



UNIVERSIDADE D  
COIMBRA

Nuno Hendrik Oliever Monteiro Branco

**THE JUVENILE NEANDERTHAL MANDIBLE  
FROM COUPE-GORGE CAVE, FRANCE  
ASSESSING AGE AT DEATH AND MANDIBULAR  
MORPHOLOGY IN PLEISTOCENE *HOMO***

**M.Sc. in Human Evolution and Biology Dissertation, supervised  
by Professor Cláudia Umbelino and Dr. Amélie Vialet, submitted  
to the Department of Life Sciences of the Faculty of Sciences and  
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*It's the job that's never started as takes longest to finish.*

By J.R.R. Tolkien

*In* The Lord of the Rings, Part 1: The Fellowship of the Ring



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## **List of Abbreviations**

**BP:** Before Period

**CIC:** Coimbra Identified Collections

**CT:** Computerized Tomography

**EVAN-SOCIETY:** European Virtual Anthropology Network Society

**FDI:** Fédération Dentaire Internationale

**IESC:** International Exchanges Skeletal Collection

**ISC:** Identified Skeletal Collection

**Kya:** Thousand years ago

**MIS:** Marine Isotope Stage

**MSCII:** Medical Schools Collection II

**NMDID:** New Mexico Decedent Image Database

**SPSS:** Statistical Package for the Social Sciences

**SR- $\mu$ CT:** Synchrotron radiation microtomography

**TIVMI:** Treatment and Increased Vision for Medical Imaging



**Resumo:** A estimativa da idade à morte desempenha um papel importante para os antropólogos que visam estudar as populações humanas do passado. Para tal, os dentes são comumente utilizados como indicadores fiáveis de maturidade, existindo vários métodos para estimar a idade biológica, cada um com as suas limitações, para a atribuição de uma estimativa de idade à morte.

A paleoantropologia, como disciplina tendencialmente comparativa, pode envolver o estudo dos padrões, semelhanças e diferenças ontogenéticas a nível dentário entre Neandertais e humanos modernos, e o mesmo caracteriza-se como um tópico de demarcada relevância.

Com o presente trabalho pretendeu-se estimar a idade à morte, a partir do estudo de um fóssil de um fragmento de sínfise mandibular de um neandertal não-adulto, identificado na caverna de Coupe-Gorge em Montmaurin (França) no século XX.

Para se estimar a idade à morte no caso de estudo, foram elaboradas duas coleções de referência compostas por mandíbulas de Neandertais não-adultos e de 31 humanos modernos não-adultos provenientes das Coleções Osteológicas Humanas Identificadas da Universidade de Coimbra e da *New Mexico Decedent Image Database* e, através da combinação das metodologias de identificação dos estádios de desenvolvimento e erupção dentárias de Moorrees e Bengston, adaptadas pelo Atlas de Londres de AlQahtani, procedeu-se à estimativa da idade à morte dos indivíduos. Posteriormente, as mandíbulas correspondentes aos neandertais foram caracterizadas tendo em conta a sua morfologia com o objetivo de examinar a presença e ausência de caracteres na espécie. Foi estimada uma idade à morte biológica no indivíduo não-adulto de Coupe-Gorge entre 3.5 a 4.5 anos, encontrando-se dentro dos valores observados em humanos anatomicamente modernos. A análise da morfologia levou-nos a concluir que os caracteres que definem os Neandertais adultos surgem e desenvolvem-se gradualmente a partir da infância.

**Palavras-chave:** desenvolvimento dentário; *Homo neanderthalensis*; sínfise mandibular



**Abstract:** Estimating age at death plays an essential role for anthropologists who aim to study past human populations. To this end, teeth are commonly used as reliable indicators of maturity, and there are several methods, each with its limitations, for estimating age at death. As a discipline that tends to be comparative, paleoanthropology can focus on the study of patterns, similarities, and ontogenetic differences at the dental level between Neandertals and modern humans, which is a topic of significant relevance. The present work aimed to estimate the age at death of a subadult Neandertal identified in the Coupe-Gorge cave in Montmaurin (France) in the XX century. Two reference collections composed of Neanderthals and 31 subadult modern humans belonging to the University of Coimbra's Human Identified Osteological Collections and New Mexico Decedent Image Database were used. By combining Moorrees and Bengston's methodologies for identifying the stages of tooth development and eruption adapted by the London Atlas of Human Tooth Development and Eruption as developed by AlQahtani, we estimated the likely ages at death in the individuals. Subsequently, the mandibles corresponding to Pleistocene hominins were characterized by their morphology to examine the presence and absence of characters in the sample. The age at death in the subadult individual of Coupe-Gorge was estimated to be between 3.5 and 4.5 years, within the values observed in anatomically modern humans. The morphological analysis led us to conclude that the characters that define adult Neanderthals emerge and develop gradually from childhood.

**Keywords:** dental development; *Homo neanderthalensis*; mandibular symphysis





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# 1. Introduction

## 1.1. Introduction

### 1.1.1. The study of Neandertals in the context of human evolution

Bearing in mind the close relationship to modern humans, when Neandertals are studied, anthropologists often resort to comparative methodologies, using the species' as an important "outgroup" to better understand biological and cultural phenomena (Roebroeks & Soressi, 2016). If done with caution, it may provide invaluable information which helps to create, sustain and falsify different hypotheses about our prehistoric past. According to French paleoanthropologist Jean Jacques Hublin, "The close phylogenetic relationship between Neandertals and *Homo sapiens* also makes this group particularly interesting as understanding its status undoubtedly sheds light on the definition of our own species", hence why anthropologists frequently look to one species when considering facets of another (Hublin, 2009, p. 16022).

For all the similarities Neandertals may share with anatomically modern humans, they differ in many aspects. One central theme that stimulates continuous research is the presence or lack thereof of ontogenetic differences (such as dental differences) between Neandertals and modern humans. The following study will thus assess the presence and degree of ontogenetic differences observed in dental development through the estimation of age at death in the Coupe-Gorge juvenile mandible and mandibular shape trajectories in this extinct *Homo* species will be discussed.

Research surrounding dental development in extinct hominins has been vigorously pursued for many reasons, 1) dental remains are often used as a reliable indicator of maturity, and 2) their highly mineralized structure makes them one of the most resistant parts of the human body against decay, thus figuring extensively in debates over hominin ontogeny (Nava et al., 2020; Ramirez Rozzi & Bermudez De Castro, 2004; Rosas et al., 2017; Smith et al., 2010).

As previously stated, dental growth can serve as a valid proxy for individuals' maturation. There are countless methodologies available to study this phenomenon that will differ in their prerequisites, potential, limitations, and conclusions. Some studies suggest that Neandertal dental ontogeny is relatively advanced when compared to modern humans and that techniques used to estimate age at death in modern humans should not

be applied to extinct hominins (Smith et al., 2007, 2010). Other authors report that some aspects of Neandertal dental ontogeny are similar, if not well encompassed to modern human dental ontogenetic patterns (Bayle et al., 2009; Dean et al., 1986; Guatelli-Steinberg et al., 2005; Smith et al., 2007, 2010; Xing et al., 2019).

For example, to establish the age at death through the study of dental development and alveolar eruption, researchers have dropped the histological sectioning of rare teeth in favor of non-destructive methods to analyze their microstructure, and for this, virtual imaging methods such as CT,  $\mu$ CT, or even SR  $\mu$ CT, which enables anthropologists to examine different features of teeth in varying degrees of resolution without compromising the stability of the materials under observation, are used. Scientists can now assess dental ontogeny through the count of incremental features in molars by virtual histology (SR  $\mu$ CT) or by examining crown development and root growth stages with the aid of an evidence-based atlas for maturation stages (Alqahtani et al., 2010, 2014; Blenkin & Taylor, 2012; Smith et al., 2007, 2010).

Besides teeth, mandibular remains figure extensively in paleoanthropological research when studying ontogeny in the cranial skeleton. The mandible is considered a valid marker for estimating variability in hominins, as it bears a considerable number of identifiable features present in different species. This permits the distinction between Neandertals and anatomically modern humans (Arnaud, 2013; Bastir, 2018; Bastir et al., 2007). Examining morphological variability in hominin mandibles thus becomes important because it permits researchers to establish at what point certain features appeared in Neandertals, at what biological age, at what pace, and how it compares to anatomically modern humans. Discussing these patterns of ontogeny is only possible after estimating age at death, hence the importance of joining these two topics in this study.

### **1.1.2. Problematic**

The following work proposes the study of mandibular remains belonging to a juvenile Neandertal under different lenses. To study dental ontogeny, tooth developmental and tooth eruption stages will be diagnosed in the Coupe-Gorge mandible in comparison with two main reference collections, one comprising of individuals from the Coimbra Identified Skeletal Collections and from individuals belonging to the New Mexico

Decedent Image Database and the other of juvenile Neandertals (Alqahtani et al., 2014; AlQahtani et al., 2010).

The following questions will be addressed: is it possible to estimate age at death for the Coupe-Gorge juvenile mandible? If so, how different their dental growth is compared to modern humans of the same age? Is anterior dental growth comparable or distinguishable between Neandertals and anatomically modern humans? Can we apply methodologies built on contemporary modern human collections to Pleistocene hominins?

Posteriorly, we will examine the Neandertal mandibular morphology of the prehistoric reference sample and discuss how different it is from modern humans.

### **1.1.3. Getting to know the Neandertals**

Ever since the discovery of the fossils later identified as Neanderthal 1<sup>1</sup> in 1856 in the Kleine Feldhofer Grotte in Germany, the Neandertals' place in hominin evolutionary history has been frequently discussed (Janković, 2004). From savages to “cognitively indistinguishable” from modern humans, they are the most well-known extinct hominin species for both researchers and the general public (Hoffmann et al., 2018; Janković, 2004; Jaubert et al., 2016).

Shrouded in mystery and controversy, anthropologists and archaeologists have relied on the continuous scientific progress of the research methodologies and technologies to cast a light on this species and to better understand their story in western Eurasia during the Middle Pleistocene up to the Last Glacial Period. Material culture aside, their phylogenetic history is a complex and hotly debated issue, with some studies suggesting new dates for the Last Common Ancestor between Neandertals and modern humans between 700 kya and 550 kya and some hypothesizing the emergence of the clade at least 800 kya (Banks et al., 2021; Gómez-Robles, 2019).

At the height of their success, they occupied territories from the Iberian Peninsula to the Altai region of Siberia, ranging an area of around 10 million km<sup>2</sup>, maintaining an archaeological record up to the MIS 3 (ca. 41kya) when we see the last traces left by them

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<sup>1</sup>While Neanderthal 1 is the species' holotype, other fossils later recognized as belonging to the same species were discovered earlier such as Engis 2 (1829) and Gibraltar 1 (1848).

in modern-day Portugal and Spain (Aubry et al., 2020; Finlayson, 2016; Hublin, 2009; Krause et al., 2007; Roebroeks & Soressi, 2016; Smith et al., 2005; Trinkaus, 2007).

#### **1.1.4. The Neandertal general anatomy**

It is worth noting that Neandertals did not exhibit their familiar characteristics when they first appeared on the fossil record. Moreover, during the Middle Pleistocene, Neandertal features appeared in a mosaic fashion throughout Eurasia. According to Hublin, we must wait until the MIS 7 for Neandertals to exhibit a combination of features and morphologies that makes them distinct (Hublin, 2009; Vialet et al., 2019). Neandertals exhibit rare autapomorphic features that are unique to them, and present a combination of apomorphic and plesiomorphic characteristics (Janković, 2004).

Regarding their overall features, they were shorter than post-WWII Europeans (averaging 164-168cm for males & 152-156 for females), had short extremities, long clavicles, their scapulae were wide with narrow glenoid fossae, their pelvis were wide with a long and narrow pubic ramus (Helmuth, 1998). Regarding their skull, some of the most notable features are their average 1450cm<sup>3</sup> cranial capacity, pronounced midfacial prognathism, occipital bun, and long and narrow foramen magnum (Harvati, 2007; Janković, 2004; Weaver, 2009).

#### **1.1.5. The Neandertal mandible**

Many of the mandibular traits that characterize adult Neandertals start manifesting early in the infancy period, reaching their potential during the juvenile and non-adult periods of development. Research suggests that some of these features can be placed in an ontogenetic timeline, such as the mandibular symphysis, which grows slowly from infancy until they reach adulthood (Bastir et al., 2007; Kondo et al., 2005; Weaver, 2009; Williams, 2006).

Some of the most researched features commonly exhibited in Neandertals are 1) the presence of a receding symphysis which results in the absence of a chin 2) the location of the mental foramen differing from modern humans, the former having it posteriorly below the first mandibular molar 3) a rounded gonial area 4) an oval-horizontal shaped mandibular foramen 5) a shallow and asymmetric sigmoid notch with a coronoid process that is higher than the condyle 6) a mandibular ramus 7) a retromolar space produced by

the forward and downward growth displacement of the molar region of the alveolar process (Bastir et al., 2007; Harvati, 2007; Kondo et al., 2005; Rosas, 2001; Schwartz & Tattersall, 2000; Weaver, 2009).

