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CHARACTERIZATION OF THE DENTAL MORPHOLOGY OF A PORTUGUESE SAMPLE FROM THE 19th AND 20th CENTURIES

UNIVERSIDADE DE COIMBRA

Characterization of the dental morphology of a Portuguese sample from the 19th and 20th centuries

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Abstract

Dental morphology analyzes a set of widely studied traits which variation was mostly determined by genetic diversity. This variation, expressed in character frequencies for each sample, differs between populations at the wider geographical scales. Therefore, it allows for the biological relations between samples to be calculated, using statistical tools.

The Arizona State University Dental Anthropology System (ASUDAS) and other complementary methodologies were used to record the dental and oral morphology of 600 identified individuals (300 males and 300 females), from two collections (Trocas Internacionais and Escolas Médicas) of the University of Coimbra, who died in Portugal in the late 19th and early to mid-20th century. Their dental morphology frequencies were analyzed and compared with others published by different authors, with the aim to enlighten the biological relations with other samples and the effects of the gene flow into and from Portugal across time. The consequences of other factors in the dental morphology of the Coimbra sample and its scoring were also analyzed. Principal components analysis, Kendall's *tau*-b, Spearman's *rho*, Pearson's *chi*-squared, Kruskal-Wallis H, Mann-Whitney U and Z-ratio were the statistical tests used.

The mean precision (overall precision: 89.4%; precision within one grade: 96.0%; presence/absence precision: 94.5%) in the scoring of the dental nonmetric traits was adequate. Only the *tuberculum dentale* presented unreliable repeatability of observation, and was removed from further analysis. The scorability of dental discrete traits between observations was precise (mean overall precision: 97.0%), as was the recording of dental wear within one grade (mean overall precision: 74.8%; precision within one grade: 99.6%).The mean precision for oral nonmetric traits presented slightly greater difficulties in their repeatability (overall precision: 82.8%; presence/absence precision: 86.4%), partially explained by methodological options. Scorability was precise for oral discrete variables (mean overall precision: 99.3%).

The dental morphology asymmetry found in the Coimbra sample was fluctuating, which can be used as a measure of developmental instability. Their general frequencies were high (mean overall asymmetry: 9.2%; mean asymmetry without bilaterally absent sites: 63.5%; mean asymmetry without bilaterally absent sites and

small samples' traits: 49.5%). The statistical difference in asymmetry between sexes was consistently significant (mean overall asymmetry: Z-ratio = 3.803, P = 0.002; mean asymmetry without bilaterally absent sites: Z-ratio = 3.432, P = 0.0006; mean asymmetry without bilaterally absent sites and small samples' traits: Z-ratio = 2.499, P = 0.0125).

Twelve of the 61 (19.7%) traits analyzed show some amount of sexual dimorphism. Intratrait correlations were only found for the frequencies of cusp number and the presence of specific cusps, as expected.

Several biological affinity analyses revealed the Coimbra sample's proximity to other Iberian samples, and to North African, Imperial Roman and Brazilian samples.

To further clarify the validity of the biological relations found, the effect of dental wear in scoring precision was tested. This revealed higher dental wear rates to be associated with lower intra-observer error and lower trait frequencies.

The individual count method was used when possible, but the tooth count and side count methods were also applied when necessary. To ascertain the legitimacy of the analyses, the different count methods were compared, and found to retain the pattern of frequency distribution. The expression count method was used to compare samples of similar background and different sizes. It allowed the biological continuity of the Coimbra sample to be demonstrated through time (generations) and space (districts, regions, foreign and Portuguese born), and for it to be estimated when dealing with individuals of low and high fluctuating asymmetry.

The observations and methods used seem generally reliable. The fluctuating asymmetry level suggests a possibly high developmental instability, and a potential childcare bias, to the detriment of female individuals. Sexual dimorphism was acceptably low, so the sexes were pooled in subsequent analyses. The dental morphology data demonstrated (a) the Portuguese frequencies correspond to Eurodonty, with the exception of Carabelli's lower frequencies and (b) historical population movements related to Portugal altered subsequent gene pools. Those data were not affected by the involvement of dental wear in the scoring precision and the trait frequencies, since its pattern should be extensible to most samples, nor by the comparison of frequencies ailing from different count methods. The genetic proximity of the several devisable subsamples within the selected individuals underlines the validity of the conclusions and the biological coherence of the Portuguese population.

Key words

Dental anthropology; Dental morphology; Coimbra identified skeletal collections; Population movements; Coimbra (Portugal); 19th and 20th centuries; Fluctuating asymmetry; Intra-observer error.

Resumo

A morfologia dentária analisa um conjunto de caracteres vastamente estudados cuja variação é determinada maioritariamente por diversidade genética. Essa variação, expressa nas frequências dos traços em cada amostra, difere entre populações em abrangentes escalas geográficas. Deste modo permite que as relações biológicas entre amostras sejam calculadas estatisticamente.

O Arizona State University Dental Anthropology System (ASUDAS) e outros métodos complementares foram usados para registar a morfologia dentária e oral de 600 indivíduos identificados (300 de cada sexo), de duas coleções (Trocas Internacionais e Escolas Médicas) da Universidade de Coimbra, que pereceram em Portugal nos finais do século XIX, e inícios a meados do século XX. Estas frequências da morfologia dentária foram analisadas e comparadas com outras de diversos autores, com o objetivo de inferir as relações biológicas com outras amostras e os efeitos do fluxo génico em Portugal ao longo do tempo. As consequências de outros fatores na morfologia dentária da amostra e no seu registo também foram analisadas. Análise de componentes principais, *tau*-b de Kendall, *rho* de Spearman, *chi* quadrado de Pearson, H de Kruskall-Wallis, U de Mann-Whitney e Z-ratio foram os testes estatísticos usados.

A precisão média (precisão geral: 89.4%; precisão com margem de um grau: 96.0%; precisão na presença/ausência: 94.5%) no registo dos caracteres não-métricos dentários foi adequada. Apenas o *tuberculum dentale* apresentou pouca fiabilidade na repetição, sendo removido de análises subsequentes. Os caracteres discretos dentários foram consistentemente considerados observáveis (precisão geral média: 97.0%), tal como o registo do desgaste dentário com margem de um grau (precisão geral média: 74.8%; precisão com margem de um grau: 99.6%). A precisão média nas variáveis não-métricas orais apresentou maiores dificuldades na repetição (precisão geral: 82.8%; precisão na presença/ausência: 86.4%), parcialmente explicada por opções metodológicas. A qualificação dos caracteres discretos orais como observáveis entre registos foi precisa (precisão geral média: 99.3%).

A assimetria na morfologia dentária encontrada na amostra de Coimbra é considerada flutuante, e portanto é uma medida de instabilidade no desenvolvimento. As suas frequências gerais foram consideradas elevadas (assimetria geral média: 9.2%; assimetria média sem ausências bilaterais: 63.5%; assimetria média sem ausências

bilaterais e amostras pequenas: 49.5%). A diferença da assimetria entre os sexos foi consistentemente significativa (assimetria geral média: Z-ratio = 3.803, P = 0.002; assimetria média sem ausências bilaterais: Z-ratio = 3.432, P = 0.0006; assimetria média sem ausências bilaterais e amostras pequenas: Z-ratio = 2.499, P = 0.0125).

Doze dos 61 traços analisados demonstram algum grau de dimorfismo sexual. As correlações entre caracteres apenas foram encontradas entre as frequências do número de cúspides e as da presença das cúspides específicas, conforme esperado.

Diversas análises de afinidade fenotípica revelaram que a amostra de Coimbra é próxima de outras amostras ibéricas e de amostras do Norte de África, do Império Romano e do Brasil.

Para esclarecer a validade das relações biológicas encontradas, o efeito do desgaste dentário na precisão do registo foi pesquisada. Este revelou que o maior desgaste está associado com um menor erro intra-observador e com frequências mais baixas das variáveis.

O método de contagem individual foi usado sempre que possível, porém as contagens por dente e por lado foram aplicadas quando necessário. Para determinar a legitimidade destas análises, os diferentes métodos foram comparados, retendo os padrões de distribuição de frequências. O método de contagem por expressão foi usado para comparar amostras de contextos semelhantes e de diferentes tamanhos. Tal permitiu a demonstração da continuidade biológica na amostra de Coimbra ao longo do tempo (gerações) e do espaço (distritos, regiões, nascidos em Portugal e no estrangeiro) e que a mesma fosse calculada em indivíduos de alta e baixa assimetria flutuante.

As observações e métodos usados surgem como fiáveis, na generalidade. O nível de assimetria flutuante sugere a possibilidade duma elevada instabilidade no desenvolvimento, e um potencial viés no tratamento das crianças, para prejuízo das do sexo feminino. O dimorfismo sexual foi aceitavelmente baixo, permitindo que nas análises subsequentes os sexos fossem combinados. A informação da morfologia dentária demonstrou que (a) as frequências correspondem a um padrão Eurodonte, à excepção da menor frequência da cúspide de Carabelli, e (b) que os movimentos populacionais históricos relacionados com Portugal alteraram os subsequentes patrimónios genéticos. Essa informação não foi afetada pelo envolvimento do desgaste dentário na precisão do registo ou nas frequências dos caracteres, uma vez que o seu padrão deve ser extensível à maioria das amostras, nem pela comparação de frequências determinadas por diferentes métodos de contagem. A proximidade genética das diversas

subamostras que dividem os indivíduos selecionados sublinha a validade das conclusões e a coerência biológica da população Portuguesa.

Palavras chave

Antropologia dentária; morfologia dentária; Coleções de esqueletos identificados de Coimbra; Movimento de populações; Coimbra (Portugal); Séculos XIX e XX; Assimetria flutuante; Erro intra-observador.

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1.Introduction

1.1.Present work

In the following research, the Arizona State University Dental Anthropology System (ASUDAS; Turner *et al.*, 1991) will be used, along with other methods and approaches (see 3.Methods), in order to analyze the dentition of the Portuguese population, using a sample kept in Coimbra, from the late 19th/early 20th century. This analysis will check for differences within this sample and compare it with other samples, and will thus contribute to establish the biological relations of the Portuguese with other groups, and how population movements to and from Portugal affected the biological composition of the groups involved. In the exposure and interpretation of findings and results, supervisors and other valid sources of guidance will be thoroughly considered (for example, see Rautman, 2012).

The aims of this work are:

- to contribute to answer anthropological, historical and archaeological questions regarding the movement of populations within, from and towards the current Portuguese territory. This task will further require the search for bibliographical sources of data on the dental morphology of pertinent populations and should, in the coming years/decades, be complemented by the utmost extent of research into geographically and chronologically varied samples of Portuguese origin;

- to inquire into biological variations within this Portuguese sample, that reflect potential diversity within chronological, regional, and developmental subgroups;

- to analyse the sexual dimorphism and intertrait correlations of the present sample's dental and oral morphology;

- to interpret the fluctuating asymmetry present on the mentioned sample, and apply it as a measure of developmental instability, to further understand the effects of early life stressors on the Portuguese population;

- to advance the discussion on the patterns of fluctuating asymmetry in the sample, by understanding sexual, temporal, regional, and health differences;

- to characterize the intra-observer error of the author in scoring each dental and oral nonmetric trait using the ASUDAS and other methodology (see 3.Methods), and contribute to understand the reproducibility of the ASUDAS as used by relatively inexperienced researchers;

- to comprehend the effect of dental wear in the sample's dental nonmetric trait frequencies, and on the proportion of intra-observer error;

- to indirectly contribute to define susceptibility to pathologies and cultural changes: the determination of genetic continuities/discontinuities between populations allows the answer of questions relating to the continuity of those factors. Buikstra and colleagues (1990) stated that biological distance analyses are important in the context of evolutionary history, bioarchaeology, palaeodemography and palaeoepidemiology, since the knowledge of the biological relations between groups is an essential tool in interpreting demography and disease in the past;

- to supply a source of valuable dental morphological information for future studies and discussions, originating from identified collections, which will benefit the fields of anthropology, archaeology, forensic anthropology, evolution, paleoepidemiology, dentistry and history, amongst others, directly and indirectly.

1.1.2.Structure of the dissertation

The overall structure of the present dissertation aims to portray a classical scientific report. Therefore, the main chapters are '1.Introduction' (the present chapter, subdivided in minor subchapters which introduce the present work, and proceed to contextualize it), '2.Sample', '3.Methods', '4.Results and discussion' and '5.Conclusions'.

The simple approach used still allows personal nuances introduced by the author, mainly represented by the subchapters in '4.Results and discussion'. Such

subchapters sometimes convey short thematic introductions and methodological clarifications that precede the results and discussion of each theme. The order in which the subchapters are inserted are again a reflection of the present author's research process.

Firstly, the quality of the observations is conveyed through the subchapter '4.5.1.Intra-observer error', which demonstrates the validity of the following results. The proportions of asymmetry, sexual dimorphism and intertrait correlations are also important in determining the validity of the results. So, subchapters '4.5.2.Fluctuating asymmetry' (despite the use of the individual count method, which is not affected by asymmetry, fluctuating asymmetry was explored as a potential measure of developmental instability), and '4.5.3.Sexual dimorphism and intratrait correlations' also precede the reports on dental morphology frequencies and their analyses.

Subchapters '4.5.4.Dental and oral nonmetric traits' and '4.5.5.Dental variation and historical migrations' address the main issues in the present dissertation. The former presents and succinctly compares the frequencies of each trait for each tooth pair or bony structure, sometimes using more than one breakpoint. The latter resumes the wide amounts of data in among-sample comparisons via PCA (principal components analysis), which allows the visualization of the biological diversity between the samples.

The study of the possible implications of dental wear in the correct scoring of dental nonmetric traits is not standard. However, it is performed to better understand the merits and limitations of the adopted methodologies, mainly ASUDAS, and communicated through '4.5.6.Dental wear'.

'4.5.7.Count method' analyzes how the comparison of data from different sources, and communicated using different count methods, may affect conclusions. Once again, this is not a standard evaluation, and is brought about by the need to compare such different information, need found in '4.5.5.Dental variation and historical migrations'.

The relations between the subsamples found on the Coimbra Portuguese sample can help further illustrate the biological diversity of late 19th and 20th century Portugal and how different phenomena could have influenced it. Subchapter '4.5.8.Intrasample biological relations' preliminarily addresses the issues of heterogeneity within the sample, and aims at prompting future research.

Finally, '4.5.9.*Ad hoc* observations' briefly describes anatomical, morphological and paleopathological findings during the observations of the present sample, again in a preliminary fashion with the objective of providing a basis for future analysis and discussion.

Results and discussion are, therefore, divided into preliminary analyses of the dental and oral morphology data; report and analysis of such information in comparison with data from other sources; further inspection of how that analysis can be affected by limitations in the methodologies or the comparisons; preliminary analysis of intrasample variation; and, finally, brief discussion of non-systematic observations outside the main scope of the present research.

1.2.On teeth and dental nonmetric traits

1.2.1.History

Dental anthropology originated in the 1930's and 1940's, through the works of Dahlberg and other dentists, as well as anatomists, and was named in a meeting set in London, in 1958 (Hillson, 2005; Scott and Turner, 2008). The term first appeared in an article in 1900, and was so coined by George Buschan (Scott and Turner, 1988). Dental anthropology is the study of teeth to garner information on social and historical backgrounds of individuals and their groups (Rodríguez, 2004, 2005).

This field studies topics as varied as morphology (see below), metrics (tooth size), pathologies, evolution (through fossil dentition and primates), growth and development, genetics, use of teeth as tools, forensic science and cultural modifications (Scott and Turner, 1988).

Even though dental anthropology only originated in the 20th century, teeth were studied long before. They were mentioned in the *Corpus Hippocraticum* (5th century BC), which described their anatomy and growth. Aristotle and Galen also described teeth in the Ancient Antiquity. Much later, in the early Modern Age, the Renaissance saw developments in the field of odontology, mainly in the University of Padua. *De humanis corporis fabrica* (1542), by Andreas Vasalius, is an example of a Renaissance work that ventures into the mouth, by providing descriptions of dental anatomy.

The first book to be written exclusively on teeth was penned in 1563 by Bartolomeo Eustachi: *Libellus de Dentibus*. Marcelo Malphighi and Anthony van Leeuwenhoek were the first people to study teeth using microscopy, in the 17th century. Finally, John Hunter began modern studies on dental anatomy with his work *The Natural History of the Human Teeth*, in 1771 (Alt *et al.*, 1998; Hillson, 2005).

Dental restorations and prosthetics are mostly found from the 16th and 17th centuries respectively, and then only on privileged classes until recently (Alt and Pichler, 1998). Wasterlain (2006) found evidences of dental extraction (root tips in reabsorbed alveoli) and prosthetic treatment (two women, one with a pivoted incisor crown and another with several prosthetic teeth, some held by vulcanized rubber and one pivoted canine) in the late 19th/early 20th century Portuguese. Restored teeth were found in 22 teeth from 12 individuals, significantly more male (10) than female (2) individuals. Marado (2010) also found restored teeth in a sample of unknown origin, presumably Portuguese and contemporary to the latter population.

Few exceptions allowed the study of teeth to enter the concerns of early age physical anthropology in the 19th century, more focused on describing perceivable distinctions among "races". Georg von Carabelli and C. S. Tomes authored some of these exceptions and were pioneers in describing and studying dental crown and root variation, having had traits named after them consequently (Scott and Turner, 1997).

Only on the early 20th century were teeth noted for their variation, and workers such as Hrdlička (with his important first article on shovel-shaped incisors) and Gregory described discrete characters of the dentition (Scott and Turner, 2008). Other researchers contributed to the advancement of the subfield during the first half of the 20th century, with emphasis on Dahlberg's *The changing dentition of man* and other works, as well as Pedersen, another prolific worker (Scott and Turner, 1997, 2008; Irish and Nelson, 2008). Studies of dental morphology and its variation among populations gave way to this subfield of dental anthropology (Schmidt, 2008). The 1940's, - besides Dahlberg and Pedersen's contribution -, also initiated a great scientific tradition in Japan (through K. Hanihara, mainly; see, for example, Hanihara [1967]), and were invaluable for dental anthropology. In the 1950's various areas of interest were developed, such as prehistoric, genetic, morphogenetic and forensic aspects of the study of dental morphology (Scott and Turner, 1997).

G. W. Lasker (1950) was the first author to associate the modern evolutionary synthesis with dental evidence, arguing the usefulness of teeth and their morphological

variation on matters of inheritance and genetics (Scott and Turner, 1997; Scott and Turner, 2008; Irish and Nelson, 2008). Lasker (1950) describes teeth as morphologically determined by genetics and very durable, and thus greatly useful in the fields of anthropology and palaeonthology. The author affirms the need for pedigree and twin studies, in order to determine the role of genetics in tooth morphology, which may be a most valuable resource in the exploration of the biological relatedness in human populations (Lasker, 1950).

The 1960's brought *Dental Anthropology*, a book edited by D. R. Brothwell in 1963 (see Dahlberg [1963], an important contribution to such classic work and to the early stages of dental morphology), and the first International Symposium on Dental Morphology. That meeting took place in Denmark in the mid-1960's, because Dahlberg and Pedersen saw a need for such international gathering.

These events defined this subfield and allowed for its breakthrough, since after that it flourished with hundreds of publications (Scott and Turner, 1997; Scott and Turner, 2008). Walker's 1997 Medline research for dental anthropology papers showed the growth of this subfield the following years, between 1966 and 1996. A high percentage (between 7.5% and 25%) of the dental anthropology articles published in the *American Journal of Physical Anthropology* (which composed up to 20% of AJPA's contents), during the mentioned time frame, were of nonmetric traits.

Biological affinity analyses are one of the aspects to which dental anthropology contributes (as developed below) and such publications have also been tracked. In a 1990 analysis, Buikstra and colleagues found that biodistance articles and abstracts were only up to 5% of the total number of articles and abstracts on the AJPA, which only rose to about 15% of the articles published on skeletal biology, during the period between 1955 and 1985. The trends in biodistance publications in AJPA demonstrate progressively less interracial studies, a diminution in interpopulation analyses and an increase in intraregional (intersite) and, more recently, intrasite research, where analytical topics are concerned. When it comes to methodological topics, trait descriptions were common in early years but decreased from 1960 to 1975, when it was replaced with studies of trait associations, error sources and distance analyses (increasing awareness on error and interpretation issues); more recently, genetic basis of biodistance analyses was frequently researched (Buikstra *et al.*, 1990).

The development of dental morphology is indelibly connected to physical anthropology, since the analysis of traits and their significance in terms of evolution and

population genetics were primarily analyzed by such experts, through the light of the historical questions they brought about. Dentists, with their expertise in oral biology are, of course, also very important to this subfield (Scott, 2008).

1.2.2.Teeth and their importance

Yet, the most important resource for the advent of dental anthropology and the morphological study of dental pieces was and is, obviously, the dentition. Teeth are composed of two main structures: crown and root. The former is covered in enamel, while the latter is covered in cement. This last material functionally belongs to the periodont while it is morphologically part of the tooth. Besides these tissues, divided in the cervical portion, the tooth is formed of dentine, which is beneath them and envelops the pulp. The pulp innerves and vascularizes the tooth, contacting the mandible or maxilla through the root apex. The superior surface of a tooth, which interacts with food, is called the incisal (when its function is shredding) or occlusal surface (when its function is crushing). Roots interact with bone through the periodont, inserting in the alveolus, an opening which is reabsorbed when the tooth is lost (Türp and Alt, 1998).

These tissues are composed of two types of materials. A tooth's inorganic material is mainly composed of apatite crystals (hydroxyapatite and fluorapatite). The organic material is collagen, a fibrous protein that connects itself very tightly with hydroxyapatite and is not easily soluble. Enamel is almost entirely composed of inorganic material, and so is very hard and easily conserved. Unlike this, dentine is softer, since it has 18% collagen, and cement has 21% collagen (Hillson, 2005).

All of this produces one of the most useful resources in the field of biological anthropology: the dentition (Scott, 2008). Attached to bone in the mouth through cementum, periodontal ligament, alveolar bone and gingiva in life (Duric *et al.*, 2004), teeth are still well preserved *post-mortem* (Scott and Turner, 1988; Silva, 2002; Avon, 2004; Hillson, 2005; Scott, 2008; Irish and Nelson, 2008), - as is the case for mandibles (Loth and Henneberg, 1996; Kemkes-Grottenthaler *et al.*, 2002), - and can be kept *in situ* through the alveolar bone alone.

Enamel is a very resistant material, able to endure almost any taphonomic environment. Sometimes it becomes the only remain left from a human inhumation (Scott and Turner, 1997). Dental specimens are easily observed (Scott, 2008), they contain a wide variation of information resources (shape, size, several morphological

traits and dental formulae, not to mention data on health and hygiene habits) and there is a strong genetic influence behind their development and expression. Due to the lack of physiological changes in size and shape, teeth are ideal for developmental studies, for example (Riga *et al.*, 2013). Some studied alterations still occur from post-occlusion exposure to the environment, like wear, for instance (Scott and Turner, 1988; 2008; Guatelli-Steinberg *et al.*, 2001; Silva, 2002; Rodríguez, 2005; Scott, 2008; Irish and Nelson, 2008). Besides, teeth are present all around the globe, allowing for generalized comparisons (Scott, 2008). Their availability, genetic control, durability and informational value make discrete dental traits more advantageous than cranial traits, for example (Alt and Vach, 1998; Silva, 2002; for example, see Wijsman and Neves, 1986).

In the past, teeth have been given symbolical importance and have been recognized as part of someone's identity. Filing, coloring, bleaching, ornamentation, ablation, amputation, germectomy and changing the position of teeth have been part of the cultural act of body decoration, traditional in some cultures, mainly in Africa, Central and South America, the Philippines and the Malayan archipelago. The importance of these practices is underlined by the disregard towards side effects and potential after-effects. Ethnologists, anthropologists and archaeologists can infer individual or population identity and social or religious affiliation through the pattern of dental modification (Alt and Pichler, 1998). Two Late Neolithic Egyptian young girls had their teeth reinserted in (wrong) *alveoli* after being disturbed to allow the burial of an older woman. Perhaps the community's reverence for the dead was the cause of this and the following actions meant to conserve the skeletons' integrity (Irish *et al.*, 2003). The same site originated what has been interpreted as an artificial human tooth. Be it an amulet, a decoration, a piece of jewelry or even a replacement for a tooth in the dental arcade, it was certainly valued. In case it was a replacement, this tooth might have been introduced in the alveolus of a superior lateral incisor lost *post-mortem*, so as to maintain the completeness of the body in the afterlife, which the Egyptians believed to be essential to house the soul eternally (Irish *et al.*, 2004). Two burials from this same Egyptian Neolithic site display teeth lost *post-mortem* inside the right orbit (18 teeth) in one case, and inside the nasal aperture (one tooth) in another. This could be interpreted as a respectful sign, again so the perished could conserve their body "intact"; in alternative, it can be seen as disrespectful or spiteful (Irish *et al.*, 2005). These examples seem to predict the biological association of teeth with identity, found at least on the group level.

Dental specimens and the measure of their post-occlusion alterations also enable the paleoanthropological characterization of the biological profile and diseases of individuals and populations. Teeth are only not applied in estimating stature, when it comes to biological profile, as the subsequent revision will underline.

Liversidge (2008) reviewed the concepts behind the measure of tooth formation timings for age estimation in sub-adults/young adults. Distinctions between growth and maturation and approaches to the treatment and comparison of data explain the process of establishment of these methods and expose their usefulness in forensic and archaeological contexts alike. Other examples of sub-adult age estimation can be found in Scheuer and Black (2000) and AlQhatani and colleagues (2010). Besides sub-adults, age estimation in adults was also found as useful and allowed for a greater age range, through a combination of methods (Lucy *et al.*, 1995), through wear analysis (Gilmore and Grote, 2012) and dental wear and alveolar resorption (Constandse-Westermann (1997), for example.

The dentition is also useful in sexual diagnosis, since they display sexual dimorphism in size, particularly. The work of Galera and Cunha (1993), using Coimbra material, is an example.

Besides age and sex, teeth can be useful in identifying someone's biotype, or ancestry. This is done by comparing the individuals' dental morphology. Forensic odontology is a part of forensic osteology, which is, in turn, a part of forensic anthropology (Scheuer, 2002). The purpose is to aid in the identification of victims of undetermined cause of death, homicide, suicide or mass disaster (Scheuer, 2002; Plourd, 2010).

Although (1) the comparison of the remains with dental records is the main way to identify a subject (Scheuer, 2002; see Cunha and Pinheiro [2007], Johansen and Bowers [2013] or Pereira and Santos [2013], for example) and (2) the identification of victims using only the pattern of missing, filled or unrestored teeth is very reliable when individuals with only healthy teeth, edentulous or without accurate dental records are removed (Adams, 2003), (3) some dental nonmetric variables are still used in ancestry estimation (which is essential in forensic profiling, despite different importance and the use of different biotype definition according to the continent: Oxenham, 2008). Carabelli's cusp, shovel-shape or premolar cusp number are some examples (Pretty and Sweet, 2001; Schmidt, 2008; Ubelaker, 2008; King, 2010). Besides, in some cases dental records are unavailable (see Djuric, 2004; Djuric *et al.*, 2007). Children and

young individuals are difficult to identify through dental records because of the lack or scarceness of interventions on teeth (Dumancic *et al.*, 2001; Adams, 2003).

DNA analysis does not replace the contribution of the fast, reliable and mostly accurate anthropological methods (Kemkes-Grottenthaler, 2001). Sometimes, DNA is destroyed with time and by soil conditions, rendering genetic techniques useless (Palo *et al.*, 2007). Dental morphology may be applied to determine ancestry, since dental nonmetric traits vary across populations. While its applicability may be limited (Edgar, 2009a; but see Edgar, 2013 and Edgar and Ousley, 2013), it can also be very useful (Kemkes-Grottenthaler, 2001). The use of other morphological traits has exposed the difficulties in individual identification (Komar and Lathrop, 2006). Besides, any technique used in forensic odontology has limitations (see Kavitha *et al.*, 2009). This is an underused resource (in forensic anthropology, morphological and osteometric craniofacial variation is mostly used: Simmons and Haglund, 2005), which can be very helpful in some forensic situations (like disasters) where teeth may be the only material remaining intact (Rodríguez, 2003; Cattaneo, 2007; Littleton and Kinaston, 2008; Scott, 2008). International wars, massacres and disasters brought (mainly from the mid-20th century onwards) a need for archaeological and anthropological methods to be applied in forensic contexts (Hanson, 2008). Anthropological methods used in forensics need to be well adjusted to the samples that undergo analyses. This requires research directed specifically at the biological groups from where the victims originate, and otherwise risk being put into question during trial (Kimmerle and Jantz, 2008; Kimmerle *et al.*, 2008). The need for research into the forensic applications of dental morphology and its usefulness, because of its solid scientific basis and potential in ancestry estimation, is thus underlined.

Nonetheless, research has been developed on the subject. Morphological and metric analysis of teeth have been used to develop discriminant functions that ascribe ancestry to European-American and African-American children with over 70% and over 80% accuracy, respectively (Lease, 2003; Lease and Sciulli, 2005). Despite providing evidence of crescent biological affinity of African Americans and European Americans through time, Edgar's 2007 work also underlines dental morphology's capabilities to distinguish between adult individuals of European and African descent. Her most recent work (Edgar, 2013) provides a tool for the distinction between African Americans and European Americans, using several formulae, with accuracy between 89.8% and 94.1% in individuals from the sample used to calculate the formulae and between 71.4% and

100% for other individuals tested. Nonmetric traits, some found on teeth, are used to distinguish "hispanics" from the Southwestern border between the USA and Mexico (Birkby *et al.*, 2008). Metrical tooth data on two Australian samples successfully distinguished between Caucasian and Mongoloid descendants, showing another application of dental anthropology to forensic cases, reliable in different ancestries with common general environmental pressures (Chiu and Donlon, 2000).

In the archaeological context, the distinction among different ancestries may also be of interest. Some victims of Lisbon's 1755 earthquake were distinguished in their dental morphology, according to their ancestry (Pereira *et al.*, 2010a; Pereira *et al.*, 2012b). A series of Araucanos (pre-Hispanic Argentina) was compared with populations from around the world and from Argentina and were most similar to the latter. They were considered hereditary of the Sinodont dental complex, from Northeast Asia (Bollini *et al.*, 2006), which informs on the hypothesis that states the origin of Native Americans as Asian.

Nonmetric dental traits can also be used to identify relatedness between individuals, as has already been found in a study of associated interments (Alt and Vach, 1998; Corruccini and Shimada, 2002 *in* Hillson, 2005). Traits that aid to identify familiarity should be low on the population from whence the sample comes and be genetically inherited (Ríos *et al.*, 2010).

An identification of typically high or low frequencies in a set of dental traits can be found in most large ancestral populations, and is usually called "dental complex". For instance, caucasoids are easier to define by trait absence or scarcity more than trait amplification (Scott and Turner, 1997; personal observation) and were recently characterized as Eurodonts by Scott and colleagues (2013). Sinodont and Sundadont dental complexes have been identified in Asia (Turner, 1990). Sub-Saharan Africa has also been characterized by Irish (in 1997, preliminarily; in 2013, definitely), as Afridont.

1.2.3.Identity, population movements and anthropological traits

Identity comes from one of the most important information found on teeth: morphology, or the study of dental nonmetric traits. Their frequencies allow anthropologists, archaeologists and historians an opportunity to glimpse at the movement of past peoples.

The current anatomical and morphological status of the human dentition, adapted to an omnivorous diet, is an evolution of the mammalian dentition with a planer occlusal surface, through the addition of rounder cusps. This was the second major type of mammalian teeth, after the sharper tricuspid format that evolved from the single-cusped conical reptilian tooth. Dental size reduction is the main trend along hominid and hominin evolution, particularly in the latter. This might be due to the adoption of cooking, initially through hearths and then using ceramics (Rodríguez, 2003).

While dental anatomy concerns itself with the normative morphology and distribution of types of teeth, dental morphology studies the variations in the number of teeth present (either by the occurrence of extra teeth – hyperodontia –, or of missing teeth – hypodontia or tooth agenesis) and, most importantly, the small variations in the morphology of crowns and roots. These latter traits have a greater significance at the evolutionary level (Scott and Turner, 1997).

Jackes and colleagues (2001) underline how dental morphology is capable to characterize genetic alterations along time and space. The authors compare several samples and contribute to questions such as the Mesolithic/Neolithic transition in Portugal. Manabe and colleagues (2003) also report the Neolithic population of Dawenkou (North China) demonstrates continuity from the Sinodont pattern found in the Paleolithic Zhoukoudian Cave, and underline the possibility that this pattern originated in this region of China. The discontinuity between the Jomon (Sundadonts) and the Yayoi (Sinodonts) cultures of Japan suggests gene flow into the Japanese islands. Dawenkou cannot be ruled out as one of the sources, despite the fact that the coexistence between Dawenkou and Jomon cultures for 3000 years demonstrates how the Japan Sea and the East China Sea caused detriment to gene flow (Manabe *et al.*, 2003). Using metric and nonmetric dental data, two southern African groups were distinguished and separation was estimated at about 12000 to 14000 years (Haeussler *et al.*, 1989). As exemplified, morphological dental traits allow for the evaluation of biological continuity, can attest for human migration and verify if cultural change is due to invasion or cultural communication between populations (Irish, 2000; Silva, 2002; Rodríguez, 2004; Ullinger *et al.*, 2005).

Dental trait variation is a biological marker which can be paired with other genetic qualities that accompany a population and evolve, across space and time. This is evidenced by its divergence when groups are isolated, and its convergence when said groups contact and interbreed. It is present in living populations and in the

archaeological, anthropological and fossil records. Therefore, dental morphology is a valid, and often unique, resource to understand population history (Scott and Turner, 1997). This prompts Formicola (1986) to deem the communication of morphological dental trait frequencies in a prehistoric Italian sample as important, so as to be used to compare groups biologically in the future, even when it was not the object of the research. Despite this, in living populations genetic studies can be undertaken. For example, genetics enlightened the relationships between Inuit groups in Alaska suggested by linguistic, archaeological and ethnographic research (Schurr *et al.*, 2012) and the origins, genetic drift and admixture in Portuguese Romani (Pereira *et al.*, 2012a). With past populations, sequencing genomes has recently become more reliable, more effective and relatively less costly, but there is still some risk of contamination (Knapp and Hofreiter, 2010), so dental nonmetric variables can be confidently and routinely used instead, with financial costs that near zero. Other approaches can be made to analysis of kinship in archaeological contexts, such as the study of metric dental traits or metric and nonmetric skeletal traits (Bondioli *et al.*, 1986; Nikita *et al.*, 2012). Family name pattern distribution is another way to infer population genetic structure and migration (Fuster, 2010).

Dental morphological traits are defined as positive (tubercles, cusps, ridges, etc.) or negative (pits, grooves, fossae, etc.) structures which can be either present or absent on a specific tooth's surface, on one or more types of teeth. Besides the present/absent dichotomization, usually there are ranks which try to reproduce the degree of variation of each trait (Scott and Turner, 1997). This will be further explored below.

Besides dental morphological traits, there are many others in the skeleton. Some oral traits, such as *torus mandibularis* and *torus palatinus*, located along the visceral side of the mandible and along the palate, respectively, are also analyzed when researching dental morphology (Turner *et al.*, 1991). The mylohyoid bridge and multiple *foramina mentales* are examples of other variables which can be usefully included (Hauser and De Stefano, 1989).

1.2.4.Genetic basis

It has been argued that the dentition is, genetically, the preferential material to use in the study of biological relations between populations or sub-groups from the past, since (1) its formation does not depend on the mother's direct, uterine, influence, (2) its

evolutions is slow, and probably neutral to natural selection (Tyrrell, 2000), (3) dental nonmetric traits present little sexual dimorphism, (4) the development of different dental traits seems generally unrelated (Tyrrell, 2000; Tocheri, 2002), and (5) dental morphological traits depend on a small and stable portion of the genome (Tyrrell, 2000).

Experiments show the connection between genotype and phenotype and also the importance of morphology during development towards the final shape of a tooth, through a morphodynamic process, the patterning cascade model. This shows the genetic quality of tooth morphology as well as the potential for asymmetry during odontogenesis (Jernvall and Jung, 2000; Salazar-Ciudad and Jernvall, 2002; 2010). The teeth of mice and voles displayed gene controlled positioning of cusp tips, from the original enamel knots, since a very early developmental stage. Evolution of different cusp spatial organization occurs by changing the position of the signaling genes that coordinate cusp formation, which may consequently alter the formation of such discrete variables as crests or patterns (Jernvall *et al.*, 2000). Therefore, genes are very involved in the shape of teeth and its evolution and development. Besides this, the role of environmental factors must not be overlooked, since it is the interplay between genomic and environmental cues that drives development (Riga *et al.*, 2013).

Initially, researchers thought discrete dental characters obeyed a simple mode of inheritance, with exceptions being justified by penetrance issues. From the 1960's on, the quasicontinuous polygenic model is considered the most likely mode of genetic inheritance, accounting for the variability on most traits (Scott and Turner, 1997; Rizk *et al.*, 2008). Today, scientists consider differing modes of inheritance may be involved, when it comes do dental variables: simple Mendelian inheritance, oligogenic and polygenic inheritances (Hillson, 2005).

In sum, the genetic factor underlining the presence of discrete dental characters is associated, theoretically, to the presence of alleles and chromosomal *loci*. Their quantity will affect the presence of a trait, its expression and the frequency with which it is present within a population, via the threshold effect (Scott and Turner, 1997, 2008; Tyrrell, 2000). Heritability in dental characters has been tested through twin and family studies, which found varying results, despite a relatively high frequency of heritability in general (Hillson, 1996; Scott and Turner, 1997; Alt *et al.*, 1998; Hughes and Townsend, 2013). Biological distance statistics calculated from the frequencies of nonmetric dental traits can be compared with those from serological similarities, linguistics and geographical proximity (Hillson, 1996). However, it should be noted the

study of genetic influence on human tooth morphology and metric variation through twin studies has frequently overlooked different events on the twinning process which can have a pronounced effect. This variation has to be measured through model-fitting, in order to take into account the intervention of non-additive genetic variance (relative to gene dominance and gene-gene interactions), additive genetic variance (relative to the effects of parents' genes), epigenetics, common environmental variance and unique environmental variance (Townsend *et al.*, 2009).

Some population studies have demonstrated that discrete dental traits are not significantly influenced by environmental change, such as when a population migrates (Scott and Turner, 1997). In spite of this, the absence of influence of external factors is questioned by research on tooth morphogenesis. Hunter *et al.* (2010) demonstrated that the intercuspal distance is negatively correlated to the expression (presence and size) of the cusp. This work aimed to prove the accuracy of the patterning cascade model of tooth morphogenesis, by studying the relation of Carabelli's cusp expression to intercuspal distances. That model suggests that a small number of genes control tooth development and are subjected to the shape of developing teeth (Hunter *et al.*, 2010). When enough space is granted by the closeness between enamel knots, other knots may be formed, which allows for the formation of more cusps (Hunter *et al.*, 2010). Fernandes (2011) also studied the relation between Carabelli's cusp expression and intercuspal distances in two Portuguese and an Irish population. Alterations in occlusal variants (such as overbite, for example) in twins also demonstrate how the environment can affect teeth during development (Corruccini *et al.*, 1986; Hughes and Townsend, 2013). External factors seem to influence trait development to some extent, according to these results.

Other workers tried to determine the influence of genetics and environment directly, like Townsend and Martin (1992), who also focused on the formation of Carabelli's cusp. The genetic model that best fit the distribution of Carabelli's trait in a sample of monozygotic and dizygotic twins is one of additive genetic influences associated with environmental influences, both general and specific to each side of the dental arcade. In other studies that involved bilateral asymmetry, genetic influences were never ruled out, though most results pointed towards environmental influence in the source of this phenomenon (Rizk *et al.*, 2008).

Fluctuating asymmetry is characterized by slight random deviations from the norm, symmetry (Groeneveld and Kieser, 1991; Graham *et al.*, 1993; Markow, 1995;

Palmer, 1996; Klingenberg and Nijhout, 1999; Gawlikowska *et al.*, 2007; Bollini *et al.*, 2009a; Jeong *et al.*, 2013). It can affect teeth, as environmental disturbances affect odontogeny (Scott and Turner, 1997; Rizk *et al.*, 2008). So, fluctuating asymmetry in dental morphology is the result of environmental factors affecting genetically controlled development (which is known as 'developmental instability'; Klingenberg and Nijhout, 1999) and can potentially be used to measure odontogenic stress, since these deviations from symmetry are induced by an incapability to translate genotypic instructions into phenotypic expression (DeLeon, 2007). This also underlines the importance of external factors, notwithstanding the role of the genome.

As summarized by Sperber (2004), the morphology and complex structure defined by a tooth is explainable through an analysis of both genetic and developmental phenomena, since the latter is the translation and adaption of the former through the filter of environment.

The role of environmental factors is not enough to justify why the frequencies of dental nonmetric traits vary between (polytipicism) and also within (polymorphism) populations (however, see Mizoguchi, 2013). This is most likely due to chance, since it has not been proved to be associated with any selective benefit (as happens to variations that accompanied hominoid dentition across evolutionary times and hundreds of generations). So, morphological dental variables are selectively neutral and only gene flow (with minor exceptions that are likely to be caused by mutation, such as the Uto-Aztecan premolar) accounts for frequency variability (Scott and Turner, 1997; Willermet and Edgar, 2009).

Nichol (1989) found the most adequate models to describe heritability of dental nonmetric variables to be polygenic and major gene inheritance. Scott (1974; through family studies) found dental crown trait variables to be most likely polygenic, and to exhibit threshold dichotomies on a quasicontinuous form. The major questions are due to divergent finds when different cut-off points are used, difficulty to interpret results due to sexual dimorphism, doubts in scorability of the traits and occasions that seem to limit conclusions due to low or high incidences of traits (Nichol, 1989). Correlated variants and the effects of a single variant that compresses the whole of the variation can also be problematic (Berry, 1976).

Trait frequencies are diversified not only on a large, world scale, on major populations, but also on smaller scales. Regionally, locally, and even familiarly and individually, differences can be found. Despite this, the last two examples are not as

useful and informative as the previous two, and apply only to particular archaeological and forensic contexts (see below). Even at the local level, when comparing subgroups within a population, dental trait frequencies are not very useful, since their differentiation depends on several *loci* and is inherently diminished on such a small scale (Scott and Turner, 1997). However, see Stojanowski and Schillaci (2006) and Stojanowski and colleagues (2013) for more recent approaches to the problematic involving interindividual and intracemetery variation, which enlighten the usefulness of the obtained results.

1.2.5.Arizona State University Dental Anthropology System

Besides the presence of teeth through the history of research, the investigation on teeth, the description and importance of dental (and oral) morphological traits, their biological value and its several scales of application, there is an important factor to introduce: methodological concerns.

Scoring methods for nonmetric dental traits were historically characterized by an evolution in their scale of measure (Scott and Turner, 1997). The nominal scale was initially used in the 19th and early 20th centuries (in biological anthropology areas other than dental anthropology, largely ignored at the time). It only determines the presence or absence of a given trait (Scott and Turner, 1997, 2008). This scale's limitations were noted by researchers such as Hrdlička, Hanihara, Campbell and Shaw, who adopted the ordinal scale. This scale is characterized by defining a list of expressions, from minimum to maximum, that refine the registry quality. There is a definition of discrete trait absence, but there are several steps to its presence (Scott and Turner, 1997).

