

THESIS

NON-METRIC CORRESPONDENCE BETWEEN NEANDERTAL PRIMARY AND
PERMANENT DENTITION

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ABSTRACT

NON-METRIC CORRESPONDENCE BETWEEN NEANDERTAL PRIMARY AND PERMANENT DENTITION

The present study aims to understand the underpinnings of dental crown morphological development and provide a dental morphological comparison between the baby and adult teeth of Krapina Neandertals with the expectations of finding a correspondence between the two dentitions based on their dental non-metric trait frequencies.

19 non-metric traits were scored utilizing the Arizona State University Dental Anthropology System (Turner et al., 1991) on both deciduous and permanent teeth of 12 KDPs (Krapina Dental Person) (n=62). Associations between the two dentitions for 11 traits were tested applying the Somers' D measure of association statistics. Also, non-metric trait occurrence frequencies with the sample sizes and their range of variation were reported.

The apparent morphological similarity between baby and adult teeth and also the inter-individual similarity observed in this study suggest a couple of points. First, it supports the assumptions that Krapina Neandertals represent a closely genetically related group. Second, it suggests that similar genes are responsible for the growth and development of the dental non-metric traits of both primary and permanent dentitions. Third, the unique and consistent dental morphological pattern at Krapina may have an adaptive significance for chewing. Lastly, the morphological similarity between deciduous second molar (dm2) and permanent first molar (M1) supports Butler (1939, 1967)'s field model which also posits that dm2 exhibits more morphological similarities with M1 than dm1 has with M1.

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TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
CHAPTER 1 INTRODUCTION.....	1
1.1 Statement of the problem.....	1
1.2 Purpose of research.....	7
1.3 Research Questions and the Hypothesis to be addressed.....	8
1.4 Scope and limitations.....	8
1.5 Organization of the study.....	9
CHAPTER 2 LITERATURE REVIEW.....	10
2.1 Introduction.....	10
2.2 Genetics of Dental Morphological Variation.....	10
2.3 Correspondence Between Deciduous and Permanent Dentitions.....	14
2.3.1 Modern Human Studies.....	14
2.4 Neandertal Dental Morphology.....	18
2.4.1 Characteristics of Neandertal Teeth and Non-metric Trait Frequencies.....	19
2.4.1.1 Anterior Dentition: Incisors and Canines.....	19
2.4.1.2 Posterior Dentition: Molars.....	21
2.4.2 Combination of Traits.....	22
2.4.3 Neandertal Autopomorphies.....	23
CHAPTER 3 MATERIALS AND METHODOLOGY.....	26
3.1 Materials.....	26
3.1.1 Sample.....	26
3.1.2 Krapina, Hušnjakovo rock-shelter: stratigraphy, chronology and archeology of the site.....	27
3.1.3 Problems with the sample.....	28
3.2 Methods.....	29
3.2.1 Non-metric data collection.....	29
3.2.1.1 ASUDAS.....	31
3.2.1.2 Dental non-metric traits and terminology.....	32
3.2.2 Statistical analysis.....	34
CHAPTER 4 RESULTS.....	36
4.1 Descriptive statistics.....	36
4.1.1 Incisors.....	39
4.1.2 Canines.....	40
4.1.3 Molars.....	40

4.1.4 Tooth Pairs.....	41
4.2 Statistical analysis	42
CHAPTER 5 DISCUSSION AND CONCLUSION	45
5.1. Summary of the Study.....	45
5.2. Concluding Remarks	49
5.3. Future Directions.....	52
REFERENCES	53
APPENDIX.....	60

LIST OF TABLES

Table 2.1: Frequencies of non-metric traits in Neandertal maxillary dentition (Percentages of presence/n). Data adapted from Bailey (2006a).	20
Table 2.2: Frequencies of non-metric traits in Neandertal mandibular dentition (Percentages of presence/n). Data adapted from Bailey (2006a).	21
Table 3.1: Krapina Neandertal sample used in the present study.	26
Table 3.2: Traits used in this study. Descriptions were adapted from Turner et al. (1991). I: incisor; C: Canine; P: Premolar; M: Molar.....	32
Table 4.1: Non-metric traits scored on the permanent dentition and their occurrence frequencies with the sample sizes and their range of variation observed in the sample.	37
Table 4.2: Non-metric traits scored on the primary dentition and their occurrence frequencies with the sample sizes and their range of variation observed in the sample.	38
Table 4.3: Comparison of trait expressions between deciduous and permanent tooth pairs. Scores in bold indicate discordance.....	41
Table 4.4: Somers' D results for the eleven tooth classes. * indicates significant associations...	43

LIST OF FIGURES

- Figure 1.1: KDP 4's occlusal view. Arrows point to (1) anterior fovea, (2) mid-trigonid crest, (3) cusp 5, and (4) labial convexity. Photo credit: Croatian National Museum..... 4
- Figure 1.2: KDP 5's occlusal view. Arrows point to (1) tuberculum dentale and (2) shoveling. Photo credit: Croatian National Museum 5
- Figure 1.3: The occlusal view of KDP 2's maxillary dentition. Arrows point to (1) deciduous first molar, (2) deciduous second molar, (3) permanent first molar. Black arrows number 4 and 5 point to the Carabelli's trait on dm2 and M1. Photo credit: Croatian National Museum..... 6
- Figure 1.4: K 100 occlusal view. Arrows point to (1) protocone, (2) paracone, (3) metacone, (4) hypocone, and (5) parastyle. Photo credit: Croatian National Museum..... 7
- Figure 3.1: An example of an ASUDAS plaque showing the level of expression of shoveling in the upper lateral incisors. 30

CHAPTER 1 INTRODUCTION

1.1 Statement of the problem

As an intensely mineralized tissue in human body, teeth preserve better than skeletal elements in geological contexts and therefore provide an important source of information about human evolution and biology (Aguirre et al., 2006; Bailey, 2006; Bailey and Hublin, 2006). One aspect of mammalian dentition, dental morphological non-metric variation, has long been studied in the major human populations, fossil hominins and non-human primates (Bailey, 2008; Hanihara, 2008; Sciullu, 1998). Dental non-metric traits are defined as;

“... phenotypic forms of the enamel that are inherited and controlled in their location, growth and orientation; they result from indirect processes of mineral secretion mediated by proteins the dental morphogenesis, and they are expressed and regulated by the human genome of each individual” (Aguirre et al., 2006:39).

Dental non-metric traits have been used for many years as population markers to identify and differentiate between the modern human populations and fossil hominins (Hanihara, 1961, 2008, Hrdlička, 1920). Previous studies have shown that dental non-metric trait frequencies vary depending on the geographic area of the human populations because dental morphology is assumed to be genetically determined (Haneji et al., 2007; Hsu et al., 1999; Lukacs and Walimbe, 1984). That is to say, genetically related individuals from the same population are expected to show similar dental morphology. For example, the marked expression of shoveling in incisors is observed approximately in 82% of Native Americans, 58% of Japanese, and 2% of Europeans which are geographically and genetically distant modern human populations. This trait is very rare among people with African descent as is the case with Europeans.

Although only few genes (such as EDA and HOXB2) that affect dental phenotype were identified to this day through “whole-genome linkage analysis or association analysis of putative

candidate loci”, hundreds of genes are known to play role in cellular communication during tooth formation and development (Hughes and Townsend, 2013:59). Therefore, the initiation and the development of dental non-metric traits are considered to be determined by genes, and consequently, it is assumed that the primary and permanent dental sets should reflect similar morphologies not only on individual level but also population level (Bader, 1965; Garn et al., 1966b; Scott and Turner, 1997). Based on this assumption, modern human studies on baby and adult teeth demonstrated that the two dentitions indeed show morphological similarities within an individual (Aguirre et al., 2006; Bailey et al., 2014). Furthermore, a few studies confirms the morphological concordance for several traits especially between the deciduous second molar (dm2) and the permanent first molar (M1) of an individual (Kieser, 1984; Saunders and Mayhall, 1982). In addition, twin and family studies also support the idea that genes are the major factor determining the dental morphology of not only within individual but also among genetically related individuals (Scott and Turner, 1997). However, some degree of variation and discordances between monozygotic twins has been reported in the literature indicating that genes are not the only factors influencing dental morphology (Hughes and Townsend, 2013; Scott and Turner, 1997; Townsend et al., 2005). Those discordances were attributed to the external factors such as the environment influencing twins differentially (Edgar and Lease, 2007; Hughes and Townsend, 2013).

If and how the morphology of the permanent dentition corresponds with the deciduous in fossil hominins is a poorly investigated question in dental anthropology. Although the literature clearly demonstrated that tooth growth and development is under strong hereditary control (Scott and Turner, 1997), and therefore, permanent and deciduous dentitions within an individual are

expected to exhibit similar morphology, it was never tested on fossil hominins. This may be primarily because of the limited sample size available for research.

Krapina, Croatia Neandertal sample used in this study provides an adult and subadult sample size which allows for comparisons between primary and permanent dentitions. The reason for using Neandertals as a sample for the current study instead of a modern human sample is because of the almost ubiquitous and consistent dental pattern that Neandertals possess. Their dental morphology is less variable, and therefore, provides a more reliable pattern to study than the modern human dentition. That is to say, Neandertal teeth are characteristic with some dental traits being in high frequencies (e.g. shoveling in incisors and Carabelli's cusp in molars) (refer to Figures 1.1 through 1.4 for illustration of the mentioned traits), and some traits in low frequencies (e.g. double shoveling in incisors and distal trigonid crest in molars) (Bailey, 2006). In addition, Krapina Neandertals were chosen for the current study because of the assumptions that they represent a group of distant relatives along multiple generations (Smith, 1976; Trinkaus and Shipman, 1993). Based on the tight time period to which Krapina individuals belong (~40k), it can be assumed that they are more closely genetically related to each other and possess a less variable morphology than they are to other Neandertals such as La Chapelle-aux-Saints Neandertal from France. Therefore, Krapina Neandertals represent an interesting test-case for an examination of the correspondence between permanent and deciduous non-metrics in closely related ancient human group.

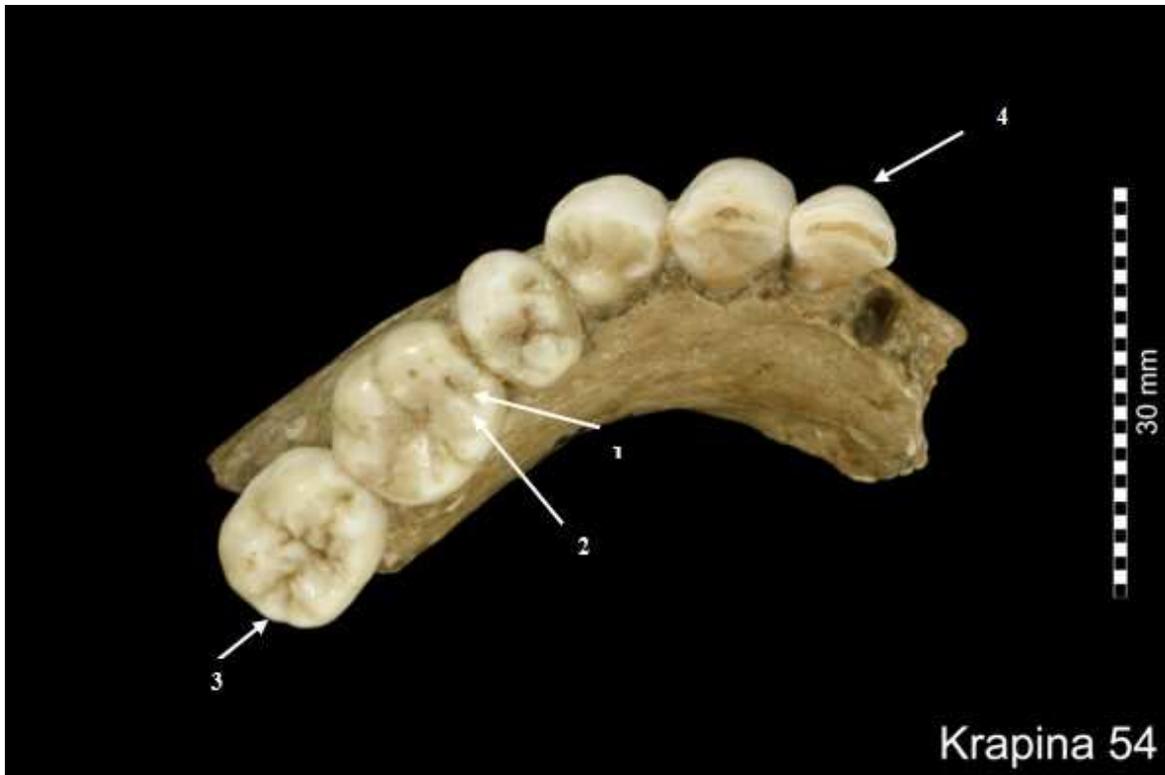


Figure 1.1: KDP 4's occlusal view. Arrows point to (1) anterior fovea, (2) mid-trigonid crest, (3) cusp 5, and (4) labial convexity. Photo credit: Croatian National Museum

