *Homo longi*, along with Dali and Jinniushan (Ni et al. 2021; Bae and Wu 2024). Even larger crania, Xujiayao 6 (ECV 1700 cm³, dated 200–160 ka) and Xuchang 1 (ECV 1800 cm³, dated 120–105 ka), have been assigned to *Homo juluensis*, along with the non-Neanderthal remains at Denisova Cave (Bae and Wu 2024). Though described as Late Middle Pleistocene these species are contemporary with Neanderthals and *Homo sapiens*.

So far the Harbin cranium from mainland China and a robust mandible found on the coast of Taiwan have been identified as Denisovan by mitochondrial DNA from dental calculus and by proteomic analysis (Fu et al. 2025a, 2025b; Tsutaya et al. 2025). Other East Asian remains contemporary with Neanderthals and early modern humans may be identified as Denisovans provisionally, unless genetic or proteomic analysis proves them to be distinct (cf. Ni et al. 2021:3).

It is beyond the scope of this study to discuss East Asian lineages further as they have limited bearing on Neanderthals,¹ although in a wider context evolutionary processes observed among these *Homo* groups during this period may well throw light on phylogenetic scenarios in other regions.

Often all groups in any continent having a broad *heidelbergensis* morphology and date are referred to as “Middle Pleistocene *Homo*”, which avoids controversy about precise phylogeny (Athreya and Hopkins 2021).

Homo heidelbergensis and its analogues in Africa and East Asia are in turn descendants of populations usually referred to as *Homo erectus s.l.*, known again from Africa and also central and eastern Eurasia and dating from around 1.5–0.6 Ma, but perhaps surviving much later in South East Asia and Australasia. These are characterized by considerable skeletal robusticity but smaller endocranial volume extending downward from the lower end of the modern human range to about half the modern human mean (Appendix E).² African and European representatives are sometimes distinguished as *Homo ergaster*, while the East Asian populations are *Homo erectus s.s.* *Homo ergaster* is thought to have originated in Africa, in which case the European groups and East Asian *Homo erectus* represent a radiation into the rest of the Old World. It is possible that *Homo erectus s.s.* survived undisturbed in Java at Ngandong, and perhaps farther afield, as late as 117–108 ka (Rizal et al. 2020),³ well into the period of Neanderthals in Europe and *Homo sapiens* in Africa and South West Asia.

All the above types of *Homo* back to early *Homo ergaster* have stature similar to that of recent humans (Bastir et al. 2020). Their ancestors in turn will have been among the habilines (*Homo habilis*, *Homo rudolfensis*) dating from ≥ 2 Ma, and before them australopithecines. The habilines and australopithecines were of smaller stature and body mass, and australopithecines had endocranial capacities not much greater than those of chimpanzees or gorillas.

¹ Morphology of Xujiayao 6 and Xuchang 1 temporal labyrinths resembles the Neanderthal pattern (§F.4.3).

² As a result of endocranial expansion in *Homo heidelbergensis (s.l.)* and later hominins, opisthocranium lies on the interparietal squama of the occipital bone, whereas in *Homo erectus s.l.* opisthocranium lies below, on the nuchal torus (Arsuaga et al. 2024:1360).

³ Previous dating results for Ngandong were ~26–150 ka (Bartstra et al. 1988) and ~27–53 ka (Swisher et al. 1996).

B.3 Morphology

Here identification of various forms of the genus *Homo* and the attribution of species names are discussed, and characteristics of the Neanderthal phenotype are considered in the context of the other forms. Apart from those classed as *Homo sapiens*, all forms of *Homo* are “archaic”, characterized by robust crania with large faces, browridges, low vaults and sometimes nuchal ridges, regardless of endocranial volume.

Generally the morphology of Neanderthals has been described in relative terms with reference to extant modern humans: e.g. long bones more bowed than ours, neurocrania longer and flatter rather than rounded like ours. These comparisons will be made later. First, earlier hominins which offer a greater contrast with modern humans are considered. *Homo sapiens* and Neanderthals are parallel branches descended from a common ancestor. So it will be useful to consider the morphology of other known types of hominin known from the last one million years, among which common ancestors may be identified. Only *Homo* from *ergaster/erectus* onward is considered here, not australopithecines or the fossils assigned to *Homo habilis* and *Homo rudolfensis*, which, it has been argued, align more closely with australopithecines than with later *Homo* (Wood and Collard 1999a, 1999b; but see Holliday 2012).

From the late nineteenth century up to the mid twentieth century, almost every fossil hominin discovery that did not conform closely to a known morphology received a binomen identifying it as a new species or even genus (Day 1977). After the publication of Mayr’s (1950) influential paper on systematics, the multi-species “splitting” trend was largely abandoned and increasingly all hominin forms other than the australopithecines were “lumped” (Mayr 1969:238–242) together into one or other of two species, the earlier, ancestral *Homo erectus* and the later, descendant, still extant *Homo sapiens* (Tattersall 1986:168; Tattersall and Schwartz 2008:50). The lumping process reached its apogee when proposals were made to sink *Homo erectus* into *Homo sapiens* (Wolpoff et al. 1994; Curnoe and Thorne 2003). In the twenty-first century, from a beginning in the late 1980s (e.g. Mellars and Stringer 1989), and partly driven by the discovery that modern human and Neanderthal mitochondrial DNA were distinct (Cann et al. 1987), a new splitting trend has gathered momentum. More morphs have been distinguished by species names, and this has appeared to be judicious given the discovery of hominins with unexpected morphology such as the small-stature forms *Homo floresiensis* in Indonesia (Brown et al. 2004; Tucci et al. 2018), *Homo naledi* in South Africa (Berger et al. 2015), and *Homo luzonensis* in the Philippines (Détroit et al. 2019).

Much work has been done on identifying criteria counting toward specific difference in hominins, and particularly on defining what the distinguishing characteristics should be for *Homo sapiens*. So below, criteria to distinguish *Homo sapiens* and *Homo erectus* are listed before moving on to Neanderthals.

In a paper principally on the Omo-Kibish remains, Day and Stringer (1982) initiated a still ongoing discussion of criteria for a specimen to be included in *Homo erectus* or *Homo sapiens*. Their definitions are listed below.

Homo erectus

1. Cranium long and low (ratio of basion-bregma height or vertex radius height to glabella-occipital length is less than 0.62 or 0.58 respectively)
2. Inion is coincident with opisthocranium
3. Thick cranial walls (for example parietal thickness at bregma exceeds 8 mm, at asterion exceeds 14 mm, on occipital at inion exceeds 14 mm)
4. Angulated occipital bone (occipital angle less than 107°)

5. Expanded nuchal portion of occipital bone (inion-opisthion chord exceeds lambda-inion chord)
6. Inion more than 25 mm above internal occipital protuberance
7. Parietal arch flat, short and low, superiorly narrow, inferiorly broad (parietal angle exceeds 145.5° , ratio of bregma-asterion chord to biasterionic breadth is less than 1.14)
8. Low frontal bone (frontal angle exceeds 136.5°)
9. Cranial capacity generally below 1150 cm^3

Homo sapiens (anatomically modern, recent)

1. Cranium short but high (ratio of basion-bregma height or vertex radius to glabello-occipital length should exceed 0.70 or 0.64 respectively)
2. Parietal arch is long and high, inferiorly narrow, superiorly broad (parietal angle less than 138° , ratio of bregma-asterion chord to biasterionic breadth greater than 1.19 [i.e. posterior region of neurocranium narrow compared with archaic hominins])
3. Frontal bone high (frontal angle less than 133°)
4. Supraorbital torus not continuous, but divided into lateral and medial portions
5. Occipital bone well curved rather than angulated (occipital angle more than 114°)
6. Mental eminence on mandible
7. Gracile limb bones: thin walled with relatively small articular surfaces

The above definitions (Day and Stringer 1982) were stated to be working definitions, not definitive. Notably, some criteria are stated in terms of absolute measurement while others are relative, so that to decide species membership a comparison is to be made between *Homo erectus* and *Homo sapiens* and between either of them and any other possible type. Also, the criteria do not correspond one to one; e.g. for *Homo erectus* a criterion of cranial capacity is given, but not for *Homo sapiens*; and for *Homo sapiens* supraorbital and limb-bone morphologies are listed, but not for *Homo erectus*.

According to Wolpoff (1986; also Kidder et al. 1992), the definition of Day and Stringer (1982) would exclude from *Homo sapiens* a considerable proportion of recent Australian and Tasmanian aboriginal crania. For example, 34% of frontal angles in Tasmanian adult females and 43% of occipital angles in Lake Alexandra Australian Aboriginal adult females fall outside the *Homo sapiens* range stated above. Some pathological cases might be expected to escape any proposed range, but not healthy members of substantial modern human communities. This case does not invalidate attempts to define *Homo sapiens*, but does illustrate the difficulty of including all phenotypes.

Later definitions of *Homo sapiens* (Tattersall 1986, 2005; Schwartz and Tattersall 2000; Tattersall and Schwartz 2008; Schwartz 2016) have emphasized cranial and mandibular characteristics such as (but not limited to) neurocranial globularity and retraction of the face below the neurocranium contrasting with all previous *Homo*, absence of browridges or presence of reduced browridges which have distinct supraciliary (medial) and supraorbital (lateral) components, presence of canine fossae, presence of a clearly defined chin, and some aspects of dental morphology. These authors acknowledge (Tattersall and Schwartz 2008; Schwartz 2016) that some hominins generally classified as early *Homo sapiens*, such as the Skhul and Qafzeh groups, would fail to meet one or more of these criteria.¹

¹ As would Herto (~157 ka), which resembles Skhul 5 (Stringer 2016), and the Jebel Irhoud fossils (~315 ka, previously dated ~160 ka), the latter once thought to be Neanderthal (Tattersall 1995:182). Stretching the definition of *Homo sapiens* to include the robust and extremely early Jebel Irhoud hominins may be worthy of review.

Characteristics of *Homo neanderthalensis* are listed below. Many of these are discussed in an ontogenetic context in Chapters 4, 5 and 6.

Homo neanderthalensis

Cranium and mandible

Apart from the first two, which are general, most of the cranial characteristics are compiled from Bräuer et al. (2020:1381–1385). Additional traits are listed with references.

1. Neurocranium long and wide but low compared with *Homo sapiens*
2. Viscerocranium long, wide and prognathic compared with *Homo sapiens* (Trinkaus 2003), but with prominent nasal bones and projecting midface, unlike other Middle and Upper Pleistocene *Homo*
3. Supraorbital torus double arched with minimally depressed glabella, unlike more linear browridge of *Homo erectus* and absent or minimal browridge in *Homo sapiens*
4. Supratoral sulcus, contrasting with absence in *Homo sapiens*
5. Frontal sinus restricted to middle half of torus, unlike highly pneumatized torus of *Homo heidelbergensis*
6. In superior view, torus curved from side to side, unlike more laterally projecting torus in Middle and Lower Pleistocene *Homo*
7. High, rounded orbits (orbital index height / breadth = 75–98) compared with Middle Pleistocene *Homo* and *Homo sapiens*
8. Inferomedially truncated orbits (lower medial part of orbit encroached upon by projecting nasal area: this is found in later Neanderthals)
9. Nasiofrontal angle 122°–139°, versus 137°–146° in Middle Pleistocene *Homo*
10. With cranium in Frankfort horizontal plane, nasion inferior rather than posteroinferior to glabella as in Middle Pleistocene *Homo*, in which nasion is depressed
11. Broad and very large nasal aperture compared with *Homo sapiens*
12. Expanded maxillary sinuses; turbinates protruding medially inside nasal cavity, unique in *Homo* (Schwartz and Tattersall 1996)
13. Infraorbital area receding posterolaterally (opposite of prominent cheekbones)
14. Anterior zygomatic roots posteriorly positioned above M2 rather than M1 or M1–M2 as in Middle Pleistocene *Homo*
15. In posterior view, parietal bones smoothly curved from temporoparietal suture to vertex so that the neurocranium has a wide oval shape, “en bombe”, in contrast to *Homo sapiens*, in which laterally the parietals are often nearly vertical, forming a quasi-pentagonal shape
16. Occipital bun (chignon)
17. Suprainiac fossa (oval depression on occipital above inion)
18. External auditory meatus at level of posterior zygomatic arch
19. In the petrous temporal, small semicircular canals with posterior canal positioned low compared with *Homo sapiens* (Quam et al. 2016)
20. Absence of projecting chin
21. Mental foramina in posterior position relative to dental arcade
22. Retromolar gap between mandibular third molar and ascending ramus

Postcrania

These are compiled: 1–6 from Pomeroy (2023), 7–24 from Weaver (2009:16031). Comparative terms are generally with reference to modern humans.

1. Larger shoulder joint than *Homo sapiens*
2. Broad and deep, flaring rib cage
3. Larger rib heads and articular tubercles (García-Martínez et al. 2020)
4. Wide pelvis with large bi-iliac breadth and mediolaterally long pubic ramus
5. Larger hip joint than *Homo sapiens*
6. Shorter distal limb segments: radius, ulna, tibia, fibula
7. Long bones with bowed shafts and thick cortical bone
8. Rugose muscle attachments
9. Vertebrae with horizontal lower cervical spinous processes
10. Robust rounded rib shafts
11. Long clavicles
12. Wide scapula with narrow glenoid fossa and dorsal axillary sulcus
13. Humerus with wide olecranon fossa and narrow dorsodistal pillars
14. Ulna with high and long olecranon process and anteriorly oriented trochlear notch
15. Radius with medially directed tuberosity and long neck
16. Trapezium with flat first metacarpal facet
17. Hamate with large hamulus
18. Third metacarpal with short styloid process
19. Subequal proximal and distal thumb phalanges
20. Large manual distal phalangeal tubercles
21. Femur with large articulations, rounded midshaft lacking pilaster, and low neck-shaft angle
22. Tibia with projecting tuberosity and absence of diaphyseal concavities
23. Relatively symmetrical medial and lateral patellar facets
24. Large pedal distal phalangeal tubercles

Weaver (2003) argues that the stocky build of Neanderthals, exemplified particularly in the long bones, is hyperpolar, i.e. an extreme adaptation to cold climate. However, Holliday (2012) found that the thorax of the *Homo ergaster* subadult skeleton KNM-WT 15000 was mediolaterally wide and anteroposteriorly deep as in Neanderthals. This trait may thus be a plesiomorphy inherited by Neanderthals via *Homo heidelbergensis* from *Homo erectus s.l.* (Bastir et al. 2020), but discontinued in *Homo sapiens*.

Trinkaus (1986:205–206) observes that the Neanderthal skeleton is similar to but slightly less robust than in the Middle Pleistocene hominins. General robusticity, thick cortical bone in the diaphyses, and the short distal limb segments contrast with living humans. He argues that these traits reflect strength and endurance capability with muscular upper and lower limbs adapted to high loadings and enabling prolonged trekking across irregular terrain, but that the growth of muscular bodies would be costly in terms of nutrition, and therefore this adaptation may have been less efficient than that of more gracile recent humans.

That Neanderthals had upright posture and gait like that of *Homo sapiens*, and that discrepancies were due to pathology, was shown by Straus and Cave (1957), disputing the then prevailing view originating from the description of the La Chapelle-aux-Saints skeleton by Boule in 1911–1913 (Boule and Vallois 1957). Recently, further study of the La Chapelle postcranial skeleton has confirmed, particularly from its lumbar lordosis, that posture was entirely upright as in modern humans, and that the individual suffered from degenerative bone

conditions such as advanced osteoarthritis in several parts of the body (Haeusler et al. 2019). The same study estimates the age of the individual to have been in the sixth or seventh decade, confirming its status, by Palaeolithic standards, as an “Old Man”. Several other Neanderthal adults are known to have had degenerative bone disease, scoliosis, and other pathologies affecting the postcrania (Haeusler et al. 2019; Gómez-Olivencia et al. 2018).

APPENDIX C

DENTITION: BACKGROUND

This appendix gives background information on types and characteristics of teeth, dental formation and associated topics.

C.1 Stages of tooth formation and dental schedules

C.1.1 Types of tooth ¹

Maxillary (upper, U) or mandibular (lower, L), left and right (L, R).

Deciduous dentition

Five tooth types: Anterior: central and lateral incisors (di1, di2), canines (dc).
Posterior: first and second molars (dm1, dm2).

Permanent dentition

Eight tooth types: Anterior: central and lateral incisors (I1, I2), canines (C).
Posterior: first and second premolars (P3, P4), first, second, and third molars (M1, M2, M3).

C.1.2 Stages and schedules

Scholars have codified stages of dental development with a view to assessing attainment of individual dental patients and populations, and these stages have been broadly correlated with chronological ages. Among the widely used systems are those of Moorrees et al. (1963), Demirjian et al. (1973) and AlQahtani et al. (2010), the last being a development of the system of Moorrees and colleagues.

Figure C.1 illustrates fourteen stages defined by Moorrees et al. (1963:1493) for multi-rooted teeth (premolars and molars). Corresponding diagrams are provided by these authors for incisors and canines with the same stages, except that the stage *cleft initiated* is omitted for incisor and canine teeth. An additional stage 0 before stage 1 is formation of a crypt but absence of a cusp. Separate root stages can be assessed for mesial and distal roots of molars. Moorrees et al. (1963) present charts showing the chronological ages at which defined stages are observed in males and females for each tooth type.

¹ Other notations for tooth type are widely used, e.g. i² and i₂ for upper and lower deciduous second incisors, M¹ and M₁ for upper and lower permanent first molars. Here the notation in the text above is used.

Like hominins, the great apes and catarrhine (Old World) monkeys have only two premolars in each quadrant. The basal primates had four, but even one of these, the first premolar, was lost early in primate evolution (Schultz 1969:104). For this reason it seems an unnecessary complication in anthropology to refer to dentists' first and second premolars as primatologists' third and fourth (P3, P4), but the convention is followed here.

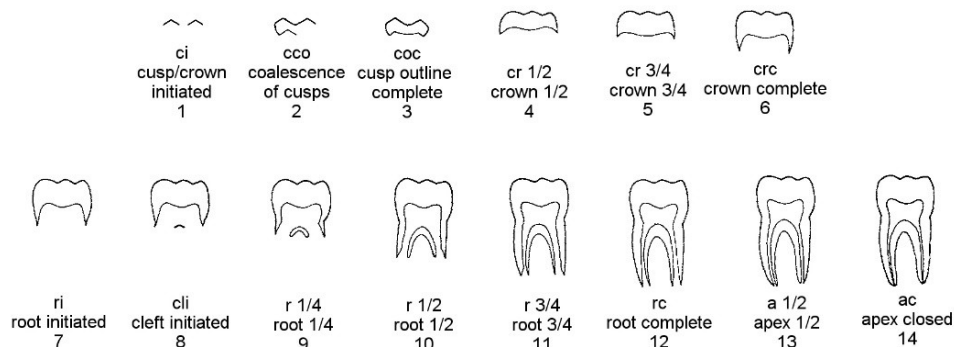


Figure C.1: Stages of tooth formation (adapted from Moorrees et al. 1963)

Similarly, Demirjian et al. (1973) identified eight stages by letters A–H, with a stage 0 for absence of a cusp. By assigning a numerical value 0–8 to each stage, an overall score of dental maturity can be obtained by summing the stages for each tooth type in the maxilla and mandible: for permanent teeth the 8 tooth types in the left and right upper and lower quadrants yield a maximum possible score of 64, which indicates completion of dental maturation. Demirjian stages and those of other systems can be identified on radiographs as well as on exfoliated teeth. For any stage the subject may have just entered that stage, be in the middle of the cohort, or be about to leave that stage, so each stage represents a range of possible ages. The range becomes wider with later emerging teeth, especially the second and third permanent molars (M2 and M3). Accuracy of various systems has been analysed by Maber et al. (2006) and Liversidge (2008b).

Tables and charts relating dental stages to age ranges have been widely used as dental schedules to estimate age at death of immature remains in forensic and archaeological contexts. In the present work the system of Moorrees and colleagues is the one most often referenced.

As the schedules linking stages and ages were initially based on samples of mostly European origin, they are not always fully applicable to subjects of other geographical populations. Known-age Australasian and Sub-Saharan African children are often advanced in dental development relative to East Asians, South Asians and Europeans, although the advancement may vary from none at all through fractions of a year to several years in the case of later developing molars (Liversidge 2003, 2008a; Brown 1978).

Dental schedules derived from observation of recent humans can provide an initial guide to age at death for a fossil immature hominin individual, but the age will be inaccurate if that population had dental formation times shorter or longer than those of living *Homo sapiens*. Chimpanzee dental formation is overall more rapid than in living humans (Kuykendall et al. 1992; Kuykendall and Conroy 1996). As all hominin genera including australopithecines and all species of *Homo* other than *Homo sapiens* are believed to have experienced more rapid growth than living humans, it has become usual to deduct some period, e.g. a year or more, from age estimates of extinct hominin subadults obtained from recent human dental schedules. A regression equation to apply this age adjustment to Neanderthals was devised by Granat and Heim (2003).

C.2 Dental formation

The following outline of tooth formation is taken from Nanci (2018:118–128,157–165), Simmer and Hu (2001:897–898), and Mahoney (2015).

Tooth structure is illustrated in Figure C.2, in this case a complete molar.

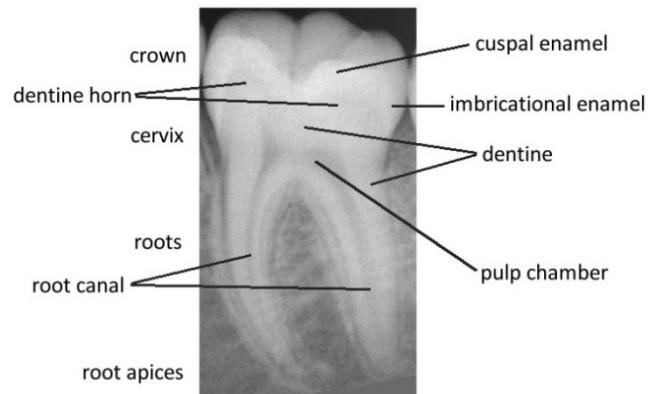


Figure C.2: Tooth structure (molar)

Within the maxilla and mandible, crypts form within which cells of the oral epithelium and adjacent ectomesenchymal tissue interact. At each site, on the basal lamina which will become the enamel-dentine junction (EDJ), an extracellular space is formed where two layers of cells differentiate from the adjacent tissues into preodontoblasts and preameloblasts. Ectomesenchymal cells adjoining the extracellular space become preodontoblasts, while on the opposite margin cells of the inner enamel epithelium become preameloblasts. As the odontoblasts develop, they begin *secretion* of predentine matrix containing collagen and non-collagenous proteins. This matrix is deposited in the direction of the ameloblasts. The developing ameloblasts are induced to activate secretion of enamel.

The first enamel is only partially mineralized and aprismatic, i.e. not orientated in any direction, and forms the base for further secretion as each ameloblast develops a wedge-shaped Tomes process at its distal end. Enamel secreted from the tip of the Tomes process forms a rod (prism) which lengthens as the ameloblast recedes from the EDJ. Enamel from the edges where ameloblasts adjoin one another extends to form inter-rod enamel, which sheaths the rods. Rod enamel crystallites are orientated to the long axis of the ameloblast, while inter-rod crystallites lie at a significantly different angle round ~75% of the circumference of the rod. Similarly, odontoblasts run in canaliculi which become dentinal tubules, forming the mineralizing dentine into the equivalent of rods surrounded by peritubular and intertubular dentine (Aiello and Dean 2002:119).

Odontoblasts and ameloblasts push away from the EDJ, secreting predentine and enamel respectively, filling the extracellular space between them. Odontoblasts recede into the dental papilla, which becomes the developing pulp chamber and will eventually be fully enclosed by dentine. Ameloblasts recede in the opposite direction all round the EDJ, and the rods and inter-rod enamel which they secrete begin to form the crown of the developing tooth.

Differentiation of odontoblasts and ameloblasts begins at limited areas on the future EDJ from which they will grow to form the cusps of those teeth. Further odontoblasts and ameloblasts differentiate and begin to secrete along the EDJ proceeding in all directions away from these initial sites. Dentine and enamel *extension* is enabled by this proliferation. The initial site becomes the tip of the dentine horn, one for an anterior tooth, multiple for premolars

C.3 Growth of dental tissues, incremental lines

Enamel grows incrementally from the cusp or cusps of a tooth to its cervix. Microstriae within the enamel represent the circadian secretion quantity (represented by CC' in Figure C.3). That this observed quantity is a daily increment was disputed (Mann et al. 1991:186) but further studies concluded in favour of this proposition (Hillson 1996:156; Fitzgerald 1998; Aiello and Dean 2002:111; Hillson 2014; Nanci 2018:149).

The circadian lines appear as cross-striations more or less perpendicular to the axes of the enamel rods, which grow in parallel by this quantity, which is a few micrometres (μm) per day (Chapter 4). Across a series of adjacent rods the cross-striations may be slanted rather than strictly perpendicular. This phenomenon occurs because adjacent ameloblasts begin enamel secretion successively, not simultaneously (Figure C.3) (Hillson 2014). Within each circadian interval a light and a dark area appear, the lighter areas representing a higher rate of secretory activity than the darker (Lacruz et al. 2012).

Within enamel the cross-striations appear within regular striae of Retzius (Hillson 2024:213–215). Each stria of Retzius contains a fixed number (the periodicity) of cross-striations. Periodicity, also designated *repeat interval* (Bromage et al. 2012), is constant across all teeth of the same organism, but varies from one individual to another. Periodicities of 6–12 days are known for recent humans, 8 and 9 being very common (Guatelli-Steinberg 2008). The circadian and long-period intervals appear to be related to organism-wide rhythms which also affect other tissues and organs and are governed by hypothalamic nuclei and the pituitary gland (Bromage et al. 2009, 2011, 2012; Lacruz et al. 2012). Small-bodied primates tend to have lower periodicity than larger-bodied primates, but the correlation is inconsistent. Even with samples of 24 and 36 respectively, orang-utans with mean body mass 57.0 kg had a mean periodicity 9.5, whereas gorillas with mean body mass 124.5 kg had a mean periodicity 8.7 (T.M. Smith 2008:213).

On the cusp later enamel layers overlie earlier layers (appositional enamel), whereas on the crown's lateral aspects layers form successively further away from the occlusal region and build the enamel surface beyond previous layers (imbricational enamel). Striae of Retzius outcropping at the lateral enamel surface form horizontal waves known as perikymata (Nanci 2018:151–153; Aiello and Dean 2002:111–112).

Within dentine, i.e. beneath the enamel crown and through the roots, the equivalent of circadian enamel cross-striations are found as von Ebner's lines, which run more or less perpendicular to the axes of the dentinal tubules and represent the daily quantity of dentine secreted by parallel odontoblasts. Von Ebner's lines appear within larger striae known as Andresen lines. Andresen lines in dentine have the same periodicity as striae of Retzius in enamel (Dean and Scandrett 1996).

Quantity of enamel secreted per day is represented by the cross-striations (short-period lines) within the striae of Retzius (long-period lines). In modern humans cross-striations generally lie $\sim 2\text{--}5\ \mu\text{m}$ apart (Hillson 2024:212), indicating the daily rate (Hillson 2014:124)

Cuspal daily secretion rate (DSR) is similar across hominoids with a lower limit of 2–3 and upper limit of 6–7 $\mu\text{m}/\text{d}$. *Homo* and *Pan* have lower mean values, *Gorilla* higher. Among hominins, the highest rates are found in the two species of *Paranthropus* (Lacruz et al. 2008:152), followed by other australopithecines, with early *Homo* intermediate, and modern humans and Neanderthals lower (T.M. Smith 2008:210).

Enamel daily secretion rate increases from the EDJ, where it begins, to the cuspal surface, where it terminates; but from the cuspal region to the cervix at equivalent depths (inner, mid and outer) within the developing enamel the rate decreases (Beynon et al. 1991:306; Reid

and Dean 2006; T.M. Smith 2008:210) (Tables D.5, D.6). The same rate differences by region and depth are found in australopithecines and early *Homo* (Lacruz et al. 2008).

Similarly, in dentine von Ebner's lines (short-period lines) within Andresen lines lie ~3–5 µm apart (Hillson 2024:260). Dean (1998b) showed that root dentine secretion is less rapid near the surface, i.e. adjacent to the granular layer of Tomes, and more rapid toward the axial plane of the cusp as seen in ground sections, i.e. toward the centre of the root (Table D.7).

Other linear and sometimes pit-shaped features appear in dentine or enamel, and these include instances of hypoplasia or deficiency of substance, which are attributed to temporary trauma, disease or episodes of undernutrition experienced by the organism, when formation or mineralization of that area of the tooth cannot be completed (Aiello and Dean 2002:112). Within the enamel of deciduous teeth and the permanent first molar, which begin formation *in utero*, the neonatal accentuated line can often be found which records the disturbance caused by birth. A neonatal line may also be visible within the dentine horn (Guatelli-Steinberg 2008).

C.4 Absolute or chronological age at death

Dental development standards have been produced indicating the expected formation stage of teeth at ages from 6 months to adulthood. However, most of these standards are based on European samples. They may not be fully compatible with other living populations or with extinct hominins. If *Homo erectus* teeth formed more quickly than those of living humans, then modern human standards would overestimate age at death of an immature *Homo erectus* specimen. Such an estimate would be a *dental age* but not an absolute or *chronological age*.