Succinctly: crown and root variables are expressed in a quasicontinuous form, allowing for the measure of different grades (Schmidt, 2008). Dahlberg developed reference plaques, and established a standardized method to evaluate the degree of presence of a given trait and give importance to the ranked scale measure of traits (see, for example, Dalhberg, 1963). Kazuro Hanihara produced similar plaques for the deciduous dentition (Scott and Turner, 2008; see, for example, Hanihara, 1967). The use of ordinal scales and the work of Al Dahlberg between the 1940's and 60's influenced the creation of the Arizona State University Dental Anthropology System, initiated by Turner in 1970 (Scott and Turner, 1997).

Christy Turner II, after having had experience with Dahlberg's plaques, started a project to develop more reference plaques of different traits, aided by students such as Scott. In 1990 they had finished this considerable task and by 1991 they had published the guidelines for the correct use of the ASUDAS (Arizona State University Dental Anthropology System; Scott and Turner, 1997, 2008; Hillson, 2005). Turner became, thusly, the main researcher in the field of dental morphology after the 1960's, because of his and his students' work and because he was the main force behind the establishment of the ASUDAS (Rose and Burke, 2006; Scott and Irish, 2013; Turner, 2013). His experience and research interests as a dental anthropologist are described in Turner (2013) and his importance, as well as that of his graduates and their appreciation, is patent in Scott and Irish (2013).

The ASUDAS, supported by reference plaques (plaster casts) that illustrate some of the observed traits, is based on giving up the present/absent dichotomy in observations and enhancing the reproducibility of results, through the consideration of equally separated grades. Reference plaques standardize observations among researchers throughout the world, and allow for a reduction in inter- (as well as intra-) observer error (Turner *et al.*, 1991; Scott and Turner, 1997, 2008; Hillson, 2005). The considered traits (1) are characteristically easy to identify and observe, (2) are conserved in spite of dental wear (but see Burnett *et al.*, 2013), (3) do not display nearly any sexual dimorphism, (4) evolve slowly, and (5) are useful in distinguishing populations biologically. Hence, valuable information is acquired with few expenses (Turner *et al.*, 1991).

In Hillson's opinion (2005), subjectivity in using ASUDAS is inherent to the method, precisely because grades are proposed in quasicontinuous variables. Experience, clear definitions and exploration of intra- and inter-observer errors diminish this factor. Practice and experience are key factors in measuring any object (Harris, 2008).

Lastly, and coming back to scales of measure, the use of metric intervals allows for a more rigorous, objective observation, in some cases, and establishes specific cut-off points between trait grades (Scott and Turner, 1997). A metric scale is, however, limited by the fact that discrete characters vary as much in shape as they do in size, as they are tridimensional objects where exact measure points are hardly defined (Scott and Turner, 1997). They can also have finer expressions, beyond the millimetric scale's reach (Scott and Turner, 1997). Because of all this, the ordinal scale, through the use of

the ASUDAS, is still applied throughout the world in the observation of dental morphological characters.

1.3. State of the Art

The study of discrete traits was initiated in 1670 by Kerkring, who considered them to be anomalies. This notion prevailed until the mid-20th century, when such traits were studied in mice by Grűneberg, which lead to their use in genetic research and their understanding as quasicontinuous morphological characters (Silva, 2002). Only from the 19th century onwards were nonmetric traits searched in order to detect biological relationships between populations (Scott and Turner, 1997, 2008). In the mid-20th century, these were studied in the context of genetics and with the notion of quasi-continuity of their manifestation (Scott and Turner, 2008).

The application of the ordinal scale in the observation of dental nonmetric traits was a development introduced by Hrdlička, Hanihara, Campbell and Shaw, that defined the absence and one or several grades of presence of a character (Turner *et al.*, 1991; Scott and Turner, 1997). This type of scale influenced the creation of the ASUDAS (Arizona State University Dental Anthropology System), initiated by Turner in 1970, and used to standardize researchers' observations (Scott and Turner, 1997).

Odontoglyphics (observed mainly in Russia from the 1960's onwards, with Zubov as a prominent author) is the study of occlusal furrows, considered unique and genetically inherited to a high degree (Hillson, 1996). Minkov (1983), using Zubov's techniques, characterizes the average dental morphology of the contemporary Bulgarians and generally compares different geographical areas in terms of dental nonmetric traits. This is a rare or unique example of a Portuguese publication on dental morphology using the Russian author's work as observation method.

The characterization of the dental morphological traits of populations throughout the world has been accomplished over the last decades, as exemplified by the work of Scott and Turner (1997), on which the second author's worldwide investigation, followed by a complete research of other authors' works, forms the international distribution of the discrete traits. Hanihara (2008) researched 15 discrete dental traits to identify their worldwide morphological variation and characterize the populations of

wide geographical areas. Later (Hanihara, 2013), the same author used these data to hypothesize on the path of human expansion Out-of-Africa.

Irish and colleagues (Irish, 1998a; Irish and Guatelli-Steinberg, 2003) contributed to the debate about the African origin of *Homo sapiens* by comparing the dental morphology of sub-Saharan Africans with other world populations', cited therein, and with the dental morphology of other hominids. Other contributions relative to taxonomy and trait frequency variation throughout human evolution were also made by Guatelli-Steinberg and Irish (2005). Bailey and colleagues (Bailey, 2000; 2002; 2006; Bailey and Hublin, 2005; Bailey *et al.*, 2008; 2011) also contributed heavily to the debate on the Out-of-Africa concept and to the affinity between *H. sapiens* and *H. neanderthalensis*. Bailey and Hublin (2013) defined the major diagnostic traits of *H. sapiens*, an important contribution towards the clarification of phylogenetic questions and identification of fossil remains. In this regard, Martinón-Torres and colleagues (2013) tried to understand through dental nonmetric data the degree of variability of Sima de los Huesos Middle Pleistocene populations and other Middle Pleistocene taxa (*H. heidelbergensis*), early and modern *H. sapiens*, and *H. neanderthalensis*. Skinner and colleagues (Skinner *et al.*, 2008; 2009; Skinner and Gunz, 2010; Bailey *et al.*, 2011; Ortiz *et al.*, 2012) played an important role in distinguishing morphological variations between modern humans, extant primates, and extinct hominids on the enamel-dentine junction. Their approach has much benefitted from the use of technological advances in inner imaging (see also Macchiarelli *et al.*, 2013 for dental imaging and subsequent analysis; and see Rizk *et al.*, 2013 for a review and a case-study of the application of geometric morphometrics in dental anthropology and dental development in general). Schroer and Wood (2013) provided predictions of dental morphology of the most recent common ancestor of hominines, of hominins and panins. They also hypothesized on the expected dental morphology of the stem taxon of the gorilla clade, and on that of the chimpanzee/bonobo clade. The authors relied on the analysis of a wide spectrum of dental nonmetric traits of extant and extinct hominines.

Hanihara and Ishida (2001a, 2001b) studied oral nonmetric traits from populations throughout the world. The expressed variability in traits such as the mylohyoid bridge and multiple *foramina mentales* may be due to genetic drift, represented through the prevalence in frequencies between current and past populations on the same geographical area. The loss, retention or increments in frequencies from the samples studied seem to be thus justified.

Lee and Zhang (2013) recently characterized the biodistances among seven Chinese and Mongolian population samples from Northeast Asia, and demonstrated the high human diversity in the region. Lukacs and Kuswandari (2013) studied the biological relations of Southeast Asia insular deciduous dentition of the Malay from Java. Their proximity to both sub-Saharan African and Indo-European samples suggested the possibility of influence from Africa, through the "Out-of-Africa" pathway to Australia, as well as later South Asian gene flow. Nelson and Fitzpatrick (2013) found that Early Paluans (3000 BP) were biologically near other Micronesians, Southeast Asians and Polynesians, and shared Sundadonty with these populations. This sample was likely biologically derived from Southeast Asia. Soltysiak and Bialon (2013) studied the biological continuity of the middle Euphrates Valley populations (Syria), and noted a population change between the Islamic rule and recent Berber populations (19th/20th centuries).

Despite the notable focus on North American and Asian dental morphology, some workers used discrete dental variables to understand population affinities throughout Europe as well. There are examples from Italy (Coppa *et al.*, 1998; 2007; Manzi *et al.*, 1997), Switzerland (Desideri and Besse, 2010), Ukraine (Haeussler, 1998), Finland (Salo, 2005), Armenia (Khudaverdyan, 2011) and Ireland (Weets, 2009), for instance. Scott and colleagues (2013) cite these and other examples.

In the Iberian Peninsula dental morphology has not been studied thoroughly, despite the recent dissertations on, or involving, the subject. The work of Silva (2002) is one of the most pertinent in the field. It presents, - amongst other relevant analyses, - data relating to dental anatomy in populations of the current Central Portuguese territory, of the Late Neolithic and Chalcolithic, that originated in funerary monuments. Despite the chronological distance, these samples contribute to testing the biological continuity of the populations within the territory. Reports by Silva and colleagues (2006a) refer to part of the material from the Praia da Samarra tomb, also from the transition between Neolithic and Chalcolithic. This will complement Silva's 2002 data.

Besides this Portuguese work from the University of Coimbra, many short reports including dental and oral nonmetric traits data were included on dissertations serving as partial fulfilment of Bachelor and Master degrees from the same University, mostly under the supervision of Professor Ana Maria Silva. Table 1.1. lists those contributions to the Portuguese dental anthropology knowledge.

Table 1.1. List of the University of Coimbra dissertations that included reports on dental and oral morphology.

Source	Site	Chronology	Sample origin	Other information
Lucas, 2006	Cerro da Vila	Romanized Iberian Peninsula	Necropolis of a *villa* or *vicus*	Located in Faro (*Ossonoba*), it was excavated in the 1960's and following decades.
Fernandes, 2006	Monte da Cegonha	Romanized Iberian Peninsula and paleo-Christian period	Necropolis of a *villa*	Beja, integrated in the *Pax Julia civitas*.
Costa, 2006; Pinto, 2006; Costa, 2007	Santo António Hospital	Modernity (17th to 20th centuries)	Hospital gardens' burials and ossuaries	The hospital was built by Santa Casa da Misericórdia.
Gomes, 2005; Rodrigues, 2005; Simão, 2005; Pombal, 2006; Tereso, 2009; Gonçalves, 2010; Graça, 2010	Santarém	Modernity	Rua dos Barcos and Largo Cândido dos Reis	From two different necropolises, these samples were aggregated because of their chronological and geographical correspondence
Marques, 2007	Batalha	Late Medieval	Santa Maria da Vitória	Chapel built to the memory of the Aljubarrota battle and Nun'Álvares Pereira, its hero.
Godinho, 2008	College of Santo Antão-o-Novo (Lisbon)	Modernity (17th and 18th centuries)	Partial Jesuit necropolis	A total of 163 individuals from the cemetery and ossuaries.
Marado, 2010 (see also Marado, 2012)	Unknown	Unknown	Museum of Natural History of the University of Porto (previously identified) collection	Presumably a late 19th/early 20th century collection from Oporto, Portugal, which record were since lost.
Cunha, 2011; Leandro, 2011	Mértola	Late Medieval (14th to 16th centuries)	Lower Alentejo necropolis	Post-Christian Reconquest sample of sixty Christian individuals.
Jesus, 2012	São João de Almedina (Coimbra)	Medieval (12th to 17th centuries)	Romanesque church	Chronological antecedent of the present sample, from the city of Coimbra.
Pinto, 2012	São Julião (Figueira da Foz)	Uncertain	Uncertain	This ossuary is most likely a post-depositional translation from the local church from the 17th to 19th centuries.

Table 1.1. (Continued.)

Source	Site	Chronology	Sample origin	Other information
Rodrigues, 2013	Shantarin (Santarém)	Medieval (8th/9th to 12th centuries)	Largo Cândido dos Reis	From the Islamic phase, since the burials accorded to the funerary practices of Muslims.
Coelho, 2013	Miranda do Corvo (Coimbra)	Modernity (18th century)	Church's bell tower ossuary	Secondary deposition following the adaption of the tower of the previous defensive wall.

In Portugal, dental morphology was applied to the field of forensic odontology by Pereira (2009). This researcher studied teeth from individuals on a mass grave dug after the 1755 Lisbon earthquake, a mass disaster in Portugal. Pereira and colleagues (2010a, 2012b; Pereira, 2009) were able to detect the presence of American Indians, Africans and Europeans in the studied sample.

In Spain, there has been recent interest in the research subfield of dental morphology. Al Oumaoui (2009) centered his work on Bronze Age populations (from the Granada province and the La Mancha region) and on Middle Age populations (from the Granada province and the Castile and León region) of Spain. García-Sívoli (2009) developed his research with material from the Mallorca Island and Catalonya, with chronologically heterogeneous populations, from the Epipaleolithic (circa 11500 BC) to the late Middle Age (16th and 17th centuries).

1.4. Present sample's historical background

In the transition from the 19th and the 20th century, Portugal was an isolated and poor country (income was in the lowest figures among European countries). Portugal was incompletely industrialized, insufficiently explored in agriculture, with a very traditional mentality and a great connection between political and clerical powers. Its colonial traditions only permitted Portugal to be a rapidly fading world power. Aristocratic and bourgeois social strata were not able to stabilize the country in terms of economy and politics, and together with a people without democratic culture, came to allow a dictatorship to take place at the end of the First Republic, which had been established in 1910 (and lasted until 1926; Cardoso, 2005).

Poor living and health conditions, particularly in the interior of the country mainland, put Portugal at the tail of Europe for such statistics as life expectancy

(Valério, 2001; see below). In a monography by Correia Pereira (1912) on a "freguesia" in northern Portugal, Palmeira (Braga), these poor conditions are described. Houses were small and generally poor and dirty. Agriculture was mainly of a subsistence quality. It relied on insufficient tools, on traditional, very dated, techniques and on a very fractioned terrain. People spent much of their income on *vendas*, a traditional "bar" or "pub" of sorts, and had very poor dietary habits, depleted of protein. Cultural and social events were restricted to those marking religious calendar. If farmers were considered poor and underfed, people (craftsmen) working out of workshops (producing nails, tiles, iron products, flour and bread, etc.) were even worse off, and were described as physically smaller and thinner still. Socially, people are described as hostile and mistrusting.

Demographically, in the 1800's the Portuguese population was young, since 43% were under 20 years of age in 1864 (Valério, 2001). Between the late 1830's and the early 1860's the mortality rate averages 2.2% per year. In Coimbra, flanked by the late 1830's and the early 1850's, the mortality rate oscillates between 1.355% and 2.463%. Average life expectancy was 31 years from birth and 43 years from the age of three in 1862 (Morais, 2002). In the late 19th and early 20th century mortality rates were 2% and birth rates were 3%. By 1920, life expectancy at birth was 35.8 years for men and 40 years for women (Valério, 2001). For example, the major demographic crisis of the period between 1820 and 1849 in the "freguesia" of the Sé de Coimbra was the cholera outbreak of 1833, which affected the country and Europe as well. The months of July and August concentrated a great number of deaths. Infants were a great part of the mortality rate in the mid-19th century, sometimes reaching 50% of the deaths recorded during a year. Many children died right after their birth, and registered little more than their baptism, that tried to take care of their "eternal soul". The oldest portion of the demographic pyramid was mostly occupied by women, who also composed the majority of widowers (Roque, 1988). These high infant mortality rates were maintained until the 20th century in Portugal. In Oporto between 1896 and 1900 deaths of 5 year olds or younger were half of all deaths, and the ones of infants until 1 year of age were a quarter of all demised (Morais, 2002). The child mortality rate was 14.5% in the early 1930's, figure similar to the rest of Western Europe. In Coimbra, though, this figure was the lowest in the country, 10% for the period of 1929-1932 (Nazareth, 1985).

Although some historians would argue that Portugal's economy and industrial tissue developed during the second half of the 19th century, through the advance of

transportation (see below), the modernization of institutions, the enlargement and betterment of markets and the apparent freeing of the productive forces, this period could be the root of later economical difficulties for this country. The observed growth was still small, when compared to the growth and development occurring on the other developed countries. The developmental scarcity in economy (both in industry and agriculture) was caused by three primary factors, according to most historians: (1) the excessive dependency on exportations, mainly because of England's need for primary products from Portugal and the importations of manufacture from that country, (2) the land ownership structure was inadequate, being too fractured in the North and underexplored in the South, since profits were high even without modern technological advances, (3) the conservative mindset of the time, resistant to advance, didn't allow for the investment in industry or agriculture to enhance profitability (Reis, 1984). In the late 19th/early 20th century most of the population, particularly men, were working in agriculture (Valério, 2001).

In the mid-19th century Coimbra district, commercial and passenger circulation was accomplished mainly through the Mondego River, an important source of traffic that allowed for essential movement of goods and people from the Beira and some of the Estremadura provinces. This movement did not occur without its many difficulties, particularly during the summer, since the river ran low. During the winter, floods were the main issue. From the mid-autumn through the spring the rains were intense, contrasting to the dryness of summer. This impacted circulation and agriculture, often penalized during the rainier months (Roque, 1982).

The opening of railways in Portugal dates to the second half of the 19th century, and allowed for a greater mobility of the population, altering the notion of time and space. If industrially (or economically), this advantage did not bring the needed development, socially the railway intensified tourism. Since early on, the major part of the ticket sales was in the third class (more than 70%), while the first and second classes occupied only less than 10% and up to 20% of their seats, respectively. This originated campaigns (in later decades of the nineteenth century) to promote day-return journeys to the beaches during summertime and travel guides, promoting tourism. Also, the fares were reduced to groups of teachers and their students or excursions, in Portugal and abroad, mainly for major events. Bicycles were already relatively popular in the late 19th century, and were the independent means of transportation that was more financially accessible. Associations promoting the use of bicycles were common in the turn to the

20th century and were only slightly affected by the new 'motoring', a sport for the rich brought about by automobiles. The automobile was introduced in Portugal in 1895 and by 1906 had reached 175 vehicles in Portugal. This came to alter the perspective on road building and originated some press of its own, despite it being mainly directed to elites. On the early 20th century, enterprises had adopted this way of transportation and there were several services across the country, complementing the limited railway (Matos *et al.*, 2010).

The lack of development in Portuguese industry, naturally not due to a lack of transportation, can be justified by several aspects: (1) a low productivity, despite Portugal's labor being the cheapest at the time, mainly caused by the low degree of education of Portuguese workers (almost entirely illiterate) and by the acquisition of inadequate machinery, (2) the inefficient support of the Government, that didn't motivate industrial development, (3) the limited internal market and the incapacity to compete abroad, caused by the mentioned aspects and causing even less productivity, since production was often altered to cater to every small niche of the Portuguese market, (4) the deficient entrepreneurship, who preferred to invest on foreign technicians and employ under-educated laborers than investing on Portuguese technicians (Reis, 1987).

The context of the Industrial Revolution didn't favor Portugal, as was demonstrated through political, social, economical and demographic revisions of the 19th and early 20th centuries. This was source to the most important population movement of the time in Portugal, immigration. Emigration, on the other hand, was not much noted, and it seemed only highly educated individuals were hired abroad, to manage some industries (Reis, 1987).

In Europe, migration laws were restrictive in the 18th century, but liberal thought in the 19th century would change this, making where to work and live an individual choice. Even so, some administrative control was maintained. Passports were always necessary to emigrate (they were free in 1896, and excused in 1907, but only when moving to one of the Portuguese colonies). In the liberal fashion, emigration was not prohibited, but in order to get a passport, minors were to be authorized by their parents, women by their husbands and employees by their hierarchical supervisors. Besides, criminals were not allowed a passport, legal work contracts and guarantee of paid voyage were necessary. Brazil, the main destination for emigrants, was never prohibited, but the Government tried to show the negative conditions there to dissuade

emigration. The main detriment to emigrants was the need to fulfill the military obligations imposed from 1855 in Portugal, taken seriously by a government that could not accomplish the planned military contingents. If someone who had not served in the military wanted to emigrate, they had to pay bail, assuring they would come back and serve or that someone could be hired instead, using that amount (Costa Leite, 1987).

So, illegal emigration could be, from the mid-19th century to the early 20th century, a widespread phenomenon, downgrading official statistics to poor estimates. This reality was imposed by the strictness of law, chastising illegal emigrants and legal ones, the latter through passports and fees. Comparing Portuguese figures and American immigration figures show consistently high correlation between them. This may be due to the fact that clandestine emigration from Portugal was of a high proportion, but could be easily accomplished by using someone else's documents. So, undocumented emigration was the only portion of illegal emigration that went without register in Portugal. This type of emigration does not affect statistics significatively (Costa Leite, 1987).

The long history of immigration in Portugal started with the conquest and discovery of new land and islands. Later, it continued with the creation of new maritime routes to Asia and the Americas. In the 19th century, Brazil witnessed the third wave of Portuguese emigration, which amounted to around 800000 people during the first half of the century and stabilized at a rhythm of about 4000 a year after that. This phenomenon was originated by the independence of Brazil in 1822 and, later on, by the end of slavery, in 1888. Many workers would find employment in the coffee and cotton plantations of São Paulo (Rocha-Trindade, 2012). Transoceanic emigration (between 1855 and the 1950's, to North and South America) had an impact on the Portuguese economy and society, because of its volume and of the amounts of money sent back by emigrants. These ranged between 2% and 4% of the gross domestic product in the first three decades of the 20th century (Baganha, 1994). Coimbra was one of the main suppliers of emigrants during this period of Portuguese emigration. Women were only 30% of the emigrants on the early portion of this period (Valério, 2001).

Only from the 1950's onward were urban centers a main concentrator of population in Portugal. Cities with more than 10000 people only congregated 11% of the population by 1890 (Valério, 2001). The city of Coimbra was the only city in its homonymous district, thus serving as its capital. The remaining area was mainly rural, with the exception of Figueira da Foz, where the Mondego River reaches the Atlantic

Ocean (Roque, 1982). In the late 1800's, Coimbra was a small city, and still conserved the boundaries from three centuries before, despite the growth noted from 1880 onward. The city's population grew from around 12000 people in 1840 to 20000 in 1911. The marked duality of Coimbra was originated in the distinction between the University uptown and the common people downtown. Uptown, around the University, clergymen, professors, students and noblemen lived, besides many servants, who undoubtedly worked for these higher social classes. There, exceptions to the popular architecture were found, through the collegiate and religious buildings. Downtown lived artisans or craftsmen (since the greatest amount of these workers concentrated in Coimbra, district capital) and other working class people, who endured the overflow of the Mondego River on an annual basis (Roque, 1988).

Despite reports of excellent conditions for agriculture in the Coimbra district (1830-1870), there were many setbacks apart from the limitations of circulation (see above). In the littoral, the progressive advance of the sea and the beaches severely impaired the reach of agriculture. This also happened in higher lands, on which more advanced methods could not be used. The weight of tributes, loan sharks and lingering feudalism presented major detriments as well (Roque, 1982). The Portuguese 19th century had constant fluctuation of the price of foodstuffs, with shortages and abundance succeeding one another. The price of wheat in the city of Oporto, for instance, fluctuated all through the century, being at its highest after the French Invasions and at a dry period in the mid-1800's. The described environmental conditions may have affected the variation in cranial morphological traits found in males of the Coimbra collections throughout the 19th century (Bocquet-Appel, 1984).

In the mid-1800's, the Coimbra district was, much like the rest of Portugal, very little industrialized. Its "factories" were usually not worthy of the name, being familiar workshops. Technical advancements were rare and not usually present in the city of Coimbra, when it came to industry. The city concentrated artisans and skilled workers, like shoe-makers, tailors, construction workers and carpenters, for example, although it kept away industries like fishing (obviously concentrated on the shore) and those that processed materials, later imported into Coimbra (Roque, 1982).

Commercially, Coimbra had, like many of the other localities throughout its district, fairs and other periodical markets, where mainly agricultural products were traded. Nonetheless, the city had a relatively strong commercial class, which sold products imported from the district and the country -, particularly from Oporto and

Lisbon -, and displayed the production of the local artisans, alluded to above. "Businessmen", at the time, displayed an important social status and played an important role as loan sharks (Roque, 1982).

The Coimbra day laborers sought work in the off seasons mainly to the South, in or around Lisbon or in Alentejo, thus migrating internally to survive. Nevertheless, emigration became a more common solution in the 1870's (see above for the situation in Portugal), particularly amongst rural workers and towards Brazil, escaping misery, no prospects and military service (Roque, 1982; for an example in Braga district: Correia Pereira, 1912). Men and particularly literates took their chances, especially when under 30 years old. People from the "concelho" (administrative division) of Coimbra weren't the largest part of this migration, but provided a numerous contribution in the 1860's and 1870's (Roque, 1982).

Since the present work intends to illuminate on the population history of Portugal and of the geographical areas with which the Portuguese contacted, the thoughts of the intellectuals of the turn of the 19th to the 20th century are of interest. When the differences between North/Center and South of Portugal were discussed in the late 19th and the early 20th century, in terms of their origins, Northerners are often acquainted with the Celts (Arians) and Southerners with Semitic, northern African (Phoenicians, Cartaginians, Arabs, Jews) influences. On the other hand, Teófilo Braga (twice President of the Portuguese Republic) maintained that the lack of Semitic biological influence and the purity of Lusitanian blood (from Celtic, Arian origin, with a background of pre-Arian peoples from the Asian continent, common with Spaniards and Berbers) justified the Portuguese unity, when compared to the independent tendency found in Spaniards. The Romans and Greeks were also an important element of the Arian contribute, for Braga, since they caused the division among the invading Visigoths, by inspiring the Northern 'lords' to follow their customs and to allow their 'serfs' in the South to be permeable to the Arabic influence. Lastly, the Mozarabs were a mixture of the Germanic influence (agriculture, cattle) with Berber influence. These were, in Braga's later view, the remainder of the main 'racial' divisions of Portugal, the Celtics and the Semitics (Sobral, 2004).

His critics viewed his perception as wrong because they recognized the contributions of many 'races' to the formation of the Portuguese people, but valued the Roman and Greek Arian the most. The superiority of Arian (Indo-European) peoples and their culture, civilization and habits is the source of later pseudo-biologically based

racism against Semitic peoples, namely Jews, but was in the 19th century the synonym of country or nation, giving the illusion of a common origin and fate. In the context of a political and economical crisis in the late 19th century, Teles brings back the question of the racial differences between North and South, suggesting the Northerner should internally colonialize the South in order to keep the country self-sufficient in terms of agriculture. Once again, Northerners are descendents of Arians, and their progress and openness to empiric knowledge; and Southerners of Semitics (here still including Arabs and Berbers, besides Jews), people of commerce and easy gain, instead of agricultural endeavor, subservient to a God instead of science, art and philosophy. This was opposed to Braga's view of the contribution of Semitics, which was mainly scientific and philosophical. Teles's view was, instead, more akin a number of works from Spain and Italy that established divisions along the same terms, the Arian civilized and progressive peoples to the North and the decadent, stagnant, Semites to the South (Sobral, 2004).

The content of Teles's work does not echo notably throughout the scientific literature, although it may reflect a popular belief in the North, mainly because politically this was the target audience for these ideas and because the anthropological approach (based in discrete and metric characters and personified by Mendes Corrêa, mainly) did not consider such subjective discourses as scientifically worthy, criticized the existence of a primitive Arian race, and thought the basis of behavior not only biological but also environmental (Sobral, 2004).

Mendes Corrêa (1919) reviews the anthropological and historical data on the Portuguese populations from the Epipaleolithic, Neolithic, Bronze and Iron Ages and historical times in the early days of the *American Journal of Physical Anthropology*. Despite his defense of science (see above), the author still advocates the national coherence of the Portuguese predates the country's formation, and seems to be connected to the Lusitanian tribes inhabiting the territory before Roman invasion. The role of Indo-European peoples is uncertain, but that of Romans, Visigoths, Suevi and Moors is merely that of adaption to the natives. The Romans, however, provided some organization and coherence, but were less able to subjugate the Lusitanians than what is normally assumed, in Mendes Corrêa's view. A variety of anthropometric evidence points to a general typing of the Portuguese as similar to other European and Mediterranean peoples, with some influence from the historical Nordic (Visigoths and Suevi) and Islamic invaders.

Sardinha, in the early 20th century, sees the Portuguese people as descendants of the Lusitanian, different from the Arians in Spain and dragged down by the biological influences of Semitics and Blacks. This author defended a country with biological unity, only questioned in the North, where the Celtic influence was greater, and limited the Lusitanian heritage. Contrarily to the authors mentioned, Sardinha was from Alentejo, in the South. Later in his life, he saw the union with Spaniards more favorable to his political intents, because of the dictatorship installed in both countries, and divided the country into "republican" and "monarchic" 'races'. The first one was biologically contaminated with Jewish and Black blood and the second with the remainder of Lusitanian purity (Sobral, 2004).

Finally, the view of the Portuguese people as a biological unity is patent from the mid-20th century onwards, mainly through the continuity from the Lusitanians. This is only questioned popularly, particularly in Oporto and through its main football club fans (from Futebol Clube do Porto), but all throughout the North, where it is relatively common to call Southerners "Mouros" (Moors) or the South "Mourolândia" (Land of Moors), for instance. This identification is mainly derived from the notion of the North as the origin and birthplace of Portugal (from the county of Portucale, around the contemporary city of Oporto), which is now ruled by Lisbon, in the Center/South. The identity of the Portuguese people as a nation is never questioned (Sobral, 2004). This controversy, typical of the late 19th/early 20th century, illustrates the population history of Portugal, which should be anthropologically tested. These analyses should not be directed towards the very unlikely biological/genetic differences between the North and South Portuguese populations, but towards the presence of biological contributions of all peoples involved to the current biological profile of the Portuguese.

2.Sample

2.1.Overall description

2.1.1.Particularities of an identified sample

The sample is composed of 600 individuals (300 males and 300 females), from 7 to 97 years old at death (although male individuals span from 11 to 84 years at death only; mean age at death: 35.84, 35.83 for female individuals and 35.84 for males), represented by their crania and mandibles. They were born between the years of 1820 and 1924, and died between 1896 and 1938. The individuals were selected among the "Trocas Internacionais" (International Trades: 300 males and 269 females) and "Escolas Médicas" (Medical Schools: 31 females) collections from the Department of Life Sciences, Faculty of Sciences and Technology, University of Coimbra (see Appendix 1). All individuals were primarily selected for having more than five dental pieces on each of the maxillary and mandibular dental arches. Then, the final 600 individuals were chosen among the total in order of serial number.

The distribution of ages at death for the whole sample, and for males and females separately, can be found on Table 2.1., divided into ten decades. The ages at death of the studied individuals vary mostly between 20 and 49 years.

Table 2.1. Ages at death. Distributions according to total sample, male and female individuals.

Age		Frequency (n = 600)	Frequency (males; n = 300)	Frequency (females; n = 300)
0-9	n	1	0	1
	%	0.2%	0%	0.3%
10-19	n	98	49	49
	%	16.3%	16.3%	16.3%
20-29	n	166	80	86
	%	27.7%	26.7%	28.7%
30-39	n	108	56	52
	%	18.0%	18.7%	17.3%
40-49	n	112	57	55
	%	18.7%	19.0%	18.4%
50-59	n	49	25	24
	%	8.2%	8.3%	8.0%
60-69	n	41	23	18
	%	6.8%	7.7%	6.0%
70-79	n	17	8	9
	%	2.8%	2.7%	3.0%
80-89	n	5	2	3
	%	0.8%	0.7%	1.0%
90-99	n	3	0	3
	%	0.5%	0%	1.0%

Table 2.2. reports the decades of birth for all individuals, and male and female individuals. Most individuals were born between the 1880's and the 1910's. The same

information for decades of death is found on Table 2.3., on which the 1920's and 1930's are predominant.

Table 2.2. Decades of birth. Distributions according to total sample, male and female individuals.

Decade of birth		Frequency (n = 600)	Frequency (males; n = 300)	Frequency (females n = 300)
1820's	n	2	0	2
	%	0.3%	0.0%	0.6%
1830's	n	5	0	5
	%	0.8%	0.0%	1.7%
1840's	n	8	2	6
	%	1.3%	0.6%	2.0%
1850's	n	22	13	9
	%	3.7%	4.3%	3.0%
1860's	n	39	16	23
	%	6.5%	5.3%	7.7%
1870's	n	61	26	35
	%	10.2%	8.7%	11.7%
1880's	n	94	47	47
	%	15.7%	15.7%	15.7%
1890's	n	119	69	50
	%	19.8%	23.0%	16.7%
1900's	n	144	77	67
	%	24.0%	25.7%	22.3%
1910's	n	96	44	52
	%	16.0%	14.7%	17.3%
1920's	n	7	3	4
	%	1.2%	1.0%	1.3%
Unknown	n	3	3	0
	%	0.5%	1.0%	0.0%

Table 2.3. Decades of death. Distributions according to total sample, male and female individuals.

Decade of death		Frequency (n = 600)	Frequency (males; n = 300)	Frequency (females; n = 300)
1890's	n	19	0	19
	%	3.2%	0.0%	6.3%
1900's	n	13	0	13
	%	2.2%	0.0%	4.3%
1910's	n	5	2	3
	%	0.8%	0.7%	1.0%
1920's	n	246	141	105
	%	41.0%	47.0%	35.0%
1930's	n	314	154	160
	%	52.3%	51.3%	53.4%
Unknown	n	3	3	0
	%	0.5%	1.0%	0.0%

Table 2.4. shows the individuals origin, either in Portuguese continental districts, or in a Portuguese archipelago (an individual from Madeira), a continent, or a country of origin. Sixty-seven percent of all individuals, a vast majority, were born in the Coimbra district. All 585 individuals, males and females, born in continental Portugal were also divided into region of origin on Table 2.5., through a strictly geographical criterion. The

Table 2.4. Sample birthplaces. Distributions according to total sample, male and female individuals.

Birthplace*		Frequency (n = 600)	Frequency (males; n = 300)	Frequency (females = 300)
Aveiro	n	16	7	9
	%	2.7%	2.3%	3.0%
Braga	n	4	1	3
	%	0.7%	0.3%	1.0%
Castelo Branco	n	9	5	4
	%	1.5%	1.7%	1.3%
Coimbra	n	402	201	201
	%	67.0%	67.0%	67.0%
Évora	n	3	3	0
	%	0.5%	1.0%	0.0%
Faro	n	2	2	0
	%	0.3%	0.7%	0.0%
Guarda	n	36	25	11
	%	0.6%	8.3%	3.7%
Leiria	n	37	16	21
	%	6.2%	5.3%	7.0%
Lisboa	n	10	3	7
	%	1.7%	1.0%	2.3%
Portalegre	n	5	5	0
	%	0.8%	1.7%	0.0%
Porto	n	11	3	8
	%	1.8%	1.0%	2.7%
Santarém	n	8	5	3
	%	1.3%	1.7%	1.0%
Setúbal	n	2	0	2
	%	0.3%	0.0%	0.7%
Viana do Castelo	n	1	0	1
	%	0.2%	0.0%	0.3%
Vila Real	n	10	8	2
	%	1.7%	2.7%	0.7%
Viseu	n	29	9	20
	%	4.8%	3.0%	6.7%
Africa	n	1	0	1
	%	0.2%	0.0%	0.3%
Brazil	n	2	0	2
	%	0.3%	0.0%	0.7%
Spain	n	5	4	1
	%	0.8%	1.3%	0.3%
France	n	1	0	1
	%	0.2%	0.0%	0.3%
Madeira archipelago	n	1	1	0
	%	0.2%	0.3%	0.0%
Unknown	n	5	2	3
	%	0.8%	0.7%	1.0%

*(Portuguese district or otherwise stated country/continent/Portuguese archipelago).

North region includes the districts of Aveiro, Braga, Guarda, Porto, Viana do Castelo, Vila Real and Viseu. As for the Centre region, it comprises the districts of Castelo Branco, Coimbra, Leiria, Lisboa and Santarém. Finally, the South region is divided into the districts of Évora, Faro, Portalegre and Setúbal. The Centre of Portugal is the birthplace of most individuals in the present sample (79.6%), while the South is rarely represented (2.1%, mostly male individuals).

Table 2.5. Birth regions. Distributions according to total sample, male and female individuals.

Birthplace*		Frequency (n = 585)	Frequency (males; n = 293)	Frequency (females; n = 292)
North	n	107	53	54
	%	18.3%	18.1%	18.5%
Centre	n	466	230	236
	%	79.6%	78.5%	80.8%
South	n	12	10	2
	%	2.1%	3.4%	0.7%

*(Continental Portuguese region of birth only).

Table 2.6. comprises succinct data on causes of death, in accordance with the World Health Organization's "International Statistical Classification of Diseases and Related Health Problems, Version 2010 (10th Revision)" online app (http://apps.who.int/classifications/icd10/browse/2010/en). The alphabetical divisions used are explained below the Table. The most commonly found diseases are those involving bacterial and parasitic infections (A; 42.2%), which is monopolized by tuberculosis, found in many forms in a total of 38.0% of the sample. Other very common causes of death are related to ailments of the circulatory (I), respiratory (J) and digestive (K) systems.

Table 2.6. Causes of death. Distributions according to total sample, male and female individuals.

Disease*		Frequency (n = 600)	Frequency (males; n = 300)	Frequency (females; n = 300)
A	n	253	139	114
	%	42.2%	46.4%	38.0%
C	n	31	13	18
	%	5.2%	4.3%	6.0%
D	n	4	1	3
	%	0.6%	0.3%	1.0%
E	n	4	3	1
	%	0.6%	1.0%	0.3%
F	n	1	1	0
	%	0.2%	0.3%	0.0%
G	n	12	6	6
	%	2.0%	2.0%	2.0%
H	n	1	0	1
	%	0.2%	0.0%	0.3%
I	n	72	33	39
	%	12.0%	11.0%	13.0%
J	n	51	28	23
	%	8.5%	9.3%	7.7%
K	n	52	26	26
	%	8.7%	8.7%	8.7%
L	n	4	3	1
	%	0.6%	1.0%	0.3%
M	n	7	3	4
	%	1.2%	1.0%	1.3%
N	n	21	13	8
	%	3.5%	4.3%	2.7%
O	n	19	0	19
	%	3.2%	0.0%	6.4%
Q	n	1	0	1
	%	0.2%	0.0%	0.3%

Table 2.6. (Continued.)

Disease*		Frequency (n = 600)	Frequency (males; n = 300)	Frequency (females; n = 300)
R	n	19	8	11
	%	3.2%	2.7%	3.7%
S	n	5	4	1
	%	0.8%	1.3%	0.3%
T	n	8	3	5
	%	1.3%	1.0%	1.7%
W	n	3	2	1
	%	0.5%	0.7%	0.3%
X	n	1	0	1
	%	0.2%	0.0%	0.3%
Y	n	2	2	0
	%	0.3%	0.7%	0.0%
Z	n	1	0	1
	%	0.2%	0.0%	0.3%
Unknown/	n	28	12	16
Unclassifiable	%	4.6%	4.0%	5.4%

* Diseases: A – Bacterial infectious and parasitic diseases (mainly tuberculous); C – Malignant neoplasms; D – In situ, benign or uncertain neoplasms and diseases of the blood and blood-forming organs, and some disorders involving the immune system; E – Endocrine, nutritional and metabolic diseases; F – Mental and behavioral disorders; G – Diseases of the nervous system; H – Diseases of the eye, the adnexa, the ear and mastoid processes; I – Diseases of the circulatory system; J – Diseases of the respiratory system; K – Diseases of the digestive system; L – Diseases of the skin and subcutaneous system; M – Diseases of the musculoskeletal system and connective tissue; N – Diseases of the genitourinary system; O – Pregnancy, childbirth and the puerperium; Q – Congenital malformations, deformations and chromosomal abnormalities; R – Symptoms, signs and abnormal clinical and laboratory findings, not elsewhere classified; S – Injuries to specific body parts; T – Injury, poisoning and certain other consequences of external causes; X – Certain other consequences of exposure to external causes, assault and intentional self-harm; Y – Legal, medical, surgical, war consequences and sequelae of other external causes; Z – Factors influencing health status and contact with health services.

In identified skeletal collections, and the study of the populations those individuals are drawn from, their occupation is relevant and can inform on the representativeness of the sample (Perréard Lopreno *et al.*, 2013). However, those data were not interpreted in the present case, due to a lack of specificity in the description of the sample's employment diversity (see the same issues in Santos [2000] and Wasterlain [2006], for instance).

2.1.2.Portuguese anthropological research history as related to identified skeletal collections

The collection of skeletons in museums and universities (through then forming Departments of Anthropology and through Departments of Anatomy) was started in the 18th century (Tobias, 1991; Cunha and Wasterlain, 2007). Western Europe was the birthplace of anthropology, namely in its opposition to ethnography (the antecedent to cultural and social anthropology and archaeology). So, "anthropology" stood for what is now physical or biological anthropology (Santos, 2012). Some values of skeletal collections are: (1) to compare populations, including the measure of their biological affinities, (2) to study sexual dimorphism, both in the metric and non-metric aspects, (3) dental studies, including variability between and within tooth groups and the field concept, the presence of diastemata and dental anatomy, for instance (Tobias, 1991).

Despite its origins lying in the 18th century, anthropology in Portugal came to be in the second half of the 19th century. Contrastingly to the remaining colonialist Europe, in Portugal the main focus was on the study of man and human evolution in the metropolis, Portugal. This is due to the fact that social and economical weaknesses hindered the blooming of Portugal's "Third Empire", the full exploitation of African colonies. The advent of a "colonialist anthropology", prompted by the realization of the "Third Empire" and Salazar's right-wing dictatorship, came about only in the 1930's, after the downfall of Portuguese monarchy in 1910 and the Republican experience in 1926 (Santos, 2012).

Carlos Ribeiro and his "Comissão Geológica" started a tradition in archaeological and anthropological field research in the beginning of the second half of the 19th century. Their work gathered attention from the political sphere, from scientists and researchers abroad (Santos, 2012; see an early 20th century review and critique in Mendes Corrêa, 1919). Ultimately, it drove to the creation of the chair of Anthropology at the then Faculty of Natural Philosophy (now "Faculdade de Ciências e Tecnologia": Faculty of Sciences and Technology) of the University of Coimbra, in 1885 (Santos, 2012). The first Portuguese human skull collection was assembled by Ferraz de Macedo, a Portuguese researcher educated in Brazil and France, between 1875 and 1877 in Lisbon, with material from two cemeteries in that capital, unfortunately mostly destroyed by fire in 1978 (Rocha, 1995; Santos, 2000; Cunha and Wasterlain, 2007;

Santos, 2012). The collection of human identified osteological material in Coimbra started in 1915 (Rocha, 1995; Santos, 2000; Cunha and Wasterlain, 2007).

The "Trocas Internacionais" collection was acquired by Eusébio Tamagnini between 1932 and 1942, from the Conchada cemetery, the largest burial ground in Coimbra (Fernandes, 1985; Rocha, 1995; Santos, 2000; Wasterlain, 2006; Cunha and Wasterlain, 2007; Santos, 2012). In Portugal, church burials were prohibited by an Act passed on the 21st of September, 1835 (Santos, 2000). The Conchada cemetery was established in 1855, after some use from 1852 onward by the Hospital, which was in great need of such an arrangement. This was due to a growing health concern surrounding burials in churches or churchyards brought from the early 19th century by scholars and knowledgeable people. Coimbra also established a cemetery on Santo António dos Olivais. Cemeteries were initially used by the lower classes, predominantly, reflecting a differentiation in death which occurred before, through the burial inside churches of the more socially important individuals and in churchyards of the common people (Roque, 1988). The 1075 individuals (524 males and 551 females) of this collection died between 1915 and 1938. These individuals were aged between 6 and 109 years. They were born, according to their ages at death, between 1818 and 1932 (Fernandes, 1985; Rocha, 1995; Wasterlain, 2006; Cunha and Wasterlain, 2007). This collection is comprised of people buried in public plots, who were to be exhumed after five years, so as to be stored in ossuaries or claimed by their relatives. Instead, due to their research importance and lack of familial intervention, it was agreed they should be studied by anthropologists and medical students or anatomists (Bocquet-Appel, 1984; Cunha and Wasterlain, 2007; Santos, 2012). The 'International Trades' collection was meant to be traded with investigators from other countries, as its name suggests (Fernandes, 1985; Rocha, 1995; Cunha and Wasterlain, 2007).