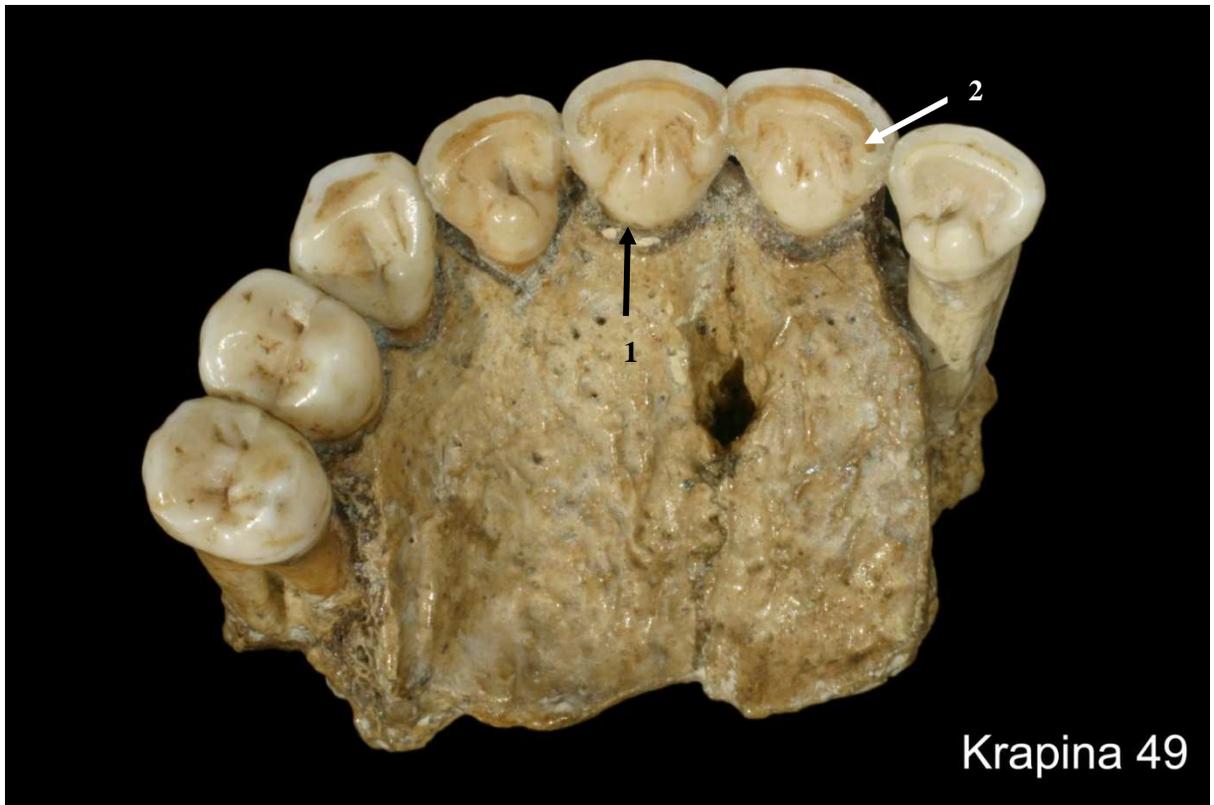


Figure 1.2: KDP 5's occlusal view. Arrows point to (1) tuberculum dentale and (2) shoveling. Photo credit: Croatian National Museum

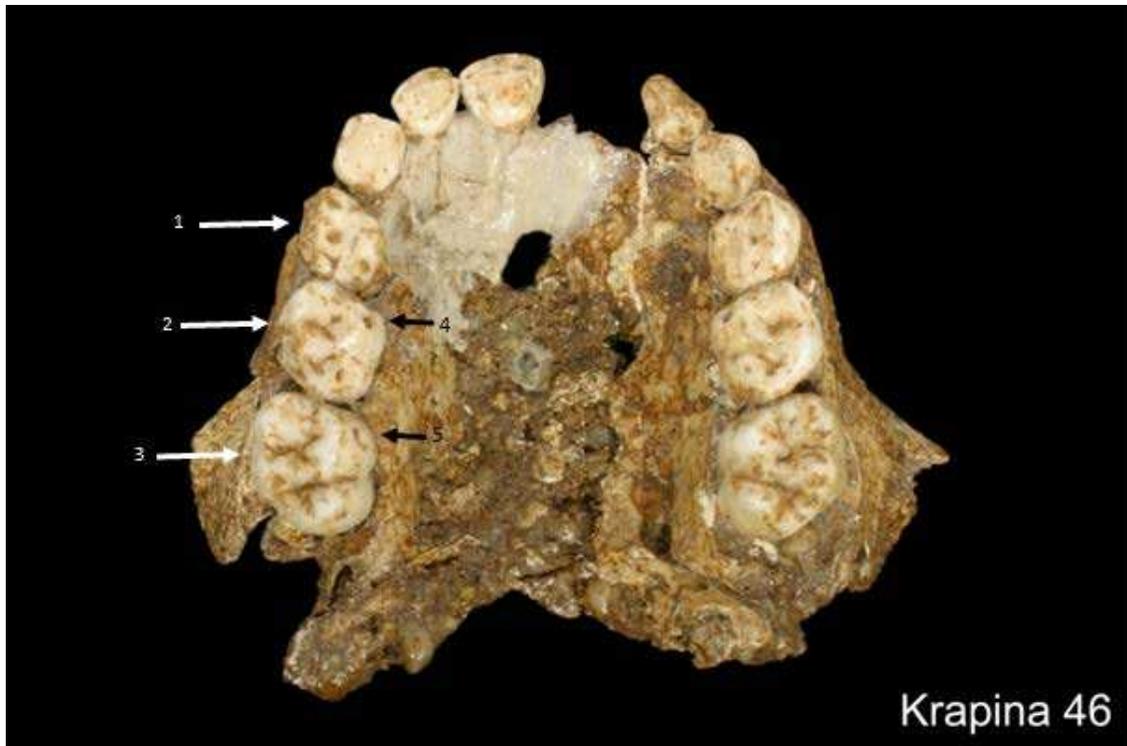


Figure 1.3: The occlusal view of KDP 2's maxillary dentition. Arrows point to (1) deciduous first molar, (2) deciduous second molar, (3) permanent first molar. Black arrows number 4 and 5 point to the Carabelli's trait on dm2 and M1. Photo credit: Croatian National Museum

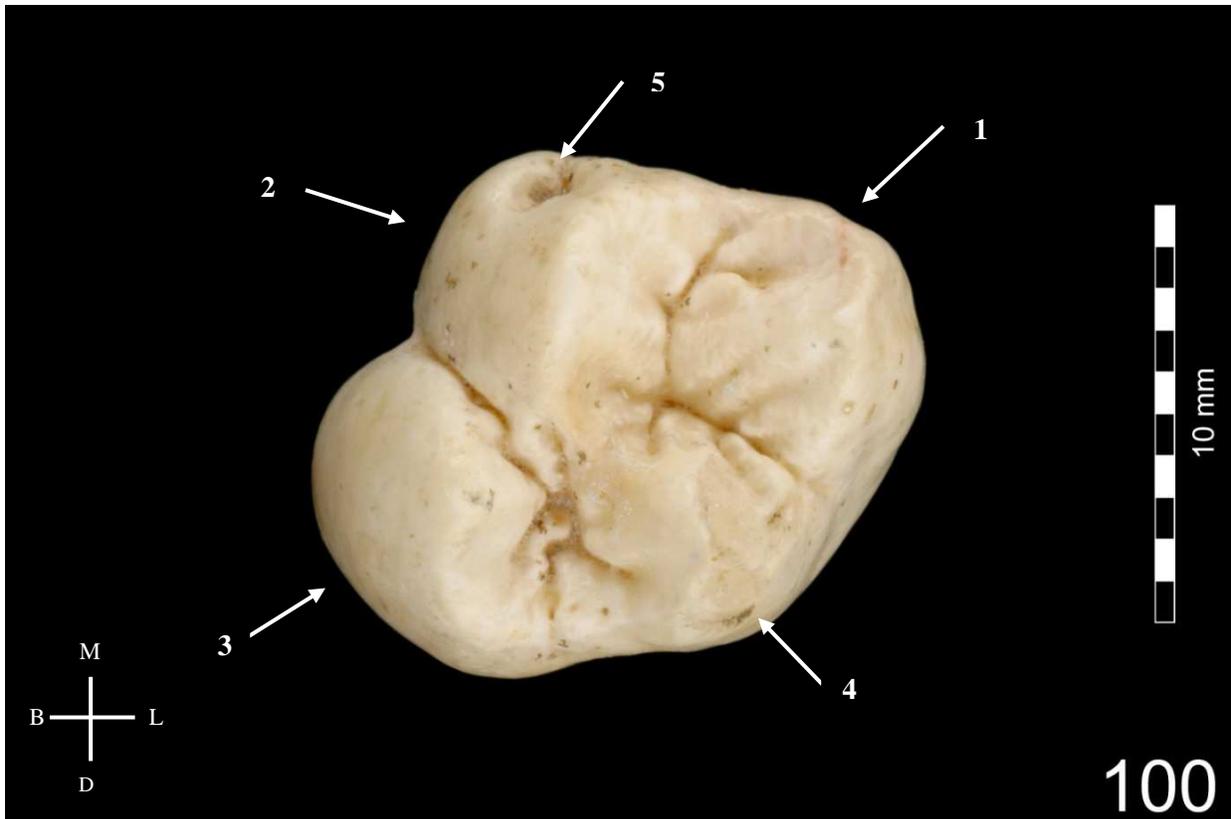


Figure 1.4: K 100 occlusal view. Arrows point to (1) protocone, (2) paracone, (3) metacone, (4) hypocone, and (5) parastyle. Photo credit: Croatian National Museum

Most of the Neandertal studies focuses on the permanent dentition (Bailey, 2002a, 2006a), and the morphological variation of the primary dentition has not been studied extensively. The study of deciduous dentition is important because deciduous teeth are thought to reflect an individual's genotype better than the permanent teeth because the latter is believed to be more open to environmental alterations (Bailey et al., 2014; Liversidge and Molleson, 1999). Given the gap in the literature, studies on the morphological comparisons between the Neandertal primary and permanent dentitions are needed.

1.2 Purpose of research

The purpose of this study is to provide a morphological comparison of the deciduous and permanent teeth of Krapina Neandertals and examine the correspondence between the two

dentitions based on their dental non-metric trait variation. Although no genetic data or method is involved to this investigation, the morphological comparison alone is a close proxy for how the development of the two dentitions is linked in a genetically related population. The implicit purpose is to test how the underlying genotype of an individual influences the dental morphology of both primary and permanent dentitions. Therefore, this study is concerned with understanding the underpinnings of dental crown morphological development.