The internal features of dentine and enamel produced by regular incremental growth offer a means of deriving the absolute age at death, provided these features can be observed and counted (Schwartz and Dean 2008). To do so requires sectioning teeth either physically or virtually, i.e. non-destructively using computed tomography.

In principle, if a section could be made from the cusp all the way to the root apex, it would be possible to count the daily cross-striations in enamel to find the total crown formation time, and similarly count von Ebner's lines in dentine from the cervix to the apex to find the time taken to grow the root. However, once the periodicity has been ascertained, the more readily visible longer period lines, striae of Retzius in enamel and Andresen's lines in dentine, can be counted and the total multiplied by periodicity to produce the number of days (Guatelli-Steinberg 2008). More particularly, if the tooth had begun formation before birth, e.g. the permanent first molar, then the neonatal line would serve as a starting point to calculate age. Decussation of the first forming inner cuspal (gnarled) enamel renders striae in this area less distinct than in lateral enamel and leads to estimation of formation time rather than determination by counting (Reid et al. 2008:226–227; Hillson 2014:123–125).

In molar teeth the earliest cusps to initiate are the paracone (upper) and paraconid (lower), and the distal root completes latest (Reid and Dean 2006:340; Liversidge 2008b:235). It would be difficult, physically or virtually, to section a tooth in one plane from earliest cusp to latest root tip, for example because of curving molar roots (cf. Dean et al. 1986:302). However, accentuated lines are likely to form in more than one of the teeth that are developing during a metabolic disturbance. These lines can be registered, i.e. cross-matched, from one tooth to another, so that later forming teeth can be used to calculate further time periods after the earlier forming teeth were completed (Guatelli-Steinberg 2008; Schwartz and Dean 2008).

In this way, even up to the last developing teeth, the third molars, it is in principle possible to calculate an absolute or chronological age at death.

APPENDIX D

DENTITION: TABLES

D.1 Neanderthals

Formation stages for the various tooth types are given in Table D.1, as a reference for all Neanderthal immatures with sufficient dentition.

Table D.1: Dental formation stages at death, Neanderthal immatures

Individuals, alphabetical order	Age (y)	Tooth types, maxillary and mandibular combined, not sided												
		dc	dm1	dm2	UI1	UI2	LI1	LI2	C	P3	P4	M1	M2	M3
Archi ⁴	2.4–3.5	a ½	ac	rc	-	-	crc	crc	cr ¾	cco	ci	cr ¾	-	-
Barakai ⁴	3	r ¾	ac	rc	-	-	crc	crc	cr ¾	ci	crypt	crc	crypt	-
La Chaise Suard ⁴	4.5	-	ac	ac	-	-	r ¼	r ¼	crc	cr ¾	coc	cli	ci	-
Châteauneuf 2	5–6	res ¼	-	-	r ¼	ri	-	-	ri	rc	cr ¾	r ½	cr ¾	-
Combe Grenal 1	5–9	res ¼	res ¼	res ¼	-	-	-	-	r ¼	crc	-	rc	-	-
Dederiyeh 1 ⁵	1.5–1.7	r ½	r ¾–rc	r ¼	cr ½	-	cr ½	cr ½	coc	-	-	cr ¾	-	-
Dederiyeh 2 ⁶	2.0	r ½	rc	r ½	crc	cr ¾	crc	cr ¾	cr ½	ci	-	cr ¾	-	-
Ehringsdorf 7/G	10–12	-	-	-	-	-	ac	ac	rc	ac	-	-	rc	crc
Engis 2 ¹	3.0	-	-	-	crc	crc	-	-	cr ¾	cr ¾	-	ri	-	-
Fate 2	8–10	-	-	-	-	-	-	-	r ½	r ¼	ri	a ½	cc	-
La Ferrassie 8	1.3–2	-	r ¾	r ½	-	-	-	-	-	-	-	cr ½	-	-
Gibraltar 2 ¹	4.6	-	-	-	ri	ri	ri	ri	crc	cr ¾	cr ½	r ¼	cr ½	-
Hortus II/III	6.5–9	-	-	-	-	-	-	-	r ¾	r ¼	r ¼	a ½	-	-
Krapina Maxilla A	6–7	-	res ½	res ¼	-	-	-	-	r ½	-	-	rc	-	-
Krapina Maxilla B	5.9	-	-	-	-	-	-	-	-	crc	cr ¾	r ¾	-	-
Krapina Maxilla C	10–12	-	-	-	-	-	-	-	-	-	-	-	r ½	-
Krapina Mandible A	5–6	ac	-	-	-	-	r ½	r ½	r ¼	ri	-	-	-	-
Krapina Mandible B	8–9.5	res ½	-	-	-	-	-	r ¾	r ½	r ¼	r ¼	ac	-	-
Krapina Mandible C	11	-	-	-	-	-	-	ac	-	-	r ½	ac	r ¾	crc
Krapina Mandible D	15–17	-	-	-	-	-	-	ac	ac	ac	ac	ac	rc	-
Krapina Mandible E	15–17	-	-	-	-	-	ac	ac	a ½	rc	a ½	ac	a ½	-
Montgaudier	12–14	-	-	res ½	-	-	-	-	r ½	r ¼	ri	a ½	ri	-
Le Moustier 1 ¹	11.86	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	r ¼ ⁷
Obi-Rakhmat 1 ¹	6–8.1	-	-	-	-	r ¾	-	-	r ¼	r ¼	r ¼	-	r ¼	-
Pech de l'Azé	1.5–2	r ½	r ¾	r ½	-	-	-	-	-	-	-	cr ¾	-	-
Pech de l'Azé ⁴	1.5	rc	ac	rc	-	-	cr ¾	cr ¾	cr ½	cco	crypt	cr ¾	crypt	-
La Quina H18	5.5–8	-	-	-	-	-	-	-	ri	crc	cr ¾	rc	cr ½	-
La Quina H18 ¹	5.5–8	-	-	-	r ¼	ri	-	-	ri	crc	cr ¾	r ¾	cr ¾	-
Roc de Marsal	2.3	r ¾	ac	rc	cr ¾	cr ½	crc	cr ¾	cr ½	cco	-	crc	-	-
Roc de Marsal ²	2.3	r ¾	res ¼	r ¾	cr ¾	cr ¾	cr ¾	cr ¾	cr ¾	coc	-	crc	-	-
Roc de Marsal ⁴	2.3	a ½	ac	a ½	ri	ri	ri	ri	cr ¾	coc	ci	crc	ci	-
Scladina	8.0	-	-	-	-	ac	ac	-	a ½	r ¾	r ½	ac	r ½	cr ¾
El Sidrón J1 ³	7.7	-	-	-	rc	r ¼	rc	r ¾	r ¼	r ¼	ri	rc	ri	crypt

Combined maxillary and mandibular dentition apart from incisors. For deciduous teeth there are stages *res* = roots resorbing. Ages from Appendix A. Ages in **bold** are derived from counts of striae in dental microstructure.

Dental stage data: Shackelford et al. (2012:249–251) from scores from radiographs by R. Tompkins, unless otherwise stated.

¹ Shackelford et al. (2012:249–251) from dental scores by T.M. Smith et al (2010).

² Shackelford et al. (2012:249–251) from Bayle et al. (2009).

³ Rosas et al. (2017 SI:36).

⁴ Faerman and Kharitonov (1994:413).

⁵ Mizoguchi (2003:226).

⁶ Kondo and Ishida (2003b:324).

⁷ r ¼ and unerupted assessed for all four M3s by Thompson and Nelson (2005:214) and Thompson and Illerhaus (2005:235–236). r ½ listed by Shackelford et al. following T.M. Smith et al (2010), who score maxillary M3s as r ½ and mandibular as r ¼.

Table D.2: Enamel thickness by tooth type, Neanderthal, fossil and recent *Homo sapiens* and European *Homo heidelbergensis*

Tooth type	Species	Area of enamel cap	EDJ length	2D AET	Area of coronal dentine	2D RET
UI1	Neanderthal	15.61	24.71	0.63	47.20	9.19
	Fossil <i>H. sapiens</i>	16.74	23.60	0.71	44.50	10.57
	Recent <i>H. sapiens</i>	13.46	21.55	0.62	32.73	10.91
UI2	Neanderthal	17.01	25.40	0.67	41.60	10.45
	Fossil <i>H. sapiens</i>	15.74	22.91	0.69	35.98	11.52
	Recent <i>H. sapiens</i>	12.16	19.04	0.64	26.78	12.51
UC	Neanderthal	20.25	24.28	0.83	55.52	11.20
	Fossil <i>H. sapiens</i>	18.83	21.67	0.97	46.89	12.71
	Recent <i>H. sapiens</i>	19.02	20.96	0.91	40.28	14.43
UP3	Neanderthal	22.95	23.49	0.98	52.31	13.57
	Fossil <i>H. sapiens</i>	26.98	21.46	1.26	45.01	18.74
	Recent <i>H. sapiens</i>	22.12	19.99	1.10	39.18	17.69
UP4	Neanderthal	23.13	22.28	1.04	48.09	15.03
	Fossil <i>H. sapiens</i>	26.81	20.42	1.31	42.61	20.11
	Recent <i>H. sapiens</i>	22.90	20.01	1.14	38.01	18.55
	Eur. <i>H. heidelberg.</i>	23.46	20.66	1.14	40.33	17.88
UM1	Neanderthal	24.36	22.97	1.06	48.08	15.29
	Fossil <i>H. sapiens</i>	28.77	22.36	1.28	49.77	18.15
	Recent <i>H. sapiens</i>	25.11	20.66	1.22	42.67	18.72
	Eur. <i>H. heidelberg.</i>	23.25	21.49	1.08	40.99	16.90
UM2	Neanderthal	26.05	22.27	1.17	47.72	17.06
	Fossil <i>H. sapiens</i>	25.97	19.82	1.31	43.63	19.83
	Recent <i>H. sapiens</i>	28.89	20.61	1.40	43.69	21.40
	Eur. <i>H. heidelberg.</i>	25.79	21.51	1.20	48.99	17.13
UM3	Neanderthal	26.16	21.33	1.22	46.30	18.07
	Fossil <i>H. sapiens</i>	-	-	-	-	-
	Recent <i>H. sapiens</i>	27.13	19.70	1.38	40.96	21.76
	Eur. <i>H. heidelberg.</i>	22.02	17.66	1.25	33.35	21.59
LI1	Neanderthal	10.88	20.63	0.53	33.35	9.14
	Fossil <i>H. sapiens</i>	10.25	19.55	0.53	29.45	9.65
	Recent <i>H. sapiens</i>	10.05	18.21	0.55	23.97	11.23
LI2	Neanderthal	12.51	21.69	0.58	36.59	9.54
	Fossil <i>H. sapiens</i>	10.75	19.95	0.53	30.13	9.77
	Recent <i>H. sapiens</i>	11.40	19.23	0.59	27.49	11.28
LC	Neanderthal	16.13	22.50	0.71	45.37	10.57
	Fossil <i>H. sapiens</i>	18.73	23.81	0.77	52.32	10.65
	Recent <i>H. sapiens</i>	16.84	20.89	0.81	40.12	12.91
LP3	Neanderthal	17.61	19.68	0.89	38.87	14.38
	Fossil <i>H. sapiens</i>	21.32	20.46	1.04	42.68	15.81
	Recent <i>H. sapiens</i>	18.08	17.85	1.01	33.16	17.78
LP4	Neanderthal	20.59	20.69	1.00	39.05	16.06
	Fossil <i>H. sapiens</i>	24.15	22.31	1.08	44.18	16.17
	Recent <i>H. sapiens</i>	21.79	18.12	1.20	32.88	21.19
LM1	Neanderthal	21.59	21.58	1.00	42.96	15.45
	Fossil <i>H. sapiens</i>	26.09	21.97	1.19	43.92	18.02
	Recent <i>H. sapiens</i>	21.95	20.37	1.08	40.51	17.02
LM2	Neanderthal	21.12	20.53	1.03	44.55	15.48
	Fossil <i>H. sapiens</i>	27.90	21.80	1.28	49.16	18.31
	Recent <i>H. sapiens</i>	22.15	18.54	1.20	34.44	20.54
LM3	Neanderthal	19.24	18.93	1.01	37.01	16.78
	Fossil <i>H. sapiens</i>	25.61	19.92	1.28	38.82	20.53
	Recent <i>H. sapiens</i>	22.86	18.32	1.25	33.37	21.72
	Eur. <i>H. heidelberg.</i>	24.05	18.98	1.27	34.58	21.55
Data from T.M. Smith et al. (2012 SI: Appendix B). Fossil <i>Homo sapiens</i> refers to specimens from Morocco, South Africa and the Levant. European <i>Homo heidelbergensis</i> refers to Heidelberg (Mauer) and Steinheim.						

Table D.3: 2D and 3D enamel thickness, Neanderthal, modern human, Sima de los Huesos, Atapuerca TD6 and Homo erectus

Tooth type	Species	2D AET (mm)		2D RET		2D % Crown that is dentine and pulp		3D AET (mm)		3D RET		3D % Crown that is dentine and pulp	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
UM1	Neanderthal	1.03	0.93–1.19	15.50	13.80–16.93	65.68	63.88–68.04	1.14	1.07–1.20	16.39	13.93–18.41	55.36	51.25–58.77
	Modern human	1.07	0.84–1.45	18.13	14.46–22.71	63.11	58.31–67.58	1.14	0.84–1.58	18.61	12.63–23.52	54.54	47.57–61.52
	Sima de los Huesos	1.04	1.03–1.06	16.76	16.03–17.21	63.82	62.81–65.37	1.30	1.28–1.30	19.65	18.00–20.65	51.87	50.63–53.91
	Atapuerca TD6	1.12	1.07–1.21	17.14	16.07–18.38	64.98	62.16–67.72	1.30	1.24–1.36	18.69	16.75–20.64	53.11	50.83–55.40
	<i>Homo erectus</i>	1.31	1.30–1.32	18.67	18.28–19.07	62.22	61.72–62.72	1.13	-	16.30	-	54.67	-
UM2	Neanderthal	1.20	1.13–1.29	18.12	15.65–20.85	62.96	59.17–66.90	1.10	0.97–1.33	15.91	13.24–20.88	58.18	50.70–62.80
	Modern human	1.32	0.82–1.80	21.75	13.72–29.59	59.59	49.69–70.02	1.33	0.96–1.78	21.93	15.06–31.63	51.03	43.24–58.46
	Sima de los Huesos	1.18	1.06–1.28	19.62	16.88–22.22	60.55	56.36–64.91	1.24	1.05–1.43	20.15	18.43–23.74	51.51	48.24–54.14 *
	Atapuerca TD6	1.39	1.27–1.52	21.74	20.26–23.22	60.65	59.35–61.94	1.44	1.32–1.54	21.30	19.01–23.59	50.92	48.24–54.14 *
	<i>Homo erectus</i>	1.49	1.48–1.51	21.47	19.42–23.52	-	-	-	-	-	-	-	-
UM3	Neanderthal	1.10	0.79–1.35	16.45	13.82–18.49	66.40	63.51–70.08	1.03	0.75–1.18	15.62	11.61–18.43	58.47	54.06–66.11
	Modern human	1.30	1.01–1.64	22.38	16.63–28.99	59.17	52.58–68.54	1.44	0.91–1.94	26.10	14.54–34.10	46.44	37.83–52.98
	Sima de los Huesos	1.30	1.04–1.46	23.84	19.88–27.56	54.49	47.48–59.92	1.36	1.18–1.50	25.39	21.24–30.02	46.10	41.43–50.82
	Atapuerca TD6	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Homo erectus</i>	-	-	-	-	-	-	1.45	-	27.64	-	42.45	-
LM1	Neanderthal	1.00	0.92–1.18	15.88	13.77–20.46	65.62	60.49–69.28	1.13	0.82–1.63	16.29	11.79–24.02	58.47	52.01–63.52
	Modern human	1.11	0.96–1.26	19.47	16.85–22.35	61.09	58.11–64.99	1.14	0.92–1.36	17.97	14.46–22.21	52.64	46.37–57.35
	Sima de los Huesos	1.00	-	17.96	-	60.51	-	1.11	-	17.74	-	54.23	-
	Atapuerca TD6	1.17	1.00–1.38	19.92	16.90–23.12	61.25	55.44–65.89	1.13	0.98–1.23	16.16	14.97–17.74	56.89	53.90–59.45
	<i>Homo erectus</i>	-	-	-	-	-	-	-	-	-	-	-	-
LM2	Neanderthal	1.01	0.90–1.19	15.59	14.21–22.24	67.25	65.28–69.69	1.06	0.81–1.32	15.17	11.88–20.92	59.50	50.97–67.53
	Modern human	1.25	1.02–1.53	22.14	16.22–28.58	58.73	50.76–66.39	1.29	0.65–2.30	20.55	12.56–40.71	50.51	36.56–57.32
	Sima de los Huesos	1.20	1.02–1.41	22.51	19.57–28.30	59.79	54.95–62.40	1.30	1.11–1.50	22.20	18.74–27.25	49.67	45.02–54.40
	Atapuerca TD6	1.16	1.02–1.37	21.60	17.65–27.25	60.01	52.53–65.98	1.27	1.16–1.37	19.85	16.36–26.04	51.70	42.14–56.80
	<i>Homo erectus</i>	1.27	1.19–1.38	22.15	18.56–24.93	59.03	56.04–63.15	1.34	1.26–1.42	21.42	18.98–23.60	48.40	45.77–51.07
LM3	Neanderthal	1.03	-	17.43	-	64.73	-	1.14	0.82–1.41	17.31	12.74–22.28	57.77	49.11–68.63
	Modern human	1.22	1.03–1.50	22.02	17.56–29.09	58.42	52.05–63.83	1.36	1.08–1.85	22.82	17.78–30.20	48.53	42.18–55.44
	Sima de los Huesos	1.32	0.93–1.48	26.88	16.68–31.98	54.70	46.60–67.28	1.40	1.05–1.53	24.54	17.12–27.90	47.95	44.81–57.50
	Atapuerca TD6	1.14	1.09–1.20	24.00	21.16–29.19	58.11	52.34–61.47	1.29	1.19–1.35	25.74	18.66–35.33	44.63	33.67–53.33
	<i>Homo erectus</i>	0.97	-	19.87	-	60.25	-	1.05	-	18.01	-	52.80	-
Neanderthal values in bold.													
Data from Martín-Francés et al. (2020:11–12).													
* The identical UM2 3D percentage ranges for TD6 and Sima de los Huesos may be a misprint.													

D.2 Early African hominins

Table D.4: Periodicity, early African hominins

Periodicity	<i>Australopithecus anamensis</i>	<i>Australopithecus africanus</i>	<i>Paranthropus robustus</i>	South and East African early <i>Homo</i>	Indeterminate hominins
5 or 6	KNM-KP 34725 (1)				
6		MLD 11/30 (1)	DNH 47, DNH 60, DNH 84 (3)		
7		MLD 2 (1)	DNH 44, DNH 108 (2)	DNH 35, DNH 100, KNM-ER 1482 ¹ (3)	
8			SK 62, EM 2368, DNH 101 (3)	DNH 67/70/71, KNM-ER 809, KNM-ER 1802, KNM-ER 1805, UR-501 ¹ (5)	StW 151 (1)
9			TM 1536 (1)	KNM-ER 3733 ¹ , KNM-WT 15000 ²	
10		Sts 24 (1)	SK 61 (1)		
11	KNM-KP 31712 (1)	Sts 2 (1)			
12			DNH 107 (1)		
12 or 13					KB 5223 (1)
Mean	8.3	8.5	7.9	7.9	10.3

Data from T.M. Smith et al. (2015 SI:Table A) unless stated.
¹ Lacruz et al. (2008:152). KNM-ER 809 and 3733 are *Homo erectus* s.l., KNM-ER 1802 and UR-501 are *Homo rudolfensis*, KNM-ER 1805 is *Homo habilis*.
² Estimate (Dean 2016:6). KNM-WT 15000 is *Homo ergaster/erectus*.

D.3 Modern humans

Table D.5: Cross-striation intervals representing enamel DSR, modern humans and chimpanzees

Species	Tooth type	Cuspal			Lateral			Cervical	
		Inner	Mid	Outer	Inner	Mid	Outer	Inner	Outer
Modern human	Premolar	2.7	4.2	4.9	2.8	4.1	4.9	2.3	3.0
	Molar	2.7	4.3	5.1	2.6	4.0	5.0	2.3	2.8
Chimpanzee	Premolar	3.1	4.2	4.4	2.5	4.7	4.4	2.7	4.2
	Molar	3.1	4.4	5.0	3.1	4.1	4.1	2.8	3.8

Data from Beynon et al. (1991:306).

Table D.6: Enamel daily secretion rates (DSR), permanent first molar, recent humans, European

		Inner		Mid		Outer	
		Mean	Range	Mean	Range	Mean	Range
Cuspal	Population						
	Roman	3.72	3.23–4.02	4.21	4.07–4.58	4.56	4.12–4.76
	Early Anglo-Saxon	3.69	3.48–4.01	3.98	3.69–4.40	4.43	4.20–4.81
	Late Anglo-Saxon	3.34	3.02–4.20	3.65	3.41–4.66	3.99	3.41–4.66
	Mediaeval	3.36	3.83–3.84	3.65	2.91–4.13	3.90	3.13–4.76
Lateral	Modern-day	3.20	2.54–3.99	3.52	2.96–4.18	3.75	3.15–4.58
	Population						
	Roman	3.66	3.30–4.36	4.19	3.67–4.78	4.57	3.97–5.13
	Early Anglo-Saxon	3.42	3.11–4.03	3.85	3.54–4.21	4.24	3.85–4.63
	Late Anglo-Saxon	3.36	2.87–3.94	3.63	2.86–4.14	3.88	2.89–4.57
	Mediaeval	3.36	2.84–3.81	3.65	3.12–4.29	3.89	3.47–4.50
	Modern-day	3.14	2.84–3.66	3.42	2.82–4.04	3.71	3.13–4.99

DSR (µm/day).
Data from Aris et al. (2020:149,151).

Table D.7: Root dentine daily secretion rate, modern humans

Zone	Mean (Range)
0–50 µm from GLT	1.8 (1.5–2.2)
100–200 µm from GLT	2.9 (2.5–3.3)
In axial plane	4.1 (3.3–4.9)
DSR (µm/day). GLT = Granular layer of Tomes. Data from Dean (1998b:1011–1015).	

Table D.8: Ages of alveolar and partial eruption, deciduous teeth, recent humans

A	Tooth type	di1	di2	dc	dm1	dm2
Maxilla	Alveolar	0.34 ±0.11	0.62 ±0.11	1.05 ±0.26	0.81 ±0.12	1.29 ±0.32
	Midpoint (Partial)	0.72 ±0.12	0.83 ±0.12	1.49 ±0.44	1.22 ±0.34	1.95 ±0.45
	Occlusal	0.85 ±0.12	1.13 ±0.30	2.19 ±0.15	1.36 ±0.11	2.56 ±0.40
Mandible	Alveolar	0.27 ±0.14	0.66 ±0.36	1.05 ±0.30	0.89 ±0.23	1.38 ±0.11
	Midpoint (Partial)	0.66 ±0.12	1.03 ±0.34	1.32 ±0.11	1.21 ±0.11	2.06 ±0.48
	Occlusal	0.90 ±0.33	1.27 ±0.12	1.93 ±0.38	1.65 ±0.25	2.49 ±0.51
Ages in years ±1SD. Data from Liversidge and Molleson (2004:178). The data for alveolar and midpoint eruption are reproduced in Liversidge (2016:161) where <i>midpoint</i> is listed as <i>partial</i> eruption.						
B	Tooth type	di1	di2	dc	dm1	dm2
Mandible	Alveolar	0.46	0.84	1.18	1.05	1.72
	Partial	0.78	1.15	1.62	1.43	2.28
Ages in years ±1SD. Data from Liversidge (2008b:248). The ages for partial eruption are later than in Part A.						

Table D.9: Gingival emergence sequence and ages, deciduous and permanent teeth, recent humans, European

Deciduous						Permanent			
Maxilla	Age (mo) emerges	Age (y) lost	Mandible	Age (mo) emerges	Age (y) lost	Maxilla	Age (y) emerges	Mandible	Age (y) emerges
						UM1	5–7	LM1	5–7
Udi1	8–12	6–7	Ldi1	6–10	6–7	UI1	7–8	LI1	6–7
Udi2	9–13	7–8	Ldi2	10–16	7–8	UI2	8–9	LI2	7–8
Udm1	13–19	9–11	Ldm1	14–18	9–11	UP3	10–11	LC	9–10
Udc	16–22	10–12	Ldc	17–23	9–12	UC	11–12	LP3	10–12
Udm2	25–33	10–12	Ldm2	23–31	10–12	UP4	11–12	LP4	11–12
						UM2	12–13	LM2	11–13
						UM3	17–21	LM3	17–21
Data from https://www.cem.scot.nhs.uk/adult/teeth.pdf , accessed 2024.11.09. These data are from a government health website and consistent with other such websites: e.g. https://www.webmd.com/children/what-to-know-eruption-childrens-permanent-teeth https://www.betterhealth.vic.gov.au/health/conditionsandtreatments/teeth-development-in-children https://my.clevelandclinic.org/health/articles/11179-teeth-eruption-timetable The ages for deciduous tooth emergence are later than for partial eruption in Table D.8.									

Table D.10: Ages at shedding deciduous teeth, recent humans (Clements et al. 1957)

	Tooth type	Male			Female		
		Mean	5% lower limit	95% upper limit	Mean	5% lower limit	95% upper limit
Maxilla	di1	6.69	5.08	8.30	6.49	5.27	7.71
	di2	7.59	5.97	9.22	7.32	5.60	9.03
	dc	11.09	8.63	13.56	10.32	8.00	12.64
	dm1	8.76	5.01	12.52	8.50	4.67	12.32
	dm2	9.60	5.67	13.54	9.37	5.63	13.11
Mandible	di1	6.04	4.68	7.41	5.60	4.72	6.65
	di2	7.15	5.86	8.43	6.66	5.29	8.22
	dc	10.17	7.99	12.36	9.10	7.27	11.15
	dm1	8.24	3.69	12.79	7.82	3.74	12.26
	dm2	8.89	4.12	13.67	8.32	4.32	12.67
Ages in years. Data from Clements et al. (1957:1509), converted from months to years. British children.							

Table D.11: Ages at shedding deciduous teeth, recent humans (Miller et al. 1965)

	Tooth type	Male		Female	
		mean	SD	mean	SD
Maxilla	di1	7.51	0.78	7.27	0.88
	di2	8.3	0.93	7.94	0.95
	dc	11.42	1.07	10.77	1.22
	dm1	11.06	1.19	10.54	1.17
	dm2	11.77	1.24	11.45	1.3
Mandible	di1	6.83	0.68	6.62	0.71
	di2	7.72	0.83	7.62	0.94
	dc	10.66	1	9.98	1.22
	dm1	10.17	1.07	10.61	1.18
	dm2	11.79	1.14	11.61	1.18
Ages in years. Data from Miller et al. (1965:809). British children.					

Table D.12: Ages of alveolar and partial eruption, permanent teeth, recent humans

		I1	I2	C	P3	P4	M1	M2	M3
Maxilla	Alveolar	6.91 ±0.75	7.63 ±0.85	10.90 ±0.98	10.05 ±1.06	10.84 ±0.95	5.27 ±0.96	10.43 ±1.09	16.73 ±2.15
	Partial	7.10 ±0.75	8.12 ±0.98	11.07 ±0.85	10.55 ±1.00	11.13 ±0.99	6.10 ±0.82	11.61 ±1.22	18.94 ±1.84
Mandible	Alveolar	5.66 ±0.77	6.78 ±0.83	10.14 ±1.14	10.47 ±1.07	10.55 ±1.17	4.80 ±0.76	10.04 ±1.02	15.35 ±2.14
	Partial	6.29 ±0.85	7.44 ±0.80	10.52 ±0.96	10.68 ±0.94	10.67 ±1.07	5.86 ±0.86	11.30 ±1.16	17.84 ±2.60
Ages in years ±1SD. Data from Liversidge 2016:161.									

Table D.13: Gingival emergence ages, permanent teeth except third molars, by quadrants, recent humans

		I1	I2	C	P3	P4	M1	M2
Upper Right, teeth 11–17	M	6.30–7.73	7.96–8.90	10.9–11.98	9.60–11.42	10.00–11.67	5.40–7.16	10.80–12.80
	F	6.10–7.46	7.10–8.85	9.40–11.81	9.10–11.35	9.6–11.64	5.00–7.12	10.39–12.45
Upper Left, teeth 21–27	M	6.30–7.73	7.97–8.85	10.60–11.87	9.50–11.41	9.30–11.72	5.40–7.98	11.20–12.81
	F	6.20–7.46	7.20–8.88	9.10–11.86	9.40–11.46	9.91–11.70	5.40–7.74	11.00–12.41
Lower Left, teeth 31–37	M	6.00–7.10	5.70–8.18	10.00–11.08	10.04–11.34	10.50–11.73	5.14–8.01	11.30–12.20
	F	5.50–7.10	6.60–7.92	9.58–10.79	9.10–11.21	10.30–11.71	5.18–7.76	6.10–11.90 ¹ 11.09–11.90
Lower Right, teeth 41–47	M	6.07–7.53	5.80–9.23	10.20–11.04	9.90–11.39	10.70–11.73	5.14–8.94	11.40–12.19
	F	5.82–7.28	6.83–9.10	9.40–10.80	9.60–11.29	5.00–11.65 ² 10.60–11.65	5.18–8.72	10.00–12.06

Ages in years. Ranges of the *means* of seven studies. Some individuals may have been earlier or later than the listed range. Data from Oznurhan et al. (2016:5). Studies include the authors' own from Turkey, and others from Spain, Jordan, India, Uganda, Pakistan and Lithuania. Often, but not always, the youngest ages are from Uganda and India, the oldest from Spain. Some of the Spanish ages, particularly for M1, seem very late.