Paleoanthropologists have proposed a variety of hypotheses to justify cranial morphology in Neandertals, such as adaptation to cold climates, adaptation to anterior dental loading, and genetic drift.

Regarding the first hypothesis, while Neandertals may have experienced colder temperatures during the Middle to Late Paleolithic, this does not mean that their cranial characteristics are adaptations to a cold climate. Moreover, the Neandertals' wide nasal aperture raises doubts if it indeed is a result of an adaptation to a cold climate, with some authors suggesting the wide nasal aperture to be the result of plesiomorphic retention of a prognathic facial skeleton (Holton & Franciscus, 2008; Weaver, 2009).

Researchers evoke the Adaptation to Anterior Dental Loading hypothesis to explain why Neandertals exhibit an accentuated degree of wear, enamel chipping, and micro-fractures on their anterior dentition rather than posteriorly (Weaver, 2009).

#### **1.1.6. The Dentition**

The statement that a Neandertal's anterior dentition (especially the incisors) is larger than a modern human one is supported by available data such as the research done on the Krapina dental remains (Wolpoff, 1979). Furthermore, the crowns of anterior teeth will be larger than modern human ones, while the posterior crown area overlaps with modern human values (Trinkaus, 1978).

The study of the morphology of the anterior dentition led anthropologists to propose the aforementioned Adaptation to Anterior Dental Loading Hypothesis – it served as an adaptation to the heavy use of the incisors and canines in processing hard foods and for other activities unrelated to feeding which commonly produced an accentuated degree of wear as well as enamel chipping and micro-fractures on their anterior dentition rather than posteriorly (Clement et al., 2012; Weaver, 2009). However, this hypothesis has been challenged. Some authors report that the degree of wear present in Neandertals' teeth is not as exceptional when compared with modern humans from the Middle Paleolithic to the Epipaleolithic. Other authors revealed that Neandertals could not produce high bite forces (Clement et al., 2012; Weaver, 2009).

Neandertals present various dental autapomorphies, including a high frequency of the mid-trigonid crest in lower molars and a distinguishable morphology of the mandibular premolars (Bailey, 2002). In addition, they present enlarged lingual tubercles, thinner enamel when compared to modern humans, skewed upper molars, third lower molars without four cusps, marked shoveling in the upper incisors, and enlarged pulp chambers (what is known as taurodontism) (Clement et al., 2012; Harvati, 2007; Harvati et al., 2011; Janković, 2004; Rak et al., 2002; Smith et al., 2010; Trinkaus, 1978).

When studying the Shanidar teeth compared to other Neandertals and modern humans, Erik Trinkaus discovered that the breadths for the anterior dentition of Neandertals were statistically more prominent than those of modern humans (Trinkaus, 1978). Regarding the posterior dentition, the area values for the premolars and molars matched those of modern humans (Trinkaus, 1978). He found that the molar size differences were reflected in the M1, M2, and M3 sizes, with modern humans exhibiting the pattern  $M1 > M2 > M3$  in the mandibular dentition. At the same time, some Neandertals showcased patterns in which the third molar is the largest, followed by M2 and M1 (Trinkaus, 1978).

Finally, when considering dental development in Neandertals, the data differs for the anterior and posterior dentitions. For the deciduous anterior teeth, recent studies on the Krapina fossils indicate that Neandertals' dental development was advanced in this region relative to humans. At the same time, "relatively rapid formation rates have also been reported for Neanderthal permanent anterior teeth" (Mahoney et al., 2021, p. 5). Mahoney reported that the permanent molars at Krapina may have erupted earlier than expected for modern humans, situating their emergence within the "faster half of the modern human range" (Mahoney et al., 2021, p. 6). However, other studies found that some Neandertals anterior and posterior permanent dentitions emerged at similar rates as modern humans (Macchiarelli et al., 2006; Mahoney et al., 2021; Rosas et al., 2017).

## 1.2. The Coimbra Identified Osteological Collections

The Department of Life Sciences of the Faculty of Sciences and Technology of the University of Coimbra (Portugal) holds 4 Identified Skeletal Collections: the Medical Schools Collection I (585 crania), II (1 skeleton and 13 non-adult crania), and III (34 adult cranium); the Identified Skeletal Collection (505 individuals), the International Exchange Collection (1144 skulls) and the 21st Century Identified Skeletal Collection (302

complete adult skeletons), totaling over 2500 individuals (Ferreira et al., 2021; Rocha, 1995; Santos, 2020).

Identified osteological collections are an invaluable tool for anthropologists to develop, test, or falsify methodologies that may be used to assess a biological profile (Popper, 2008). For that reason, the Department of Life Sciences grants access to graduate students and other researchers to conduct their work. This work will include mandibular remains from the Medical Schools Collection II, the Identified Skeletal Collection, and the International Exchange Collection.

#### **1.2.1. The Medical Schools Collection II**

The Medical Schools Collection II was created by the former President of the first Portuguese Republic, Bernardino Machado. This small collection is comprised of a ~ 20-month-old skeleton and 13 non-adult crania, the oldest being 12 years old at death and the youngest stillborn. They entered the Anthropological Museum between 1897 and 1901 (Rocha, 1995).

#### **1.2.2. The Identified Skeletal Collection**

The osteological remains, which are part of this collection, come from Coimbra's biggest cemetery (Cemitério da Conchada). They were gathered by the former Director of the Anthropological Museum, Dr. Eusébio Tamagnini. The collection holds 505 skeletons belonging to individuals born between around 1826 and 1922 and that died between 1904 and 1938. They were exhumed between 1915 and 1942 (Rocha, 1995).

#### **1.2.3. The International Exchange Skeletal Collection**

With the prospect of making exchanges with collections from other countries, Dr. Eusébio Tamagnini also organized the collection between 1932 and 1942. These 1144 skulls come from Cemitério da Conchada (Santos, 2020).

### **1.3. The New Mexico Decedent Image Database**

In 2010, the Office of the Medical Investigator (OMI), a medical examiner's office for New Mexico, moved to new installations. In the same year, the newly created Center for Forensic Imaging (CFI) received a grant to fund CT scanning to determine if the traditional autopsy could be supplemented or replaced by Computerized Tomography (Berry & Edgar, 2017; *The New Mexico Decedent Image Database*, n.d.). Thus, every



deceased individual received a full-body high-resolution CT scan of ~12,000 2D images (Berry & Edgar, 2017; *The New Mexico Decedent Image Database*, n.d.). The collection now houses 150,000,000 images of 15,000 New Mexicans who died between 2010 and 2017 (Berry & Edgar, 2017; *The New Mexico Decedent Image Database*, n.d.).

#### 1.4. The Coupe-Gorge Cave

The Coupe-Gorge cave is part of a karst system of caves connected to each other such as Boule, La Terrasse, le Putois, and La Niche, located near the village of Montmaurin, southwest of Toulouse (Figure 1.2) (Gaillard, 1982; Granat & Peyre, 2012). Located 25 meters above the Seygouade river, the partially excavated site is well known for its lithic assemblages, and for the faunal remains recovered (Billy, 1985; Gaillard, 1982).

From 1946 to 1961, systematic excavations were undertaken in Coupe-Gorge and led by L. Méroc, who opened the cave the previous year, and was responsible not only for the discovery of Middle Paleolithic archaeological artifacts but also for hominin remains, namely an incomplete adult right maxillary, three teeth and a fragmentary mandibular symphysis which serves as the case study of this work (Figure 1.1) (Billy, 1982; Granat & Peyre, 2012; Vialet et al., 2019). The cave, with 25 meters in length and 9 meters wide and with a sediment depth between 7 to 8 meters was divided into layers 1, 2 and 3, and according to Méroc all human remains came from layer three during the cultural transition of the Acheulean to Micoquien and Mousterian (Figure 1.3) (Billy, 1985; Gaillard, 1982; Granat & Peyre, 2012; Vialet et al., 2019). Layer 1 holds an archaeological record from the Neolithic to the Gallo-roman period. In contrast, layer 2, sometimes isolated from the more recent layer by a stalagmitic floor is characterized by reddish-brown silt with intrusions of limestone. The first two layers are around 1 meter each, while the oldest layer exceeds 7 meters. For this reason, Méroc subdivided it into nine sub-layers, setting into motion one of the first instances someone recorded cartesian coordinates of human remains in a grading system (Granat & Peyre, 2012; Vialet et al., 2019).

The sediment characteristics for layer 3Z (where the mandibular symphysis was found) are somewhat like those of layer 2, with the difference that this level is rich in artifacts. Sub-layer 3T, where the maxillary fragment and isolated teeth were found, has a clayish consistency with a few intrusions of limestone elements. With these sedimentological characteristics, Méroc suggested a paleoclimatic and chronological interpretation level of sub-layer 3Z corresponding to a cold climate, that is, it

corresponding it to the end of the Riss- Würm or the beginning of the Würm (Gaillard, 1982; Girard & Renault-Miskovsky, 1979; Granat & Peyre, 2012; Méroc, 1963; Vialet et al., 2019). However, new dates have been proposed for Complex III where all hominin remains were found, thus setting back the age of the fossils to 200,000 years, based on U-Th/ESR methodologies (Vialet et al., 2023).



Figure 1. 1: Osteological material recovered from Coupe-Gorge cave (photo taken from the MNHN collection database).

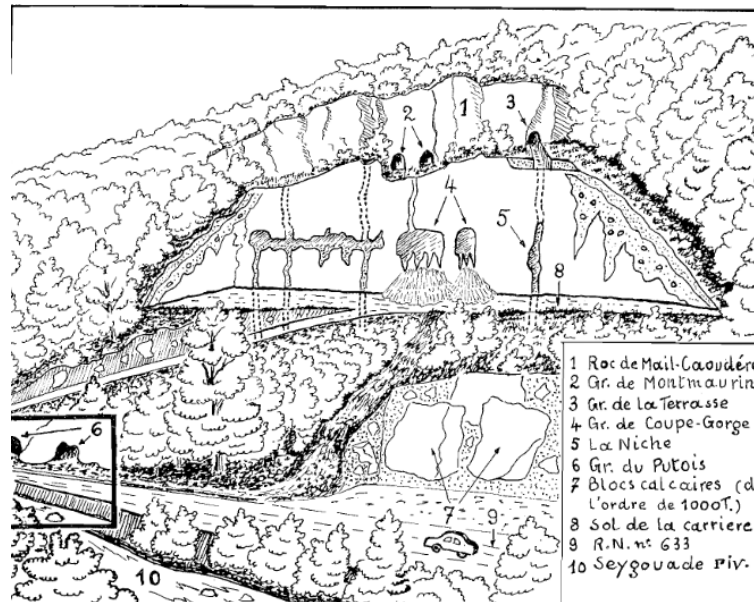


Figure 1. 2: Representation of Montmaurin caves, Coupe-Gorge being n°4 (taken from Méroc, 1963).

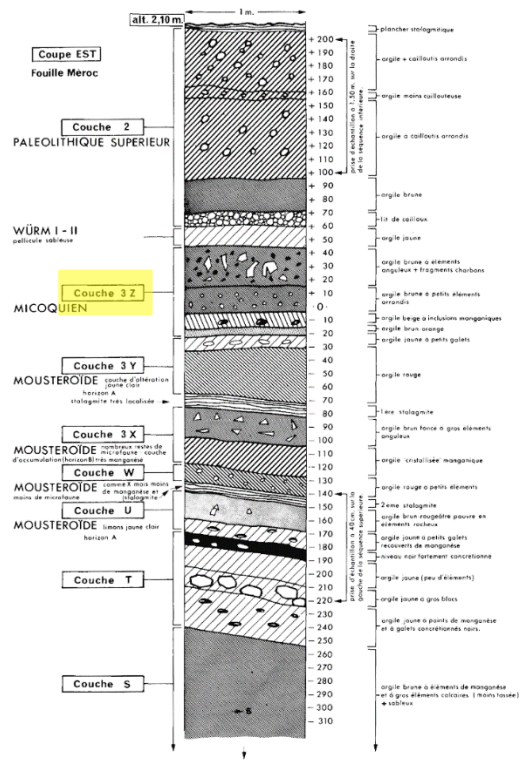


Figure 1. 3: Stratigraphic succession of Coupe-Gorge(Girard & Renault-Miskovsky, 1979).

## 2. Materials and methods

### 2.1. The Coupe Gorge mandible

The subject of study of this work consists of a fragment of a mandibular symphysis (C.G.3Z6281) belonging to a young Neandertal child associated with a late Acheulean culture known as the Micoquien Industry and dated to around 200kya (Billy, 1985; Gaillard, 1982; Granat & Peyre, 2012; Vialet et al., 2023). The fossil (Figure 2.1), recovered in sub-layer 3Z from Coupe-Gorge cave, belonging to an individual that lived roughly 200kya<sup>2</sup>, only presents the germs of the permanent central incisors within the mandible, being the only dentition associated with the fossil (Billy, 1985; Granat & Heim, 2003; Granat & Peyre, 2012; Vialet et al., 2023). The fossil (MNHN-HA-28116) is housed in the National Museum of Natural History in Paris.