1.3 Research Questions and the Hypothesis to be addressed

The following research questions were addressed in this study: What are the morphological similarities and differences between the deciduous and permanent teeth of Krapina Neandertals? Does the deciduous non-metric variation correspond to the adult non-metric variation? In other words, do the Neandertal primary and permanent dentitions show the same frequency and level of variation of those non-metric traits that characterize most Neandertals?

Based on the assumptions that Krapina Neandertals are biologically related individuals (Smith, 1976; Trinkaus and Shipman, 1993), and if we consider the genetic inheritance to be the case for Neandertal dentition, a testable hypothesis is that there is a correspondence between primary and permanent non-metric frequencies and level of variation. And, the null hypothesis is that there is not a correspondence or association between the two dentitions in the incidence and the level of expression of non-metric traits.

1.4 Scope and limitations

The morphological variation and associations only within the Krapina Neandertals will be examined in this study. Therefore, it is not the scope of this study to determine the phylogenetic or taxonomic relationships of this population with other fossil hominins. Although the sample

size at Krapina is large overall, sample size for the current research will be limited to the individuals with mixed dentition. In addition, to prevent any inflated sample sizes, only one side of the dentition was used. Therefore, the sample size decreases and introduces problems for the statistical analysis. The problems with the sample were discussed in more detail in subsection 3.1.3 of Chapter 3.

1.5 Organization of the study

Chapter 2 provides a comprehensive literature review by summarizing the genetic grounds of the dental morphological variation, the modern human studies which compare the primary and permanent dentitions, and the previous descriptive and comparative studies on Neandertal dental morphology.

Chapter 3 introduces the materials and methods used in this study. The Krapina Neandertal sample and the ASUDAS dental scoring method was presented in this chapter. Also, the problems with the sample (in subsection 3.1.3) and the method (in subsection 3.2.1.1) were discussed. Subsequently, the dental non-metric trait terminology descriptions were provided. Lastly, the Somers' D statistical method that measures the association between two ordinal variables was presented.

Chapter 4 presents the results of this study. It begins with summarizing the descriptive statistics of observations on Krapina sample. Observed frequencies of non-metric traits were compared between deciduous and permanent teeth. Also, statistical results were summarized in this chapter.

Chapter 5 presents the summary of the study, discussion of the statistical results along with the concluding remarks and the future directions.

CHAPTER 2 LITERATURE REVIEW

2.1 Introduction

The study of dental morphological variation is a central theme in paleoanthropology, and biological anthropology more broadly. For example, global patterns of dental variation among geographical regions help to elucidate the biological relationships among human populations (Saunders and Mayhall, 1982; Zubov, 1992b). The dental morphology of not only modern humans but also fossil hominins has been studied extensively (Ahern, 2006; Bailey, 2002a, b, 2006a; Hanihara, 2008; Hsu et al., 1999; Stringer et al., 1997). Although the literature covers many aspects of the hominin dentition such as the metric variation (e.g. Brace, 1979), root morphology (e.g. Kupczik and Hublin, 2010) and dental wear patterns (e.g. Krueger and Ungar, 2012), this literature review will focus particularly on (1) the genetic explanations for the dental morphological variation, (2) the modern human studies which cover the morphological relationships between permanent and primary dentitions, and (3) the descriptive and comparative studies concerning Neandertal dental crown morphology and the non-metric trait frequencies.

2.2 Genetics of Dental Morphological Variation

Human dentition is a complex system starting its development *in utero*, and continues developing until the early years of adulthood (Scott and Irish, 2013). It is mostly agreed that the initiation and development of the dental traits are strictly genetically controlled during odontogenesis (Bader, 1965; Garn et al., 1966b; Scott and Turner, 1997; Thesleff and Nieminen, 1996). Although which particular genes operate in the presence or absence of a dental trait is still mostly unknown, the twin and family studies indicate that genes are the major factor in tooth growth and development (Scott and Turner, 1997; Townsend et al., 2009). However, there is also

evidence that tooth size and shape can be influenced by not only genes but also the environment of an individual such as the diet (Moller, 1967; Riga et al., 2013).

In the early 1900s, the inheritance pattern of most of the dental traits was thought to have simple dominant or recessive modes of inheritance (Scott and Turner, 1997). However, this kind of inheritance was only explaining the presence or absence of a dental trait in the offspring, and was not accounting for the varying level of expression. Therefore, researchers started to think that there must have been other factors influencing dental phenotype. It is now mostly agreed that the mode of inheritance is polygenic, which indicates that dental trait development is controlled by more than one gene at many loci with the additive effect of each locus (Scott and Turner, 1997). Recently, new candidate genes are identified to be associated with several dental phenotypes through the genome-wide association studies (GWAS) (Scott and Irish, 2013). However, they are still under investigation.

Kimura et al. (2009) conducted a study in order to clarify whether genetic polymorphism accounts for the geographic distribution of tooth shoveling. They examined a specific allele of ectodysplasin A receptor (EDAR) gene which is also known for Asian hair thickness, and examined the association between crown diameters and shoveling grades of the two Japanese populations. They found that this particular allele of EDAR gene was strongly associated with shoveling expression, and it was responsible for 18.9% of the total variance observed in the two populations.

It is the dental anthropologists' assumption that phenotype reflects genotype. This assumption was supported by the global scale studies which use both genetic and morphological data to estimate biodistance between major human populations such as Sinodonts of North Asia and Sundadonts of Southeast Asia (Scott and Turner, 1997). It has been shown that either data

(i.e. genetic or morphological) is useful to differentiate and account for the dental morphological variation observed between regions (Hubbard et al., 2015). To test whether or not dental morphological data corresponds with the nuclear DNA data at regional scale, Hubbard et al. (2015) compared four ethnic populations in Kenya. This study is different from the earlier studies in that it uses paired genetic and morphological data of the same individuals and utilizes a standardized dental scoring method (i.e. Arizona State University Dental Anthropology System which is the same standard used in the current study). They used a living sample of which population histories are known rather than an archaeological sample, so that predictions were possible regarding their biodistance estimates with each other. The study showed that both genetic and morphological data is correlated and efficient in identifying the already known ethnic differences between the four groups. The results in the study can be interpreted as dental phenotypes can be used as another line of evidence to infer an individual's or a population's genotype.

To what extent dental trait variation in a population (not in an individual) is due to genetics and/or environmental determinants were established by heritability studies (Mizoguchi, 1978; Scott and Turner, 1997). Heritability is a population concept, and it does not imply anything about how a dental trait is inherited between generations (Scott and Turner, 1997). For example, the heritability value for shoveling was calculated as approximately 75 percent (Scott and Turner, 1997). This value indicates that the occurrence frequency variation for shoveling in a population is due to genetic factors in 75 percent and due to environmental effects in 25 percent. A value of 75 percent indicates a strong genetic contribution to the observed population variation. However, again, it does not imply whether or not the trait expression is controlled by genes. As Scott and Turner (1997:154) exemplify:

“Say, for example, the development of trait X is controlled by genes at three loci, A, B, and C. Assume further that all individuals in a population are homozygous at these three loci (i.e. AAbbCC). In such a population, any variation in trait expression is entirely environmental in origin – genetic variance and heritability both equal zero. A heritability of zero does not vitiate the fact that the development of the trait is controlled by genes – it is only the within group variation in trait expression that is determined by environmental factors”.

Scott and Turner (1997) further argue that the phenotypic traits with low heritabilities are the most essential for survival of a population, and the traits with high heritabilities are the least essential. If a trait’s heritability is low, this means that the trait is less subject to genetic change. For instance, the timing of odontogenesis has a prime importance in a population’s survival, and the genes that act during odontogenesis are strictly conserved in nature meaning that they have not the luxury to be subject to change. If they change, the population would be open to some anomalies such as no tooth formation. However, the heritability values for dental crown features range between 0.40-0.80 (Mizoguchi, 1978) indicating a moderate to strong genetic contribution which makes them subject to change over time, and therefore, least important features for survival.

It was argued that if the same genotype is responsible for the development of the deciduous and permanent dentitions within an individual, the two dentitions would be expected to exhibit similar trait expressions (Scott and Turner, 1997). However, it is highly common that the two dentitions may show morphological variation and discordance of traits within individuals or populations. As a matter of fact, the dentition of monozygotic twins who share all of their genes can show discordance in their trait expression (Scott and Irish, 2013; Scott and Turner, 1997; Townsend et al., 2005). At this point, the morphological differences between deciduous and permanent dentitions of an individual or between monozygotic twins are believed to be the result of environmental and epigenetic alterations to a major gene responsible for the development of a particular trait (Edgar and Lease, 2007; Scott and Irish, 2013).

It is assumed that the genetic make-up of the permanent teeth which develops postnatally is more open to the alterations (Edgar and Lease, 2007). As a result of these alterations, some traits might be absent in permanent dentition but present in deciduous. Townsend and Brown (1981b) looked at the Carabelli's trait expression in the two dentitions of the Australian Aboriginal population. One of their results showed that in 80% of their sample, the trait was either present in both deciduous and permanent teeth or it was absent in both of the dentitions. The rest of the individuals showed discordance in their trait expressions meaning that only one of the dentitions exhibited Carabelli's trait. They pointed out that 90% of the time the trait was present on deciduous teeth and absent on permanents. This result was consistent with the assumption that deciduous teeth reflect the genotype better than the later developing permanents (Liversidge and Molleson, 1999).

Based on the literature reviewed above, several traits seem to be shared between the primary and permanent dentitions although some traits may show discordance. Although not all of the non-metric traits have been studied to this day, in the light of genetic information, Krapina Neandertals would be expected to show the same morphological similarity or dissimilarity for some certain traits between the two dentitions as modern human dentition shows.

2.3 Correspondence Between Deciduous and Permanent Dentitions

2.3.1 Modern Human Studies

One of the many reasons why the study of deciduous dentition is of particular importance is that for some sites the only remains can be the deciduous teeth (Bailey et al., 2014). It is critically important to identify the remains correctly and attribute them to a group (Bailey, 2006). In addition, it was asserted that deciduous teeth are valuable in that they are "morphologically conservative" (Bailey et al., 2014: 1; Smith 1978, Smith et al., 1987; Smith and Tillier, 1989).

What this means is that because their development is initiated earlier *in utero*, and the crowns develop faster than those of the permanent teeth, it is assumed that they depict individual's genotype better than the permanent dentition. And, in addition, because of this accelerated development, deciduous teeth are less impacted by environmental disturbance (Bailey et al., 2014; Liversidge and Molleson, 1999).

Studies on primary teeth predominantly focus on modern human dental metrics excluding morphology (Bailey et al., 2014). Few existing deciduous non-metric studies focus on assessing inter- and intra-group affinities and variation (Aguirre et al., 2006; Delgado-Burbano, 2008; Kitagawa et al., 1995; Lukacs and Walimbe, 1984; Paul and Stojanowski, 2015); within-individual mixed dentition non-metric trait variations (Edgar and Lease, 2007; Kieser, 1984; Saunders and Mayhall, 1982; Smith et al. 1987); ancestral determination (Lease, 2003; Lease and Sciulli, 2005); taxonomic differences between hominins (Bailey et al., 2014); and dental growth and development (Baile et al., 2009; Machiarelli et al., 2006; Smith et al., 2015). Studies which cover the morphological relationship between deciduous and permanent dentitions are summarized in this subsection.