¹Uganda. Male mean is 11.50, so female 6.10 years may be questioned. Otherwise the youngest female mean reported is 11.09.

²Uganda. Male mean is 11.00, so female 5.00 years may be questioned. Otherwise the youngest female mean reported is 10.60. The Ugandan values come from Kutesa et al. (2013:4). In their Table 2 the female emergence ages are: Tooth number 45 (LRP4) 5.0, 46 (LRM1) 10.5, 47 (LRM2) 6.2. Clearly values have been transposed. Oznurhan et al. interpreted 10.5 as the M2 emergence age and 6.2 as the M1, the male value also being 6.2. However, 5.0 for the P4 is allowed to stand but is unlikely to be correct. As the female lower left M1 emergence age in their Table 2 is 5.3, 5.0 is not impossible for the LRM1. However, the LLM2 is listed as 6.1, which seems unlikely.

Table D.14: Gingival emergence ages, permanent teeth except third molars, by continent, recent humans

		I1	I2	C	P3	P4	M1	M2	
Africa	U	M	6.42–7.38	7.42–8.60	10.06–11.29	9.6–10.45	10.74–11.25	5.50–6.67	11.00–12.32
		F	6.42–7.13	7.32–8.10	9.70–11.00	9.30–10.06	10.10–10.73	5.06–6.27	10.30–11.67
	L	M	5.23–6.57	6.5–7.52	9.95–10.58	9.90–10.70	10.90–11.44	5.15–6.47	10.60–11.96
		F	5.31–6.34	6.40–7.19	8.50–10.00	8.87–10.09	10.30–11.00	4.74–6.08	10.74–11.50
Europe	U	M	6.65–8.64	7.50–9.70	10.40–12.94	9.10–12.16	9.86–13.24	6.00	11.40
		F	6.20–8.23	7.15–9.40	9.72–12.69	8.60–11.53	9.60–12.35	4.98–7.30	10.75–13.33
	L	M	5.75	6.78–8.86	9.52–12.19	9.25–12.42	10.15–13.41	5.70	10.75–13.58
		F	4.95–7.35	6.55–8.55	8.75–11.20	8.83–11.96	9.55–12.79	5.45	10.25–12.97
East Asia	U	M	6.29–9.99	7.34–10.27	9.83–13.26	8.64–13.42	9.64–14.14	6.12–7.78	11.47–14.49
		F	6.17–9.99	7.19–10.27	9.23–13.11	8.64–12.57	9.64–13.59	5.74–8.36	11.12–14.49
	L	M	6.15–7.79	5.84–9.14	9.25–13.11	9.06–13.52	9.85–13.86	6.12–7.78	10.83–14.04
		F	6.15–7.79	6.08–9.44	9.25–12.51	9.06–12.93	9.85–13.86	5.74–8.36	10.83–13.91

Ages in years. M = male, F = female, U = maxillary, L = mandibular.

Data from Liversidge (2003:85–86).

Ranges here are each composed from several country means. Lower ages are lowest obtainable from the data, either the lowest mean or a low mean minus 1 standard deviation. Higher ages are highest obtainable, either the highest mean or a high mean plus 1 standard deviation.

Africa = Gambia, Ghana, Kenya, Ivory Coast, Uganda, Zambia only. Europe = Italy, Russia. East Asia = China, Tibet. Nigeria is excluded because ages listed are ~1 year older than the other West African values, which may indicate a difference in method. The USA African diaspora is omitted.

Table D.15: Gingival emergence ages, permanent first molar, by geography/continent, recent humans

	Europe	Africa	Asia	Indo-Mediterranean	Australasia
Median	6.0	5.7	5.8	6.0	5.4
Range	5.4–6.3	4.7–6.2	5.4–6.5	5.7–6.9	5.1–5.8
Ages in years. Ranges are for all four quartiles excluding outliers. Data from Liversidge (2003:91).					

Table D.16: Gingival emergence ages, permanent first and second molars, recent humans, African

			Ghana 1967	Nigeria 1971	Uganda 1971	Uganda 2013
M1	Maxilla	M	5.0	6.3	5.1	6.4
		F	5.0	5.8	5.4	5.3
	Mandible	M	4.7	6.0	5.3	6.0
		F	4.4	5.8	5.4	5.2
M2	Maxilla	M	10.9	11.8	10.5	10.0
		F	10.9	11.4	9.8	10.7
	Mandible	M	10.6	11.3	10.2	11.5
		F	10.5	10.9	9.4	10.3
Mean ages in years. Data from Kutesa et al. (2013:6).						

Table D.17: Gingival emergence ages, permanent molars, by geography, recent humans

			Male		Female	
Continent	Population		Maxillary	Mandibular	Maxillary	Mandibular
Africa	Cameroon, Baka ¹	M1	5.33 (5.17–5.48)	5.18 (5.01–5.34)	5.15 (5.01–5.28)	4.95 (4.81–5.09)
		M2	10.97 (10.72–11.22)	10.76 (10.52–11.00)	9.98 (9.48–10.41)	9.88 (9.49–10.23)
		M3	19.63 (18.60–21.74)	18.33 (17.61–19.46)	16.66 (16.10–17.43)	16.13 (15.52–16.94)
	Ghana ²	M1	5.0 ±1.5	5.0 ±1.6	4.9 ±1.2	4.5 ±1.2
		M2	10.9 ±1.9	10.9 ±2.0	10.8 ±1.9	10.5 ±1.8
		M3	16.7 ±1.7	-	16.5 ±1.5	-
	Kenya ³	M1	5.4	5.4	5.3	5.1
		M2	11.3	11.2	10.8	10.3
	Kenya ⁴	M3	18.76 ±2.45	17.95 ±2.53	17.63 ±2.81	18.47 ±2.38
	Nigeria, rural ⁵	M3	16 (15–21+)	16 (14–21+)	16 (14–21+)	16 (13–21+)
	South Africa ⁶	M1	5.26 ±0.68	5.19 ±0.64	5.74 ±0.59	5.49 ±0.74
		M2	11.33 ±1.21	11.04 ±1.09	10.93 ±1.32	10.61 ±1.52
	Southern African ⁷	M1	6.27 ±0.29	6.11 ±0.28	6.04 ±0.89	5.37 ±1.13
		M2	12.75 ±1.78	12.64 ±2.07	12.07 ±1.20	11.69 ±1.51
		M3	18.82 ±1.45	18.45 ±1.97	19.56 ±2.89	18.58 ±2.49
	Uganda, Kampala ⁸	M1	6.4	6.0	5.3	5.2
		M2	10.0	11.5	10.7	10.3
Uganda ⁹	M1	5.1 ±1.1	5.3 ±1.7	5.4 ±1.5	5.4 ±1.9	
	M2	10.5 ±1.9	10.2 ±2.1	9.8 ±1.6	9.4 ±1.5	
Uganda ¹⁰	M3	13–24		-		
Asia	India, North-East ¹¹	M3	17.33 ±2.00	17.76 ±2.89	18.40 ±1.82	18.36 ±1.29
	Japan ¹²	M3	21.4 (15.9–25.8)	21.4 (16.8–25.9)	21.2 (16.1–26.3)	21.4 (18.1–25.9)
	Pakistan, Peshawar ¹³	M1	7.6	7.2	6.3	6.6
		M2	10.1	11.8	8.3	11.2
	Thailand, Bang Chan ¹⁴	M1	7.0	7.0	7.0	7.0
		M2	12.2	11.7	12.1	11.6
Australasia	Australia, Yuendumu ¹⁵	M1	6.4 ±0.7	6.4 ±0.7	5.7 ±1.1	5.1 ±0.0
		M2	11.5 ±1.0	11.2 ±1.1	11.0 ±1.1	10.8 ±1.0
		M3	16.8 ±1.3	16.5 ±1.3	16.1 ±1.3	16.1 ±1.0
	Australia ¹⁶	M1	6.0 (5–7)	6.0 (5–7)	6.5 (5–8)	6.0 (5–7)
		M2	11.5 (9–14)	11.0 (9–13)	13.0 (10–16)	(9–14)
		M3	18.0 (16–20)	17.5 (16–19)	19.0 (15–19)	19.0 (13–19)
	Australia, Yuendumu ¹⁷	M1	6.1 ±0.3	6.5 ±0.9	5.7 ±1.2	5.1
		M2	11.3 ±1.0	11.0 ±1.1	10.7 ±1.2	10.5 ±1.0
		M3	16.6 ±1.2	16.4 ±1.3	15.9 ±1.2	15.9 ±1.1
	New Guinea, Kaiapit ¹⁸	M1	5.7 (5.3–6.1)	5.2 (4.9–5.4)	5.7 (5.4–6.0)	5.5 (5.3–5.8)
		M2	11.3 (10.8–11.9)	11.3 (10.8–11.9)	10.3 (9.9–10.7)	10.3 (9.9–10.7)
		M3	19.2	18.6	17.2 (16.3–18.0)	17.0 (15.4– ?)
	New Guinea, Bundi ¹⁹	M1	5.85 ±0.68	5.85 ±0.74	5.52 ±0.77	5.41 ±0.81
		M2	11.53 ±1.28	11.45 ±1.21	10.88 ±1.33	10.88 ±1.06
		M3	18.65 ±2.38	18.53 ±2.58	18.49 ±2.06	18.41 ±2.24
	New Guinea, Siassi Islands ²⁰	M1	-	5.48 ±0.33	-	5.29 ±0.45
		M2	-	10.83 ±0.62	-	10.13 ±0.51
	New Guinea, Baiyer River ²⁰	M1	-	5.27 ±0.47	-	5.31 ±0.49
		M2	-	10.65 ±0.53	-	10.25 ±0.59
New Guinea, Papuan Gulf ²⁰	M1	-	5.49 ±0.50	-	5.36 ±0.42	
	M2	-	10.68 ±0.67	-	9.97 ±0.65	
New Guinea, Bougainville ²¹	M1	5.91 (5.42–6.44)	5.91 (5.38–6.48)	5.77 (5.06–6.57)	5.76 (5.06–6.56)	
	M2	11.31 (9.96–12.93)	11.02 (9.55–12.71)	10.92 (10.07–11.86)	10.54 (9.78–11.38)	
Europe	Belgium, Flemish ²²	M1	6.30 (6.23–6.37)	6.28 (6.21–6.39)	6.13 (6.04–6.22)	6.10 (6.00–6.19)
		M2	12.22 (12.13–12.31)	11.81 (11.75–11.88)	11.91 (11.83–11.98)	11.43 (11.37–11.49)
	Denmark ²³	M1	6.20 ±0.70	6.24 ±0.70	6.04 ±0.68	6.01 ±0.66
		M2	12.24 ±1.21	11.91 ±1.21	11.81 ±1.16	11.43 ±1.15
	USA, Boston ²⁴	M3	15.0–20.0+	14.0–20.0+	15.0–20.0+	14.0–20.0+
Age (y), mean and 1SD or range, unless stated. If source reports antimeres, earlier emerging age is listed. Third molars in bold.			⁷ Esan et al. (2018). ⁸ Kutesa et al. (2013). ⁹ Krumholt et al. (1971). ¹⁰ Chagula (1960). ¹¹ Putul et al. (2021). ¹² Olze et al (2008). ¹³ Khan et al. (2019). ¹⁴ Kamalanathan et al. (1960) cited by Houpt et al. (1967). ¹⁵ Brown (1978).		¹⁶ Abbie (1975) cited by Collier (1982), median. ¹⁷ Jenner (1972). ¹⁸ Malcolm (1969a). ¹⁹ Malcolm (1969b). ²⁰ Brook and Barker (1972). ²¹ Friedlaender and Bailit (1969), median and 95% CI. ²² Leroy et al. (2003), median and 95% CI. ²³ Heidmann (1986). ²⁴ Fanning (1962).	

Age (y), mean and 1SD or range, unless stated. If source reports antimeres, earlier emerging age is listed. Third molars in bold.
¹ Ramírez-Rozzi (2016:2).
² Houpt et al. (1967).
³ MacKay and Martin (1952) cited by Krumholt et al. (1971).
⁴ Hassanali (1985).
⁵ Otuyemi et al. (1997).
⁶ Suk (1919) cited by Krumholt et al. (1971).

⁷ Esan et al. (2018).
⁸ Kutesa et al. (2013).
⁹ Krumholt et al. (1971).
¹⁰ Chagula (1960).
¹¹ Putul et al. (2021).
¹² Olze et al (2008).
¹³ Khan et al. (2019).
¹⁴ Kamalanathan et al. (1960) cited by Houpt et al. (1967).
¹⁵ Brown (1978).

¹⁶ Abbie (1975) cited by Collier (1982), median.
¹⁷ Jenner (1972).
¹⁸ Malcolm (1969a).
¹⁹ Malcolm (1969b).
²⁰ Brook and Barker (1972).
²¹ Friedlaender and Bailit (1969), median and 95% CI.
²² Leroy et al. (2003), median and 95% CI.
²³ Heidmann (1986).
²⁴ Fanning (1962).

APPENDIX E

ENDOCRANIAL VOLUMES, FOSSIL *HOMO*

This appendix contains the following tables, discussed in Chapter 4.

1. *Homo neanderthalensis* immatures
2. *Homo neanderthalensis* adults
3. *Homo neanderthalensis* adults, male
4. *Homo neanderthalensis* adults, female
5. *Homo neanderthalensis* adults before 100 ka
6. *Homo neanderthalensis* lower-ECV adults after 100 ka
7. *Homo neanderthalensis* higher-ECV adults after 100 ka
8. *Homo sapiens*, Upper Palaeolithic, Eurasia, down to 15ka
9. *Homo sapiens*, Middle Stone Age/Middle Palaeolithic, Africa and Eurasia
10. *Homo heidelbergensis sensu lato*, Middle Pleistocene, Eurasia
11. *Homo heidelbergensis sensu lato/Homo rhodesiensis*, Middle Pleistocene, Africa
12. *Homo erectus*, Lower and Middle Pleistocene, Asia
13. *Homo erectus sensu lato/Homo antecessor*, Lower Pleistocene, Europe
14. *Homo erectus sensu lato/Homo ergaster*, Lower Pleistocene, Africa

Tables cover all available endocranial volumes (ECV) from *Homo ergaster/erectus* onward. Mean ECV, especially for *Homo erectus (s.l.)*, covering such a long time scale, is not always informative. Alternative values from sources are listed for completeness. For adult and subadult Neanderthals compromise values are presented in the first ECV column. The compromise values are used in Chapter 5. Dates are taken from Lieberman (2011) where possible, and if not then from Holloway et al. (2004), and the other sources from left to right in the tables. Assignment to male and female is sometimes on the basis of ECV itself, since not all specimens have diagnostic postcrania or viscerocrania.

Table E.1: Endocranial volumes, *Homo neanderthalensis immatures*

Specimen	Age (y)	Date (ka)	Endocranial volume (cm ³)													
			<i>Compromise value</i>	Lieberman (2011)	Holloway et al. (2004)	Madre-Dupouy (1992)	Tillier (1988)	Minugh-Purvis (1988)	Heim (1982)	Thompson and Illerhaus (2005)	Ponce de León and Zollikofer (1999)	Ponce de León et al. (2008)	Gunz et al. (2012)	Debetz and Sinelnikov in Gremyatskii (1949)	Rosas et al. (2017)	Cofran et al. (2021)
Le Moustier 2	0	40–45	418										408–428			
Mezmaiskaya 1	0	57–68	422									422–436	414–423			
Pech de l'Azé	1.5	43–51	1150	1150		1198	1150–1200	1115	1115			1135				
Dederiyeh 1	1.5	>54	1096									1096				
Dederiyeh 2	2.0	48–54	1089									1089				
Roc de Marsal	2.3	40–60	1250	1260		1270										
Subalyuk	3.0	70 ?	1187				1000–1100	1000–1100				1187				
Engis 2	3.0	60	1362	1362	1362	1256	1290	1392								
Gibraltar 2	4.6	30–50	1400	1400	1400											
La Quina H18	5.5	60	1200	1200	1200	1284	1250	1166–1188, 1249	1188							
Krapina 1 (Skull A)	6–8	130	1419													1419
Krapina 2 (Skull B)	6–8	130	1286		1450 ¹											1286
El Sidrón J1	7.7	49	1330												1330	
Teshik Tash	8.0	70	1490		1525	1569	1475–1490	1389, 1490	1389	1440				1490		
Le Lazaret	8.5	160–200	1250	1250	1250											
La Ferrassie 3	10	40–54	1444					1444	1444							
Le Moustier 1	12	41	1540	1565	1565			1564		1540	1590–1650					

Ages at death from Appendix A are those from counts of daily increments in dental microstructure when these are available, otherwise the best evidenced ages from published estimates.

¹ Cofran et al. (2021) state that this estimate 1450 cm³ first applied to a Krapina adult cranium, then was mistakenly attributed to the juvenile, and was in any case unreliable.

Table E.2: Endocranial volumes, *Homo neanderthalensis adults*

Specimen	Date (ka)	Endocranial volume (cm ³)						
		<i>Compromise value</i>	Lieberman (2011)	Holloway et al. (2004)	Neubauer et al. (2018)	Heim (1970, 1989)	Cofran et al. (2021)	Miguel and Henneberg (2001)
Reilingen	125–250	1430	1430	1430				1430, 1434
Vértesszöllös 2	186	1328						1115–1437, 1300, 1325, 1328, 1350, 1363, 1400
Biache	160–190	1200		1200				1200
La Chaise (Suard)	151	1065						1065
Krapina 3 (C)	130	1255		1255			1247 (1247–1310)	1200
Krapina 5 (D)	130	1397					1397	1450
Krapina 6 (E)	130	1205		1205			1178 (1135–1207)	
Saccopastore 1	122–129	1245	1245	1245				<1200, 1245, 1258
Saccopastore 2	122–129	1300	1300	1300				1280–1300, 1300
Tabun 1	110	1271		1271				1270, 1271
Ganovce	90	1320		1320				1320
La Ferrassie 1	60–75	1641	1640	1640	1643	1681 ³		>1600, 1640, 1641, 1681, 1689
La Quina H5	65	1350	1350	1172				1307, 1345, 1350, 1367
Shanidar 1	60	1600		1600				1600, 1700
Shanidar 5	60	1550		1550				1550
Monte Circeo (Guattari 1)	50–60 65–66 ⁵	1360	1550	1360 ¹	1421			1550, 1552
Spy 1 ²	50 or 68	1305	1553	1305	1287			1300, 1305, 1500, 1525, 1562, 1553
Spy 2 ²	50 or 68	1553	1305	1553	1531			1305, 1425, 1504, 1553, 1650
Gibraltar 1	50	1200	1200	1200	1213			1075, 1080, 1200, 1260, 1270, 1296, 1300, 1333
La Chapelle-aux-Saints	47–56	1625	1625	1625	1490	1593 ⁴		1600, 1610, 1620, 1625, 1626, 1550–1600
Amud 1	41	1740		1740	1747			1740, 1750
Neanderthal (Feldhofer)	40	1525	1525	1525	1261			1033, 1230, 1234, 1370, 1408, 1450, 1452, 1525
Mean		1384.8	1429.4	1396.4	1449.1			

For the Krapina specimens, designations are taken from Holloway et al. (2004:299) and Cofran et al. (2021:121).

¹ Monte Circeo (Guattari), usually quoted as 1550 (after Sergi 1974), was revised downward by Recheis et al. (1999).

² Spy 1 and 2 ECVs are reversed between (a) Holloway et al. (2004) and Neubauer et al. (2018) and (b) Lieberman (2011). Also, Holloway et al. date the Spy remains to 68 ka. The ambiguity of the Spy designations may be explained by the assignment of each cranium Spy 1 and 2 to one or the other of two sets of postcrania Spy 1 and 2, either way forming only two individuals, one of each sex (F.H. Smith 1980:368).

³ Heim (1970).

⁴ Heim (1989).

⁵ Rolfo et al. (2023).

Table E.3: Endocranial volumes, *Homo neanderthalensis* adults, male

Specimen	Date (ka)	ECV (cm ³)
Reilingen	125–250	1430
Vértesszöllös 2	186	1328
Krapina 5 (D)	130	1397
Saccopastore 2	122–129	1300
La Ferrassie 1	60–75	1641
La Quina H5	65	1350
Shanidar 1	60	1600
Shanidar 5	60	1550
Monte Circeo (Guattari 1)	50–60 or 65–66	1360
Spy 2 ²	50 or 68	1553
La Chapelle-aux-Saints	47–56	1625
Amud 1	41	1740
Neanderthal (Feldhofer)	40	1525
Mean		1492.2

Table E.4: Endocranial volumes, *Homo neanderthalensis* adults, female

Specimen	Date (ka)	ECV (cm ³)
Biache	160–190	1200
La Chaise (Suard)	151	1065
Krapina 3 (C)	130	1255
Krapina 6 (E)	130	1205
Saccopastore 1	122–129	1245
Tabun 1	110	1271
Ganovce	90	1320
Spy 1	50 or 68	1305
Gibraltar 1	50	1200
Mean		1229.6

Table E.5: Endocranial volumes, Homo neanderthalensis adults before 100 ka

Specimen	Date (ka)	ECV (cm ³)
Reilingen	125–250	1430
Vértesszöllös 2	186	1328
Biache	160–190	1200
La Chaise (Suard)	151	1065
Krapina 3 (C)	130	1255
Krapina 5 (D)	130	1397
Krapina 6 (E)	130	1205
Saccopastore 1	122–129	1245
Saccopastore 2	122–129	1300
Tabun 1	110	1271
Mean		1269.6

Table E.6: Endocranial volumes, Homo neanderthalensis lower ECV adults after 100 ka

Specimen	Date (ka)	ECV (cm ³)
Ganovce	90	1320
La Quina H5	65	1350
Monte Circeo (Guattari 1)	50–60 or 65–66	1360
Spy 1	50	1305
Gibraltar 1	50	1200
Mean		1307.0

Table E.7: Endocranial volumes, Homo neanderthalensis higher ECV adults after 100 ka

Specimen	Date (ka)	ECV (cm ³)
La Ferrassie 1	60–75	1641
Shanidar 1	60	1600
Shanidar 5	60	1550
Spy 2	50	1553
La Chapelle-aux-Saints	47–56	1625
Amud 1	41	1740
Neanderthal (Feldhofer)	40	1525
Mean		1604.9

Table E.8: Endocranial volumes, *Homo sapiens*, Upper Palaeolithic, Eurasia, down to 15ka

Specimen	Date (ka)	Endocranial volume (cm ³)			
		Lieberman (2011)	Holloway et al. (2004)	Neubauer et al. (2018)	Miguel and Henneberg (2001)
Nazlet Khater	37		1420		1420
Hofmeyr	36			1498	
Mladeč 1 (16–17y)	31		1540	1606	1540, 1559, 1620
Mladeč 2 (17–18y)	31		1390		1390
Mladeč 5	31		1650		1500, 1650
Mladeč range	31	1390–1650			
Předmost 3	30		1580		1580, 1608
Předmost 4	30		1250		1250, 1500, 1518
Předmost 9	30		1555		1555
Předmost 10	30		1452		1452
Předmost range	30	1250–1580			
Grimaldi 4	25–30				1715, 1775
Grimaldi 5	25–30				1375, 1518
Grimaldi 6	25–30				1500, 1580
Grimaldi range	25–30	1375–1880			
Combe Capelle	28		1570		1440
Cro-Magnon 1	27		1730	1574	1590, 1593, 1600, 1636, 1660
Cro-Magnon 2	27				1402
Cro-Magnon 3	27		1590	1813	1730
Cro-Magnon range	27	1600–1730			
Dolni Vestonice 3	26		1285		1293, 1322
Dolni Vestonice 13	26			1590	
Dolni Vestonice 14	26		1538	1663	
Dolni Vestonice 15	26			1385	
Dolni Vestonice 16	26			1542	
Dolni Vestonice 18	26		1481		
Dolni Vestonice 20	26		1378		
Dolni Vestonice 21	26		1547		
Dolni Vestonice range	26	1285–1547			
Pavlov 1	26		1472		1522
Brno 1	18				1600
Brno 2	18				1543
Brno female	18				1250
Brno range	23–27	1304–1600			
Sungir 1	24		1464		
Sungir 2 (10–12y)	24		1267		
Sungir 3 (9–10y)	24		1361		
Sungir 5	24		1453		
Arene Candide 1	23				1490
Arene Candide range	23	1414–1520			
Abri Pataud	22	1380		1323	1383
Ohalo 2	22			1475	
Kostenki 2	20		1605		
Kostenki 14	20		1222		
Barma Grande 2	18				1748, 1880
Minotagawa 1	16–18	1390	1390		1390
Minotagawa 2	16–18	1170	1170		1170
Minotagawa 4	16–18	1090	1090		1090
Taza 1	16				1125
Zhoukoudian 1	15		1500		1500
Zhoukoudian 2	15				1380
Zhoukoudian 3	15				1290, 1300
Mean			1442.6	1546.9	
Lieberman's ranges are for multiple individuals at a given site.					
The relative sizes of Cro-Magnon 1 and 3 are reversed between some authors.					

Table E.9: Endocranial volumes, Homo sapiens, Middle Palaeolithic/Middle Stone Age, Africa and South West Asia

Specimen	Date (ka)	Endocranial volume (cm ³)				
		Lieberman (2011)	Holloway et al. (2004)	Neubauer et al. (2018)	Rightmire (1985)	Miguel and Henneberg (2001)
Jebel Irhoud 1	281–349 ¹	1305	1305	1375		1305, 1420, 1480, 1500
Jebel Irhoud 2	281–349 ¹	1450	1400	1467		1305, 1450
KNM-ER3884	270					1400
Laetoli 18 (Ngaloba)	200–300	1367	1367	1237		1200, 1367
Omo 1	130 ?					1400
Omo 2	195	1435	1435	1491	1430	1430, 1435
Herto 1/16	160	1450	1450			
Florisbad	150					1280
KNM-ES11693 (Eliye Springs)	150					1300–1450
Singa 1	140–150	1550	1550			1550
Yinkou	130		1390			
Skhul 1	100		1450			
Skhul 2	100					1300
Skhul 4	100		1554			1554, 1555
Skhul 5	100		1520	1363		1450, 1510, 1518, 1520
Skhul 9	100		1590			1585, 1587, 1590
Qafzeh 6	90		1568	1524		1535, 1554, 1560, 1568, 1569, 1570
Qafzeh 9 (immature)	90		1531	1497		1531
Qafzeh 11 (immature, 12–13y)	90		1280			1280
Border Cave	70	1510	1510			1450, 1507
Liujiang	40		1480			1480
Eyasi	35					1220–1250
Mean		1438.1	1461.3	1422.0	1430.0	
¹ Revised dates from Hublin et al. (2016) and Richter et al. (2017).						

Table E.10: Endocranial volumes, Homo heidelbergensis sensu lato, Middle Pleistocene, Eurasia

Specimen	Date (ka)	Endocranial volume (cm ³)				
		Lieberman (2011)	Holloway et al. (2004)	Neubauer et al. (2018)	Rightmire (1985)	Miguel and Henneberg (2001)
Sima de los Huesos 4	430 ¹	1390				
Sima de los Huesos 5	430 ¹	1125				
Arago 21	350–600	1166	1166		1166	1166, 1100, 1100–1200
Petralona	200–700	1220	1230	1162	1200	1155, 1170, 1200, 1220, 1230, 1384, 1400, 1440, 1190–1210
Hexian	412		1025			1000, 1025
Swanscombe	400	1250	1325			1250, 1275, 1300, 1325, 1375
Yunxian	350					1100
Steinheim	250–350	900	1200			900, 922, 950, 1000, 1070, 1100, 1110, 1163, 1170, 1239, 1150–1175, 1184–1214, 1460
Jinniushan	200–300	1300	1390			1260, 1300, 1390
Dali	180–230	1120			1120	1120, 1200
Ehringsdorf 9	200–205	1450	1450			1450
Mean		1213.4	1255.1	1162.0	1162.0	

¹ Date from Arsuaga et al. (2014).