The "Escolas Médicas" collection was acquired by Bernardino Machado, between 1896 and 1903, with the purpose of gathering samples from every district of continental Portugal (Fernandes, 1985; Rocha, 1995; Santos, 2000; Wasterlain, 2006; Cunha and Wasterlain, 2007; Santos, 2012). Bernardino Machado, like Ferraz de Macedo (see above), also had Brazilian links, since he was born and lived there almost a decade of his childhood. He was, however, educated in the University of Coimbra, and taught there. The creation of the chair of "Anthropology, human paleontology and prehistoric archaeology" was proposed by him. Machado was very involved in politics throughout his life, which sometimes led to his absence from academic activity (Santos,

2012). The "Escolas Médicas" collection came from the Medical Schools of Oporto and Lisbon and the Anatomical Museum of the Faculty of Medicine of the University of Coimbra. All 585 individuals (366 males and 219 females) perished between 1895 and 1903. These individuals were aged between 11 and 99 years, although 10 of them were not aged. They were born, as their ages suggest, from 1803 to 1890 (Fernandes, 1985; Rocha, 1995; Santos, 2000; Wasterlain, 2006; Cunha and Wasterlain, 2007).

Another assortment, the "Colecção de Esqueletos Identificados" (Identified Skeletal Collection), which includes 505 complete or almost complete skeletons that belonged to individuals who died in Coimbra between 1904 and 1938 (Fernandes, 1985; Rocha, 1995; Santos, 2000; Wasterlain, 2006; Cunha and Wasterlain, 2007), was not included in the present study.

The Coimbra series belongs to the most complete set of osteological collections, because of the good preservation of the samples and because of the complete records that detail the description of each case (Cunha and Wasterlain, 2007). When created, these collections were essential to study the anthropology of the Portuguese "metropolitan" population, - in opposition to colonial "indigenous" populations, which would be researched at a later period -, focused on the biological unity of the Portuguese and their placement among the dominant European "white race", which was paired with the interest in the natural history of the Portuguese in the anthropological research of the time (Santos, 2012; for an example of this, see Mendes Corrêa, 1919).

Santos (2000) suggests the individuals in the Coimbra series might have been registered later than their actual date of birth, so as to avoid a late fee. This author also warns to the possibility of long stays in hospital installations without change in the recorded age. Most individuals in the Identified Skeletal Collection (not included in the present sample) were interred in flat graves, not on mausoleums, which again testify to the generally low social status of the individuals (Santos, 2000).

*2.1.3.Dental conservation of the present sample (*ante- *and* post-mortem *tooth loss)*

Both referred collections are well kept and in good condition, but there is a good deal of *post-mortem* tooth loss (PMTL = 14.0%; corroborating the idea reported by Cunha and Wasterlain [2007]), particularly among the crania and mandibles of the "Escolas Médicas" (Wasterlain [2006] found 16.4% of PMTL in the "Escolas Médicas"

Table 2.7. *Post-* and *ante-mortem* tooth loss frequencies. Distributions according to total sample, male and female individuals.

Tooth		PMTL frequency (n = 600)	AMTL frequency (n = 600)
11	n	220	21
	%	36.7%	3.5%
21	n	211	33
	%	35.2%	5.5%
31	n	175	28
	%	29.3%	4.7%
41	n	173	25
	%	28.8%	4.2%
12	n	150	16
	%	25.0%	2.7%
22	n	136	23
	%	22.7%	3.8%
32	n	130	8
	%	21.7%	1.3%
42	n	144	5
	%	24.0%	0.8%
13	n	91	11
	%	15.2%	1.8%
23	n	85	14
	%	14.2%	2.3%
33	n	78	1
	%	13.0%	0.2%
43	n	92	3
	%	15.3%	0.5%
14	n	70	78
	%	11.7%	13.0%
24	n	62	72
	%	10.3%	12.0%
34	n	86	21
	%	14.3%	3.5%
44	n	88	27
	%	14.7%	4.5%
15	n	85	92
	%	14.2%	15.3%
25	n	51	103
	%	8.5%	17.2%
35	n	87	43
	%	14.5%	7.2%
45	n	89	50
	%	14.8%	8.3%
16	n	13	134
	%	2.2%	22.3%
26	n	12	131
	%	2.0%	21.8%
36	n	10	192
	%	1.7%	32.0%
46	n	20	192
	%	3.3%	32.0%
17	n	22	86
	%	3.7%	14.3%
27	n	21	71
	%	3.7%	11.8%
37	n	17	131
	%	2.8%	21.8%
47	n	28	117
	%	4.7%	19.5%
18	n	81	152
	%	13.5%	25.3%
28	n	77	142
	%	12.8%	23.7%
38	n	35	175
	%	5.8%	29.2%
48	n	43	164
	%	7.2%	27.3%

collection, and only 11.5% on "Trocas Internacionais"), making it less valuable to the projected investigation, which justifies its minimal use.

Table 2.7. displays frequencies and percentages of PMTL and *ante-mortem* tooth loss (AMTL) per predictable tooth in the sample. PMTL diminishes from anteroposteriorly, with the rise of the right UP4 and of all M3 as exceptions. This trend is probably due to root number and shape. Between upper and lower teeth, PMTL affects the former most, except for the right LI2, right LC, right LM1 and LM2, and for all LP, which are more affected. This pattern is most likely due to the influence of gravity, and the exceptions may be due to the finger placement of researchers or students who manipulated the specimens. Duric and colleagues (2004) associated PMTL with *post-mortem* interval and teeth root number (and type, since the UI1 is more affected because of its conical root). Excavation technique and expertise did not show significant differences (Duric *et al.*, 2004). Even so, when establishing a skeletal collection, if possible, it is very important to exhume the skeletons using archaeological and anthropologically adequate techniques, in order to preserve the skeleton and the dentition, besides identifying any alterations or associated phenomena (Bosio *et al.*, 2012). If this advice had been followed, probably there would be less *post-mortem* tooth loss (even if not significantly), but the time frame of the inhumations (second quarter of the 20th century) most likely did not allow for such preclusions. The handling of the crania and mandibles by many researchers and students throughout the years (see Fernandes, 1985) probably contributed to PMTL.

The *chi*-square test was used to infer the differences in PMTL and AMTL proportions between sexes, dental arcades, sides and anterior and posterior dentition. When sexes were compared for PMTL (M: 12.9%, 1234/9600; F: 15.1%, 1448/9600), differences were found to be unlikely caused by any random effect ($\chi^2 = 19.848$; df = 1; P = 0.000), which allows the conclusion that women present more PMTL, possibly due to less robust roots. The same discrepancy was found in Carvalho's (2013) sample, and noted as unusual. Despite the reported differences affecting the upper (14.4%; 1387/9600) more than the lower dentition (13.5%; 1295/9600), as observed, this difference could be due to random sampling ($\chi^2 = 3.668$; df = 1; P = 0.055). Differences between sides are found (L: 13.3%, 1273/9600; R: 14.7%, 1409/9600), and are statistically shown as not random ($\chi^2 = 8.016$; df = 1; P = 0.005), which may again be due to the handedness of the researchers who manipulated these specimens (assuming most people handling them were right handed, and held teeth on the left side better), but

this issue requires more research. PMTL occurred with a much greater frequency on the anterior teeth (23.4%, 1685/7200; posterior teeth: 8.3%, 997/12000), as previously described, and this difference is now shown as clearly indicative of a non-random trend (χ^2 = 853.165; df = 1; P = 0.000).

AMTL diminishes anteroposteriorly within the anterior dentition, following the order of eruption of these teeth (the first to erupt is the one lost the most, and so on). In the posterior dentition, there is an overall anteroposterior increase in AMTL. However, there are the exceptions of all M2 and both LM3, showing decrease in AMTL when compared to M1's. These teeth (all first molars), as the first to erupt, are the most affected. The remaining molars may justify their relatively high AMTL with greater susceptibility to caries and other oral pathologies, due to their anatomy. The figures might be slightly exaggerated for all M3, since radiological analyses were not used (due to a lack of time and resources) to distinguish AMTL from tooth agenesis.

Upper teeth (except for all molars and the right UI1) are more subject to AMTL. This may be related to the effect of gravity when the alveolar bone has been compromised. Lower molars are lost in life in greater number than their upper counterparts. The depth of their central *fossae* and a greater accumulation of plaque (assured by gravity and the larger crevice space) may be the cause of this. Teeth attach to bone in the mouth through cement, the periodontal ligament, alveolar bone and gingiva (Duric *et al.*, 2004). A review of the aging process in bone culminates with a lack of causality between oral bone loss (and osteoporosis in general) and age. There is, however, an association, since bone loss is facilitated by age, through several molecular and cellular modifications. For it to occur, though, there has to be some other etiology, a precipitating factor further aggravated by age (Boskey and Coleman, 2010). The occurrence of these precipitating factors (oral pathologies) may justify the degree of AMTL in this sample with only 19.2% of individuals over 50 years.

The differences found for AMTL between sexes (M: 11.8%, 1131/9600; F: 12.8%, 1230/9600) reveal a slight tendency for a greater female loss of teeth during life which is not occasioned by random sampling (χ^2 = 4.733; df = 1; P = 0.030). As for dental arches, *ante-mortem* tooth loss in general is identical in both (L: 12.3%, 1182/9600; U: 12.3%, 1179/9600), as is demonstrated statistically (χ^2 = 0.004; df = 1; P = 0.947). This feature is also identical in both sides (L: 12.4%, 1188/9600; R: 12.2%, 1173/9600) and a difference is not statistically detected either (χ^2 = 0.109; df = 1; P = 0.742). AMTL is, however, much more frequent on the posterior dentition (18.1%,

2173/12000; anterior dentition: 2.6%, 188/7200), which is most likely not a random effect ($\chi^2 = 1002.098$; df = 1; P = 0.000).

This analysis hails, for PMTL and AMTL alike, some very different results from those obtained by Wasterlain (2006). It is vital to keep in mind the prerogative of this study to select the individuals with the most teeth available. Wasterlain (2006), on the other hand, obeyed a strict age structure and took a more cautious approach to these results, since they were part of the bulk of her research.

The mentioned differences were more noticeable on AMTL results. This author found 37.5% of the total observable alveoli showed some indication of resorption, which is much greater than what was found presently (12.3%). The patterns of results present some likeness, since women tend to lose more teeth *ante-mortem*, sides do not reveal notable differences, and anterior teeth are much less frequently loss than posterior teeth, according to both studies. Another difference in the results of both studies is found when dental arcades are compared, since Wasterlain (2006) found significant differences between them and the present sample demonstrates equal AMTL on both. Carvalho (2013) analyzed a Medieval sample from Coimbra and found 20.7% of AMTL. Males loss teeth more frequently (although females loss more teeth overall) and the upper dental arch was the one that lost the most teeth, which may be related to higher frequencies of dental caries and periapical inflammation. Otherwise, the result patterns were similar: more posterior teeth were lost *ante-mortem* and AMTL affected both sides equivalently (Carvalho, 2013).

These final considerations have the objective of reminding the reader of the character of this chapter, where the sample is merely described and scarcely discussed. The differences between the samples of Wasterlain (2006) and the present one, which share provenience and number of individuals, are justified by the different purposes of each investigation. In the matter of the paleoepidemiology of oral disease(s), the results discussed by Wasterlain (2006) are much more informative.

3.Methods

3.1.Descriptive methodology

3.1.1.Discrete dental traits

The Arizona State University Dental Anthropology System (ASUDAS: Turner *et al.*, 1991) will be used to characterize the dental nonmetric traits of the dentition. This system, supported by plaques that illustrate some of the traits, intends to avoid the present/absent dichotomy safely and increase the possibility of replicating results, when considering several evenly distributed grades (Turner *et al.*, 1991). The chosen traits distinguish themselves through an ease in identification and observation (Turner *et al.*, 1991). They are also harder to obliterate through dental wear, they display low (or no) sexual dimorphism, evolve slowly and are useful in distinguishing population groups biologically (Turner *et al.*, 1991). This allows for valuable information to be acquired with a low cost. Information relative to each dental morphological trait was complemented with aid from the second chapter of Scott and Turner's 1997 work when possible and, occasionally, with other pertinent sources.

Dental wear is physiologically normal, and allows for some functionality of affected teeth to be preserved (Kaidonis, 2008). The importance of wear in dental morphology studies is underlined by the decrease it causes on a tooth's representation (as happened with the maxillary first molar, when compared to the maxillary second molar, on Edgar's 2007 work, for example). Occlusal wear originates difficulty in determining if a tooth is possible to score or observe accurately (Burnett *et al.*, 2010; Marado, 2010).

Dental wear will be accounted for, and teeth that contribute towards augmenting intra-observer error due to great dental wear will be removed from the results. The effect of dental wear on dental nonmetric trait frequencies will be tested. In measuring dental wear, the method proposed and described by Smith (1984) was used. This method to collected data on dental wear is recommended, in particular for premolars and the anterior dentition, because of its ease and useful application in several dental researches (Rose and Ungar, 1998). Hillson (2001) also recommends it as the "simplest to use" (Hillson, 2001: p. 275), in his thorough method for recording dental caries.

Dental discrete traits were selected so as to appropriately fit the described sample. No root traits were selected, since loose teeth are not a part of this sample.

Traits are to be selected (or removed, if necessary) according to the sample or group. When a trait is present or absent in every individual analyzed, statistical analysis will be negatively affected (Tyrrell, 2000). Not all traits could be included for this sample, whether they would be present in very low frequencies or absent altogether (like Uto-Aztecan premolar or Bushman canine), or because of the difficulty in scoring them in a skeletal collection without using radiological analyses. One such example is agenesis of the third molar. It is difficult to diagnose, since other phenomena can mimic the lack of tooth development, like impaction or ectopia (Alt and Türp, 1998). Another example is LM1 lingual cuspule, a very rare trait that would be difficult to evaluate in relation to genetic inheritance and variation, so would be useless in population biological affinities (Irish, 1991). Every selected trait, grading system and corresponding dichotomy is listed on Table 3.1.

Selected traits (maxillary dental arch):

- *Winging* of the central incisors (Turner *et al.*, 1991; Scott and Turner, 1997; Scott, 2008): bilateral rotation of the mesial margins of the incisors, forming a V with the tip pointed towards the palate. It may be unilateral, which can be caused by anterior tooth crowding. That may also be the cause of counterwinging. These variables are also scored, but should be interpreted carefully and are not as important in population studies;

- *Shoveling* of the central incisors (Hillson, 1986; Turner *et al.*, 1991; Scott and Turner, 1997): protuberant lingual margins of incisors, enclosing a deep fossa in the lingual surface of incisors (and canines, occasionally);

- *Double shoveling* of the central incisors (Turner *et al.*, 1991; Scott e Turner, 1997): protuberant lingual margins of incisors, particularly the mesial margin, where a greater expression or sole appearance is possible;

- *Midline diastema* of the central incisors (Irish, 1998b): occurrence of a space between the central incisors, which should be greater than 0.5 mm, and is usually linked to African populations;

Table 3.1. Selected traits, methodologies, grading systems and breakpoints used.

Trait (teeth observed)	Method	Grades	Presence
Midline diastema	Irish, 1998b	N/A	> 0.5 mm
Winging (I^1)	ASU	1(a and b)-4	1a and 1b
Shoveling (I^1; I_1; I_2)	ASU	0-6	2-6
Double shoveling (I^1)	ASU	0-6	2-6
Interruption grooves (I^1; I^2)	ASU	0; M; D; MD; Med.	~= 0
Peg incisors (I^2)	ASU	0-2	1-2
Tuberculum dentale (I^2)	ASU	0-6 (including 5-)	2-6 (including 5-)
Distal accessory ridge (^{C}; c)	ASU	0-5	1-5
Accessory cusps (P^3; P^4)	ASU	0-1	1
Accessory crests (P^3; P^4)	Scott and Turner, 1997	0-1	1
Tricuspid premolars (P^3; P^4)	ASU	0-1	1
Odontome (P^3; P^4; P_3; P_4)	ASU	0-1	1
Carabelli's trait (M^1)	ASU	0-7	2-7
C5/metaconule (M^1)	ASU	0-5	2-5
Mesial marginal accessory tubercles (M^1)	Scott and Turner, 1997	0; mesial paracone tubercle (MPT); protoconule (PL); mesial accessory tubercle (MAT); lingual paracone tubercle (LPT).	~= 0
Enamel extensions (M^1; M^2; M^3)	ASU	0-3	1-3
C4/hypocone (M^2)	ASU	0-5 (including 3.5)	3-5 (including 3.5)
Parastyle (M^3)	ASU	0-6	1-6
Lingual cusp number (P_3; P_4)	ASU	A-9 (0 follows A)	2-9
Deflecting wrinkle (M_1)	ASU	0-3	1-3
Anterior fovea (M_1)	ASU	0-4	1-4
Cusp/groove pattern (M_1; M_2; M_3)	ASU	Y; +; X	Y (M_1; M_3) + and X (M_2)
Distal trigonid crest (M_1; M_2; M_3)	ASU	0-1	1
Protostylid (M_1; M_2; M_3)	ASU	0-7	1-7
MMPT (M_1; M_2; M_3)	Weets, 2009 (adapted)	0-3+	1-3+
Cusp number (M_1; M_2; M_3)	ASU	4-6	4 and 6 (M_1) 5 and 6 (M_2; M_3)
C5 (M_1; M_2; M_3)	ASU	0-5	1-5
C6 (M_1; M_2; M_3)	ASU	0-5	1-5
C7 (M_1; M_2; M_3)	ASU	0-4 (including 1A)	1-4
Mandibular *torus*	ASU	0-3	1-3
	Galera *et al.*, 1995	Ausente-Fuerte	Débil-Fuerte
Palatine *torus*	ASU	0-4	1-4
	Galera *et al.*, 1995	Ausente-Fuerte complete	Débil incomplete-Fuerte complete
Foramina mentales	Hauser and De Stefano, 1989	N/A	2 or more *foramina*
Mylohyoid bridge	Hauser and De Stefano, 1989	0-complete bridge	Incomplete or complete bridge(s)

- *Interruption groove* of the maxillary incisors (Turner *et al.*, 1991; Scott and Turner, 1997): groove crossing the *cingulum* (that may continue down the root). It may be related to the *tuberculum dentale* trait. More common on the lateral incisors;

- *Tuberculum dentale* of lateral incisors (Turner *et al.*, 1991; Scott and Turner, 1997): may appear as ridges along the lingual margins of incisors (and canines), originating from the *cingulum*, and are susceptible to be as large as cusps. The variation is difficult to classify, so this trait is prone to intra- and inter-observer error;

- *Peg shape* of lateral incisors (Turner *et al.*, 1991; Scott and Turner, 1997; Alt and Türp, 1998): progressive reduction in size of lateral incisors, with ultimate abnormal crown morphology (microdontia), probably culminating with the congenital absence of the tooth (Figure 3.1., p. 87);

- *Distal accessory ridge* of canines (Scott, 1977; Turner *et al.*, 1991; Scott and Turner, 1997): ridge on the distolingual fossa, between the cusp apex (tip of the medial lingual ridge) and the distolingual crest, or distal marginal ridge. It is somewhat of a problematic trait, which can easily disappear. It is not reflected on dentine when worn, and is the most sexually dimorphic trait;

- *Accessory cusps* on premolars (Turner *et al.*, 1991; Scott and Turner, 1997): small cusps at each end (distal and mesial) of the sagittal groove of the premolars may appear, being clearly divided from the buccal and lingual cusps, strongly separated;

- *Accessory ridges* on premolars (Scott and Turner, 1997; Burnett *et al.*, 2010): ridges that can be identified on the mesial and distal accessory lobe segments of the buccal cusp of premolars. The presence of each ridge is not independent, but the distal accessory ridge is more common. Maxillary premolar accessory ridges are more common and useful to distinguish between populations than other premolar nonmetric traits but are ignored in most dental morphology studies;

- *Tricuspid* premolars (Turner *et al.*, 1991; Scott and Turner, 1997): rare variation of premolars with three cusps (the extra cusp is lingual);

- *Odontome* on premolars (Turner *et al.*, 1991; Scott e Turner, 1997): small enamel and dentine projection (which can be accompanied by a pulpar projection as well), on the occlusal surface of premolars. It can be visualized even when it breaks off or the tooth has moderate dental wear. It is approximately pinhead-shaped, over a conical tubercle;

- *Carabelli's trait* on first molars (Dahlberg, 1963; Turner *et al.*, 1991; Scott and Turner, 1997): trait that occurs on the mesiolingual or lingual facet of molars, on cusp 1 (protocone), and is morphologically something from a groove (see Figure 3.2.) to a free apex cusp. This trait is the most studied morphological variant on teeth;

- *Cusp 5* (metaconule) on first molars (Turner *et al.*, 1991; Scott and Turner, 1997): cusp located in the distal marginal ridge, between cusps 3 and 4. It varies a great deal, from a faint cuspule to a relatively large cusp. The trait can be detected even when the tooth is worn, because of the grooves usually adjacent to it;

- *Mesial marginal accessory tubercles* on first molars (Scott and Turner, 1997): tubercles expressed in the mesial and lingual margins of the upper molars that should be considered independently. The mesial paracone tubercle is an independent part of the mesial accessory ridge of cusp 2; the protoconule is the augmented form of the accessory ridge of cusp 1; the mesial accessory tubercle is located in the mesial marginal ridge; the lingual paracone tubercle is lingual and mesial to the median ridge of cusp 2;

- *Cusp 4* (hypocone) on second molars (Turner *et al.*, 1991; Scott and Turner, 1997): distolingual cusp, which can be reduced in the first, and particularly the second molars. It was the last cusp added to the molar crown during the evolution of primates, and now is often reduced or missing, as it tends to disappear in hominin evolution;

- *Enamel extensions* on molars (Turner *et al.*, 1991; Scott and Turner, 1997): enamel projections that derive from the tooth crown towards the apex of the roots. Their formation prevents the maintenance of a horizontal cement-enamel junction. They may

occur buccally or lingually (cases where enamel pearls or enamel not contacting coronal enamel appear should not be registered as enamel extensions);

- *Parastyle* on third molars (Turner *et al.*, 1991; Scott and Turner, 1997): trait that develops from a pit to a separate crown attached to the root of the molar. It can be on the buccal surface of cusp 2 or on the same surface on the third cusp, more rarely;

Figure 3.1. Detail of the upper dental arch of individual 164 of the International Trade collection (ITC), a 52 year-old female. Both upper lateral incisors are peg-shaped; the left I2 is a grade 1 peg, while the right I2 is a grade 2 peg.

Figure 3.2. Detail of the upper right dental arcade of individual 138 ITC (a 24 year-old female). Near the center of the image a grade 3 Carabelli's trait is visible on the upper right first molar.

Selected traits (mandibular dentition):

- *Shoveling* on incisors (described above);

- *Distal accessory crest* on canines (Turner *et al.*, 1991; Scott and Turner, 1997; described above): not as expressive on the inferior canine as in the superior;

- *Odontome* on premolars (described above);

- *Variation on premolar lingual cusp number* (Turner *et al.*, 1991; Scott and Turner, 1997): there is variation between none and three lingual cups and on their relative expression. When dental wear occurs it may become difficult to distinguish between some of the possible classifications, so the record should indicate information is inexistent;

- *Anterior fovea* on first molars (Turner *et al.*, 1991; Scott and Turner, 1997): groove located in the mesial portion of the occlusal surface. The trait can be removed by wear of the enamel, due to the precocious occlusion of the first molar, mainly when its manifestation is not expressive;

- *Cusp pattern* on molars (Turner *et al.*, 1991; Scott and Turner, 1997): Y pattern occurs when cusps 2 and 3 meet at the central fossa, + pattern is patent when such happens with all four primary cusps and X pattern is present when the contact is between cups 1 and 4. This trait may be observed even when the tooth has severe wear. The variability is greater on the second molar and the third molar is more difficult to observe;

- *Deflecting wrinkle* on first molars (Turner *et al.*, 1991; Scott and Turner, 1997): the medial occlusal crest on cusp 2 follows a straight path from the cusp apex to the tooth's central fossa. When that path starts on a more mesial direction and, half way through, it deflects towards the central fossa, forming a wrinkle, it is called a "deflecting wrinkle". This trait is difficult to observe when some wear is present;

- *Distal trigonid crest* on molars (Turner *et al.*, 1991; Scott and Turner, 1997): a small crest or bridge between the first and second cusps, difficult to identify when dental wear is present. It is more common on the decidual dentition (not analyzed here);

- *Protostylid* on molars (Dahlberg, 1963; Turner *et al.*, 1991; Scott and Turner, 1997): this trait is patent in the buccal surface of cusp 1 and the sulcus that separates cusps 1 and 3, in the same buccal surface. It can appear as a depression, in a lesser expression of the trait, and may be a cusp with a free apex, which is rare. When a depression occurs, caries commonly affect it. In the plaques issued by the Zoller Memorial dental clinic laboratories for the record of the *protostylid*, the pit/depression form was large and found at the base of the buccal groove;

- *Mandibular molar pit-tubercle* on molars (MMPT; Weets, 2009 [adapted]): trait located on cusp 1, mesial and closer to the occlusal surface in relation to the *protostylid*. The MMPT varies between a small pit and a tubercle without a free apex. This should not be confused with the *protostylid*, since it can occur at the same time as this trait (Marado, 2010). The recording method was adapted by the present author, since some of the tubercles have a free apex, and could thus be described as cusps. This prompted the introduction of a further grade, '3+'.

   Grading system used:
0 – Absence of the trait;
0-1 – Slight indentation in place of the trait;
1 – Small pit;
1-2 – Distally and inferiorly elongated pit mouth;
2 – Groove in the distal-inferior direction;
2-3 – Two grooves seem to demarcate a slight tubercle;
3 – Small tubercle without a free apex;
3+ – Slightly larger tubercle, with a free apex.

- *Cusp number* on molars (Turner *et al.*, 1991; Scott and Turner, 1997): number of cusps, from 4 to 6 cusps (cusp 7 is not taken into account here, because it may be present regardless of the presence of cusps 5 and 6). The variation is due to the evolutionary tendency to reduce molar crowns, which affects the second molar most;

- *Cusp 5* (hypoconulid) on molars (Turner *et al.*, 1991; Scott and Turner, 1997): it occurs on the distal side of the occlusal surface, and is registered through the ASUDAS plaque in the absence of cusp 6. The progressive disappearance of the fifth cusp obeys the evolutionary tendency to reduce mandibular molars, which can be considered through the several grades of the ASUDAS plaques;

- *Cusp 6* (entoconulid or *tuberculum sextum*) on molars (Turner *et al.*, 1991; Scott and Turner, 1997): it occurs only when cusp 5 is present, is positioned relatively lingual and occupies the distal fossa of the occlusal surface;

- *Cusp 7* (metaconulid or *tuberculum intermedium*) on molars (Turner *et al.*, 1991; Scott and Turner, 1997): it occurs on the sulcus between cusps 2 and 4, and is not used in determining a tooth's total cusp number, contrarily to cusps 5 and 6. It is easily identified, even when the observer is faced with considerable dental wear. When the trait is limited to a small cusp (grade 1a) some authors consider it to be a different trait, the post-metaconulid, and both can be present in the same tooth.

3.1.2.Morphological mandibular and maxillary traits

The following paragraphs describe the morphological traits of both mandible and maxilla along with the methodology for their scoring.

- *Foramina mentales* (Hauser and De Stefano, 1989): found on the external side of the mandible, generally under the premolars, they enable the exterior passage of blood vessels and the inferior alveolar nerve, which travel through the mandibular canal. This trait may vary in relation to number, relative position, size, shape and distance between openings. It is clearly defined after the fifth gestational month, although it only assumes its vertical position after the teeth erupt. Generally, this character (double or multiple *foramina*) is more frequent in males. It is asymmetrical in its expression and may be more commonly identified as the sample's mean age is higher. When inferior and vertically misaligned, the orifice may correspond to the anterior termination of a Serres' canal;

- Mylohyoid bridge (Hauser and De Stefano, 1989): on the interior side of the mandibular ramus, starting with the mandibular *foramen*, a diagonal groove crosses it posteroanteriorly. The mylohyoid groove descends through the ramus and can be partially (on several positions and, occasionally, more than one position) or totally covered by a mylohyoid bridge. This groove receives the muscular branch of the inferior alveolar nerve and the accompanying blood vessels. The bridge may be the ossification of a ligament or of the periosteum, which probably happens in adolescence. It has never been registered in children and tends to increase with age in adults. The base for the suggested genetic relationship comes from the standardization of population variability. The trait is scored as present, but can also be scored for position and grade

of bridging. There are enough data to demonstrate sexual differences in the trait's frequency, but that is sample dependent;

- Palatine *torus* (Turner *et al.*, 1991): the palatine suture is accompanied, totally or partly, with bone growth. This is developed with age and only adults should be used for comparisons. Methodology adapted for the Portuguese sample kept in the Coimbra collections (Movsesjan *et al.*, 1975 *in* Galera *et al.*, 1995) will be used, grading the trait from absent ("Ausente") to a strong presence ("Fuerte), although the trait can also be of weak and medium expressions ("Débil" and "Medio", respectively). Each of these grades, concerning thickness and wideness, can still be divided into "complete" or "incomplete", categorizations referring to their length along the palatine suture. The ASUDAS is also used, in order to further opportunities for comparisons. The five grades go from absence of the trait to a very marked 10 mm high and 10 to 20 mm wide *torus*, which is to be measured in order to be inserted into one of these categories;

- Mandibular *torus* is a bony excrescence on the internal face of the mandible, under the second premolar, which shape and size vary (Hauser and De Stefano, 1989). Its function is doubtful, as is the relevance of external factors in its formation, depending on the consulted author (Silva, 2002). The mandibular *torus* will be evaluated as proposed by Galera *et al.* (1995), authors who adapted the method of Movsesjan *et al.* (1975 *in* Galera *et al.*, 1995). This methodology was considered appropriate for the Portuguese population of Coimbra by its authors. Four grades characterize the variation of the trait: the first one is the absence of the *torus* and the following describe an increasingly marked presence of the character. This begins with one or several small notches, which require palpation, and culminate in marked prominences, clearly visible and extensive to the length of the mandible (Galera *et al.*, 1995). The method proposed in the ASUDAS (Morris, 1970 *in* Turner *et al.*, 1991) will also be used, so as to permit bibliographical comparisons as wide as possible. The scale develops from absent or 0 to a *torus* with more than 5 mm, recorded even if only one of the sides is as large.

3.2.Statistical and quantitative approach

The use of statistical interpretation in dental morphology was initiated by tooth measures (odontometrics) at the end of the 19th century. The search for different patterns on the coronal size of diverse "races" prevails until the mid-20th century. Later, measurements increased in technological advance and became more specific. Mesiodistal and buccolingual measures are replaced by cusp measure, amongst other metrical approaches. The 21st century, with computerized tomography, will allow for tridimensional information (such as areas and tissue volume) to be easily collected from teeth (Harris, 2008).

Yet, this subfield is not exclusively made up of metric data, and discrete data also require interpretation and validation. The study of morphologic variability in teeth is, in the context of the general study of nonmetric variables, relatively reliable and effectively dependent on genotype. This justifies the acceptance of the results found through dental morphology and the need to use the most adequate statistical tests, so as to guarantee the correct interpretation and transmission of such results. In order to assure this, a large sample and a vast battery of discrete traits are recommended. Despite this, statistically significant results are produced with few individuals and few observed nonmetric traits. These results are naturally subjected to greater question (Tyrrell, 2000).

The quantitative approach used to estimate the biological affinities between the analyzed sample and frequencies reported by other authors for other samples and populations was the PCA. Principal components analysis (PCA) is a form of reducing data. Variables are compounded and re-expressed as combinations of themselves along composite axes, in a smaller and more coherent form, commonly easier to interpret. Besides this, another important benefit is the identification of those dental morphological traits most responsible for the distinctions between the sampled population groups, because PCA analyzes correlations between the original variables and the resulting components (Irish and Guatelli-Steinberg, 2003; Harris, 2008). PCA produces factors that depict the interrelation between variables, expressing the information within the original data, reducing the volume of data and eliminating variables of little use (Delgado-Burbano, 2007b). The main advantage of using PCA is that it underlines the variation among the included samples (Delgado-Burbano, 2007a).

Although the use of PCA implies the analysis of quantitative variables, dichotomous dental morphology data can also be studied with this method, once it is in the form of percentages or frequencies. Such approach has been conducted in several previous researches (as explained by Irish and Guatelli-Steinberg, 2003).

Descriptive statistics allow the study of data distribution, attesting if it is as expected, and the verification of which biological and/or cultural causes originated a hypothetical deviation from normal distribution (Harris, 2008).

All the count methods were used to calculate frequencies (see 4.7.Count method). These are the individual count, the tooth count, the unilateral count, and the expression count methods. The individual count method was the primary methodology used in the current work, and the tooth count and the unilateral count methods were applied in a merely comparative capacity, so as to comprehend their effect on the trait frequencies of the present sample. The expression count method (Turner, 1985) was applied in intrasample comparisons, which involve the search for low grade variation that demands strong discriminatory power.

To test for significant correlations between both sides for every variable, Kendall's *tau*-b and Spearman's *rho*, rank correlation coefficients, were used. Sex differences were tested using Pearson's *chi*-square test, which results are appraised according to the corresponding statistical significance.

Statistics also provide tests to verify the occurrence of observation error, *i. e.*, the precision and reproducibility of observations, in the inter- and intra-observer capacities (Harris, 2008). The precision rate for the comparison between all observations (the "preliminary" observation of 100 individuals and the "first" and "second" full observations) was calculated for each variable, through the division of the number of teeth to observe by the number of corresponding observations. Kendall's *tau*-b and Spearman's *rho* was be used in the comparison between observations to calculate the statistical significance of any hypothetical differences. The former test, Kendall's *tau*-b was also used to calculate intertrait correlations.

The Kruskal-Wallis H test of analysis of variance by ranks was used to understand the statistical significance of the differences between mean FA percentages of several sample categories. The paired comparisons of these categories were accomplished using the Mann-Whitney U test, another rank-sum statistic.

The z-ratio, a test of independence of proportions, was used to compare the difference of proportions between the sexes' and age range differences within the

summed fluctuating asymmetry results. This statistic test was calculated using http://www.vassarstats.net/propdiff_ind.html . All other statistics were computed using IBM SPSS Statistics 19.0.0, sometimes with aid from Microsoft Excel 2007.

4.Results and Discussion

4.1.Intra-observer error

Intra- and inter-observer errors should be determined for each study, since reliability depends on the observers, the traits chosen and the conditions of the observation (Hillson, 1996). Reproducibility of observations is one of the most relevant purposes of scientific methods. Some studies have been carried out in order to test intra- and inter-observer errors, and precision varies from around 85% and 100%, when it comes to the presence-absence dichotomy. Experience is a relevant factor, some variables' results are easier to replicate and the threshold manifestations are harder to score consistently. To add difficulty, altered dental surfaces offer a dilemma: the investigator wants to collect as much data as possible, without compromising the results. This leads to situations when on one of the observations, or by one of the observers, a trait is registered, and not on/by the other. The capacity to set aside dubious situations is essential, guaranteeing the quality of the observation (Scott and Turner, 1997).

So, subjectivity in using ASUDAS is inherent to the method, since grades are proposed in quasicontinuous variables. Experience, clear definitions and exploration of scoring errors diminish this factor (Scott and Turner, 1997; Hillson, 2005).

Pertinent issues when dealing with previously published data from others authors include the inexistence of intra- or inter-observer error calculation (Irish and Guatelli-Steinberg, 2003). This investigation will be subjected to such issue, because the use of data collected by other authors without known precision figures.

In the present investigation, the author proceeded with three observations: a preliminary observation and two others of the whole sample. The "preliminary observation" was intended to prepare the present author and to allow for further analysis of the intra-observer error. It consisted of the observation of the full battery of non-metrical traits, both dental and oral (palatine and mandibular), on 100 individuals (50 of each sex), a part of the complete sample. It was completed between the 23rd of February 2011 and the following March 10th. The final 600 individual sample was observed twice, during what were called the "first" and "second" observations. The objectives behind this zealous approach were to ensure the preparedness of the observer and present author, as well as to allow for the greater amount of knowledge of the intra-observer error still prevalent. Usually, error is calculated with repetition of only a subsample. Repetition of all observations is recommended, since it can be highly informative and reveal the effect of the method (Harris and Smith, 2009). The first

observation occurred between March 30th and August 3rd of 2011. The second one was accomplished between the 5th of September and November 18th of the same year.

Table 4.1.1. shows the intra-observer precisions and statistical significance, calculated for the comparison between the preliminary and the first observations, the first and the second observations and the preliminary and the second observations.

Precision is presented in the form of the percentage of corresponding results between compared observations. Precision is defined as the correspondence of repeated measures of the same trait (Harris and Smith, 2009). The "Overall" result refers to exact correspondence of grade. The "Within one grade" percentage pertains to the correspondence of the compared observations allowing the error margin of one grade. The "Dichotomized" value is equivalent to the proportion of teeth correctly classified as either present or absent. As for the "Observable trait", it equals the frequency of teeth deemed observable or unobservable in both instances for each trait (meaning teeth were not alternately considered observable and unobservable).

Correlation was attested through Kendall's *tau*-b and Spearman's *rho* (rank correlation coefficients), and the coefficient is displayed for both, along with asterisks representing statistical significance was found for the 0.05 level (one asterisk) and the 0.01 level (two asterisks). These statistical tests were used to compare raw data ("(overall)" in the Table) and also to compare dichotomized data (present and absent; appearing as "(dichot.)" in the Table).

Table 4.1.1. Precision and correlation values of the analyzed traits for each tooth pair.