Earlier studies on modern humans showed that dm2 and M1 in a mixed dentition show morphological similarities for several traits (Aguirre et al., 2006; Edgar and Lease, 2007; Kieser, 1984; Saunders and Mayhall, 1982). For example, Aguirre et al. (2006) conducted a study on 100 children with mixed dentition from Cali, Colombia. They gathered the frequencies of five non-metric traits (Carabelli's trait, protostylid, groove pattern, and cusps 6 and 7) on dm2 and M1 of the same individual. According to the study, among the five traits examined, Carabelli's trait and protostylid show a significant correspondence between the two teeth suggesting that their development is predominantly genetically controlled. They found no meaningful

association regarding the groove pattern of the two dentitions, and the frequencies for cusp 6 and 7 were low. Also, their data showed that the expressions of the five traits are not sexually dimorphic (i.e. there is no sex differences), and there is bilateral symmetry (i.e. there is no difference between the right and left sides of the dentition). Symmetrical dental morphology and the lack of sexual dimorphism are particularly useful for fossil studies because of the limited number of fossil findings. In the absence of the one side of a tooth class, the presence of bilateral symmetry allows for the consideration of the both right and left sides of the dentition. Likewise, the lack of sexual dimorphism allows for ignoring the sexual identification of the individuals when the sample size is limited.

Similarly, Kieser (1984)'s study on children of European descent showed a high degree of morphological similarity regarding the presence of Carabelli trait in permanent and deciduous teeth within the same individual. It was indicated that high frequencies of the trait and the similar degree of expression suggest that development of the Carabelli trait is controlled by genetic mechanisms. As is the case with Aquirre et al. (2006), Kieser (1984) also reported a lack of sexual dimorphism in his sample. However, there are some studies that reported sexual dimorphism in the occurrence of Carabelli trait (e.g. Goose and Lee, 1971).

Saunders and Mayhall (1982) examined the dentition of American white children. They scored Carabelli's trait, cusps 6 and 7, protostylid in molars, and shoveling in incisors. Their results showed that maxillary central incisors demonstrate a concordance between primary and permanent teeth in terms of shoveling. Maxillary lateral incisors showed less association with regard to trait presence due to their variable nature. Their data also showed a concordance for Carabelli trait, cusps 6 and 7, and protostylid between dm2 and all of the molars (i.e. M1, M2, and M3). In addition, they found that the frequencies of Carabelli's trait decrease starting from

the deciduous second molar to the permanent third molar. They argue that their results agree with Butler (1939)'s field theory which provides a good approximation of causal explanation of the directionality of variation within the tooth classes. The field theory divides permanent dentition into three fields: incisor, canine and molar. According to this model, there is a gradient of variation starting from the most mesial to the most distal tooth in each field, and each field has a least variable tooth which is called "the key tooth" (Edgar and Lease, 2007). This model emphasizes a system in which teeth are dependent to each other in lieu of individual organs (Townsend et al., 2009). It is postulated that each field has its own "field-inducing substance" (Saunders and Mayhall, 1982:48), and as the cells that initiate tooth growth get older, morphological differences occur between the molar teeth, including deciduous molars. In this context, Saunders and Mayhall (1982) believe that deciduous second molars belong to the molar field, and that permanent molars are the continuation of the deciduous molars in terms of their development and morphology. Smith et al. (1987) points out that the directionality of the trait frequency is specified according to the trait. In other words, there are certain traits that increase in frequency mesiodistally whereas the frequency decreases for other traits in the same direction. They observed that hypocone, Carabelli's cusp, Y pattern, fifth and seventh cusps were higher in frequency in dm2 than M1 while marginal ridge cusps (metaconules) and occlusal tubercles were higher in M1 than dm2 (Smith et al., 1987). According to them, earlier developing traits are more frequently observed on dm2 than M1, and later developing traits are more frequently observed on M1 than dm2. This pattern supports the assumption that the ontogenetic timing of the dental trait initiation *in utero* affects the frequency and direction of dental traits.

2.4 Neandertal Dental Morphology

Neandertal dentition has long been the focus of attention since the discovery of the first Neandertal individual from Neander Valley, Germany in the 19th century (Bailey, 2006). From the 19th century to the present, an abundance of fossils have been added to the Neandertal collection from the different regions of the world. Among them, Krapina Neandertal site in Croatia yielded one of the largest fossil collections from a single site. During the excavations (1899-1905) at Krapina, Gorjanovic-Kramberger, discoverer of the site, recovered dozens of Neandertal specimens including young individual fossils (Bailey, 2006; Molnar and Molnar, 1985; Rougier et al., 2006; Trinkaus and Shipman, 1993; Wolpoff, 1979). Since the recovery, a tremendous amount of skeletal and dental remains allowed anthropologists to study them in detail, and the detailed descriptions of the Krapina Neandertals were reported by several researchers such as Smith (1976) and Wolpoff (1979).

It was Gorjanović-Kramberger first to recognize the unique morphology of the Krapina dental remains (Bailey, 2006; Gorjanović-Kramberger, 1906). He reported several dental characteristics including shovel-shaped incisors (i.e. a unique Neandertal shoveling not being identical to Asian shoveling), lingual tubercles, and taurodont molars. Although Neandertals in general possess a human-like dentition, they are also well known for their consistent dental pattern with some morphological traits being in high frequencies (e.g. shoveling in incisors and Carabelli's cusp in molars), and some traits in low frequencies (e.g. double shoveling in incisors and distal trigonid crest in molars) (Bailey, 2006). Bailey (2002a, 2006, 2006a) pointed out that Neandertal dentition also exhibits a unique combination of some traits, which is very uncommon among modern humans, such as the incidence of incisor shovel shaping, lingual tubercles and labial convexity on the same individual. In addition to the high and low trait frequencies, they are

characteristic with the marked expression of some of the traits (Bailey, 2000a). For example, Bailey (2000a) observed that Neandertal incisors exhibit shovel shaping in high frequencies, and it is markedly expressed (refer to the Figure 3.1 through 3.5 for illustrations of mentioned traits). In the later studies, new dental non-metric traits were recognized in the Neandertals (e.g. mid-trigonid crest on mandibular molars) (Bailey, 2006a; Zubov, 1992a), and their frequencies were established (Bailey, 2002a, b, 2006a, Bailey et al., 2011).

Despite the abundance of the studies regarding Krapina Neandertals, most attention was given to the permanent dentition, and deciduous dentition took comparatively less notice (Bailey et al., 2014). The primary dentition of both modern humans and Neandertals in general is recently getting more attention among anthropologists (Aguirre et al., 2006; Bailey et al., 2014; Edgar and Lease, 2007; Kieser, 1984; Saunders and Mayhall, 1982; Smith et al., 1987; Thomas et al., 1986). However, regarding the correspondence between Neandertal deciduous and permanent non-metric traits, almost no data can be found in the literature.

Following sections 2.4.1, 2.4.2 and 2.4.3 summarizes Neandertal dental morphology and Neandertal dental trait frequencies in more detail.

2.4.1 Characteristics of Neandertal Teeth and Non-metric Trait Frequencies

2.4.1.1 Anterior Dentition: Incisors and Canines

Neandertal anterior teeth are characterized by their marked expression of shoveling, lingual tubercles and labial convexity (Bailey, 2002a, 2002b, 2006a; Bailey and Hublin, 2006; Rosas et al., 2006; Wolpoff, 1979). Wolpoff (1979) states that development of the strong lingual tubercles in Krapina Neandertals contributes to the size increase of anterior dentition, and results in enlarged incisors and canines. The overall morphology of the upper incisors and canines is more complex, and exhibit higher marked trait expression than the lower incisors and canines.

Therefore, lower anterior dentition is not usually preferred for assessing taxonomy or biological affinities among Neandertals (Bailey, 2006a).

Bailey (2006a) reported dental trait frequencies of both European and non-European Neandertals (n=347). Frequencies in her study were adapted and tabularized in Tables 2.1 and 2.2. In her sample, 100% of both lateral and central incisors exhibited at least grade 2 shoveling. The frequency of marked expression of this trait is typically high in Neandertals. 54% of the upper central incisors (I¹) and 81% of the upper lateral incisors (I²) showed grade 4 or greater marginal ridge development. Double shoveling in both incisors and canines is very rare among Neandertals. If present, it is weakly expressed. She also reported that the presence of lingual tubercles and labial convexity is also in high frequencies being 100% and 96%, respectively. Canines and incisors are quite similar in their morphology. In the study sample (Bailey, 2006a), shovel shape was present in 96% of the canines, and 42% of them showed grade 3 and higher expression. Similar to incisors, the presence of lingual tubercles in canines are high in frequencies. 84% of the sample exhibited at least grade 2 and 32% of them showed marked expression of this trait (grade 4 and above). Also, the canine mesial ridge (Bushman canine) (43%) and distal accessory ridge (67%) are common in Bailey (2006a)'s sample.

Table 2.1: Frequencies of non-metric traits in Neandertal maxillary dentition (Percentages of presence/n). Data adapted from Bailey (2006a).

Traits	I¹	I²	C¹	P³	P⁴	M¹	M²	M³
Shoveling	91.7/24	100/31	95.8/24					
Double shoveling	4.3/23	3.7/27	0/24					
Lingual tubercles	100/24	96/25	84/25					
Labial convexity	95.8/24							
Canine mesial ridge			42.9/21					
Distal acc. ridge			66.7/15					
M/D acc. ridges				63.2/19	77.8/18			
Accessory cusps				66.7/21	47.6/21			
Cusp 5						63.6/22	68.2/22	35.3/17
Carabelli's trait						68/25	50/22	14.3/14

Hypocone reduction	0/39	6.1/33	68.4/19
Mesial accessory cusps	40/10	100/10	70/10

Table 2.2: Frequencies of non-metric traits in Neandertal mandibular dentition (Percentages of presence/n). Data adapted from Bailey (2006a).

Traits	I ₁	I ₂	C ₁	P ₃	P ₄	M ₁	M ₂	M ₃
Distal accessory ridge			84.6/13	90/20	87.5/16			
Mesial accessory ridge				23.5/17	12.5/16			
Transverse crest				96.7/30	93.5/31			
Asymmetry				94.4/18	93.5/31			
Lingual cusp number				20.6/34				
Groove pattern (Y)						97.3/37	75/36	41.2/17
Mid-trigonid crest						93.5/31	96.2/26	93.3/15
Cusp 6						36.4/22	50/22	50/10
Cusp 7						36.1/36	20/35	40/15
Anterior fovea						88.6/35	88.5/26	92.9/14
Cusp number (4)						2/49	0/39	0/23

2.4.1.2 Posterior Dentition: Molars

Premolars were excluded from this review simply because it is the purpose of this study to compare the deciduous and permanent dentitions, and premolars are not present in the primary dental set. Therefore, there are not analogue premolars in primary teeth to compare with adult premolars.

Neandertal upper molars exhibit well-developed protocone, paracone, metacone and hypocone except for the third molars. Bailey (2006a) reports that hypocone is commonly reduced in M³s (68%). However, reduced hypocone is very rare for M¹s (0%) and M²s (6%). Cusp 5 (hypoconule) and Carabelli's trait are more frequently present in M¹s (64% and 68%, respectively) and M²s (68% and 50%) than it is in M³s (35% and 14%). 100% of Bailey

(2006a)'s M^2 sample exhibited mesial accessory cusps which are less frequent in M^1 s (40%) and M^3 s (70%).

For the lower molars, the most frequently present traits observed by Bailey (2006a) was mid-trigonid crest (M_1 : 94%; M_2 : 96%; M_3 : 93%), anterior fovea (M_1 : 89%; M_2 : 89%; M_3 : 93%), and the presence of at least five cusps (M_1 : 98%; M_2 : 100%; M_3 : 100%). Bailey et al. (2011) indicate that Neandertals are unique and divergent from *H. sapiens*, *A. africanus* and *Pan* species in terms of their middle trigonid crest origins. In Neandertals, trigonid crest starts forming from the “mesial” segment of the metaconid, and ends in the “mesial” segment of the protoconid. In other taxa, a “true” form of middle trigonid crest occurs starting from the “middle” segment of the metaconid, and ending in the “medial” segment of protoconid (Bailey et al., 2011). In Neandertals, it is characteristic with their undisturbed continuity, building a bridge between metaconid and protoconid. In modern humans, when occurs, this bridge is disrupted by the sagittal sulcus (Bailey, 2002a).