Table E.11: Endocranial volumes, Homo heidelbergensis sensu lato/Homo rhodesiensis, Africa

Specimen	Date (ka)	Endocranial volume (cm ³)				
		Lieberman (2011)	Holloway et al. (2004)	Neubauer et al. (2018)	Rightmire (1985)	Miguel and Henneberg (2001)
Elandsfontein	500–1000	1225				
Ternifine	750					1300
Bodo	600	1250	1250			1250, 1300
Saldanha	500		1225			1200, 1225, 1200–1250
Ndutu	400	1100			1100	1100
Salé	400	880				860, 880, 925, 945, 930–960
Kabwe	300–600	1280	1325	1249	1285	1270, 1280, 1285, 1300, 1325, 1400
Mean		1147.0	1266.7	1249.0	1192.5	

Table E.12: Endocranial volumes, Homo erectus, Asia

Specimen	Date (ka)	Endocranial volume (cm ³)			
		Lieberman (2011)	Holloway et al. (2004)	Neubauer et al. (2018)	Miguel and Henneberg (2001)
Sangiran 2	1000–1600	813	813	793	745, 750, 775, 800, 813, 815, 850
Sangiran 3 (immature)	1000–1600	950	950		890
Sangiran 4	1000–1600	908	908		750, 808, 880, 890, 900, 908
Sangiran 9	1000–1600				856
Sangiran 10	1000–1600	855	855		700, 855, 900, 913, 975
Sangiran 12	1000–1600	1059	1059		900, 915, 930, 1059
Sangiran 17	1000–1600	1004	1004		1004, 1027, 1029
Trinil 2	900–1200	940	940		850, 855, 896, 900, 914, 935, 940, 943, 953, 1000
Gongwangling (Lantian)	1000	780	780		780, 778, 775–783
Zhoukoudian 2	600–780	1030			1030
Zhoukoudian 3	600–780	915	915		915, 960
Zhoukoudian 10	600–780	1225	1225		1225
Zhoukoudian 11	600–780	1015	1015		1015
Zhoukoudian 12	600–780	1030	1030		1030
Zhoukoudian 5	400–500	1140			1140, 1300
Zhoukoudian 6	300				850
Yunxian 1	400–800	1200	1200		
Narmada	236		1260		1200, 1260, 1155–1421
Sambungmacan 1	50–100	1035	1035		1034, 1035, 1100
Sambungmacan 3	50–100	917	917	902	900
Sanbungmacan 4	50–100	1006	1006		
Ngawi 1	50–100	1000	870	952	
Ngandong 1	27–125	1172	1120		1000, 1035, 1140, 1143, 1160, 1172, 1200
Ngandong 6	27–125	1251	1251		1225, 1250, 1251, 1255, 1300, 1316
Ngandong 7	27–125	1013	1013		1013, 1035, 1087, 1150, 1160, 1175, 1190
Ngandong 10	27–125				1135
Ngandong 11	27–125				1055, 1231
Ngandong 12	27–125	1135	1135		1060, 1090
Ngandong 13	27–125	1231	1231		
Ngandong 14	27–125	1090	1090	1127	
Mean		1028.6	1025.9	943.5	

Table E.13: Endocranial volumes, *Homo erectus sensu lato/Homo antecessor, Europe*

Specimen	Date (ka)	Endocranial volume (cm ³)		
		Lieberman (2011)	Holloway et al. (2004)	Miguel and Henneberg (2001)
Dmanisi A	1800			775–780
Dmanisi B	1800			650
Atapuerca 4	800–900 ¹		1390	1390
Atapuerca 5	800–900 ¹		1125	1125
Atapuerca 6 (immature)	800–900 ¹		1140	1100, 1140, 1220
Ceprano	500–900	1185	1165	1185
Mean		1185.0	1218.3	

¹ Dates from Lieberman, who does not give ECVs for these specimens. Holloway et al. give a date 350 ka.

Table E.14: Endocranial volumes, *Homo erectus sensu lato/Homo ergaster, Africa*

Specimen	Date (ka)	Endocranial volume (cm ³)			
		Lieberman (2011)	Holloway et al. (2004)	Neubauer et al. (2018)	Miguel and Henneberg (2001)
KNM-ER3733	1780			878	800, 804, 848, 850, 800–850
KNM-ER3833	1570			838	
KNM-ER3883	1570				804, 848, 800–850
KNM-WT15000 (immature)	1500		900	850	880
Olduvai 9	1200		1067	1013	1000, 1067, 1060–1070, 1100–1200
Olduvai 12	900–1200	725–750	727		720, 727, 700–800
Buia	1000	750–800			
Daka	1000	995	995		
Mean			922.3	931.5	

APPENDIX F

NEUROCRANIAL GROWTH AND APOMORPHIES: SUPPLEMENT

F.1 Cranial base and vault

The base of the cranium includes elements of the occipital, temporal, frontal, sphenoid and ethmoid bones. Most parts of it, including the petrous temporals and the supraoccipital part of the occipital squama are endochondral bone, arising from cartilaginous precursors, like most of the postcrania, whereas the calvaria, formed by the frontal, temporal and parietal squamae and only the interparietal part of the occipital squama, is of intramembranous origin (Gunz and Harvati 2007:154; Lieberman 2011:26–28; Cunningham, Scheuer and Black 2016:45,48). Development of endochondral bone is believed to be more closely under genetic control, so the morphology of the cranial base may be largely constrained by inheritance while the calvarial bones may be more readily influenced by epigenetic factors (Lieberman et al. 2000b:158). The cranial base is the first part of the neurocranium to reach adult size, in modern humans at ~6–8 years (Lieberman et al. 2000b:144,158; Rightmire 2012:4).¹

During ontogeny expansion of the cerebrum is constrained inferiorly by the brainstem and medulla and by the cranial base, to which the viscerocranium is attached anteroinferiorly (Lieberman et al. 2000b:137). The cerebellum lies in the posterior cranial fossa, which rests above the nuchal musculature, yet expands throughout childhood (Tiemeier et al. 2010; Kranioti et al. 2009:1764,1768). The frontal bone is constrained inferiorly by orbital and nasal structures (Rightmire 2012), while the rest of the cranial vault has no external constraints to expansion, so that temporal, parietal and occipital squamae can grow superiorly, laterally and posteriorly through drift (deposition and resorption) of the bony plates and deposition at the sutures (Lieberman 2011:177–178).

In non-human primates the cranial base determines the breadth and length of the neurocranial vault. During ontogeny the nuchal plane formed by the supraoccipital part of the occipital bone tilts superoposteriorly, carrying the foramen magnum posteriorly with respect to the rest of the skull (Lieberman et al. 2000b:124), so that most of the brain lies anterior to it. In *Homo* this tilting is expressed to a much lesser degree, enabling the interparietal part of the occipital to expand above the nuchal plane, where posterior growth is no longer constrained. Even so, in *Homo erectus* the most posterior point on the cranium is usually inion rather than on the interparietal squama of the occipital as it is in more encephalized later hominins (Coon 1962:342).

As listed in Table F.1, cranial base width, measured as biauricular breadth, is wider in *Homo erectus* than in living humans, and remains at least as wide in the Middle Pleistocene hominins and Neanderthals. In living and most, but not all, fossil *Homo sapiens* the width is reduced. Three of the Upper Palaeolithic (~35 ka) Mladeč specimens are included in the table to illustrate the variation in these early modern Europeans: Mladeč 5 exceeds the means of earlier groups.²

¹ Although the occipital bone immediately lateral and posterior to the foramen magnum is by its position and endochondral origin part of the base of the cranium (Keith 1927), only the area anterior to basion, i.e. from basion to the foramen caecum, is strictly termed the cranial base or basicranium (Scott 1958; Lieberman 2011).

² The Mladeč 5 and 6 crania are long and very wide. Mladeč 6 biauricular breadth is not available (Freyer et al. 2006:207–208; 227–228). They may be male and Mladeč 1 and 2 female (Freyer 1986).

Table F.1: Cranial base (biauricular) breadth

	AUB mean (mm)	AUB range (mm)
<i>H. erectus</i> ¹	133.8	
Middle Pleistocene ¹	134.0	
Neanderthals ²	139.2	127.6–146.6
Skhul/Qafzeh ² (S)	131.1	123.8–135.0
Mladeč 5 ² (S)	150.0	
Mladeč 1 ³ (S)	128.8	
Mladeč 2 ³ (S)	130.4	
Living humans ¹	117.3	
S = sapiens. ¹ Rightmire 2012.	² Frayer et al. 2006. ³ Frayer 1986.	

In the genus *Homo*, the cranial base partly determines the morphology of the base of the brain while the brain determines the morphology of the vault (Moss and Young 1960:282; Bruner et al. 2015:268). The cranial base also affects upper facial width and neurocranial vault width but not vault length, which is determined by anteroposterior growth of the brain (Lieberman 2000a:296–297,306, 2011:569; Rightmire 2012).

The anterior (prechordal) and posterior (postchordal) areas of the cranial base are separated by the hypophyseal fossa within the sella turcica (Figure F.1). While the anterior cranial base, supporting the frontal lobes, lies horizontally, the posterior cranial base inclines posteroinferiorly into the clivus leading to the foramen magnum. The angulation (measured inferiorly) between these planes affects the shape of the neurocranium. The more obtuse the angulation, the more the cranial base is flattened or extended and the neurocranium is likely to be more elongated. A tighter angle will tend to induce a more globular neurocranium. The *cranial base angle*, illustrated in Figure F.1, is intended to quantify this angulation. It is measured in the midline, from basion to a vertex at the sella turcica and anteriorly to one of various landmarks on the anterior base: the cribriform plate, foramen caecum, or nasion (Aiello and Dean 1990:62). Much recent work has used sella, the midpoint of the sella turcica, readily identified radiographically, and anteriorly the foramen caecum (Lieberman 2011:103,616). This is the CBA1 of Lieberman et al. (2000a; 2000b; Lieberman 2011), who also defined alternative cranial base angles CBA2–4 using other points.

Table F.2 lists cranial base angles for *Homo* samples. Neanderthals either fall into the distribution of earlier *Homo* or exceed those values. Only with *Homo sapiens* does a distinctly smaller angle appear. Bastir et al. (2008:131) point out that basicranial flexion is evidently not a consequence of encephalization alone, otherwise *Homo heidelbergensis* and Neanderthals would manifest it.

Earlier anthropologists defined a cranial base angle using nasion as anterior point (e.g. Keith 1927; McCown and Keith 1939; Heim 1989). As nasion lies anteroinferiorly to the foramen caecum, an angle using nasion should be slightly tighter. Also, in these cases tuberculum sellae,¹ the anterior margin of the sella turcica, has been used (Heim 1989) rather than sella midpoint. Measurements are therefore not always fully comparable.²

¹ Strictly the superior midline point of the tuberculum sellae, named *ephippion*.

² Some interpretations have included extra points not strictly on the cranial base such as staphylion (Laitman 1985; cf. Houghton 1993 and Albanese 1994).

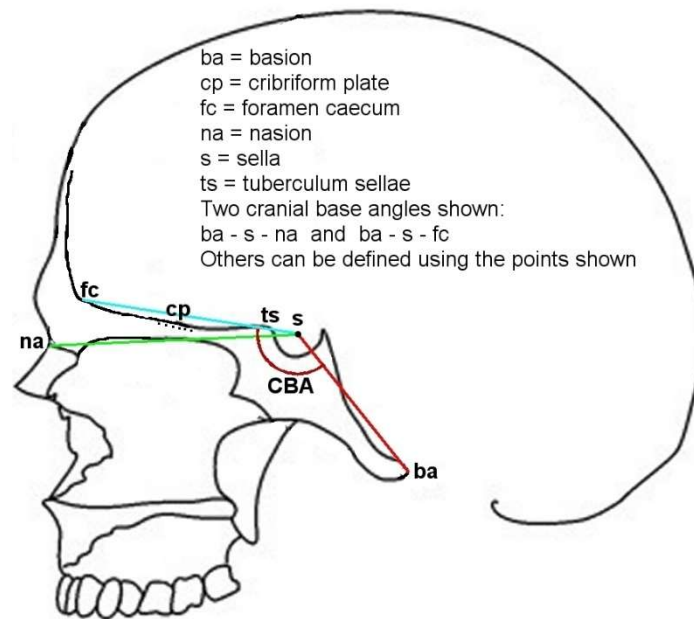


Figure F.1: Cranial base angle (CBA)

Table F.2: Cranial base angle

Angles in degrees	CBA1 mean	CBA1 range	CBA1, individual Neanderthals	Angle basion–tuberculum sellae–nasion, individual Neanderthals
<i>H. erectus</i>	141	133–145		
Middle Pleistocene (<i>H. heidelbergensis</i>)	142.5	139–145		
Neanderthals	150	150–150		
Gibraltar 1 (Forbes Quarry)			150	140 ¹ , 142 ²
Monte Circeo (Guattari)			150	
La Chapelle				137.5 ²
La Ferrassie 1				135 ²
Early <i>H. sapiens</i>	134	127–135		
Living humans	134±3.1			
CBA1 = angle basion–sella–foramen caecum All CBA1 angles from Lieberman 2011:570. ¹ Keith 1927:219; McCown and Keith 1939:361. ² Heim 1989:105.				

When the cranial base angle is wide, the brain extends anteroposteriorly from above the sella turcica and the skull is platycephalic. When the angle is less obtuse, the posterior cranial base is bent anteroinferiorly, which creates relatively more vertical space posterior to it. The foramen magnum and therefore also the supraoccipital plate should be drawn anteriorly, and the brain is induced to grow more vertically, expanding the calvaria superiorly.

Lengthening of the cranial base is mediated by growth at the spheno-ethmoid, mid-sphenoid, and spheno-occipital synchondroses. Whereas the mid-sphenoid fuses within the first year or so postnatally and the spheno-ethmoid by ~7 years, the spheno-occipital fuses at ~11–18 years (Cunningham, Scheuer and Black 2016:66,68,96–97). It is proposed that flexion is

produced by differential growth at the superior and inferior aspects of the synchondroses (Lieberman et al. 2000b:129–130; Lieberman 2011:170).¹ Although the growing brain may influence the growing cranial base and vice versa, it is suggested that bone predominates (Bruner et al. 2015:268). Otherwise, possibly the neuropil of the infant brain, with a genetic tendency to globularize (Chapter 4), exerts sufficient pressure or tension on the synchondroses to increase flexion.

The anterior cranial fossae, which form the roofs of the orbits, align with the upper part of the face. Cranial base extension leads to dorsal rotation, in relation to the posterior cranial base, of the anterior cranial base along with the facial block, as in chimpanzees and gorillas. Flexion induces ventral rotation, most clearly seen in recent *Homo sapiens*, in which facial reduction has also taken place (Lieberman et al. 2000b:139).² The face is thus retracted below the anterior cranial fossa rather than projected in front of it as in African apes and earlier hominins. Ponce de León and Zollikofer (2001:537) suggest that pronounced flexion at the sphenoccipital synchondrosis, taking place before 2 years, accounts for facial retraction.

Orientation of the orbits is constrained to maintain the *Neutral Horizontal Axis* at close to perpendicular to the posterior maxillary plane, which defines the posterior margin of the facial block,³ so that when the head is held in natural posture the central line of sight is straight ahead (McCarthy and Lieberman 2001; Lieberman 2011:171). The Neutral Horizontal Axis appears to be aligned with the semicircular canals in the petrous temporals (Lieberman et al. 2000b:150–151).

Only the orbital region, not the nasomaxillary region below, is closely tied to the cranial base, so that a retracted upper face may be combined with a prognathic lower face.

F.2 Frontal lobes and bone

The frontal lobes contain posteriorly the motor and premotor cortices and anteriorly the prefrontal association areas. Prefrontal areas, dorsal, ventral and medial, have reciprocal connections with association cortex in the parietal and temporal lobes and to medial and dorsal thalamic nuclei, providing processed sensory information. Connections with the cingulate gyrus, lying posterior to the prefrontal area, and to the hypothalamus, amygdala and hippocampus give access to motivation, emotion and memory.

Efferent and reciprocal connections from the prefrontal cortex to posterior frontal areas and the thalamus and cerebellum enable the initiation and control of motor and other activity. Lateral prefrontal gyri, particularly, have long been regarded as the site of a central executive process which contributes to the sense of self, evaluates information and possible action, and makes decisions (Fuster 1987, 2002; Allen 2009:16,22; Arain et al. 2013; Hrvoj-Mihic et al. 2013). Critchley (2005) reports that dorsal anterior cingulate cortex may contribute to consciousness and executive control, while ventromedial prefrontal cortex may subserve a self-

¹ The mid-sphenoid or intrasphenoidal synchondrosis, which closes earliest, is close to the vertex of the cranial base angle, however measured.

² Some early *Homo sapiens* skulls exhibit extreme ventral rotation of the face without facial reduction: Skhul 2, 4, 7 and 9, which Coon (1962:569–571) describes as hyperorthognathous. Corrucini (1976, 1990, 1992) observes a marked contrast of these crania with the prognathous Skhul 5 which, being more complete, has served as the type of the Skhul population.

³ The posterior maxillary plane is projected coronally from a line connecting upper and lower points combined radiographically from left and right sides: the most inferoposterior point on the maxillary tuberosities and the point of the anteriormost extent of the greater wings of the sphenoid (McCarthy and Lieberman 2001:247).

referential state of rest and disengagement, a basal state for further activity, sometimes designated the *default mode process*.

The frontal lobes press upon the vault via the meningeal tissue, but also are cradled in and leave impressions on the anterior fossae of the cranial base. The endocranial surface of the frontal bone is the inner table, which assumes the contour of the frontal lobe, while the outer table forms the exterior of the frontal squama and, below it, the anterior component of the orbital roof. In most modern humans, with their small faces, the eyes lie almost entirely below the anterior cranial fossae. When the face is large relative to the neurocranium, as it is in all archaic *Homo*, the orbits are carried upward to a position anteroinferior to the anterior cranial fossae, so that the frontal outer table must extend outward to protect the eyes (Moss and Young 1960; Coon 1962:350). The result is the browridges characteristic of archaic humans, including Neanderthals (§6.5.2).

In contrast to outer-table developments, the endocranial sagittal profile of the inner table in *Homo* seems to have remained largely unchanged from *Homo heidelbergensis* onward to the present day (Bookstein et al. 1999), a period of roundly half a million years. Endocranial volume has significantly increased, but the shape of the anterior contour of the frontal lobe has not. Albessard et al. (2016:13) concur, but caution that these results, including their own, apply to the sagittal plane and not necessarily to lateral frontal areas.

According to Bruner and Holloway (2010:141), width of the anterior cranial fossae is relatively larger in both modern humans and Neanderthals than in *Homo erectus s.l.*, and this enlargement is not due to allometry in line with increased endocranial volume.

Studies by Semendeferi et al. (1997, 2001, 2002) and Semendeferi and Damasio (2000) compare sizes of lobes in monkeys, apes and hominins. They conclude that the frontal lobe has not increased in relative size in modern humans compared with the great apes, but has increased compared with gibbons, macaques and cebus monkeys (cf. Allen et al. 2004:248). Holloway (2002:400) observes that Brodmann Area 10 of the prefrontal in living humans is absolutely ~7 times as large as in chimpanzees (cf. Semendeferi et al. 2001:234–235). The prefrontal is enlarged relatively as well as absolutely in humans compared with other primates, as are certain other brain structures to which it projects, suggesting coevolution of those components (Ramnani 2006:513).

Bastir et al. (2011:3–4) find that the anterior cranial fossa (ACF) is wider in modern humans and Neanderthals than in earlier *Homo* (cf. Bruner and Holloway 2010), but that in modern humans it is relatively longer than in Neanderthals, owing to a retraction of the medial cranial base with lengthening of the cribriform plate to extend more posteriorly. As a result, maximum width of the ACF transects the cribriform plate near the midpoint longitudinally of the ACF, whereas in Neanderthals maximum width lies within the posterior half of the ACF. Such a condition would be consistent with greater postorbital constriction in Neanderthals.

The size of the cribriform plate varies with the size of the olfactory bulbs, which project to rhinal and pyriform cortex medial to the temporal poles, and thence to the limbic system, where emotional and memory content can be added; and connections reach orbital prefrontal cortex (Bastir et al. 2011:5–6). On the basis that modern human olfactory bulbs, scaling with the larger cribriform plates, are larger than those of Neanderthals, these authors suggest that modern humans developed more effective odour detection and that this contributed to high-level cognitive and emotional processes, in learning, decision-making, social interaction,

detecting fear in others, and discerning potential mates, all of which would have offered a selective advantage.¹

Turetsky et al. (2000:829) found olfactory bulbs of mean volume 104.3 mm³ in a sample of healthy living humans. In African apes the volume is 2.5–3 times as much: chimpanzee mean quoted as 257 mm³, and gorilla 316 mm³ (Stephan et al. 1981, cited by Allen 2009:86).² Modern humans have smaller olfactory bulbs than expected in relation to other primates, absolutely and relative to body or brain size (Allen 2009:86). If Neanderthals had even smaller olfactory bulbs than modern humans, then in respect of olfactory function Neanderthals appear to be more distant from the apes and lower mammals (one might say more highly evolved) than modern humans are. At any rate, the smaller cribriform plate in Neanderthals suggests that their large nasal cavity did not evolve to subserve the sense of smell.

F.3 Parietal lobes and bones

The parietal lobes contain the somatosensory cortex immediately posterior to the central sulcus, which divides the parietal from the frontal lobes. More posterior parietal areas are association cortex, which integrates information from the somatosensory cortex, the visual, auditory and olfactory areas in other lobes, and subcortical structures. The sense of position and orientation in space, and the capacity to move and act on the basis of that orientation appear to be enabled by the superior and inferior parietal lobules (Lynch 1987; Cavanna and Trimble 2006; Allen 2009:33).

The parietal lobes contribute substantially to globularization. In the course of evolution from *H. heidelbergensis*, parietal expansion took place in the modern human and Neanderthal lineages. However, in *H. sapiens* the upper parietal, specifically the precuneus, Brodmann Area 7, underwent further expansion. This area lies sagittally at the superior edge of the parietal lobe, some of the surface external and some descending within the longitudinal fissure, and is bounded inferiorly by the cingulate gyrus. Expansion of the upper parietal squamae heightens the vault (Bruner et al. 2003:15537–15538; Cavanna and Trimble 2006:565). According to Gogtay et al. (2004:8175,8177) the precuneus matures early in the sequence of brain development. The parietal lobe is relatively longer anteroposteriorly in *H. sapiens* than in *H. neanderthalensis* (Bruner et al. 2015a:274; Albessard et al. 2016:9). In recent humans a longer parietal is paired with a shorter frontal lobe, and vice versa (Allen et al. 2004:250)

The precuneus has extensive reciprocal connections with other parietal areas and the frontal lobe, including prefrontal, supplementary motor and premotor cortex, and with subcortical structures, including the dorsal thalamus, caudate nucleus and putamen. Notably there is a lack of connections to sensory thalamic nuclei, indicating that the precuneus is not part of a primary sensory system (Cavanna and Trimble 2006:566–568).

The precuneus is involved in spatial awareness and spatially guided motor behaviour, attention, reaching and grasping. However, functional imaging studies also indicate that it contributes to higher-order cognition: memory retrieval, the sense of self and other, perspective-taking and theory of mind. It is quiescent during sleep and anaesthesia and most active not during demanding activity but during the resting conscious state when the subject is

¹ On the hypothesis cited, body odour must have played a large part in early modern human society. If Neanderthals had been found to have *larger* cribriform plates than modern humans, would the presumed large olfactory bulbs have drawn comparison with apes and lower mammals, and would greater olfactory sense have been attributed to a primitive mentality and mode of life rather than an indication of superior cognitive fitness?

² Primates are microsmatic and in them the laminated structure seen in the olfactory bulbs of macrosmatic animals such as canids and ursids is undeveloped (Vanderah and Gould 2021:322).

not concentrating on a task. It therefore appears to subserve conscious awareness, which is represented neurally by a baseline state or *default mode* of processing involving or even centred on superior parietal and prefrontal regions (Cavanna and Trimble 2006:572–578; Bruner et al. 2015b:350; Bruner et al. 2017a).

The *default network* or *default mode network* (DMN) is identified as an anatomically defined brain system preferentially active when individuals are not focused on the external environment. Core functional areas of this system include the hippocampal formation and a number of cortical regions: ventral and dorsal medial prefrontal, inferior parietal lobule, lateral temporal, and posterior cingulate (Buckner et al. 2008). Later studies additionally implicate the precuneus as one of the hubs or cores of the DMN (Utevsky et al. 2014, 2016; Jitsuiishi and Yamaguchi 2021). The thalamus is also connected to the DMN (Cunningham et al. 2017).

The superior parietal lobule has been identified as a major locus of activity corresponding to meditative (Cavanna and Trimble 2006:577) and putative spiritual (Newberg and d'Aquili 2001; Clark 2006) experience.

The absence of comparable upper parietal expansion in Neanderthals (Bruner et al. 2017b) suggests that modern humans may have superior control of behaviours managed by the precuneus.

Bruner et al. (2010) emphasize hand-eye coordination and visuospatial integration together with recognition and codification of the spatial environment. However, chimpanzees have absolutely and relatively much smaller superior parietal areas than modern humans. Yet, in addition to knuckle walking, sometimes at speed and dodging trees and undergrowth, they expertly brachiate in trees. They are able to navigate as a predator group to likely locations, spot colobus monkeys in the canopy and cooperatively pursue, kill and eat them. Recent observations in the wild show that in groups they are able to attack gorillas and kill their infants (Southern et al. 2021). These behaviours would appear to demand highly developed and coordinated visuospatial, motor and social abilities.

Hand-eye coordination is again emphasized by Bruner and Iriki (2016:104–105), who suggest that Neanderthals were deficient in this area, as they appear habitually to have held skins and perhaps other materials with their front teeth while processing them with cutting tools, using the mouth as a third hand: this practice, bringing a sharp edge close to the face, is highly dangerous.¹

Bruner et al. (2015b:345–348) observe that in living subjects precuneal surface area and thickness is not correlated with intelligence, working memory, attention control or task processing speed, and the length of the precuneus is not correlated with the subject's intelligence.

F.4 Temporal lobes and bones, and insula

F.4.1 Temporal lobes and middle cranial fossa

The temporal lobes are almost entirely formed of association cortex. On each side the lobe is posteriorly continuous with the parietal and occipital lobe, from which it receives processed sensory information, and separated anterosuperiorly from the frontal lobe by the Sylvian

¹ Alternatively, perhaps hand-eye-mouth coordination would require more complex engagement of neural centres subserving visuospatial and motor abilities than only hand-eye coordination.

fissure, in the depth of which lies the insula. The temporal lobe presses laterally upon the temporal squama and inferiorly nestles within the middle cranial fossa, bounded posteriorly by the petrous pyramid, which forms the posterolateral part of the cranial base. Surrounded by temporal neocortex superiorly, laterally and inferiorly are two major limbic structures: the amygdala, principal centre for emotion, and the hippocampus, principal centre for memory.

The inferior and middle temporal gyri process and interpret visual information originating in occipital cortex, while the superior temporal gyrus including its superior surface, the planum temporale, contains primary auditory cortex, with auditory association cortex lying inferiorly (Vanderah and Gould 2021:63–64). The posterior extremity of the superior gyrus including the planum temporale is the focal centre for interpretation and production of language, in most subjects on the left side only (Rodman and Gross 1987; Guenther 2016:79; Price 2012:820,824). Some studies implicate superior, middle and inferior temporal gyri along with the superior and inferior sulci, and occipitotemporal cortex (Price 2012:824,828). However, neural control of speech, requiring both language production and motor activity with auditory feedback, appears to be widely distributed, extending to temporal, prefrontal and insular areas of the neocortex, basal ganglia, brainstem and cerebellum (Guenther 2016).

Pearson et al. (2020) state that temporal lobe size can be predicted from the size of the middle cranial fossa (MCF). In *Homo* the MCF is 20% larger relative to the whole endocranium than in apes, but there is no significant difference in relative volume of the MCF for any living or fossil *Homo* taxa (Bastir et al. 2008:138). However, the MCF is 20% wider¹ in anatomically modern humans than in *H. neanderthalensis* and *H. heidelbergensis* relative to overall cranial size (Lieberman et al. 2002:1137; Bastir et al. 2008:131). The anteromedial area of the Neanderthal temporal lobe extends more inferiorly than in modern humans (Kochiyama et al. 2016:5). Although most traits of the MCF are similar, in the El Sidrón Neanderthals the postarcuate fossa is narrower and smaller than in modern humans and the middle and inferior temporal gyri extend into the temporal pole rather than the superior and middle temporal gyri as in modern humans (Rosas et al. 2014:2339), perhaps indicating an emphasis on visual rather than auditory and linguistic processing.

According to Bastir et al. (2008:137), in *Homo sapiens* the temporal pole is positioned more anterolaterally than in other hominins; while Bruner et al. (2017b) and Pereira-Pedro et al. (2017) state that the pole is positioned more anteromedially. The interpretation perhaps is that the middle cranial fossa is wider but shorter and the temporal pole is more anteriorly positioned relative to the optic chiasm and foramen rotundum (Bastir et al. 2008:130,132), but the pole may be diverted medially by being compressed against the posterior wall of the orbit (Pereira-Pedro et al. 2017:956).

F.4.2 Insula and limbic structures

The insula is not part of the frontal, temporal or parietal lobes but is neocortex continuous with all three, located on both lateral aspects of the brain and exposed in lower primates such as galagos and lorises, but in cercopithecoids and hominoids covered by the opercula,² which meet to form the Sylvian fissure. Evidence indicates that the posterodorsal insula integrates interoceptive information from the brainstem and other centres to produce a representation of the body's homeostatic state, which is subsequently communicated to orbitofrontal cortex; and that the ventral anterior insula is involved in empathy and social awareness (Bauernfeind et al.