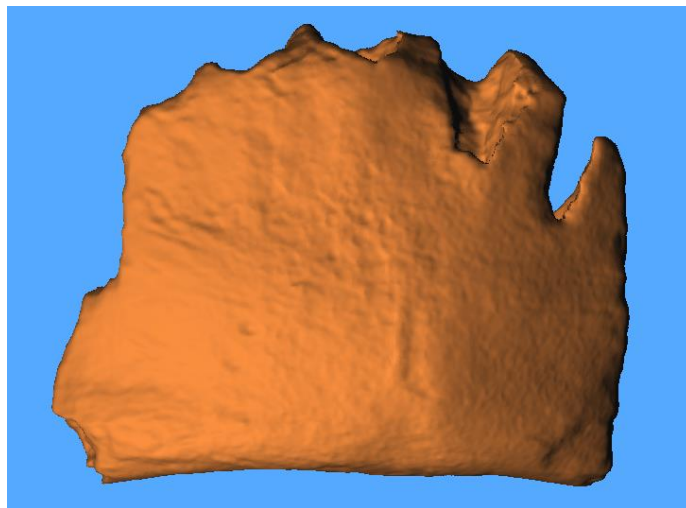


Figure 2. 1: Coupe-Gorge mandible

### 2.2. The Human Sample

#### 2.2.1. The Coimbra Collections

A total of 24 mandibles belonging to individuals situated in their first and second infancy were selected for this study, from which 9 (37.5%) were male, 8 (33.3%) were

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<sup>2</sup> The most recent proposed chronology for the Coupe-Gorge mandibular symphysis is based on new U-Th/ESR performed on the alternating layers of the stratigraphy and the stalagmitic floor (Vialet et al., 2023).

female, and seven individuals (29.2%) belonging to the Medical Schools II collection had no information regarding sex (Table 2.1).

The criteria used to create the following reference collection were not random. Only Portuguese individuals were selected with a recorded age at death between around two months up to 9 years (these individuals died between 1897 and 1931), thus encompassing a relatively broad spectrum to study dental development, with individuals relatively close to the first proposed age at death of the Coupe-Gorge fossil (Billy, 1985). Factors that could influence bone growth and dental development, such as sex, geographical origin, and health status, were considered when choosing the individuals to be part of the sample. Individuals who presented evidence of lesions or chronic illnesses that could potentially affect the cranial skeleton were excluded from the sample (such as severe burns and gangrene of the face). All the mandibular fragments come from juvenile individuals who lived between the XIX and XX centuries in the center-south region of Portugal.

Table 2. 1: Distribution of individuals by sex, age group and osteological collection (MSCII= Medical Schools Collection II; ISC= Identified Skeletal Collection; IESC = International Exchange Collection).

Coimbra Identified Collections						Total
Age	MSCII	ISC		IESC		
	Indetermined.	♂	♀	♂	♀	
±2 months.	1	0	0	0	0	1
±1 year	1	0	0	0	0	1
~2-3 years	5	0	0	0	0	5
6 years	0	0	0	1	0	1
7 years	0	0	3	2	2	7
8 years	0	1	0	4	2	7
9 years	0	1	1	0	0	2
<b>Total</b>	7	2	4	7	4	24

### 2.2.2. The New Mexico Decedent Image Database

A total of 7 mandibles of individuals situated in their first infancy were selected for this work, from which 5 (71.4%) were male and 2 (28.6%) were female (Table 2.2). The criteria used to develop this reference collection followed similar procedures to the collections described in the previous sample. The selected individuals, from ages 3 to 5 years old, died between 2011 and 2017 (see Table 2).

Table 2. 2: Distribution of individuals by sex and age group (New Mexico Decedent Image Database also identified with NMDID).

New Mexico Decedent Image Database			Total
Age	♂	♀	
3 years	2	0	2
4 years	3	1	4
5 years	0	1	1
<b>Total</b>	5	2	7

### 2.3. The Neandertal Reference Collection

Estimating age at death in the Coupe-Gorge mandible was done with two primary reference samples: modern humans born between the XIX and XXI centuries and fossil hominins commonly ascribed to the Neandertal taxa (Table 2.3). Given the impossibility of examining the actual fossil remains, data regarding their mandibular morphology and dental ontogenetic patterns were gathered mainly from research publications and to a lesser extent from surface scans<sup>3</sup>, which were utilized for morphometric analyses when possible. The sample encompasses hominins from various regions, from modern-day Portugal to Syria and from age ranges from ~ two years up to ~ eight years old at death. Excluding the Coupe-Gorge mandible, which is about 200,000 years old, the reference sample covers the Late Middle Paleolithic up to the Early Upper Paleolithic stages.

Table 2. 3: Pleistocene Homo Reference Collection for age at death estimate.

Specimen	Location	Chronology
<b>Dederiyeh 1</b>	Dederiyeh Cave, Syria	60ka (Akazawa & Muhsen, 2003)
<b>Dederiyeh 2</b>	Dederiyeh Cave, Syria	48.1-53.6ka (Akazawa & Muhsen, 2003)

<sup>3</sup> Surface scans for the Pech de l’Azé and Archi 1 Neandertals were shared with the author by Dr. Julie Arnaud from the Università Degli Studi di Ferrara in Italy. The surface scan for the Teshik-Tash, and surface scan plus  $\mu$ CT data for the Roc de Marsal fossils were obtained from the NESPOS digital database. The remaining specimens had their data gathered from publications.

<b>Roc de Marsal</b>	Roc de Marsal, France	60-70ka (Guérin et al., 2012)
<b>Pech de l'Azé</b>	Pech de l'Azé I, France	41-51ka (Soressi et al., 2007)
<b>Barakai</b>	Barakai Cave, Western Caucasus	38-36ka cal BP (S. Bailey et al., 2014)
<b>Archi 1</b>	San Francesco d'Archi, Italy	40,000ka (Mallegni & Trinkaus, 1997)
<b>Gibraltar 2</b>	Devil's Tower, Gibraltar	60-120ka (Bokelmann et al., 2019)
<b>El Sidrón J1</b>	Cueva del Sidrón, Spain	49,000ka (Rosas et al., 2017)

#### 2.4. Methods

This study involved a combination of methodologies to answer the questions posed in the introduction. Before gathering the data, a period of learning was reserved to better familiarize with the description of Moorrees' tooth developmental stages for single and multi-rooted teeth, with Bengston's stages for classifying tooth eruption stage in relation to bone level and with AlQahtani's evidence based atlas for age estimation using the stages mentioned above (AlQahtani et al., 2010; Moorrees et al., 1963). A learning period was also reserved to better understand the functionalities of the software used in this study, TIVMI<sup>4</sup> and Slicer<sup>5</sup>, the most important being the segmentation of the mandibles, 3D reconstruction, and analysis in 2D (observation of the dental development) (Dutailly et al., 2009; Fedorov et al., 2012).

An application was sent to the curator of the Identified Osteological Collections from Coimbra to have access to the mandibular remains. Then, each mandible was photographed with an associated 10-centimeter scale and with a tag containing the individual's record identification, the provenance collection, a number that would identify the individual in the CT scan, and the date when the photograph was taken (Figure 2.2).

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<sup>4</sup> TIVMI (Treatment and Increased Vision for Medical Imaging) is a software developed by the University of Bordeaux. This freely downloadable software allows the user to treat DICOM files, and 3D HMM reconstruction and segmentation, along with various other operations.

<sup>5</sup> Slicer is a software application that enables researchers to visualize and perform geometric morphometric analyses using high-resolution data from volumetric scans and 3D surface scans.





Figure 2. 2: Example of photographic record of mandibles (Mandible belonging to individual number 54 from the International Exchange Collection).

In order to evaluate dental growth, all mandibles had regular CT scans<sup>6</sup> performed at the Coimbra Hospital and University Centre by Rosa Ramos Gaspar.

Regarding the New Mexico Decedent Image Database, after searching the metadata for the individuals, an application was sent to access the individuals' high-resolution CT scan data<sup>7</sup>.

The Coupe Gorge mandible already had an associated  $\mu$ CT scan<sup>8</sup>, and although comparable to computerized tomography, it provides greater detail (Weber & Bookstein, 2011). The advantage of using computed tomography as an analytical tool is its high resolution and the fact that it is non-destructive, thus permitting researchers to work with a specimen without risking its preservation (Bayle et al., 2009). Digitizing specimens through CT and  $\mu$ CT scans allow for surface and internal analysis by anthropologists and makes the data available at all times (Godinho & Gonçalves, 2020; Weber & Bookstein, 2011).

After gathering all the CT data from the human reference collections, we created a database for the individuals, containing information about their identification code, CT number, recorded age at death, cause of death, and location.

In the first stage, using the TIVMI and Slicer software, deciduous and permanent teeth were assessed for their presence in the mandible. The dental notation followed in this

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<sup>6</sup> The parameters of the CT from the CIC scans were: 0.390625 (width), 0.390625 (height), 0.8 (thickness), and 0.800049 (space between slices).

<sup>7</sup> The parameters of the CT scans from the NMDID were: 0.386719 (width), 0.386719 (height), 1 (thickness), and 0.5 (space between slices).

<sup>8</sup> The parameters of the CT scan from the Coupe-Gorge mandible were: 0.021 (width), 0.021 (height), 0.0210001 (thickness), and 0.0210001 (space between slices).



work was established by the FDI (*Fédération Dentaire Internationale*). Then, we individually examined each tooth of the left arcade with the mandible in lateral and posterior views. The examination was done under good light conditions and repeated. Finally, to get a more credible evaluation with no external influences, the data regarding the chronological ages of the individuals was only consulted after the classification of the stages of Moorrees, Bengston and AlQahtani (AlQahtani et al., 2010; Moorrees et al., 1963).

#### 2.4.1. Intra and inter-rater reliability

When examining the specimens, part of the sample had the Moorrees' stages reexamined for the 36 by the author and by a second rater<sup>9</sup> with no previous experience in the methodology to assess intra and inter-rater reliability of the observations. Twelve mandibles (37%) from the Identified Osteological Collections of the University of Coimbra and the New Mexico Decedent Image Database, with ages ranging from 3 to 9 years, were selected to evaluate the reliability of the data collection. The second rater observed the sample with no previous knowledge of the classifications made by the author.

We gathered the date and inserted it in SPSS (version 28.0.1.1), followed by an analysis of Cohen's kappa ( $\kappa$ ) (Table 2.4), a robust, valuable statistic for measuring the "chance-adjusted" agreement between one or more observers (Byrt, 1996; McHugh, 2012).

Table 2. 4: Kappa description (Byrt, 1996).

<i>Kappa value</i>	<i>Agreement</i>
<i>0.93-1.00</i>	Excellent agreement
<i>0.81-0.92</i>	Very good agreement
<i>0.61-0.80</i>	Good agreement
<i>0.41-0.60</i>	Fair agreement
<i>0.21-0.40</i>	Slight agreement
<i>0.01-0.20</i>	Poor agreement
<i>0.00, or less</i>	No agreement

<sup>9</sup> Anita Viktorovna Bondarenko.

#### **2.4.2. On the Pleistocene specimens**

The procedures used for the sample of Pleistocene specimens varied slightly. Due to the impossibility of gathering tomographic files on most individuals excepting for the Roc de Marsal child, we gathered data concerning the developmental stages of their dentition from selected publications that used Moorrees' stages to classify tooth formation.

After assessing each human mandible and estimating the age at death, and after analysis of the results of the intra and inter-rater reliability, we studied the Coupe-Gorge mandible following the methods proposed in AlQahtani et al. (2010). The data of the Paleolithic hominins chosen for the comparative sample was inserted into tables provided by the London Atlas software application version 2. Their estimated age at death was then confronted with previously proposed ages at death.

#### **2.4.3. Morphological assessment**

The study of mandibular remains figures extensively in research, and anthropologists have discovered that while the postcranial skeleton of Neandertals reflects an adaptation to increased stress in the harsh climate of Pleistocene Eurasia, their craniofacial morphology owes its trajectory to either genetic or environmental influences or a combination of both, or, how Bastir puts it, a result of "random drift" (Bastir, 2018; Weaver, 2009). The study of mandibular morphology is central to better understanding evolutionary processes (Rosas, 2001). Neandertal mandibles express many features that distinguish them from earlier species' and anatomically modern humans (Walker et al., 2010).

After estimating age at death, this study assessed Neandertal mandibular morphology from a modified reference sample (Table 2.5). The first step constituted the actual description of the features. The data for this section came mainly from previous peer-reviewed publications with some exceptions, and all the individuals constituting the sample were studied.