Tooth (FDI) /Structure	Precision				Correlation			
	Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
	Winging							
	Pre-1st	95.8% 113/118	-	+=1a/1b 100.0% 118/118	94.5% 189/200	0.599**	0.601**	N/A	N/A
	1st-2nd	94.5% 588/622	-	+=1a/1b 100.0% 622/622	97.3% 1167/1200	0.505**	0.509**	N/A	N/A
	Pre-2nd	93.4% 113/121	-	+=1a/1b 100.0% 121/121	98.0% 196/200	0.431**	0.439**	N/A	N/A
11/21	Shoveling							
	Pre-1st	68.4% 52/76	97.4% 74/76	+=2-7 94.7% 72/76	89.0% 178/200	0.277*	0.283*	-0.027	-0.027
	1st-2nd	86.3% 320/371	99.7% 370/371	+=2-7 97.3% 361/371	92.9% 1115/1200	0.485**	0.494**	0.486**	0.486**
	Pre-2nd	73.6% 53/72	97.2% 70/72	+=2-7 97.2% 70/72	91.5% 183/200	0.363**	0.368**	N/A	N/A

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure		Precision				Correlation			
		Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
11/21					Double shoveling				
	Pre-1st	84.3% 86/102	99.0% 101/102	+=2-6 97.1% 99/102	93.5% 187/200	0.343**	0.349**	-0.014	-0.014
	1st-2nd	95.6% 366/383	99.5% 381/383	+=2-6 100.0% 383/383	91.2% 1094/1200	0.476**	0.478**	1.000**	1.000**
	Pre-2nd	82.2% 60/73	95.9% 70/73	+=2-6 95.9% 70/73	83.5% 167/200	0.241*	0.244*	-0.020	-0.020
					Diastema				
	Pre-1st	97.8% 44/45	-	+>=0.5mm 97.8% 44/45	94.0% 94/100	0.883**	0.883**	0.883**	0.883**
	1st-2nd	99.5% 421/423	-	+>=0.5mm 99.5% 421/423	96.2% 577/600	0.971**	0.971**	0.971**	0.971**
	Pre-2nd	97.8% 45/46	-	+>=0.5mm 97.8% 45/46	96.0% 96/100	0.902**	0.902**	0.902**	0.902**
					Interruption grooves				
	Pre-1st	98.3% 113/115	-	+=1 98.3% 113/115	93.5% 187/200	N/A	N/A	N/A	N/A
	1st-2nd	96.8% 517/534	-	+=1 97.4% 520/534	92.0% 1104/1200	0.685**	0.691**	0.685**	0.685**
	Pre-2nd	98.0% 98/100	-	+=1 98.0% 98/100	89.0% 178/200	N/A	N/A	N/A	N/A
					Attrition				
	Pre-1st	66.7% 72/108	100.0% 108/108	-	-	0.786**	0.838**	-	-
	1st-2nd	69.0% 368/533	99.4% 530/533	-	-	0.766**	0.810**	-	-
	Pre-2nd	67.0% 75/112	100.0% 112/112	-	-	0.803**	0.848**	-	-
12/22					Interruption grooves				
	Pre-1st	87.6% 120/137	-	+=1 89.1% 122/137	98.5% 197/200	0.448**	0.459**	0.458**	0.458**
	1st-2nd	92.0% 644/700	-	+=1 93.7% 656/700	94.6% 1135/1200	0.685**	0.702**	0.704**	0.704**
	Pre-2nd	81.5% 101/124	-	+=1 83.1% 103/124	93.0% 186/200	0.252**	0.261**	0.266**	0.266**
					Tuberculum dentale				
	Pre-1st	54.0% 74/137	76.6% 105/137	+=2-6 75.9% 104/137	98.5% 197/200	0.429**	0.467**	0.383**	0.383**
	1st-2nd	39.4% 287/728	81.5% 593/728	+=2-6 65.2% 475/728	96.6% 1159/1200	0.417**	0.468**	0.360**	0.360**
	Pre-2nd	23.9% 32/134	53.7% 72/134	+=2-6 53.7% 72/134	97.5% 195/200	0.410**	0.455**	0.324**	0.324**
					Peg incisors				
	Pre-1st	97.1% 134/138	100.0% 138/138	+=1-2 97.8% 135/138	99.0% 198/200	0.763**	0.766**	0.760**	0.760**
	1st-2nd	96.2% 753/783	100.0% 783/783	+=1-2 96.8% 758/783	97.0% 1164/1200	0.498**	0.500**	0.493**	0.493**
	Pre-2nd	95.6% 131/137	100.0% 137/137	+=1-2 97.1% 133/137	99.0% 198/200	0.600**	0.604**	0.598**	0.598**

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure	Precision				Correlation			
	Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
				Attrition				
12/22 Pre-1st	76.4% 94/123	100.0% 123/123	-	-	0.772**	0.806**	-	-
1st-2nd	64.6% 441/683	99.4% 679/683	-	-	0.653**	0.682**	-	-
Pre-2nd	52.8% 65/123	100.0% 123/123	-	-	0.676**	0.712**	-	-
				Distal accessory ridge				
13/23 Pre-1st	55.1% 65/118	83.9% 99/118	+=1-5 80.5% 95/118	94.0% 188/200	0.624**	0.697**	0.639**	0.639**
1st-2nd	57.4% 413/720	90.8% 654/720	+=1-5 85.0% 612/720	94.6% 1135/1200	0.647**	0.726**	0.691**	0.691**
Pre-2nd	44.0% 51/116	75.9% 88/116	+=1-5 68.1% 79/116	93.5% 187/200	0.536**	0.610**	0.434**	0.434**
				Attrition				
Pre-1st	74.8% 101/135	99.3% 134/135	-	-	0.817**	0.862**	-	-
1st-2nd	77.7% 663/853	99.3% 847/853	-	-	0.757**	0.786**	-	-
Pre-2nd	61.8% 84/136	97.8% 133/136	-	-	0.714**	0.759**	-	-
				Accessory cusps				
14/24 Pre-1st	97.5% 119/122	-	+=1 97.5% 119/122	96.5% 193/200	0.388**	0.389**	0.396**	0.396**
1st-2nd	98.7% 734/744	-	+=1 98.7% 734/744	97.5% 1170/1200	0.294**	0.295**	0.292**	0.292**
Pre-2nd	98.3% 118/120	-	+=1 98.3% 118/120	96.0% 192/200	N/A	N/A	N/A	N/A
				Accessory crests				
Pre-1st	98.4% 124/126	-	+=1 98.4% 124/126	96.0% 192/200	0.562**	0.563**	0.573**	0.573**
1st-2nd	96.5% 715/741	-	+=1 96.5% 715/741	95.9% 1151/1200	0.428**	0.430**	0.428**	0.428**
Pre-2nd	96.7% 118/122	-	+=1 96.7% 118/122	95.0% 190/200	-0.014	-0.014	-0.014	-0.014
				Tricuspid premolars				
Pre-1st	100.0% 133/133	-	+=1 100.0% 133/133	97.5% 195/200	1.000**	1.000**	1.000**	1.000**
1st-2nd	99.9% 834/835	-	+=1 99.9% 834/835	98.8% 1186/1200	0.707**	0.707**	0.707**	0.707**
Pre-2nd	100.0% 134/134	-	+=1 100.0% 134/134	98.0% 196/200	1.000**	1.000**	1.000**	1.000**
				Odontome				
Pre-1st	100.0% 132/132	-	+=1 100.0% 132/132	99.0% 198/200	N/A	N/A	N/A	N/A
1st-2nd	100.0% 818/818	-	+=1 100.0% 818/818	98.6% 1183/1200	1.000**	1.000**	1.000**	1.000**
Pre-2nd	100.0% 133/133	-	+=1 100.0% 133/133	98.5% 197/200	N/A	N/A	N/A	N/A

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure		Precision				Correlation			
		Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
				Attrition					
14/24	Pre-1st	66.7% 88/132	97.7% 129/132	-	-	0.684**	0.731**	-	-
	1st-2nd	75.2% 624/830	99.2% 823/830	-	-	0.675**	0.696**	-	-
	Pre-2nd	44.8% 60/134	97.0% 130/134	-	-	0.588**	0.619**	-	-
				Accessory cusps					
15/25	Pre-1st	95.1% 117/123	-	+=1 95.9% 118/123	97.5% 195/200	0.708**	0.714**	0.697**	0.697**
	1st-2nd	97.8% 709/725	-	+=1 97.9% 710/725	98.1% 1177/1200	0.659**	0.661**	0.656**	0.656**
	Pre-2nd	98.4% 120/122	-	+=1 98.4% 120/122	96.5% 193/200	0.853**	0.855**	0.848**	0.848**
				Accessory crests					
	Pre-1st	87.3% 110/126	-	+=1 88.1% 111/126	97.0% 194/200	0.567**	0.579**	0.578**	0.578**
	1st-2nd	87.4% 638/730	-	+=1 90.3% 659/730	96.3% 1156/1200	0.683**	0.710**	0.695**	0.695**
	Pre-2nd	86.8% 105/121	-	+=1 90.1% 109/121	95.5% 191/200	0.610**	0.631**	0.638**	0.638**
				Tricuspid premolars					
	Pre-1st	99.2% 128/129	-	+=1 99.2% 128/129	96.0% 192/200	N/A	N/A	N/A	N/A
	1st-2nd	99.8% 804/806	-	+=1 99.8% 804/806	99.2% 1190/1200	-0.001	-0.001	-0.001	-0.001
	Pre-2nd	100.0% 129/129	-	+=1 100.0% 129/129	96.5% 193/200	N/A	N/A	N/A	N/A
				Odontome					
	Pre-1st	100.0% 127/127	-	+=1 100.0% 127/127	96.5% 193/200	N/A	N/A	N/A	N/A
	1st-2nd	99.7% 790/792	-	+=1 99.7% 790/792	98.8% 1186/1200	-0.001	-0.001	-0.001	-0.001
	Pre-2nd	100.0% 127/127	-	+=1 100.0% 127/127	97.5% 195/200	N/A	N/A	N/A	N/A
				Attrition					
	Pre-1st	74.0% 97/131	98.5% 129/131	-	-	0.736**	0.772**	-	-
	1st-2nd	76.4% 610/798	99.6% 795/798	-	-	0.670**	0.687**	-	-
	Pre-2nd	45.5% 60/132	99.2% 131/132	-	-	0.641**	0.672**	-	-
				Carabelli's trait					
16/26	Pre-1st	57.9% 77/133	88.0% 117/133	+=2-7 84.2% 112/133	98.0% 196/200	0.694**	0.755**	0.649**	0.649**
	1st-2nd	70.1% 570/813	93.4% 759/813	+=2-7 90.8% 738/813	98.8% 1185/1200	0.771**	0.819**	0.747**	0.747**
	Pre-2nd	58.2% 78/134	82.1% 110/134	+=2-7 84.3% 113/134	99.0% 198/200	0.650**	0.717**	0.642**	0.642**

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure	Precision				Correlation			
	Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
			C5					
	Pre-1st	89.6% 121/135	97.8% 132/135	+=2-5 97.0% 131/135	98.0% 196/200	0.688**	0.700**	0.707**	0.707**
	1st-2nd	93.9% 760/809	97.9% 792/809	+=2-5 96.5% 781/809	98.3% 1179/1200	0.646**	0.655**	0.375**	0.375**
	Pre-2nd	88.9% 120/135	100.0% 135/135	+=2-5 96.3% 130/135	97.0% 194/200	0.804**	0.814**	0.601**	0.601**
			Mesial marginal accessory tubercles					
	Pre-1st	95.3% 123/129	-	+=1 95.3% 123/129	98.0% 196/200	0.378**	0.381**	0.369**	0.369**
	1st-2nd	96.4% 728/755	-	+=1 96.6% 729/755	96.3% 1156/1200	0.362**	0.365**	0.365**	0.365**
16/26	Pre-2nd	91.4% 117/128	-	+=1 91.4% 117/128	98.0% 196/200	0.100	0.102	0.109	0.109
			Enamel extensions					
	Pre-1st	92.3% 72/78	98.7% 77/78	+=1-3 92.3% 72/78	79.5% 159/200	N/A	N/A	N/A	N/A
	1st-2nd	96.7% 529/547	99.1% 542/547	+=1-3 97.4% 533/547	89.9% 1079/1200	0.641**	0.645**	0.638**	0.638**
	Pre-2nd	98.8% 79/80	98.8% 79/80	+=1-3 98.8% 79/80	82.5% 165/200	N/A	N/A	N/A	N/A
			Attrition					
	Pre-1st	58.1% 79/136	99.3% 135/136	-	-	0.645**	0.680**	-	-
	1st-2nd	83.8% 708/845	99.8% 843/845	-	-	0.773**	0.794**	-	-
	Pre-2nd	45.7% 63/138	97.8% 135/138	-	-	0.679**	0.722**	-	-
			C4					
	Pre-1st	55.8% 87/156	80.8% 126/156	+=3-5 92.9% 145/156	97.5% 195/200	0.678**	0.783**	0.866**	0.866**
	1st-2nd	59.9% 548/915	83.8% 767/915	+=3-5 90.3% 826/915	98.4% 1181/1200	0.709**	0.810**	0.807**	0.807**
	Pre-2nd	47.8% 75/157	75.8% 119/157	+=3-5 84.7% 133/157	98.0% 196/200	0.633**	0.750**	0.705**	0.705**
			Enamel extensions					
	Pre-1st	84.8% 78/92	91.3% 84/92	+=1-3 87.0% 80/92	79.5% 159/200	0.429**	0.439**	0.416**	0.416**
17/27	1st-2nd	88.9% 559/629	96.8% 609/629	+=1-3 94.0% 591/629	88.7% 1064/1200	0.789**	0.811**	0.787**	0.787**
	Pre-2nd	91.0% 81/89	95.5% 85/89	+=1-3 93.3% 83/89	78.5% 157/200	0.499**	0.506**	0.482**	0.482**
			Attrition					
	Pre-1st	56.7% 89/157	98.1% 154/157	-	-	0.616**	0.656**	-	-
	1st-2nd	81.4% 768/944	99.8% 942/944	-	-	0.690**	0.702**	-	-
	Pre-2nd	37.3% 60/161	94.4% 152/161	-	-	0.550**	0.583**	-	-

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure	Precision				Correlation			
	Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
	Enamel extensions							
18/28	Pre-1st 94.7% 36/38	94.7% 36/38	+=1-3 94.7% 36/38	84.5% 169/200	N/A	N/A	N/A	N/A
	1st-2nd 95.0% 285/300	99.7% 299/300	+=1-3 99.7% 299/300	91.7% 1100/1200	0.952**	0.969**	0.973**	0.973**
	Pre-2nd 95.1% 39/41	97.6% 40/41	+=1-3 95.1% 39/41	84.5% 169/200	N/A	N/A	N/A	N/A
	Parastyle							
	Pre-1st 97.5% 77/79	100.0% 79/79	+=1-6 97.5% 77/79	94.5% 189/200	0.582**	0.585**	0.570**	0.570**
	1st-2nd 98.2% 434/442	99.3% 439/442	+=1-6 98.6% 436/442	94.7% 1136/1200	0.722**	0.724**	0.724**	0.724**
	Pre-2nd 95.9% 70/73	98.6% 72/73	+=1-6 95.9% 70/73	92.0% 184/200	0.402**	0.405**	0.388**	0.388**
	Attrition							
	Pre-1st 68.2% 60/88	97.7% 86/88	-	-	0.712**	0.756**	-	-
	1st-2nd 73.4% 413/563	99.5% 560/563	-	-	0.748**	0.787**	-	-
	Pre-2nd 39.8% 37/93	91.4% 85/93	-	-	0.606**	0.660**	-	-
31/41	Shoveling							
	Pre-1st 82.9% 97/117	99.1% 116/117	+=2-7 99.1% 116/117	97.5% 195/200	0.482**	0.484**	N/A	N/A
	1st-2nd 96.3% 578/600	100.0% 600/600	+=2-7 100.0% 600/600	94.7% 1136/1200	0.405**	0.405**	N/A	N/A
	Pre-2nd 74.8% 80/107	99.1% 106/107	+=2-7 99.1% 106/107	93.5% 187/200	0.222*	0.223*	N/A	N/A
	Attrition							
	Pre-1st 70.0% 84/120	100.0% 120/120	-	-	0.714**	0.748**	-	-
	1st-2nd 65.8% 434/660	99.7% 658/660	-	-	0.603**	0.625**	-	-
	Pre-2nd 75.4% 89/118	98.3% 116/118	-	-	0.718**	0.752**	-	-
32/42	Shoveling							
	Pre-1st 72.4% 89/123	99.2% 112/123	+=2-7 99.2% 122/123	91.5% 183/200	0.271**	0.272**	N/A	N/A
	1st-2nd 95.9% 661/689	100.0% 689/689	+=2-7 100.0% 689/689	94.5% 1134/1200	0.313**	0.313**	N/A	N/A
	Pre-2nd 66.7% 80/120	99.2% 119/120	+=2-7 99.2% 119/120	94.5% 189/200	N/A	N/A	N/A	N/A
	Attrition							
	Pre-1st 74.1% 100/135	100.0% 135/135	-	-	0.796**	0.842**	-	-
	1st-2nd 68.4% 507/741	99.7% 739/741	-	-	0.667**	0.701**	-	-
	Pre-2nd 68.4% 93/136	100.0% 136/136	-	-	0.735**	0.774**	-	-

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure		Precision				Correlation			
		Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
				Distal accessory ridge					
33/43	Pre-1st	71.5% 93/130	94.6% 123/130	+=1-5 82.3% 107/130	94.5% 189/200	0.636**	0.669**	0.618**	0.618**
	1st-2nd	73.5% 615/837	95.7% 801/837	+=1-5 81.4% 681/837	97.3% 1168/1200	0.607**	0.639**	0.583**	0.583**
	Pre-2nd	67.2% 88/131	90.8% 119/131	+=1-5 80.2% 105/131	93.0% 186/200	0.622**	0.662**	0.594**	0.594**
				Attrition					
	Pre-1st	77.2% 112/145	100.0% 145/145	-	-	0.788**	0.820**	-	-
	1st-2nd	72.4% 633/874	99.7% 871/874	-	-	0.645**	0.675**	-	-
	Pre-2nd	61.6% 90/146	97.7% 143/146	-	-	0.655**	0.694**	-	-
				Odontome					
34/44	Pre-1st	100.0% 149/149	-	+=1 100.0% 149/149	96.5% 193/200	N/A	N/A	N/A	N/A
	1st-2nd	100.0% 922/922	-	+=1 100.0% 922/922	99.2% 1190/1200	N/A	N/A	N/A	N/A
	Pre-2nd	100.0% 149/149	-	+=1 100.0% 149/149	97.0% 194/200	N/A	N/A	N/A	N/A
				Lingual cusp number					
	Pre-1st	79.6% 113/142	90.8% 129/142	+=2-9 93.0% 132/142	95.5% 191/200	0.630**	0.660**	0.743**	0.743**
	1st-2nd	80.6% 722/896	86.7% 777/896	+=2-9 90.1% 807/896	98.1% 1177/1200	0.676**	0.709**	0.718**	0.718**
	Pre-2nd	73.9% 105/142	85.2% 121/142	+=2-9 83.1% 118/142	94.5% 189/200	0.546**	0.582**	0.527**	0.527**
				Attrition					
	Pre-1st	71.1% 106/149	100.0% 149/149	-	-	0.684**	0.706**	-	-
	1st-2nd	79.0% 720/911	100.0% 911/911	-	-	0.653**	0.667**	-	-
	Pre-2nd	55.7% 83/149	100.0% 149/149	-	-	0.618**	0.641**	-	-
				Odontome					
35/45	Pre-1st	99.3% 147/148	-	+=1 99.3% 147/148	97.0% 194/200	0.814**	0.814**	0.814**	0.814**
	1st-2nd	99.8% 863/865	-	+=1 99.8% 863/865	98.8% 1185/1200	0.706**	0.706**	0.706**	0.706**
	Pre-2nd	100.0% 149/149	-	+=1 100.0% 149/149	98.0% 196/200	1.000**	1.000**	1.000**	1.000**
				Lingual cusp number					
	Pre-1st	64.3% 92/143	85.3% 122/143	+=2-9 83.9% 120/143	95.0% 190/200	0.605**	0.653**	0.650**	0.650**
	1st-2nd	68.7% 576/839	84.5% 709/839	+=2-9 86.5% 726/839	97.9% 1175/1200	0.718**	0.763**	0.727**	0.727**
	Pre-2nd	55.2% 79/143	80.4% 115/143	+=2-9 79.7% 114/143	97.0% 194/200	0.602**	0.667**	0.562**	0.562**

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure		Precision				Correlation			
		Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
				Attrition					
35/45	Pre-1st	69.8% 104/149	100.0% 149/149	-	-	0.650**	0.676**	-	-
	1st-2nd	78.2% 678/867	99.9% 866/867	-	-	0.614**	0.627**	-	-
	Pre-2nd	53.0% 80/151	99.3% 150/151	-	-	0.525**	0.546**	-	-
				Deflecting wrinkle					
	Pre-1st	89.5% 94/105	100.0% 105/105	+=1-3 93.3% 98/105	94.5% 189/200	0.682**	0.695**	0.655**	0.655**
	1st-2nd	94.2% 598/635	98.6% 626/635	+=1-3 95.7% 608/635	95.9% 1151/1200	0.509**	0.515**	0.509**	0.509**
	Pre-2nd	86.4% 89/103	98.1% 101/103	+=1-3 91.3% 94/103	95.5% 191/200	0.552**	0.572**	0.545**	0.545**
				Anterior fovea					
	Pre-1st	66.7% 70/105	93.3 % 98/105	+=1-4 84.8% 89/105	96.0% 192/200	0.713**	0.771**	0.695**	0.695**
	1st-2nd	80.2% 556/693	94.5% 655/693	+=1-4 87.6% 607/693	98.7% 1184/1200	0.657**	0.686**	0.659**	0.659**
	Pre-2nd	63.5% 66/104	84.6% 88/104	+=1-4 80.8% 84/104	96.0% 192/200	0.666**	0.726**	0.656**	0.656**
				Cusp/groove pattern					
36/46	Pre-1st	98.2% 112/114	-	+=Y 98.2% 112/114	100.0% 200/200	0.809**	0.809**	0.809**	0.809**
	1st-2nd	92.8% 662/713	-	+=Y 92.8% 662/713	99.0% 1188/1200	0.470**	0.470**	0.470**	0.470**
	Pre-2nd	93.8% 106/113	-	+=Y 93.8% 106/113	98.5% 197/200	0.348**	0.348**	0.348**	0.348**
				Distal trigonid crest					
	Pre-1st	97.3% 108/111	-	+=1 97.3% 108/111	96.5% 193/200	-0.013	-0.013	-0.013	-0.013
	1st-2nd	97.5% 690/708	-	+=1 97.5% 690/708	98.8% 1186/1200	0.425**	0.425**	0.425**	0.425**
	Pre-2nd	100.0% 111/111	-	+=1 100.0% 111/111	97.5% 195/200	1.000**	1.000**	1.000**	1.000**
				Protostylid					
	Pre-1st	73.6% 81/110	92.7% 102/110	+=1-7 75.5% 83/110	98.0% 196/200	0.431**	0.446**	0.497**	0.497**
	1st-2nd	87.7% 629/717	98.7% 708/717	+=1-7 88.7% 636/717	99.2% 1190/1200	0.567**	0.572**	0.576**	0.576**
	Pre-2nd	66.4% 73/110	96.4% 106/110	+=1-7 66.4% 73/110	98.5% 197/200	0.321**	0.326**	0.352**	0.352**
				MMPT					
	Pre-1st	98.2% 110/112	98.2% 110/112	+='0-1'-'3+' 98.2% 110/112	99.5% 199/200	0.572**	0.572**	0.572**	0.572**
	1st-2nd	98.6% 698/708	98.7% 699/708	+='0-1'-'3+' 98.6% 698/708	99.3% 1191/1200	0.291**	0.292**	0.292**	0.292**
	Pre-2nd	96.4% 107/111	96.4% 107/111	+='0-1'-'3+' 96.4% 107/111	97.5% 195/200	0.315**	0.315**	0.315**	0.315**

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure		Precision				Correlation			
		Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
				Cusp number					
	Pre-1st	94.9% 111/117	100.0% 117/117	+~=5 94.9% 111/117	99.5% 199/200	0.815**	0.820**	0.796**	0.796**
	1st-2nd	96.2% 687/714	100.0% 714/714	+~=5 96.2% 687/714	99.3% 1191/1200	0.837**	0.839**	0.828**	0.828**
	Pre-2nd	95.7% 112/117	100.0% 117/117	+~=5 95.7% 112/117	99.5% 199/200	0.844**	0.851**	0.824**	0.824**
				C5					
	Pre-1st	65.0% 76/117	96.6% 113/117	+=1-5 96.6% 113/117	99.5% 199/200	0.768**	0.827**	0.830**	0.830**
	1st-2nd	66.9% 476/711	95.4% 678/711	+=1-5 95.9% 682/711	99.1% 1189/1200	0.720**	0.769**	0.792**	0.792**
	Pre-2nd	71.8% 84/117	98.3% 115/117	+=1-5 98.7% 115/117	99.5% 199/200	0.784**	0.833**	0.907**	0.907**
				C6					
	Pre-1st	97.4% 114/117	98.3% 115/117	+=1-5 98.3% 115/117	99.5% 199/200	0.731**	0.734**	0.741**	0.741**
36/46	1st-2nd	98.6% 703/713	99.3% 708/713	+=1-5 99.0% 706/713	99.2% 1190/1200	0.714**	0.717**	0.720**	0.720**
	Pre-2nd	97.5% 114/117	97.4% 114/117	+=1-5 97.4% 114/117	99.5% 199/200	0.651**	0.652**	0.658**	0.658**
				C7					
	Pre-1st	94.9% 111/117	96.6% 113/117	+=1-4 97.4% 114/117	99.5% 199/200	0.302**	0.304**	-0.012	-0.012
	1st-2nd	95.1% 686/721	96.5% 696/721	+=1-4 96.7% 697/721	99.3% 1192/1200	0.685**	0.697**	0.631**	0.631**
	Pre-2nd	96.6% 112/116	96.6% 112/116	+=1-4 97.4% 113/116	98.0% 196/200	0.877**	0.888**	-0.012	-0.012
				Attrition					
	Pre-1st	75.6% 90/119	99.2% 118/119	-	-	0.693**	0.725**	-	-
	1st-2nd	74.9% 561/749	100.0% 749/749	-	-	0.689**	0.708**	-	-
	Pre-2nd	63.6% 77/121	100.0% 121/121	-	-	0.651**	0.682**	-	-
				Cusp/groove pattern					
	Pre-1st	86.8% 118/136	-	+=+/X 86.8% 118/136	97.0% 194/200	0.592**	0.596**	0.663**	0.663**
	1st-2nd	90.2% 738/818	-	+=+/X 90.2% 738/818	97.8% 1174/1200	0.749**	0.749**	0.749**	0.749**
	Pre-2nd	86.2% 119/138	-	+=+/X 87.0% 120/138	97.5% 195/200	0.641**	0.645**	0.650**	0.650**
37/47				Distal trigonid crest					
	Pre-1st	96.2% 128/133	-	+=1 96.2% 128/133	95.5% 191/200	0.600**	0.600**	0.600**	0.600**
	1st-2nd	95.4% 783/821	-	+=1 95.4% 783/821	98.0% 1176/1200	0.432**	0.432**	0.432**	0.432**
	Pre-2nd	94.7% 125/132	-	+=1 94.7% 125/132	95.0% 190/200	0.387**	0.387**	0.387**	0.387**

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure		Precision				Correlation			
		Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
				Protostylid					
	Pre-1st	87.5% 118/135	94.8% 128/135	+=1-7 91.1% 123/135	99.0% 198/200	0.681**	0.695**	0.703**	0.703**
	1st-2nd	84.6% 708/837	89.7% 751/837	+=1-7 86.6% 725/837	98.3% 1179/1200	0.429**	0.441**	0.461**	0.461**
	Pre-2nd	78.5% 106/135	90.4% 122/135	+=1-7 80.7% 109/135	97.5% 195/200	0.381**	0.395**	0.368**	0.368**
				MMPT					
	Pre-1st	91.0% 121/133	92.5% 123/133	+='0-1'-'3+' 92.5% 123/133	97.5% 195/200	0.426**	0.435**	0.459**	0.459**
	1st-2nd	97.6% 818/838	97.6% 818/838	+='0-1'-'3+' 97.9% 820/838	97.8% 1174/1200	0.628**	0.630**	0.634**	0.634**
	Pre-2nd	94.1% 127/135	96.3% 130/135	+='0-1'-'3+' 96.3% 130/135	98.0% 196/200	0.672**	0.682**	0.699**	0.699**
				Cusp number					
	Pre-1st	91.2% 125/137	100.0% 137/137	+~=4 91.2% 125/137	98.5% 197/200	0.662**	0.665**	0.650**	0.650**
	1st-2nd	95.6% 804/841	100.0% 841/841	+~=4 95.8% 806/841	98.5% 1182/1200	0.867**	0.870**	0.863**	0.863**
	Pre-2nd	93.5% 130/139	100.0% 139/139	+~=4 94.2% 131/139	100.0% 200/200	0.784**	0.789**	0.776**	0.776**
37/47				C5					
	Pre-1st	90.5% 124/137	95.6% 131/137	+=1-5 92.7% 127/137	98.5% 197/200	0.721**	0.736**	0.696**	0.696**
	1st-2nd	90.0% 757/841	95.6% 804/841	+=1-5 95.0% 799/841	98.5% 1182/1200	0.805**	0.823**	0.816**	0.816**
	Pre-2nd	90.6% 126/139	96.4% 134/139	+=1-5 95.7% 133/139	100.0% 200/200	0.827**	0.843**	0.825**	0.825**
				C6					
	Pre-1st	100.0% 138/138	100.0% 138/138	+=1-5 100.0% 138/138	99.0% 198/200	N/A	N/A	N/A	N/A
	1st-2nd	99.2% 835/842	99.4% 837/842	+=1-5 99.4% 837/842	98.6% 1183/1200	0.664**	0.665**	0.665**	0.665**
	Pre-2nd	99.3% 138/139	99.3% 138/139	+=1-5 99.3% 138/139	100.0% 200/200	N/A	N/A	N/A	N/A
				C7					
	Pre-1st	97.0% 131/135	98.5% 133/135	+=1-4 99.3% 134/135	97.0% 194/200	0.558**	0.562**	0.813**	0.813**
	1st-2nd	98.9% 845/854	99.3% 848/854	+=1-4 99.4% 849/854	99.3% 1192/1200	0.445**	0.446**	0.533**	0.533**
	Pre-2nd	99.3% 136/137	100.0% 137/137	+=1-4 99.3% 136/137	97.5% 195/200	0.818**	0.820**	0.813**	0.813**
				Attrition					
	Pre-1st	66.2% 92/139	98.6% 137/139	-	-	0.572**	0.588**	-	-
	1st-2nd	81.3% 715/879	99.3% 873/879	-	-	0.658**	0.674**	-	-
	Pre-2nd	51.1% 72/141	97.9% 138/141	-	-	0.475**	0.490**	-	-

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure	Precision				Correlation			
	Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
	Cusp/groove pattern							
Pre-1st	89.1% 90/101	-	+=Y 90.1% 91/101	97.0% 194/200	0.692**	0.695**	0.705**	0.705**
1st-2nd	86.1% 477/554	-	+=Y 86.1% 477/554	96.7% 1160/1200	0.615**	0.615**	0.624**	0.624**
Pre-2nd	87.0% 87/100	-	+=Y 87.0% 87/100	95.5% 191/200	0.545**	0.548**	0.604**	0.604**
	Distal trigonid crest							
Pre-1st	82.7% 86/104	-	+=1 82.7% 86/104	97.0% 194/200	0.575**	0.580**	0.499**	0.499**
1st-2nd	85.4% 496/581	-	+=1 85.4% 496/581	97.2% 1166/1200	0.518**	0.518**	0.518**	0.518**
Pre-2nd	78.4% 80/102	-	+=1 78.4% 80/102	94.5% 189/200	0.502**	0.506**	0.440**	0.440**
	Protostylid							
Pre-1st	88.3% 83/94	96.8% 91/94	+=1-7 90.4% 85/94	97.5% 195/200	0.591**	0.602**	0.611**	0.611**
1st-2nd	91.8% 481/524	95.0% 498/524	+=1-7 92.6% 485/524	96.5% 1158/1200	0.477**	0.485**	0.490**	0.490**
Pre-2nd	87.0% 80/92	95.7% 88/92	+=1-7 89.1% 82/92	94.0% 188/200	0.450**	0.459**	0.472**	0.472**
	MMPT							
Pre-1st	87.2% 82/94	91.5% 86/94	+='0-1'-'3+' 92.6% 87/94	95.5% 191/200	0.781**	0.803**	0.805**	0.805**
1st-2nd	89.2% 479/537	91.6% 492/537	+='0-1'-'3+' 92.0% 494/537	96.9% 1163/1200	0.764**	0.776**	0.777**	0.777**
Pre-2nd	85.4% 82/96	91.7% 88/96	+='0-1'-'3+' 93.8% 90/96	95.0% 190/200	0.829**	0.854**	0.834**	0.834**
	Cusp number							
Pre-1st	85.7% 90/105	99.0% 104/105	+~=4 88.6% 93/105	98.0% 196/200	0.813**	0.832**	0.756**	0.756**
1st-2nd	86.7% 495/571	99.6% 569/571	+~=4 89.8% 513/571	97.3% 1168/1200	0.852**	0.875**	0.801**	0.801**
Pre-2nd	84.0% 89/106	100.0% 106/106	+~=4 89.6% 95/106	98.5% 197/200	0.840**	0.868**	0.762**	0.762**
	C5							
Pre-1st	67.9% 72/106	86.8% 92/106	+=1-5 90.6% 96/106	98.5% 197/200	0.691**	0.756**	0.813**	0.813**
1st-2nd	77.2% 441/571	90.9% 519/571	+=1-5 92.1% 526/571	97.3% 1167/1200	0.799**	0.849**	0.845**	0.845**
Pre-2nd	66.4% 71/107	88.8% 95/107	+=1-5 92.5% 99/107	98.5% 197/200	0.709**	0.780**	0.843**	0.843**

The "Tooth (FDI)/Structure" value **38/48** spans the full block of rows.

Table 4.1.1. (Continued.)

Tooth (FDI) /Structure		Precision			Correlation			
	Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
38/48	C6							
Pre-1st	91.5% 97/106	95.3% 101/106	+=1-5 96.2% 102/106	98.0% 196/200	0.796**	0.813**	0.812**	0.812**
1st-2nd	95.1% 542/570	96.7% 551/570	+=1-5 96.8% 552/570	97.2% 1166/1200	0.829**	0.838**	0.836**	0.836**
Pre-2nd	88.8% 95/107	95.3% 102/107	+=1-5 94.4% 101/107	98.5% 197/200	0.777**	0.789**	0.765**	0.765**
	C7							
Pre-1st	96.1% 98/102	99.0% 101/102	+=1-4 96.1% 98/102	95.5% 191/200	-0.017	-0.017	-0.017	-0.017
1st-2nd	98.3% 573/583	98.3% 573/583	+=1-4 98.6% 575/583	97.0% 1164/1200	0.305**	0.307**	0.347**	0.347**
Pre-2nd	96.0% 96/100	99.0% 99/100	+=1-4 96.0% 96/100	94.5% 189/200	0.397**	0.398**	-0.018	-0.018
	Attrition							
Pre-1st	66.4% 73/110	97.3% 107/110	-	-	0.762**	0.810**	-	-
1st-2nd	75.0% 465/620	99.4% 616/620	-	-	0.740**	0.770**	-	-
Pre-2nd	41.4% 46/111	98.2% 109/111	-	-	0.781**	0.839**	-	-
Mandible	*Foramina mentales*							
Pre-1st	97.5% 194/199	-	+>=2 97.5% 194/199	100.0% 200/200	0.697**	0.697**	0.694**	0.694**
1st-2nd	97.8% 1172/1198	-	+>=2 98.4% 1179/1198	99.9% 1199/1200	0.642**	0.644**	0.700**	0.700**
Pre-2nd	96.0% 191/199	-	+>=2 96.0% 191/199	100.0% 200/200	0.489**	0.489**	0.484**	0.484**
	Mylohyoid bridge							
Pre-1st	93.8% 167/178	-	-	97.0% 194/200	0.611**	0.620**	-	-
1st-2nd	98.6% 1088/1104	-	-	97.6% 1171/1200	0.907**	0.907**	-	-
Pre-2nd	88.1% 156/177	-	-	96.5% 193/200	0.546**	0.555**	-	-
	Mandibular torus (ASUDAS)							
Pre-1st	87.0% 87/100	-	+=1-3 88.0% 88/100	100.0% 100/100	0.515**	0.520**	0.510**	0.510**
1st-2nd	78.0% 467/599	-	+=1-3 81.0% 485/599	100.0% 600/600	0.535**	0.546**	0.504**	0.504**
Pre-2nd	85.0% 85/100	-	+=1-3 86.0% 86/100	100.0% 100/100	0.486**	0.492**	0.479**	0.479**
	Mandibular *torus* (Galera *et al.*, 1995)							
Pre-1st	86.0% 86/100	-	+='Débil'- 'Fuerte' 87.0% 87/100	100.0% 100/100	0.484**	0.489**	0.488**	0.488**
1st-2nd	78.1% 468/599	-	+='Débil'- 'Fuerte' 81.0% 485/599	100.0% 600/600	0.542**	0.553**	0.504**	0.504**
Pre-2nd	82.0% 82/100	-	+='Débil'- 'Fuerte' 85.0% 85/100	100.0% 100/100	0.460**	0.468**	0.456**	0.456**

Table 4.1.1. (Continued.)

Tooth (FDI)/Structure	Precision				Correlation			
	Overall	Within one grade	Dichotomized	Observable trait	Kendall's *tau*-b (overall)	Spearman's rho (overall)	Kendall's *tau*-b (dichot.)	Spearman's rho (dichot.)
	Palatine *torus* (ASUDAS)							
	Pre-1st 84.0% 84/100	-	+=1-4 91.0% 91/100	100.0% 100/100	0.784**	0.809**	0.822**	0.822**
	1st-2nd 80.8% 480/594	-	+=1-4 85.5% 508/594	99.2% 595/600	0.632**	0.645**	0.621**	0.621**
	Pre-2nd 78.0% 78/100	-	+=1-4 82.0% 82/100	100.0% 100/100	0.690**	0.704**	0.668**	0.668**
	Palatine *torus* (Galera *et al.*, 1995)							
Maxilla	Pre-1st 75.0% 75/100	-	+='Débil inc.'-'Fuerte comp.' 90.0% 90/100	100.0% 100/100	0.713**	0.772**	0.801**	0.801**
	1st-2nd 63.7% 379/595	-	+='Débil inc.'-'Fuerte comp.' 85.9% 511/595	99.3% 596/600	0.664**	0.611**	0.634**	0.634**
	Pre-2nd 59.0% 59/100	-	+='Débil inc.'-'Fuerte comp.' 81.0% 81/100	100.0% 100/100	0.564**	0.630**	0.643**	0.643**

*: P <= 0.05; **: P <= 0.01.

4.1.1. Paired observations' precision(s) on dental nonmetric variables

The overall precision (on 58 dental traits) ranges from 54.0% (UI2 *tuberculum dentale*) to 100% (several traits) on "Pre-1st", with a mean of 87.2%; from 39.4% (UI2 *tuberculum dentale*) to 100% (odontome on all P3's) on "1st-2nd", with a mean of 89.4%; and from 23.9% (UI2 *tuberculum dentale*) to 100% (several traits), with a mean of 83.8% on "Pre-2nd". Despite the low minimum value, the mean precision of the "1st-2nd" comparison is the highest.

Nichol and Turner's (1986) reported overall precision ascends to 74.1% (between the second and third observations), which is lower than the lowest precision found for the present study. This may mean the present author is more experienced and more accurate than Nichol, the mentioned observer, at the time of the cited work. The difference may also be caused by the conditions of the casts used by Nichol (high dental wear) and the different samples scored.

Precision within one grade on "Pre-1st" has a mean of 94.5%, and ranges from 76.6% (UI2 *tuberculum dentale*) to 100% (several traits); on "1st-2nd" it presents a mean

of 96.0%, and ranges from 81.5% (UI2 *tuberculum dentale*) to 100% (several traits); on "Pre-2nd" the mean is 93.1% and the range is 53.7% (UI2 *tuberculum dentale*) to 100% (several traits). Once again, "1st-2nd" is the most precise pair of observations, with the highest mean precision within one grade.

Nichol's highest precision within one grade was 94.4%, a value similar to the ones reported here for the present author's observations (Nichol and Turner, 1986). This suggests reliability of the ASUDAS method, which "prototype" was used by Nichol (since the methods used by these authors were later adapted and coordinated into ASUDAS), given a one grade margin of error.

Dichotomized data observed with precision averaged 93.4% on the "Pre-1st" comparison, and ranged from 75.5% (LM1 protostylid) to 100% (several traits); it averaged 94.5% on the "1st-2nd", ranging from 65.2% (UI2 *tuberculum dentale*) to 100% (several traits); it averaged 92.1% on the "Pre-2nd" paired observations, with a range from 53.7% (UI2 *tuberculum dentale*) to 100% (several traits). The "1st-2nd" comparison overcomes the other two on this precision calculation as well, thus making it the most well reproduced and precise pair of observations. On the other hand, precision percentages are always lower for the "Pre-2nd" comparison. Ranges demonstrate these precision values to be widely diversified in results and dependent on traits, which is particularly evident by the near omnipresence of UI2 *tuberculum dentale* as the lowest score.

The mean precision of dichotomized results of 89.8% found by Nichol's reliability test is somewhat lower than the present author's trend (Nichol and Turner, 1986). This may again be suggestive of a greater experience of the present author or of the effect of the sample of Kodiak Island casts used by Nichol, or a combination thereof.

When the overall precision amongst comparisons (only dental traits) is scrutinized, a pattern is evident. Percentages of "1st-2nd" comparison are very frequently higher than either one of the other comparisons ("Pre-1st" and "Pre-2nd") or very near those of the higher one (allowing up to 4% variation). Exceptions are found only on UI2 *tuberculum dentale* (Pre-1st: 54.0%; 1st-2nd: 39.4%; and Pre-2nd: 23.9%) and the LM1 cusp/groove pattern (Pre-1st: 98.2%; 1st-2nd: 92.8%; and Pre-2nd: 93.8%) and LM1 cusp 5 (Pre-1st: 65.0%; 1st-2nd: 66.9%; and Pre-2nd: 71.8%). As this was the comparison relying on the greater sample (600 individuals), it is suggestive of its quality when compared to the others, and merely reflects the means stated above.

Analysis of the comparisons' precision within one grade (when the used scale had more than one grade of presence) reveals the same pattern, reinforcing the previous finding. LP4 lingual cusp number (Pre-1st: 90.8%; 1st-2nd: 86.7%; and Pre-2nd: 85.2%) and LM2 protostylid (Pre-1st: 94.8%; 1st-2nd: 89.7%; and Pre-2nd: 90.4%) are the only exceptions.

The precision of dichotomized data for the three comparisons again revealed the same pattern: the "1st-2nd" comparison is consistently high, being either higher than the others or near the highest. Again there are exceptions. These are limited to UI2 *tuberculum dentale* (Pre-1st: 75.9%; 1st-2nd: 65.2%; and Pre-2nd: 53.7%), LM1 cusp pattern (Pre-1st: 98.2%; 1st-2nd: 92.8%; and Pre-2nd: 93.8%), LM2 protostylid (Pre-1st: 91.1%; 1st-2nd: 86.6%; and Pre-2nd: 80.7%), and finally LM3 cusp pattern (Pre-1st: 90.1%; 1st-2nd: 86.1%; and Pre-2nd: 87.0%).

The results so far seem to indicate the intention of the "preliminary" observation was successful, since subsequent observations were more accurate, despite being much more dispersed through time (which is justified by the fact that they were six times larger in sample number). The most different sets of results were the "Pre-2nd", which can be because the degree of observation quality was greater when the "second" observation was carried out, since presumably the "preliminary" observation is the least reliable.

As for the precision of observable traits, the mean for the "Pre-1st" comparison is 96.0%, and ranges from 79.5% (UM1 and UM2 enamel extensions) to 100% (LM1 cusp pattern); the mean for the "1st-2nd" is 97.0%, with the minimum precision at 88.7% (UM2 enamel extensions) and the maximum at 99.3% (LM1 MMPT and cusp number, and LM1 and LM2 C7); the mean for the "Pre-2nd" is 95.6%, and its range is from 78.5% (UM1 enamel extensions) to 100% (LM2 cusp number, C5 and C6).

When compared for each trait, the paired observations' precision of observable traits unveils the same pattern as before, without any exception: for every dental nonmetric trait the "1st-2nd" is either higher than the other comparisons or very near the highest percentage. This was expected, since it had the highest mean of the three paired comparisons and the narrowest range between the minimum and maximum recorded percentages (due to having the highest minimum by 9.2%). So, despite not reaching 100% precision, contrarily to the other comparisons, the "first" and "second" observations have high reliability in sites deemed sufficiently preserved for observation between them.

In Nichol and Turner's study (1986), inter-observer discrepancy between the amounts of observable casts was due to the most inexperienced observer's attempt to score more casts. This error is also precipitated by the frequency of dental wear and caries. According to the authors, ability to restrain from scoring a dubious cast is gained with experience. Results suggest experience helped the present author slightly, since they gradually improved.

Intra-observer mean precision when corresponding scorable sites between observations was lower on Nichol and Turner's (1986) study, since the highest precision was 93.3% (second-third scoring sessions), when compared to the present one. Molars were more affected by error in Nichol's observations, probably due to caries, dental wear and casting errors. These differences may be caused by the discrepancies in samples and observed materials, since casts are prone to error, as noted, and dental attrition was high on the Kodiak Island Inuit studied by the mentioned authors.

4.1.2. Paired observations' correlation(s) on dental nonmetric variables

As for the rank correlation coefficients, Kendall's *tau*-b and Spearman's *rho*, of the overall error between dental nonmetric variables observations, correlations are generally moderate to strong (correlations near or above 0.4) and statistically significant (P < 0.01), particularly within the "1st-2nd" comparison, with few major exceptions: tricuspid premolars and UP4 odontome (both statistics on both traits present negative association of -0.001, without statistical significance, meaning the result can be influenced by small sample size), LP3 odontome (coefficients unavailable for either test). Relatively weaker associations (coefficients between 0.2 and 0.4) were found for the "1st-2nd" paired observations, on some traits: UP3 accessory cusps, UM1 mesial marginal accessory tubercles, LI2 shoveling, LM1 MMPT and LM3 C7. All of the previous traits have consistently high precision values, and so are considered reliable results despite lower (mostly slightly lower) correlation coefficients.

When establishing rank correlations on dichotomized data, although general results are similar for "1st-2nd", more unavailable coefficients (UI1 winging, LI1 and LI2 shoveling, and LP3 odontome) and the same negative, not significant, associations (UP4 tricuspid premolars and odontome) occur.

The results on the "Pre-1st" pair of observations for overall ranked data correlation are similar to the ones presented for "1st-2nd". Exceptions are UI1 shoveling with lower statistical significance ($P < 0.05$), probably due to smaller samples; UI1 interruption grooves, UP3 odontome, UP4 tricuspid premolar and odontome, UM1 and UM3 enamel extensions, LP3 odontome, and LM2 C6 with unavailable coefficients; LM1 distal trigonid crest and LM3 C7 with non-significant, negative associations. Once again, there are some slightly weaker associations between observations: UI1 shoveling and double shoveling, UP3 accessory cusps, UM1 mesial marginal accessory tubercles, LI2 shoveling and LM1 C7. Some are accompanied by relatively low (under 90.0%) precision values, but most are not, and these results are not threatening to either observations' validity, despite showing the diminishment of intra-observer error with passing observations (since the comparison between the "1st-2nd" and final observations yielded slightly more consistent associations).

The correlations found for dichotomized data again reflect the ones for the original data for "Pre-1st", with several exceptions. Unavailable results for the statistical tests occurred with UI1 winging and interruption grooves, UP3 odontome, UP4 tricuspid premolars and odontomes, UM1 and UM3 enamel extensions, UI1 and UI2 shoveling, LP3 odontome, and LM2 C6; negative and non-significant correlation was found for UI1 shoveling and double shoveling, LM1 distal trigonid crest and C7, and for LM3 C7.

Coefficients found for the "Pre-2nd" comparison of non-dichotomized data are, once again, generally high. Notable differences reside on results with lower significance ($P < 0.05$), such as UI1 double shoveling; unavailable results, such as UI1 interruption grooves, UP3 accessory cusps and odontome, UP4 tricuspid premolars and odontome, UM1 and UM3 enamel extensions, LI2 shoveling, LP3 odontome, and LM2 C6; low negative correlations, namely UP3 accessory crests; and not significant coefficients: UM1 mesial marginal accessory tubercles and LI1 shoveling. The weakest associations (coefficients between 0.2 and 0.4) were found on the following traits' comparisons: UI1 shoveling and double shoveling; UI2 interruption grooves; LI1 shoveling; LM1 groove pattern, protostylid and MMPT; LM2 distal trigonid crest and protostylid. Mostly, these lower associations are accompanied by high overall precision values (above 90.0%), but the increase in the number of traits with relatively low correlation coefficients illustrates once again the difference in observations with each try, emphasizing the quality of the

"1st-2nd" observations, with the least lower correlations and all of them in situations where high precision values guaranteed generally low intra-observer error.