Y groove pattern is common for M_1 (97%) and M_2 s (75%). However, M_3 s exhibit X pattern (59%) more than Y pattern. Cusps 6 and 7 are not very commonly present (M_1 : 36% and 36%; M_2 : 50% and 20%; M_3 : 50% and 40%, respectively). The deflecting wrinkle and distal trigonid ridge are either absent or in very low frequencies if present (Bailey, 2006a).

2.4.2 Combination of Traits

Bailey (2002a, 2006, 2006a) points out that what makes Neandertals unique and distinctive is that they not only possess some traits in high frequencies, but they also exhibit a combination of these traits. Bailey (2006a)'s study showed that 100% of the Neandertal sample exhibits at least grade 2 shovel shaping in both lateral and central incisors, and the trait is almost always accompanied with lingual tubercles and labial convexity in Neandertals. She reported that

the frequency of occurrence of all the three traits within the same individual is 96% in upper central incisors.

In a study, Bailey (2002a) looked at Neandertal, modern human, *Homo heidelbergensis* and *Homo erectus* specimens to understand the uniqueness of the Neandertal dental pattern in the sense of phylogenetics. In terms of premolars, she found that Neandertal mandibular P₄'s not only show a high frequency of some traits such as “multiple lingual cusps (93%), transverse crest (88%), and asymmetrical lingual crown contour (96%)” (Bailey, 2002a:151), but they also show a combination of the above mentioned traits. In modern humans, P₄'s are simpler and frequencies of the above mentioned traits are lower. Also, combination of these traits is highly uncommon for modern humans with being only 2.4%.

2.4.3 Neandertal Autopomorphies

The differences between the modern human and Neandertal dentition raise the question of whether or not Neandertal morphology is a primitive one. The debate has been mostly around whether or not Neandertals are a distinct species from *Homo sapiens*. Some argued that Neandertals are not very different from modern humans regarding their dentition. That is to say, every trait (except for the large tooth size and taurodontism) observed in Neandertals can be seen in modern humans as well (Smith, 1976). On the other hand, others believed that Neandertal teeth and their overall morphology is significantly different from modern humans and therefore they cannot be ancestral species to moderns (Boule, 1923 in Bailey, 2002b).

To address this question, Bailey (2002a) compared Neandertal postcanine teeth with *Homo erectus* sample which serves as an outgroup, and found no resemblance between them. Therefore, she concluded that Neandertal dental features are unique and derived (autapomorphic) rather than primitive. This implies that if those unique traits observed in Neandertals are

autapomorphic to them, Neandertals should be designated as a separate species from moderns. If this was the case, one should expect to see those traits in almost all Neandertals and not to see them in modern humans (e.g. Upper Paleolithic people in Europe) (Ahern, 2006). However, Frayer (1992) and Wolpoff et al. (2004) state that Neandertal cranial traits can also be observed in Upper Paleolithic moderns indicating a genetic exchange between the two groups. Therefore, it is plausible to consider Neandertals as the same species with modern humans.

Another study by Bailey (2008) suggests that Neandertals are more divergent from modern humans than modern human groups are divergent from each other based on their non-metric dental variation. In addition, this distance between Neandertals and modern humans is greater than the distance between two *Pan* species and two *Pan* subspecies. Therefore, the conclusion was that Neandertals are taxonomically distinct species (i.e. *Homo neanderthalensis* instead of *Homo sapiens neanderthalensis*) from modern humans.

However, recent genetic studies showed that Neandertals and modern humans exchanged genes meaning that they could interbreed and produce offsprings (Green et al., 2010; Kuhlwilm et al., 2016). Green et al. (2010) indicated that modern humans and Neandertals shared a last common ancestor 800,000 years ago, and they split 270,000-440,000 years ago. They also showed that Neandertals are genetically more close to modern non-Africans than sub-Saharan Africans, which means that the gene flow between Neandertals and moderns occurred after modern humans migrated from Africa. It was found that 1-4% of the modern human genome comes from Neandertals. Reich et al (2010) compared Neandertal, Denisovan, African and Eurasian genome to each other. Denisovans are an extinct archaic hominin group of which genes are found in Melanesians in ~5% and not found in other non-African populations. They found that Neandertals, rather than Denisovans, are more closely related to the ancestors of Eurasians.

This result indicates that intermixture between Neandertals and Eurasians occurred before the intermixture between Neandertals and Denisovans. With the recent genetic evidence briefly summarized here, the idea of Neandertals being subspecies of modern humans is receiving wider acceptance (Wolpoff, 2009) than the idea of them being separate species.

Discrepancies between the genetic evidence and the utility of only non-metric traits in cladistic studies draw into the question of usefulness alpha taxonomy (detecting and classifying a new species). Recently, there is a tendency among scientists to use different lines of evidence such as genetic or ecological data to classify a new species when the population histories are complex as of Neandertals.

CHAPTER 3 MATERIALS AND METHODOLOGY

3.1 Materials

3.1.1 Sample

The Neandertal dental sample used in this study is from Krapina, Croatia, and includes isolated deciduous and permanent teeth as well as the teeth observable from the mandibular and maxillary samples in the jaws. The Krapina collection consists of 281 teeth in total. Only 90 of them are intact in jaws, and the rest are isolated teeth. Wolpoff (1979) managed to associate some of the isolated teeth to a possible maxilla or mandible based on the resemblance in their morphology and wear pattern. Also, he gathered several teeth together and created dental sets according to their morphological similarity. In a subsequent study, Radovčić et al. (1988) assigned the groups of teeth to 35 dental persons which are named as Krapina Dental People (KDP). 26 isolated teeth remained unassigned to a dental person (Stringer et al., 1997). For the purposes of the current study, only the individuals with a mixed dentition were used. As listed in Table 3.1, the sample consists of a total of 62 individual permanent and deciduous teeth which belongs to 12 Krapina Dental Persons.

Table 3.1: Krapina Neandertal sample used in the present study.

Individuals	Teeth
KDP 1	<i>K 11, 14, 15, 17, 21, 24, 98, 174, 182, 187, Max A (left M1, dm1, dm2)</i>
KDP 2	Max B (right I1, I2, i1, i2, M1, dm1, dm2)
KDP 3	K 102, 107, 119, 131, 134, 189, Max C (left M1, M2, dm2)
KDP 4	Max D (left M1, M2)
KDP 5	Max E (right I1, I2, left C)
KDP 8	K 62, 74, 103, 120
KDP 9	<i>K 66, 73, Mand C (R M1)</i>
KDP 10	Mand E (left M1, M2)

KDP 21	K 93, 95, 181, 186, 190
KDP 22	K 12, 16, 23, 68, 94, 100, 183, 185, 188
KDP 27	K 6, 64, 81
KDP 28	K 63, 168

3.1.2 Krapina, Hušnjakovo rock-shelter: stratigraphy, chronology and archeology of the site

Krapina is a town located in the northern Croatia (Yugoslavia) and well known with its Pleistocene site, Hušnjakovo rock-shelter. The site provides the largest Neandertal collection with more than 800 fossil fragments (Smith, 1976). Gorjanović-Kramberger conducted excavations at the site between 1899 and 1905. His research on Krapina Neandertals was published in his monograph (1906) which is considered to be one of the most comprehensive and detailed works in the hominin paleontology. In his day, his excavations were well planned and he kept detailed records of the findings including their stratigraphic locations (Smith, 1976). However, instead of assigning the findings to a particular stratigraphic level, he divided cultural levels into 9 zones based on the faunal remains. The reason for that would be that he thought the site belongs to only one time period, which was Riss-Würm interglacial period, therefore, he may have assumed that stratigraphic terms within that time period was not of prime importance. The faunal remains found in Krapina and the comparisons to the neighboring sites in the area led him to date Krapina to the Riss-Würm (130k-115k). Although his way of keeping records and excavating was criticized, his techniques were ahead of his time, such as using fluorine dating for Krapina remains. The fluorine analysis confirmed that hominin and faunal remains were contemporaneous (Smith, 1976). However, Malez (1967a, b in Smith, 1976)'s analysis of the stratigraphic position of the fauna revealed that the site was occupied in different time periods from the late Riss-Würm to the early Würm II (from 80k to 27k). A more recent work of Rink et

al. (1995) showed that the levels 1-8 date to the last interglacial (average of 130 ± 10 kyr). Most of the Neandertal material was found in levels 3 and 4, but a few Neandertal fossils were found in the other levels as well.

Gorjanović observed that most of the stone tools from Krapina are Mousterian which starts to appear from stratum 5 (Würm I stadial). Also, he discovered that the size of the tools decreases, and the tools become more specialized from the lowest stratum to the highest. Along with the stone tools, bone tools were also discovered at the site.

3.1.3 Problems with the sample

Although Krapina is one of the most informative samples with its large specimen number, it introduces some problems for the current study. In order to test the correspondence between the deciduous and primary dentition non-metric variation, the sample should be examined longitudinally. In other words, it would be ideal to have the non-metric scorings of the both permanent and primary teeth within the same individual over time. Krapina dental sample is impressive with the large number of teeth available for study, but it is not the perfect sample in that it does not provide an adequate sample size for mixed dentition due to the preservation matters. However, the number of individuals with mixed dentition at Krapina ($n=12$) is close to adequate which allows for testing the associations between the two dentitions.

Also, it is not clear whether the Krapina Neandertals are a true biological population. Based on the tight time period (~40k) and the abundance of the findings, Krapina Neandertals were considered to be a biological population, i.e., they are genetically related individuals (Smith, 1976; Trinkaus and Shipman, 1993). Smith (1976) indicates that since the majority of the fossils were recovered from the 3rd and 4th strata, there is a high degree of probability that Krapina fossils represent a group of distant relatives throughout many generations over the

course of 40 thousand years. If they are genetically related, one would expect to see less variation in their morphology. In this context, Smith (1976) draws attention to the fact that morphological variation observed in Krapina cranial bones (except the mandibles and maxillae) cannot be explained with the geographic and temporal factors. He suggests that sexual dimorphism accounts for the Krapina's cranial variation. He compared Krapina cranial size with the total Neandertal (which includes European and Tabun specimens) and Upper Paleolithic samples. Krapina crania showed slightly less sexual dimorphism than the total Neandertals. He found that the level of dimorphism in Krapina is closer to the Upper Paleolithic sample which is thought to be a biological population unlike the total Neandertals.

On the other hand, Wolpoff (1979) posits that Krapina does not look like a biological population based on their age distribution and average age at death. 0-3 age group and individuals older than 27 years old are absent in Krapina. Absence of the former group is not unusual since the mortality rate is higher, and the preservation of the juvenile fossils is expected to be poor. However, the absence of the individuals older than 27 years old cannot be explained with poor preservation. In addition, Wolpoff (1979) argues that the birth rate in Krapina also does not demonstrate a "true" biological population, either. Bocquet-Appel and Arsuaga (1999) attempted to explain the mortality profile in Krapina. According to them, the underrepresentation of particular age groups may be due to "a demographic crisis of a local group for a meta-population in nature, caused by severe environmental fluctuation." (p. 327).

3.2 Methods

3.2.1 Non-metric data collection

The non-metric scorings of both primary and permanent teeth were recorded by my advisor, Dr. Michelle M. Glantz (Colorado State University) in the Croatian National Museum in

Zagreb, utilizing the Arizona State University Dental Anthropology System (ASUDAS) (Turner et al., 1991), and the dental wear was scored based on Smith (1984)'s classification. Teeth with the high level of dental wear were excluded from the study since it makes the scoring procedure impossible for some traits such as the molar groove pattern. However, some worn teeth were scored if the trait was observable. In order to enlarge the sample size, both the right and left sides of the teeth in the same individual (when present) were scored but only the side which exhibits the greatest expression was included in the analysis. Since the aim of this study is to compare deciduous and permanent dentitions, premolars and third molars were not scored and included in the analysis.