The second part, dedicated to morphometrics, focused on linear distances and indices. Considering the fragmentary state of the Coupe-Gorge mandible, only the assessment of the height and breadth of the symphysis were studied. The morphometric analysis used a modified version of the Neandertal reference sample, excluding El Sidrón J1 and

including the fossils known as Teshik-Tash and Ehringsdorf G. This was because linear measurements and virtual data of the El Sidrón mandible were not available. Data concerning these measurements were taken from published works and, when possible, directly from STL files downloaded from the NESPOS digital database. Individuals belonging to the NMDID and the CIC were selected for this stage. The CT data belonging to the modern human individuals were converted to 3D using Slicer, and the results between modern humans and Neandertals were later confronted.

Table 2. 5: Morphometrics sample (Modified sample using a selection of Modern human and Neandertal specimens).

<b>Morphometrics Sample</b>	
Modern Human Sample	Pleistocene <i>Homo</i> Sample
NMDID106974	Coupe-Gorge
NMDID110163	Dederiyeh 1
NMDID110562	Dederiyeh 2
NMDID119072	Roc de Marsal
NMDID119553	Pech de L'Azé
NMDID134483	Barakai
NMDID114998	Archi 1
CT2b.670	Gibraltar 2
CT06.552	Teshik-Tash
CT10.338	Ehringsdorf G
CT24.368	

### **3. Results**

#### **3.1. Quantifying the modern human sample**

We combined a set of methodologies to assess age at death in 31 mandibles belonging to modern human individuals from the center-south region of Portugal and New Mexico.

We studied a total of 275 teeth in the modern human sample, the most represented deciduous teeth being the first and second molars (74, 75) and in the case of the permanent teeth the canine (33) and the first permanent molar (36) with the deciduous central incisors being the least represented teeth in the sample (Table 3.1). The minor presence of these deciduous anterior teeth is mainly because the sample contains a lesser number of individuals whose ages imply the presence of these teeth.

Table 3. 1: Distribution of observed teeth by type (Tooth identification follows the dental notation of the World Dental Federation).

Distribution of teeth by type		
Tooth	Amount	%
71	12	4%
72	16	6%
73	15	5%
74	27	10%
75	26	9%
31	25	9%
32	25	9%
33	30	11%
34	25	9%
35	22	8%
36	29	11%
37	23	8%
TOTAL	275	

### 3.2. Error analysis

#### 3.2.1. Intra-rater reliability

We assessed intra-rater reliability for classifying the Moorrees' stage for developing multirrooted teeth (Table 3.2). For this exercise, a sample consisting of 12 individuals from the ISC, IESC, and NMDID had their first permanent molar (36) observed in two isolated sessions. Of all twelve teeth observed, only one was classified differently during both sessions. Having done this, we proceeded to analyze the results of Cohen's  $\kappa$ . The values presented indicate a very good agreement for the identification of tooth developmental stages.

Table 3. 2: Intra-rater reliability results.

<b>Symmetric Measures</b>					
		Value	Asymptotic Standard Error <sup>a</sup>	Approximate T <sup>b</sup>	Approximate Significance
Measure of Agreement	Kappa	.894	.099	6,336	<.001
N of Valid Cases		12			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

### 3.2.2. Inter-rater reliability

The same way intra-rater reliability was studied, the sample comprising of 12 permanent first molars was examined by a second rater (Table 3.3). Using again Cohen’s statistic to analyze agreement between two raters, the results indicate a good agreement.

Table 3. 3: Inter-rater reliability results.

		<b>Symmetric Measures</b>			
		Value	Asymptotic Standard Error <sup>a</sup>	Approximate T <sup>b</sup>	Approximate Significance
Measure of Agreement	Kappa	,789	,122	5,871	<,001
N of Valid Cases		12			

a. Not assuming the null hypothesis.

b. Using the asymptotic standard error assuming the null hypothesis.

### 3.3. Age at death estimate in the modern human sample

#### 3.3.1. The individuals from the New Mexico Decedent Image Database

The 7 New Mexican individuals who comprise this reference sample range from 3 to 5 years old at death, thus constituting a vital sample to help study the Coupe-Gorge mandibular symphysis, whose age was estimated in 1985 to be around 4 to 5 years (Billy, 1985). These mandibles were observed in the software and the identification of the Moorrees and Bengston stages were inserted in the London Atlas software application, developed by the Queen Mary University of London. The age ranges suggested by the software were then observed with the “Atlas of Human Tooth Development and Eruption” and with the tooth development data provided by AlQahtani (AlQahtani et al., 2010).

The results for 106974 belong to a male individual who died at the age of 4 years. The study of their mandibular dentition allowed us to estimate the age at death between 3.5 and 4.5 years (Table 3.4).

Table 3. 4: Age at death for individual 106974.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	Ac	Ac	Ac	Ri	Ri	Crc	Cr 1/2	Coc	Ri	Coc	
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1	1	1	1	

The results for 110163 belong to a male individual who died at the age of 4 years. The study of their mandibular dentition suggests an estimated age at death between 3.5 and 4.5 years (Table 3.5).

Table 3. 5: Age at death for individual 110163.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	Ac	Ac	Ac	Ri	Ri	Crc	Cr 1/2	Coc	Ri	Coc	
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1	1	1	1	

The results for 110562 belong to a male individual who died at the age of 4 years. The study of their mandibular dentition suggests an estimated age at death between 3.5 and 5.5 years (Table 3.6).

Table 3. 6: Age at death for individual 110562.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	Ac	Ac	Ac	Ri	Crc	Cr 3/4	Cr 1/2	Coc	R 1/4	Cco	
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1	1	1	1	

The results for 114998 belong to a female individual who died at the age of 5 years. The study of their mandibular dentition suggests an estimated age at death between 4.5 and 6.5 years (Table 3.7).

Table 3. 7: Age at death for individual 114998.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	Ac	Ac	Ac	R 1/4	R 1/4	Ri	Cr 3/4	Cr 3/4	R 1/4	Cr 1/2	
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1	1	3	1	

The results for 119072 belong to a male individual who died at the age of 3 years. The study of their mandibular dentition suggests an estimated age at death between 2.5 and 4.5 years (Table 3.8).

Table 3. 8: Age at death for individual 119072

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	Ac	Ac	Ac	Cr 3/4	Cr 1/2	Cr 1/2	Cr 1/2	Cco	Crc	Ci	
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1	1	1	1	

The results for 119553 belong to a female individual who died at the age of 4 years. The study of their mandibular dentition suggests an estimated age at death between 4.5 and 5.5 years (Table 3.9).

Table 3. 9 Age at death for individual 119553.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	Ac	Ac	Ac	Ri	Cr 3/4	Cr 3/4	Cr 1/2	Coc	R 1/4	Coc	
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1	1	1	1	

The results for 134483 belong to a male individual who died at the age of 3 years. The study of their mandibular dentition suggests an estimated age at death between 2.5 and 4.5 years (Table 3.10).

Table 3. 10: Age at death for individual 134483.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	Ac	Ac	Ac	Cr3	Cr3/4	Cr1/2	Cr1/2	Ci	Ri	Ci	
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1	1	1	1	

### 3.3.2. The Identified Collections of the University of Coimbra

The individuals that comprise the Identified Osteological Collections of the University of Coimbra make up 24 mandibular remains with associated CT scans. The individuals belonging to the Identified Skeletal Collections and International Exchange Skeletal Collections did not have their data inserted in the software app and were instead recorded in individual tables. The reason is that the current version of the software does not yet allow the user to insert Moorrees' stages used to classify tooth resorption which is needed given the fact that the sample from the ISC and IESC is made up from mandibles belonging to individuals older than 6 years old and 14 of them had Moorrees' stages for tooth resorption identified in their deciduous dentition.

#### 3.3.2.1. *The Medical Schools Collection II*

A total of 52 teeth belonging to 7 individuals from the MSCII constituted the comparative sample for this study. However, there is an important drawback to mention regarding these individuals. While we know how many individuals constitute this collection, their ages at death, sex, and year of death, their crania were separated from the mandibles in their original container, thus making it impossible in this work to know to which exact individuals the mandibular remains belong.

The study of the mandibular dentition belonging to the individual with CT number 32 provided us with a broad age range. While the deciduous dentition suggests an age range between 1.5 to 4.5 months, if we compare the developmental stage for 36 with AlQahtani's data, we observe it from 1.5 months to 1.5 years old (Table 3.11).

Table 3. 11: Age at death for CT32.



	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Crc	Crc		Coc	Crc						Cco		
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		1	1		1	1						1		

The study of the mandibular dentition belonging to CT33 gave us an age range between 2.5 and 4.5 years at death (Table 3.12).

Table 3. 12: Age at death for CT33

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Ac	Ac	R 3/4	R 3/4	R 1/2	Crc	Crc	Cr 1/2	Cco		Cr 3/4		
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1	1		1		

The individual known as CT34, similar to CT33, had an estimated age at death between 2.5 and 4.5 years (Table 3.13).

Table 3. 13: Age at death for CT34.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
					Ac	Ac	Cr 3/4	Crc	Cr 1/2	Cco		Cr 3/4		
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
					4	4	1	1	1	1		1		

The tooth developmental stages of CT35 permit us to establish an age at death between 1.5 and 2.5 years old (Table 3.14).

Table 3. 14: Age at death for CT35.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		R 3/4	R 3/4	R 1/2	R 1/2		Cr 3/4	Cr 1/2	Coc			Cr 3/4		
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4		1	1	1			1		

The individual known as CT36 allowed us to estimate age at death between 10.5 months and 1.5 years (Table 3.15).

Table 3. 15: Age at death for CT36.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
			R 3/4		R 1/2		Cr 1/2	Coc	Cr			Cco		
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
			4		4		1	1	1			1		

The study of the mandibular dentition belonging to CT37 permitted us to suggest an age at death between 1.5 and 3.5 years (Table 3.16).

Table 3. 16: Age at death for CT37.

	Jaw	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		Rc	Ac	R 1/2	R 3/4	R 1/2	CrC	CrC	Cr 1/2			CrC		
Eruption	Lower Left	7.1	7.2	7.3	7.4	7.5	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8
		4	4	4	4	4	1	1	1			1		

### 3.3.2.2. *The Identified Skeletal Collection and the International Exchange Skeletal Collection*

We present below the results of the identification of the developmental stages as well as the corresponding age at death estimates for the 17 individuals belonging to the ISC and IESC that comprise the modern human comparative sample.

The following results belong to a 6-year-old male individual from the IESC (Table 3.17). By assessing the development of his dentition, we reached an estimated age at death between 4.5 and 6.5 years. The lowest age is related to the permanent first (36) and second permanent molars (37) who express their identified developmental stages in individuals

of that age in their median and maximum values for tooth formation stages as seen in (AlQahtani et al., 2010).

Table 3. 17: Age at death for CT01.N688.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					Ac	Ac			Crc	Cr 3/4	Crc	R 1/2	Coc	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					4	4			1	1	1	4	1	

The following results belong to a 7-year-old female individual from the IESC (Table 3.18). By assessing the development of her dentition, we reached an estimated age at death between 4.5 and 6.5 years. The lowest age is related to the permanent first premolar (34) who expresses its identified developmental stage in individuals of that age in their maximum values for tooth formation stages.

Table 3. 18: Age at death for CT2-2b.N670.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					Res 1/4	Res 1/4	R 3/4	R 1/2	R 1/4	Crc	Crc	Crc	Cr 3/4	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					4	4	4	4	1	1	1	4	1	

The following results belong to a 7-year-old female individual from the ISC (Table 3.19). By assessing the development of her dentition, we reached an estimated age at death between 4.5 and 7.5 years. The lowest age is related to the permanent first premolar (34) and second molar (37) who express their identified developmental stages in individuals of that age in their median and maximum values for tooth formation stages.

Table 3. 19: Age at death for CT03.N5.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				Ac	Ac	Ac	R 1/2	R 3/4	R 1/4	Crc	Crc		Coc	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				4	4	4	1	1	1	1	1		1	

The following results belong to a 7-year-old female individual from the ISC (Table 3.20). By assessing the development of her dentition, we reached an estimated age at death between 6.5 and 8.5 years.

Table 3. 20: Age at death for CT04.N305.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
						Res 1/4			R 1/4	R 1/4	Crc	R 3/4	Cr 3/4	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
						4			1	1	1	4	1	

The following results belong to a 7-year-old female individual from the ISC (Table 3.21). By assessing the development of her dentition, we reached an estimated age at death between 5.5 and 7.5 years. The lowest age is related to the permanent lateral incisor (32) and second molar (37) who express their identified developmental stages in individuals of that age in their median and maximum values for tooth formation stages.

Table 3. 21: Age at death for CT05.N352.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					Res 1/4	Res 1/4		R 1/4	R 1/4	Ri	Cr 1/2	R 3/4	Cr 1/2	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					4	4		1	1	1	1	4	1	

The following results belong to a 7-year-old female individual from the IESC (Table 3.22). By assessing the development of her dentition, we reached an estimated age at death between 4.5 and 7.5 years. The lowest age is related to the permanent premolars (34,35) as well as the first molar (36) who express their identified developmental stages in individuals of that age in their median and maximum values for tooth formation stages.