¹ And correspondingly shorter anteroposteriorly, if relative volume is conserved across *Homo*.

² Exteroinferior extensions of the frontal and parietal and an exterosuperior extension of the temporal.

2013:263; Critchley 2005:154–156,162–164). The insula is also implicated in some aspects of speech (Price 2012).

In the course of encephalization from lower to higher primates, the insula has increased in volume slightly relative to the brain overall, and in great apes and humans is 5–22% larger than predicted by isometry (Bauernfeind et al. 2013:263,271).

As the insula and limbic structures such as the amygdala and hippocampus (medial to the temporal gyri), and lateral cingulate gyrus (superior to the corpus callosum) are located in the interior of the endocranium, no evidence exists about their size in fossil hominins. As an example, some nuclei of the amygdala are relatively enlarged in humans compared with the great apes (Hrvoje-Mikic et al. 2013:4), but when in hominin phylogeny this enlargement occurred is unknown. However, owing to their mediolateral position underlying the neocortex, evolutionary enlargement of any of these structures at a gross level would tend to expand the neurocranium laterally, as seen in *Homo sapiens* and Neanderthals.

F.4.3 Petrous temporal

External temporal bone morphology varies distinctively between *Homo* species, including Neanderthals, as analysed by Elyaqine (1996). Since these differences minimally, if at all, affect sensation, proprioception or cognition, they are not discussed here.

The petrous temporal bone contains the middle-ear and inner-ear (labyrinthine) organs. The middle-ear ossicles transmit vibrations to the inner-ear cochlea, enabling auditory sensation. The semicircular canals of the labyrinth enable perception of orientation and rotation of the head and stabilization of gaze (Spoor 2003:93–95; Spoor et al. 2003:142). The bony labyrinth encloses the membranous labyrinth forming the cochlea and three semicircular ducts conjoined at the vestibule (Vanderah and Gould 2021:329–331). All these structures are fully formed at birth (Quam et al. 2013:260), which suggests that their morphology is genetically defined with negligible influence from environment or behaviour (Spoor et al. 2003:158).

The ossicular chain (malleus, incus and stapes) of Neanderthals seems to differ from that of modern humans in some respects: e.g. the malleal head is larger; the stapedial anterior crus is shorter than the posterior, rather than equal length (Quam et al. 2013:258; Gómez-Olivencia et al. 2018a). While stapedial asymmetry may be a derived feature in Neanderthals, it occurs as a rare variant in modern humans. Both species evince a similar incudal lever arm ratio, with incudal length greater than in chimpanzees.

Neanderthal morphology is consistent with a modern human pattern of hearing including sensitivity in mid-range frequencies where chimpanzees appear to have a deficiency (Quam et al. 2013:260). Analysis of middle-ear configuration in the Sima de los Huesos hominins, generally regarded as ancestral to Neanderthals, also indicates a hearing pattern similar to that of modern humans (Martínez et al. 2004, 2013).

Compared with modern humans, Neanderthals exhibit smaller vertical (anterior and posterior) semicircular canal arcs, larger horizontal (lateral) canal arcs, the posterior canal more inferiorly located relative to the others, and a more vertically inclined ampullar line, while the orientation of the planes to one another is the same (Spoor et al. 2003:155,159). The common crus between anterior and posterior canals is shorter (Quam et al. 2016:5,10). Small vertical canals and a large lateral canal are features shared with the earlier Sima de los Huesos population and possibly other European Middle Pleistocene hominins, but the low placement of the posterior canal, shorter common crus and inclination of the ampulla are generally not present in the Middle Pleistocene populations. Evidence overall therefore suggests that the

Neanderthal suite of features is derived and had begun to develop in the earlier Europeans (Quam et al. 2016:1,5,8,13; Spoor et al. 2003:162). This conclusion is supported by the modern human dimensions seen in *Homo erectus* (Hublin et al. 1996:225; Spoor 2003:98; Quam et al. 2016:2). Contrastingly, cochlear height in the Sima de los Huesos hominins is low, but increased in Neanderthals (Quam et al. 2016:1).¹

The infants Arcy sur Cure, Dederiyeh 2, Pech de l'Azé, Petit Puymoyen 5, and adult Gibraltar 1 show the full Neanderthal labyrinthine morphology, but the Le Moustier 1 child and to a lesser degree the adult Spy 1 have a morphology within Holocene human range, Le Moustier 1 being the closest to moderns in all measurements (Hublin et al. 1996; Spoor et al. 2003:142,154–155; Wu et al. 2014:10511).

Relative to body mass, primates have larger semicircular canals than mammals generally (Spoor 2003:97–98), but the genus *Homo* has smaller canals than expected of a primate with its body mass (Quam et al. 2016:8). Large canals, as found in primates, are thought to be related to increased agility. Considerations of balancing a head longer than in modern humans and stabilizing line of sight during locomotion have to be taken into account, but the small vertical canals of Neanderthals may imply lesser agility, which would be consistent with their wide pelves and short distal limbs, less suited perhaps to running than to endurance trekking (Spoor 2003:101; Spoor et al. 2003:159–161; cf. Stock and Shaw 2012). The larger lateral canal in both Neanderthals and their putative ancestors does not necessarily invalidate this hypothesis, since it may be related to the wide cranial base shared by these populations, and the rest of the full Neanderthal labyrinthine morphology may have been induced later by further encephalization (Quam et al. 2016:2).

F.5 Occipital lobes and occipital cerebral fossa

The occipital lobes are the smallest lobes of the modern human cerebrum, at only up to ~12% of the neocortex (Allen et al. 2004:248,250), and are concerned with visual processing. Primary visual striate cortex (V1, Brodmann Area 17) occupies both banks of the calcarine sulcus, which appears centrally on each occipital pole but lies mostly within the inter-hemispheric fissure, where it extends anteriorly. Located superiorly and inferiorly to V1 are the bands of V2 (Brodmann Area 18). Further visual areas with interpretative and associative functions extend both medially and on the external surface of the occipital lobe, continuing anteriorly into the temporal lobe within the occipitotemporal and inferior temporal gyri (Vanderah and Gould 2021:524,526).

If brain sizes of *Homo sapiens* and Neanderthals are similar and Neanderthal temporal and parietal lobes and cerebellum are relatively smaller, then their frontal and/or occipital lobes must be relatively larger. Neanderthals had relatively larger occipital lobes than modern humans (Balzeau et al. 2012; García-Tabernero et al. 2018). Quam et al. (2016:11) observe a reduction in length and width of the occipital lobes in Neanderthals relative to their Middle Palaeolithic ancestors. Peirce et al. (2013) argue that the occipital lobes in Neanderthals must be larger than in *Homo sapiens* because Neanderthals had larger orbits.

If the occipital cortex is larger in Neanderthals than in modern humans, then Neanderthals may have possessed greater visual acuity and sensitivity, and their way of life may have emphasized the visual sense, perhaps at the expense of the strong olfactory capability

¹ The East Asian archaic cranium Xujiayao 15 has a low position of the posterior semicircular canal, a more vertical ampullar line, and some other Neanderthal traits, but its overall morphology is not Neanderthal (Wu et al. 2014). Xujiayao 6 (XJY 6) and Xuchang 1 also have Neanderthal-like semicircular canals (Li et al. 2017; Wu Xiujie 2024; Bae and Wu 2024).

alleged for *Homo sapiens* (§F.2). An extant modern human population may provide an example of what could be expected from enhanced occipital function. Australian Aboriginals are reported to have larger visual cortex than Caucasians (Klekamp et al. 1994), which may enable their independently assessed greater visual acuity (Taylor 1981) and stronger visual memory and sense of place (Kearins 1981).

Dural venous sinus drainage patterns of the occipital region in Neanderthals are described by Rosas et al. (2008), Peña-Melián et al. (2011), and García-Tabernero et al. (2018). The most common pattern is that the superior sagittal sinus drains via the right transverse sinus. In many specimens there is no indication that the left transverse sinus has any connection with the superior sagittal sinus, although in living humans with a right sinus drainage pattern there are often anastomoses which provide that connection. Recent humans have a high incidence of confluence, where the superior sinus drains into both left and right transverse sinuses. This has not been found in Neanderthals, in whom the superior sagittal sinus, rather than coursing vertically toward the internal occipital protuberance, tends to divert to the right, cutting across the cerebral fossa.

In recent and fossil hominins, the cerebral hemispheres often show asymmetries (Holloway 1981). There is a common pattern of left occipital petalia, often associated with right frontal petalia, discernible on the cranium where the right frontal boss is more prominent than the left and the left occipital more prominent than the right; this pattern applies to fossil as well as recent modern humans (LeMay 1976; Balzeau et al. 2012:703). Peña-Melián et al. (2011:1372–1373) list only four Neanderthal specimens with right occipital petalias: El Sidrón SD-1149, La Chapelle-aux-Saints, Salzgitte, and Le Moustier 1. Of these, Salzgitte combines the right petalia with a left sinus drainage pattern, while the other three have right sinus drainage patterns. A study of recent humans by Ventrone (2011:137–140) finds a right occipital petalia more common in infants up to adolescents, then a reversal to the left side by adulthood. If this phenomenon occurred in Neanderthals, the right occipital petalias might have become reversed in Le Moustier 1 and perhaps SD-1149, had they survived. The adult male La Chapelle would then be a unique case.

F.6 Cerebellum and occipital cerebellar fossa

Traditional opinion held that the cerebellum was concerned, primarily if not exclusively, with sensorimotor functions, managing locomotion, modulating adjustments of body movement according to perceived position and attitude, and enabling fine control of the vocal apparatus (Chan-Palay and Palay 1987; Dow 1987; Allen 2009:14) on a millisecond timescale (D'Angelo 2011). However, as well as being a component of a motor loop along with the premotor and motor cortex, it receives visual, auditory and even visceral inputs and has projections via the thalamus to prefrontal cortex (Vanderah and Gould 2021:484,489). The cerebellum contains as many neurons as the rest of the brain combined (Ramnani 2006:511), and compared with the rest of the brain has a highly regular structure (Ramnani 2006:512; Vanderah and Gould 2021).

It has been proposed that the cerebellum prefigures and models bodily movement, so that during the course of physical movements, e.g. of the limbs, proprioceptive feedback about position can be compared with the model and ongoing muscular movements adjusted directly to compensate for deviations, without the delay inherent in engaging motor cortex (Guenther 2016:52–56).

In recent years it has been argued that the cerebellum is also involved in higher cognitive functions (Allen 2009:15; Price 2012; Barton 2012; Vanderah and Gould 2021:489).

These principally centre upon language, but are not limited to mechanical aspects of speech production: they extend to vocabulary and the structure, timing and sequencing of utterances (Ramnani 2006; Price 2012). However, the facility for planning and modelling is extended to learning: so that when an activity has been learned, whether mechanical or even intellectual, the cerebellum manages that activity with reduced input from prefrontal cortex (Ramnani 2006; Price 2012; Barton 2012). Altogether, it appears that the cerebellum is able to process large quantities of data in a regular or automatic manner without reference to context or content (Ramnani 2006; Price 2012). If this is so, then presumably the cerebellar contribution to cognition is not directly to produce sensation, understanding or thought but to provide processed information for neocortical structures to act upon.¹

The cerebellum in apes is relatively larger than in monkeys; but in recent humans it is smaller than expected relative to overall brain volume, whereas relative to body mass it is very large (Rilling and Insel 1998; Rosas et al. 2008:510). During primate evolution, including that of the hominins, there has broadly been coevolution of the neocortex and cerebellum (Barton 2012; cf. Hofman 2014:1–2). In absolute volume both have expanded dramatically in comparison with apes. In particular, lateral cerebellar areas such as crus I and II of lobule VII are disproportionately large (Vanderah and Gould 2021).

Weaver (2005) finds that, compared with living humans, the cerebellum is relatively small in both monkeys and apes, and this condition continued up to Late Pleistocene *Homo*. Neanderthals and at least one Upper Palaeolithic modern human (Cro-Magnon 1) have the lowest ratio of cerebellum to cerebrum of all hominins. Since ~30 ka humans have developed relatively and absolutely larger cerebella and smaller cerebral hemispheres (Table F.3).² Weaver (2005:3579) suggests that with cultural advances after the initial Upper Palaeolithic the required quantity of processing exceeded the capacity of the neocortex, which had by then attained the maximum mean dimensions known in human evolution. On this hypothesis the cerebellum was recruited to undertake intensive computation, presumably carried out unconsciously. A question arises whether, prior to this development, the cerebral computation was in some way more conscious and how this would have been experienced in everyday life.

Table F.3: Cerebellar versus cerebral volume (Weaver 2005)

Volume (cm ³)	Cerebrum	Cerebellum	Brain (cerebrum + cerebellum)	% Cerebellum / Cerebrum	% Cerebellum / Brain	Cerebellar Quotient
Recent humans	1116.92±15.72	139.76±2.54	1256.68	12.51	11.12	0.91±0.01
Cro-Magnon 1	1289.08	118.92	1408.00	9.22	8.44	0.75
Neanderthals	1197.52±101.66	106.35±12.32	1303.87	8.88	8.15	0.71
African apes						1.13±0.08
Cercopithecoids						0.77±0.03
Data (columns 2, 3, 7) from Weaver 2005. Cerebellar quotient is actual versus predicted value for each species (Weaver 2005:3577–3578).						

Alternative values from Kochiyama et al. (2016:2) are given in Table F.4. From their research, size-adjusted volumes indicate that both recent and early modern humans have

¹ In a computing analogy, the cerebrum may be viewed as the general-purpose main processor, which receives inputs and delivers processed output, while the cerebellum is the floating-point processor, specialized for repetitious large-scale and parallel calculations outsourced from the main processor.

² This research used digital scans of physical endocasts and CT scans of some specimens, identifying the cerebral-cerebellar boundary by positions where the tentorium would have inserted.

significantly larger cerebella (vermis and posterior hemispheres) than Neanderthals. On this evidence, cerebellar expansion to modern levels began at the latest by 100 ka (Kochiyama et al. 2016:2–3). As cerebellar activity seems to be involved in the processing of a wide range of cognitive tasks, including those associated with executive function, language and working memory, they deduce that Neanderthals were deficient in all those capacities. A further finding is that in Neanderthals the right side of both anterior and posterior cerebellum was smaller than the left. As the fibres from the cerebellar peduncles cross over at the level of the pons, the right cerebellum communicates with the left hemisphere of the cerebrum. In most subjects capacity for language processing is a left-hemisphere function, so deficiency of the right cerebellum may indicate lesser capacity. However, the authors acknowledge that the cerebellar regions of the fossils may be incompletely preserved (Kochiyama et al. 2016:5).¹

Table F.4: Cerebellar versus cerebral volume (Kochiyama et al. 2016)

Volume (cm ³)	Cerebrum	Cerebellum	Brain (cerebrum + cerebellum)	% Cerebellum / Cerebrum	% Cerebellum / Brain
Recent <i>sapiens</i> mean	1097±115	149±15	1246	13.58	11.96
Early <i>sapiens</i> mean	1135±83	153±9	1288	13.48	11.88
Neanderthal mean	1161±177	149±33	1310	12.83	11.37
Qafzeh 9 (S)	1075	147	1222	13.67	12.03
Skhul 5 (S)	1053	146	1199	13.87	12.18
Mladeč 1 (S)	1205	165	1370	13.69	12.04
Cro-Magnon 1 (S)	1208	156	1364	12.91	11.44
Amud 1 (N)	1304	182	1486	13.96	12.25
La Chapelle (N)	1159	140	1299	12.08	10.78
La Ferrassie 1 (N)	1268	166	1434	13.09	11.58
Gibraltar 1 (N)	912	106	1018	11.62	10.41
Data (columns 2 and 3) from Kochiyama et al. 2016. Values in italics are calculated here. S = sapiens, N = Neanderthal.					

Notably, some Neanderthals have larger cerebellar volumes than some *Homo sapiens* representatives.² The significance of proportions versus absolute volume seems unclear.

A comparison of Tables F.3 and F.4 showing relative cerebellar volumes raises questions about divergent methods, beginning with delimitation of the structures in question. Weaver (2005) uses the fossils as a proxy for brain structure volumes. Kochiyama et al. (2016) use a succession of complex techniques from imaging to statistical treatments, so that the results are in a sense more remote from the original material. The choice to estimate each fossil human volume from a warp of a recent human brain may introduce uncertainty because variation of gyral and sulcal patterns between modern individuals is large, as Kochiyama and colleagues acknowledge; it is unclear whether the relation of Middle or even Upper Palaeolithic brain structures to endocranial features was entirely like that of recent humans (cf. Bruner et al. 2003:15338); and it is unverifiable whether a warp function can reproduce the internal brain configuration of a given prehistoric individual.

¹ These results are produced by scanning fossil and modern crania, and complex processing of virtual data. The principal task appears to have been to derive a deformation function which produces a matching virtual fossil endocast from an average modern cranium, and then applying a comparable deformation to the virtual 3D modern brain itself to produce a virtual brain for each fossil, thereby allowing volumes of lobes, lobules and cerebellum to be calculated.

² In Manot 1, a Levantine early modern human skull dated to ~54.7 ka, the cerebellar fossae occupy less of the internal aspect of the supraoccipital than in later moderns (Hershkowitz et al. 2015 SI:22).

APPENDIX G

GESTATION AND BIRTH

G.1 Introduction

Compared with modern humans, most extinct hominins well represented in the fossil record have had either smaller body size and much smaller endocranial capacity (e.g. all the australopithecines, including even the robust species) or similar body size combined with smaller endocranial capacity (e.g. *Homo ergaster*, *Homo erectus*, *Homo antecessor*). From the Middle Pleistocene onward, species are found whose ranges of both body size and brain size fit within the ranges known for modern extant humans: in the earlier period *Homo heidelbergensis/rhodesiensis*, and in the Upper Pleistocene *Homo neanderthalensis*, and early *Homo sapiens* in Africa and South West Asia.

Palaeoanthropological research on gestation and birth has centred upon the following topics: brain size at birth; gestation length; the obstetric dilemma, i.e. conflict between pelvic requirements for birth and for upright posture and locomotion; the birth process, which in modern humans involves rotation of the fetus during passage through the birth canal; and whether Neanderthals had assisted birth and concomitant social relationships.

G.2 Brain size at birth

Living modern humans frequently have difficult births owing to the very tight fit of the large-brained fetal head as it passes down the birth canal within the pelvis. True *cephalopelvic disproportion* resulting in fatality is caused by a large fetus or a small pelvic canal. Worldwide, the rate of maternal death among living humans, from this and other causes, during natural birth in the absence of medical intervention, is as high as 1.0–1.5% (Kurki 2011:139–145).

This difficulty is absent for chimpanzees, gorillas and orang-utans, which, owing to large adult body size, have large internal pelvic diameters in relation to the head of their comparatively small-brained fetuses. Gibbons and siamangs, however, with their much smaller adult body size, and similarly some small-bodied monkeys, especially rhesus monkeys, approach the human condition, and death of the neonate during birth has been reported for some species (Schultz 1949:415–418; Rosenberg and Trevathan 2002:1199). Chimpanzee and gorilla neonates weigh only as much as 4.0% and 2.4% respectively of mean adult female weight, while in modern humans the neonate weighs 5.5% and in gibbons 7.5% (Schultz 1949:412). Unlike apes and monkeys, whose neonates are very lean and wrinkled (Schultz 1969:152), human babies are born plump, with body fat 11–14% of birth weight (Cunnane and Crawford 2003), which buffers them as an energy reserve through infancy (Kuzawa 1998).

G.2.1 Fetal and adult brain size

Fetal brain sizes, and consequently external dimensions of the fetal neurocranium, are correlated with adult brain size (Trinkaus 1984:510). While actual external dimensions of the fetal cranium at term are the genuinely determining factors, these are largely not to be found in the literature, and for fossil hominins brain sizes are expressed as endocranial capacities.

Endocranial volumes (ECV) of neonates and adults in apes and hominins are listed in Table G.1. For extant ape species and modern humans neonatal ECV is directly available, but for extinct hominin species the researchers cited derive ECV for neonates from adult mean ECV.

Table G.1: Endocranial volumes at birth and percentages of adult ECV

Species	Neonate ECV (DeSilva and Lesnik 2008)	Neonate % adult ECV (DeSilva and Lesnik 2008)	Adult ECV (DeSilva and Lesnik 2008)	Neonate ECV (Gunz et al. 2011)	Neonate ECV (Ponce de León et al. 2008)	Neonate ECV (Zollikofer and Ponce de León 2010)	Neonate % adult ECV (Zollikofer and Ponce de León 2010)	Adult ECV (Zollikofer and Ponce de León 2010)
<i>Hylobates lar</i>	65.0		102.5					
<i>Pongo pygmaeus</i>	165.1		419.4					
<i>Pan paniscus</i>	154.9	40.1	381.7			145		340
<i>Pan troglodytes</i>		40.1				155	40	median 360 (330–450)
<i>Gorilla gorilla</i>	217.0		522.7					
<i>Sahelanthropus tchadensis</i>	148.3*		365.0					360–370
<i>Ardipithecus ramidus</i>								300–350
<i>Australopithecus afarensis</i>	173.8*	38.1	455.6					
<i>Australopithecus africanus</i>	177.1*	38.1	466.8		180* (158–205)			460
<i>Australopithecus garhi</i>	172.6*	38.1	450.0					
<i>Paranthropus aethiopicus</i>	161.4*		410.0					
<i>Paranthropus robustus</i>	194.4*		530.0					
<i>Paranthropus boisei</i>	186.2*		499.6					
<i>Homo habilis</i> and <i>Homo rudolfensis</i>	225.4*	35.2	651.6					
Early <i>Homo erectus</i>	270.5*	33.1	839.6					
<i>Homo erectus</i> , Mojokerto						270–320* (663 at 1 year postnatal)	35	900
Late <i>Homo erectus</i>	320.0*	30.5	1056.7					
Mid-Pleistocene <i>Homo</i>	355.0*	29.5	1218.9					
<i>Homo neanderthalensis</i> , Mezmaiskaya 1					400* (382–416) (422 – 436 at 2 weeks postnatal)			
<i>Homo neanderthalensis</i> , Le Moustier 2				406–428				1500
Mid and Upper Pal. <i>Homo sapiens</i>								1500
Recent <i>Homo sapiens</i>		28.0		380–420	400 (380–420)		29	1350 (1150–1650)
* indicates ECV for fossil species predicted by cited authors from given values.								

Notably, gorilla neonatal mean ECV is higher than for any australopithecine, and gorilla adult ECV is only exceeded by one australopithecine species, *Paranthropus robustus*. On the basis of known fossils, *Sahelanthropus tchadensis* has a slightly higher ECV than *Ardipithecus ramidus*, which is dated at least two million years later. Selection for increased brain size seems not to have applied in the earlier stages of the hominin lineage (Zollikofer and Ponce de León 2010:447).

Generally, in less encephalized species a higher proportion of total brain growth takes place before birth. For chimpanzees ~40% of brain growth is achieved *in utero*, whereas for modern humans the proportion is ~28–29%. The result for humans is that more brain growth has to take place in the first year of life, when fetal-like rates of growth continue. For australopithecines the expected figure is ~38%, and for Lower and Middle Pleistocene *Homo* the percentage is intermediate, and practically reaches modern human level by the Middle Pleistocene, i.e. in *Homo heidelbergensis*, when adult ECV comes firmly within modern range. The Neanderthal range of adult ECV is a subset of that of modern humans. Modern human exemplars exist having smaller ECV and others larger ECV than any known Neanderthals.

G.2.2 Fetal and adult body weight and brain size

The value ~400 cm³ for modern human neonatal brain size has recently been used by a number of anthropologists, sourced from Huppi et al. (1998:227). This is larger than neonatal values from some other sources (Table G.2). The specific gravity of brain tissue is ~1.0365 g per cm³ (Leigh 2006), so the value for weight should be higher than the value for volume: e.g. 400 cm³ should weigh 414.6 g. Most researchers have stated lower weights. Jerison (1987:168) gives 350 grams; Boyd (1962) gives 353 g (male), 347 g female); Dekaban and Sandowsky (1978) give 380 g (male), 360 g (female); Martin (1983:24) gives 384 g. Dekaban (1977) lists calculated endocranial volumes at 7 postnatal days 410 (male) and 398 (female) cm³, and at 28 days 522 and 510 cm³, an increment of 112 cm³ in 3 weeks (21 days). If the same rate of growth is assumed for the first week, 112/3 can be deducted from the 7-day values to derive 383 (male) and 361 (female) cm³ at birth.

The percentage of adult brain size attained at birth in *Homo erectus* has been a subject of discussion (Coqueugniot et al. 2004; Balzeau et al. 2005; Leigh 2006; Hublin and Coqueugniot 2006; DeSilva and Lesnik 2006; O’Connell and DeSilva 2013; Hublin et al. 2015). Chimpanzees have been determined to have ~40% of adult brain size at birth, while modern humans average ~28%. The percentages for modern humans using the data from sources above turn out well below 30 unless the 400 cm³ value is used (Table G.2).

It has been suggested that extinct hominins such as *Homo erectus* most likely exemplified an intermediate value (Table G.1). Given that adult *Homo erectus s.l.* including the Dmanisi specimens exhibits endocranial volumes ~600–1250 cm³ (Chapter 4 and Appendix E), and there are no neonate specimens, the question is not easy to resolve. Dating from as early as ~1.81Ma (Coqueugniot et al. 2004), there is a Javanese *Homo erectus* infant calvaria, Mojokerto (Perning 1), but its age at death is difficult to estimate, as no dentition or postcrania were recovered. Age has been estimated as 0.5–1.5 years (Coqueugniot et al. 2004) or as much as 4–6 years (Antón 1997). The percentage of adult ECV attained also depends on the selection of one *Homo erectus* group or another, by dating and geography, to represent adult ECV (Leigh 2006).

Table G.2: Neonatal brain size, living humans

	Adult male	Neonate male	%	Adult female	Neonate female	%
Dekaban and Sadowsky (1978), weights g	1449	380	26.2	1309	360	27.5
Neonate 400		400	27.6		400	30.6
Jerison (1987), neonate 350		350	24.1		350	26.7
Boyd (1962), weights g	1430	353	24.7	1318	347	26.3
Neonate 400		400	28.0		400	30.3
Dekaban (1977), ECV cm ³	1548	383	24.7	1425	361	25.3
7 days		(410)	26.5		(398)	27.9
1 month		(522)	33.7		(510)	35.8
Neonate 400		400	25.8		400	28.1

According to Jordaan (1976), in the neonates of recent humans brain mass varies with body mass according to the formula

$$\log_{10}(\text{brain mass}) = 0.64 \times \log_{10}(\text{body mass}) + 0.35$$

Table G.3 illustrates expectations on this basis.

Table G.3: Neonatal brain mass expected from neonatal body mass

Body mass		Brain mass
pounds	grams	grams
5.51	2500	334.7
6.61	3000	376.1
7.71	3500	415.1
8.81	4000	452.2
Formula from Jordaan (1976).		

Across species, neonatal body weight may also very broadly be expected to scale with maternal body weight. This expectation does not apply among individuals within human populations, as large mothers sometimes give birth to small neonates and vice versa. Formulae have been derived to predict neonatal weight from mother's weight (Little 1987; Nahum and Stanislaw 2002). A major factor is mother's body mass index (Koepp et al. 2011), which would be affected by adiposity and health conditions. Hunter-gatherer mothers are unlikely to have been subject to obesity and diabetes, so lean body mass may reasonably be considered on its own, and can be estimated from lower limb dimensions (e.g. Ruff et al. 1997; Will et al. 2017). For exploratory purposes only, Table G.4 gives expected neonatal brain weights, using linear proportion from mean adult body weight (sexes combined) taken from Will et al. (2017:9).

Table G.4: Hypothetical mean neonatal brain mass from adult body mass

	Adult mean body mass (kg)	Neonatal brain mass (g)		
Typical modern human taken to be either 350, 380, or 400 g		Modern human 350	Modern human 380	Modern human 400
Holocene foragers (representing modern humans)	61.86	350.0	380.0	400.0
Upper Palaeolithic <i>H. sapiens</i>	68.23	386.0	419.1	441.2
Middle Palaeolithic <i>H. sapiens</i>	62.67	354.6	385.0	405.2
<i>Homo neanderthalensis</i>	70.52	399.0	433.2	456.0
Middle Pleistocene <i>Homo</i>	70.47	398.7	432.9	455.7
<i>Homo erectus</i> (s.l.)	60.80	344.0	373.5	393.1
<i>Homo naledi</i>	37.53	212.3	230.5	242.7
Early <i>Homo</i>	51.22	289.8	314.6	331.2
<i>Homo habilis</i>	48.43	274.0	297.5	313.2
<i>Australopithecus africanus</i>	31.07	175.8	190.9	200.9
<i>Pan troglodytes</i>	53.60 (f)	303.3	329.3	346.6
<i>Pan troglodytes</i>	53.60 (f)	152.6 actual		
Adult body mass from Will et al. (2017), except <i>Pan troglodytes</i> from DeSilva (2011).				