A total of 19 dental traits which are either in high or low frequencies in Neandertals were scored with the help of the reference plaques ASUDAS provides (see Figure 3.1 for an example plaque). The list of traits scored in this study and definition for each trait were provided in section 3.2.1.2.



Figure 3.1: An example of an ASUDAS plaque showing the level of expression of shoveling in the upper lateral incisors.

High quality digital photographs of the Krapina dental sample were provided by the Croatian National Museum. Thus, I could also find the opportunity to score the Krapina teeth,

and compare my ASUDAS scorings with Dr. Glantz's scorings. Our scorings showed an inter-observer agreement.

3.2.1.1 ASUDAS

ASUDAS (Arizona State University Dental Anthropology System), designed by Turner et al. (1991), is a commonly used standard for scoring dental discrete traits, and it was originated based on the work of Dahlberg (1956) (Bailey, 2002b). Figure 3.1 presents an example of the ASUDAS plaques. It provides ordinal scales for dental traits starting from the grade of the lowest expression of the trait, and ending with the grade of the highest expression. The system includes more than 36 dental traits with the reference plaques of more than half of the traits. The ASUDAS is particularly useful for dental morphological studies because it enables researchers to quantify the non-metric dental traits and do comparative studies by deriving trait frequencies from both fossil hominins and contemporary humans (Ahern, 2006; Bailey, 2000, 2002a, b, 2006a, 2008; Bailey et al., 2011; Smith, 1987).

Although the ASUDAS was originally designed to determine the dental morphological variation in modern humans, it was also utilized for a number of fossil hominid phylogenetic studies (Bailey, 2000; Irish, 1998; Stringer et al., 1997). Despite the common utilization of the ASUDAS in dental morphological studies, it may introduce some problems when applied for fossil hominids. Bailey (2002a, 2006) asserted that using the ASUDAS standards for Neandertals may cause biased results primarily because several traits that are present and variable in fossil hominids are not included in the ASUDAS. Bailey (2002b) indicates that although several additional traits should be included in the system in order to adequately capture the Neandertal dental variation, the system's efficiency on detecting the biological distance between Neandertals and modern humans was well-attested by the earlier studies (Bailey, 2000; Irish, 1998).

3.2.1.2 Dental non-metric traits and terminology

Table 3.2 presents the dental traits used in this study with their descriptions, tooth classes on which the traits were scored and the presence/absence breakpoints. Although most of the ASUDAS crown traits were scored, only the traits that are uniquely in high frequencies in Neandertals were included in the statistical analysis. Traits that are known to be variable among Neandertals were excluded from the analysis. Presence/absence breakpoints are used following Bailey (2006a) except for the metacone, mid-trigonid crest, parastyle and protostylid. Several dental traits mentioned in Table 3.2 were illustrated in the Figures 1.1 through 1.4 in Chapter 1.

Table 3.2: Traits used in this study. Descriptions were adapted from Turner et al. (1991). I: incisor; C: Canine; P: Premolar; M: Molar

Traits	Trait descriptions	Teeth scored	Breakpoint grades
Shoveling	The presence of lingual marginal ridges	I ¹ , I ² , I ₁ , I ₂ , C ¹	2-7
Double Shoveling	The presence of labial marginal ridges	I ¹ , I ² , I ₁ , I ₂	2-6
Labial Curve	The degree of convexity when viewed from the occlusal aspect	I ¹ , I ²	2-4
Tuberculum Dentale	Projection of the lingual cingulum which varies in the form of ridges or a cusp	I ¹ , I ² , C ¹	2-6
C Mesial Ridge (Bushman)	Mesial ridge is larger than the distal ridge	C ¹ , C ₁	2-3
C Distal Accessory Ridge	Occurs in the distolingual between the tooth apex and the distolingual marginal ridge	C ¹ , C ₁	1-5
Metacone	The presence of the cusp 3 and its expression	M ¹ , M ²	3-5

Hypocone	The presence of the cusp 4 and its expression	M^1, M^2	3-5
Cusp 5 (Metaconule)	A fifth cusp occurs between the metacone and hypocone	M^1, M^2	1-5
Cusp 5 (Hypoconulid)	A fifth cusp occurs between entoconid and hypoconid	M_1, M_2	1-5
Cusp 6 (Entoconulid)	A sixth cusp occurs between hypoconulid and entoconid	M_1, M_2	1-4
Cusp 7 (Metanoculid)	A seventh cusp occurs between metaconid and entoconid	M_1, M_2	1-4
Carabelli's Cusp	Occurs on the lingual surface of protocone	M^1, M^2	3-7
Groove Pattern	Y: cusps 2 and 3 are in contact; +: cusps 1 and 4 are in contact; X: cusps 1 and 4 are in contact	M_1, M_2	Presence of Y pattern
Anterior Fovea	Precuspidal fossa occurs distally to the mesial marginal ridge	M_1, M_2	2-4
Parastyle	A cusp-like feature occurs on the buccal surface of paracone	M^1, M^2	1-6
Protostylid	A cusp-like feature occurs on the buccal surface of protoconid	M_1, M_2	2-7
Mid-trigonid crest	A ridge connects metaconid and protoconid	M_1, M_2	Presence of 1B
Deflecting Wrinkle	Medial ridge on cusp 2	M_1, M_2	1-3

3.2.2 Statistical analysis

In this study, associations between permanent and deciduous teeth were established using Somers' D statistics. Somers' D (or Somers' delta) is a non-parametric measure of association for ordinal variables. It measures the strength and direction of association between a predictor (X) and outcome variable (Y). It can be used to estimate "the effect of X on Y", or alternatively, it may be used "as a performance indicator of X as a predictor of Y" (Newson, 2006:1). Somers' D values range between -1 and +1, where the value of -1 reflects the strongest negative association and +1 reflects the strongest positive association. A "0" value indicates an independence and no association between the variables (Agresti and Finlay, 2009). The association becomes weaker as the value of the measure converges to zero. A negative association occurs when the values of the independent variable increase on the x scale as the values for the dependent variable decrease on the y scale, or vice versa. Similarly, a positive association occurs when the values of a variable increase as the other variable also increases (Agresti and Finlay, 2009).

Negative associations for each trait are the result of the disagreement between the deciduous and permanent teeth in their direction of grade scores. In other words, an inverse relationship (which is a negative association in this case) occurs when the deciduous teeth get higher scores on the grade scale for a given trait, and the permanent teeth get lower grades, or vice versa. This kind of association creates more discordant pairs of units than the concordant pairs. Because Somers' D's original formula relies on the difference between the number of concordant and discordant pairs (C-D), in a case where there is more discordant pairs than the concordant pairs, it would result in negative values.

A total of 11 traits which are characteristic of Neandertals were included in the statistical analysis. These traits and their abbreviations used in the subsection 4.2 of Chapter 4 are as follows: shoveling in upper central incisors (SSUI1/i1), shoveling in upper lateral incisors (SSUI2/i2), labial curve in upper central incisors (LCUI1/i1), tuberculum dentale in upper central incisors (TDUI1/i1), tuberculum dentale in upper lateral incisors (TDUI2/i2), tuberculum dentale in upper canines (TDUC/c), metacone (MUM1/dm2), hypocone (HUM1/dm2), Carabelli's trait (CTUM1/dm2) in the upper permanent first molars and deciduous second molars, anterior fovea (AFLM1/dm2), and mid-trigonid crest (MTCLM1/dm2) in the lower permanent first molars and deciduous second molars.

As discussed in subsection 3.1.3 of this chapter, the sample introduces some problems for the statistical analysis. Because the sample size is small per trait, the majority of the results are expected to lack statistical power. At this point, a weighted average of Somers' D values for all of the tooth comparisons were included in the analysis in order to get an overall association value. For this purpose, following formula was used:

$$\text{Weighted average of Somers' D} = \frac{\sum_{i=1}^n |D_i| * W_{Ti}}{\sum_{i=1}^n W_i}$$

Where $|D_i|$ is the absolute value of Somers' D for a given trait, W_{Ti} is the sum of the concordant and discordant pairs for a given trait, and W_i is the sum of the concordant and discordant pairs of all of the trait comparisons.

CHAPTER 4 RESULTS

The purpose of this chapter is to describe the data set and provide the quantitative summary of the observed frequencies of the non-metric traits in Krapina Neandertals in the subsection 4.1. Also, this chapter presents the statistical analysis applied in order to examine the associations between the permanent and deciduous dentitions in the subsection 4.2.

4.1 Descriptive statistics

A total of 62 teeth belonging to 12 Krapina Dental Persons (KDP) was scored. Although the total of dental sample size is large at Krapina (n=281), this study only used the individuals with mixed dentition. The sample had to be divided into groups in order to get the trait frequencies for each tooth class (from either the left or right side). Consequently, the sample size per trait decreased when the dentitions are divided into groups such as mandibular and maxillary teeth.

Tables 4.1 and 4.2 present the non-metric traits scored on the primary and permanent dentitions, their frequencies with the sample sizes, and the range of variation observed for each tooth class and trait. Tables 4.1 and 4.2 were summarized in the following subsections 4.1.1, 4.1.2, and 4.1.3.

Table 4.1: Non-metric traits scored on the permanent dentition and their occurrence frequencies with the sample sizes and their range of variation observed in the sample.

Traits	%/n	Range of variation
I¹		
Shoveling	100/4	4-5
Double shoveling	0/4	0
Labial convexity	100/4	4
Tuberculum dentale	100/4	4
I²		
Shoveling	100/4	4-5
Double shoveling	0/4	0
Labial convexity	100/4	4
Tuberculum dentale	100/4	2-4
C¹		
Shoveling	100/3	2-3
Tuberculum dentale	100/3	3-4
Canine Mesial Ridge (Bushman)	33.3/3	0-2
Canine Distal Accessory Ridge	100/3	3-4
M¹		
Cusp 5	20/5	0-3
Metacone	100/5	4
Hypocone	100/5	4-5
Carabelli's trait	100/5	4-6
Parastyle	40/5	0-6
M²		
Cusp 5	33.3/3	0-3
Metacone	100/3	3-5
Hypocone	100/3	3
Carabelli's trait	100/3	3-4
Parastyle	0/3	0
I₁		
Shoveling	50/2	1-3
Double shoveling	0/2	0
Labial convexity	100/2	4
Tuberculum dentale	0/2	0
C₁		
Shoveling	50/2	0-2
Tuberculum dentale	100/2	2
Canine Mesial Ridge	0/2	0
Canine Distal Ridge	100/2	2
M₁		
Groove pattern	75/4	+, Y
Anterior fovea	100/4	3-4
Deflecting wrinkle	50/2	0-3

Mid-trigonid crest	100/4	1B
Cusp 6	0/2	0
Cusp 7	0/2	0
M₂		
Groove pattern	33.3/3	+, Y
Anterior fovea	100/3	3-4
Deflecting wrinkle	50/2	0-2
Mid-trigonid crest	33.3/3	0, 1A, 1B
Cusp 5	66.6/3	0-3
Cusp 6	0/3	0
Cusp 7	0/3	0

Table 4.2: Non-metric traits scored on the primary dentition and their occurrence frequencies with the sample sizes and their range of variation observed in the sample.