Table 3. 22 : Age at death for CT06.N552.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				Ac	Res 1/4	Ac	R 3/4	R 3/4	R 1/4	Crc	Coc	R 1/2	Cr 3/4	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				4	4	4	4	1	1	1	1	4	1	

The following results belong to an 8-year-old male individual from the IESC (Table 3.23). By assessing the development of his dentition, we reached an estimated age at death between 7.5 and 8.5 years.

Table 3. 23: Age at death for CT07.N54.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			Ac	Ac	Res 1/2	Res 1/4	Rc	R 1/4	R 1/4	Ri	Crc	R 3/4	Ri	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			4	4	4	4	4	1	1	1	1	4	1	

The following results belong to a 7-year-old male individual from the IESC (Table 3.24). By assessing the development of his dentition, we reached an estimated age at death between 5.5 and 8.5 years. The lowest age is related to the second permanent molar (37) who expresses its identified developmental stage in individuals of that age in their median values for tooth formation stages.

Table 3. 24: Age at death for CT08.N805.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			Ac		Res 1/4	Res 1/4	Rc	R 1/2	R 1/4	Ri	Ri	R 3/4	Cr 1/2	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			4		4	4	4	2	1	1	1	4	1	

The following results belong to a 7-year-old male individual from the IESC (Table 3.25). By assessing the development of his dentition, we reached an estimated age at death between 5.5 and 8.5 years. The lowest age is related to the lateral incisor (32), as well as

the first (36) and second molars (37) who express their identified developmental stages in individuals of that age in their median and maximum values for tooth formation stages.

Table 3. 25: Age at death for CT09.N227.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
						Res 1/4	R 3/4	R 1/4	R 1/4	Ri	Cr	R 1/2	Cr 1/2	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
						4	2	1	1	1	1	3	1	

The following results belong to an 8-year-old male individual from the IESC (Table 3.26). By assessing the development of his dentition, we reached an estimated age at death between 8.5 and 9.5 years.

Table 3. 26: Results for CT10.N338.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					Res 1/4	Res 1/4	Ac		R 3/4	R 1/4	R 1/4	A 1/2	Ri	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					4	4	4		2	1	1	4	1	

The following results belong to an 8-year-old male individual from the ISC (Table 3.27). By assessing the development of his dentition, we reached an estimated age at death between 6.5 and 7.5 years. The lowest age is related to the permanent central incisor (31), the canine (33), the second premolar (35) as well as the first molar (36) who also express their identified developmental stages in individuals of that age in their median and maximum values for tooth formation stages.

Table 3. 27: Results for CT11.N126.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			Ac	Ac	Res 1/2	Ac	Rc	R 1/2	R 1/4	Ri	Cr	R 3/4	Cr 3/4	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			4	4	4	4	4	1	1	1	1	4	1	

The following results belong to an 8-year-old male individual from the IESC (Table 3.28). By assessing the development of his dentition, we reached an estimated age at death between 7.5 and 8.5 years.

Table 3. 28: Results for CT12-12. N616.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			Ac		Res 1/4	Res 1/4	A 1/2	R 3/4	R 1/2	R 1/4	Crc	R 3/4		
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
			4		4	4	4	1	1	1	1	4		

The following results belong to an 8-year-old male individual from the IESC (Table 3.29). By assessing the development of his dentition, we reached an estimated age at death between 7.5 and 8.5 years.

Table 3. 29: Age at death for CT13.N609.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					Res 1/2	Res 1/4			R 1/4	R 1/4	Ri	R 3/4	Ri	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					4	4			1	1	1	4	1	

The following results belong to an 8-year-old female individual from the IESC (Table 3.30). By assessing the development of her dentition, we reached an estimated age at death between 7.5 years and 8.5 years.

Table 3. 30: Age at death for CT14.N317.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
							Rc	R 3/4	R 1/4	R 1/4	Crc	R 3/4	Ri	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
							4	4	1	1	1	4	1	

The following results belong to an 8-year-old female individual from the IESC (Table 3.31). By assessing the development of her dentition, we reached an estimated age at death between 6.5 and 8.5 years. The lowest age is related to the permanent lateral incisor (32), canine (33), second premolar (35) and first molar (36) who express their

identified developmental stages in individuals of that age in their median and maximum values for tooth formation stages.

Table 3. 31: Age at death for CT15.N622.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				Ac	Res 1/4	Res 1/4	R 3/4	R 3/4	R 1/4	R 1/4	Cr	R 3/4	Cr 3/4	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				4	4	4	4	1	1	1	1	4	1	

The following results belong to a 9-year-old male individual from the ISC (Table 3.32). By assessing the development of his dentition, we reached an estimated age at death between 8.5 and 9.5 years.

Table 3. 32: Age at death for CT16.N372.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					Res 1/4				R 1/4	R 1/4			R 1/4	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
					4				1	1			1	

The following results belong to a 9-year-old female individual from the ISC (Table 3.33). By assessing the development of her dentition, we reached an estimated age at death between 7.5 and 8.5 years. The lowest age is related to the permanent lateral incisor (32), canine (33) and first molar (36) who express their identified developmental stages in individuals of that age in their minimum, median and maximum values for tooth formation stages.

Table 3. 33: Age at death for CT18.N22.

	Mandible	DECIDUOUS TEETH					PERMANENT TEETH							
Development	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				Res 1/4			Ac	R 3/4	R 1/4	R 1/4	Ri	R 3/4	Ri	
Eruption	Lower Left	71	72	73	74	75	31	32	33	34	35	36	37	38
				4			4	4	1	1	1	4	1	

### 3.4. Age at death estimate for the Pleistocene *Homo* reference sample



The Pleistocene *Homo* reference collection for estimating age at death comprises seven individuals. However, contrary to the modern human reference sample, only the Roc de Marsal child has an associated CT scan. This data was gathered from the NESPOS database, using the author's Evan-Society credentials. The data gathered were inserted in individual tables, which included the rated teeth, the Moorrees' stages, the estimated age at death in the specimens, and the tooth formation stages for each tooth by age.

### 3.4.1. Dederiyeh 1

The following results belong to a Neandertal individual known as Dederiyeh 1 (Table 3.34). The remains were previously aged between no more than two years and above one year and less than three by examining the dentition and the postcranial skeleton respectively (Akazawa et al., 1995). The age at death for the Dederiyeh 1 specimen was later proposed to be around 1 year and 7 months after studying incremental lines in the specimen's permanent molar (Sasaki et al., 2002). However, by assessing the development of their mandibular dentition, an estimated age at death between 1.5 and 3.5 years was reached, thus showing no significant divergence from previous estimates.

Table 3. 34: Age at death results for Dederiyeh 1.

<b>Specimen: Dederiyeh 1</b>		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
71	A 1/2	2.5 Minimum
72	Rc	1.5 Maximum; 2.5 Minimum
73	R 1/2	1.5 Maximum
74	Rc	2.5 Median
75	R 1/4	1.5 Maximum
31	Cr 1/2	1.5 Minimum-Median 2.5 Minimum
32	Cr 1/2	1.5 Median-Maximum 2.5 Minimum
33	Coc	1.5 Median-Maximum 2.5 Minimum 3.5 Minimum
36	Cr 3/4	2.5 Median

### 3.4.2. Dederiyeh 2

The following results belong to a Neandertal individual known as Dederiyeh 2, discovered four years after Dederiyeh 1 (Table 3.35). The remains were previously aged around 2.5 years old, by examining the dentition, the sutures of the skull, and the ossification of the postcranial bones (Akazawa et al., 1999). The estimated age at between 1.5 and 4.5 years was reached by assessing the development of their mandibular dentition.

The highest value is observed in the permanent canine (33), where the tooth developmental stage can be expressed in human individuals from 2.5 to 4.5 years.

Table 3. 35: Age at death results for Dederiyeh 2.

<b>Specimen: Dederiyeh 2</b>		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
71	Ac	2.5 Median- Maximum
72	Re	1.5 Maximum; 2.5 Minimum
73	R 1/2	1.5 Maximum
74	Re	2.5 Median
75	R 1/2	2.5 Minimum
31	Crc	2.5 Maximum 3.5 Median
32	Cr 3/4	2.5 Median 3.5 Median
33	Cr 1/2	2.5 Median- Maximum 3.5 Median 4.5 Minimum
36	Cr 3/4	2.5 Median

### 3.4.3. Roc de Marsal

The following results belong to a Neandertal individual known as the Roc de Marsal child (Table 3.36). The remains were previously aged between 2.5 and 4 years, using SR- $\mu$ CT, volumetric measurements, and the scoring system proposed by Demirjian (Bayle et al., 2009). By assessing the development of their mandibular dentition and observing the SR- $\mu$ CT of the Roc de Marsal child, an estimated age at death between 2.5 and 5.5 years was reached. The highest value is observed in the permanent central incisor (31) and the first premolar (34), where the tooth developmental stage can be expressed in human individuals from 3.5 to 5.5 years and 5.5 respectively.

Table 3. 36: Age at death results for Roc de Marsal.

Specimen: Roc de Marsal		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
71	Ac	2.5 Median-Maximum
72	Ac	2.5 Median-Maximum
73	A 1/2	2.5; 3.5
74	Ac	2.5 Maximum
75	A 1/2	2.5
31	Ri	3.5 Maximum; 4.5 Median; 5.5 Minimum
32	Ri	4.5 Median-Maximum;
33	Cr 3/4	3.5 Median-Maximum; 4.5 Median
34	Coc	5.5 Minimum
35	Ci	3.5 Median; 4.5 Minimum
36	Crc	2.5 Maximum
37	Ci	2.5 Median-Maximum

#### 3.4.4. Pech de l'Azé

The following results belong to a Neandertal individual known as the Pech de l'Azé child (Table 3.37). The remains were previously aged around 18 ½ months ± two months, using two methods, one that used mathematical formulas and another which used a new table which allowed researchers to directly obtain the age at death of Neandertals from the deciduous and permanent teeth degree of maturation data (Granat & Heim, 2003). By assessing the development of their mandibular dentition, the estimated age at death between 1.5 and 4.5 years was reached. These results are slightly higher than the previous ones, however they still encompass the previous estimated age for the specimen.

Table 3. 37: Age at death results for Pech de l'Azé.

<b>Specimen: Pech de l'Azé</b>		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
71	Ac	2.5 Median-Maximum
72	A 1/2	2.5 Minimum-Median
73	Rc	2.5 Median-Maximum
74	Ac	2.5 Maximum
75	Rc	2.5 Median-Maximum
31	Cr 3/4	1.5 Maximum 2.5 Median 3.5 Minimum
32	Cr 3/4	2.5 Median; 3.5 Median
33	Cr 1/2	2.5 Median- Maximum; 3.5 Median; 4.5 Minimum
34	Cco	2.5 Median-Maximum
36	Cr 3/4	2.5 Median

### 3.4.5. Barakai

The following results belong to a Neandertal individual known as Barakai (Table 3.38). The remains were aged around three years based on the dentition (Faerman et al., 1994). The estimated age between 2.5 and 4.5 years was reached by assessing the development of their mandibular dentition. Therefore, these results encompass the previous age estimation.

Table 3. 38: Age at death results for Barakai.

<b>Specimen: Barakai</b>		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
71	Ac	2.5 Median-Maximum
72	Ac	2.5 Median-Maximum
73	R 3/4	2.5 Minimum
74	Ac	2.5 Maximum
75	Rc	2.5 Median-Maximum
31	Crc	2.5 Maximum 3.5 Median
32	Crc	2.5 Maximum 3.5 Maximum
33	Cr 3/4	3.5 Median-Maximum 4.5 Median
34	Ci	2.5 Minimum 3.5 Minimum
36	Crc	2.5 Maximum

### 3.4.6. Archi 1

The following results belong to a Neandertal individual known as Archi 1 (Table 3.39). The remains received different estimates for age at death since their discovery. When the mandible was discovered, the specimen was aged between 5 and 6 years, based on the germs of 31, 32, 33, 34, 35 and 36 (Ascenzi & Segre, 1971). A few years later, in 1994, the mandible was characterized as belonging to a 3-year-old individual, and in 1997 Mallegni and Trinkaus aged the specimen to circa 3 years old (Mallegni & Trinkaus, 1997). The estimated age at death between 2.5 and 5.5 years was reached by assessing the development of their mandibular dentition. The expression of stage Ri ('Initial root formation with diverge edges) in individuals around 5.5 years as a minimum value of tooth formation stage for the permanent central incisor varies slightly from the previously observed ages. However, the age estimate still encompasses the previous estimates for the specimen.

Table 3. 39: Age at death results for Archi 1.

Specimen: Archi 1		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
31	Crc	2.5 Maximum 3.5 Median
32	Crc	2.5 Maximum 3.5 Maximum
33	Cr 3/4	4.5 Median 5.5 Minimum 6.5 Minimum
34	Cco	2.5 Median-Maximum
35	Ci	2.5 Median-Maximum 3.5 Median 4.5 Minimum
36	Cr 3/4	

### 3.4.7. Gibraltar 2

The following results belong to a Neandertal individual known as Gibraltar 2 or Devil's Tower child (Table 3.40). Different ages were attributed to this specimen: Dean, Stringer, and Bromage proposed an age at death of 3 years, based on histological observations (Dean et al., 1986). A recent article proposed an age at death of 4.6 years based on the application of synchrotron virtual histology to calculate age at death from the microstructure of the dentition (T. M. Smith et al., 2010).