As for dichotomized data for "Pre-2nd", there are some deviations from the generally high correlations found: not available coefficients as UI1 winging, shoveling and interruption grooves, UP3 accessory cusps and odontome, UP4 tricuspid premolars and odontomes, UM1 and UM3 enamel extensions, LI1 and LI2 shoveling, LP3 odontome, and LM2 C6; not significant negative correlations as UI1 double shoveling, UP3 accessory crests, LM1 and LM3 C7; not significant coefficients as UM1 mesial marginal accessory tubercles.

Rank correlation coefficients show the most consistent results for the "1st-2nd" paired observations, which may not only be related to a greater quality of the observations, but also be dependent on the greater variability found therein. A greater amount of total presence or absence of a trait sometimes justifies low or unavailable coefficients. These may also occur when presence is low and, due to an error, detected only on one of the observations, for instance. Kendall's *tau*-b and Spearman's *rho* are therefore better with greater samples, as well as with non-dichotomized data, presenting more than two ranks and tending to a greater variability. These coefficients testify to a general lack of gross and systemic intra-observer error, hence evaluating the statistical meaning of the precision calculations.

Despite these considerations, "1st-2nd" is again the best ranking set of observations, when it comes to intra-observer error, consolidating earlier finds.

4.1.3.Paired observations' precision(s) and correlation(s) on oral nonmetric variables

Overall precision for mandibular and palatine traits averages 87.2% and ranges from 75.0% (palatine *torus* [Galera *et al.*, 1995]) to 97.5% (*foramina mentales*) for the "Pre-1st" pair; it averages 82.8% and ranges from 63.7% (palatine *torus* [Galera *et al.*, 1995]) to 98.6% (mylohyoid bridge) for the "1st-2nd"; finally, it averages 81.4% and ranges from 59.0% (palatine *torus* [Galera *et al.*, 1995]) to 96.0% (*foramina mentales*) for "Pre-2nd".

The osseous nonmetric traits' dichotomized data precision that compare the "Pre-1st" observations range from 87.0% (mandibular *torus* [Galera *et al.*, 1995]) to

97.5% (*foramina mentales*), averaging 90.7%; the "1st-2nd" comparison ranges from 81.0% (mandibular torus [Galera *et al.*, 1995]) and mandibular *torus* (ASUDAS) to 98.4% (*foramina mentales*), averaging 86.4%; the "Pre-2nd" observation pair ranges from 81.0% (palatine *torus* [Galera *et al.*, 1995]) to 96.0% (*foramina mentales*), averaging 86.0%.

Objective traits, *foramina mentales* and the mylohyoid bridge, are more consistently recorded than the *tori* on the "1st-2nd" observation pair. The mandibular *torus* (using both methods) has its least reliable pair of observations on the "1st-2nd" comparison, and the palatine *torus* (again using either method) shows a descending precision percentage from "Pre-1st" to "Pre-2nd", with "1st-2nd" in the middle. This suggests a decrease in the quality of the observation, although this can be misleading. In case of the observer's excessive incursion in error during the "preliminary" and "first" observations, any correction would cause a diminished precision. This find may be caused by a number of factors, from a difficulty with the methods to a greater attention of the author and observer on dental traits, his main concern. The palpatory character of the detection of the smallest *tori* may be a sufficient contrast to the visual nature of the remaining evaluations, lending greater difficulty and inaccuracy to the task.

Traits considered observable on both observations achieve a mean precision of 99.5%, with a minimum of 97.0% (mylohyoid bridge) and a maximum of 100% (every other trait) on pair "Pre-1st"; for pair "1st-2nd" this precision test ascends to an mean of 99.3%, ranging from 97.6% (mylohyoid bridge) to 100% (mandibular *torus*, for both methods); for the final comparison ("Pre-2nd"), the mean precision is 99.4%, ranging from 96.5% (mylohyoid bridge) to 100% (all other traits). Despite having the highest minimum precision percentage, the lowest mean is "1st-2nd", although only differing 0.1% and 0.2% from "Pre-2nd" and "Pre-1st", respectively. A rarity of 100% precision justifies this.

For *foramina mentales* and the palatine *torus* (both methods), the "1st-2nd" had the lowest precision of all three comparisons, although with few difference. The mylohyoid bridge precision percentage for the "1st-2nd" pair was the highest (97.6%). For the mandibular *torus* (either method) all paired observations attained 100% precision. This precision measure was very high throughout, verifying the observer's capacity to distinguish observable from unobservable trait sites on oral bones.

Showing a slight contrast to the previous results, the rank correlation coefficients show consistently strong associations and a consistently high ($P < 0.01$) statistical

significance between each of the paired observations for every trait of the maxilla and mandible, either using non-dichotomized or dichotomized data. This concedes greater guaranty on the quality of the observations and allows the use of all the traits on biological affinity analyses, despite some lower precision results.

4.1.4.Paired observations' precision(s) and correlation(s) on dental wear

Exact correspondence precision on dental attrition classification averages 69.5%, ranging from 56.7% (UM2) to 77.2% (LC) for "Pre-1st"; it averages 74.8% and ranges from 64.6% (UI2) to 83.8% (UM1) on "1st-2nd"; it averages 54.1%, ranging from 37.3% (UM2) to 75.4% (LI1) on "Pre-2nd".

Precision within one grade for dental attrition on the "Pre-1st" comparison averages 99.1%, with a minimum percentage of 97.3% (LM3) and a maximum percentage of 100% (several teeth); on the "1st-2nd" paired observations it averages 99.6%, ranging from 99.2% (UP3) to 100% (UP3 and LM1); on "Pre-2nd" its mean is 98.1% and its range varies from 91.4% (LM3) to 100% (several teeth).

Precision of the exact replication of the grade attributed to dental attrition (or wear) was low, overall. This may be due to the difficulty in deciding between nearing grades, which is largely demonstrated by the within one grade precision, which is very high (consistently above 90.0%). On both precision results, the "1st-2nd" observations were once again the most precise, which is most likely due to the experience gained beforehand. If for the within one grade precision the minimum and mean percentages were slightly higher than the ones involving the "preliminary" observation, for the exact precision these were even higher, with a mean more than 5.0% higher than "Pre-1st" and more than 20.0% higher than "Pre-2nd" as well as notably higher minimum and maximum percentages. When analyzing this comparison, it was found that molars' mean overall precision (78.3%) is higher than the mean for teeth with less complex crowns (72.7%), which may mean the method (Smith, 1984) is easier to correspond to observed reality when more reference points (cusps and crevices) are present.

The Kendall's *tau*-b and Spearman's *rho* coefficients produced for the exact correspondence between dental wear grades always detect strong correlations and high statistical significance (P < 0.01), for every tooth and comparison. Intra-observer error

is, thus, at an acceptable level for the determination of the degree of dental attrition of the observed sample.

4.1.5.Single trait precision(s) and correlation(s)

Although the analysis undertaken above, in general, allows for an understanding of the range and general reliability of the observations' intra-observer error, each dental and osseous non-metric variation will be reviewed, so as to identify any particular difficulty with the reproduction of trait classification. This approach will only consider the intra-observer error of the "1st-2nd" pair of observations, since the results of the "second" observation will be used for subsequent biological affinity analyses.

Some of the traits will not be reported on individually, since their precision was over 90.0% on all (or nearly all) accounts and the rank correlation coefficients were highly significant, or justifiably not so. These are: UI1 winging (the results for rank correlation tests of dichotomized data are unavailable, which is probably an artifact of the low presence of the trait and its cut-off point for dichotomization), UI1 double shoveling, UI1 midline diastema, UI1 and UI2 interruption grooves, UI2 peg incisors, UP3 and UP4 accessory cusps (the former tooth displays a correlation coefficient under 0.4, but has consistently high precision values); UP3 and UP4 tricuspid premolars (negative [-0.001] coefficients on UP4, probably an artifact of the very low presence of the trait, at 0.1%/0.2%), odontomes (all P; negative [-0.001] coefficients on UP4 and LP3, probably an artifact of the very low presence of the trait, at 0.1%/0.2%), UM1 mesial marginal accessory tubercles (its precision values compensate a moderate correlation), UM1 C5, enamel extensions (all UM; overall precision of only 88.9% on UM2, a negligible exception, most likely due to slight difficulty in determining presence of the first grade: the dichotomized precision, dividing absence from every grade of presence, is 94.0%), UM3 parastyle, LM1 deflecting wrinkle, C6 (all LM), C7 (all LM; the relatively weak association between observations is compensated for high precisions), *foramina mentales* and mylohyoid bridge.

Shoveling, despite high precisions for every parameter and high correlation for overall correspondence (coefficients for dichotomized correspondence are unavailable, the exception is a moderate association on LI2) on lower incisors, presents an overall precision of 86.3% on UI1. This is most likely due to the difficulty in distinguishing

from grades 0 and 1 (probably brought about by dental wear), both considered as absence of this trait. On the other hand, dichotomized precision is 11.0% higher, with 97.3%. Nichol's UI1 shoveling overall precision was 57.1% (first-third observations), but his dichotomized precision was 98.0% (Nichol and Turner, 1986). This lack of overall precision, therefore, does not affect the accuracy of the trait frequency.

Table 4.1.2. Precision and correlation of dichotomized data with different breakpoints on selected traits.

Tooth (FDI)/Structure	Precision (dichotomized)	Kendall's *tau*-b	Spearman's *rho*
	Tuberculum dentale		
12/22	+=3-6 87.4% 636/728	0.394**	0.394**
	Distal accessory ridge		
33/43	+=2-5 90.4% 757/837	0.613**	0.613**
	Anterior fovea		
	+=2-4 90.5% 627/693	0.590**	0.590**
	Protostylid		
36/46	+=2-7 98.2% 704/717	0.429**	0.429**
	C7		
	+=1a-4 96.8% 698/721	0.692**	0.692**
	Protostylid		
	+=2-7 89.7% 751/837	0.262**	0.262**
37/47	C7		
	+=1a-4 99.1% 846/854	0.445**	0.445**
	Protostylid		
	+=2-7 94.5% 495/524	0.308**	0.308**
38/48	C7		
	+=1a-4 98.5% 574/583	0.309**	0.309**
	Mandibular *torus* (ASUDAS)		
	+=2-3 96.5% 578/599	0.586**	0.586**
Mandible	Mandibular *torus* (Galera *et al.*, 1995)		
	+='Medio'-'Fuerte' 97.0% 581/599	0.696**	0.696**
	Palatine *torus* (ASUDAS)		
	+=2-4 95.3% 566/594	0.580**	0.580**
Maxilla	Palatine *torus* (Galera *et al.*, 1995)		
	+='Medio inc.'-'Fuerte comp.' 89.1% 530/595	0.551**	0.551**

*: P <= 0.05; **: P <= 0.01.

Distal accessory ridge on both upper and lower canines presents very low overall precision (57.4% for UC; 73.5% for LC) and low dichotomized precision (85.0% for UC; 81.4% for LC), despite precisions within one grade above 90.0% (90.8% for UC; 95.7% for LC) and very high correlations. When determining the dichotomized precision for LC differently, by considering present grades from 2 above only (see Table 4.1.2), it improves to 90.4%. This reflects the difficulty in identifying the trait when even the slightest amount of attrition has affected the site (and particularly if the trait is poorly expressed). Filtering out teeth that had suffered amounts of attrition greater than grade 4, 3, 2 and even 1 did not reflect itself on the results (author's personal observation; see 4.6.Dental wear for the role of dental wear in dental morphological analyses), underlining the trait's subjection to localized attrition. Scott's (1997) original review of this trait found only presence errors of 0.0% (UC) and 2.4% (LC), 100% for precision within one grade and overall precisions of 79.1% (UC) and 64.3% (LC). The better results achieved by this author may be related to his creation of the plaques (conducing to a better analysis of scorability and easier reproducibility) and his only focus being this trait, for said study.

Nichol's best overall precision (54.5%), precision within one grade (84.1%) and dichotomized precision (90.9%) are similar to the ones presented here for the upper canine. This author's best overall precision (52.4%) and precision within one grade (92.9%) for the lower canine are lower than the present ones, but dichotomized precision (88.1%) is somewhat higher (Nichol and Turner, 1986). In general, results are similar. Nichol and Turner (1986) justify these results with difficulties relating to dental wear, corroborating the above findings.

Accessory crests (on both UP) present high precision and correlation results, with the exception of the overall precision on UP4 (87.4%). This is probably caused by occasional confusion relating to where these crests are present, since they were not recorded in a graded scale, but according to their position. Burnett and colleagues (2010) have recently provided a set of graded plaques for the scoring of this trait, but they were not yet available to the author at the time of his observations. These crests' presence (or dichotomized) precision for the same premolar is 90.3% in the present sample, and are 97.0% for either premolar on the mentioned work (Burnett *et al.*, 2010).

Carabelli's trait (UM1) has poor overall precision (70.1%), despite very strong correlation coefficients. Its cause may be mainly indecision on whether to pick one grade or the next, since precision within one grade is 93.4% and dichotomized precision

(presence from grades 2 to 7) is 90.8%. Threshold expressions as analyzed through complex grading systems make it difficult to consistently score the same tooth.

A 66.7% overall precision was the best result obtained by Nichol in his three observations. Precision within one grade was also low (82.1%). Despite this, he was able to correctly reproduce presence and absence 94.9% of the time on his best attempt. The slight difference from the present observer's and Nichol's best result may be due to the breakpoint, since Nichol considered the trait present from grade 1 to 7 (Nichol and Turner, 1986). The presence-absence scoring concordance of Carabelli's trait found by Scott (1980) was 97.6%, using the Dahlberg plaques and considering grades 1 through 7 present. The ASUDAS should, therefore, be reliable at detecting the presence of the trait at least on either of these cut-off points (+ = 2-7 and + = 1-7).

The hypocone (UM2 C4) is affected by the same difficulty in overall precision (59.9%), corrected by dichotomization (90.3%) and very strong correlations. Precision within one grade is not high, but only 83.8%, which may mean the difference in proportion between cusps on the grades considered present (3-5) may be difficult to reproduce or detect accurately, at least for the present observer. Presence of the trait was not hindered by any difficulty distinguishing the trait threshold, between grades 2 and 3, which seems sufficient to ensure correct detection of the trait's frequency. Nichol's best result with this trait on UM1 was 76.3% overall precision and 100% precision within one grade and of presence (Nichol and Turner, 1986). Discrepancies may be the result of different methodology and breakpoints, and may demonstrate Nichol's greater scoring precision for this trait.

Premolar lingual cusp variation is shown as difficult to reproduce, mainly on LP4, since precision results are low for overall precision (LP3: 80.6%; LP4: 68.7%) and relatively low for precision within one grade (LP3: 86.7%; LP4: 84.5%) and dichotomized data precision (LP3: 90.1%; LP4: 86.5%), despite very strong association between observations. The 10-graded scale is complex and, therefore, may be prone to some confusion in reproduction of observations. Differences between grades 1 and 2, the cut-off point for dichotomization, may be difficult to ascertain when some attrition is present, resulting on a slightly lower presence precision. Nonetheless, the frequencies presented for the trait are thought as acceptable, given the high correlation coefficient between the two main observations for both teeth and both overall and dichotomized data.

Nichol's best overall precisions are 90.0% (LP3) and 69.4% (LP4), precisions within one grade are 96.0% (LP3) and 95.9% (LP4) and dichotomized data precisions are 94.0% (LP3) and 81.6% for LP4 (Nichol and Turner, 1986). Present results are generally lower, except for the dichotomized data precision for LP4. Again, particularly for LP4 the scoring of this trait is portrayed as somewhat confusing. Careful reading of instructions and consultations of the plaques is hence recommended.

Anterior fovea (LM1) is a trait which poses difficulties when coronal wear is present, since it is a crevice which depth may be under or overestimated when the cusps and the mesial ridge, functioning as references, have eroded away. This justifies an overall precision of 80.2%, accompanied by precision within one grade of 94.5%, but again showing a percentage of merely 87.6% for the presence precision. On Table 4.1.2., a different breakpoint is tested (+ = 2-4, instead of: + = 1-4), and presents a dichotomized data (or presence) precision of 90.5%, revealing the greater difficulty on these observations was accurately detecting the difference between grades 0 and 1.The consistently high and statistically significant (P < 0.01) coefficients allow for the validity of this trait's frequency not to be put into question.

Nichol and Turner (1986) found a best overall precision of 53.3%, precision within one grade of 96.7%, and dichotomized precision of 100.0%. They thought this trait's plaque should be reviewed, since it was one of the least precisely reproduced. However, their results were definitely lower than the present ones for overall precision but higher for the dichotomized data precision. Nichol could better determine presence and had a greater difficulty distinguishing among the grades defining it. This difference may have been due to attrition, reported as high for the sample used by Nichol and Turner (1986). Only 83.3% of the teeth were deemed scorable from one observation to the other on the comparison with best results (first-third). That may mean the exclusion of the LM1's most affected by attrition was sufficient to allow for better results on presence precision. If the present sample is less affected by attrition, the decision to dismiss a tooth as unscorable may have been harder on the present observer, who tended towards including most teeth.

Cusp/groove pattern (all LM) posits high correlation and statistical significance (P < 0.01) for all lower molars and only on LM3 does it present overall and dichotomized data precisions under 90.0% (both 86.1%). The high morphological variability of the third molar crowns is well known, and inadequacy in reproduced

observations may be partly justified by such variability and the difficulty in characterizing it objectively (noted by Scott and Turner [1997]).

Morphological variability of the LM3 also influences the recording of the distal trigonid crest, which presents low precision values for overall and dichotomized data (85.4% on both). Correlations are high throughout tests and comparison types (*tau*-b/*rho* = 0.518, P < 0.01).

The protostylid (all LM) shows overall precision values under 90.0% for LM1 (87.7%) and LM2 (84.6%). On LM1, protostylid precision within one grade corresponds to a high 98.7%, which contrasts with 89.7% on LM2. This percentage is very near 90.0, but 9% lower than the same parameter on LM1. Strong correlations are found for this trait on both teeth. Besides the breakpoint for presence definition at Table 4.1.1. (+ = 1-7), another one is presented at Table 4.1.2. (+ = 2-7). Precision on dichotomized data is 88.7% for presence between grades 1 and 7 and 98.2% from grades 2 to 7 on LM1, illustrating imprecision in determining protostylid grades 0 and 1. The latter grade is considered the first expression of the trait, since it is present on dentine (Skinner *et al.*, 2009). However, it is difficult to pinpoint consistently. As for LM2, the definition of grade 1 does not seem to be the only issue, given a slight increase from 86.6% (+ = 1-7) to 89.7% (+ = 2-7) once the calculation of dichotomized data precision is altered. Correlation for this trait on LM2 and LM3 when using the latter breakpoint drops below 0.4, the threshold used here to determine a strong correlation. So, a strong correlation between observations (using grades 1 through 7 as presence) shows their reliability, in spite of the somewhat lower precision values, indicating the indistinct nature of the first two grades of presence.

Nichol achieved high results for overall precision and dichotomized data precision (both 93.0%) and precision within one grade (100.0%) for LM2. As for protostylid on LM1, exact precision was only 62.9% at best, with 91.4% precision within one grade and dichotomized precision at 65.7%. This trait at this particular tooth was identified as one of the difficulties for Nichol, related to his poor results (Nichol and Turner, 1986). So, these results are another testimony that the major difficulty is to locate the first instance of presence, grade 1, since Nichol also displays a great amount of difficulty when distinguishing presence (dichotomized precision only slightly improved the percentage found for overall precision).

MMPT (all LM) is another trait slightly affected by the variability on M3's. The overall precision on LM3 is 89.2%, which is compensated by a 92.0% dichotomized

data precision and 91.6% precision within one grade. On LM1 an LM2, all calculated precisions are above 90.0% and there are strong coefficients with high significance (P < 0.01) for LM2 and LM3.

Lower molar cusp number has high precision and correlation values on LM1 and LM2. On LM3, despite highly significant and very strong correlation values (P < 0.01), overall precision is 86.7% and precision of dichotomized data is 89.8%. High variability on M3's again is the most likely explanation for this situation.

The cusp 5 trait (all LM) is also difficult to grade precisely, despite that it seems easy to identify as present and presents very strong correlations. Doubt arises on LM1 (overall precision: 69.6%; precision within one grade: 95.4%; dichotomized precision: 95.9%) and LM3 (overall precision: 77.2%; precision within one grade: 90.9%; dichotomized precision: 92.1%) only. Expressions of the trait that would be better qualified as being between grades (given the quasicontinuous nature of dental discrete traits) redound on such results, corrected by the definition of presence for this variable, between grade 1 and the highest, grade 5. The same pattern is found on the results reported by Nichol and Turner (1986) for LM1.

The lowest precision figures proceed from UI2 *tuberculum dentale*. Overall precision is 39.4%, precision within one grade is 81.5% and dichotomized data precision is 65.2% (+ = 2-6) and 87.4% (+ = 3-6), according to each breakpoint used. Despite relatively strong and highly significant (P < 0.01) coefficients for this trait, the reported precision values are too low. Low intra-observer precision with this trait's graded scale has occurred before, and has shown its low reliability. *Tuberculum dentale* can be expressed as a tubercle or as one or more lingual ridges, of varied expression, which makes its standardization very difficult (Hillson, 1986; Scott, 2008). The value of this trait for further analyses is severely hindered, even if the individual count method will be used to obtain the frequencies of trait presence and could diminish the effect of this error margin, by using only the highest expression from every pair of upper lateral incisors present. Therefore, this trait will not be used for the calculation of the biological relations between groups.

Nichol and Turner (1986) place this trait as one of the most difficult to replicate accurately, and hypothesize the cause as a fault with the developed plaque. The best overall precision for UI2 was 59.6%, with 83.0% precision within one grade and 87.5% precision using dichotomized results. Despite accepting presence from grades 0 to 8 of the used method, the dichotomized precision result is similar to the one reported here

for results including ASUDAS grade 3 through 6. Precision within one grade is also similar, and overall precision is still low, despite 20.2% higher than the present author's comparison. These results and the authors' conclusion stated above reinforce the idea of inadequacy with the method when using ASUDAS.

Mandibular *torus*, in terms of intra-observer error calculations, obtained very similar results using both methods (ASUDAS and Galera *et al.*, 1995). Overall precision is 78.0% for ASUDAS and 78.1% for Galera and colleagues' (1995) method, and dichotomized data (+ = 1-3 and + = 'Débil'-'Fuerte', respectively) was 81.0% for both. When different dichotomization was applied, not considering the least trace of mandibular *torus* present (but + = 2-3 and + = 'Medio'-'Fuerte', respectively; see Table 4.1.2.), results were 96.5% and 97.0%. This illustrates how the main difficulty resided in determining presence when the trait was barely detectable. Visually it was virtually undetectable, sometimes, due to the alterations on bone from the long interval of time past since exhumation and to the handling of the material by many people throughout the decades.

Using a method similar to ASUDAS, Nichol and Turner (1986) found inter-observer overall precision to be 89.6% and dichotomized data precision to be 91.7%. These results are about 10.0% higher than the ones found in the present study. This may be due to differences in the methods or to a greater reliability of casts when compared to the present sample, as well as due to a greater difficulty in scoring the trait for the present author.

The palatine *torus* evaluated using ASUDAS was exactly agreeable 80.8% of the time, and precise using presence, or dichotomized data, 85.5% (+ = 1-4) and 95.3% (+ = 2-4) of the cases. Although affected by the difficulty in detecting smaller expressions of the trait, the results are near 90.0%, when dichotomized data is used, as will occur with further analyses.

The use of the Galera and colleagues' (1995) method was not as successful (overall precision: 63.7%; + = 'Débil' incomplete-'Fuerte' complete: 85.9%; + = 'Medio' incomplete-'Fuerte' complete: 89.1%). The intricacy and multiple variables (assessing thickness and wideness, but also length of the trait) evaluated may have caused some lack of reliability on threshold or trace cases.

Nichol's overall precision and dichotomization precision, using a different method, was 93.6% at his best comparison, indicating once again the possibility of a

difference between methods or a greater ease in identifying presence with the use of casts.

4.1.6.Final considerations

The results here analyzed correspond to the expected results, with error margins between 0.0% and 15.0%, and generally corresponding to the results published by Nichol and Turner (1986). Dichotomized data is generally reproduced with precision, with only two dental non-metric traits (*tuberculum dentale* on I^2 and distal canine ridge on $_C$) and one osseous discrete variable (mandibular *torus*) with less than 85.0% precision. Correlations between observations were also generally strong to very strong, with a minimum amount of moderate results. All these data gives strength to the results used for further analyses.

This demonstrates the ASUDAS method as easily reproducible and scorable, despite the moderate amount of training and experience of the present author and the fact he was not trained by one of the method's authors and main promoter (as was Nichol).

The use of the individual count method (that considers only the highest expression of each trait for each tooth in an individual) to determine trait frequency will further diminish the error margin, since the highest expression is usually easier to detect accurately (confirm above) and the lowest expression will sometimes be eliminated from consideration. This analysis considered the tooth count method so as to effectively account all the available data for intra-observer error calculations.

The "second" observation is thought as potentially the most accurate, since it encompasses the peak of the observer's experience, accumulating the "preliminary" observation and the "first" full observation (besides the work done on a prior dissertation: Marado, 2010). As previously stated, further evaluation of the samples variability and comparisons with other samples will only consider the "second" observation.

4.2.Fluctuating asymmetry

Symmetry is the reproduction of a structure in size, shape and position relative to a dividing point. Asymmetry is the divergence in size, shape and position of a part of this structure (Bollini *et al.*, 2009a). Asymmetry is largely unrelated to handedness, despite numerous attempts to finds an association (Ubelaker and Zarenko, 2012).

In dental morphology, one of the applications of measuring symmetry is its contribution to the decision on which count method to better suit each sample (Scott and Turner, 1997; see below: 4.7.Count method). Theoretically, tooth morphology should be a symmetrical mirror image between antimeric teeth (Groeneveld and Kieser, 1991; Bollini *et al.*, 2009a). Despite this, fluctuating asymmetry (FA) occurs in dentition, since a given character can be found on a left side tooth and not on its antimere. Research on this matter has shown that this is a relatively constant phenomenon amongst populations, and that it is not genetic in origin, but rather due to environmental factors that intervene in the expression of genes during odontogeny (Scott and Turner, 1997; Rizk *et al.*, 2008). Several studies that involved the dental phenotype have demonstrated the very relevant role of environmental factors on odontogenesis, despite of the influence of genomic factors. This is due to the interplay between these sets of factors and their reflection on phenotypic results (Riga *et al.*, 2013). When tooth morphology is concerned, bilateral asymmetry is a form of qualitative FA (Bollini *et al.*, 2009a). Processes behind FA may explain part of the variability within monozygotic twins' dental morphology, which depends on environment (Scott and Potter, 1984). FA occurs when there are slight deviations from normal symmetry without left or right side preference and is measured as the difference between the expression on the right side and that of the left ($FA = R - L$). The mean difference found throughout a population should be zero, plotting a normal distribution, and its variance is considered a measure of development instability, or noise (Groeneveld and Kieser, 1991; Graham *et al.*, 1993; Markow, 1995; Palmer, 1996; Klingenberg and Nijhout, 1999; Gawlikowska *et al.*, 2007; Bollini *et al.*, 2009a; Jeong *et al.*, 2013).

Developmental instability is the proportion of the reaction of developmental systems to internal or external disturbances (Klingenberg and Nijhout, 1999), as it may be caused by external perturbations or by a lack of genomic adaptation (Van Dongen and Gangestad, 2011). Despite the emphasis given to developmental instability, the dynamics of development begin with a different notion, developmental precision. This is the proximity to which an organism develops when compared to its genotype, and is affected by two opposing forces: (1) developmental noise, affecting precision, (2)

developmental homeostasis, correcting for this disruption towards bilateral symmetry. Developmental noise is summarized as the inability of an organism to provide an exactly identical developmental path for both sides, which allows some degree of variation to cellular physiological processes. Developmental homeostasis may be the genetic component to FA, since the capability of this process to actually correct developmental noise may be genetically determined (Palmer, 1996). FA is heightened by developmental morbidity or anomalies and by homozygosity, which corresponds to the genetic factor. Environmental factors play a very important role, since their effect on development is also reflected on FA (Livshits and Kobyliansky, 1991). So, FA is modulated both by genetic and environmental factors, since it is a response to the latter that has to be within the variability of the former (Klingenberg and Nijhout, 1999).

Genotype and phenotype are connected through morphology during development towards the final shape of a tooth, through the "patterning cascade model". This demonstrates the genetic quality of tooth morphology as well as the potential for asymmetry during odontogenesis, since it posits the formation of new enamel knots (and the formation of traits such as Carabelli's trait, for example) are dependent on the relative position of the main cusps (Jernvall and Jung, 2000; Salazar-Ciudad and Jernvall, 2002; 2010). Perturbations during development (environmental factors, which can be nutritional stress, extreme temperatures and high parasitic load, for instance) may require or hinder available resources during ontogeny, which thus potentially causes deviations from symmetry, known as FA. These deviations are due to an incapability of the full phenotypic expression of the genome, and are more frequent as environmental stress increases (DeLeon, 2007). Environmental conditioning of tooth development (which can both be evaluated by, and inform on, dental morphology) is a part of dental ecology, the study of the effect environment has on dentition (Cuozzo *et al.*, 2012).

Developmentally, FA could still be further explained as two different processes that occur at different times: (1) asymmetry could begin with tooth buds, *in utero*, which would only mineralize later, after birth, and (2) mineralization could bring about further asymmetry, due to disturbances in development affecting one side differently from the other (Noss *et al.*, 1983).

Although most authors hypothesize FA is caused by environmental factors during odontogeny, the results are sometimes difficult to interpret with certainty, because of the usually low number of individuals observed (Bermúdez de Castro, 1989). Such random asymmetry is thought to mean the genes that control trait development are

the same for each side of the jaw, and only environmental factors, either in the jaw or *in utero*, could explain the variation among sides (Baume and Crawford, 1980). FA may, on the other hand, be a result of nonlinear dynamics within developing organisms, resulting from the various cellular processes inherent to them, and not generated by developmental instability (Graham *et al.*, 1993). So, Markow (1995) seems to not overstate her conclusion that the degree and type of genetic influence on FA is unknown, and its study a priority. Such considerations show the link between FA (as a measure of developmental instability) and stress is still diffuse. One of the main aspects in the study of FA and its potential correlation to stress is the test for directional asymmetry or antisymmetry, both of which can be caused by different catalysts (Palmer, 1996; Van Dongen *et al.*, 1999).

Directional asymmetry is the normal overdevelopment of one side in relation to the other in the majority of a population (Graham *et al.*, 1993; Markow, 1995; Palmer, 1996; Klingenberg and Nijhout, 1999; Gawlikowska *et al.*, 2007; Jeong *et al.*, 2013). Antisymmetry is the consistent occurrence of asymmetry across a population, with side defined randomly for each individual (Graham *et al.*, 1993; Markow, 1995; Palmer, 1996; Klingenberg and Nijhout, 1999; Gawlikowska *et al.*, 2007; Jeong *et al.*, 2013). Antisymmetry and directional asymmetry may also be related to stress. Its bias may not be genetically determined but resulting from the very stimuli causing asymmetry, depending on its degree or direction and the organism's susceptibility at early development (Graham *et al.*, 1993).

A small sample of five patients with genetic mosaicism (45, X/46, XX patients) displayed directional asymmetry in dental morphology, as measured by first molar cuspal distances and angles. This is in agreement with findings from other parts of the bodies of such patients (Pirttiniemi *et al.*, 1998). The same types of measurements were applied to 27 children, which displayed some instances of directional asymmetry related to handedness (Pirila-Parkkinen *et al.*, 2001). Another example of directional asymmetry in tooth morphology was found in an Australian woman. Her posterior dentition was asymmetrical, with the left side typically smaller, presenting small intercuspal distances and changes in the roots. This could have been caused by a developmental issue and is not, most likely, an extreme case of the normal range of variability in human dental asymmetry (Wetherell *et al.*, 2004). These are atypical situations, and would commonly be diluted within large population studies.

Studies reveal awareness in measurement error and possible directional asymmetry within their sample as possible obstacles to their conclusions' validity (Van Dongen and Gangestad, 2011). The calculation of intra-observer error (see 4.1.Intra-observer error) demonstrated its degree to be, in general, relatively low and within expected. The author expects observation error to be small when it comes to differences among sides, due to their paralleled observation (direct comparison between sides facilitates the definition of each side's precise grade, through comparison of their difference or likeness). Directional asymmetry and antisymmetry will be ruled out statistically, so as not to hinder this study's results and interpretations.

4.2.1.Overall sample's fluctuating asymmetry

Table 4.2.1. shows the results for fluctuating asymmetry (FA) found in the present sample. Asymmetry was determined for the overall sample of observable paired teeth or mandibles (thus using the individual count method and excluding individuals with only one of the sides represented), by subtracting the grade found on the left side to that found on the right. Each individual calculation produced null, positive and negative outcomes, depending on the correspondence between sides, a greater right side grade or the opposite, respectively. The same sample was evaluated including present traits only (therefore excluding bilateral absences, so as to diminish the effect of either low or high trait presence within the sample on the overall asymmetry, and make the sample comparable to biologically distinct populations, as proposed by Mayhall and Saunders, 1986). Rank correlation coefficients (Kendall's *tau*-b and Spearman's *rho*) were calculated for the overall asymmetry, to check the correlation between sides. Overall grade frequencies and grade frequencies for each side are reported as well (using the tooth count method). Traits were selected when one side could be independently measured from the other (excluding midline diastema, maxillary *torus* and mandibular *torus*; the *tori* were recorded as unilateral, since nonmetric ordinal measure of these traits tends to be symmetric, according to personal observation) and when intra-observer error was acceptable (so excluding UI2 *tuberculum dentale*; see 4.1.Intra-observer error).

Table 4.2.1. Overall FA, Comparable FA, rank correlations, and grade frequencies for bilateral dental and oral nonmetric traits.

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
Winging (11/21)	7.3% (18/247)	+ = ASU 1a and 1b 75.0% (9/12)	0.416**	0.423**	3: 93.7% (592/632) 1a: 0.3% (2/632) 1b: 1.6% (10/632) 2: 1.1% (7/632) 4: 3.3% (21/632)	3: 93.6% (291/311) 1b: 1.6% (5/311) 2: 1.3% (4/311) 4: 3.5% (11/311)	3: 93.8% (301/321) 1a: 0.6% (2/321) 1b: 1.6% (5/321) 2: 0.9% (3/321) 4: 3.1% (10/321)
Shoveling (11/21)	3.5% (5/141)	+ = ASU 2-6 0.0% (0/4)	0.865**	0.866**	0: 86.4% (348/403) 1: 11.2% (45/403) 2: 2.5% (10/403)	0: 86.7% (176/203) 1: 11.3% (23/203) 2: 2.0% (4/203)	0: 86.0% (172/200) 1: 11.0% (22/200) 2: 3.0% (6/200)
Double shoveling (11/21)	2.1% (3/140)	+ = ASU 2-6 100.0% (2/2)	0.737**	0.739**	0: 97.7% (381/390) 1: 1.5% (6/390) 2: 0.3% (1/390) 3: 0.3% (1/390) 4: 0.3% (1/390)	0: 97.4% (185/190) 1: 1.6% (3/190) 2: 0.5% (1/190) 3: 0.5% (1/190) 4: 0.5% (1/190)	0: 98.0% (196/200) 1: 1.5% (3/200) 3: 0.5% (1/200)
Interruption grooves (11/21)	5.5% (11/200)	+ = ASU 1 91.7% (11/12)	0.268**	0.271**	0: 96.2% (537/558) Mesial: 1.3% (7/558) Distal: 0.5% (3/558) Mesial/Distal: 0.2% (1/558) Medial: 1.8% (10/558)	0: 96.3% (260/270) Mesial: 0.7% (2/270) Distal: 0.7% (2/270) Medial: 2.2% (6/270)	0: 96.2% (277/288) Mesial: 1.7% (5/288) Distal 0.3% (1/277) Mesial/Distal: 0.3% (1/288) Medial: 1.4% (4/288)
Interruption grooves (12/22)	15.6% (40/256)	+ = ASU 1 87.0% (40/46)	0.337**	0.348**	0: 87.3% (618/708) Mesial: 3.8% (27/708) Distal: 6.6% (47/708) Mesial/Distal: 0.4% (3/708) Medial: 1.8% (13/708)	0: 87.1% (316/363) Mesial: 3.9% (14/363) Distal: 6.3% (23/363) Mesial/Distal: 0.6% (2/363) Medial: 2.2% (8/363)	0: 87.5% (302/345) Mesial: 3.8% (13/345) Distal: 7.0% (24/345) Mesial/Distal: 0.3% (1/345) Medial: 1.4% (5/345)
Peg incisors (12/22)	3.3% (10/306)	+ = ASU 1-2 66.7% (10/15)	0.785**	0.792**	0: 96.6% (771/798) 1: 2.6% (21/798) 2: 0.8% (6/798)	0: 96.8% (393/406) 1: 2.5% (10/406) 2: 0.7% (3/406)	0: 96.4% (378/392) 1: 2.8% (11/392) 2: 0.8% (3/392)

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Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
Distal accessory ridge (13/23)	30.2% (87/288)	+ = ASU 1-5 41.4% (87/210)	0.662**	0.719**	0: 35.8% (271/757) 1: 19.7% (149/757) 2: 30.4% (230/757) 3: 13.1% (99/757) 4: 1.1% (8/757)	0: 34.5% (130/377) 1: 19.9% (75/377) 2: 29.4% (111/377) 3: 14.9% (56/377) 4: 1.3% (5/377)	0: 37.1% (141/380) 1: 19.5% (74/380) 2: 31.3% (119/380) 3: 11.3% (43/380) 4: 0.8% (3/380)
Accessory cusps (14/24)	1.3% (4/302)	+ = ASU 1 100.0% (4/4)	N/A	N/A	0: 99.3% (752/757) Mesial: 0.4% (3/757) Distal: 0.3% (2/757)	0: 98.7% (376/381) Mesial: 0.8% (3/381) Distal: 0.5% (2/381)	0: 100.0% (376/376)
Accessory crests (14/24)	5.2% (16/290)	+ = 1 84.2% (16/19)	0.393**	0.396**	0: 96.2% (730/759) Mesial: 0.7% (5/759) Distal: 2.8% (21/759) Mesial/Distal: 0.4% (3/759)	0: 96.1% (365/380) Mesial: 1.3% (5/380) Distal: 1.8% (7/380) Mesial/Distal: 0.8% (3/380)	0: 96.3% (365/379) Distal: 3.7% (14/379)
Tricuspid premolars (14/24)	0.0% (0/349)	+ = ASU 1 N/A	N/A	N/A	0: 99.9% (841/842) 1: 0.1% (1/842)	0: 99.8% (423/424) 1: 0.2% (1/424)	0: 100.0% (418/418)
Odontome (14/24)	0.6% (2/343)	+ = ASU 1 100.0% (2/2)	-0.003	-0.003	0: 99.8% (828/830) 1: 0.2% (2/830)	0: 99.8% (415/416) 1: 0.2% (1/416)	0: 99.8% (413/414) 1: 0.2% (1/414)
Accessory cusps (15/25)	4.4% (12/274)	+ = ASU 1 85.7% (12/14)	0.345**	0.348**	0: 97.6% (722/740) Mesial: 0.8% (6/740) Distal: 1.5% (11/740) Mesial/Distal: 0.1% (1/740)	0: 97.9% (373/381) Mesial: 0.5% (2/381) Distal: 1.3% (5/381) Mesial/Distal: 0.3% (1/381)	0: 97.2% (349/359) Mesial: 1.1% (4/359) Distal: 1.7% (6/359)
Accessory crests (15/25)	21.4% (61/285)	+ = 1 72.6% (61/84)	0.440**	0.462**	0: 79.7% (601/754) Mesial: 4.8% (36/754) Distal: 9.9% (75/754) Mesial/Distal: 5.4% (41/754) Medial: 0.1% (1/754)	0: 79.2% (309/390) Mesial: 5.6% (22/390) Distal: 9.0% (35/390) Mesial/Distal: 5.9% (23/390) Medial: 0.3% (1/390)	0: 80.2% (292/364) Mesial: 3.8% (14/364) Distal: 11.0% (40/364) Mesial/Distal: 4.9% (18/364)
Tricuspid premolars (15/25)	0.3% (1/316)	+ = ASU 1 100.0% (1/1)	N/A	N/A	0: 99.9% (811/812) 1: 0.1% (1/812)	0: 99.8% (420/421) 1: 0.2% (1/421)	0: 100.0% (391/391)
Odontome (15/25)	0.3% (1/312)	+ = ASU 1 100.0% (1/1)	N/A	N/A	0: 99.9% (800/801) 1: 0.1% (1/801)	0: 99.8% (415/416) 1: 0.2% (1/416)	0: 100.0% (385/385)

Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
Carabelli's trait (16/26)	20.1% (69/343)	+ = ASU 2-7 53.3% (40/75)	0.742**	0.773**	0: 52.7% (433/822) 1: 28.1% (231/822) 2: 6.2% (51/822) 3: 5.2% (43/822) 4: 3.2% (26/822) 5: 2.6% (21/822) 6: 0.7% (6/822) 7: 1.3% (11/822)	0: 54.8% (223/407) 1: 25.8% (105/407) 2: 6.6% (27/407) 3: 4.2% (17/407) 4: 3.7% (15/407) 5: 2.9% (12/407) 6: 0.7% (3/407) 7: 1.2% (5/407)	0: 50.6% (210/415) 1: 30.4% (126/415) 2: 5.8% (24/415) 3: 6.3% (26/415) 4: 2.7% (24/415) 5: 2.2% (9/415) 6: 0.7% (3/415) 7: 1.4% (6/415)
C5 (16/26)	6.1% (21/342)	+ = ASU 2-5 81.4% (10/14)	0.638**	0.644**	0: 92.8% (761/820) 1: 4.6% (38/820) 2: 2.4% (20/820) 3: 0.1% (1/820)	0: 93.5% (377/403) 1: 3.0% (12/403) 2: 3.5% (14/403)	0: 92.1% (384/417) 1: 6.2% (26/417) 2: 1.4% (6/416) 3: 0.2% (1/417)
Mesial marginal accessory tubercles (16/26)	4.9% (15/308)	+ = Scott and Turner (1997) 1 88.2% (15/17)	0.235**	0.235**	0: 97.0% (742/765) MPT: 1.3% (10/765) PL: 0.8% (6/765) MAT: 0.8% (6/765) PL/MAT: 0.1% (1/765)	0: 98.4% (375/381) MPT: 1.3% (5/381) PL: 0.3% (1/381)	0: 95.6% (367/384) MPT: 1.3% (5/384) PL: 1.3% (5/384) MAT: 1.6% (6/384) PL/MAT: 0.3% (1/384)
Enamel extensions (16/26)	1.7% (4/229)	+ = ASU 1-3 50.0% (4/8)	0.760**	0.764**	0: 96.7% (563/582) 1: 1.0% (6/582) 2: 0.5% (3/582) 3: 1.7% (10/582)	0: 96.9% (283/292) 1: 0.7% (2/292) 2: 0.7% (2/292) 3: 1.7% (5/292)	0: 96.6% (280/290) 1: 1.4% (4/290) 2: 0.3% (1/290) 3: 1.7% (5/290)
C4 (17/27)	36.4% (145/398)	+ = ASU 3-5 42.6% (104/244)	0.707**	0.802**	0: 15.0% (139/928) 1: 14.1% (131/928) 2: 15.3% (142/928) 3: 14.3% (133/928) 3.5: 10.0% (93/928) 4: 23.4% (217/928) 5: 7.9% (73/928)	0: 14.8% (69/466) 1: 13.9% (65/466) 2: 16.3% (76/466) 3: 12.2% (57/466) 3.5: 9.0% (42/466) 4: 26.2% (122/466) 5: 7.5% (35/466)	0: 15.2% (70/462) 1: 14.3% (66/462) 2: 14.3% (66/462) 3: 16.5% (76/462) 3.5: 11.0% (51/462) 4: 20.6% (95/462) 5: 8.2% (38/462)

Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
Enamel extensions (17/27)	11.9% (31/261)	+ = ASU 1-3 58.5% (31/53)	0.720**	0.741**	0: 83.8% (570/680) 1: 2.6% (18/680) 2: 5.0% (34/680) 3: 8.5% (58/680)	0: 84.5% (289/342) 1: 2.3% (8/342) 2: 4.4% (15/342) 3: 8.8% (30/342)	0: 83.1% (281/338) 1: 3.0% (10/338) 2: 5.6% (19/338) 3: 8.3% (28/338)
Enamel extensions (18/28)	5.3% (6/114)	+ = ASU 1-3 66.7% (6/9)	0.680**	0.689**	0: 93.7% (314/335) 1: 2.1% (7/335) 2: 3.6% (12/335) 3: 0.6% (2/335)	0: 93.3% (154/165) 1: 1.8% (3/165) 2: 3.6% (6/165) 3: 1.2% (2/165)	0: 94.1% (160/170) 1: 2.4% (4/170) 2: 3.5% (6/170)
Parastyle (18/28)	4.3% (7/161)	+ = ASU 1-6 100.0% (7/7)	0.239**	0.240**	0: 97.6% (446/457) 1: 1.3% (6/457) 3: 0.7% (3/457) 4: 0.2% (1/457) 5: 0.2% (1/457)	0: 97.1% (232/239) 1: 1.3% (3/239) 3: 1.3% (3/239) 5: 0.4% (1/239)	0: 98.2% (214/218) 1: 1.4% (3/218) 4: 0.5% (1/218)
Shoveling (31/41)	0.4% (1/253)	+ = ASU 2-7 N/A	0.941**	0.941**	0: 97.2% (599/616) 1: 2.8% (17/616)	0: 97.5% (308/316) 1: 2.5% (8/316)	0: 97.0% (291/300) 1: 3.0% (9/300)
Shoveling (32/42)	1.8% (5/272)	+ = ASU 2-7 N/A	0.757**	0.757**	0: 97.0% (685/706) 1: 3.0% (21/706)	0: 97.7% (341/349) 1: 2.3% (8/349)	0: 96.4% (344/357) 1: 3.6% (13/357)
Distal accessory ridge (33/43)	19.2% (67/349)	+ = ASU 1-5 45.0% (67/149)	0.675**	0.699**	0: 64.7% (556/860) 1: 20.1% (105/860) 2: 12.2% (105/860) 3: 3.0% (26/860)	0: 63.0% (279/443) 1: 21.4% (95/443) 2: 12.9% (57/443) 3: 2.7% (12/443)	0: 66.4% (277/417) 1: 18.7% (78/417) 2: 11.5% (48/417) 3: 3.4% (14/417)
Odontome (34/44)	0.0% (0/392)	+ = ASU 1 N/A	N/A	N/A	0: 100.0% (927/927)	0: 100.0% (468/468)	0: 100.0% (459/459)
Lingual cusp number (34/44)	15.4% (58/377)	+ = ASU 2-9 54.7% (58/106)	0.617**	0.643**	0: 78.5% (709/903) 1: 0.3% (3/903) 2: 10.3% (93/903) 3: 3.8% (34/903) 4: 0.6% (5/903) 5: 1.4% (13/903) 6: 3.1% (28/903) 7: 0.3% (3/903) 8: 1.6% (14/903) 9: 0.1% (1/903)	0: 80.2% (365/455) 2: 10.8% (49/455) 3: 3.1% (14/455) 4: 0.2% (1/455) 5: 1.3% (6/455) 6: 2.4% (11/455) 7: 0.4% (2/455) 8: 1.3% (6/455) 9: 0.2% (1/455)	0: 76.8% (344/448) 1: 0.7% (3/448) 2: 9.8% (44/448) 3: 4.5% (20/448) 4: 0.9% (4/448) 5: 1.6% (7/448) 6: 3.8% (17/448) 7: 0.2% (1/448) 8: 1.8% (8/448)

Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
Odontome (35/45)	0.0% (0/365)	+ = ASU 1 0.0% (0/1)	1.000**	1.000*	0: 99.8% (874/876) 1: 0.2% (2/876)	0: 99.8% (441/442) 1: 0.2% (1/442)	0: 99.8% (433/434) 1: 0.2% (1/434)
Lingual cusp number (35/45)	27.4% (95/347)	+ = ASU 2-9 39.7% (95/239)	0.572**	0.602**	0: 41.9% (356/849) 1: 0.1% (1/849) 2: 37.9% (322/849) 3: 11.1% (94/849) 4: 2.6% (22/849) 5: 0.5% (4/849) 6: 3.8% (32/849) 7: 0.1% (1/849) 8: 1.9% (16/849) 9: 0.1% (1/849)	0: 47.0% (202/430) 2: 35.3% (152/430) 3: 10.7% (46/430) 4: 2.3% (10/430) 5: 0.2% (1/430) 6: 2.6% (11/430) 8: 1.6% (7/430) 9: 0.2% (1/430)	0: 36.8% (154/419) 1: 0.2% (1/419) 2: 40.6% (170/419) 3: 11.5% (48/419) 4: 2.9% (12/419) 5: 0.7% (3/419) 6: 5.0% (21/419) 7: 0.2% (1/419) 8: 2.1% (9/419)
Deflecting wrinkle (36/46)	4.7% (12/258)	+ = ASU 1-3 66.7% (12/18)	0.519**	0.523**	0: 94.9% (609/642) 1: 2.8% (18/642) 2: 1.9% (12/642) 3: 0.5% (3/642)	0: 97.2% (315/324) 1: 2.2% (7/324) 2: 0.6% (2/324)	0: 92.5% (294/318) 1: 3.5% (11/318) 2: 3.1% (10/318) 3: 0.9% (3/318)
Anterior fovea (36/46)	7.1% (20/283)	+ = ASU 1-4 33.3% (20/62)	0.832**	0.843**	0: 82.6% (578/700) 1: 6.1% (43/700) 2: 8.0% (56/700) 3: 2.9% (20/700) 4: 0.4% (3/700)	0: 83.1% (295/355) 1: 5.4% (19/355) 2: 8.2% (29/355) 3: 2.8% (10/355) 4: 0.6% (2/355)	0: 82.0% (283/345) 1: 7.0% (24/345) 2: 7.8% (27/345) 3: 2.9% (10/345) 4: 0.3% (1/345)
Groove pattern (36/46)	7.2% (21/292)	+ = ASU Y 7.6% (21/278)	0.545**	0.545**	Y: 92.1% (661/718) X: 7.9% (57/718)	Y: 93.4% (342/366) X: 6.6% (24/366)	Y: 90.6% (319/352) X: 9.4% (33/352)
Distal trigonid crest (36/46)	1.7% (5/290)	+ = ASU 1 55.6% (5/9)	0.625**	0.625**	0: 97.9% (699/714) 1: 2.1% (15/714)	0: 98.4% (359/ 365) 1: 1.6% (6/365)	0: 97.4% (340/349) 1: 2.6% (9/349)
Protostylid (36/46)	11.3% (33/293)	+ = ASU 1-7 50.0% (33/66)	0.606**	0.606**	0: 83.9% (605/722) 1: 15.8% (114/722) 3: 0.4% (3/722)	0: 83.9% (308/367) 1: 15.5% (57/367) 3: 0.5% (2/367)	0: 83.7% (297/355) 1: 16.1% (57/355) 3: 0.3% (1/357)
MMPT (36/46)	2.8% (8/289)	+ = Weets (2009) [adpt.] 1 – '3+' 100.0% (8/8)	-0.014	-0.014	0: 98.7% (704/713) 1: 1.1% (8/713) 3: 0.1% (1/713)	0: 98.4% (359/365) 1: 1.4% (5/365) 3: 0.3% (1/365)	0: 99.1% (345/348) 1: 0.9% (3/348)

Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
Cusp number (36/46)	3.8% (11/293)	+ ~= ASU 5 28.9% (11/38)	0.819**	0.820**	4: 9.3% (67/717) 5: 89.1% (639/717) 6: 1.5% (11/717)	4: 8.5% (31/364) 5: 89.6% (326/364) 6: 1.9% (7/364)	4: 10.2% (36/353) 5: 88.7% (313/353) 6: 1.1% (4/353)
C5 (36/46)	18.1% (53/293)	+ = ASU 1-5 19.1% (53/267)	0.859**	0.894**	0: 10.2% (73/716) 1: 0.3% (2/716) 2: 3.2% (23/716) 3: 17.3% (124/716) 4: 45.7% (327/716) 5: 23.3% (167/716)	0: 9.3% (34/364) 1: 0.3% (1/364) 2: 3.8% (14/364) 3: 16.8% (61/364) 4: 46.7% (170/364) 5: 23.1% (84/364)	0: 11.1% (39/352) 1: 0.3% (1/352) 2: 2.6% (9/352) 3: 17.9% (63/352) 4: 44.6% (157/352) 5: 23.6% (83/352)
C6 (36/46)	0.7% (2/292)	+ = ASU 1-5 40.0% (2/5)	0.890**	0.891**	0: 98.5% (705/716) 1: 0.7% (5/716) 2: 0.8% (6/716)	0: 98.1% (357/364) 1: 1.1% (4/364) 2: 0.8% (3/364)	0: 98.9% (348/352) 1: 0.3% (1/352) 2: 0.9% (3/352)
C7 (36/46)	4.4% (13/294)	+ = ASU 1-4 59.1% (13/22)	0.639**	0.647**	0: 94.5% (686/726) 1a: 1.1% (8/726) 1: 0.1% (1/726) 2: 1.4% (10/726) 3: 1.7% (12/726) 4: 1.2% (9/726)	0: 94.6% (351/371) 1a: 0.8% (3/371) 1: 0.3% (1/371) 2: 1.1% (4/371) 3: 1.9% (7/371) 4: 1.3% (5/371)	0: 94.4% (335/355) 1a: 1.4% (5/355) 2: 1.7% (6/355) 3: 1.4% (5/355) 4: 1.1% (4/355)
Groove pattern (37/47)	16.0% (56/346)	+ = ASU + and X 20.2% (56/277)	0.610**	0.610**	Y: 27.1% (225/829) X: 72.9% (604/829)	Y: 25.5% (105/412) X: 74.5% (307/412)	Y: 28.8% (120/417) X: 71.2% (297/417)
Distal trigonid crest (37/47)	2.6% (9/352)	+ = ASU 1 60.0% (9/15)	0.565**	0.565**	0: 96.9% (807/833) 1: 3.1% (26/833)	0: 97.3% (400/411) 1: 2.7% (11/411)	0: 96.4% (407/422) 1: 3.6% (15/422)
Protostylid (37/47)	12.2% (44/360)	+ = ASU 1-7 67.7% (44/65)	0.448**	0.456**	0: 88.0% (748/850) 1: 7.8% (66/850) 2: 2.1% (18/850) 3: 1.5% (13/850) 5: 0.4% (3/850) 7: 0.2% (2/850)	0: 88.8% (372/419) 1: 7.2% (30/419) 2: 1.7% (7/419) 3: 1.9% (8/419) 5: 0.2% (1/419) 7: 0.2% (1/419)	0: 87.2% (376/431) 1: 8.4% (36/431) 2: 2.6% (11/431) 3: 1.2% (5/431) 5: 0.5% (2/431) 7: 0.2% (1/431)

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Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
MMPT (37/47)	3.3% (12/365)	+ = Weets (2009) [adpt.] 1 – '3+' 75.0% (12/16)	0.456**	0.459**	0: 97.4% (834/856) 1: 2.0% (17/856) 1-2: 0.1% (1/856) 2: 0.2% (2/856) 3: 0.2% (2/856)	0: 97.2% (413/425) 1: 1.9% (8/425) 2: 0.5% (2/425) 3: 0.5% (2/425)	0: 97.7% (421/431) 1: 2.1% (9/431) 1-2: 0.2% (1/431)
Cusp number (37/47)	9.2% (33/359)	+ ~= ASU 4 42.9% (33/77)	0.696**	0.698**	3: 0.5% (4/850) 4: 82.2% (699/850) 5: 16.5% (140/850) 6: 0.8% (7/850)	3: 0.5% (2/425) 4: 80.7% (343/425) 5: 18.1% (77/425) 6: 0.7% (3/425)	3: 0.5% (2/425) 4: 83.8% (356/425) 5: 14.8% (63/425) 6: 0.9% (4/425)
C5 (37/47)	11.1% (40/359)	+ = ASU 1-5 55.6% (40/72)	0.713**	0.731**	0: 83.1% (706/850) 1: 0.6% (5/850) 2: 2.7% (23/850) 3: 7.3% (62/850) 4: 4.5% (38/850) 5: 1.9% (16/850)	0: 81.9% (348/425) 1: 0.2% (1/425) 2: 2.4% (10/425) 3: 8.9% (38/425) 4: 4.7% (20/425) 5: 1.9% (8/425)	0: 84.2% (358/425) 1: 0.9% (4/425) 2: 3.1% (13/425) 3: 5.6% (24/425) 4: 4.2% (18/425) 5: 1.9% (8/425)
C6 (37/47)	0.3% (1/359)	+ = ASU 1-5 33.3% (1/3)	0.815**	0.815**	0: 99.2% (843/850) 2: 0.8% (7/850)	0: 99.3% (422/425) 2: 0.7% (3/425)	0: 99.1% (421/425) 2: 0.9% (4/425)
C7 (37/47)	0.3% (1/365)	+ = ASU 1-4 100.0% (1/1)	1.000**	1.000**	0: 99.8% (859/861) 2: 0.1% (1/861) 3: 0.1% (1/861)	0: 99.8% (425/426) 3: 0.2% (1/426)	0: 99.8% (434/435) 2: 0.2% (1/435)
Groove pattern (38/48)	22.6% (48/212)	+ = ASU Y 66.7% (48/72)	0.356**	0.356**	Y: 24.8% (144/581) X: 75.2% (437/581)	Y: 28.2% (82/291) X: 71.8% (209/291)	Y: 21.4% (62/290) X: 78.6% (228/290)
Distal trigonid crest (38/48)	15.5% (35/226)	+ = ASU 1 59.3% (35/59)	0.485**	0.485**	0: 82.9% (499/602) 1: 17.1% (103/602)	0: 82.9% (247/298) 1: 17.1% (51/298)	0: 82.9% (252/304) 1: 17.1% (52/304)
Protostylid (38/48)	8.0% (16/201)	+ = ASU 1-7 94.1% (16/17)	0.065	0.066	0: 95.4% (522/547) 1: 2.6% (14/547) 2: 0.7% (4/547) 3: 0.7% (4/547) 5: 0.2% (1/547) 7: 0.4% (2/547)	0: 94.9% (258/272) 1: 2.2% (6/272) 2: 1.5% (4/272) 3: 1.1% (3/272) 5: 0.4% (1/272)	0: 96.0% (264/275) 1: 2.9% (8/275) 3: 0.4% (1/275) 7: 0.7% (2/275)

Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
MMPT (38/48)	27.1% (55/203)	+ = Weets (2009) [adpt.] 1 – '3+' 78.6% (55/70)	0.285**	0.297**	0: 77.0% (428/556) 1: 16.7% (93/556) 1-2: 2.0% (11/556) 2: 2.2% (12/556) 2-3: 1.1% (6/556) 3: 0.4% (2/556) 3+: 0.7% (4/556)	0: 78.9% (217/275) 1: 14.9% (41/275) 1-2: 2.9% (8/275) 2: 2.5% (7/275) 2-3: 0.4% (1/275) 3+: 0.4% (1/275)	0: 75.1% (211/281) 1: 18.5% (52/281) 1-2: 1.1% (3/281) 2: 1.8% (5/281) 2-3: 1.8% (5/281) 3: 0.7% (2/281) 3+: 1.1% (3/281)
Cusp number (38/48)	30.2% (67/222)	+ ~= ASU 4 47.9% (67/140)	0.619**	0.619**	2: 0.2% (1/589) 3: 4.2% (25/589) 4: 46.3% (273/589) 5: 38.0% (334/589) 6: 11.2% (66/589)	3: 3.4% (10/290) 4: 46.2% (134/290) 5: 38.3% (111/290) 6: 12.1% (35/290)	2: 0.3% (1/299) 3: 5.0% (15/299) 4: 46.5% (139/299) 5: 37.8% (113/299) 6: 10.4% (31/299)
C5 (38/48)	32.0% (71/222)	+ = ASU 1-5 55.5% (71/128)	0.635**	0.692**	0: 51.0% (301/590) 1: 1.0% (6/590) 2: 3.9% (23/590) 3: 6.8% (40/590) 4: 15.8% (93/590) 5: 21.4% (126/590) 6: 0.2% (1/590)	0: 50.0% (145/290) 1: 1.4% (4/290) 2: 2.8% (8/290) 3: 5.5% (16/290) 4: 15.9% (46/290) 5: 24.1% (70/290) 6: 0.3% (1/290)	0: 52.0% (156/300) 1: 0.7% (2/300) 2: 5.0% (15/300) 3: 8.0% (24/300) 4: 15.7% (47/300) 5: 18.7% (56/300)
C6 (38/48)	14.4% (32/222)	+ = ASU 1-5 82.1% (32/39)	0.413**	0.426**	0: 88.8% (524/590) 1: 0.8% (5/590) 2: 6.3% (37/590) 3: 1.7% (10/590) 4: 1.5% (9/590) 5: 0.8% (5/590)	0: 87.6% (254/290) 1: 1.0% (3/290) 2: 7.6% (22/290) 3: 1.4% (4/290) 4: 1.4% (4/290) 5: 1.0% (3/290)	0: 90.0% (270/300) 1: 0.7% (2/300) 2: 5.0% (15%300) 3: 2.0% (6/300) 4: 1.7% (5/300) 5: 0.7% (2/300)
C7 (38/48)	2.2% (5/228)	+ = ASU 1-4 100.0% (5/5)	-0.011	-0.011	0: 99.2% (599/604) 1a: 0.2% (1/604) 1: 0.2% (1/604) 2: 0.3% (2/604) 3: 0.2% (1/604)	0: 99.3% (298/300) 1: 0.3% (1/300) 2: 0.3% (1/300)	0: 99.0 (301/304) 1a: 0.3% (1/304) 2: 0.3% (1/304) 3: 0.3% (1/304)

Table 4.2.1. (Continued.)

Trait and tooth (FDI)	Overall FA	Comparable FA+	Kendall's *tau*-b	Spearman's *rho*	Grade frequencies	Grade frequencies (left)	Grade frequencies (right)
Foramina mentales	3.8% (23/598)	+ = >1 82.1% (23/28)	0.296**	0.296**	1: 97.2% (1165/1198) 2: 2.7% (32/1198) 3: 0.1% (1/1198)	1: 98.0% (586/598) 2: 1.8% (11/598) 3: 0.2% (1/598)	1: 96.5% (579/600) 2: 3.5% (21/600)
Mylohyoid bridge	12.3% (64/520)	+ = >0 63.4% (64/101)	0.529**	0.541**	0: 86.6% (962/1111) Incomplete: 4.8% (53/1111) 1: 8.6% (96/1111)	0: 88.2% (493/559) Incomplete: 4.3% (24/559) 1: 7.5% (42/559)	0: 85.0% (469/552) Incomplete: 5.3% (29/552) 1: 9.8% (54/552)

*: P <= 0.05; **: P <= 0.01; +: Assymetry excluding bilateral absences.

Table 4.2.2. reports on means for all traits, upper and lower arches, mandibular traits, and traits of each tooth. Means are calculated using overall asymmetry (Overall FA), asymmetry excluding bilateral absences (Comparable FA) and asymmetry excluding bilateral absences and reduced samples (Large sample comparable FA; traits with frequencies under 40 individuals, when bilateral absences were excluded; this cut-off was chosen so as to not include most of the smaller resulting samples and still allow for the contribution of as many traits as possible towards such means).

Table 4.2.2. Mean Overall FA, Comparable FA, and Large sample comparable FA for the sample, upper and lower arches, mandibular traits and each tooth.

Site	Mean Overall FA	Mean Comparable FA	Mean Large sample comparable FA
Overall	9.3%	63.5%	49.5%
Upper arch	8.3%	74.8%	59.2%
Lower arch	10.1%	54.6%	46.5%
Mandible	8.1%	72.8%	63.4%
UI1	4.6%	66.7%	N/A
UI2	9.5%	76.9%	87.0%
UC	30.2%	41.4%	41.4%
UP3	1.8%	94.7%	N/A
UP4	6.6%	89.6%	72.6%
UM1	8.2%	68.2%	53.3%
UM2	24.2%	50.6%	50.6%
UM3	4.8%	83.4%	N/A
LI1	0.4%	N/A	N/A
LI2	1.8%	N/A	N/A
LC	19.2%	45.0%	45.0%
LP3	7.7%	54.7%	54.7%
LP4	13.7%	19.9%	39.7%
LM1	6.2%	46.0%	27.5%
LM2	6.9%	56.8%	46.6%
LM3	19.0%	73.0%	61.6%

4.2.1.1.Rank correlation coefficients

The correlation coefficients are mostly statistically significant (P < 0.01). Exceptions are some not-calculable coefficients (UP3 accessory cusps and tricuspid premolars; UP4 tricuspid premolars and odontome; LP3 odontome); negative associations (UP3 odontome: -0.003 on both tests; LM1 MMPT: -0.014 on both tests; LM3 C7: -0.011 on both tests), probably an artifact of low trait presence; and a low statistically insignificant coefficient (LM3 protostylid; Kendall *tau*-b: 0.065; Spearman's *rho*: 0.066), probably because the low presence of this trait is divided by different expressions per side. Other relatively weak associations are also found in traits where presence on each side is similar, but expression is different, due to different positioning or size (UI1 and UI2 interruption grooves; UP4 accessory cusps; UM1 mesial marginal accessory tubercles; UM3 parastyle; LM3 MMPT, and *foramina mentales* on the mandible). Still, the weakest association is both Kendall's *tau*-b and Spearman's *rho* of 0.235, which is a moderate to weak association, found on a "trait", mesial marginal accessory tubercles, made out of four tubercles, the mesial paracone tubercle (MPT), the protoconule (PL), the mesial accessory tubercle (MAT) and the lingual paracone tubercle (LPT, absent from this sample), and any combination of them.

These results demonstrate the existence of either directional asymmetry or antisymmetry is very unlikely, and thus facilitates further discussion. As shown above, developmental instability is likely to be involved in the occurrence of FA, thus making the measure of FA useful in the calculation of a sample's degree of developmental stress, although only when directional asymmetry and antisymmetry are ruled out.

4.2.1.2.Trends on asymmetry frequencies

Overall FA and Comparable FA are very variable when different traits and teeth are compared. Shoveling displays low asymmetry, but this could result from the trait presence of only four pairs (or individuals) for comparison.

When Overall FA is analyzed, interruption groove's frequencies increase from the central to the lateral upper incisor, from mesial to distal within tooth district (UI1: 5.5%; UI2: 15.6%), as do accessory cusps (UP3: 1.3%; UP4: 4.4%) and accessory crests

(UP3: 1.3%; UP4: 4.4%) for upper premolars, shoveling (LI1: 0.4%; LI2: 1.8%) for lower incisors, lingual cusp number (LP3: 15.4%; LP4: 27.4%) for lower premolars and cusp/groove pattern (LM1: 7.1%; LM2: 16.0%; LM3: 22.6%), distal trigonid crest (LM1: 1.7%; LM2: 2.6%; LM3: 15.5%), MMPT (LM1: 2.8%; LM2: 3.3%; LM3: 27.1%) and cusp number (LM1: 3.8%; LM2: 9.2%; LM3: 30.2%) for lower molars.

The same trend is detected within Comparable FA: in enamel extensions (UM1: 50.0%; UM2: 58.5%; UM3: 66.7%) for upper molars, although this find is hindered by low samples on UM1 (8 individuals) and UM3 (9 individuals); in cusp/groove pattern (LM1: 7.6%; LM2: 20.2%; LM3: 66.7%) for lower molars; protostylid (LM1: 50.0%; LM2: 67.7%; LM3: 94.1%) for lower molars, despite a low sample on LM3 (17 individuals); cusp number (LM1: 28.9%; LM2: 42.9%; LM3: 47.9%), affected by a borderline low sample on LM1 (38 individuals).

The overall presence-absence asymmetry found in Carabelli's trait for several populations from most major ethnic backgrounds averages 5.5% and ranges from 1.5% to 7.8%. The total asymmetry averages 20.6% and ranges from 9.2% and 26.4% (Scott, 1980). Overall asymmetry (20.1%) for this sample is in agreement with this range, and even slightly below the ones for Caucasian groups (American whites: 24.3%; South African Whites: 26.4%; Scott, 1980).

4.2.1.3.Mean frequencies

The use of traits from the same area of an organism to calculate FA is less representative of an organism's developmental instability as a whole, since it can over- or underestimate it because of an excessive correlation between traits. The value of FA used to search for relations between developmental instability and adaptability can, usually, be a mean of all asymmetries measured, but this probably will not be as fruitful when dealing with traits from the same body area (Van Dongen and Gangestad, 2011). In the particular case of dental morphology, the growth of teeth occurs for a relatively long period of time, and is affected between the gestation and late adolescence/early adulthood (see Scheuer and Black [2000] or AlQahtani *et al.* [2010], for example). Besides, dental nonmetric variables are expected not to be correlated to each other, in general (Scott and Turner, 1997; for the analysis of the Coimbra sample, see 4.3.Sexual dimorphism and intertrait correlations). These characteristics allow for means to be

calculated in order to simplify and better represent the samples' FA, as suggested by Van Dongen and Gangestad (2011).

The mean Overall FA is relatively low (9.3%), although it can be considered deceiving, since absent sites are rarely measured for rank (since they usually comprise grade 0 only), as opposed to metric measures of asymmetry, which consider all existing and well kept surfaces. In order to correct for such great error (trait presence is most frequently low on Caucasian samples, the present one being no exception) and to allow for comparisons with other author's results, the mean FA was calculated without the consideration of individuals with no trait presence on either side (Comparable FA). The result is a much higher value (63.5%), even when potentially deceiving results are removed (Large sample comparable: 49.5% asymmetry).

The "functionality hypothesis" theory suggests that greater symmetry is found on functionally relevant traits, to insure efficiency. This has been verified for some traits, namely related with locomotion. The importance of symmetry of the masticatory apparatus for functional efficiency is also high (DeLeon, 2007). The proportion of FA found in this sample seems to be high, which can suggest this is a sample highly affected by developmental instability or that the functionality hypothesis is not applicable, at least to dental morphology. However, Moskona and colleagues (1996) hypothesize different susceptibility of certain traits (as those related to number of cusps and delineation of crowns) when compared to others (related tubercle configuration, for instance) may be related to the genetic control placed upon them, and therefore to their functional importance. This does not appear to be the case in the Coimbra sample: in the upper dentition, despite the fact UM1 C5 presents an overall FA (6.1%) below the mean, UM2 C4 presents a very high FA (36.4%). So, two different cusps (C4 and C5), which can add functionality to mastication, show different FA levels. This duality is again displayed by UP4 accessory crests, that present high FA (21.4%), and UM1 mesial marginal accessory tubercles, with a low FA (4.9%). This variation of FA levels seems to be much more related to the number of individuals with present traits for each case (C4: 244; accessory crests: 84; C5: 14; mesial marginal accessory tubercles: 17), than with functionality. That trend is repeated throughout the dentition and again justifies the exclusion of low sample data.

The upper dental arch (8.3%) has a slightly lower overall asymmetry than the lower dental arch (9.3%), but for either of the absence excluded FA averages the reverse is observed. So, the lower arch has a lower asymmetry by 20.2% (Comparable FA) and

12.7% (Large sample comparable FA) when compared to the upper dental arch. In children from Bedouin groups, upper teeth show higher overall FA frequencies than lower teeth (Moskona *et al.*, 1996), but these frequencies are not corrected for bilateral absence of the traits.

The mandibular traits (*foramina mentales* and mylohyoid bridge) average a low frequency Overall FA (8.1%), severely increased for Comparable FA (72.8%), and for Large sample comparable FA (in this case, it includes only mylohyoid bridge: 63.4%).

In a medieval Nubian population, medial and facial landmarks were more symmetrical, which can be related to their greater functional importance or to better chances in sexual selection, as both aspects can be modeled by natural selection (DeLeon, 2007). In the case of dental morphology in the Coimbra sample, the same trend is not clear for any analysis taken, except for the overall mean of the lower incisors, which present lower values than the rest of the dentition. Even considering this exception, these results suggest such pattern of selective asymmetry does not affect tooth morphology.

For the mean Overall FA, in almost every case there is an increased asymmetry from mesial to distal in each tooth district. The exceptions are the upper molars (unless UM3's are excluded). This trend is only observed for lower molars when Comparable FA means are considered and only for the latter in Large sample comparable FA. The opposite (FA decrease from mesial to distal) is found on all premolars for the Comparable FA mean and on lower premolars for the mean Large sample comparable FA.

Mayhall and Saunders (1986) and Moskona and colleagues (1996) find FA corresponds to the field concept proposed by Dahlberg. Asymmetry, therefore, is enhanced the more distal the tooth is, except in the case of mandibular incisors. The latter authors found central mandibular incisors present greater asymmetry than lateral incisors, which is in accord with this field reference tooth. Other authors, using exclusively metric traits, also found this pattern (Pirzigian, 1977; Harris and Nweeia, 1980; Khalaf *et al.*, 2005; Peiris *et al.*, 2013). Peiris and colleagues (2013) found most stable portion of LM1 and LM2 to be the trigonid, with the talonid showing greater FA.

When analyzed using the ASUDAS ordinal scale, the present FA results seems to obey this scheme only when Overall FA between all observed grades is compared. Then, the only exceptions are upper molars and all incisors, as noted. These are an exception to the exception, since indeed such teeth are more asymmetric when more

distal, like most other fields, instead of demonstrating the opposite as predicted. It should be noted the finds of the cited Mayhall and Saunders (1986) are mostly derived from metric finds, and incisor shoveling, with a small difference. Such a difference is also found here, on the other direction, and could be meaningless. So, with the exception of the poorly represented incisors (very few individuals display shoveling grades above zero, and even fewer display trait presence) and the UM3's (also conditioned by the only traits observed, enamel extensions and parastyle, which were only present in 9 and 7 individuals, respectively), the Dahlberg's field concept is verified within the pattern of FA, which testifies the most stable tooth to be the most bilaterally symmetric as well.

Moskona and colleagues (1996) relate the number of grades the traits are measured by with FA, which tends to be enhanced the more grades there are. They also reflect on the possibility the quasicontinuous variability of dental morphologic traits may subject them to lesser discrimination due to difficulties in the distinction of slightly different expressions on antimeric teeth. Care when comparing the present results with others obtained using different traits will be taken, since the concerns expressed above alert to the relative lack of standardization in dental morphology studies previous to the ASUDAS. These authors also state comparability among FA studies using dental morphology will only be achieved when standards are set on which methods to use. The very work of Moskona and colleagues (1996, 1997), following the standardization of this scientific sub-area, uses a divergent set of traits and methodologies than ASUDAS, providing a good example of their very warning.

Baume and Crawford (1980) found dental discrete trait FA is negatively correlated with tooth size, which they interpreted to mean asymmetry could be genetically determined (or caused by crowding, in some traits, such as winging). They studied four Mexican related populations (descendent from natives, hybridized with Spanish and, to a lesser extent, African groups) and two Belizean hybrid populations, Caribs (of native and, predominantly, West African, ascendance) and Creoles (of European and West African ascendance). The cited authors posit asymmetry could also be environmentally determined (since they report environmental stress had been suggested as a factor contributing to FA). They are, however, puzzled by the fact that very different environmental conditions within each major group result in homogeneous results, with differences noted only when major groups are compared. They suggest a

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hypothesis aside from genetic background differences: intrauterine developmental factors affecting Mexicans more than Belizeans.

When the overall FA mean of the Coimbra sample is compared to Mexicans and Belizeans, it is located nearer the Belizeans, despite being placed between each group's mean (Coimbra: 9.3%; Belizeans: 8.3%; Mexicans: 11.0%). Since the Mexican sample is a trihybrid mixture of indigenous peoples, Spanish and African populations, as opposed to the hybridization process between indigenous and West African groups in Belize, in a strictly genetic point of view, Mexicans should have an FA mean nearer the Coimbra sample (due to the Iberian contribution). The larger difference (1.7%) than the one recorded between the Portuguese and the Belizeans (1.0%) may be justified by environmental factors that provide developmental noise, such as nutritional stress or viral load, for example. The Creoles (one of the Belizean samples) have some European genetic admixture, which would predictably approximate their mean FA to the Coimbra samples' FA. Yet, their mean (7.93%) is approximately 1.4% different, which is a larger difference than the one between the Portuguese sample and the Belizian mean. The most likely justification would again be environmental factors, tending towards the dismissal of the genetic component's central part in FA frequency.

The occasionally very high asymmetry found on Bedouin isolated groups, which are highly inbred and subjected to environmental pressures, is difficult to relate to a single factor, since all these genetic and environmental stresses could intervene (Moskona *et al.*, 1996).

Tocheri (2002) analyzed the deciduous dentition of 100 dental casts of mid-20th century Pima Indian children, finding only a small degree of asymmetry. This was mostly due to his criteria, since this author only considered unilateral tendencies as impediment of MMD analysis and only considered the presence/absence dichotomy. Unilateral tendencies are found only when more than half the individuals display asymmetry for a trait. When looking at the data, 13.8% of trait presence Overall FA mean (six traits) is found for samples containing more than 40 individuals, a higher value than that found for the Coimbra sample (9.3%). If it is assumed FA predominantly results from how environmental factors affect development, the first interpretation of this comparison is Pima Indians are more affected by developmental instability than the Coimbra population. In case the results found for the deciduous dentition are not directly comparable to the results of another sample's permanent dentition, the

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difference in proportion may be due to a greater susceptibility of the former to environmental/intrauterine influence.

The Pima Indian's permanent dentition had been analyzed by Noss and colleagues (1983). The overall FA is approximately 11.8%, which indicates that although the first dentition may be subjected to more FA, due to a greater susceptibility, this American indigenous sample may indeed be more affected by developmental instability than the presently analyzed Portuguese sample, which indicates more biologically stressful environmental conditions.

Bollini and colleagues (2009a) found less than 8.0% FA in 44 discrete dental variables (since only 12 presented values fewer than 100% symmetry) from 376 individuals from several pre-conquest Argentinean archaeological sites. These traits' FA mean was only 0.9%, when only samples with more than thirty individuals are counted. Despite the fact that to consider traits to be unilateral only when one side is present and the other absent is reductive (although appropriate for their intended use, to show all traits as reliable markers with taxonomic value in biological affinity analyses), the reported figures are surprisingly low and developmental instability should be minimal, when compared to Coimbra (9.3% overall).

Foxe Basin Inuit (Canada) are an isolated sample from two villages, whose casts were collected between 1968 and 1973 (Mayhall and Saunders, 1986). Their study shows an Overall FA mean of 25.4% (excluding trait samples under 40 individuals), a much greater proportion than the one found for Coimbra (9.3%). The Large sample comparable FA mean was 36.8%, below the 49.5% mean found for Coimbra. This demonstrates the relevance of the frequency of selected traits in each population to the overall mean, and the need for a calculation without bilateral absences to correct for that. Despite this, the Coimbra and this Inuit sample are not directly comparable. The authors of the latter study only considered it FA when one of the sides presented and the other did not, and the present author thought it more informative to display the results of total asymmetry, even when there was simply a difference of expression amongst sides. This probably produced an enhanced, and presumably more accurate, proportion of FA.

Indian Knoll hunter-gatherers revealed greater FA in dental mesiodistal and buccolingual measures than Campbell/Larson agriculturalists and Hamann-Todd 20th century Americans. This was expected by Perzigian (1977), since Indian Knoll displayed large frequencies of Harris lines and linear enamel hypoplasias, slow long bone growth, small adult stature and high infant mortality, which probably reflected

metabolic stress due to reduced nutritional resources. In the Indian Knoll sample, FA is inversely correlated with femur size and tooth size, again indicating environmental factors might be more relevant than genetic ones in causing FA.

A comparison between Pueblo Natives, an Inuit population, Ohio Caucasians and Neanderthals aimed to infer the differences in the FA frequencies of mesiodistal and buccolingual breadths caused by inbreeding (Doyle and Johnston, 1977). The latter two samples had already been compared, and their differences (greater asymmetry in Neanderthals) were attributed to greater inbreeding in Neanderthals. Doyle and Johnston (1977) found greater FA in Inuits and Puebloans, concluding the difference may hail from a source other than inbreeding, such as developmental stress.

Inbreeding may enhance FA, because any blockage to pathways of protein production on one side of the organism would be met with fewer alternatives, due to a limitation of the variability within the population. However, this phenomenon is more likely when developmental stress, induced by environmental conditions, is introduced, and causes the initial blockage. So, the greater technological handle on the environment mustered by Ohio Caucasians, when compared to Pueblo Natives, Inuit and Neanderthals, should be the most important factor to grant them less FA (Doyle and Johnston, 1977).

These considerations should be taken into account when comparing Coimbra with other samples. First, because lack of variability in breeding patterns seems not to be an issue in Coimbra sample, due to inclusion in a relatively large community and a European Modern age country. Second, the greater FA found in Coimbra (when compared to most samples available in the literature; see above), could counter the thesis of greater technological domain over the environment allowing for lesser FA. The Coimbra of the early 20th century could be less developed than the leading European potencies, but was technologically more advanced than most samples compared. The differences in FA could therefore be originated by social inequalities and the nutritional deficits that hence resulted.

4.2.2.Fluctuating asymmetry differences between sexes

Fluctuating asymmetry frequencies for each of the 58 dental and mandibular nonmetric variables are separated by sex on Table 4.2.3., that shows Overall FA and

Comparable FA. Table 4.2.4. displays the means for these frequencies as well as the Large sample comparable FA mean frequency, for all traits and for trait means for each tooth.

Only 20 out of the total 58 traits (34.5%) display equal or greater overall FA for male individuals, since the remaining 38 show greater frequencies for the female individuals. All three instances of shoveling (UI1 - F: 2.9%, M: 4.2%; LI1 – F: 0.0%, M: 0.8%; LI2 – F: 1.5%, M: 2.2%), the two instances of interruption grooves (UI1 – F: 4.4%, M: 6.4%; UI2 – F: 15.2%, M: 16.1%), all three accounts of protostylid (LM1 – F: 8.1%, M: 14.0%; LM2 – F: 11.5%, M: 12.9%; LM3 – F: 5.1%, M: 10.7%) and both mandibular characters (*foramina mentales* – F: 3.0%, M: 4.7%; mylohyoid bridge – F: 11.7%, M: 13.0%) are most asymmetric for male individuals, for example. Traits that display most asymmetry for female individuals with a greater disparity are on LM1 (anterior fovea – F: 11.4%, M: 3.3%; C5 – F: 22.6%, M: 14.4%) and LM3 (MMPT – F: 33.3%, M: 21.5%; C6 – F: 19.3%, M: 9.7%). The mean frequency is 9.8% for females and 8.6% for males.

Scott (1977) studied the canine distal accessory ridge in seven Southwest Native American and two European American samples. For the upper canine, asymmetry occurred mainly with one degree of difference, and in 11.0% of males and 14.6% of females. Presence-absence asymmetry for that work occurred in 2.5% of males and 3.4% of females. As for the lower canine, asymmetry occurred overall on 14.6% of males and 13.2% of females and in presence-absence asymmetry on 5.3% and 8.5% respectively. The Coimbra sample male individuals are more asymmetric on both accounts and it displays greater FA proportions for this trait (UC – F: 26.0%, M: 35.1%; LC – F: 17.0%, M: 21.6%).

Difference in asymmetry on the Carabelli's trait for each sex is statistically too small to identify a tendency in several populations from almost all different major ethnic backgrounds (Scott, 1980).

In the present results, the proportion of variables with equal or greater male frequency diminishes to 18 (out of 58: 31.0%) in Comparable FA. In Large sample comparable FA, male individuals only demonstrate greater asymmetry for distal accessory ridge on both C (UC – F: 34.5%, M: 50.0%; LC – F: 43.7%, M: 46.2%). Female individuals are most asymmetric in the remaining 10 traits meeting such conditions. Some examples are lingual cusp number on both LP (LP3 – F: 60.4%, M:

Table 4.2.3. Female and male Overall FA and Comparable FA frequencies.

Trait and tooth (FDI)	Female Overall FA	Male Overall FA	Female Comparable FA	Male Comparable FA
Winging (11/21)	9.4% (11/117)	5.4% (7/130)	+ = ASU 1 and 2 100.0% (5/5)	+ = ASU 1 and 2 57.1% (4/7)
Shoveling (11/21)	2.9% (2/69)	4.2% (3/72)	+ = ASU 2-7 0.0% (0/2)	+ = ASU 2-7 0.0% (0/2)
Double shoveling (11/21)	2.8% (2/71)	1.4% (1/69)	+ = ASU 2-6 100.0% (2/2)	+ = ASU 2-6 N/A
Interruption grooves (11/21)	4.4% (4/90)	6.4% (7/110)	+ = ASU 1 80.0% (4/5)	+ = ASU 1 100.0% (7/7)
Interruption grooves (12/22)	15.2% (20/132)	16.1% (20/124)	+ = ASU 1 83.3% (20/24)	+ = ASU 1 90.9% (20/22)
Peg incisors (12/22)	4.5% (7/154)	2.0% (3/152)	+ = ASU 1-2 70.0% (7/10)	+ = ASU 1-2 60.0% (3/5)
Distal accessory ridge (13/23)	26.0% (40/154)	35.1% (47/134)	+ = ASU 1-5 34.5% (40/116)	+ = ASU 1-5 50.0% (47/94)
Accessory cusps (14/24)	0.7% (1/148)	1.9% (3/154)	+ = ASU 1 100.0% (1/1)	+ = ASU 1 100.0% (3/3)
Accessory crests (14/24)	4.1% (6/148)	6.3% (10/158)	+ = 1 66.7% (6/9)	+ = 1 100.0% (10/10)
Tricuspid premolars (14/24)	0.0% (0/159)	0.0% (0/190)	+ = ASU 1 N/A	+ = ASU 1 N/A
Odontome (14/24)	1.3% (2/158)	0.0% (0/185)	+ = ASU 1 100.0% (2/2)	+ = ASU 1 N/A
Accessory cusps (15/25)	5.0% (7/139)	3.7% (5/135)	+ = ASU 1 100.0% (7/7)	+ = ASU 1 71.4% (5/7)
Accessory crests (15/25)	21.8% (32/147)	21.0% (29/138)	+ = 1 80.0% (32/40)	+ = 1 65.9% (29/44)
Tricuspid premolars (15/25)	0.6% (1/156)	0.0% (0/160)	+ = ASU 1 100.0% (1/1)	+ = ASU 1 N/A
Odontome (15/25)	0.6% (1/156)	0.0% (0/156)	+ = ASU 1 100.0% (1/1)	+ = ASU 1 N/A
Carabelli's trait (16/26)	23.8% (43/181)	16.0% (26/162)	+ = ASU 2-7 59.5% (25/42)	+ = ASU 2-7 45.5% (15/33)
C5 (16/26)	7.3% (13/179)	4.9% (8/163)	+ = ASU 2-5 77.8% (7/9)	+ = ASU 2-5 60.0% (3/5)
Mesial marginal accessory tubercles (16/26)	4.9% (8/164)	4.9% (7/144)	+ = Scott and Turner (1997) 1 100.0% (8/8)	+ = Scott and Turner (1997) 1 77.8 (7/9)
Enamel extensions (16/26)	2.3% (3/130)	1.0% (1/99)	+ = ASU 1-3 42.9% (3/7)	+ = ASU 1-3 100.0% (1/1)
C4 (17/27)	27.0% (74/200)	25.9% (71/198)	+ = ASU 1-5 41.8% (74/177)	+ = ASU 1-5 39.4% (71/180)

Table 4.2.3. (Continued.)