The chimpanzee case illustrates that a smaller-brained primate with body mass in the lower half of modern human range may give birth to much smaller, leaner, and smaller-brained offspring than modern humans. At some point during evolution of the hominins, a transition, gradual or abrupt, must have been made to longer gestation and more rapid fetal growth leading to birth of substantially larger and fatter neonates. With a body weight and stature very similar to modern humans, *Homo erectus*, all else being equal including pelvic dimensions (discussed below), may have been able to gestate as long and give birth to offspring at the same body weight and stage of brain development as modern humans (cf. Leigh 2006). If this were the case, then, because the target adult brain size was lower (~650–1250 instead of ~1100–1700 cm³), postnatal brain growth could have proceeded at a slower pace or for a shorter period than in modern humans.

Hominins and panins diverged ~7 million years ago, and the ancestral line of modern humans passed through some population of *Homo erectus* s.l. probably in Africa ~2.0–0.8 million years ago. That and the comparable body size of *Homo erectus* are sufficient reasons to expect, *prima facie*, that in *Homo erectus* gestation and fetal development more closely followed the modern human than chimpanzee pattern. Such reasoning applies *a fortiori* to Neanderthals.

G.3 Gestation length

The question of extended gestation length in Neanderthals has receded from active research at the time of writing, but is reviewed here to clarify how understanding of differences between Neanderthal and modern human childbirth has been refined. It has particular bearing on time available for fetal brain growth.

Examining the pelves of the female Tabun C1 adult and the adult male Shanidar 1, Wolpoff (1980a:268,286,288) drew attention to the mediolaterally elongated pubis, as compared with modern humans, which in theory should enlarge the diameter of the birth canal. This he explained as a response to the increase in cranial capacities observed in Neanderthals relative to earlier hominins, which would have resulted in larger fetal head sizes. The upper part of the pubis is anteroposteriorly wider but superoinferiorly thinner than in modern humans and earlier hominins, as if to resist bending, since pressure would be applied horizontally. Neanderthal ilia and ischia are less massive than in the Middle Pleistocene pelves and follow patterns of sexual dimorphism and size with respect to stature similar to those of modern humans, but the distinctively elongated pubic bones subtend hyper-female subpubic angles (Trinkaus 1984:509–510).

On the basis that adult body mass and endocranial capacity was similar between early modern humans (e.g. the Skhul population) and Neanderthals, pelvic diameters relating to the birth canal might also have been similar, but they are not. A Neanderthal pelvis should have allowed a normal human 39-week fetus to be delivered without constriction. However, early modern humans, including the large-brained Upper Palaeolithic population, with reduced overall pelvic dimensions compared with Neanderthals, would have had more difficult births and therefore would have required assistance, giving rise to the custom of practical midwifery, which differs from all other primates (Trinkaus 1984:510,512).

In chimpanzees gestation typically lasts ~32 weeks, in gorillas and orang-utans ~37 weeks, (Rosenberg and Trevathan 2002:1205; Wells et al. 2012:49). Human gestation length is shorter than expected for a mammal of our brain and body size (Leonard et al. 2003:11). According to Trinkaus (1984), primate correlations of brain size to gestation length¹ imply that modern humans and Neanderthals, with adult endocranial capacity 1300–1500 cm³, should have a gestation period of 12 months or more. In that case they would have given birth to larger, more developed neonates, with additional body and brain growth achieved *in utero* (Trinkaus 1984:510,512). The neonates would still be altricial, but would remain so presumably for a shorter time than modern human babies.

However, a consequence of very long gestation and larger fetuses at term would be increased risk of cephalopelvic disproportion, with greater infant or maternal mortality. So, even if extended gestation producing large fetuses had come about in a population, either mothers would have had to acquire the social habit of assisted birth like modern humans, or natural selection would have begun to favour those individuals with smaller heads at birth and so a lower percentage of adult brain size (Collins 1976:128). Such selection would most likely have reduced gestation length in descendants, or have prevented extended gestation from developing in the first place.

Maternal energy expenditure increases as pregnancy progresses and reaches a metabolic ceiling in the third trimester, when energy requirements approach twice basal metabolic rate, which is at or close to maximum sustainable metabolic rate. It is suggested that reaching this limit induces labour. It appears from these results that gestation could not continue

¹ Allman and Hasenstaub (1999:447) assess correlations of primate gestation length with adult and neonatal brain size as very weak.

with an ever growing fetus beyond the nine-month stage, because it would exceed the mother's metabolic capacity (Dunsworth and Eccleston 2015:61–62; cf. Wells et al. 2012:52–54).

Middle Pleistocene hominins seem to have been very large-bodied, some more so than Neanderthals, with lean body mass among the Sima de los Huesos population up to ~90 kg (Arsuaga et al. 1999:256–257). The female individual from Jinniushan (dated 260 ka) is estimated to have weighed 78.9 kg (Rosenberg et al. 2006:3554), and members of this species or grade were possibly the largest humans who have ever lived (Gallagher 2013:559). Adult endocranial volumes, however, were lower than the mean of modern humans (Table G.1). The possibility arises that, if Middle Pleistocene mothers were larger and stronger than modern humans, they could have given birth to neonates with a slightly larger proportion, say ~32%, of their population's adult ECV, to an absolute size of ~400 cm³ or even more. If this is so, then, with a slight decrease in body mass but increase in brain size as Middle Pleistocene populations evolved into early and still robust *Homo sapiens* and collaterals including Neanderthals, the limits of maternal strength and endurance may have been reached sooner, so that *Homo sapiens* and Neanderthal fetuses would have had to be delivered at a more truncated state of brain development. Their ECV at birth remained ~400 cm³, but representing only ~29% or less of adult size.

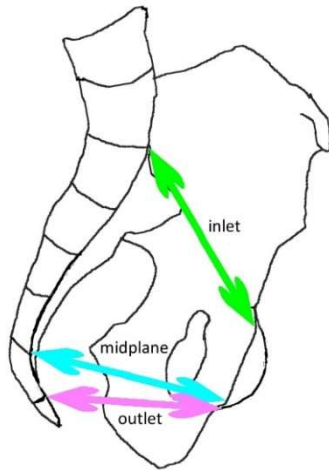
Greene and Sibley (1986) argue that acetabulosity length is related to postural and locomotory adaptation, varies with overall body size, and cannot be used to predict the dimensions of the most constricted apertures of the birth canal, i.e. the pelvic midplane and outlet. Following the discovery and description of the Kebara 2 pelvis (Rak and Arensburg 1987), Trinkaus remarked that greater acetabulosity length does not predict a larger pelvic aperture (comment on Rosenberg 1988:611).

With the discovery of further exemplars, it appears that Neanderthal neonates were skeletally much the same size as modern human ones, suggesting similar length of gestation. A number of fossil pelvises have been reconstructed, allowing comparison with neonatal head size, to be discussed below.

G.4 Obstetric dilemma

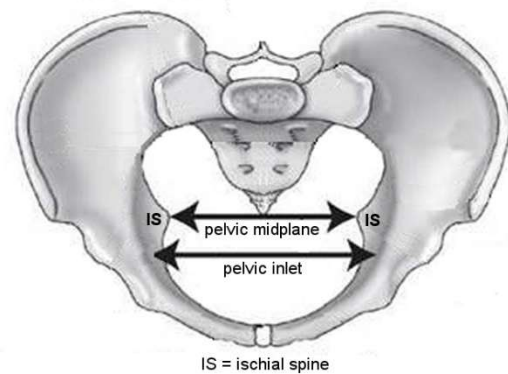
The *obstetric dilemma*, also known as the reproductive dilemma (Trinkaus 1984), refers to conflicting demands between childbirth and upright posture with bipedal locomotion, which could potentially result in a compromise female pelvic shape (Kurki 2007, 2011; DeSilva and Lesnik 2008:1071; Zollikofer and Ponce de León 2010:449; Dunsworth and Eccleston 2015; Gruss and Schmidt 2015). Apart from childbirth in females, stabilization of the vertebral column, and anchorage of and interaction with the lower limbs, the pelvis has the function in upright hominins, in contrast to apes and monkeys, of supporting the lower abdominal viscera and bodily orifices (Abitbol 1988; Chene et al. 2015).

Within the birth canal in the bony pelvis there are three levels which the fetus must negotiate (Figures G.1 and G.2): the *inlet*, defined anteriorly by the posterosuperior surface of the pubic symphysis and posteriorly by the sacral promontory; the *midplane*, defined anteriorly by the posteroinferior surface of the pubic symphysis and medially by the ischial spines; and the *outlet*, again defined anteriorly by the posteroinferior surface of the pubic symphysis and posteriorly by the anterior surface of the fifth sacral element (Tague 1992; Franciscus 2009; Capelle et al. 2020).



Redrawn from Chene et al. (2014),

Figure G.1: Pelvic planes, lateral (R) view



Adapted from online image (doctorlib.org)

Figure G.2: Pelvic planes, superior view

The great apes are not habitually bipedal, and have tall pelves with inferior openings large enough for the small-headed, narrow-shouldered fetus to pass through the birth canal unobstructed. In contrast, modern humans with their vertically shorter pelves have openings that are both anteroposteriorly and mediolaterally constricted in relation to the dimensions of the large fetal head and shoulders. At a gross level, the modern human pelvic configuration is shared with all other member species of the genus *Homo* and at least the later australopithecines of the genus *Australopithecus*, all of which would have been habitually bipedal. However, ratios of anteroposterior versus transverse diameters at levels within the birth canal may differ between hominin species.

Australopithecine females had mediolaterally wide (platypelloid) pelves, with transversely greater diameters at all levels, as exemplified by the female *Australopithecus afarensis* AL-288-1 and *Australopithecus africanus* Sts-14 (Rosenberg and Trevathan 2002:1204). They would have been able to give birth to their small-brained neonates with relative ease, at least not requiring assisted birth (Tague and Lovejoy 1986). On the grounds that australopithecines and Neanderthals (then the only hominins with fossil pelves available) exhibit the same mediolateral elongation of the pubic bones and share other pelvic proportions, Trinkaus (1984:510) stated that the reproductive dilemma does not exist except for modern humans. There is clearly no conflict *prima facie* between the needs of bipedalism and childbirth, in view of the fact that bipedal hominins, australopithecines and *Homo*, successfully reproduced for at least four million years. However, with increased body size and greater degree of encephalization in later species, *Homo heidelbergensis* and especially *Homo neanderthalensis* and *Homo sapiens*, the risk of cephalopelvic disproportion is likely to have become more common, unless pelvic internal dimensions continually expanded to accommodate the fetus at term. Although Neanderthal pelves are robust, dimensions of the birth canal are not necessarily larger, as various reconstructions have shown.

In Lovejoy's (1975) assessment, hominin pelvic shape is determined by requirements of bipedal posture and locomotion, and the dimensional differences between australopithecines and *Homo sapiens* are related to encephalization.

Efficient bipedal locomotion is held to require limited biacetabular breadth, whereas a wide pelvic opening like that of *Australopithecus afarensis* (Ayala and Cela-Conde 2017:76),

scaled up to *Homo* dimensions with further allowance for large-headed fetuses, would have increased biacetabular breadth. During walking and running the pelvis tends to rotate away from the limb that is in contact with the ground (Warrener et al. 2015:2): this effect exaggerated by a large biacetabular diameter might be expected to produce an energetically inefficient gait (cf. Dunsworth and Ecclestone 2015:57; Arsuaga et al. 1999:257), which potentially would compromise the ability to pursue prey and evade predators.

A recent study of biomechanical demands on the pelvis concludes that pelvic width does not predict hip abductor mechanics and that modern human females and males are equally efficient in locomotion. It is suggested that factors other than the requirements of bipedal locomotion must account for transverse constriction of the birth canal in modern humans (Warrener et al. 2015). Two such factors may perhaps be identified: (1) support of the abdominal viscera and (2) thermoregulation in tropical climates, discussed later in this chapter.

In modern humans the ischial spines project medially into the pelvic cavity and serve to anchor the major ligaments of the pelvic floor (Figure G.2). Their prominence varies from one individual to another, 0.9–3.0 cm. In apes and australopithecines the projection so far found is much less: *Pan* 0.2–0.7 cm, *A. afarensis* 0.6 cm, *A. africanus* 0.8 cm. In some individuals the ischial spines develop from separate centres of ossification, but in others are an outgrowth of the body of the ischium. This difference of origin may account for variability of prominence: when a separate ossification centre is present, the pelvic-floor ligaments pulling medially on that centre and therefore on the cartilage connecting it to the ischial body may cause greater medial growth by the end of development (Abitbol 1988). The transverse breadth between the ischial spines at the midplane is the narrowest diameter in the birth canal for modern humans (Abitbol 1988; Kurki 2007, 2011).

In an upright hominin the ligaments of the pelvic floor have to support the viscera, genitalia, and sphinctres of elimination. Too wide a bony outlet in any orientation may increase risk of prolapse (Xu et al. 2011; Kolesova et al. 2013). This factor may have induced selection to minimize the diameters of the lower pelvic internal planes which these ligaments have to span, a process which appears to have included increasing prominence of the ischial spines. Yet a narrower outlet conflicts with the need to maintain wide enough apertures to give birth to large-headed babies. This conflict appears to be a distinct obstetric dilemma, one which arises from the requirements not of bipedal locomotion as such but of upright posture itself.

G.5 Birth process

In all primates the greatest dimension of the fetal neurocranium is its sagittal length. In monkeys the greatest diameter of the pelvic cavity at all planes is anteroposterior, so the fetus descends the birth canal all the way with the cranium aligned sagittally, generally facing anteriorly. In the great apes the process is similar, but without the constrictions experienced by smaller-bodied primates. In contrast, the inlet plane in modern humans is widest mediolaterally, but the mid-pelvic and outlet planes are larger anteroposteriorly (Abitbol 1988; Rosenberg and Trevathan 2002). Modern human fetuses typically descend into the birth canal with the cranium transversely or obliquely orientated, but turn through up to ninety degrees to make their way in sagittal orientation through the midplane and outlet, usually facing posteriorly, though sometimes anteriorly. Sometimes the neck is flexed, so as to present inferiorly the shorter suboccipitobregmatic cranial diameter (Laudicina et al. 2019:2). To enable the relatively rigid and broad shoulders (as compared with other primates) to pass through the midplane and outlet, the emerging baby may again rotate (Rosenberg and Trevathan 2002; 1201), and the anterior shoulder may temporarily locate in the hollow of the obturator foramen while the posterior

shoulder is delivered (Smeltzer 1986 cited by Trevathan, comment on Rosenberg 1988:611). Rotation is not unique to humans, since fetal entry into the inlet at various angles has been observed in baboons and other monkeys, followed by rotation into sagittal orientation facing ventrally (Rosenberg and Trevathan 2002:1200). Chimpanzee babies are sometimes born facing posteriorly like modern humans (Wells et al. 2012:43).

Table G.5 lists pelvic plane dimensions for hominins in which these are available, with modern humans and chimpanzees for comparison.

Table G.5: pelvic plane diameters

Species	Specimen	Sex	Source	Inlet AP	Inlet ML	Midplane AP	Midplane ML	Outlet AP	Outlet ML
<i>Pan trogl.</i>	recent sample	F		136	90	117	71	122.4	105.0
<i>Aus. afarensis</i>	AL-288-1	F	Tague & Lovejoy 1986	76	132	72	101	71	96
	AL-288-1	F	Häusler & Schmid 1995	79–81	123–126	112–115	86–89	90–92	83–86
	AL-288-1	F	Chene et al. 2015	76.8	129	73	104.5	72	94.5
<i>Aus. africanus</i>	Sts-14	F		83	116.8	73.3	93.1	NA	105
	Sts-65	F	Claxton et al. 2016	82.7, 82.8 ^a	101.5, 109 ^a	NA	NA	NA	NA
<i>Aus. sediba</i>	MH2	F	Laudicina et al. 2019:4	81.7	117.6	97.9	NA	97.4	NA
	MH2	F	Laudicina et al. 2019, Supp. Inf.	80.8	112.4	97.5	96.9	97.4	104.2
<i>Homo erectus</i>	BSN49/P27 (Gona)	F		98	124.5	111.5	114.5	111.5	133.3
<i>Homo heidelberg.</i>	SH1	M	Arsuaga et al. 1999	109.4	138	133	108	126.5	135
	SH1	M	Bonmatí et al. 2010	108.3	139.3	131.2	116.4, 125.1 ^b	127.5	133.6
<i>Homo neanderthal.</i>	Kebara 1	M	Rak and Arensburg 1987	117	141	NA	NA	NA	NA
	Kebara 1	M	Tague 1992	118	142	94	NA	88	114
	Tabun C1	F	Ponce de León et al. 2008	109–121	143–145	131–141	114–122	123–134	116–126
	Tabun C1	F	Weaver and Hublin 2009	104	131	NA	NA	93	132
<i>Homo sapiens</i>	recent sample	F		91–112	123–135	112.9–138	NA	NA	111.9–127

Data from Laudicina et al. (2019 including SI), unless otherwise stated.
AP = anteroposterior, ML = mediolateral, NA = not available.
a = Sts-65 first with Sts-14 sacrum, then with AL-288-1 sacrum.
b = SH1 first with restoration of ischial spines, then without.

During labour, the placenta and ovaries secrete the hormone relaxin, which has the effect of loosening pelvic ligaments as well as widening the cervix. As the descending fetus imposes pressure, eversion of the ischia can widen the subpubic angle and increase bispinous breadth by several millimetres, and backward nutation, i.e. tilting, of the sacrum can increase anteroposterior diameters of the midplane and especially the outlet. This way even a birth canal which would appear to be dystocic may become sufficient (Tague 1992:15; Gruss and Schmitt 2015). To assess how this factor may have affected Neanderthal mothers, it would be necessary to have reliable diameters at all planes. It may be that relaxation of the pelvis was rarely needed until the increase in endocranial volume observed in Middle Pleistocene *Homo*, but would apply from then onward with the continued increase in ECV up to modern humans and Neanderthals.

The skull of a fetus at term is flexible since the vault sutures are unfused, and it is even possible for the squamae to overlap one another slightly (Tague 2012; Claxton et al 2016),

aiding passage through a constrained birth canal. Open sutures of the vault and basicranium are observed in the Le Moustier 2 neonate (Gunz et al. 2011). It is notable that several Neanderthal infants continue to exhibit an unfused metopic suture several years after birth (§5.2).

Rotational birth as above seems not to have occurred in australopithecines, and possibly also not in *Homo* other than *Homo sapiens*. While some researchers have argued that australopithecines had rotational birth, others have not accepted this view (§G.5.1). It would seem anomalous if it were present in australopithecines and modern humans but absent in intermediate forms of *Homo*. The question arises at what stage the modern human pattern of rotational birth became established, and in particular whether it applied to Neanderthals. Below, diagnostic specimens from australopithecines onward are considered.

G.5.1 Australopithecines

The two specimens with fairly complete pelves, AL-288-1 (*Australopithecus afarensis*) and Sts-14 (*Australopithecus africanus*), are platypelloid. In most reconstructions, the pelvic transverse diameter is greater than the anteroposterior diameter at all three obstetric levels of the cavity (Figures G.1 and G.2, Table G.5). Despite AL-288-1 having distinct ischial spines, the bispinous diameter is as much as 104.5 mm (Chene et al. 2015:976–977), 101 mm (Tague and Lovejoy 1986:243), or at least 86 mm (Häusler and Schmid 1995:368). It is therefore expected that australopithecine fetuses descended all the way with the head orientated transversely, rather than sagittally like monkeys and modern humans (Rosenberg and Trevathan 2002:1204; Tague 1992:19). However, Häusler and Schmid (1995) reconstruct AL-288-1 with an anteroposterior diameter at the midplane of 94 mm and transverse (bispinous) 86 mm (1995:368), and propose rotational birth as in modern humans. Berge and Goularas (2010) virtually reconstruct Sts-14 with an anteroposterior diameter at the midplane of only 73.3 mm with transverse 93.1 mm, but argue that forces from muscular contractions would have induced the small fetal head into an anteroposterior orientation as it entered the midplane.¹

Fossils assigned to the species *Australopithecus sediba*, dated to ~1.98 Ma, one of the later australopithecines, are said to combine features of earlier species of this genus with features of *Homo*. MH1 represents a male juvenile, and MH2 an adult female including a pelvis (Churchill et al. 2018). The pelvis shows a narrowing of the midplane transverse diameter toward the human pattern owing to greater development of the ischial spines. Even so, this diameter is 96.9 mm. Neonatal head size is derived by regression from the MH1 juvenile, whose endocranial capacity is 420 cm³, to give neonatal endocranial capacity 162 cm³, with biparietal width 73 mm and fronto-occipital length 89 mm. The fetal head could therefore have passed easily through the midplane in either orientation (Laudicina et al. 2019). There is no evident reason to expect that the fetus would have presented sagittally.

Whereas in great apes the metopic suture fuses soon after birth, in the Taung child, aged 3–4 years and attributed to *Australopithecus africanus*, the suture remains unfused, as it does in modern humans until ~2 years (Falk et al. 2012). The authors propose that fetuses at term of this species and its successors in the genus *Homo* had flexible cranial vault bones to aid passage through a pelvic canal adapted for bipedalism. In Neanderthal infants the metopic suture is incompletely fused (Thoma 1963).

¹ Muscular influences on the orientation of the fetus during the birth process arguably deserve more attention, with analysis of their applicability in different species of hominins and to birth canals with different proportions of anteroposterior versus transverse diameters and with different dimensions of anterior and posterior areas of each pelvic plane. Pelvic asymmetries also exist (Tobolsky et al. 2016) and may affect fetal orientation, although in fossils often only one side of the pelvis is preserved and the other is reconstructed by mirroring.

G.5.2 Early Homo

The earliest female fossil pelvis attributed to *Homo* is the specimen BSN49/P27 from Gona, Ethiopia, dated to 0.9–1.4 Ma and assigned to *Homo ergaster*.¹ It comprises a sacrum and os coxae with a complete pubis. The pelvis is transversely broad but is said to share with later *Homo* an anteroposteriorly wider birth canal, and could permit passage of a fetus with an endocranial capacity of 315 cm³, which would be 30–50% of adult value 600–1067 cm³ for early *Homo erectus*. It appears intermediate between australopithecines and modern humans (Simpson et al. 2008). The small body weight and stature of the Gona individual (33.2 kg and 120–146 cm), below those hitherto known for *Homo* (52–82 kg and 150–185 cm) but within the range of australopithecines, are emphasized by Ruff (2010). Even the body mass of the sole diagnostic adult from the small-bodied Dmanisi *Homo* sample is 58% larger than BSN49/P27.

Ruff (2010) also draws attention to the wide pelvic midplane and outlet diameters relative to overall size. The midplane anteroposterior diameter is 111.5 mm and the bispinous 114.5 mm; and the outlet has a transverse diameter of 133.3 mm (Simpson et al. 2008 SI:11). These very large diameters in a small body add support to Ruff's (2010) observation that archaic hominins including *Homo erectus* were very wide-bodied compared with *Homo sapiens*. There appears to be no reason to assume rotational birth in the population represented by BSN49/P27.

G.5.3 Middle Pleistocene Homo

Sima de los Huesos Pelvis 1 (SH1) is a fairly complete pelvis, with associated lumbar spine, of a mature male from a population most probably ancestral to Neanderthals, and dated to ~430 ka, usually included in *Homo heidelbergensis* (§B.2). Arsuaga et al. (1999) describe the pelvis as having a very long pubic ramus, robust, wide, undistorted and probably representing a primitive pattern from which modern humans departed. A modern human fetus at term would pass through with ease (1999:256,258), and the birth canal of a female pelvis would be expected to be wider. At the midplane the largest diameter is sagittal: the bispinous diameter is estimated to be 108 mm and the anteroposterior is 133 mm (Arsuaga et al. 1999:257–258; Simpson et al. 2008, SI:11). This very capacious pelvis belonged to a subject with a stature of 168.9–171.2 cm and body mass 90.3–92.5 kg, over 45 years old and suffering from pathologies of the lumbar spine (Bonmatí et al. 2010). Levels of sexual dimorphism in Middle Pleistocene hominins were similar to those of recent humans (Ruff 2010:174), so a female counterpart would likely also have been large-bodied.

The Middle Pleistocene archaic *Homo* female from Jinniushan dated to 260 ka is very robust (Rosenberg et al. 2006; Ruff 2010). Though missing the sacrum, it possesses a complete left os coxae. Virtual reconstruction of the pelvis and computer simulation of the birth process are said to indicate constraints indicative of rotational birth (Rosenberg et al. 2010).²

Arsuaga et al. (1999:258) suggest rotational birth was likely in SH1 on the expectation that the fetus would orientate to the largest diameter at the midplane. However, Weaver and Hublin (2009:8158) observe that the inlet and outlet are transversely wider, and suggest that a female pelvis would have a larger midplane transverse diameter than the male, as in modern humans, so that rotational birth was not necessarily implied by the SH1 configuration. They

¹ The relatively complete skeleton KNM-WT15000 from Nariokotome dated to ~1.3–1.5 Ma and assigned to *Homo ergaster*, possesses a pelvis. It has been studied from an obstetric viewpoint but is not discussed here, because it is male and aged only ~8 years (Walker and Leakey (eds.) 1993; Simpson et al. 2008; cf. Frémondrière and Marchal 2013:164).

² No measurements are given and I have not found a more recent publication on this research.

also note that the ischial spines had to be reconstructed, and were made to be large and pointing (Arsuaga et al. 1999:257), which they imply may not be accurate. Given the absolutely large diameters, a human fetus could pass down the birth canal with its head and shoulders in transverse or oblique positions, so modern rotational birth is not shown to be obligate in this population.

If the SH1 pelvis is typical, then *Homo heidelbergensis* females could have given birth to neonates with crania as large as those of modern humans, although no evidence has been presented that they did. Hypothetically, the higher percentage of brain growth achieved in utero would result in considerably earlier attainment of adult volume during postnatal life, especially since the adult target size would be smaller. Arsuaga et al. (1999:257) give adult endocranial volumes of 1125–1390 cm³ for the Sima hominins.

G.5.4 Neanderthals

Neanderthals largely retain the overall wide bodies and general pelvic characteristics of their Middle Pleistocene predecessors, including the elongated pubic ramus, with an additional feature of superoinferior thinning of the ramus (Trinkaus 2006; Rosenberg 2007). With respect to previous *Homo* and australopithecines, the narrow pelvises of modern humans, and notably the short pubic bones of modern males, are apomorphic.

While Neanderthal pelvises are expected to be wide, reassessment of the La Chapelle-aux-Saints adult male postcrania by Trinkaus (2011:464–466) results in a pelvis narrower than the Kebara 2 adult male and fitting within the early modern human distribution, with bi-iliac breadth 292 mm and outlet diameter 125 mm. Yet these dimensions do not pertain to a small individual, since the right femoral head diameter, a prime indicator of body mass, is 52.4 mm, lying at the upper end of the Neanderthal sample (2011:464 and SI). Incompleteness of the La Chapelle pelvis does not allow midplane measurements.

Two skeletons, both from the Levant, have pelvises complete enough to have been the subject of reconstructions and birth simulations: Kebara 2 and Tabun C1. The skeleton of a female from Spain, Palomas 96, recovered in 2006–2007, also preserves much of the pelvis (Walker et al. 2011a), but the fossils were encrusted in breccia (Appendix A). To the present writer's knowledge no obstetric studies of it have yet appeared.

Kebara 2 is a male aged ~32 years (Rak and Arensburg 1987; Gómez-Olivencia et al. 2018b), dated to 60–64 ka (Schwarcz et al. 1989). The sacrum and right os coxae are preserved.

Kebara 2 pelvic inlet dimensions are anteroposterior 117 mm and mediolateral 141 mm (Rak and Arensburg 1987). Tague (1992:17) observes that Rak's (1990:327–328) graphs show the anteroposterior diameter of the inlet lying in the middle of the modern male distribution and the transverse diameter at the upper end. Tague (1992:15) lists Kebara 2 anteroposterior dimensions as inlet 118 mm, midplane 94 mm, outlet 88 mm. Transverse dimensions are unavailable for the midplane and outlet, but would be wider. The anteroposterior diameters are lower than for any modern human males in Tague's study. Citing Abitbol (1996), Arsuaga et al. (1999) list modern human neonatal cranial diameters as 93 mm biparietal and 94 mm suboccipitobregmatic. A Neanderthal fetus with similar dimensions would only just negotiate the midplane with the cranium sagittally orientated, and the outlet seems scarcely negotiable at all, unless there were nutation (tilting) of the sacrum and ischial eversion to widen the lower pelvic opening during birth (Tague 1991:170–171; Chene et al. 2014:319). It is not clear whether a rotation to sagittal orientation would facilitate the birth process. The fetal head could have remained in a transverse orientation all through the birth canal, as would have applied in australopithecines and probably Lower and Middle Pleistocene *Homo*. Tague (1992:19)

suggests that a sagittal orientation might have been possible if Neanderthal females had greater anterior space at the lower planes than males. To enable this, as Neanderthal males have longer pubic bones than females, unlike modern humans, females would have had to have longer ischia.