Traits	%/n	Range of variation
i¹		
Shoveling	100/2	4-5
Double shoveling	0/2	0
Labial convexity	100/2	4
Tuberculum dentale	100/2	4
i²		
Shoveling	100/3	3-4
Double shoveling	0/2	0-1
Labial convexity	100/3	4
Tuberculum dentale	100/2	2-3
c¹		
Tuberculum dentale	50/2	1-5
Canine Mesial Ridge (Bushman)	0/2	0-1
Canine Distal Accessory Ridge	100/2	2
dm¹		
Cusp 5	50/2	0-2
Metacone	100/2	3-5
Hypocone	100/2	3-4
Carabelli's trait	75/4	0-3
Parastyle	0/2	0
dm²		
Cusp 5	40/5	0-3
Metacone	100/5	4-5
Hypocone	100/5	4-5
Carabelli's trait	100/5	3-6
Parastyle	0/5	0
i₂		
Shoveling	100/2	2-3

Double shoveling	50/2	0-2
Labial convexity	100/2	4
dm₂		
Groove pattern	100/5	Y
Anterior fovea	80/5	1-4
Deflecting wrinkle	33.3/3	0-2
Protostylid	20/5	0-2
Mid-trigonid crest	50/4	1A, 1B
Cusp 5	100/5	3-4
Cusp 6	20/5	0-2
Cusp 7	0/5	0

4.1.1 Incisors

The current study found that shoveling is markedly expressed (at least grade 3) in all of the upper central and lateral incisors in both permanent and deciduous teeth. Similarly, 100% of the deciduous and permanent upper incisors exhibit labial convexity and tuberculum dentale, and they are often markedly expressed in both dentitions. Also, the combination of shoveling, tuberculum dentale and labial convexity was observed to be common among Krapina Neandertals. All three traits were present in 100% of the deciduous and permanent upper central and lateral incisors. Double shoveling was not present any of the upper incisors in both dentitions.

There was no permanent lower lateral incisor (I_2) and deciduous central incisor (i_1) available for scoring. Therefore, no analogue teeth were present for comparison between the deciduous and permanent dentitions. When compared with the upper incisors, shoveling was less expressed in the lower incisors of both deciduous and permanent teeth. Scorings for the trait did not exceed grade 3 for both central and lateral incisors. In addition, labial convexity was present in 100% of the permanent central incisors and deciduous lateral incisors. The trait was equally expressed in both dentitions (grade 4). Tuberculum dentale was not observed in the permanent central incisors.

4.1.2 Canines

All of the upper permanent canines exhibited shoveling, tuberculum dentale and canine distal accessory ridge. Tuberculum dentale was more frequent in permanent teeth (100%) than the deciduous (50%). Canine mesial ridge (Bushman canine) was absent in upper deciduous canines (0%) and it was not common in permanents (33.3%). None of the deciduous canines and only one permanent canine exhibited this trait.

4.1.3 Molars

Although all of the deciduous and permanent molars were scored, for the purposes of this study, only the deciduous second molars (dm2) and the permanent first molars (M1) were summarized in this subsection.

Observed frequencies of traits for the upper dm2s and M1s were similar between the two dentitions. Metacone and hypocone were never absent in both dentitions, and they were expressed as either large (grade 4) or very large (grade 5) cusps. Cusp 5 was more frequent in deciduous teeth (40%) than the permanent (20%). Carabelli's trait was always present in all of the upper dm2 and M1s, and the trait was almost equally expressed in both dentitions. Parastyle was not observed in dm2s, and it was observed in 40% of the M1s. One M1 possessed a grade 6 parastyle expression which is the highest grade in the ASUDAS.

In the lower molars, "Y" groove pattern was more common in both dm2s (100%) and M1s (75%) than the "+" and "x" pattern. Mid-trigonid crest grade 1B which is more rounded and wider than grade 1A was more common in the sample. All of the dm2s and half of the M1s exhibited 1B mid-trigonid crest trait expression. Cusp 6 was present 20% of the dm2s, and absent in M1s. cusp 7 was not observed in any of the lower deciduous and permanent molars.

4.1.4 Tooth Pairs

Out of 12 KDPs, 4 individuals possessed their upper dm2s and M1s; 3 individuals possessed their lower dm2s and M1s; and 1 individual possessed its upper deciduous and permanent central (I1/i1) and lateral incisors (I2/i2) within the same individual. Table 4.3 shows the comparisons of the deciduous and permanent scores of the tooth pairings for each individual.

Any trait expression in the tooth pairs was considered as a demonstration of correspondence between the two dentitions. In KDP 1 and KDP 22, all of the tooth comparisons, except for parastyle, show a correspondence in their trait expressions. KDP 2, KDP 27 and KDP 28 show a perfect correspondence where all of the trait expressions are the same in the deciduous and permanent teeth. All of the traits but one in KDP 3 and KDP 9 also show correspondence between tooth pairs. Based on these observations, majority of the comparisons in all of the 12 KDPs indicate an overall correspondence between the two dentitions.

Table 4.3: Comparison of trait expressions between deciduous and permanent tooth pairs. Scores in bold indicate discordance.

Specimen (KDP)	Deciduous scores	Permanent scores
KDP 1		
Metacone dm ² /M ¹	4	4
Hypocone dm ² /M ¹	5	5
Cusp 5 dm ² /M ¹	3	3
Carabelli's cusp dm ² /M ¹	3	4
Parastyle dm ² /M ¹	0	2
KDP 2		
Shoveling i ¹ /I ¹	4	4
Double-shoveling i ¹ /I ¹	0	0
Labial convexity i ¹ /I ¹	4	4
Lingual tubercles i ¹ /I ¹	4	4
Shoveling i ² /I ²	4	4
Labial convexity i ² /I ²	4	4
Metacone dm ² /M ¹	4	4
Hypocone dm ² /M ¹	5	5
Cusp 5 dm ² /M ¹	0	0

Carabelli's cusp dm^2/M^1	4	4
Parastyle dm^2/M^1	0	0
KDP 3		
Metacone dm^2/M^1	5	4
Hypocone dm^2/M^1	4	5
Cusp 5 dm^2/M^1	0	2
Carabelli's cusp dm^2/M^1	6	5
Parastyle dm^2/M^1	0	0
KDP 9		
Groove Pattern dm_2/M_1	Y	Y
Anterior Fovea dm_2/M_1	1	4
KDP 22		
Metacone dm^2/M^1	4	4
Hypocone dm^2/M^1	5	5
Cusp 5 dm^2/M^1	0	0
Carabelli's cusp dm^2/M^1	6	6
Parastyle dm^2/M^1	0	6
KDP 27		
Groove Pattern dm_2/M_1	Y	Y
Anterior Fovea dm_2/M_1	3	3
Distal trigonid crest dm_2/M_1	0	0
Mid-trigonid crest dm_2/M_1	1B	1B
KDP 28		
Groove Pattern dm_2/M_1	Y	Y
Anterior Fovea dm_2/M_1	4	4
Deflecting wrinkle dm_2/M_1	0	0
Distal trigonid crest dm_2/M_1	0	0
Mid-trigonid crest dm_2/M_1	1B	1B

4.2 Statistical analysis

Somers' D statistic was applied for the 11 traits in order to examine how strongly related is the grade score to whether it is deciduous and permanent teeth. Results were presented in Table 4.4. In addition, cross-tabulations for each trait were provided in the Appendix A.

Table 4.4: Somers' D results for the eleven tooth classes. * indicates significant associations.

Traits	Coef.	Std. Err.	Z	P> z	[95% Conf. Interval]	
SSUI1/i1	.25	.5676844	0.44	0.660	-.8626411	1.362641
SSUI2/i2	-.6428571*	.1562125	-4.12	0.000	-.9490279	-.3366863
LCUI1/i1	0	(omitted)				
TDUI1/i1	0	(omitted)				
TDUI2/i2	-.1818182	.4120852	-0.44	0.659	-.9894904	.625854
TDUC/c	0	.7027284	0.00	1.000	-1.377322	1.377322
MUM1/dm2	.5555556*	.1964186	2.83	0.005	.1705823	.9405288
HUM1/dm2	-.2380952	.3916183	-0.61	0.543	-1.005653	.5294626
CTUM1/dm2	0	.3173691	0.00	1.000	-.622032	.622032
AFLM1/dm2	-.3478261	.2975725	-1.17	0.242	-.9310575	.2354053
MTCLM1/dm2	-.6666667*	.2400274	-2.78	0.005	-1.137112	-.1962215

Somers' D results yielded negative associations for the traits shoveling (SSUI2/i2) and tuberculum dentale (TDUI2/i2) in upper lateral incisors, hypocone (HUM1/dm2) in upper permanent first molars and deciduous second molars, anterior fovea (AFLM1/dm2), and mid-trigonal crest (MTCLM1/dm2) in the lower permanent first molars and deciduous second molars. For the tuberculum dentale in upper canines (TDUC/c) and Carabelli's trait in upper molars (CTUM1/dm2), Somers' D yielded zero values, which reflects no association between the grade scores of the permanent and deciduous teeth.

In addition, as can be seen in Table 4.4, several comparisons were not significant and did not provide enough evidence against the null hypothesis. Somers' D omitted the traits labial curve and tuberculum dentale in the upper central incisors (LCUI1/i1 and TDUI1/i1) from the analysis because there was no variation in trait expression amongst the deciduous and permanent teeth, and thus, no comparisons were available for the analysis.

Among eleven traits, only three traits were statistically significant (MUM1/dm2 and MTCLM1/dm2). Only for the metacone (MUM1/dm2) in upper molars, the statistical test results allowed rejecting the null hypothesis that there is not a positive association between primary and permanent trait expressions. Grade scores for metacone showed a moderate positive association

between M1 and dm2 (Somers' D=.55). For MTCLM1/dm2, the associations was moderately negative (Somers' D=-.66).

Lastly, two traits (labial curve and tuberculum dentale on upper central incisors) were excluded from the calculations of the weighted average of Somers' D because these traits showed no variation between deciduous and permanent teeth as mentioned above. Therefore, the formula, mentioned in subsection 3.2.2, was applied for nine out of eleven traits. The weighted average calculation yielded a value of 0.28. This result indicates a weak positive association across all of the Somers' D values.

CHAPTER 5 DISCUSSION AND CONCLUSION

5.1 Summary of the Study

The literature makes it clear that deciduous and permanent teeth have several characteristics in common within an individual (Bailey et al., 2014; Saunders and Mayhall, 1982). These morphological similarities are assumed to be the result of the actions of genes during the growth and development process (Bader, 1965; Garn et al., 1966b; Scott and Turner, 1997), although very few genes that influence dental development were identified to this day (e.g. Kimura et al., 2009). Based on this assumption, several modern human studies explore the morphological relationships between the deciduous and permanent dentitions (Edgar and Lease, 2007; Kieser, 1984; Saunders and Mayhall, 1982; Smith et al. 1987). However, it was never tested on fossil hominins including Neandertals.

In this regard, the present study is conducted with the purpose of providing a dental morphological comparison between the baby and adult teeth of Krapina Neandertals. In addition, this study examines the Krapina individuals with the expectations of finding a correspondence between the two dentitions based on their dental non-metric trait variation. In line with this purpose, several steps are taken. First, several non-metric traits were scored utilizing the ASUDAS (Arizona State University Dental Anthropology System) (Turner et al 1991) on both deciduous and permanent dentitions of 12 KDPs. Then, the associations of the two dentitions were tested applying the Somers' D measure of association. The results were presented in subsection 4.2 of Chapter 4.

In the present study, the results of Somers' D range from -0.66 (moderate to high negative relationship) to 0.55 (moderate positive relationship) (see Table 4.4 on page 38). In the

upper dentition, shoveling in incisors (except for the lateral incisors) and tuberculum dentale in upper incisors and canines showed either weak or no association between the primary and permanent dentitions. This result agree with Edgar and Lease (2007)'s findings. Their results also did not show any significant correlation for shoveling and tuberculum dentale in any of the upper incisors and canines. However, Saunders and Mayhall (1982) found a significant association for shoveling in upper central incisors. In addition, the moderate to high negative association between upper lateral incisors for shoveling in the current study does not support Saunders and Mayhall (1982)'s results which suggested a less association between the two teeth. They attribute this discordance between deciduous and permanent lateral incisors to the variable nature of this tooth class. Nevertheless, the only significant result among the anterior tooth classes in the present study was shoveling in upper lateral incisors. The majority of the upper tooth classes do not provide enough evidence against the null hypothesis of there is not a correspondence between the two dentitions.