The estimated age at death between 3.5 and 5.5 years was reached by assessing the development of their mandibular dentition. These results are close to the age estimate which used SR- $\mu$ CT to assess crown and root formation time.

Table 3. 40: Age at death results for Gibraltar 2.

<b>Specimen: Gibraltar 2</b>		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
74	Ac	
75	Ac	
31	R 1/4	4.5 Maximum 5.5 Median
32	Ri	4.5 Median-Maximum
33	Crc	3.5 Maximum 5.5 Median
34	Cr 3/4	5.5 Median
35	Cr 1/2	4.5 Maximum
37	Cr 1/2	4.5 Maximum 5.5 Median

### 3.4.8. El Sidrón J1

The following results belong to a juvenile Neandertal known as Sidrón J1 (Table 3.42). The specimen has attributed an age at death of 7.7 years using dental histology (Rosas et al., 2017).

By assessing the development of the mandibular remains of El Sidrón J1, the estimated age at death between 6.5 and 9.5 years was reached. The expression of stage Ri in individuals around 9.5 years as a minimum value of tooth formation stage for the permanent second molar (37) slightly extends the previous estimate, nonetheless, the results encompass the previous estimates for the specimen.

Table 3. 41: Age at death results for El Sidrón J1.

<b>Specimen: El Sidrón J1</b>		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
31	Rc	6.5 Maximum 7.5 Median
32	R 3/4	6.5 Maximum 7.5 Median
33	R 1/4	7.5 Median-Maximum 8.5 Minimum-Median
36	Rc	7.5 Maximum 8.5 Maximum
37	Ri	8.5 Median 9.5 Minimum

### 3.5. Estimating age at death in the Coupe-Gorge specimen

Having applied the London Atlas, together with Moorrees' and Bengston's stages to identify tooth development and eruption in the previous specimens, we observed the Coupe-Gorge mandibular dentition. In 1985, Billy reported the results of the study of the

Coupe-Gorge mandible. An X-Ray was performed on the mandibular symphysis to allow observation of the non-erupted dentition. The crowns of the central incisors (34, 41) were classified as completed and described as being in a high position. Considering these results, Billy estimated the Coupe-Gorge specimen to be between 4 and 5 years old per dental developmental stages seen in modern humans (Billy, 1985).

Later, in 2003, Granat and Heim proposed two new methods for estimating age at death in Neandertals without resorting to modern human tables of tooth formation stages and eruption chronology (Granat & Heim, 2003). The first method involves the use of two mathematical formulas whilst the second method proposes the use of a table. Besides studying the permanent central incisors<sup>10</sup>, casts of the imprints left by the germs of the two permanent lateral incisors (32, 42) and of the left canine (33) were made (Granat & Heim, 2003). The results of their analysis indicated an age at death of 3 years and ten months (Granat & Heim, 2003).

We assessed the  $\mu$ CT of the Coupe-Gorge mandible to identify the tooth developmental and eruption stages (Figures 3.1 and 3.2). Our observations of the permanent central incisors are consistent with Granat and Heim, identifying the tooth developmental stages of 31 and 41 as Ri. By assessing the dentition of the Coupe-Gorge individual, the estimated age at death between 3.5 and 4.5 years was reached. The results encompass Granat and Heim's three years and ten months estimate.

Table 3. 42: Age at death results for Coupe-Gorge mandible.

<b>Coupe-Gorge Mandible</b>		
Dentition	Moorrees' Stage	London Atlas - Tooth Formation Stage
31	Ri	3.5 Maximum 4.5 Median
41	Ri	3.5 Maximum 4.5 Median

<sup>10</sup> Contrary (Billy, 1985), Granat and Heim's description of the developmental stage of the permanent central incisors relates more to Moorrees' Ri stage ("Initial root formation with diverge edges) rather than Crc ("Crown root completed with defined pulp roof").

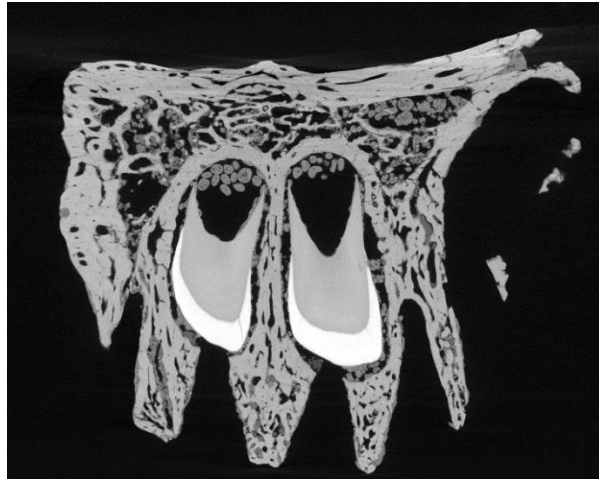


Figure 3. 1:  $\mu$ CT scan image of the Coupe-Gorge mandible (posterior view).



Figure 3. 2:  $\mu$ CT scan image of the Coupe-Gorge mandible (lateral view).

### 3.6. Morphology

#### 3.6.1. The Coupe-Gorge mandibular morphology

The Coupe-Gorge remains correspond to a fragmentary mandibular symphysis belonging to a juvenile Neandertal (see Appendix A for a list of traits shared with other Pleistocene *Homo* specimens) (Figure 3.3). It extends from the distal edge of the left deciduous canine (73) to the interalveolar interstice which separates the right deciduous



lateral incisor (82) and canine (83) (Figure 3.4) (Billy, 1985; Granat & Peyre, 2012). The alveolar edge shows damage on the lingual surface of the deciduous left incisor (72) (Billy, 1985; Granat & Peyre, 2012). The germs of the permanent central incisors (31, 41) had begun root initiation; however, the lateral incisors (32, 42) and the left canine (33) appear to have fallen post-mortem during fossilization, as evidenced by the damage which left opened areas on the lingual surface, leaving only the imprints of the germs (Figures 3.6 and 3.7) (Billy, 1985; Granat & Peyre, 2012).

The symphysis is characterized by its vertical profile with a slight depression in the center, showing anterior alveolar flattening, and below, we observe a discrete outline of a mental trigone. A slightly inclined planum alveolare can be seen, limited by a torus transversus superior which separates it from a from a genioglossus fossa. Below, we can detect the genioglossus and geniohyoid (Billy, 1985; Granat & Peyre, 2012).

The inferior edge is thick, and the imprints of the digastric muscles are in the internal half of both sides of the midline (Figure 3.5). This display is different from the one seen in recent modern humans, where the digastric fossae are located on the internal and inferior section of the symphysis (Billy, 1985; Granat & Peyre, 2012).

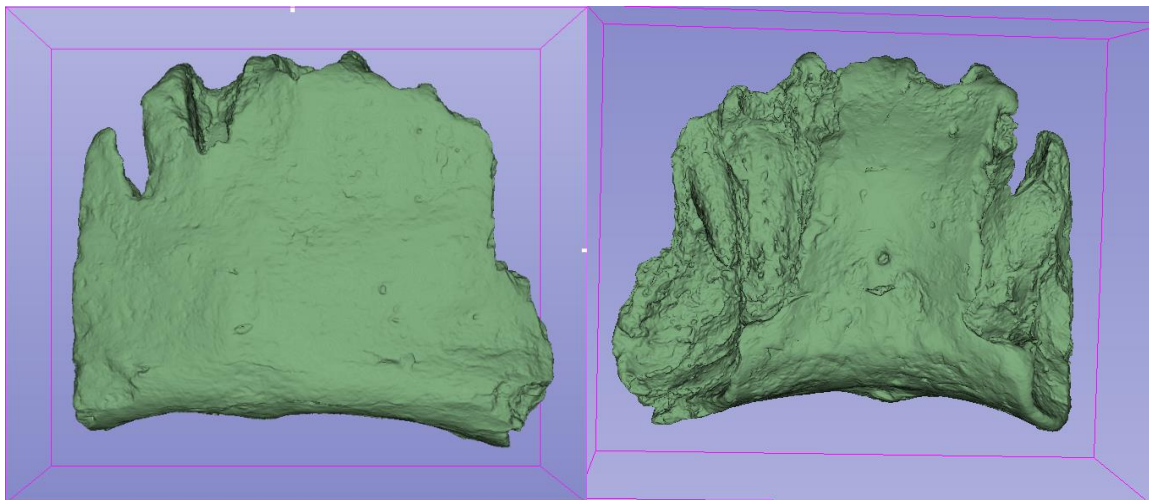
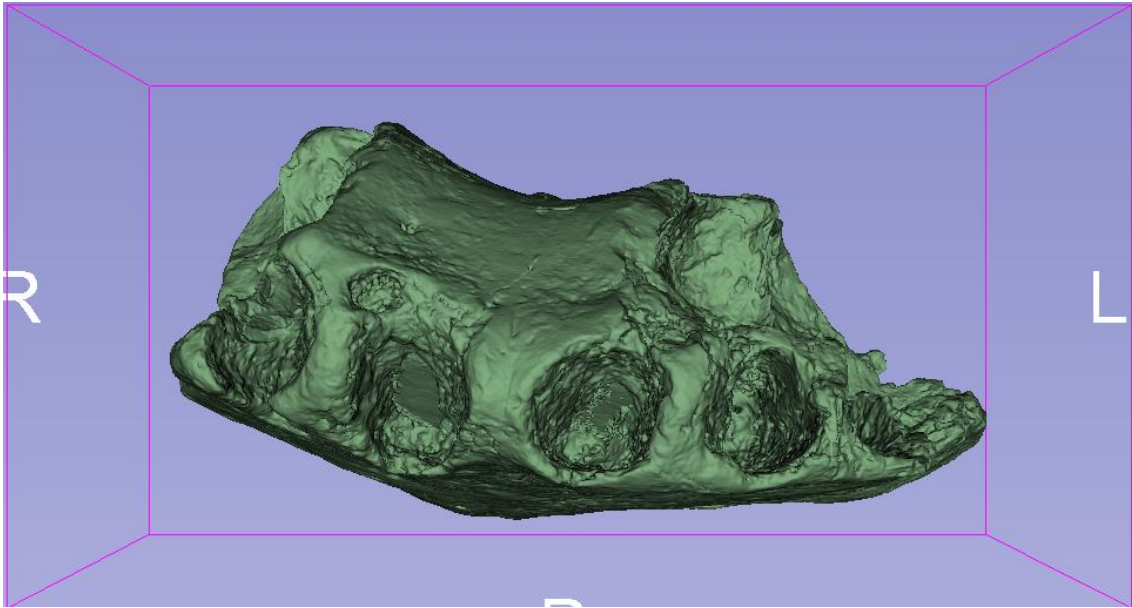
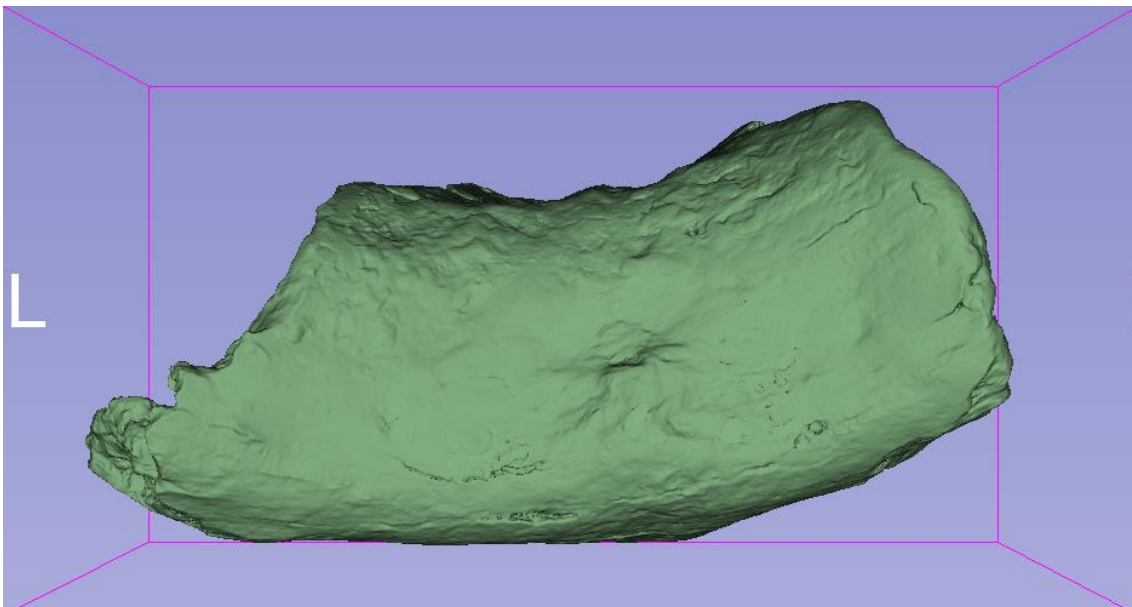


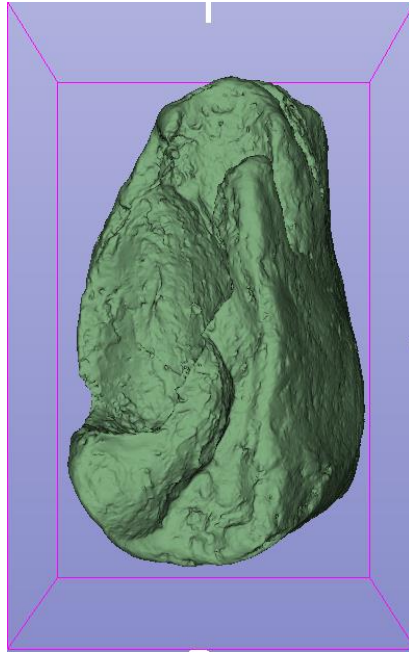
Figure 3. 3: Anterior and posterior views of the Coupe-Gorge mandible.