The accuracy of the earlier reconstruction of the Kebara 2 pelvis has been questioned. Detecting lateral displacement of the midplane and outlet area and distortion midway along the ischiopubic ramus, Ruff (1995:564–566) suggests that correcting the distortion would position the inferior edge of the pubic symphysis 1–2 cm more anteriorly. His view then was that fetal rotation to sagittal orientation through the midplane and outlet was likely a precondition for giving birth to larger-brained offspring from the Middle Pleistocene onward. With the constraints of platypelloid pelvises until then, *Homo erectus* populations would have been limited to the smaller endocranial volumes which prevailed from 1.5 to 0.5 Ma with only a gradual increase. Trinkaus (2011:466) observes that in the Kebara 2 pelvis the original angles of articulation between the sacrum and the ossa coxae are unknown because there is sacral deformation and the auricular surfaces are eroded, leaving scope for different reconstructions.

Tabun C1 is a female aged ~30 years, dated to ~122ka, possibly 82–143 ka (Grün and Stringer 2000; Coppa et al. 2007; Been et al. 2017). The right ilium, pubis and ischium and the left ilium and pubis are preserved. Mezmaiskaya 1 is a 2-week-old infant. Ponce de León et al. (2008) virtually reconstructed the skull with an ECV of 422–436 cm³, from which they derived the value which it would have had at birth: 382–416 cm³. This derived value is consistent with the estimate of ECV by Gunz et al. (2011) for the neonate Le Moustier 2 (Table G.1).

To study the birth process, Ponce de León et al. (2008) utilized the preserved elements of Tabun C1, mirrored where necessary and supplemented with a sacrum and ischial part, including the spines, from modern humans. The authors observe that the birth canal has a wide inlet and probably wide outlet, but conclude that rotational birth, with the head entering the inlet in transverse orientation but passing through the midplane and outlet in sagittal orientation, was most likely. Their dimensions for Tabun C1 are shown in Table G.5. The anteroposterior diameter at the midplane is ~19 mm greater than the transverse diameter, but both are large, although the authors state that Tabun C1 is small for a Neanderthal female. Diameters at all levels are 109 mm or more, so it is reasonable to assume that a modern human or Neanderthal fetus at term could have descended in either orientation.¹

Weaver and Hublin (2009) take issue with the above conclusions from Tabun C1, arguing that the reconstruction of the pelvis was deliberately designed to allow the Mezmaiskaya 1 neonate to pass through. In their view, the preserved portions do not justify reconstruction with the large anteroposterior diameter for the lower planes, and they conclude that transverse orientation throughout should be assumed, as they do for Middle Pleistocene *Homo* (cf. Franciscus 2009).

Given that modern human babies may turn on exit to enable the shoulders to pass through the midplane and outlet orientated to the longer diameter, in their case anteroposterior, one would expect Neanderthal fetuses to do the same, although in their case the longer diameter would be transverse, so that the head would become more sagittally oriented during passage of the shoulders.

¹ The article and supporting information contain many measurements, but no ectocranial diameters or circumferences (as opposed to ECV) for Mezmaiskaya 1, either those of the specimen as preserved or those which it would have had at birth. Yet these would be informative and presumably must have been available from the virtual reconstruction.

A new virtual reconstruction of Kebara 2 has been announced by Adegboyega et al. (2018), which is said to result in a rounder pelvic inlet and outlet with a slightly more anterior position of both the sacral promontory and the pubic symphysis. It is not stated whether the anteroposterior lengths of the midplane or outlet are increased.¹

G.5.5 Neanderthals with early *Homo sapiens*

Observing an increase of anteroposterior breadth at the pelvic outlet from australopithecines to *Homo erectus*, Ruff (1995:566) suggested that modern rotational birth would have begun in the Middle Pleistocene. It would then be expected in the descendant species *Homo sapiens* and *Homo neanderthalensis*. This view was widely accepted.

Rosenberg (2007) states that it is *Homo sapiens*, especially male, pelvic morphology that needs explanation, since Neanderthals, represented by Kebara 2, Tabun C1, and fragmentary remains from Krapina, seem to have followed a pattern which includes the long pubic ramus and large bi-iliac breadth, plesiomorphic with earlier *Homo* and shared with all archaic hominins across the world. Neanderthal males have longer pubic rami than females, the reverse of the condition in recent humans.

Following later discoveries and analysis, Ruff (2010) proposes that high-latitude, robust, wide-bodied populations of *Homo* from the Middle Pleistocene onward retained the primitive pelvic morphology of large transverse diameters at all obstetric planes. As their large-headed fetuses could descend in transverse or oblique orientation, there was no need to develop modern rotational birth. These populations were the Neanderthals (and perhaps in East Asia Denisovans). In hot low-latitude regions such as South and East Africa, where *Homo sapiens* developed, there was need for effective thermoregulation and so selection for a more slender physique to dissipate body heat. The resulting narrower pelves required a reorientation of maximum internal diameter of the lower planes to the anteroposterior axis to continue to allow birth of large-headed fetuses. As modern humans migrated northward, some eventually reached temperate to cold and arctic regions, where their descendants adapted by developing stockier, wider bodies. However, although pelves became relatively wider, they did not redevelop the transverse pattern of birth but retained the anteroposterior rotation pattern of their low-latitude ancestors (Gruss and Schmitt 2015; cf. Churchill and Vansickle 2017).

The male Qafzeh 11 pelvis, dated to roundly ~100ka, exemplifies the slender pelvic morphology of early *Homo sapiens*, contrasting with Kebara 2 (Rak 1990). Neanderthal pelvic and lumbar morphology is characterized by other features, including a straighter, more vertical sacrum and an apparently less curved lumbar spine (Been et al. 2010; Gómez-Olivencia et al. 2018b:6). The wide bi-iliac breadth is matched superiorly by the wide rib cage, which, in Kebara 2 at least, is not larger than in modern humans but craniocaudally shorter (Gómez-Olivencia et al. 2018b). The result is the stocky, theoretically cold-climate physique, which is yet found more or less unchanged in Neanderthals inhabiting warmer regions such as the Levant and Spain (Walker et al. 2011a:10090).

¹ I have not found a follow-up publication by any of the authors.

G.6 Conclusion

In so far as there is consensus, it appears that Neanderthals experienced the same gestation period as modern humans. They may have retained the primitive hominin pattern of transverse orientation of the fetal head throughout the birth process, although one reconstruction of the only adult female pelvis (Tabun C1) has anteroposterior diameters conspicuously larger than transverse diameters, which may indicate modern rotational birth.

Like most mammals, monkeys, gibbons, siamangs, and the great apes generally seek solitude when about to give birth. This contrasts with modern human practice, whereby in all documented societies mothers almost invariably expect to be assisted by other community members, traditionally females (Rosenberg and Trevathan 2002:1201,1203). It is not clear at what stage in prehistory this uniquely human practice began.

Owing to the high degree of encephalization coupled with skeletal robusticity of Neanderthals, fetuses at term had heads and shoulders at least as large as those of modern human babies, while the birth canal remained no larger than that of their Middle Pleistocene ancestors. Whichever orientation the fetus presented in, mothers may often have experienced difficult births and have sought and expected assistance from other females (Weaver and Hublin 2009:8154). Such practice implies developments in family and social relationships, communication, general mental capability, and emotional engagement with and commitment to conspecifics.

Virtual reconstructions allow non-destructive experimentation on the fragmentary remains of pelvises and neonates, and may bring to light possible configurations which otherwise could not be elaborated. Further potentially informative specimens are being found, especially in Spain, and discovery of more complete Neanderthal pelvises and neonate skeletons will help to resolve remaining uncertainties.

Appendix H

STATURE AND BODY MASS, FOSSIL *HOMO*

H.1 Introduction

Immature data is given in Chapter 6, only adult data here. Data are tabulated for the following groups:

- Neanderthals
- Upper Palaeolithic *Homo sapiens*
- West Asian Middle Palaeolithic *Homo sapiens* (Qafzeh and Skhul)
- East African Middle Stone Age *Homo sapiens*
- East and South African *H. rhodesiensis/heidelbergensis*
- European *H. heidelbergensis*, excluding Sima de los Huesos
- European *H. heidelbergensis*, Sima de los Huesos
- East Asian archaic *Homo* 500 – 200 ka
- East Asian *Homo erectus* 1 Ma – 500 ka
- East African archaic *Homo* 1 Ma – 500 ka

The data on individuals are taken from Will et al. (2017 Supplementary Information). Where numbers of a group are sufficient, individuals assigned female and male by these authors are listed in separate tables, and a third table lists those unassigned, each table with mean, minimum and maximum. In these cases a further table gives overall mean, minimum and maximum.

La Quina H5 (Neanderthal) is listed here as female, following Will et al., while Trinkaus (2016) regards it as a small male on the grounds of robusticity.

Not all individuals yield both body mass and stature. Some specimens are otherwise very incomplete but include diagnostic long bone diaphyses for stature and femoral or tibial heads or components of the pelvis for body mass. For example, Fond-de-Forêt 1 is an isolated femur.

Dating information is taken from Will et al. without change, except that years are rounded to whole thousands. Specimens from before 1 million years ago or after 15,000 years ago are not covered here.

Stature and body mass estimates and their degree of uncertainty

Generally these estimates are derived by regression formulae using direct measurements on fossils as independent variables (Carretero et al. 2012). Stature can be based upon the length of the femur, tibia, or even humerus, radius or ulna, or on vertebral superoinferior diameters (ibid.). Body mass can be based upon dimensions of load-bearing bone parts such as femoral or tibial head diameter or diaphyseal cross-sectional diameter, or sometimes a combination of stature and bi-iliac breadth (Ruff et al. 2005). Estimates from regression equations can be tested against recent human reference samples (Ruff et al. 1991). Carretero et al. (2012:346–348) discuss methods of stature calculation using different techniques and reference samples. R.J. Smith (1996) critiques methods of estimating body mass and the derivation of further traits from it.

Researchers have preferred as reference samples recent human groups possessing body characteristics more likely to be found among particular extinct hominins. So McHenry (1992) used pygmy and Khoisan individuals as a reference sample for estimating body size of the small-boned australopithecines and *Homo habilis*. On the basis that the physique of Middle and Upper Pleistocene hominins would have emphasized strength, speed, agility and endurance, Ruff (2000) used Olympic athletes to estimate body mass from stature and bi-iliac breadth. Ruff et al. (2005) used Finns and Alaskan Inupiat to approximate robust Middle and Upper Palaeolithic hominins. Pomeroy et al. (2018) studied female athletes as a sample to estimate lean and fat body mass from cross-sections of the femur, tibia and humerus.

Deriving body mass in kilograms for their recent human sample Ruff et al. (1991:406) reported standard errors of the estimate (SEE) between 9.8 and 18.3. In a later study of Inupiat and Finns using new equations, SEE was 3.6 for males, 4.1 for females (Ruff et al. 2005:385). Mean body mass for all three groups Sima de los Huesos hominins, Neanderthals, and Pleistocene *Homo sapiens* centres on ~70 kg, with 95% confidence intervals of the means lying within the range 56.42–84.63 kg. (Will et al. 2017:12). There are differences of up to ~10 kg (nearly 14%) between estimates from different sources (ibid. SI:file 004). Some individuals have had estimates based upon very limited fossil material: e.g. Sima de los Huesos “SH foot association 2” which consists of two tali and two calcanei (ibid. SI: file 001). Heyes and MacDonald (2015) review uncertainties of body mass estimation, noting underestimation reported in several studies and SEE up to 14.11 (ibid.:194).

In view of the uncertainty of individual estimates, means for groups, populations or species in the tables are intended to be illustrative rather than definitive.

H.2 Tables

Table H.1: Neanderthal, male

	Individual	Dating (ka)	Body mass	Stature
1	Lezetxiki	164		166.8
2	Krapina 207	130	66.0	
3	Krapina 237	130	77.5	171.1
4	Kiik-Koba 1	100	80.2	162.7
5	Regourdou 1	66	64.4	162.3
6	Regourdou 2	66		181.2
7	Kebara 2	60	72.4	172.0
8	Amud 1	60	72.1	175.7
9	La Chapelle-aux-Saints 1	51	81.7	162.5
10	El Sidrón SDR-035+SDR-041	49		160.4
11	El Sidrón SDR-054+SDR-055+SDR-056	49		167.2
12	Shanidar 1	47	67.8	167.2
13	Shanidar 2	47		154.8
14	Shanidar 3	47	72.7	166.4
15	Shanidar 4	47	74.6	162.5
16	Shanidar 5	47	71.2	163.6
17	La Ferrassie 1	47	90.5	171.6
18	Neandertal 1 (Feldhofer)	40	81.4	165.6
19	Spy 2	33	82.6	158.6
	Mean		75.4	166.2
	Minimum		64.4	154.8
	Maximum		90.5	181.2

Table H.2: Neanderthal, female

	Individual	Dating (ka)	Body mass	Stature
1	Sedia del Diavolo 2	250		159.7
2	Le Prince 1	200	76.2	
3	Tabun C1	170	54.2	153.1
4	Krapina foot A	130	59.2	163.2
5	Krapina 236	130	59.7	160.0
6	Subalyuk 1	66		160.5
7	Kebara 9	60		158.0
8	La Ferrassie 2	47	67.8	148.7
9	Shanidar 6	47		150.5
10	Shanidar 8	47		159.3
11	Moros de la Gabasa (Gal. Rev.439)	45		157.9
12	Sima de las Palomas 96	45	61.0	149.2
13	La Quina H5	42		161.0
	Mean		60.4 excluding Le Prince 1 otherwise 63.0	156.8
	Minimum		54.2	148.7
	Maximum		67.8 excluding Le Prince 1 otherwise 76.2	163.2

The body mass of Le Prince 1 is calculated from femoral head diameter estimated from the acetabular diameter (Will et al. 2017 SI) of the isolated right os coxae from the Grotte du Prince, Grimaldi, Italy. It is unequivocally assigned female by De Lumley (1973:232–233). However, the specimen is incomplete. De Lumley comments on the height of the acetabulum, 59 mm, which just exceeds that of Krapina males and females (1973:236–237). Although it is included here for completeness, in the rest of this work the female mean *excluding* this specimen is used, because Le Prince 1 is an outlier to the rest of the sample, the date is marginally early, and the diagnostic value could not be measured directly. The even older Sedia del Diavolo specimen fits within the rest of the sample range and makes little difference to the mean for stature.

Table H.3: Neanderthal, sex unassigned

	Individual	Dating (ka)	Body mass	Stature
1	Krapina 208	130	68.5	
2	Krapina 209	130	67.4	
3	Krapina 213	130	83.0	
4	Krapina 214	130	63.7	
5	Krapina 238.1	130	53.0	
6	Krapina 238.2+238.7	130		164.2
7	Krapina 248.1	130		169.9
8	Moula Guercy M-D2-587	72		173.0
9	Combe Grenal 30	70	63.5	
10	Fond-de-Forêt 1	50	73.5	
11	El Sidrón SDR-1609	49	82.6	
12	Sima de las Palomas 77	45	66.9	
13	Sima de las Palomas 92	45	63.7	152.6
14	La Quina H1	42	72.7	168.8
15	Spy 25B	33		161.2
16	Spy 25C	33		157.9
17	Spy 25D	33		160.3
	Mean		69.0	163.5
	Minimum		53.0	152.6
	Maximum		83.0	173.0
?	Gesher Benot Ya'acov 1 (Possible Neanderthal, not included in mean etc.)	70	52.0	149.9

Table H.4: Neanderthal, all

	Body mass	Stature
Mean	70.7	162.7
Minimum	53.0	148.7
Maximum	90.5	181.2

Table H.5: Upper Palaeolithic H. sapiens, male

	Individual	Dating (ka)	Body mass	Stature
1	Paviland 1	28	74.0	176.5
2	Cro-Magnon 1 (CM-1)	28	70.3	172.1
3	Cro-Magnon 4314	28	70.1	
4	Cro-Magnon 4315	28	73.5	
5	Sunghir 1	27	78.9	183.6
6	Dolní Věstonice 13	26	71.2	171.6
7	Dolní Věstonice 14	26	79.4	185.0
8	Dolní Věstonice 15	26	69.8	160.1
9	Dolní Věstonice 16	26	78.0	174.2
10	Předmostí 3	25	70.1	182.0
11	Předmostí 9	25	58.8	169.9
12	Předmostí 14	25	68.5	173.6
13	Barma Grande 2	24	82.3	188.8
14	Veneri 1	24	77.1	177.1
15	Ohalo 2	19	74.9	175.0
16	Minatogawa 1	17	63.3	152.9
	Mean		72.5	174.5
	Minimum		58.8	160.1
	Maximum		82.3	188.8

Table H.6: Upper Palaeolithic H. sapiens, female

	Individual	Dating (ka)	Body mass	Stature
1	Abri Pataud 1	31	69.7	162.2
2	Mladeč 21	31	65.6	
3	Cro-Magnon 4337	28	81.1	170.2
4	Dolní Věstonice 3	26	55.8	163.4
5	Caviglione 1	25	68.1	175.1
6	Předmostí 1	25	56.5	153.7
7	Předmostí 4	25	70.5	168.2
8	Předmostí 10	25	71.9	163.4
9	Veneri 2	24	74.2	173.2
10	Paglicci 25	23	61.7	170.4
11	Minatogawa 2	17	48.6	144.8
12	Minatogawa 3	17	50.8	149.3
13	Minatogawa 4	17	47.4	147.7
14	Mirón 1	15	56.9	160.7
	Mean		62.8	161.7
	Minimum		47.4	144.8
	Maximum		81.1	175.1

Table H.7: Upper Palaeolithic H. sapiens, sex unassigned

	Individual	Dating (ka)	Body mass	Stature
1	Maladeč 22	31	78.5	
2	Maladeč 24	31		191.6
3	Maladeč 27	31		176.9
4	Maladeč 30	31	91.3	173.3
5	Rochette 1	30	66.7	
6	Cro-Magnon 4293	28		173.8
7	Cro-Magnon 4297	28		178.0
8	Cro-Magnon 4317	28	61.7	
9	Cro-Magnon 4321	28	61.3	
10	Cro-Magnon 4322	28		178.9
11	Cro-Magnon 4324	28		160.0
12	Cro-Magnon 4330	28		173.7
13	Cro-Magnon 4345	28		171.9
14	Cro-Magnon 4345-Bis	28		170.6
15	Cro-Magnon 4346	28		169.6
16	Cro-Magnon 4347	28		169.8
17	Cro-Magnon 4348	28		170.0
18	Pavlov 1	26		186.3
19	Kubbaniya 1	19	71.8	
20	Mittlere Klause 1	19	72.0	
21	Zhoukoudian-UC 105	18	71.8	
22	Zhoukoudian-UC 117	18	59.0	
23	Minatogawa Q	17		162.1
	Mean		70.4	173.8
	Minimum		59.0	160.0
	Maximum		91.3	191.6

Table H.8: Upper Palaeolithic H. sapiens, all

	Body mass	Stature
Mean	68.5	170.3
Minimum	47.4	144.8
Maximum	91.3	191.6

Table H.9: Middle Palaeolithic H. sapiens, Qafzeh, male

	Individual	Dating (ka)	Body mass	Stature
1	Qafzeh 8	91	59.9	191.4
Low body mass, very high stature.				

Table H.10: Middle Palaeolithic H. sapiens, Qafzeh, female

	Individual	Dating (ka)	Body mass	Stature
1	Qafzeh 3	91	46.7	164.8
2	Qafzeh 7	91		171.8
3	Qafzeh 9	91	64.4	172.5
	Mean		55.6	169.7
	Minimum		46.7	164.8
	Maximum		64.4	172.5

Table H.11: Middle Palaeolithic H. sapiens, Qafzeh, all

No unassigned sex.	Body mass	Stature
Mean	57.0	175.1
Minimum	46.7	164.8
Maximum	64.4	191.4

Table H.12: Middle Palaeolithic H. sapiens, Skhul, male

	Individual	Dating (ka)	Body mass	Stature
1	Skhul 3	119		180.6
2	Skhul 4	119	72.4	182.0
3	Skhul 5	119	76.9	181.6
4	Skhul 6	119	69.0	177.9
5	Skhul 9	119	74.0	
	Mean		73.0	180.5
	Minimum		69.0	177.9
	Maximum		76.9	182.0

Table H.13: Middle Palaeolithic H. sapiens, Skhul, female

	Individual	Dating (ka)	Body mass	Stature
1	Skhul 7	119	57.9	158.5

Table H.14: Middle Palaeolithic H. sapiens, Skhul, all

No unassigned sex.	Body mass	Stature
Mean	70.0	176.1
Minimum	57.9	158.5
Maximum	76.9	182.0

Table H.15: Middle Palaeolithic H. sapiens, Skhul and Qafzeh, all

No unassigned sex.	Body mass	Stature
Mean	65.1	175.7
Minimum	46.7	158.5
Maximum	76.9	191.4

Table H.16: East African Middle Stone Age H. sapiens

	Individual	Sex	Dating (ka)	Body mass	Stature
1	Omo Kibish 1	F	195	54.1	163.3
2	Klasies River (Mt I)	M	100		164.1
3	Klasies River (Mt II)		100		178.6
	Mean			54.1	168.7

Table H.17: East and South African H. rhodesiensis/heidelbergensis

	Individual	Sex	Dating (ka)	Body mass	Stature
1	Broken Hill E689 (Femur)		400	75.8	
2	Broken Hill E691 (Tibia)	M	400		184.2
3	Broken Hill E907 (Femur)		400	82.6	
4	Thl94-UA28-7		400	59.8	
	Mean			72.7	184.2

Table H.18: European H. heidelbergensis, excluding Sima de los Huesos

	Individual	Sex	Dating (ka)	Body mass	Stature
1	Boxgrove	M	500	82.8	175.3
2	Arago 44		475	79.6	
	Mean			81.2	175.3

Table H.19: European H. heidelbergensis, Sima de los Huesos, male

	Individual	Dating (ka)	Body mass	Stature
1	AT-800 (coxal)	430	75.8	
2	AT-835+AT-2501 (coxal)	430	77.8	
3	AT-2350 (coxal)	430	75.8	
4	AT-2803	430	80.3	174.0
5	SH Pelvis 1 ¹⁰	430	78.7	
6	SH Femur X	430	83.3	170.0
7	SH Femur XII/XIII	430	73.8	167.8
8	SH Tibia III / AT-848 (Tibia)	430		171.7
9	SH Tibia VI	430		164.5
10	SH Tibia XI	430		162.8
11	SH Tibia XII	430		168.4
12	SH Fibula I	430		162.3
13	SH Fibula III	430		164.5
14	SH foot association 1	430	73.0	173.7
15	SH foot association 3	430		175.6
16	SH foot association 5	430	90.7	175.3
17	SH foot association 7	430		177.8
18	SH foot association 8	430	65.7	173.7
	Mean		77.5	170.1
	Minimum		65.7	162.3
	Maximum		90.7	177.8

Table H.20: European H. heidelbergensis, Sima de los Huesos, female

	Individual	Dating (ka)	Body mass	Stature
1	AT-860	430	62.5	161.0
2	AT-1004 (coxal)	430	66.2	
3	AT-1930	430	66.1	162.8
4	AT-2466	430		160.0
5	AT-3132	430	75.6	164.3
6	AT-4425	430	72.1	163.6
7	SH Coxal I	430	56.9	
8	SH Femur XI	430	58.3	
9	SH Femur XVI	430	56.9	
10	SH Tibia I	430		157.9
11	SH Tibia IV	430		154.3
12	SH Fibula II	430		153.7
13	SH foot association 2	430	57.6	161.3
14	SH foot association 9	430	62.6	159.8
	Mean		63.5	159.9
	Minimum		56.9	153.7
	Maximum		75.6	164.3

Table H.21: European H. heidelbergensis, Sima de los Huesos, sex unassigned

	Individual	Dating (ka)	Body mass	Stature
1	AT-489	430		166.3
2	AT-575	430	64.8	167.0
3	AT-859	430	63.8	
4	AT-1480	430	72.4	
5	AT-1700	430		170.9
6	AT-1832	430	65.8	
7	AT-3130	430		165.1
8	AT-3131	430		165.1
9	AT-3133	430	58.5	166.3
10	SH Femur IV/V	430	69.0	
	Mean		65.7	166.8
	Minimum		58.5	165.1
	Maximum		72.4	170.9

Table H.22: European H. heidelbergensis, Sima de los Huesos, all

	Body mass	Stature
Mean	69.4	166.0
Minimum	56.9	153.7
Maximum	90.7	177.8

Table H.23: East Asian archaic Homo 500 – 200 ka

	Individual	Sex	Dating (ka)	Body mass	Stature
1	Sambungmacan 2		500	68.2	165.1
2	Jinniushan 1	F	200	77.4	168.8
	Mean			72.8	167.0

Table H.24: East Asian Homo erectus 1 Ma – 500 ka

	Individual	Sex	Dating (ka)	Body mass	Stature
1	Trinil I	M	900	51.7	171.1
2	Trinil II		900	50.0	
3	Trinil III		900	49.3	
4	Trinil IV		900	51.8	
5	Zhoukoudian Femur 1		770	54.8	154.3
6	Zhoukoudian Femur 4		770	54.3	156.2
7	Zhoukoudian VI		770	51.6	
	Mean			51.9	160.5
	Minimum			49.3	154.3
	Maximum			54.8	171.1

Table H.25: East African archaic Homo 1 Ma – 500 ka

	Individual	Sex	Dating (ka)	Body mass	Stature
1	OH 34		975	55.3	160.5
2	KNM-ER 999		750		176.5
3	Ain Maarouf 1		700	53.3	151.2
4	OH 28	F	700	62.2	164.8
5	KNM-BK 66		650	55.9	165.0
	Mean			56.7	163.6
	Minimum			53.3	151.2
	Maximum			62.2	176.5

Appendix I

AETIOLOGY AND FUNCTION OF THE SUPRAORBITAL TORUS

Alternative hypotheses have been put forward to explain torus development in hominins and across the higher primates. Here a summary is given of hypotheses on aetiology and function, but it is not intended to argue for a specific conclusion.

Although they vary, hypotheses can be divided into *spatial disjunction* (between neurocranium and viscerocranium) models and *biomechanical* (usually masticatory stress) models (Ravosa 1988:535). Some models emphasizing spatial disjunction allow a role for some degree of stress on the frontal bone produced by the action of masticatory musculature (e.g. Ravosa 1991b). Biomechanical models tend to have a spatial disjunction component as a basis for the torus to develop as a connection between face and forehead to transmit increasing stresses during growth (e.g. Russell 1985; Picq 1994).

The spatial disjunction explanation of browridge development emphasizes growth of the viscerocranium in relation to the neurocranium. The central structure around which both of them grow is the cranial base, sagittally the region between basion and the foramen caecum (Chapter 4). In recent humans the face is largely retracted below the anterior cranial fossae, the thin bone of which also serves as the roofs of the orbits, whereas in chimpanzees the orbits lie largely in front of the anterior cranial fossae (Pereira-Pedro et al. 2017:956). In all archaic *Homo* also, the face grows to some degree anteriorly to the anterior cranial fossae. In Neanderthals the face is reduced and retracted more than in *Homo heidelbergensis* but less than in *Homo sapiens* (Trinkaus 1987, 2003).

The inner and outer tables of the frontal bone belong to different functional matrices (Moss and Young 1960): the inner table is in contact with the brain via the meninges, while the outer table is continuous with the orbits and nasal structure. The inner table grows according to a neural schedule, expanding to accommodate the growing frontal lobes, and its growth slackens dramatically when brain growth, passing ~90%, slows down during the juvenile stage, while the outer table continues to grow on a skeletal schedule as facial structure extends inferoanteriorly, and reaches maximum growth velocity during the adolescent skeletal growth spurt (Young 1957; Baume et al. 1983; Enlow 1990:110–113; Lieberman 2000:99–101).

The facial block expands vertically, transversely, and anteroposteriorly (Enlow 1990:118–120, 128, 138–142). Because of the constraint imposed by the posterior cranial base, spine and pharynx, expansion in the last dimension is anteriorly directed. Throughout ontogeny depository fields cover the anterior surface of the frontal bone immediately above the orbits (Enlow 1990:112). As the anterior surfaces and components of the viscerocranial structure drift anteriorly with respect to the cranial base, the orbits are carried anteriorly. Above the supraorbital region, from the juvenile stage onward no growth process exists to induce the frontal squama, enclosing the prefrontal regions of the brain, also to move anteriorly. The roofs of the orbits, containing and protecting the eyes, thus come to project beyond the neurocranial vault, in archaic humans and some early *Homo sapiens* forming a torus.

The above is the essence of the spatial disjunction hypothesis, which depends upon configuration of facial elements and upon growth processes.

A basis for the biomechanical model, treating the higher primate face as a rigid frame structure, was set out in detail by Endo (1965, 1966, 1970). Intensive stresses are generated in the inferior region of the maxilla, nasal root, inferomedial and inferolateral orbital margins, and the orbital margin formed by the zygomatic process of the frontal (Endo 1965). According

to Endo (1970) the masseter muscle produces tensile stress on the lateral supraorbital margin and the medial part of the infraorbital margin, while the temporalis produces compressive stress around the rest of the orbital margin. Greaves (1985) makes the case that chewing with the masseter and pterygoid muscles creates asymmetric loads and lateral torsional effects, which are reduced when the temporalis muscle is dominant.