Trait and tooth (FDI)	Female Overall FA	Male Overall FA	Female Comparable FA	Male Comparable FA
Enamel extensions (17/27)	14.4% (20/139)	9.0% (11/122)	+ = ASU 1-3 64.5% (20/31)	+ = ASU 1-3 50.0% (11/22)
Enamel extensions (18/28)	5.6% (3/54)	5.0% 3/60)	+ = ASU 1-3 60.0% (3/5)	+ = ASU 1-3 75.0% (3/4)
Parastyle (18/28)	4.1% (3/73)	4.5% (4/88)	+ = ASU 1-6 100.0% (3/3)	+ = ASU 1-6 100.0% (4/4)
Shoveling (31/41)	0.0% (0/124)	0.8% (1/129)	+ = ASU 2-7 N/A	+ = ASU 2-7 N/A
Shoveling (32/42)	1.5% (2/135)	2.2% (3/137)	+ = ASU 2-7 N/A	+ = ASU 2-7 N/A
Distal accessory ridge (33/43)	17.0% (31/182)	21.6% (36/167)	+ = ASU 1-5 43.7% (31/71)	+ = ASU 1-5 46.2% (36/78)
Odontome (34/44)	0.0% (0/195)	0.0% (0/197)	+ = ASU 1 N/A	+ = ASU 1 N/A
Lingual cusp number (34/44)	17.1% (32/187)	13.7% (26/190)	+ = ASU 2-9 60.4% (32/53)	+ = ASU 2-9 48.1% (25/52)
Odontome (35/45)	0.0% (0/169)	0.0% (0/196)	+ = ASU 1 0.0% (0/1)	+ = ASU 1 N/A
Lingual cusp number (35/45)	29.2% (47/161)	25.8% (48/186)	+ = ASU 2-9 41.6% (47/113)	+ = ASU 2-9 38.1% (48/126)
Deflecting wrinkle (36/46)	6.0% (7/117)	3.5% (5/141)	+ = ASU 1-3 63.6% (7/11)	+ = ASU 1-3 71.4% (5/7)
Anterior fovea (36/46)	11.4% (15/132)	3.3% (5/151)	+ = ASU 1-4 44.1% (15/34)	+ = ASU 1-4 17.9% (5/28)
Groove pattern (36/46)	9.6% (13/135)	5.1% (8/157)	+ = ASU Y 10.2% (13/127)	+ = ASU Y 5.3% (8/151)
Distal trigonid crest (36/46)	3.8% (5/133)	0.0% (0/157)	+ = ASU 1 62.5% (5/8)	+ = ASU 1 0.0% (0/1)
Protostylid (36/46)	8.1% (11/136)	14.0% (22/157)	+ = ASU 1-7 37.9% (11/29)	+ = ASU 1-7 59.5% (22/37)
MMPT (36/46)	3.6% (5/137)	2.0% (3/152)	+ = Weets (2009) [adpt.] 1 – '3+' 100.0% (5/5)	+ = Weets (2009) [adpt.] 1 – '3+' 100.0% (3/3)
Cusp number (36/46)	4.5% (6/133)	3.1% (5/160)	+ ~= ASU 5 35.3% (6/17)	+ ~= ASU 5 23.8% (5/21)
C5 (36/46)	22.6% (30/133)	14.4% (23/160)	+ = ASU 1-5 24.4% (30/123)	+ = ASU 1-5 16.0% (23/144)
C6 (36/46)	0.0% (0/132)	1.2% (2/160)	+ = ASU 1-5 0.0% (0/2)	+ = ASU 1-5 66.7% (2/3)
C7 (36/46)	2.9% (4/137)	5.7% (9/157)	+ = ASU 1a-4 66.7% (4/6)	+ = ASU 1a-4 56.2% (9/16)
Groove pattern (37/47)	19.8% (34/172)	12.4% (22/177)	+ = ASU + and X 25.6% (34/133)	+ = ASU + and X 15.3% (22/144)

Table 4.2.3. (Continued.)

Trait and tooth (FDI)	Female Overall FA	Male Overall FA	Female Comparable FA	Male Comparable FA
Distal trigonid crest (37/47)	4.0% (7/174)	1.1% (2/178)	+ = ASU 1 63.6% (7/11)	+ = ASU 1 50.0% (2/4)
Protostylid (37/47)	11.5% (21/182)	12.9% (23/178)	+ = ASU 1-7 75.0% (21/28)	+ = ASU 1-7 62.2% (23/37)
MMPT (37/47)	4.9% (9/184)	1.7% (3/181)	+ = Weets (2009) [adpt.] 1 – '3+' 81.8% (9/11)	+ = Weets (2009) [adpt.] 1 – '3+' 60.0% (3/5)
Cusp number (37/47)	8.5% (15/177)	9.9% (18/182)	+ ~= ASU 4 46.9% (15/32)	+ ~= ASU 4 40.0% (18/45)
C5 (37/47)	10.2% (18/177)	12.1% (22/182)	+ = ASU 1-5 60.0% (18/30)	+ = ASU 1-5 52.4% (22/42)
C6 (37/47)	0.6% (1/177)	0.0% (0/182)	+ = ASU 1-5 100.0% (1/1)	+ = ASU 1-5 0.0% (0/2)
C7 (37/47)	0.0% (0/183)	0.5% (1/182)	+ = ASU 1a-4 N/A	+ = ASU 1a-4 0.0% (1/1)
Groove pattern (38/48)	24.5% (25/102)	20.9% (23/110)	+ = ASU Y 69.4% (25/36)	+ = ASU Y 63.9% (23/36)
Distal trigonid crest (38/48)	13.4% (15/112)	17.5% (20/114)	+ = ASU 1 53.6% (15/28)	+ = ASU 1 64.5% (20/31)
Protostylid (38/48)	5.1% (5/98)	10.7% (11/103)	+ = ASU 1-7 83.3% (5/6)	+ = ASU 1-7 100.0% (11/11)
MMPT (38/48)	33.3% (32/96)	21.5% (23/107)	+ = Weets (2009) [adpt.] 1 – '3+' 78.0% (32/41)	+ = Weets (2009) [adpt.] 1 – '3+' 79.3% (23/29)
Cusp number (38/48)	33.9% (37/109)	26.5% (30/113)	+ ~= ASU 4 57.1% (37/66)	+ ~= ASU 4 40.5% (30/74)
C5 (38/48)	32.1% (35/109)	31.9% (36/113)	+ = ASU 1-5 60.3% (35/58)	+ = ASU 1-5 51.4% (36/70)
C6 (38/48)	19.3% (21/109)	9.7% (11/113)	+ = ASU 1-5 87.5% (21/24)	+ = ASU 1-5 73.3% (11/15)
C7 (38/48)	3.7% (4/107)	0.8% (1/121)	+ = ASU 1a-4 100.0% (4/4)	+ = ASU 1a-4 100.0% (1/1)
Foramina mentales	3.0% (9/298)	4.7% (14/300)	+ = >1 75.0% (9/12)	+ = >1 87.5% (14/16)
Mylohyoid bridge	11.7% (32/273)	13.0% (32/247)	+ = >0 66.7% (32/48)	+ = >0 60.4% (32/53)

48.1%; LP4 – F: 41.6%; M: 38.1%), two instances of groove pattern (LM1 – F: 10.2%, M: 5.3%; LM2 – F: 25.6%, M: 15.3%) and of C5 (LM1 – F: 24.4%, M: 16.0%; LM3 – F: 60.3%, M: 51.4%) and the mylohyoid bridge (F: 66.7%, M: 60.4%).

When Comparable FA is considered, the female mean is 64.8%, which is 7.8% greater than the male mean (57.0%). In Large sample comparable FA the difference decreases (5.8%) along with female (45.5%) and male means (39.7%).

These figures demonstrate female individuals are affected by a greater FA in this large sample more often, with a 14.6% increase (5.8% as proportionately related to 39.7%) in the asymmetry shown by the mean Comparable FA in the larger male sample.

Table 4.2.4. Female and Male mean Overall FA, Comparable FA, and Large sample comparable FA for the sample and each tooth.

Site	Mean Overall FA	Mean Comparable FA	Mean Large sample comparable FA
Females	9.8%	64.8%	45.5%
Males	8.6%	57.0%	39.7%
UI1/sex	F: 4.9%	F: 70.0%	F: N/A
	M: 4.4%	M: 52.4%	M: N/A
UI2/sex	F: 9.9%	F: 76.7%	F: N/A
	M: 9.1%	M: 75.5%	M: N/A
UC/sex	F: 26.0%	F: 34.5%	F: 34.5%
	M: 35.1%	M: 50.0%	M: 50.0%
UP3/sex	F: 1.5%	F: 88.9%	F: N/A
	M: 2.1%	M: 100.0%	M: N/A
UP4/sex	F: 7.0%	F: 95.0%	F: 80.0%
	M: 6.2%	M: 68.7%	M: 65.9%
UM1/sex	F: 9.6%	F: 70.1%	F: N/A
	M: 6.7%	M: 70.8%	M: N/A
UM2/sex	F: 20.7%	F: 53.2%	F: 41.8%
	M: 17.5%	M: 44.7%	M: 39.4%
UM3/sex	F: 4.9%	F: 80.0%	F: N/A
	M: 4.8%	M: 87.5%	M: N/A
LI1/sex	F: 0.0%	F: N/A	F: N/A
	M: 0.8%	M: N/A	M: N/A
LI2/sex	F: 1.5%	F: N/A	F: N/A
	M: 2.2%	M: N/A	M: N/A
LC/sex	F: 17.0%	F: 43.7%	F: 43.7%
	M: 21.6%	M: 46.2%	M: 46.2%
LP3/sex	F: 8.6%	F: 60.4%	F: 60.4%
	M: 6.9%	M: 48.1%	M: 48.1%
LP4/sex	F: 14.6%	F: 20.8%	F: 41.6%
	M: 12.9%	M: 38.1%	M: 38.1%
LM1/sex	F: 7.3%	F: 44.5%	F: 17.3%
	M: 5.2%	M: 41.7%	M: 10.7%
LM2/sex	F: 7.3%	F: 64.7%	F: 25.6%
	M: 6.3%	M: 35.0%	M: 15.3%
LM3/sex	F: 20.7%	F: 73.7%	F: 58.7%
	M: 17.4%	M: 71.6%	M: 46.0%

The statistical test performed to verify the independence of proportions was the Z test. When the trait results for Large sample comparable FA of each sex are summed, the percentage is 38.8% (437/1125) for females and 33.6% (407/1210) for males. This yields a z-ratio of 2.617, equivalent to a two-sided P-value of 0.0089 (P < 0.01), which shows with a 99.1% confidence there is a difference in FA proportion between sexes, and female individuals display a greater rate of FA. To test the independence of these proportions for Overall FA results (F: 9.9%, 831/8435; M: 8.6%, 754/8740) provides an even lower P-value (0.0056 < 0.01), with a very high confidence level (>99.4%; z-ratio: 2.773). When Comparable FA results (F: 47.6%, 797/1676; M: 41.7%, 726/1742) are tested, an even higher z-ratio (3.456) and lower P-value (0.0005) are found, which again underlines the difference between sexes in FA proportions. Women demonstrate, consistently and without statistical contradiction, higher FA frequencies.

Mayhall and Saunders (1986) found metric dental trait asymmetry is not correlated with nonmetric dental trait asymmetry. Nonmetric traits are theoretically uncorrelated between themselves (for the present sample, see 4.3.Sexual dimorphism and intertrait correlations), so it is feasible that mimicking of the patterned behavior found on metric data is unlikely. Noss and colleagues (1983) found the same lack of correlation (between metric and nonmetric dental FA) and hypothesized the genesis of such independence could be the diverse formation of each part of the tooth bud. Mayhall and Saunders (1986) add that the different timings of the odontogenesis of a single trait and the tooth that carries it allow for very different stimuli to be a part of the dynamic behind FA.

This reasoning related to the timing of tooth odontogenesis shows FA may be a long term measure of developmental stress, as opposed to episodic stress markers such as enamel hypoplasia (Barrett *et al.*, 2012). Jeong and colleagues (2013) fail to find a difference in odontometric FA between two groups, one with LEH and another without LEH. This can be due either to the type of stressor that can differently affect teeth, and cause LEH or FA independently; or to the determination of odontometric FA by measuring mesiodistal and buccolingual distances, which can be insufficiently diagnostic of the true size of the FA that affects the teeth of the sample (Jeong *et al.*, 2013). Hoover and colleagues (2005) sought for a connection between hypoplasias and odontometric FA in individuals, but found only few traits that exemplified that association. Many hypotheses can justify that, including the fact that these two

phenomena may record environmental stresses of different time lengths or nature (Hoover *et al.*, 2005).

If this is so, socio-cultural biases could be as effective as, or more effective than genetic control over FA, since they can filter environmental stress, by enhancing or diminishing it. This can be a partial justification to the difference found between Mexicans and Belizeans by Baume and Crawford (1980), mentioned above. Noss and colleagues (1983) found differences in frequencies of asymmetry between sexes are difficult to detect statistically, but should not be overruled when such significance is found. These differences could indicate differential treatment of children or biological differences within a population. Culture could, then, be a crucial part of such differences.

Pima Indians display an overall presence/absence FA of 11.4% for males and 12.8% for females (Noss *et al.*, 1983). The differences in individual traits were not statistically significant, but these means differ in an order of magnitude greater to the one found for the overall FA of the present sample for each sex. It seems an accurate statement that among Pima Indians female individuals are also the most asymmetric.

An impoverished population of African Americans (Gullah) was found to display greater FA in mandibular canine dimensions of female individuals, when odontogenic timings and evolutionary trends suggested otherwise. This difference could be caused by some sex-bias in childcare. The Gullah were found to be more asymmetric than Native American archaeological samples, in accordance with historical and archaeological evidence (Guatelli-Steinberg *et al.*, 2006).

Ticuna Indian female individuals had significantly larger FA frequencies than males for the mesiodistal diameter, and show larger overall FA (Harris and Nweeia, 1980). The authors think this sexual difference may predate the gender definition of roles within this culture, because it is expressed since the earliest forming crowns (M1's and I1's), so it may not be a socio-cultural, but a biological phenomenon.

The Coimbra sample does not display such a clear pattern, since the traits whose mean Overall FA is greater for males than female individuals are mostly located on the I1's and the LM1. The teeth that form their crowns earlier (M1's, I1's and I2's, according to Scheuer and Black [2000] and AlQahtani *et al.* [2010]), until about three or four years of age, show relatively small mean FA differences between male and female individuals, with some larger means for males (see Table 4.2.4.). The following permanent crowns to form (canines and premolars: Scheuer and Black, 2000; AlQahtani

et al., 2010) show mixed results, with canines (which initiate and finish formation slightly earlier) persistently more asymmetric among males, and premolars showing a greater tendency towards asymmetry in females, with the exception of UP3. It should be noted that the P4's develop slightly later than the P3's, with all these crowns of canines and premolars forming between the approximate ages of 2 and 6 years (Scheuer and Black, 2000; AlQahtani *et al.* [2010] report canine crown formation from 1 to 5.5 years and premolar crowns from around 3 to 6.5 years). M2's (crowns forming completely until the age of 6 through 10 years [Scheuer and Black, 2000]; crown formation between 3.5 and 8.5 years, approximately [AlQahtani *et al.*, 2010]) clearly display more asymmetry in female individuals. UM3's are difficult to compare, due to a lack of traits with large samples, but are nearly equal between sexes, while LM3's again display the tendency of more asymmetric female individuals. The crowns of both these teeth start forming around 10 and finish at about 15 years of age (+- 30 months [Scheuer and Black, 2000]; crown formation from about 9.5 to 14.5 years [AlQahtani *et al.*, 2010]). Besides, *foramina mentales* (formed during gestation: Hauser and De Stefano, 1989) are also more asymmetric in males. Therefore, the pattern is clearly different, and almost opposite to the one found by Harris and Nweeia (1980), which indicates the possibility that the definition of the role of females affects their exposure to environmental stress and developmental instability. Dental age calculations show a (statistically insignificant) delay of nearly half a year on the growth of low socioeconomic status children when compared to those of high socioeconomic status (Cardoso, 2007), which can explain the seemingly early age of this gender role definition as slightly underestimated.

Wasterlain (2006) studied enamel hypoplasia in the population of Coimbra, sampled from the same identified collections as the present study. This researcher found a greater frequency of hypoplasias in male LM1 (F: 13.9%, 28/202; M: 16.3%, 46/282) and UM1 (F: 9.1%, 26/285; M: 14.6%, 42/288). Slightly greater male frequencies are also present for UI2 (F: 51.8%, 146/282; M: 52.8%, 161/305), but lower male frequencies appear on UI1 (F: 58.2%, 152/261; M: 51.3%, 143/279), LI1 (F: 57.8%, 160/277; M: 43.4%, 138/314) and LI2 (F: 61.7%, 205/332; M: 51.0%, 183/359). As for canines (UC – F: 61.6%, 223/362; M: 63.2%, 237/375; LC – F: 73.2%, 278/380; M: 74.7%, 304/407) and premolars (UP3 – F: 41.7%, 116/278; M: 44.2%, 133/301; LP3 – F: 54.2%, 180/332; M: 55.4%, 214/386), only for the fourth premolars, UP4 (F: 35.4%, 99/280; M: 33.6%, 100/298) and LP4 (F: 50.5%, 154/305; M: 43.4%, 151/348), does

the female frequency surpass the male. The remaining teeth are more hypoplastic in women on UM2 (F: 11.0%, 34/308; M: 9.5%, 31/327) and LM3 (F: 8.2%, 15/184; M: 4.6%, 11/238), with the opposite occurring on LM2 (F: 12.1%, 29/239; M: 12.7%, 41/323) and UM3 (F: 3.7%, 7/188; M: 10.1%, 24/237).

This is not a relatively clear pattern, like the one found for FA in the same population, and does not suggest any particular trend. Wasterlain (2006) also found that slightly more female individuals display any hypoplasia (F: 93.8%, 240/256; M: 91.9%, 237/258) and that more female teeth are affected, with a high statistical probability (F: 41.2%, 1852/4495; M: 38.7%, 1959/5067; P = 0.011). Historical context (explored below) suggest the reasons for the high incidence of enamel hypoplasia are nutritional deficiencies, trauma, parasitism and infection (among other insults). The difference between the sexes suggests male infants and children were better treated and given preferential access to essential care. Alternatively boys could die more often when afflicted by disease, resulting in a differential adult frequency of enamel hypoplasia (see below). The overall frequency of this enamel defect, above that of a Medieval Coimbra population and of other countries' contemporary samples, suggests the poor socioeconomic status of the sample caused a worse health condition during growth (Wasterlain, 2006). This is underlined by the results found by Carvalho (2013) for a Medieval (11th/12th to 15th/16th century) Coimbra sample of 58 adult individuals, with 58.6% of them showing hypoplastic defects. This author also found a difference between the sexes, with female individuals showing greater frequencies than males. This is attributed to different social roles that could prompt perceived differences in the necessity of nutritional input, favoring males. The timing of these individuals' hypoplasias can be related to the weaning period adopted by that population (Carvalho, 2013).

The recorded variations may be due to biological or cultural sex biases, as noted above. When mean frequencies are concerned, female individuals seem to be more prone to developmental instability. The male individuals in these samples, including the Coimbra one addressed herein, are either more capable of buffering stress or are subjected to less stress due to some socio-cultural bias. Women can also be more resilient to disease in infancy, and thus display greater exposure to developmental noise than men as adults, on average. Age differences found by Wasterlain (2006) for linear enamel hypoplasias are due to a greater LEH frequency on older individuals. If LEH

was related to an early death, the opposite would be expected. This suggests the early death of male individuals when affected by higher frequency of LEH is not likely.

Comparing populations or population classes in measures of stress or developmental instability should be done carefully. If a subsample displays a greater amount of stress evidences it may be a sign of better health status, as the least affected subsample could have been biased by high childhood mortality (King *et al.*, 2005).

Hope and colleagues (2013) found evidence that in males, lower socioeconomic status in early life may be reflected in facial symmetry to a further extent than midlife socioeconomic status. In females, this connection was not supported by the statistical analysis. This could be justified by a greater resistance to developmental stress at an early age in females or by a different tradeoff system involving women's reproductive success and bodily maintenance (Hope *et al.*, 2013). Female individuals, as shown through research from several viewpoints, are able to buffer environmental and nutritional stress better than male individuals. This is not, however, clearly corroborated by results in studies analyzing the difference in enamel hypoplasia frequencies between male and female individuals (Guatelli-Steinberg and Lukacs, 1999). The frequencies reviewed by Guatelli Steinberg and Lukacs (1999) suggest differences in parental investment may have a stronger effect on sex differences than a greater male susceptibility to stress. This strengthens the possibility of a greater buffering of environmental stress by female individuals, which would again underline the difference found in the present sample, and contradict a male biological advantage in counteracting developmental noise with developmental homeostasis.

As was explored within the Introduction to this dissertation, Portugal in the 19th and first half of the 20th century was a poor country, with underfed populations mostly relying on subsistence agriculture (Correia Pereira, 1912; Cardoso, 2005). Mortality rates were high, and life expectancy was subsequently low, in particular for men. Women composed the higher portions of the demographic pyramid, when infant mortality was at 50.0% (in the mid-19th century, dropping to around 10% in the first decades of the 20th century; Roque, 1988; Valério, 2001).Thus, they could have outlived men as suggested above, resisted illness in infancy and childhood, and suffered the biological consequences while developing. This is a classic conundrum posed by the osteological paradox. Evidences of disease or stress are only informative when the lesions or healing lesions can be related to frailty (susceptibility to morbidity and mortality), otherwise they are difficult to interpret (Wood *et al.*, 1992).

Men are more vulnerable to disease, stress, injury, and infection, and are more prone to sickness and death than women, despite the latter's special health needs and investments related to offspring. Different mortality rates between sexes across human life history should be viewed in a sexual selection standpoint, since it molds behavior, which affects the probability of exposure to dangerous situations. Trade-offs between greater competitiveness and risk-taking behavior at the expense of longevity are translated into greater reproductive success. This is particularly true of underprivileged populations, such as the one sampled in the present study. A mortality male:female ratio increase shows individuals of a lower socioeconomic status incur in risky behavior with the potential for high payoff in reproductive success because of the perception of a general likeliness for extrinsic mortality and morbidity, which would not justify a long-term strategy (Kruger and Nesse, 2006). Despite this, Kruger and Nesse (2006) found childhood mortality caused by internal factors (susceptibility to disease and injury) was higher for males, but only slightly, in United States individuals in 2001. So, this biological interpretation of the general difference between male and female mortality rates and their life expectancies may affect individuals predominantly from late adolescence and adulthood onward, because of the onset of sexual competition for mates.

The Portuguese society was still a very conservative one, as is suggested by the social, political and economical points of view of the time (Correia Pereira, 1912; Reis, 1987; Cardoso, 2005). Agriculture was constantly affected by difficulties related to transportation, tributes, loan sharks, environmental hardship, inadequate techniques and feudalist tradition (Roque, 1982). This originated subsequent shortages and abundances, with fluctuating prices of foodstuffs (Bocquet-Appel, 1984). Both these realities, a conservative and poor society, are possible explanations for the degree of FA presence in the sample and its greater expression on the female individuals, since from an early age girls were probably charged with greater responsibilities than young boys, especially within the household. Besides, they could have been considered as needing or deserving a lesser nutrition in times of food shortage.

As testified through dental FA differences, Neanderthals and modern humans might have suffered the same level of developmental stress at the time of birth, but modern humans suffered less so during later childhood, which can be due to less exposure to stress or to greater ability in buffering such stress (Barrett *et al.*, 2012). Environmental stress is shown as greater for the Early Christian cemetery in Kulubnarti

(Sudanese Nubia), and FA is significantly greater on the specimens from that necropolis than from the Late Christian cemetery. These diachronic samples are expected to be biologically related (DeLeon, 2007). The importance of environmental effects on occlusal variants (such as overbite, for example) in twins also demonstrates how the environment can affect teeth during development (Corruccini *et al.*, 1986). Genetic relatedness is not completely responsible for differences in FA or susceptibility to developmental instability, as has been repeatedly shown throughout this text, and particularly by the last two examples.

Different frequencies of linear enamel hypoplasia for males and females may mean they differ in vulnerability or record stress episodes differently, in differential mortality or in preferential treatment and access to nutritional and medical resources (King *et al.*, 2005). 18th and 19th century London surviving female individuals display enamel hypoplasia more frequently than surviving males. King and colleagues (2005) stressed this can be interpreted as a result of subjection to unhealthier nutrition, care and habits or as a greater mortality for male children, which removed those subjected to stress from the surviving males.

In Medieval Croatia (Slaus, 2000), mortality was higher for female than male individuals during the late adolescence and early adulthood, presumably due to health issues related to pregnancy and childbirth, but also to differential social status. Subadult individuals have a greater frequency of hypoplasia than adult individuals in the Nova Raca (Croatia) Late Medieval sample. Hypoplasia was, to some point, related with mortality. Female individuals also presented greater frequencies of hypoplasia than males, particularly in subadults, and a higher mean number of defects per tooth. Dental caries evidence also suggests differential access to foodstuffs between sexes. Food shortages, due to tax pressure from the feudal lords, were common, and are widely recorded in historical data. The raids from the Ottoman Turkish Empire disrupted trading routes and forced men into military and construction service, to protect the Austrian Habsburg Kingdom. This supposedly granted men tax exemption, and could be the reason for a perceivable health distinction between the sexes, favoring men in food access and (probably) social status, despite subjecting them to great effort (noted in spinal lesions, mainly). In the work here summarized, Slaus (2000) finds the difference in socio-cultural gender roles as the most likely explanation for stress event (and other indicators of health) differences.

Three hundred children from rural communities in Mexico were analyzed for enamel hypoplasia frequencies and timing of development. In this impoverished non-Western population with high enamel hypoplasia frequencies (46.7% of children), girls presented greater frequencies overall and kept high frequencies after two years, while boys' dropped. This is not a common trend, according to the bibliographic review provided by the authors, and may signify boys were given preferential access to health, nutritional and habitation resources (Goodman *et al.*, 1987).

Guatemalan children with nutritional supplementation present lower linear enamel hypoplasia (LEH) frequency, when compared with a non-supplemented group. Females display greater prevalence of maxillary incisors and canines LEH. Girls received less mean calorie supplementation and were ill longer than boys. However, the difference in LEH was disproportionate, with females demonstrating greater LEH frequency than frequently ill or inadequately supplemented males. This is most likely not due to biological differences in enamel formation when subjected to illness or inadequate supplementation. The fact that frequently ill males show an LEH frequency equal to that of frequently healthy males prompted the authors to suggest culturally mediated preferential treatment of boys, particularly when sick, may have confounded the results. Frequently sick female children were not taken to supplementation centers as frequently as males (May *et al.*, 1993).

Directional (DA) and fluctuating asymmetries in skull shape of an Early Medieval sample from Czech Republic (Mikulcice) demonstrate socioeconomic differences in access to food resources and exposure to environmental stress. Males and females from the sub-castle region displayed enhanced DA and dental wear that indicated the chewing of harder and grittier foods, when compared to the castle population, of theoretically greater socioeconomic status. Males and females show different patterns in FA, with males characterized by homogeneity among the two groups and females displaying more FA in the castle sample. This could be due to the external origin of the castle females, due to strategic, political marriages. It could also be indicative of some of the castle females' low status, since these could be serfs or slaves. There seems to be a low environmental stress in the overall population (Bigoni *et al.*, 2013). The higher FA in women in the Mikulcice castle could be indicative of cultural distinctions in gender, as hypothesized for the Coimbra population.

Pirzigian (1977) found no sex differences in mesiodistal and buccolingual diameters for Indian Knoll hunter-gatherers, Campbell/Larson prehistoric

agriculturalists and contemporary Hamann-Todd identified individuals. In a Japanese contemporary population, mesiodistal and buccolingual dimensions of LM1 and LM2 produced insignificant FA differences between males and females (Peiris *et al.*, 2013). A study relating handedness to asymmetry in occlusal morphology (distances and angles) in left and right handed American children from the 1960's found FA to be similar between these handedness groups, except for two instances of larger FA for left-handed children. Female and male individuals did not differ significantly in FA frequency (Pirila-Parkkinen *et al.*, 2001). These results again suggest FA sex differences are not common or biologically determined, since they do not occur in these chronologically and biologically diverse populations.

Buchwald and Grubska (2012) provide an example of FA research in the soft tissue, from skin patterns. Dermatoglyph asymmetry suggests Polish males are more subjected to or more susceptible to developmental stress during early ontogeny (as 3 to 4 month fetuses). This underlines the origin of female FA in later forming structures as not of a likely biological origin, since that is predictably independent of ontogenic phase.

In order to evaluate differences in dental morphology FA within the present sample, the author tested the proportions of the sum of FA between the 18.2% (109 individuals) of the sample under the age of 21 years (7 to 20 year olds) and those that died at 21 years or older (the remaining 81.8%, from 21 to 97 years of age, 491 individuals). In all accounts of FA there was no statistically detectable difference, with all presumably caused by random sampling. Overall FA (7-20: 9.6%, 356/3721; 21-97: 9.3%, 1142/12230) produced a z-ratio of 0.42, with a two-tailed P-value of 0.6745, and thus revealed a very low confidence level for the difference (approximately 32.5%). The differences between these age ranges in Comparable FA is negligible (7-20: 40.7%, 333/818; 21-97: 40.6%, 1065/2625), and statistically meaningless (z-ratio: 0.07; P = 0.9442). When Large sample comparable FA (in this case it includes samples of 20 or more individuals, since the younger age range has much less individuals overall) is considered, the difference is still small (7-20: 30.2%, 170/563; 21-97: 29.2%, 498/1705) and statistically unreliable (z-ratio: 0.446; P = 0.6556). So, despite the younger age range slightly greater FA proportions, these results demonstrate consistent statistical equivalence between both age ranges, and therefore show there is continuity in the frequency of FA despite of age. Developmental instability, as expressed by FA, is not connected with early mortality in Coimbra, so the difference in FA between male and

female individuals should not be caused by the former's greater childhood mortality, causing misrepresentation of the incidence of FA in adult males. In light of the osteological paradox (Wood *et al.*, 1992), greater susceptibility to disease could have resulted in differential mortality, and affected infant male individuals more than female individuals, precluding them from inclusion in the present sample and being accounted in this FA comparison. If this frailty was connected to FA (as a measure of DI), it should still be represented in the individuals who survived infanthood but died before reaching mature ages.

This is yet another piece of evidence pointing towards a gender difference in access to nutrition, health, sunlight exposure, adequate rest and exercise, and other culturally defined biases which may result in biological differentiation.

Brazilian boys were found to display higher body trait FA in accordance to early life, and birth to nine years of age, compensatory growth. So, fast growth rate was connected with higher FA. This may mean that FA is a measure of "good development" for potential future sexual mates, since body size does not reflect growth pattern, while FA does. Growth pattern is connected to fitness and longevity, and is thus a useful reference for potential mates (Wells *et al.*, 2006). This finding may unveil a further hypothesis. If dental nonmetric trait FA of the permanent dentition is related to compensatory *post-partum* growth, sex differences may mean female children were either more affected by lower birth weight than males, or grew at a faster rate (or were more affected by fast growth) than males, despite sharing a low birth weight with them. This hypothesis is more difficult to interpret, because of a lack of reasonable explanations for such patterns. The greater presence of compensatory growth in female children could still be evidence of childcare bias, which depends on when the stalled growth that anteceded it occurred. If as infants, female children had access to fewer resources, later compensatory growth could justify the timing and higher incidence of FA.

Historically accurate depictions of children's day-to-day activities and gender role differences from early on need to be established for the 19th and 20th century in Portugal, in order to test which of the presented hypotheses is most likely. Before such research is conducted, and despite environmental factors (which could be differentially filtered for each gender by cultural behavior) being the most likely cause of developmental instability, genetic differences in buffering stress cannot be overruled. Differential mortality seems unlikely; however it should not be completely overruled.

The increase of the gap in FA frequencies between female and male individuals along odontogenesis (shown above), with the greater values always pending toward females with a mean statistically significant difference, may be too strong an evidence to ignore. It demonstrates a high likeliness that gender roles were defined early on in the late 19th and early 20th century, and were pervasive towards the health of the female population.

ASUDAS standard protocol allows individual trait presence to be determined through the consideration of the most expressive side when both are present, since it better represents the genotype of these polygenic variables (Irish and Guatelli-Steinberg, 2003). Thus, FA is not represented in the analyzed trait frequencies.

4.2.3. Fluctuating asymmetry differences among causes of death

In evolutionary medicine, changes in environment are considered detrimental to the health status of individuals, which indicates modernization, like other major changes in living habits throughout human history, can cause health problems (Gage, 2005). Historical mortality trends in post-Industrial Revolution Western countries, as analyzed by Gage (2005) indicate a decrease in infectious disease and degenerative disease related mortality, when the figures are corrected for classification errors. This indicates the artificial environments of modern Western societies should not be detrimental to human health. On the contrary, it should in general be favorable to it. There are no clear causes for the decreases of mortality, and specifically for mortality related to infectious or degenerative diseases (Gage, 2005). Yet, environmental factors that include nutrition and other developmental mediators could play a role.

High FA may be associated with parasitism, an increased prevalence of disease and a diminution on immune responses, on several organisms (Moller, 2006). Developmental instability is correlated to phenotypic plasticity, which is translated by a greater variation in phenotypes through a lessened heritability (affecting how genotype is mapped into phenotype). This effect is contrary to stabilizing selection, and therefore lessens the fitness of the overall population (Tonsor *et al.*, 2013).

The "fetal origins hypothesis" states that developmental pace and pathway is a risk factor for a group of chronic diseases, mainly of cardiac diseases. Malnutrition

between gestation and early childhood can affect the structure and function of the organism, a process called "programming" (Barker *et al.*, 2009).

This process can generate some pathological effects in later life. Low birth weight is related to coronary heart disease. A reduced number of nephrons in people who were born small can be a cause of hypertension. Undernourishment can lead to a trade-off in organ development which hinders kidney, lung and muscle growth to protect brain development, and in turn may be related to hormone processing and metabolism alterations that can cause diabetes. Individuals of low birth weight are also less resilient to harsh environmental conditions in later life (Barker *et al.*, 2009).

Barker and colleagues (2009) found other such effects. Both low birth weight and high BMI at age 11 are related to type 2 diabetes, hypertension and coronary heart disease. Girls' growth is related to the next generation's chronic disease. The mother's low rate of protein synthesis can affect fetal growth, leading to a low BMI during life, hypertension and higher stroke hazard. A higher concentration of sex hormones in the mother, due to catch-up pre-pubertal growth, may increase the probability of breast or ovarian cancer in female children. The mother's under average body size may also condition the size of the placenta, which is related to hypertension in children.

In the Hertfordshire birth cohort, individuals born with higher birth weight were less likely to die from circulatory disease. Male individuals also presented less risk of death from accidental falls (due to a greater resistance of the bones), and females were less prone to pneumonia, injury, diabetes and musculoskeletal disease-related deaths. Despite this, high birth weight was related to increased cancer-related mortality in men (Syddall *et al.*, 2005).

So, environmental conditions during early development can influence life history. Besides, this affects future generations, since birth weight and adult body size are predictors for offspring birth weight (Kuzawa, 2007).

Kieser and colleagues (1997) found prejudicial effects in children of overweight mothers as well. The children of obese mothers show higher FA than those of non-obese mothers. When the mother was obese and smoked during the pregnancy, FA levels were even higher than those of non-smoking obese mothers (Kieser *et al.*, 1997).

In a Filipino cohort, male children who gained weight faster during the first six months of life had lower birth weight than the remaining sample. Despite this, they became taller, more muscular, had higher sex hormone levels and reached sexual maturity sooner. Besides, the reproductive behavior of these male adult individuals was

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altered in relation to their middle and low weight gain counterparts: they tended to have sex for the first time sooner, to have had more sexual partners and to have had sex within the last month when interviewed (Kuzawa *et al.*, 2010). This may be indicative of an organic detection of environmental signals which leads to a compensation in sexual development and reproductive behavior, to allow gene transmission to the next generation before a possible early death. This again exemplifies how environmental hardship during gestation and early growth can condition development and life history.

The apparent contradiction between the prediction of future disease by birth weight or compensatory growth rate is actually the reflection of a complex dynamic. Fetal growth most likely models metabolic capacity, while postnatal growth models metabolic load. Poor metabolic capacity (derived from low fetal growth) and/or excessive metabolic load can increase the propensity to certain diseases of cardiovascular or metabolic natures. An adequate and balanced nutrition during ontogeny should minimize or eliminate either risk (Wells, 2009).

Developmental instability is often connected to fluctuating asymmetry. The relation between dental morphology FA percentage and cause of death can be analyzed in the present sample, since it is identified for most individuals, albeit through dubious and outdated diagnostic criteria and terminology. The reports on cause of death are difficult to interpret because of the continuous changes in conventions used within them and the early difficulties in the classification of causes of death by medical staff (Gage, 2005). If these data are sufficiently accurate, the relations between these variables may yield important results in historical epidemiological trends.

The World Health Organization "International Statistical Classification of Diseases and Related Health Problems, Version 2010 (10th Revision)" online app (http://apps.who.int/classifications/icd10/browse/2010/en) was used to attribute a classification to each available and classifiable cause of death of the present sample (see the distribution of classified causes of death on Table 2.6., on chapter 2.Sample). The attributed classification consists only of the letters used to distinguish each of the blocks, which define a broad type of disease.

An individual fluctuating asymmetry (FA) overall percentage was calculated by determining the total instances of FA (with any degree of asymmetry) per individual. Then, this figure was divided by the total number of possible FA sites (the number of bilaterally scored traits, independently of their presence or expression) per individual. The resulting percentage was called "Individual overall FA".

The Individual overall FA mean ranks of each death causing disease were compared through a Kruskal-Wallis H test, which demonstrated those means differ at a high level of confidence: χ^2 (21) = 38.207, P = 0.012. This suggests developmental instability (DI) may be related to cause of death, since FA means differ significatively at a degree of confidence greater than 95% among causes of death (see Table 4.2.5.).

Table 4.2.5. Mean Individual overall FA, standard deviation, and mean rank for each disease and Kruskal-Wallis H test results.

Disease classification	Mean Individual overall FA	n	Standard deviation	Mean rank
A	10.1209	253	7.08947	309.77
C	6.8812	31	5.38654	240.00
D	12.2262	4	14.94375	286.13
E	10.7655	4	7.38449	320.63
F	12.5000	1	-	422.50
G	5.7239	12	4.92914	203.71
H	17.6471	1	-	508.00
I	9.3062	72	9.70976	273.13
J	10.0498	51	8.15218	297.39
K	7.1019	52	6.63463	228.38
L	12.0120	4	.43885	406.75
M	10.2750	7	5.91681	323.64
N	6.8318	21	5.61576	241.12
O	7.7327	19	8.32399	226.76
Q	4.7619	1	-	152.00
R	11.7886	19	6.67964	363.16
S	6.9963	5	6.93250	225.40
T	6.0276	8	5.51520	212.63
W	6.8571	3	6.18095	248.17
X	7.1429	1	-	239.00
Y	20.1681	2	11.88415	480.75
Z	14.2857	1	-	468.00
Total	9.3029	572	7.49382	

Kruskal-Wallis H	χ^2	38.207	P	0.012
	df	21		

A further figure was calculated, the "Individual comparable FA" percentage. The total instances of FA were divided by the total number of FA sites with trait presence (the only accepted sites were bilaterally scored and expressed at least unilateral trait presence).

The Individual comparable FA mean ranks of each ailment identified as cause of death were tested for differences via a Kruskal-Wallis H test. This statistical test showed the mean ranks did not differ: χ^2 (21) = 26.863, P = 0.175 (see Table 4.2.6.). Contrarily to the previous result, this indicates DI can have no relation to cause of death, since the null hypothesis, which stated there would be no difference among each disease's mean

Table 4.2.6. Mean Individual comparable FA, standard deviation, and mean rank for each disease and Kruskal-Wallis H test results.

Disease classification	Mean Individual comparable FA	n	Standard deviation	Mean rank
A	43.8788	253	25.18213	297.29
C	39.4307	31	35.40469	261.53
D	40.0000	4	43.20494	247.88
E	54.1667	4	31.54949	330.38
F	0.0000	1	-	49.00
G	32.2538	12	31.59161	224.29
H	100.0000	1	-	548.50
I	40.8606	72	30.37796	279.67
J	48.3584	51	32.71332	316.76
K	36.1512	52	26.26894	247.89
L	64.4345	4	29.21067	411.50
M	53.4418	7	24.56460	346.93
N	32.7778	21	28.34844	234.86
O	39.0476	19	30.56772	260.24
Q	33.3333	1	-	207.00
R	45.8839	19	23.37030	318.42
S	29.8571	5	23.23433	218.00
T	32.4405	8	24.64314	238.31
W	33.3333	3	28.86751	255.67
X	42.8571	1	-	301.00
Y	83.3333	2	23.57023	512.25
Z	66.6667	1	-	476.00
Total	42.3561	572	28.12056	

Kruskal-Wallis H	χ^2	26.863	P	0.175
	df	21		

ranks, could not be rejected. The previous result could have been an artifact resulting from the lack of specificity of the statistical comparison, which did not remove bilateral absences. This inclusion can alter any individual's FA percentage by overstating his/her

Table 4.2.7. Mean Individual comparable FA, standard deviation, and mean rank for each disease and Kruskal-Wallis H test results (with individuals with more than three comparable sites only).

Disease	Mean Individual comparable FA (> 3 comparable	n	Standard	Mean
A	45.2803	201	20.92644	193.44
C	47.0456	15	23.72659	198.03
D	30.0000	2	14.14214	100.50
G	31.4827	7	18.61653	121.57
I	45.6101	36	17.59915	202.28
J	46.3599	23	17.41743	199.91
K	41.5703	36	19.99761	174.47
L	45.5357	2	23.99112	202.75
M	48.1518	5	15.07136	215.20
N	37.1667	10	16.05930	154.35
O	37.1429	11	25.93097	135.32
Q	33.3333	1	-	110.50
R	46.5483	13	13.60244	206.88
S	37.3214	4	18.66392	150.75
T	41.9048	5	18.64150	178.60
W	33.3333	3	28.86751	160.33
X	42.8571	1	-	190.00
Y	66.6667	1	-	331.50
Total	44.1783	376	20.05433	

Kruskal-Wallis H	χ^2	13.278	P	0.717
	df	17		

symmetry, when in fact the individual most likely lacked the genetic requirements for trait expression.

So as to further filter useless data from the comparison, individuals with less than four traits with at least unilateral presence were removed from analysis. The resulting Kruskal-Wallis H test provided an even lower likeliness of a connection between DI and cause of death: χ^2 (17) = 13.278, P = 0.717 (all of the compared data can be seen in Table 4.2.7.).

When individuals with less than six traits with at least unilateral presence were removed, the probability that greater DI would condition an individual's cause of death was lowered even further: χ^2 (17) = 11.507, P = 0.829 (see Table 4.2.8.).

Table 4.2.8. Mean Individual comparable FA, standard deviation, and mean rank for each disease and Kruskal-Wallis H test results (with individuals with more than five comparable sites only).