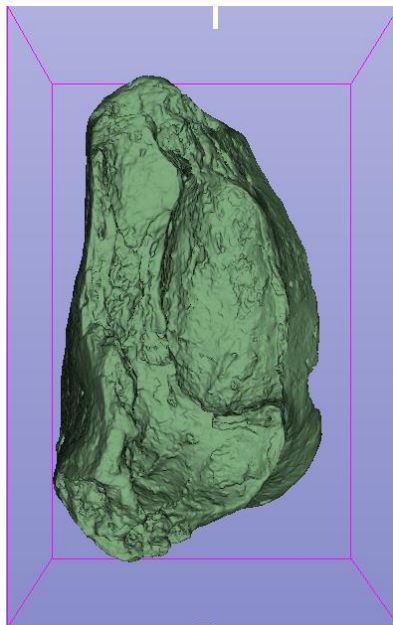
*Figure 3. 4: Superior view of the Coupe-Gorge mandible.*



*Figure 3. 5: Inferior view of the Coupe-Gorge mandible.*



*Figure 3. 6: Lateral right view of the Coupe-Gorge mandible.*



*Figure 3. 7: Lateral left view of the Coupe-Gorge mandible.*

### **3.6.2. Dederiyeh 1**

The Dederiyeh 1 child's mandible is characterized by its receding symphyseal profile with a minor indication of a mental trigone (Akazawa et al., 1995). Two mental foramina are located on each side of the mandible below the first molar (Akazawa et al., 1995). Shoveling of the permanent central incisors was observed in the specimen, considered a high-frequency trait in Neandertals, as well as an enlarged pulp chamber of the first deciduous molar (taurodontism) (Akazawa et al., 1995; S. E. Bailey, 2002). The symphyseal inclination angle in the specimen is lower when compared to anatomically modern humans (Akazawa et al., 1995; Fukase et al., 2015).

### **3.6.3. Dederiyeh 2**

The Dederiyeh 2 child's mandibular remains do not present a mental protuberance on the anterior surface. In the mandibular body and ramus, a mental foramen is located on each side of the mandible, under the first deciduous molars (74, 84), and a medial pterygoid tubercle is present internally (Akazawa et al., 1999).

### **3.6.4. Roc de Marsal**

The Roc de Marsal mandibular remains contain two mental foramina on each side of the mandible, posteriorly to the position observed in modern humans and the characteristic retromolar gap (Tillier, 1996). The specimen presents a developed planum alveolare with a vertical profile above (and a clearly present tuber symphyseos), resulting below in a receding symphysis (Schwartz & Tattersall, 2002; Tillier, 1996). Externally, the symphysis is described as "smooth and featureless" (Schwartz & Tattersall, 2002). Inferiorly, the symphysis is somewhat thick and broad anteroposteriorly with a gentle curvature (Schwartz & Tattersall, 2002). In addition, the digastric fossae are clearly present, and the mandible contains a large medial pterygoid tubercle (Schwartz & Tattersall, 2002).

### **3.6.5. Pech de L'Azé**

The Pech de l'Azé is characterized by a gracile symphyseal region on both surfaces. The anterior profile is almost vertical, and the tuber symphyseos is clearly present. There is no planum alveolare on the posterior surface (Mallegni & Trinkaus, 1997; Tillier, 1996). The right side of the mandible shows a mental foramen below the first deciduous molar (86) (Tillier, 1996). A medial pterygoid tubercle is present, and the digastric fossae are developed (Schwartz & Tattersall, 2002).

### **3.6.6. Barakai**

This mandible discovered in Barakai cave is firstly described as large and rounded with a symphyseal contour which results in an obtuse angle. Although the mandible lacks a chin, a slight mental trigone is present in the median line (Faerman et al., 1994). The mandible contains a large mental foramen with three foramina associated on the right side of the mandible under the first deciduous molar (Faerman et al., 1994). Lastly, the inner surface is characterized as convex and ‘saddle-shaped’ (Faerman et al., 1994).

### **3.6.7. Archi 1**

The mandible belonging to Archi 1 is characterized as thick on all sides (Schwartz & Tattersall, 2002). Looking at its profile, the symphyseal region slopes backward, and a slight convexity is expressed towards the inferior border. The inferior surface is also elevated in the regions of the deciduous incisors (73, 83) (Schwartz & Tattersall, 2002). A torus marginalis clearly developed is present in the mandible as is the development of the torus transversus inferior (Mallegni & Trinkaus, 1997). A clearly present planum alveolare is evident in the Archi 1 mandibular remains.

### **3.6.8. Gibraltar 2**

The mandibular remains belonging to Gibraltar 2, also known as the Devil’s Tower child have been thoroughly studied since their discovery at the beginning of the XX century. The imprints of the insertions of the pterygoid muscle are clearly present. Externally, the proeminentia lateralis is slightly protruding and is extended by a clearly present torus lateralis superior (Schwartz & Tattersall, 2002; Tillier, 1982). Three mental foramina can be observed on both sides of the mandible. In addition, there is a clear indication of anterior alveolar flattening (Schwartz & Tattersall, 2002; Tillier, 1982). Looking at the mandible in profile, a receding symphysis is denoted (Schwartz & Tattersall, 2002).

The posterior surface presents a weak planum alveolare which is interrupted by a torus transversus superior (Schwartz & Tattersall, 2002; Tillier, 1982). The mandible is also characterized by the lack of a chin and constant height of the mandibular body (Tillier, 1982).

### **3.6.9. Teshik-Tash**

The remains belonging to the Teshik-Tash specimen consist of a virtually complete mandible. It is described as broad and flat vertically across the symphyseal region (Schwartz & Tattersall, 2005). A mental foramen lies on each side of the mandible, below

the deciduous second molar (75, 85) (Schwartz & Tattersall, 2005). By observing from below, the symphyseal region is thinner anteroposteriorly than the bone of the corpora behind (Schwartz & Tattersall, 2005). The mandible presents also a broad and long digastric fossa that faces straight down (Schwartz & Tattersall, 2005). The gonial region is characterized as smooth and inflected medially with different tubercle-like structures along the external margin and the medial pterygoid tubercle is prominent (Schwartz & Tattersall, 2005).

### 3.6.10. Ehringsdorf G

The Ehringsdorf G remains consist of a partial mandibular fragment missing most of the right side and part of the left corpus and ramus (Schwartz & Tattersall, 2002). The symphyseal region is described as broad and arced from side to side, and its profile is clearly vertical with a slight protrusion of the alveolar region of the incisors (Schwartz & Tattersall, 2002). The digastric fossa left little traces in the mandible. The gonial margin deflects inwards and the fragment bears a medial pterygoid tubercle of considerable size (Schwartz & Tattersall, 2002).

### 3.6.11. Morphometrics

Below are the results of the linear measurements associated with the modern human and Pleistocene *Homo* morphometrics sample (Tables 3.8, and 3.9).

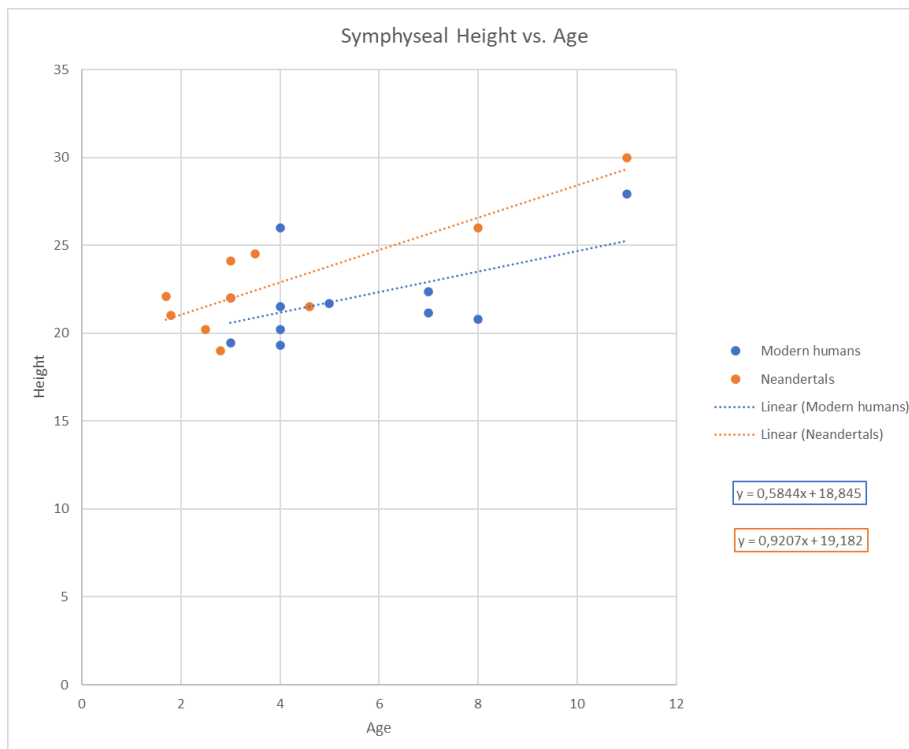


Figure 3. 8: Scatterplot of symphyseal height versus age for Modern humans and Neandertals

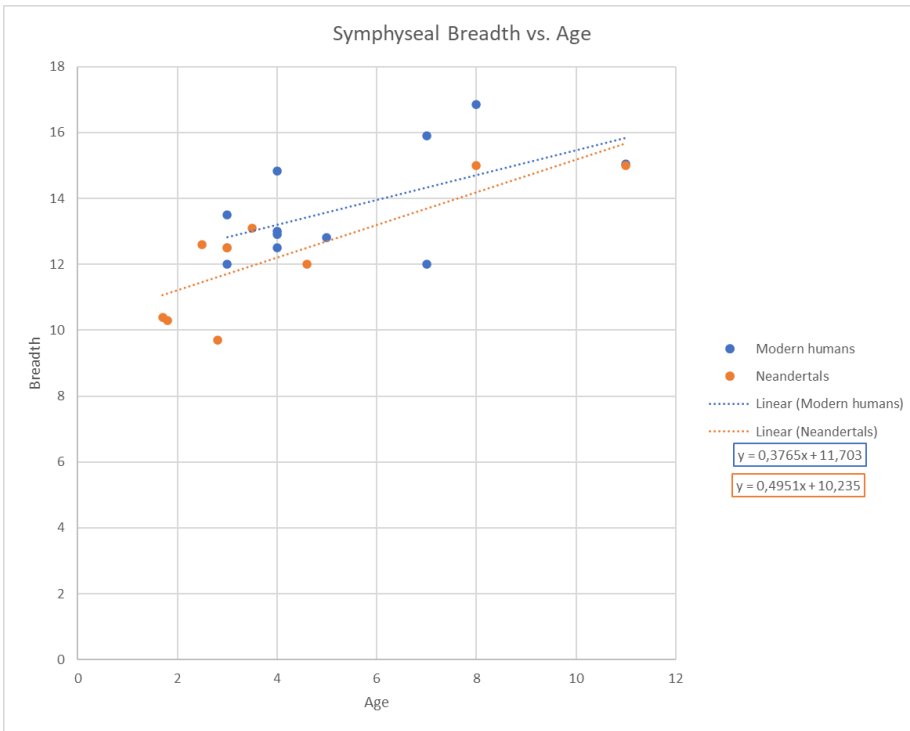


Figure 3. 9: Scatterplot of symphyseal breadth versus age for Modern humans and Neandertals

## 4. Discussion

The study of dental and mandibular remains to assess Neandertal and anatomically modern human ontogenetic patterns and sequences figures extensively in paleoanthropological research.

Compared to bone development, dental development is less affected by environmental and hormonal factors (Cunha & Wasterlain, 2015; Hillson, 1996; Ramirez Rozzi & Bermudez De Castro, 2004). Moreover, after the death of the organism, teeth are the most resistant part of the body against decay, being one of the most common remains found in prehistoric archaeological excavations. Therefore, teeth are an invaluable subject to study to assess the somatic development of an individual.