In the posterior dentition, results for two out of five traits were significant as can be seen in Table 4.4. Metacone in upper dm2 and M1 showed a significant moderate positive relationship meaning that trait expressions are in agreement by being systematically either higher or lower in both dentitions. For mid-trigonid crest in lower dm2 and M1, results indicated a significant moderate to high negative relationship suggesting a discordance in trait expression of the two dentitions. The rest of the results for posterior teeth should be interpreted with caution since the results are not statistically significant. Unexpectedly, Carabelli's trait showed no relationship although the result was not significant. In addition, hypocone and anterior fovea showed negative weak insignificant associations between dm2 and M1. These results both agree and disagree with previous studies. They disagree with Edgar and Lease (2007)'s results which indicate a

significant positive relationship for Carabelli's trait between deciduous and permanent teeth. On the contrary, the present study's results agree with Smith et al. (1987)'s findings for hypocone and Carabelli's trait. According to their results, dm2 and M1 do not show any positive association for any of the traits observed on these tooth classes.

The weighted average of Somers' D did not also provide enough evidence to reject the null hypothesis. A value of 0.28 indicates a weak positive association between deciduous and permanent dentitions concerning the nine tooth class comparisons.

The results in the present study are both expected and unexpected at the same time. They were expected because the sample size for each trait is very small, and therefore, the statistical measure of association used in this study cannot tell whether or not there is an association between the dentitions. Therefore, the majority of the results are not statistically reliable and do not reflect reality because they lack statistical power. This is not to blame the statistical method used in this study for the insignificant results, it is rather the small sample size that prevents establishing an appropriate association test.

On the other hand, these results were unexpected simply because there is a clear and repeatable trend observed among Krapina, and the trend is that primary and permanent teeth express the dental traits in a similar pattern. This morphological similarity is also evident from the individual comparisons of the trait expressions between the tooth pairs within individuals (see subsection 4.1.4 of Chapter 4 for the tooth pair comparisons). As can be seen from Table 4.3 in Chapter 4, 34 out of 37 tooth pair comparisons belonging to 7 KDPs indicate a correspondence in their trait expressions. Not even one individual among 7 KDPs exhibits a perfect discordance of trait expression where all of the individual tooth comparisons show disagreement between baby/adult tooth pairs. Although this is a small sample size and there is no

statistical power associated with these results, it is clear that there is a trend toward the deciduous and permanent trait correspondence in the sample.

In this regard, the results in this study beg the questions of “What is the perfect sample for testing the morphological correspondence between primary and permanent dentitions? Does it exist?” It should be noted that it can be quite challenging to find such a sample even in a historical collection far from finding in a fossil collection. At this point, the question becomes: “Should this fact prevent us to ask the question of fossils?” It should be admitted that a better and more appropriate way to conduct a research as the current one might have been by using a modern human sample with an adequate sample size. In order to increase the sample size, several additional steps could have been taken. For example, data from the previous studies concerning dental morphology of fossils with mixed dentition could have been included in the statistical analysis. In addition to that, a modern human or a non-human primate group with mixed dentition could have been used as an out-group. At this point, Krapina was the sample available for research, and it provided a close to adequate sample size with a couple of mixed dentitions which allows for testing the patterns of dental crown morphological development among Neandertals. Also, if the sample size were not an issue, Neandertals are a better sample for the current study than a modern human sample because there are no modern human groups that have such a high number of non-metric features expressed as Neandertals have. For example, 80% of Native Americans are characterized by incisor shoveling, and 20% of Sub-Saharan Africans are characterized by Bushman canines, and Europeans have a very simple and not complex dentition when compared to Neandertals. These frequencies (80% and 20%) are relatively high when compared to other human groups. But these are the almost only traits that are in high frequencies

in these groups. With such a low number of traits, a comparison between primary and permanent dentition would not say much.

5.2 Concluding Remarks

This study is conducted to understand the underpinnings of dental development by comparing the permanent and primary dentitions of Krapina Neandertals. The central prediction in the current study is that there is a correspondence between the two dentitions. Although the majority of results did not allow rejecting the null hypothesis of no association between the two dentitions, the apparent morphological similarity between baby and adult teeth and also the inter-individual similarity at Krapina suggests a couple of points. First, it suggests that they are actually a closely genetically related group of individuals because they share a genetic make-up that is similar about dental morphology. Although this study does not involve any genetic methods such as sequencing genes of Krapina Neandertals, the study of morphology is also close proxy for inferring about their genetic relatedness. If the opposite was true and they were not a biological population, it would be expected to see a more variable dental morphology across all individuals. However, the very low level of dental morphological variation at Krapina is reminiscent of a variation that can be observed only in a true biological population.

Not only the morphological similarity observed in this study but also the previous studies regarding the dentition of Krapina Neandertals strengthen the assumption that they may be a closely related population. For example, first Gorjanović-Kramberger (1906), and then Wolpoff (1979) noticed that mandibular premolars (P_{3s}) at Krapina are unusually rotated clockwise. Rougier et al. (2006) examined the frequency of rotated P_{3s} at Krapina, and compared it to a modern human sample and to the total Neandertal sample. Their results showed that the proportions of rotated P_{3s} of Krapina Neandertals are unique and very different from the modern

human sample as well as the total Neandertal sample. They suggest that the rotated premolars are an inherited feature among Krapina people, implying that they might be a biological population. However, they argue that not all of the Krapina people might be related because only the mandibles from the stratigraphic levels 3, 4 and 5 exhibit rotated premolars, and the mandible from level 6 do not. Nevertheless, tooth rotation is a rare anomaly, and its presence in Krapina individuals supports that they might be a genetically related population.

Second of all, the apparent but not statistically significant correspondence between the two dentitions suggests that similar genetic mechanisms are responsible for the growth and development of the dental non-metric traits of both primary and permanent dentitions. It is known that interactions between the tissues during odontogenesis are controlled by not only one gene but also multiple genes acting in concert (Hughes and Townsend, 2013). As Jernvall and Jung (2000: 171) put it:

“Much of the genetic machinery of development uses the same genes among different organs, including teeth, limbs, and feathers. Furthermore, within a tooth, the development of individual cusps repeatedly uses the same set of developmental genes, forming a ‘developmental module’”.

Therefore, the morphological similarity observed in this study could be the reflection of the repeated use of the same genes during tooth development. Although which particular genes produce a particular dental trait is mostly unknown, several genetic loci which can be directly linked to the dental morphology were determined to this day. However, they are still under investigation (Hughes and Townsend, 2013). Among the few studies, a study on Japanese population confirmed that a particular allele of a gene (EDAR) is associated with the presence of shoveling (Kimura et al., 2009). Apparently, more genetic studies are needed to account for the genotype-phenotype relationship of dental crown traits.

Thirdly, it is reasonable to suggest that the consistent dental pattern observed among Krapina individuals might have an adaptive significance. The function of these dental traits is not known. It might be just a random variation that identifies and characterizes a biological population so that it can be used as a population marker which is a reflection of genetic drift or gene flow. The other way to think about the function of these dental traits is to consider the idea that there may be an adaptive value to the combination of these dental traits. The unique Neandertal dental morphology could have been a reflection of some sort of chewing adaptation. This notion emphasizes the “Anterior Dental Loading Hypothesis” which proposes that the anatomy of Neandertal face is the resultant of the strong force applied on anterior teeth during masticatory and paramasticatory behavior (Rak, 1986; Trinkaus, 1987). Their highly and evenly worn front teeth were interpreted as they were being used as a third hand during food preparation and material processing such as producing stone tools. It was suggested that their large anterior teeth compared to the posterior teeth as regards to modern humans, the presence of strong shoveling as well as lingual tubercles as a whole have the function of making anterior teeth stronger in order to counter the force applied to the teeth. In addition, a more complex posterior dentition when compared to modern humans might be an adaptive response for chewing. That is to say, extra crests or cusps that are frequently observed in Neandertal posterior dentition might have helped them increase the occlusal chewing efficiency. However, although feasible, it is better to be cautious before any conclusions are drawn because this kind of suggestion would be a high level of inference from a small sample such as the current one.

Lastly, the morphological similarity observed in the current study between the deciduous second molar and permanent first molar is corroborative of Butler (1939)’s field model which proposes that each tooth share the same morphogenetic field with the tooth nearby to it, and

therefore, they are expected to show morphological similarities. Butler (1967) also argues that premolars are the earlier developing members of the molar field, and dm2 is similar to M1 in morphology. In agreement with the model, the results here also suggest that the morphology of dm2 is more similar to M1 than dm1 (see Figure 1.3 for illustration). The tooth pair comparisons in the current study (see Table 4.3 on page 36) also support the similarity between dm2 and M1.

5.3 Future Directions

This study demonstrated a clear and consistent trend toward the deciduous and permanent dental non-metric trait correspondence among Krapina Neandertals although the sample size created statistically insignificant results. It is recommended that the trend observed here can be tested with a more appropriate sample size by including data from the previous studies concerning dental morphology of fossils or by examining a modern human sample with mixed dentition. In addition, identifying the key genes that act during the dental development would help to account for the morphological similarity between primary and permanent dentitions observed in this study.

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APPENDIX

Crosstabulations for the 11 tooth class comparisons

SSUI1/i1	Permanent	Deciduous	Total
4	3 75.00	1 50.00	4 66.67
5	1 25.00	1 50.00	2 33.33
Total	4 100.00	2 100.00	6 100.00

SSUI2/i2	Permanent	Deciduous	Total
3	0 0.00	2 66.67	2 28.57
4	3 75.00	1 33.33	4 57.14
5	1 25.00	0 0.00	1 14.29
Total	4 100.00	3 100.00	7 100.00

LCUI1/i1	Permanent	Deciduous	Total
4	4 100.00	2 100.00	6 100.00
Total	4 100.00	2 100.00	6 100.00

TDUI1/i1	Permanent	Deciduous	Total
4	4 100.00	2 100.00	6 100.00
Total	4 100.00	2 100.00	6 100.00

TDUI2/i2	Permanent	Deciduous	Total
2	2 50.00	1 50.00	3 50.00
3	0 0.00	1 50.00	1 16.67
4	2	0	2

	50.00	0.00	33.33
Total	4 100.00	2 100.00	6 100.00

TDUC/c	Permanent	Deciduous	Total
1	0 0.00	1 50.00	1 20.00
3	1 33.33	0 0.00	1 20.00
4	2 66.67	0 0.00	2 40.00
5	0 0.00	1 50.00	1 20.00
Total	3 100.00	2 100.00	5 100.00

MUM1/dm2	Permanent	Deciduous	Total
4	5 100.00	4 80.00	9 90.00
5	0 0.00	1 20.00	1 10.00
Total	5 100.00	5 100.00	10 100.00

HUM1/dm2	Permanent	Deciduous	Total
4	1 20.00	2 40.00	3 30.00
5	4 80.00	3 60.00	7 70.00
Total	5 100.00	5 100.00	10 100.00

CTUM1/dm2	Permanent	Deciduous	Total
3	0 0.00	1 20.00	1 10.00
4	3 60.00	1 20.00	4 40.00
5	0 0.00	1 20.00	1 10.00
6	2 40.00	2 40.00	4 40.00
Total	5	5	10

	100.00	100.00	100.00
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AFLM1/dm2	Permanent	Deciduous	Total
1	0 0.00	1 20.00	1 11.11
3	1 25.00	2 40.00	3 33.33
4	3 75.00	2 40.00	5 55.56
Total	4 100.00	5 100.00	9 100.00

MTCLM1/dm2	Permanent	Deciduous	Total
0	0 0.00	2 50.00	2 25.00
1	4 100.00	2 50.00	6 75.00
Total	4 100.00	4 100.00	8 100.00