Some authors attribute much of the Neanderthal facial structure – midfacial projection involving the maxillary and nasal bones, apparently more sagittally swept back zygomatic bones, and the almost vertical maxillary clivus – to a need to resist stress created by use of the anterior dentition for biting tough food items and paramasticatory activity such as habitually holding objects between upper and lower anterior teeth (F.H. Smith 1983; Rak 1986; Trinkaus 1987). These are versions of the *anterior dental loading* hypothesis. These models do not necessarily focus on the supraorbital torus but emphasize mandibular, maxillary and malar morphology, although F.H. Smith (1983) explains the expansion of the torus laterally at the frontal trigone as a continuation of the ascending lateral pillar (equivalent to the lower primate postorbital bar) formed by the thickened zygomatic to transmit load to the frontal.

Hylander et al. (1991) and Picq (1994), partly on the basis of experiments on monkeys, state that evidence is lacking to show that enlarged browridges develop to counter masticatory forces, and argue that torus development is unrelated to the masticatory apparatus, diet or paramasticatory usage. Ravosa (1988, 1991a, 1991b) rejects the masticatory stress and anterior dental loading hypotheses on the grounds that calculated stresses on the circumorbital region are much lower than on the zygomatic arch or mandible. Facial and neurocranial size are the prime determinant of torus development. However, he suggests that there is moderate support for an effect on browridge height of neurofacial torsion caused by unilateral chewing and reaction at the condyle of the non-chewing side (Ravosa 1991b, cf. Picq 1994).

With a combined hypothesis, Russell (1985) seeks to account for the fact that some hominins and some non-hominin primates have distinct browridges and others do not, apparently without a correlation to the relative sizes of neurocranium and viscerocranium. She argues that it is the mutual positioning of the neurocranium and viscerocranium that determines the extent of supraorbital development, but that such development is in response to stresses generated by the masticatory musculature. In particular, she identifies the *craniofacial angle* between the chords prosthion–nasion and nasion–metopion. In Figure I.1 the angle prosthion–nasion–metopion (PNM) is defined on the posterior side. When the craniofacial angle is 180°, i.e. a straight line (condition A), muscular forces from the jaw region are transmitted directly to the anterior neurocranium, i.e. the forehead, which is able to absorb the stress. When the angle is significantly different from 180°, e.g. >185° or <175°, then browridge development has to occur to ensure structural integrity of the anterior cranium. In most modern humans condition A prevails, with the anterior cranial fossa positioned above the face. Condition C with an angle PNM <175° characterizes most of the extinct species of *Homo* including Neanderthals. This principle explains why the orang-utan, fitting condition B, does not have browridges like the gorilla or even the chimpanzee. Although it is prognathic, its viscerocranium is dorsally deflected (Shea 1985; Ravosa 1988:539–540), keeping the angle PNM to a straight line. For condition B tilting the whole head ventrally to maintain line of sight (~ neutral horizontal axis, Chapter 4) produces condition E. According to Russell (1985:349), this model also explains why a browridge can develop in relatively prognathic modern humans even when the forehead is vertical (condition D). However, Upper Palaeolithic people and Australian Aboriginals exhibit much less lower facial prognathism than the great apes and remain close to condition A.

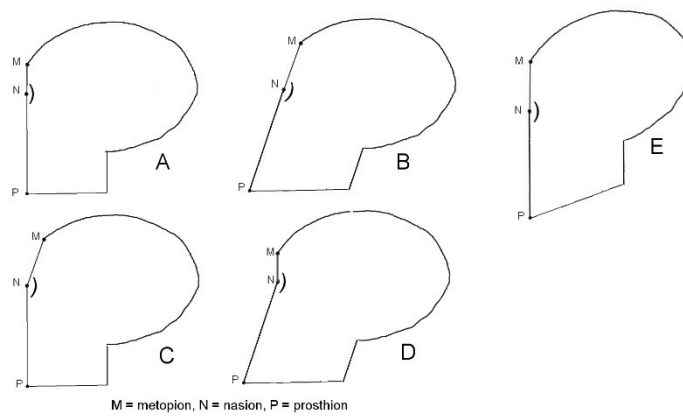


Figure I.1: Craniofacial angle, adapted from Russell (1985)

Russell (1985:341) refers to the above hypothesis as a “bent-beam” model. It allows for both genetic and ontogenetic influences. Among comments on the paper, Girgis and Turkel (ibid.:352) suggest that a solid beam may not be a suitable analogue for upper facial structure because stability is compromised by sutures (metopic, frontonasal, zygomaxillary, etc.) and the frontal sinuses. Osteogenic response to experienced cranial stresses during ontogeny, suggested by Ravosa, is questioned in another comment by F.H. Smith (ibid.:354), on the grounds that stresses would not be great enough in younger subadults. Another interesting objection to biomechanical models is raised by Brown (ibid.:350), who observes that even in osteogenesis imperfecta, rickets, and other forms of osteopenia the face does not distort because of masticatory stresses.

Viðarsdóttir (1999:351,355) discounts the anterior loading hypothesis partly on the grounds that Neanderthals have no greater affinities in facial morphology with modern humans noted for their use of the anterior dentition as a tool (Inupiaq and Aleutians) than with other modern human groups. Clement et al. (2012) studied dental wear patterns in recent Canadian Inuit, Late Pleistocene modern humans and Neanderthals. All demonstrated heavy wear on the anterior relative to posterior dentition, but this was more evident in the modern humans and especially the recent sample. Neanderthals exhibited a pattern whereby wear was spread more evenly across the whole anterior dentition. Their results do not support the anterior dental loading hypothesis as an explanation for Neanderthal facial morphology. A study by Wroe et al. (2018) found few differences in the capacity to sustain high anterior dental loading between modern humans, Neanderthals and *Homo heidelbergensis*, but concludes that Neanderthals had the capacity to condition cold dry air and to inhale and exhale greater air volumes than their predecessors, suggesting that their midfacial configuration evolved to cope with colder climate and enable very high energetic activity rather than to manage biomechanical stress.

Godinho et al. (2018) compared crania of *Homo heidelbergensis* and modern humans on masticatory musculature, force production and resulting strains and potential deformation of cranial structure. The modern human configuration, though having smaller musculature, proves more efficient in converting muscle force into bite force, but the modern human cranium deforms more readily. Given the relative gracility of the modern human cranium, these results, not referencing Neanderthals as such, seem to leave open the question whether archaic morphology, including the supraorbital torus, contributed to stabilize cranial structure against masticatory stresses. Examining dental microwear textures from early modern humans, Neanderthals and seven bioarchaeological samples, Krueger et al. (2019) find that early moderns and Neanderthals both engaged in similar non-dietary use of the anterior dentition, thus rejecting the paramasticatory wear component of the anterior dental loading hypothesis.

To summarize, the supraorbital torus develops primarily as an extended orbital roof when during ontogeny a large viscerocranium expands in front of the neurocranium and the angle between them is such that the orbital contents would otherwise be unprotected. It would be expected in smaller-brained anthropoids such as gorillas, chimpanzees, australopithecines and early *Homo*. It develops in Neanderthals because they combine a large neurocranium similar in overall volume to that of *Homo sapiens* with a viscerocranium considerably larger than that of *Homo sapiens* (Trinkaus 2003; Lieberman 2000:112). The torus maintains structural integrity of the cranium, particularly the orbits, whether or not it enables resistance to transient stresses from mastication or other use of the jaws (F.H. Smith and Ranyard 1980:600). It remains possible that biomechanical factors play a part. Stresses generated by the mandibular musculature, whether direct or torsional, whether transmitted medially through the maxilla and nasal region or laterally through the zygomatic and temporal bones and frontal trigone, may exert influence on the shape and size of the torus. It is suggested that the presence of a distinctively shaped torus is genetically determined, but that final form may be affected by muscularly induced stresses during ontogeny.

It has also been proposed that the torus serves a social function: as an aid to intimidating a rival (Russell 1985:339) or for sexual selection as a signal of a robust and therefore capable provider (F.H. Smith, comment, *ibid.*:355), and that reduction of this and other robust features indicates greater tolerance or placidity in the community (Cieri et al. 2014).

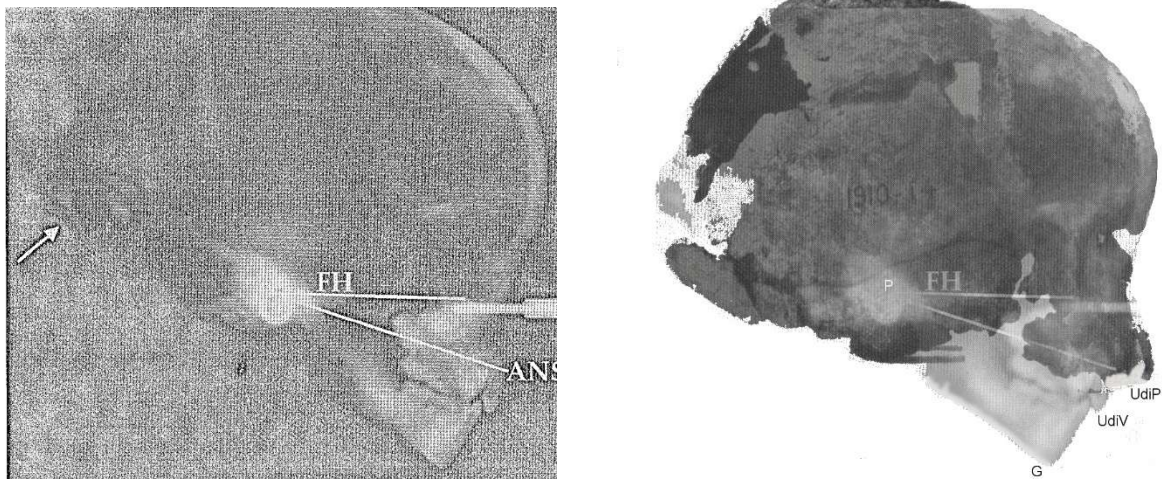
APPENDIX J

ILLUSTRATIONS

The following illustrations of Neanderthal immature and adult crania may be useful in visualizing some of the characteristics and processes described in the thesis. They are redrawn from photographs, unless otherwise noted from Von Koenigswald, G.H.R. (ed.), *Hundert Jahre Neanderthaler: Neanderthal Centenary 1856–1956*, Utrecht: Kemink en Zoon N.V. Ages are from Appendix A. Figures are not kept to scale.



Figure J.1: Pech de l'Azé, 1.5–2 years, Patte (1957)

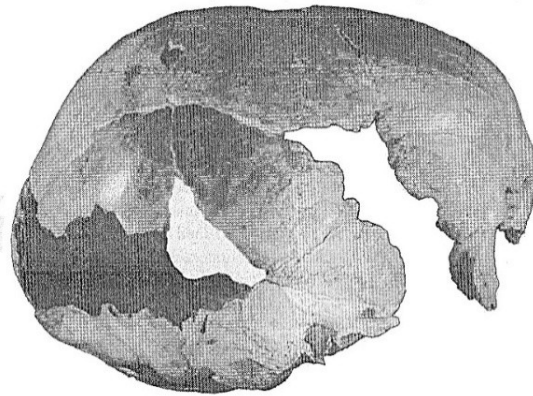


FH = Frankfort Horizontal, ANS = anterior nasal spine, P = porion, G = gnathion, Udi1-P, Udi-V = upper deciduous first incisor Patte position and Vlček position. The later (Vlček) reconstruction has lower cranial height. The earlier reconstruction showing Udi-P exhibits gross maxillary prognathism but the Vlček reconstruction has the maxilla retracted enabling the mandible to articulate at the glenoid fossae and with the maxilla. The later reconstruction showing Udi-V has a slight maxillary overbite.

Figure J.2: Pech de l'Azé: LEFT Cuozzo (2005) radiograph of Vlček 1962 reconstruction; RIGHT overlay of Cuozzo/Vlček and Patte reconstructions



Figure J.3: Roc de Marsal, 2.3 years



Absence of brow ridges in Pech de l'Azé and Roc de Marsal, and "bulbing" begun in Engis 2.

Figure J.4: Engis 2, 3 years

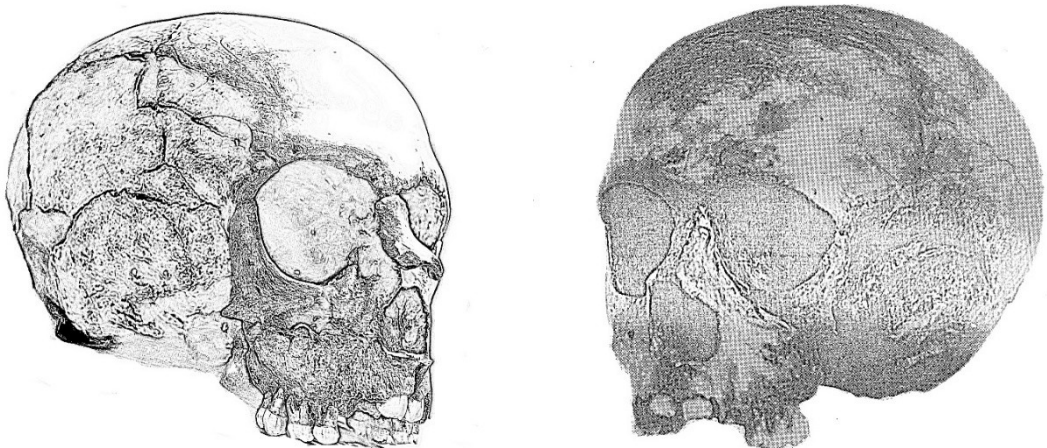


Figure J.5: La Quina H18, 5.5–6 years



Figure J.6: El Sidrón J1, 7.7 years

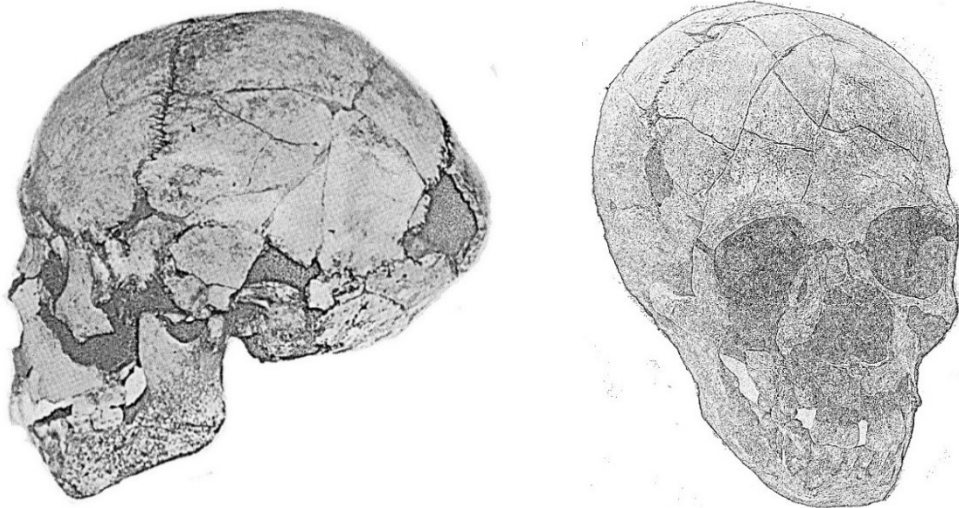


Figure J.7: Teshik-Tash, 8–9 years

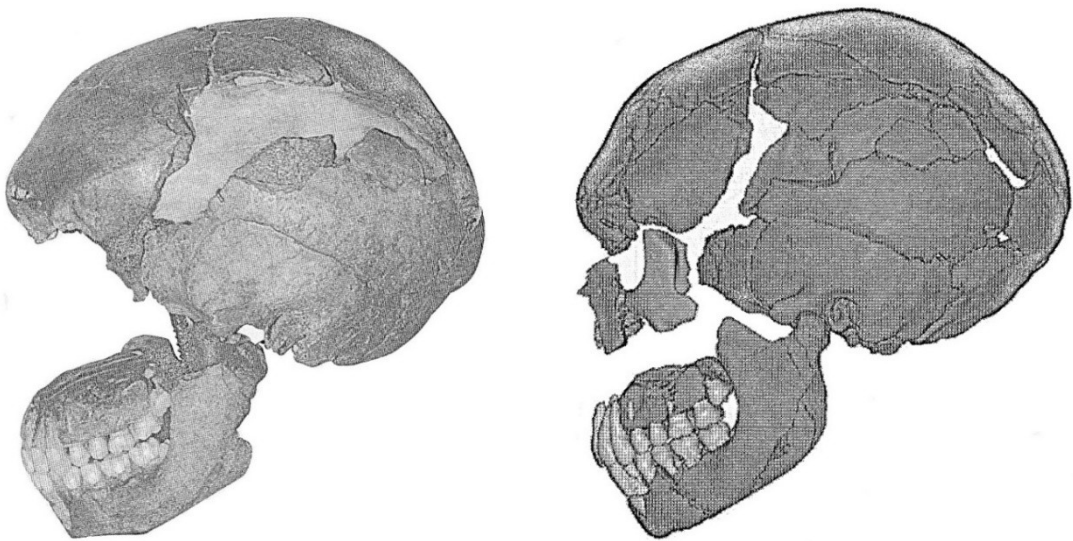


Figure J.8: Le Moustier 1, 11.86 years: LEFT in 1965; RIGHT Ponce de León and Zollikofer (2005)

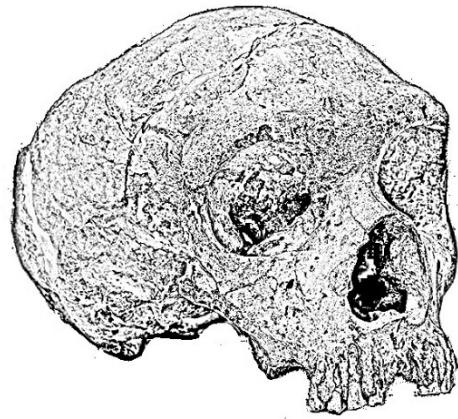
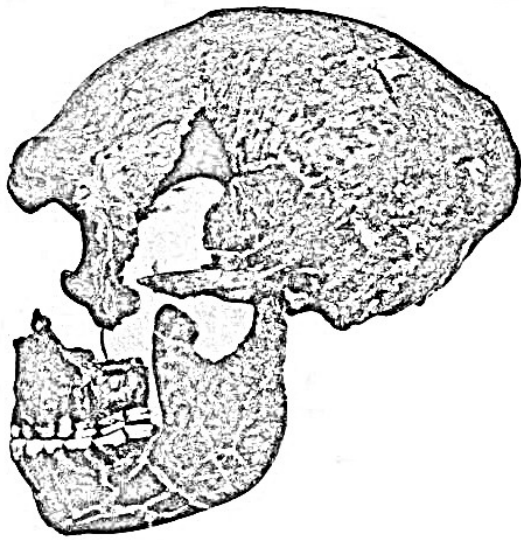


Figure J.9: Adults: LEFT La Quina H5 (male or female), RIGHT Gibraltar 1 (female)

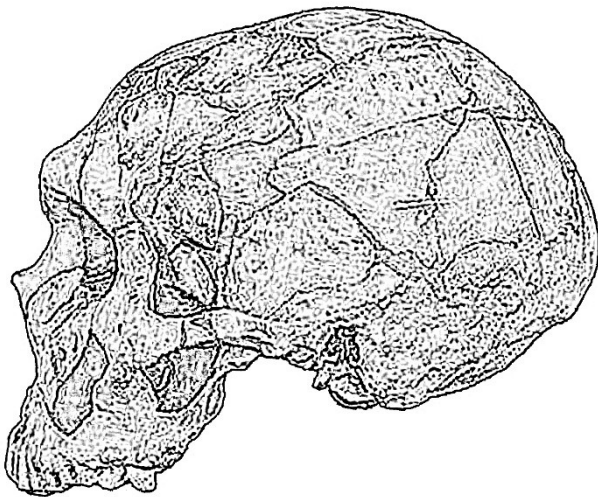
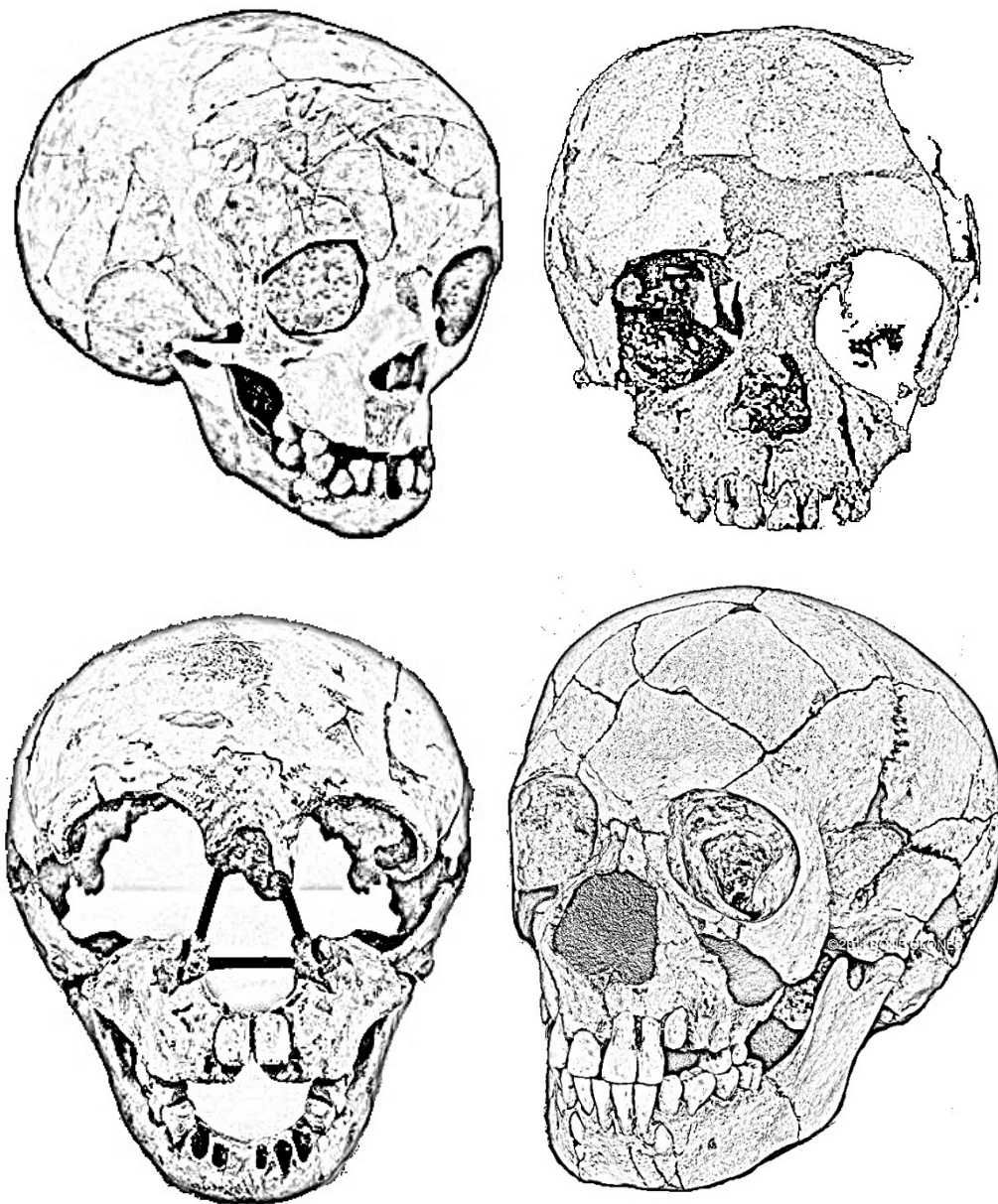


Figure J.10: Adult males: LEFT La Chapelle-aux-Saints, RIGHT La Ferrassie 1



The “en bombe” appearance of the wide and rounded neurocranium is best viewed posteriorly, but it is evident in these subadults in anterior view.

Figure J.11: “Family” resemblance of Neanderthal immatures: UPPER LEFT Dederiyeh 1, 1.5 years, UPPER RIGHT Roc de Marsal, 2.3 years, LOWER LEFT Gibraltar 2, 4.6 years, LOWER RIGHT Teshik-Tash, 8–9 years



Minimal development of browridges in child, browridges in adult female with projecting occipital.
British Museum of Natural History.

Figure J.12: LEFT Frontal of Gibraltar 2, male 4.6 years; RIGHT Gibraltar 1, adult female



Absence of browridges in child and adult, almost vertically sloping and inferiorly rounded occipital.
Skulls from University of Sheffield Archaeology.

Figure J.13: Modern human, European, LEFT Frontal and sphenoid of child ~2–3 years, RIGHT Adult female

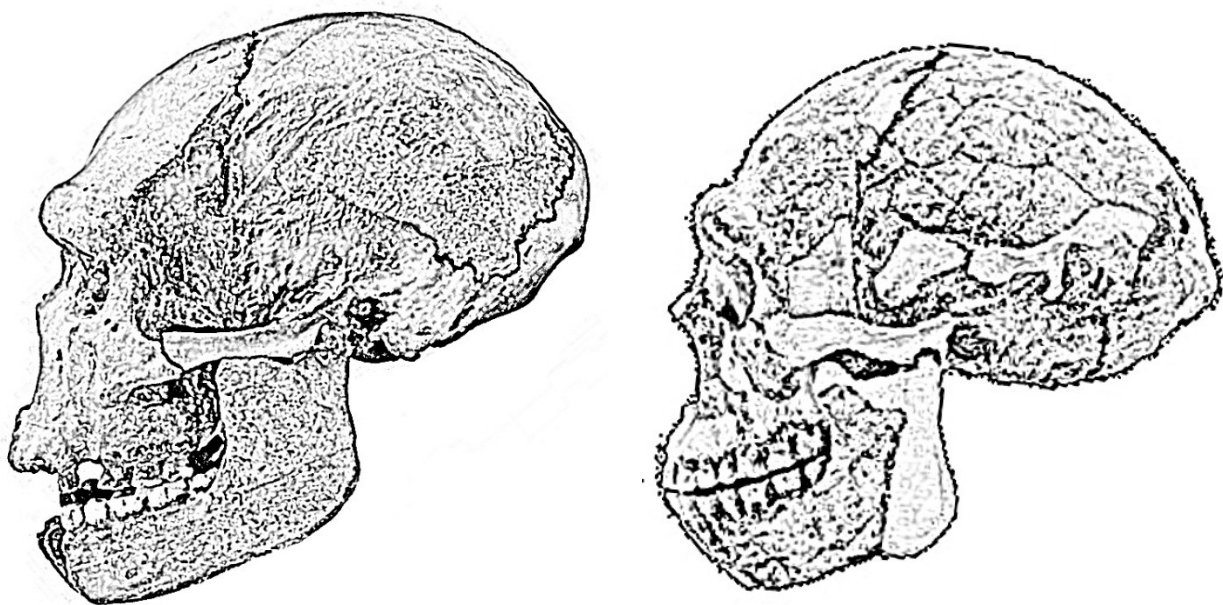


Figure J.14: LEFT Homo heidelbergensis (or Homo erectus) adult, Arago; RIGHT Homo erectus adult female, Peking (Beijing)

GLOSSARY AND ABBREVIATIONS

±	plus or minus (followed by value of one standard deviation)
AET	average enamel thickness
aka	also known as
BP	before present
C	permanent canine
¹⁴ C	Carbon isotope atomic weight 14
dc	deciduous canine
DEH	dental enamel hypoplasia
di1	deciduous first (central) incisor
di2	deciduous second (lateral) incisor
dm1	deciduous first molar
dm2	deciduous second molar
DSR	daily (enamel or dentine) secretion rate
ECV	endocranial volume
EDJ	enamel-dentine junction
Eemian	last interglacial, aka Riss-Würm (Alpine sequence)
EER	enamel extension rate
Entoconid	cuspid 4 distolingual, lower molar
hGH	human growth hormone
Hypocone	cuspid 4 distolingual, upper molar
Hypoconid	cuspid 3 distobuccal, lower molar
Hypoconulid	cuspid 5 distobuccal, lower molar
I1	permanent first (central) incisor
I2	permanent second (lateral) incisor
IBI	inter-birth interval
IGF-1	insulin-like growth factor 1
ka	thousand years (ago)
LEH	linear enamel hypoplasia, form of dental enamel hypoplasia
L	lower (dentition); LL lower left; LR lower right
M1	permanent first molar
M2	permanent second molar
M3	permanent third molar
Ma	million years (ago)
Metacone	cuspid 3 distobuccal, upper molar
Metaconid	cuspid 2 mesiolingual, lower molar
Metaconule	cuspid 5 distal, upper molar
MIS	marine isotope stage (dating period) = OIS
OIS	oxygen isotope stage (dating period) = MIS
OSL	optically stimulated luminescence (dating method)
P3 = PM1	permanent third premolar (primatology) = first premolar (dentistry)
P4 = PM2	permanent fourth premolar (primatology) = second premolar (dentistry)
Paracone	cuspid 2 mesiobuccal, upper molar
Protocone	cuspid 1 mesiolingual, upper molar
Protoconid	cuspid 1 mesiobuccal, lower molar
RET	relative enamel thickness
Riss	penultimate glaciation (Alpine sequence)
SI	Supplementary Information
TL	thermoluminescence (dating method)
U	upper (dentition); UL upper left; UR upper right
U/Th	uranium/thorium (dating method)
Würm	last glaciation (Alpine sequence)

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