The mandible is a reliable marker to assess variability in hominin populations. Paleoanthropologists aim to study the different features present in the mandibles of distinct species of hominins as well as the ontogenetic sequence of these features, if they occur mainly prenatally through adulthood or if the most important differences appear postnatally (Bastir et al., 2007).

Unlike modern primates, modern humans benefit from a prolonged period of infant and childhood ontogenetic growth (Smith et al., 2010). Knowing this, paleoanthropologists have continuously debated the possible similarities and differences in ontogenetic patterns and sequences between *Homo sapiens* and Neandertals.

Several techniques are available to help researchers assess age at death from the study of dental remains. Using a combination of radiographs of mandibular teeth, Moorrees established the chronology of the formation of teeth in 14 developmental stages and presented them in graphic form to allow researchers to determine an individual's dental maturation (Hillson, 1996; Moorrees et al., 1963). Demirjian developed a methodology to assess dental maturity in a study of human children. New dental formation stages and weighted scores were defined for each tooth that, when summed, these quantitative values from 0 to 100 can be converted into a dental age (Cunha & Wasterlain, 2015; Hillson, 1996). Regarding traditional tooth histology, the physical sectioning of teeth has ceased, and anthropologists currently favor nondestructive techniques, considering the value of hominin dental remains as a rare find in paleoanthropological excavations (Dean et al., 1986). The observation of the microstructure of teeth to determine tooth formation and age at death is now performed with methods such as SR- $\mu$ CT, which are considered highly reliable (Smith et al., 2010).



This study employed AlQahtani's atlas of human tooth development and eruption to estimate age at death in a Neandertal specimen discovered in the XX century in Coupe-Gorge cave in Montmaurin, France. The use of atlas is not new, one of the most well-known being the Schour and Massler atlas with an age range from 5 months in utero to 35 years (AlQahtani et al., 2010; Schour & Massler, 1940). Ubelaker's atlas is another example of a diagram of the chronology of dental eruption (AlQahtani et al., 2010; Cunha & Wasterlain, 2015; Ubelaker, 1978). Despite criticisms, such as the possibility of identification of different tooth developmental stages by multiple raters, the London Atlas has been tested against similar methodologies, and the latest results have shown that AlQahtani's atlas represents a considerable improvement in accuracy of estimation of age at death and that it performs better than other methods such as Schour and Massler's atlas (Alqahatani et al., 2014; Cunha & Wasterlain, 2015). Furthermore, the atlas has also been tested for its effectiveness in multiple modern human populations and has proved to be a reliable tool for estimating age at death (AlQahtani et al., 2017; McCloe et al., 2018). Moreover, the London Atlas has been employed in Pleistocene *Homo* specimens, from anatomically modern humans to Denisovans and Neandertals (Demeter et al., 2022; Estalrich & Marín-Arroyo, 2021; Šešelj, 2017).

In order to estimate age at death in the Coupe-Gorge mandibular symphysis, modern human individuals from the University of Coimbra's Identified Skeletal Collection, International Exchange Skeletal Collection, Medical Schools Collection II and from the New Mexico Decedent Image Database were selected to be part of a reference sample to test the methodology, before moving on to test it in a sample consisting of Pleistocene *Homo* specimens attributed to the Neandertal taxa. For the sake of assessing the level of agreement in rating the teeth' developmental stages using Moorrees' stages, the left permanent first molar (36) from 12 individuals was selected to test out inter-rater and intra-rater reliability. Despite the author of this study and the second rater not having previous experience, good  $\kappa$  values were obtained (,789; ,894). A total of 275 teeth were rated, the most common of the deciduous dentition being the first molar (10%) and the least common the first incisor (4%), while the most common of the permanent dentition were the canine (11%) and first molar (11%) and the less frequent was the second premolar (8%). We succeeded in applying Moorrees and Bengston's stages, together with the London Atlas, to estimate age at death in the modern human individuals comprising the reference sample. However, it is essential to restate

those confirmations could not be made in the Medical Schools Collection II records. Sex differences were observed, as was the case of the New Mexican individuals 106974 and 110163 (both 4-year-old males) and 119553 (4-year-old female), where the developmental stage of the permanent first molar (36) was Ri for the males and R ¼ for the female individual, however, those differences are not unexpected. They can be consulted on the software application in the comparison section, where diagrams for both sexes can be accessed for different maturational stages. Besides that, differences were observed in individuals of the same age and sex, which can be attributed to expected variation between individuals. Most estimates encompassed the chronological age at death of the individuals.

A total of 7 individuals comprising a Pleistocene *Homo* reference sample had their ages at death estimated based on the London Atlas. The tooth developmental stages of Moorrees were obtained from previous publications that assessed these individuals via X-rays and CT scans for all specimens. However, a  $\mu$ CT scan performed on the Roc de Marsal child was obtained via the NESPOS database, and the published Moorrees' stages for the specimen were confirmed via observation of the  $\mu$ CT data. Previously attributed ages at death were mentioned for the Pleistocene specimens ranging from estimates based on dental development data, to age estimates based on postcranial remains to results based on the analysis of the microstructure of the teeth as was the case of Dederiyeh 1 and Gibraltar 2 for example.

Overall, all estimates encompassed the previously proposed ages at death, some closer than others. In the case of Dederiyeh 1, the specimen received several ages at death estimates, from 2 years to more than one year and less than three, to 1.7 years based on the analysis of cross striations of the first molar (Sasaki et al., 2002). Our assessment resulted in an age at death between 1.5 and 3.5 years old. The 3.5-year (minimum value for tooth formation) mark is based on the canine, who reports the Coc stage in modern humans from the ages of 1.5 to 3.5 years, therefore slightly overestimating the specimen's age. Another example concerns Gibraltar 2. The specimen was assessed using synchrotron virtual histology and the analysis yielded an estimated age at death of 4.6 years. With AlQahtani's atlas, the individual received an age at death estimate between 3.5 and 5.5 years, a positive result which encompasses the previous estimate.

The development and timing of the dentition of Neandertals remain a controversial subject, and the way one looks at it might influence how one uses the

London Atlas. A hypothesis proposes that Neandertals might have a more advanced dental development than modern humans. Wolpoff was one of the first to hypothesize this when he reported an earlier eruption of the third molar in the Krapina Neandertals (Wolpoff, 1979). Some authors defend a rapid growth of the anterior dentition in Neandertals relative to modern humans, with Ramirez Rozzi & Bermudez De Castro (2004) proposing that Neandertals grew their anterior teeth 15% faster than modern humans. Another study involving the analysis of anterior teeth support the hypothesis that Neandertals experienced a faster growth of anterior teeth, based on their shallower perikymata and linear enamel hypoplasia defects (McGrath et al., 2021). In contrast, a study involving the Scladina Neandertal reported that their permanent anterior teeth (except for the incisor) formed over a greater period of time than modern human population mean times while the molars developed over a shorter time, something which was also attested for the Dederiyeh 1 molar and the Roc de Marsal child (Bayle et al., 2009; Šešelj, 2017; Smith et al., 2007). On a study which employed SR- $\mu$ CT virtual histology, Smith (2010) stated that recent modern human dental standards overestimate age at death in Neandertals and thus should not be used to assess ages in juvenile Neandertals. A recent paper involving the study of five deciduous teeth from Krapina using virtual histology reported that the deciduous teeth of the specimens formed quickly and a deciduous incisor emerged at the “advanced end of the modern human schedule” (Mahoney et al., 2021).

Some studies contradict the hypothesis of a more accelerated pace of growth of Neandertal teeth. The El Sidrón J1 juvenile dental maturation was reported to fall within the expected range of modern humans of the same age (Rosas et al., 2017). Challenging the proposal of Neandertals expressing an accelerated molar growth, a virtual histological assessment of two molars from the site of La Chaise de Vouthon (85 from Abri Suard, 36 from Abri Bourgeois-Delaunay) found that the timing of the crown formation in both teeth was almost identical with the data reported for large samples of modern humans (Macchiarelli et al., 2006).

By describing the morphology of the Pleistocene *Homo* sample and the Coupe-Gorge mandible, we aimed to assess and highlight the different aspects of mandibular ontogeny in subadult Neandertals. The sample for this study encompassed Neandertals from three main geographical regions, Europe (6), Central Asia/Caucasus (2), and the Middle East (2). The specimens expressed a mixture of traits commonly attributed to

Neandertals in varying degrees (see Appendix A). The Coupe-Gorge mandibular morphology shares some features with other mandibular remains such as Roc de Marsal, Archi 1, and Gibraltar 2. Despite being separated from around 200kya to 40kya these European Neandertals share a present tuber symphyseos, a clearly present planum alveolare and torus transversus inferior and an expression of anterior alveolar flattening. These differ from the Pech de L'Azé mandible, which exhibits a more gracile symphyseal region (Billy, 1985; Tillier, 1996). The Central Asian specimens differ from the European ones in not having a tuber symphyseos yet they express a very strong tubercula lateralia, a feature only shared with the European Archi 1 child. A total of five individuals from the European and Middle eastern geographical regions share the presence of a medial pterygoid tubercle with the weakest expression of this feature being found in Dederiyeh 2 and Pech de l'Azé Neandertals which constitute some of the more recent fossil Neandertals in the sample.

The presence of these features in specimens ranging from around 1.7 to 12 years shows that many of the traits usually associated with adult Neandertals are manifested early in infancy, with some authors proposing they start their development prenatally (Williams, 2006).

Regarding the morphometrics sample, our results show that the Pleistocene *Homo* sample expresses a higher median symphyseal height value than modern humans. In contrast, the median values for the symphyseal breadth of the modern human sample were slightly superior to the former specimens.

## 5. Conclusion

The present work aimed to estimate age at death and assess the morphology of a fragmentary mandibular symphysis belonging to a subadult Neandertal individual from the Coupe-Gorge cave in Montmaurin, France.

We tested the London Atlas for human tooth development and eruption for its suitability in estimating age at death in the Coupe-Gorge mandible. AlQahtani's atlas was developed using a combination of radiographs belonging to English and Bangladeshi individuals up to 24 years of age. Earlier, in 2008, Liversidge reported tooth maturation differences between English, Bangladeshi, and South African populations. His study demonstrated that black children from south Africa initiate and complete maturation of the third molar significantly earlier than white and Bangladeshi individuals (Liversidge, 2008). Still on population differences, Tompkins demonstrated that the advanced sequence of third molar eruption in African populations potentially resembled those seen in past populations (Tompkins, 1996).

A comparative sample consisting of modern human individuals and Pleistocene *Homo* specimens were selected to test the method.

Results for the modern human reference sample were compared with the recorded ages at death. In contrast, for the Pleistocene *Homo* specimens, results were compared with age estimates based on skeletal remains and results from the observation of the microstructure of dental remains. The use of the London Atlas to estimate age at death was shown to be suitable for the modern human Portuguese and New Mexican individuals. It also proved reliable for providing age ranges for the Pleistocene *Homo* sample although some cases of overestimation were observed. The case-study of this work yielded an age at death estimate between 3.5 and 4.5 years, encompassing previous estimates and being similar to modern human values.

The ongoing research about ontogenetic differences between Neandertals and modern humans' dental development has not entirely falsified either hypothesis concerning dental maturation in Neandertals. However, overall, the different results that stem from estimating age at death and dental eruption sequences in Neandertals could likely be interpreted as an individual's ontogenetic variation, an aspect that is not exclusive to modern humans. Regarding potential cases where an overestimation is verified compared to other analyses, the minimum, median, and maximum values for tooth formation stages

can be consulted to narrow down the estimate. Nonetheless, the London Atlas should be further tested with past human populations and extant African populations.

We propose that the London Atlas can be used with caution to estimate age at death in Neandertals, especially when other methods are unavailable, such as SR- $\mu$ CT virtual histology (as it requires the first molar). A greater certainty might be reached if the methodology is applied in tandem with other methods of estimating age at death from fossil remains.

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## Appendix

General traits of the Coupe-Gorge mandible and their distribution across Pleistocene <i>Homo</i> specimens							
	Tuber symphyseos	Tubercula lateralia	Planum alveolare	Torus transversus inferior	Mental foramen	Pterygoid tubercle	Anterior alveolar flattening
Coupe-Gorge	±		+	+			+
Dederiyeh 1					2_2		
Dederiyeh 2					1_1	±	
Roc de Marsal	+	-	+		2_2	+	
Pech de l'Azé			-		1	±	+
Barakai	+				1_1		-
Archi 1	±	±	+	+	1_1		+
Gibraltar 2	+	-	±	+	3_3	+	+
Teshik-Tash	-	+	-	-	1_1		-
Ehringsdorf G						+	

A: General traits of the Coupe-Gorge mandible and their distribution across Pleistocene *Homo* specimens. (± weak expression, + clearly present, - absent). Modified version with data gathered from (Akazawa et al., 1995, 1999; Billy, 1985; Faerman et al., 1994; Granat & Peyre, 2012; Mallegni & Trinkaus, 1997; Schwartz & Tattersall, 2002, 2005; Tillier, 1996).