Disease classification	Mean Individual comparable FA (> 5 comparable sites)	n	Standard deviation	Mean rank
A	43.2641	149	18.29284	137.74
C	42.5685	10	17.35243	138.75
D	40.0000	1	-	125.00
G	43.8447	4	10.05216	141.38
I	46.4216	26	12.76935	156.52
J	46.1198	19	17.22850	151.34
K	43.8612	25	21.42108	141.62
L	45.5357	2	23.99112	146.75
M	48.1518	5	15.07136	161.40
N	35.2778	6	3.67675	91.00
O	39.1964	8	29.48070	103.00
Q	33.3333	1	-	75.50
R	50.5128	10	11.16826	180.10
S	37.3214	4	18.66392	114.38
T	41.9048	5	18.64150	135.30
W	33.3333	3	28.86751	124.17
X	42.8571	1	-	145.00
Y	66.6667	1	-	254.50
Total	43.6823	280	17.80860	

Kruskal-Wallis H	χ^2	11.507	P	0.829
	df	17		

These results demonstrate the likeliness that the differences among the mean Individual comparable FA resulted from a sampling artifact is high. The better the data (including only highly informative individuals), the further is the null hypothesis from being rejected.

However, the significant results from the first test, performed on Individual overall FA, remain unexplained. With the aim to test why those data may be misleading, a Kruskal-Wallis H test compared the mean ages at death for each disease. The results prove those mean ranks as different: χ^2 (21) = 38.207, P = 0.012 (see Table 4.2.9.). If

each disease caused death at a statistically significant different time in life, *ante-mortem* tooth loss or greater wear rates may have caused some mean Individual overall FA to be artificially enhanced. The lack of antimeres for FA evaluation may have caused some individuals to have lost symmetrical sites, which might diminish their FA percentage if

Table 4.2.9. Mean age at death, standard deviation, and mean rank for each disease and Kruskal-Wallis H test results.

Disease classification	Mean age at death (in years)	n	Standard deviation	Mean rank
A	29.49	253	12.807	222.31
C	45.52	31	13.902	395.27
D	30.75	4	12.527	245.25
E	53.75	4	21.777	428.13
F	67.00	1	-	543.50
G	39.00	12	16.749	323.25
H	18.00	1	-	76.50
I	46.53	72	21.580	369.91
J	41.82	51	16.573	347.81
K	39.35	52	14.309	332.38
L	40.75	4	11.644	365.88
M	28.57	7	25.559	167.43
N	45.10	21	16.634	379.86
O	31.11	19	8.185	256.21
Q	34.00	1	-	303.50
R	37.42	19	21.180	289.05
S	26.80	5	9.602	200.60
T	37.63	8	13.617	321.00
W	20.67	3	13.429	120.33
X	37.00	1	-	333.00
Y	32.00	2	15.556	253.00
Z	55.00	1	-	485.50
Total	36.00	572	16.824	

Kruskal-Wallis H	χ^2	107.091	P	0.000
	df	21		

still present. This hypothesis was tested through rank correlation coefficients, which evaluated the correlation between age at death and remaining number of bilaterally scored traits (Kendall's *tau*-b: -0.349, P = 0.000; Spearman's *rho*: -0.519, P = 0.000), and age at death and remaining bilaterally scored and at least unilaterally present traits (Kendall's *tau*-b: -0.360, P = 0.000; Spearman's *rho*: -0.513, P = 0.000). Those results demonstrate age at death to be inversely correlated to the maintenance of bilaterally scorable traits, which is the possible cause of the difference in Individual overall FA mean ranks for at least some causes of death.

FA in the craniofacial skeleton of the Lisbon collection of identified skeletons was higher on people who died from degenerative diseases than on people who died of infectious diseases (Weisensee, 2013). The Developmental Origins of Health and Disease (DOHaD) hypothesis predicts people who suffered DI in pre- and early post-

natal age, also suffer adult health consequences, explaining the results. This population is particularly appropriate for this analysis, since its timeframe encompasses the modern health transition. These individuals were thus born in a health environment prone to nutritious deficiencies and died in an environment of either continuity of under-nutrition or greater food supply. When the latter was verified, individuals who were already adapted to a depleted nutrition could be more prone to degenerative disease, particularly of cardiovascular etiology (Weisensee, 2013).

This result was not repeated in the dental morphology FA of the Coimbra sample of the same chronology. This might be because the DOHaD hypothesis is incorrect, because there are other factors to consider, or because dental morphology FA is not measuring the same type of DI as craniofacial skeletal FA. In fact, the latter FA measure may reflect alterations in symmetry occurring much later in life than dental morphology FA, which might influence the results.

4.2.4. Fluctuating asymmetry differences among places of origin

High school students from two different socioeconomic origins, from Ankara, Turkey, were compared by Ozener and Fink (2010). Individuals from the slums presented higher facial FA than individuals from an urban area, denoting the affected development of individuals from poorer means.

So, individuals hailing from different origins within a same area or country can be differently affected by DI. Those differences in DI, as measured by FA, may be related to environmental or cultural causes and may be highly informative of a country's past socioeconomic inequalities.

The Individual overall FA means for the Portuguese continental districts of origin (birth) were compared. Again, the Kruskal-Wallis H test was used to verify the existence of differences among mean ranks. Test results were as follows (mean Individual overall FA and mean ranks per district can be seen in Table 4.2.10.): χ^2 (15) = 20.330, P = 0.160. These results do not allow the rejection of the null hypothesis. So, the mean ranks do not present any difference. The place of birth of the studied individuals seems not to influence their individual dental morphological FA.

Table 4.2.10. Mean Individual overall FA, standard deviation, and mean rank for each district and Kruskal-Wallis H test results.

District of origin	Mean Individual overall FA	n	Standard deviation	Mean rank
Aveiro	5.3438	16	4.82857	202.81
Braga	5.9183	4	4.82165	217.75
Castelo Branco	7.4032	9	6.73772	255.28
Coimbra	10.0064	402	7.76034	309.25
Évora	11.7647	3	20.37707	226.33
Faro	9.2632	2	1.78638	325.25
Guarda	8.7822	36	8.15821	268.35
Leiria	7.3743	37	4.95439	250.57
Lisboa	10.8313	10	9.47949	315.20
Portalegre	9.8011	5	4.10503	339.80
Porto	7.2777	11	6.63324	255.32
Santarém	9.8713	8	6.28496	321.44
Setúbal	12.5397	2	13.69318	332.50
Viana do Castelo	6.2500	1	-	204.00
Vila Real	5.0565	10	3.81664	184.95
Viseu	7.9214	29	6.70499	257.40
Total	9.3490	585	7.53752	

Kruskal-Wallis H	χ2	20.330	P	0.160
	df	15		

However, the more specific Individual comparable FA means were also used to compare districts of origin, through the application of the same test (Kruskal-Wallis H). The Individual comparable FA removes bilaterally absent traits from comparison. That impedes individual means to be affected by a lack or a greater amount of trait presence throughout the dental arcade. The results indicate the same conclusions, since there seems not to be any difference between district mean ranks: χ2 (15) = 18.084, P = 0.258 (see Table 4.2.11.).

Table 4.2.11. Mean Individual comparable FA, standard deviation, and mean rank for each district and Kruskal-Wallis H test results.

District of origin	Mean Individual comparable FA	n	Standard deviation	Mean rank
Aveiro	26.3874	16	23.82816	202.97
Braga	24.8512	4	16.96429	174.38
Castelo Branco	37.9630	9	35.13642	265.78
Coimbra	44.8742	402	28.25143	308.29
Évora	25.0000	3	43.30127	205.17
Faro	34.2857	2	8.08122	227.75
Guarda	42.7351	36	31.47811	290.36
Leiria	37.1408	37	23.50094	258.92
Lisboa	43.6905	10	31.10362	304.65
Portalegre	48.5000	5	20.61890	346.40
Porto	33.1494	11	27.24476	245.55
Santarém	35.0974	8	24.71784	262.31
Setúbal	55.5556	2	62.85394	330.50
Viana do Castelo	33.3333	1	-	215.50
Vila Real	37.9563	10	29.42015	266.90
Viseu	33.1373	29	25.78080	238.22
Total	42.3398	585	28.21367	

Kruskal-Wallis H	χ2	18.084	P	0.258
	df	15		

As was done before, in previous comparisons, some individuals were removed from the test in order to understand if those individuals yielding more comparable data are more informative, and provide different conclusions. The first such test excluded individuals with less than four bilaterally scorable traits. The results suggest there is definitely no difference between the mean ranks of birth districts: χ^2 (14) = 9.108, P =

Table 4.2.12. Mean Individual comparable FA, standard deviation, and mean rank for each district and Kruskal-Wallis H test results (with individuals with more than three comparable sites only).

District of origin	Mean Individual comparable FA (> 3 comparable sites)	n	Standard deviation	Mean rank
Aveiro	37.2198	10	19.16096	160.75
Braga	33.0357	2	6.31345	117.50
Castelo Branco	41.6667	5	27.63854	194.00
Coimbra	44.9366	272	20.70207	198.46
Évora	75.0000	1	-	358.50
Faro	34.2857	2	8.08122	129.25
Guarda	43.5898	20	19.76892	184.35
Leiria	42.7888	29	15.48625	180.47
Lisboa	50.8929	4	16.00515	247.75
Portalegre	47.5000	3	23.84848	225.67
Porto	40.5159	9	24.33265	179.89
Santarém	46.7965	6	14.08493	213.75
Setúbal	55.5556	2	62.85394	200.00
Vila Real	35.9127	5	13.67609	147.90
Viseu	38.1864	16	19.55243	165.66
Total	44.0900	386	20.28969	

Kruskal-Wallis H	χ^2	9.108	P	0.824
	df	14		

0.824 (see Table 4.2.12.).

When individuals with less than six bilaterally scorable traits are removed from analysis, similar conclusions are drawn, despite of a slightly lower P-value: χ^2 (14) = 12.836, P = 0.540 (see Table 4.2.13.).

The Portuguese continental districts were divided into three regions. The North region includes the districts of Aveiro, Braga, Guarda, Porto, Viana do Castelo, Vila Real and Viseu. The Centre region is composed of the districts of Castelo Branco, Coimbra, Leiria, Lisboa and Santarém. The South region encompasses the districts of Évora, Faro, Portalegre and Setúbal. These regions of origin were also compared in terms of mean Individual overall FA, through the use of the Kruskal-Wallis H statistic. This time, a difference was found between the mean ranks: χ^2 (2) = 11.084, P = 0.004 (see Table 4.2.14.). This statistically very significant result suggests DI could be greater

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Table 4.2.13. Mean Individual comparable FA, standard deviation, and mean rank for each district and Kruskal-Wallis H test results (with individuals with more than five comparable sites only).

District of origin	Mean Individual comparable FA (> 5 comparable sites)	n	Standard deviation	Mean rank
Aveiro	44.0247	8	13.37370	143.13
Braga	33.0357	2	6.31345	79.50
Castelo Branco	36.1111	3	37.57708	117.67
Coimbra	44.1226	202	17.71662	145.22
Évora	75.0000	1	-	269.50
Faro	28.5714	1	-	49.00
Guarda	37.4360	11	13.82323	107.27
Leiria	42.4227	21	14.77729	129.48
Lisboa	51.1905	3	19.58867	180.00
Portalegre	62.5000	1	-	245.50
Porto	34.1071	6	23.15453	110.33
Santarém	44.1558	5	13.98865	142.90
Setúbal	55.5556	2	62.85394	145.00
Vila Real	32.3909	4	12.91094	91.13
Viseu	43.7257	11	16.68651	145.14
Total	43.4475	281	17.81962	

Kruskal-Wallis H	χ^2	12.836	P	0.540
	df	14		

on the Centre and South regions. To determine specific differences between regions, pairwise comparisons were computed using the Mann-Whitney U test. The North and Centre regions were different to a high degree of confidence (U = 19819, P = 0.001). On the other hand, the North and South regions were not statistically distinguished (U = 506, P = 0.227), most likely due to the latter's small sample. Finally, the Centre and South regions were not different (U = 2754.5, P = 0.930). These results indicate people who were born in the North during the 19th and early to mid-20th centuries were likely to suffer from less DI than individuals born in the Centre of Portugal, which can indicate regional differences in access to resources.

Table 4.2.14. Mean Individual overall FA, standard deviation, and mean rank for each region and Kruskal-Wallis H test results.

Region of origin	Mean Individual overall FA	n	Standard deviation	Mean rank
North	7.4011	107	6.72108	243,95
Centre	9.7626	466	7.58862	303,88
South	10.6588	12	10.03117	307,79
Total	9.3490	585	7.53752	

Kruskal-Wallis H	χ^2	11.084	P	0.004
	df	2		

Such findings were again sought, through the application of the same tests to the Individual comparable FA data. The Kruskal-Wallis H test yielded significant results once again: χ^2 (2) = 8.113, P = 0.017 (see Table 4.2.15.). These figures, while not

Table 4.2.15. Mean Individual comparable FA, standard deviation, and mean rank for each region and Kruskal-Wallis H test results.

Region of origin	Mean Individual comparable FA	n	Standard deviation	Mean rank
North	35.5008	107	27.78588	251.33
Centre	43.9334	466	28.04786	302.68
South	41.4319	12	31.66211	288.67
Total	42.3398	585	28.21367	

Kruskal-Wallis H	χ^2	8.113	P	0.017
	df	2		

significant at a more conservative 99% degree of confidence, are still well over the 95% degree of confidence threshold. This underlines the previous findings. As for the Mann-Whitney U test, results were similar. The North and Centre regions were the only pair to differ (U = 20548, P = 0.004), while the North and South regions (U = 566, P = 0.499) and the Centre and South regions (U = 2668, P = 0.786) do not. Once again, the Northern and Central areas of Portugal seem to be different in developmental conditions, which may have caused a difference between individual FA percentages (when bilateral trait absences are excluded).

The removal of individuals with less than four bilaterally scorable traits, however, produced figures that suggest mean ranks not to be statistically divergent. The Kruskal-Wallis H test yielded results reinforcing the null hypothesis (absence of mean rank differences): χ^2 (2) = 3.421, P = 0.181 (see Table 4.2.16.). None of the Mann-Whitey U pairwise comparisons resulted in differences. The North and Centre regions (U = 8382.5, P = 0.072), the North and South regions (U = 203, P = 0.405), and the Centre and South regions (U = 1163, P = 0.699) were similar in mean rank, when considering their sample sizes.

Table 4.2.16. Mean Individual comparable FA, standard deviation, and mean rank for each region and Kruskal-Wallis H test results (with individuals with more than three comparable sites only).

Region of origin	Mean Individual comparable FA (> 3 comparable sites)	n	Standard deviation	Mean rank
North	39.7622	62	19.22935	169.98
Centre	44.7985	316	20.15960	197.65
South	49.6478	8	30.12305	211.75
Total	44.0900	386	20.28969	

Kruskal-Wallis H	χ^2	3.421	P	0.181
	df	2		

The individuals with less than six bilaterally scorable traits were also removed from comparison in further tests. When the differences between Individual comparable FA mean ranks for Portuguese regions were compared, the Kruskal-Wallis H test

produced the following results, similar to the most immediate precedent: χ^2 (2) = 3.368, P = 0.186 (see Table 4.2.17.). North and Centre (U = 4127, P = 0.098), North and South

Table 4.2.17. Mean Individual comparable FA, standard deviation, and mean rank for each region and Kruskal-Wallis H test results (with individuals with more than five comparable sites only).

Region of origin	Mean Individual comparable FA (> 5 comparable sites)	n	Standard deviation	Mean rank
North	39.1727	42	15.64126	121.60
Centre	43.9586	234	17.60657	143.85
South	55.4365	5	35.72465	170.80
Total	43.4475	281	17.81962	
Kruskal-Wallis H	χ^2	3.368	P	0.186
	df	2		

(U = 77, P = 0.331) and Centre and South (U = 464, P = 0.428) were consistently not different, when compared by the Mann-Whitney U statistic. Contrarily to the first two analyses, the following question the premise of regional difference in DI. Perhaps the differences seen between the mean Individual overall FA and the mean Individual comparable FA of the regions are merely coincidental, an artifact of the smaller samples of the North and South regions. When the individuals with the least complete dentitions are removed, that is suggested. On the other hand, the statistically significant differences found require further research, to determine the effect of comparing larger North (and South) samples to the Centre region, the better represented.

4.2.5. Fluctuating asymmetry differences between sexes in different places of origin

Ozener and Fink (2010) found male high school students from the slums of Ankara, Turkey, to have higher facial FA than females. The same difference was found for the urban sample, but was not statistically significant. This indicates that even within the same environment, there can be differences in the magnitude of sexual differences in FA. This can be informative of the cultural practices of a population or the sex-specific effects of DI.

The FA differences between sexes were found not to be random for the Coimbra sample (see above). However, the birthplace of an individual may have had an influence in the degree or direction of difference. That premise was tested by repeating the Z test to understand the FA independence of proportions between males and females for each

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district. Table 4.2.18. displays all the frequencies and their corresponding z-ratios, for Overall FA (which considers all bilaterally compared traits) and Comparable FA (excludes bilateral trait absences).

The sample includes individuals who were born in 16 different Portuguese continental districts, although some of these did not have a large enough sample (Braga and Vila Real) or did not have representation for one of the sexes (Évora, Faro, Portalegre, Setúbal and Viana do Castelo), which left nine districts to analyze.

Aveiro, Castelo Branco, Lisboa, Porto and Santarém have small samples. So, despite some interesting results, analyses are hindered. Aveiro shows low Overall FA results (F = 7.7%, M = 4.2%), with interesting differences in male and female FA proportions for Overall FA and Comparable FA (F = 40.7%, M = 21.7%). Castelo Branco also display seemingly large FA proportion differences for Overall FA (F = 9.9%, M = 8.0%) and Comparable FA (F = 47.8%, M = 40.0%), as do Porto (Overall FA: F = 8.4%, M = 5.8%; Comparable FA: F = 44.7%, M = 33.3%), and particularly Santarém (Overall FA: F = 14.1%, M = 7.2%; Comparable FA: F = 52.0%, M = 32.4%). While all these districts provide data which demonstrate larger FA frequencies for females, as found for the total Portuguese sample (see above), Lisboa displays the reverse: the female individuals have much lower FA frequencies than the male individuals (Overall FA: F = 7.7%, M = 19.6%; Comparable FA: F = 39.4%, M = 69.2%). The Overall FA Z test yielded results which indicate an independence of proportions (z = -2.389, P = 0.0169). However, since the sample number for each sex is small and the strength of the statistical test is most likely due to the consideration of number of sites as sample size, this result is questionable. The small Comparable FA sample hindered the computation of the Z test, which does not allow a confirmation or proper denial of the Overall FA comparison.

The Viseu sample is not as small as the previous ones; nonetheless, the Z test does not identify a statistically significant difference, either for Overall FA (F = 9.4%, M = 6.9%, z = 1.233, P = 0.2176) or for Comparable FA (F = 44.2%, M = 31.1%, z = 1.499, P = 0.1339), despite the relatively large differences.

On the other hand, the largest sample is precisely the one from Coimbra, with 402 individuals, 201 of each sex. The other two fairly large samples hail from the Guarda and Leiria districts. Table 4.2.18. shows the Coimbra sample corresponds to the results found for the total sample, which comprises every individual.

Table 4.2.18. Sex differences in Overall FA and Comparable FA, and respective z-ratios, for districts of origin.

District of origin	Overall FA	Comparable FA
Aveiro n (F) = 9 n (M) = 7	F: 7.7% (24/312) M: 4.2% (6/142) z-ratio = 1.585 P = 0.113	F: 40.7% (22/54) M: 21.7% (5/23) z-ratio = 1.599 P = 0.1098
Braga n (F) = 3 n (M) = 1	F: 5.3% (3/57) M: 10.8% (4/37) z-ratio = N/A P = N/A	F: 25.0% (3/12) M: 37.5% (3/8) z-ratio = N/A P = N/A
Castelo Branco n (F) = 4 n (M) = 5	F: 9.9% (12/121) M: 8.0% (7/87) z-ratio = 0.462 P = 0.6441	F: 47.8% (11/23) M: 40.0% (6/15) z-ratio = 0.474 P = 0.6355
Coimbra n (F) = 201 n (M) = 201	F: 10.4% (586/5649) M: 9.0% (558/6174) z-ratio = 2.454 P = 0.0141	F: 49.3% (563/1141) M: 42.2% (541/1283) z-ratio = 3.541 P = 0.0004
Évora n (F) = 0 n (M) = 3	F: - M: 15.0% (6/40) z-ratio = N/A P = N/A	F: - M: 60.0% (6/10) z-ratio = N/A P = N/A
Faro n (F) = 0 n (M) = 2	F: - M: 9.1% (4/44) z-ratio = N/A P = N/A	F: - M: 33.3% (4/12) z-ratio = N/A P = N/A
Guarda n (F) = 11 n (M) = 25	F: 7.9% (29/366) M: 8.1% (47/578) z-ratio = -0.114 P = 0.9092	F: 40.0% (26/65) M: 45.0% (45/100) z-ratio = -0.634 P = 0.5261
Leiria n (F) = 21 n (M) = 16	F: 9.3% (56/599) M: 7.3% (37/507) z-ratio = 1.225 P = 0.2206	F: 43.5% (54/124) M: 42.0% (37/88) z-ratio = 0.218 P = 0.8274
Lisboa n (F) = 7 n (M) = 3	F: 7.7% (14/182) M: 19.6% (9/46) z-ratio = -2.389 P = 0.0169	F: 39.4% (13/33) M: 69.2% (9/13) z-ratio = N/A P = N/A
Portalegre n (F) = 0 n (M) = 5	F: - M: 9.5% (14/148) z-ratio = N/A P = N/A	F: - M: 50.0% (12/24) z-ratio = N/A P = N/A
Porto n (F) = 8 n (M) = 3	F: 8.4% (17/203) M: 5.8% (6/103) z-ratio = 0.799 P = 0.4243	F: 44.7% (17/38) M: 33.3% (6/18) z-ratio = 0.81 P = 0.4179
Santarém n (F) = 3 n (M) = 5	F: 14.1% (13/92) M: 7.2% (12/167) z-ratio = 1.811 P = 0.701	F: 52.0% (13/25) M: 32.4% (11/34) z-ratio = 1.518 P = 0.129
Setúbal n (F) = 2 n (M) = 0	F: 11.3% (7/62) M: - z-ratio = N/A P = N/A	F: 46.7% (7/15) M: - z-ratio = N/A P = N/A
Viana do Castelo n (F) = 1 n (M) = 0	F: 6.3% (1/16) M: - z-ratio = N/A P = N/A	F: 33.3% (1/3) M: - z-ratio = N/A P = N/A

Table 4.2.18. (Continued.)

District of origin	Overall FA	Comparable FA
Vila Real n (F) = 2 n (M) = 8	F: 5.4% (3/56) M: 5.5% (13/235) z-ratio = N/A P = N/A	F: 42.9% (3/7) M: 36.4% (12/33) z-ratio = N/A P = N/A
Viseu n (F) = 20 n (M) = 9	F: 9.4% (48/511) M: 6.9% (16/239) z-ratio = 1.233 P = 0.2176	F: 44.2% (46/104) M: 31.1% (14/45) z-ratio = 1.499 P = 0.1339

Guarda, on the other hand, is a district where the differences found between male and female individuals could be random. The results for Overall FA (F = 7.9%, M = 8.1%, z = -0.114, P = 0.9092) and for Comparable FA (F = 40.0%, M = 45.0%, z = 0.634, P = 0.5261) are still interesting, because they show male individuals had higher FA frequencies. Further research into the Guarda district is required to understand if this difference is representative of the population; however, this underlines the possibility Coimbra could be a district where male individuals were beneficiated in resource access, or where males died at an early age, from exposure to DI (which has been demonstrated as unlikely). The Guarda district males, on the other hand, may have been affected by socio-cultural standards which granted females a broader access to resources important for their adequate development, when compared to them.

The Leiria district also contrasts with Coimbra, mainly in the Comparable FA differences. The Overall FA frequencies (F = 9.3%, M = 7.3%, z = 1.225, P = 0.2206), while large, could be uninformative due to sample size. The Comparable FA frequencies (F = 43.5%, M = 42.0%, z = 0.218, P = 0.8274) are small when compared to those of other samples, and yield an accordingly high P-value, which indicates FA is identical for males and females. This could also be due to the inexistence or lesser importance of socio-cultural differences in childcare and early gender role definition.

These results, with the exception of Coimbra, are preliminary and can only be further considered upon the analysis of more data. They still indicate a need for future investment in this area, as it could be highly informative in regards to Portuguese recent historical childcare standards.

The regions of origin of the individuals in the present sample were also considered as possible sources of more widely set distinctions in the sexual differences in FA. Table 4.2.19. displays the comparison between Overall FA and Comparable FA frequencies for males and females and the corresponding z-ratios.

The North region, despite the large (not statistically significant) difference in Overall FA frequencies (F = 10.1%, M = 6.9%, z = 1.28, P = 0.2005), presents closer Comparable FA frequencies for males and females (F = 41.7%, M = 37.4%, z = 0.975,

Table 4.2.19. Sex differences in Overall FA and Comparable FA, and respective z-ratios, for regions of origin.

Region of origin	Overall FA	Comparable FA
North n (F) = 54 n (M) = 53	F: 10.1% (125/1531) M: 6.9% (92/1334) z-ratio = 1.28 P = 0.2005	F: 41.7% (118/283) M: 37.4% (85/227) z-ratio = 0.975 P = 0.3296
Centre n (F) = 236 n (M) = 230	F: 10.3% (681/6643) M: 8.9% (623/6981) z-ratio = 2.632 P = 0.0085	F: 48.6% (654/1346) M: 42.1% (604/1433) z-ratio = 3.408 P = 0.0007
South n (F) = 2 n (M) = 10	F: 11.3% (7/62) M: 10.3% (24/232) z-ratio = 0.215 P = 0.8298	F: 46.7% (7/15) M: 47.8% (22/46) z-ratio = -0.078 P = 0.9378

P = 0.3296). The Centre region, with by far the largest sample, conveys non-random large differences for both Overall FA (F = 10.3%, M = 8.9%, z = 2.632, P = 0.0085) and Comparable FA (F = 48.6%, M = 42.1%, z = 3.408, P = 0.0007). The South region, with a very small sample (ten male and two female individuals), displays very similar frequencies for Overall FA (F = 11.3%, M = 10.3%, z = 0.215, P = 0.8298) and Comparable FA (F = 46.7%, M = 47.8%, z = -0.078, P = 0.9378).

The results for regional FA differences between males and females demonstrate Central Portugal may have been particularly prone to the often mentioned socio-cultural trend of providing preferential access to nutritional, health and habitat resources to male individuals, in detriment of female development. This contrasts with the North and South data, which have to be further enhanced so as to allow conclusive considerations.

4.2.6. Fluctuating asymmetry differences between "generations"

After reviewing data for Western countries (developed and less developed) and hunter-gatherer groups, Fenner (2005) suggested an overall human generation interval of 28 to 30 years or a conservative approach of 28 years, when intervals are not appropriate, which accounts for the past variation in generation intervals. The female and male generation intervals were also calculated by Fenner (2005), but population

divergence studies using autosomal or X-linked chromosomal genetic data should use the overall human generation interval, the mean number of years between successive generations including both male and female data.

Despite that Fenner's work focused on the determination of the number of generations that separate populations from a shared ancestor using genetic data, the definition of generation and its mean interval was adopted. The aim was to understand the changes in FA through time, so as to take advantage of the variation between birth years found on the Coimbra sample. Those individuals were born between 1820 and 1924, dates which spread over 100 years.

Each "generation" was defined as lasting 28 years. So, (a) Generation One (G1) is composed of individuals who were born between 1820 and 1847, (b) Generation Two (G2) is made up of those born between 1848 and 1875, (c) Generation Three (G3) is formed by people who came to life between 1876 and 1903, and (d) Generation Four (G4) comprised those which were born between 1904 and 1924 (which makes this generation shorter in span than the others, with a duration of 21 years as opposed to the usual 28).

These "generations" were compared in terms of the mean ranks of Individual overall FA of their samples. The Kruskal-Wallis H test was used: χ^2 (3) = 8.643, P = 0.034 (see Table 4.2.20.). This result is significant at the 95% level of confidence, which indicates only 5% likeliness that the differences among "generations" result from random sampling. Furthermore, it suggests that at least one of the generations may

Table 4.2.20. Mean Individual overall FA, standard deviation, and mean rank for each "generation" and Kruskal-Wallis H test results.

Generation	Mean Individual overall FA	n	Standard deviation	Mean rank
1	5.5403	13	5.95126	209.85
2	9.3815	96	9.61263	285.50
3	9.1587	294	7.78530	291.15
4	9.8258	194	5.76944	323.56
Total	9.3325	597	7.51171	

Kruskal-Wallis H	χ^2	8.643	P	0.034
	df	3		

present different proportions of DI than the others. In order to test that possibility, pairwise Mann-Whitney U tests were performed. Statistically significant results were only found for the comparisons between G1 and G4 (U = 756.5, P = 0.016), and G3 and G4 (U = 25389.5, P = 0.040). The mean Individual overall FA of G4 is higher than the

means of G1 and G3, which suggests individuals born after 1904 may have been more affected by DI than those from previous generations (although not significantly more than the G2).

The same analysis was performed with Individual comparable FA data. The Kruskal-Wallis H test provided different results: χ^2 (3) = 2.894, P = 0.408 (see Table 4.2.21.). This questions the preliminary conclusions drawn from the previous analysis.

Table 4.2.21. Mean Individual comparable FA, standard deviation, and mean rank for each "generation" and Kruskal-Wallis H test results.

Generation	Mean Individual comparable FA	n	Standard deviation	Mean rank
1	31.4103	13	31.84050	232.58
2	43.3333	96	35.37600	299.52
3	41.8353	294	29.23966	294.67
4	43.5511	194	21.63660	309.76
Total	42.4067	597	28.19852	
Kruskal-Wallis H	χ^2 df	2.894 3	P	0.408

Those individuals with less than four bilaterally scorable traits were removed prior to a re-analysis. The Kruskal-Wallis H test resulted in an even higher P-value: χ^2 (3) = 0.427, P = 0.935 (see Table 4.2.22.). This indicates there is as very low probability that the differences found are not due to a sampling error.

The individuals with less than six bilaterally scorable traits were also excluded. The Kruskal-Wallis H test provided a lower P-value, which is nonetheless well below the 95% level of confidence: χ^2 (3) = 3.965, P = 0.265 (see Table 4.2.23.). The lowered P-value is most likely the result of the very small samples of G1 and G2 used in the statistical test.

Table 4.2.22. Mean Individual comparable FA, standard deviation, and mean rank for each "generation" and Kruskal-Wallis H test results (with individuals with more than three comparable sites only).

Generation	Mean individual comparable FA (>3 comparable sites)	n	Standard deviation	Mean rank
1	48.3333	5	16.49916	228.80
2	44.5714	35	21.88923	198.54
3	44.4737	175	20.49536	197.20
4	43.7205	178	19.84886	195.61
Total	44.1904	393	20.22502	
Kruskal-Wallis H	χ^2 df	0.427 3	P	0.935

Despite the removal of potentially confounding data, in the latter three analyses, that dismissed the existence of FA (and DI) difference between the "generations", the

significant differences found for the first analysis remain unexplained. A test of the differences in mean ranks of ages at death of each "generation" was performed, to try to

Table 4.2.23. Mean Individual comparable FA, standard deviation, and mean rank for each "generation" and Kruskal-Wallis H test results (with individuals with more than five comparable sites only).

Generation	Mean individual comparable FA (>5 comparable sites)	n	Standard deviation	Mean rank
1	58.3333	2	11.78511	224.75
2	50.0000	16	18.65858	170.19
3	42.7393	127	17.84297	139.67
4	43.0161	140	17.40841	141.75
Total	43.3923	285	17.68456	
Kruskal-Wallis H	χ^2 = 3.965		P	0.265
	df = 3			

demonstrate once again how *ante-mortem* tooth loss and high mean wear levels may have influenced the results. A Kruskal-Wallis H test was performed: χ^2 (3) = 419.747, P = 0.000 (see Table 4.2.24.). The results state to a 99% level of confidence there is a

Table 4.2.24. Mean age at death, standard deviation, and mean rank for each "generation" and Kruskal-Wallis H test results.

Generation	Mean age at death	n	Standard deviation	Mean rank
1	78.85	13	13.297	577.62
2	56.78	96	14.453	491.70
3	37.73	294	8.728	350.29
4	19.74	194	5.030	107.24
Total	35.84	597	16.721	
Kruskal-Wallis H	χ^2 = 419.747		P	0.000
	df = 3			

difference between mean ages at death between the "generations". Pairwise Mann-Whitney U tests all resulted in very high statistically significant differences among age at death means (P = 0.000). Age at death is strongly negatively correlated to the "generation" number (Kendall's *tau*-b = -0.710, P = 0.000; Spearman's rho = -0.835, P = 0.000): between G1 and G4, ages at death diminish. These results demonstrate how only the most inclusive FA percentage, the Individual overall FA, provided significant differences. With the advance of age at death, the *ante-mortem* destruction or loss of teeth gave an increasing proportional relevance to the remaining scorable traits, to the point of becoming difficult to objectively compare older to younger individuals.

Gawlikowska and colleagues (2007) were surprised by greater FA levels in cranial measures on a modern sample (early 20th century), when compared to a medieval one from the same origin, Gródek, in Poland. This illustrates how in the early

20th century nutrition levels had not been much improved and how some other stressful environmental factors related to modernity could have caused an increase in FA levels in Poland. The maintenance of the FA level across the former tests of the present Portuguese sample should also testify to the general maintenance of DI levels along this period of time, between the early 19th to the early 20th century. Living conditions possibly remained constant along this period, although further research is necessary to allow for conclusive statements.

4.2.7. Fluctuating asymmetry differences between sexes in different "generations"

The "generations" were also compared in Overall FA and Comparable FA frequency differences between males and females. The Z test was performed to compare each "generation's" FA sex difference. Table 4.2.25. presents frequencies, proportions and z-ratios on each comparison.

Table 4.2.25. Sex differences in Overall FA and Comparable FA, and respective z-ratios, for "generation" of birth.

Generation	Overall FA	Comparable FA
G1 n (F) = 12 n (M) = 1	F: 6.0% (14/233) M: 13.3% (4/30) z-ratio = N/A P = N/A	F: 43.8% (14/32) M: 50.0% (4/8) z-ratio = N/A P = N/A
G2 n (F) = 53 n (M) = 43	F: 9.9% (105/1059) M: 7.7% (57/739) z-ratio = 1.604 P = 0.1087	F: 52.9% (100/189) M: 44.2% (53/120) z-ratio = 1.498 P = 0.1341
G3 n (F) = 139 n (M) = 155	F: 9.8% (362/3687) M: 8.3% (354/4267) z-ratio = 2.365 P = 0.018	F: 47.8% (351/734) M: 40.7% (339/833) z-ratio = 2.835 P = 0.0046
G4 n (F) = 96 n (M) = 98	F: 10.1% (350/3456) M: 9.1% (332/3637) z-ratio = 1.426 P = 0.1539	F: 46.0% (332/721) M: 42.1% (323/768) z-ratio = 1.55 P = 0.1211

G1 has a very small sample (12 females and one male) and did not allow the computation of the Z test. Therefore, it will not be further discussed.

The largest difference between males and females on Overall FA (F = 9.9%, M = 7.7%, z = 1.604, P = 0.1087) and Comparable FA (F = 52.9%, M = 44.2%, z = 1.498,

P = 0.1341) is displayed by G2; nevertheless, those differences are not statistically significant, because of the relatively small sample.

The only statistically demonstrated differences were provided by G3, the "generation" with the largest sample. The Overall FA (F = 9.8%, M = 8.3%, z = 2.365, P = 0.0018) and Comparable FA (F = 47.8%, M = 40.7%, z = 2.835, P = 0.0046) relay the possibility that individuals born on the late 19th century and turn of the 20th century were the most susceptible, or the most exposed, to DI.

The most recent individuals, from G4, display the most similar frequencies for Overall FA (F = 10.1%, M = 9.1%, z = 1.426, P = 0.1539) and Comparable FA (F = 46.0%, M = 42.1%, z = 1.55, P = 0.1211) alike.

The trend between G2 and G4 seems to be that of a progressive descent in the differences of both types of FA frequencies. The most recent "generation" (G4) was largely sampled and is not statistically significant in FA sex differences. G3, the largest sample, is statistically different. G2, while not statistically different, is the smallest of these three "generations" and may be affected by that. In order to fully state a valid conclusion more individuals from those years of birth must be added to the analysis.

Preliminarily, the results suggest that during the 19th and early 20th centuries childrearing habits changed progressively. Initially, families may have provided better access to developmental resources to male individuals; however, in later periods that preferential treatment may have been ceased or greatly reduced.

4.3.Sexual dimorphism and intertrait correlations

4.3.1. Sexual dimorphism

Sexual dimorphism is a common feature in animals, and especially in primates. Usually, this is expressed through size differences, not through shape. Simians, particularly the gorilla (*Gorilla gorilla*) and the orangutan (*Pongo pygmaeus*), but also the chimpanzee (*Pan troglodytes*), display a greater deal of sexual dimorphism, although this indicator is faint in humans (Wood *et al.*, 1991). Darwin explained some apparently unnecessary and costly features as the product of sexual selection. That works through the competition between males for the access of females and the selection by females of the most apt males. Although in other simians and in human evolution sexual dimorphism was great (up to 60% in gorillas and more than that in australopithecines), in *H. sapiens* it comes only to about 4-7%. The mandible is fairly affected, and the dentition is among the less conditioned structures. The inferior canine is the most affected, with 6.4% of sexual dimorphism in mesiodistal diameter, while the least dimorphic is the inferior central incisor (1.3%) (Rodríguez, 2003).

Sexual dimorphism was found between the proportion of dentine and enamel on mandibular canines and third premolars, showing the possible hormonal influence at the time of these crowns' formation (Saunders *et al.*, 2007). The Y chromosome enables tooth crown enamel and dentin growth, while the X chromosome is involved in enamel formation. The chromosomes display differential effects on growth, which can produce differences in traits such as the *tori*, for example (Alvesalo, 2013). This demonstrates the degree to which sexual dimorphism can be expressed on teeth. This is due to X and Y chromosomes being involved in enamel and dentine development. Even so, their influence is relatively small when it comes to sex dimorphism in nonmetric dental traits. This allows for the pooling of sexes when reporting a sample's frequencies, just like autosomal traits, to enhance the sample size. Sex dimorphism in dental morphologic characters occurs in some populations, for some traits, but the results are not usually consistent across populations. The exception is the distal accessory ridge of the canines, which is systematically dimorphic. The dimensions of the canines are also the most dimorphic in the definitive dentition (Scott and Turner, 1997).

Pearson's *chi*-square test was applied in cross tabulations comparing the proportion of each trait's grade for each sex. The results are presented on Table 4.3.1. Grade frequencies are displayed (using the tooth count method) for each sex when the

difference between them was statistically significant (P < 0.05 or P < 0.01). Twelve of the 61 traits (19.7%) displayed on the table have some degree of sexual dimorphism. Three of these display a very high statistical significance (P < 0.01), and the remaining nine still display a sufficiently high significance (P < 0.05), both usually accepted as thresholds bellow which the probability of the result being attributable to chance is very limited (1.0% and 5.0%, respectively).

The upper dental arch only has three dimorphic traits: UP4 accessory crests (P < 0.01) and UM1 and UM3 enamel extensions (both with P < 0.05). As for the lower dental arch, it harbors eight traits showing sexual dimorphism: distal accessory ridge (LC: P < 0.05), deflecting wrinkle (LM1: P < 0.01), groove pattern (LM1 and LM2: P < 0.05), distal trigonid crest (LM1 and LM2: P < 0.05), protostylid (LM2: P < 0.05) and MMPT (LM3: P < 0.01). The maxillary *torus* is not dimorphic, according to these results, and the mandible is dimorphic only in respect to the mandibular *torus*, as attested by the results found using both methods (P < 0.05).

Scott (1977) found sexual dimorphism in seven Native American and two European American samples for the canine distal accessory ridge, which is considered by Scott and Turner (1997) the single trait to be consistently dimorphic. The Coimbra sample only shows significant results for the lower canine (P < 0.05), with male frequency of 39.0% and female frequency of 31.9%. As for the upper canine, the opposite is found (M: 61.4%, F: 67.8%), but the difference is not relevant to a 95.0% degree of confidence. This is, however, an exception and therefore an example of the variability of dental morphology dimorphism found throughout populations.

Although in most populations the difference is not statistically significant, in others male individuals present greater frequency of Carabelli's trait than females (in the Canary Islands, for example). The contrary may also occur (Bermúdez de Castro, 1989). For example, Kondo and Townsend (2006) advise caution when using standardized observations to compare Carabelli's trait between groups, since Australians have been found to differ in the frequency and degree of expression among sexes. In the present Portuguese sample, Carabelli's trait is not statistically significantly dimorphic. The sexual dimorphism found for Carabelli's trait by Scott (1980) in several populations from diverse ethnic backgrounds was statistically demonstrated as occurring randomly as well. So, once again variability in dimorphism of dental

Table 4.3.1. Pearson's *chi*-square test for dimorphism between sexes on each trait, with grade frequencies when dimorphism occurs.

Trait and tooth (FDI)	Female grade frequencies	Male grade frequencies	Pearson's *chi*-square
Winging (11/21) + = ASU 1a-1b	-	-	$\chi2 = 1.024$ df = 1 P = 0.312
Shoveling (11/21) + = ASU 2-6	-	-	$\chi2 = 0.380$ df = 1 P = 0.537
Double shoveling (11/21) + = ASU 2-6	-	-	$\chi2 = 2.872$ df = 1 P = 0.090
Diastema (11/21) + = Irish (1998) > 0.5 mm	-	-	$\chi2 = 2.678$ df = 1 P = 0.102
Interruption grooves (11/21) + = ASU 1	-	-	$\chi2 = 0.294$ df = 1 P = 0.588
Interruption grooves (12/22) + = ASU 1	-	-	$\chi2 = 0.175$ df = 1 P = 0.675
Peg incisors (12/22) + = ASU 1-2	-	-	$\chi2 = 1.989$ df = 1 P = 0.158
Distal accessory ridge (13/23) + = ASU 1-5	-	-	$\chi2 = 2.532$ df = 1 P = 0.112
Accessory cusps (14/24) + = ASU 1	-	-	$\chi2 = 0.193$ df = 1 P = 0.660
Accessory crests (14/24) + = 1 (truncated ridges excluded)	-	-	$\chi2 = 0.268$ df = 1 P = 0.605
Tricuspid premolars (14/24) + = ASU 1	-	-	$\chi2 = 0.932$ df = 1 P = 0.334
Odontome (14/24) + = ASU 1	-	-	$\chi2 = 2.145$ df = 1 P = 0.143
Accessory cusps (15/25) + = ASU 1	-	-	$\chi2 = 1.122$ df = 1 P = 0.289
Accessory crests (15/25) + = 1 (truncated ridges excluded)	0: 83.6% (326/390) Mesial: 4.6% (18/390) Distal: 8.7% (34/390) Mesial/Distal: 2.8% (11/390) Medial: 0.3% (1/390)	0: 75.5% (275/364) Mesial: 4.9% (18/364) Distal: 11.3% (41/364) Mesial/Distal: 8.2% (30/364)	$\chi2 = 7.525**$ df = 1 P = 0.006
Tricuspid premolars (15/25) + = ASU 1	-	-	$\chi2 = 1.001$ df = 1 P = 0.317
Odontome (15/25) + = ASU 1	-	-	$\chi2 = 0.974$ df = 1 P = 0.324
Carabelli's trait (16/26) + = ASU 2-7	-	-	$\chi2 = 1.441$ df = 1 P = 0.230
C5 (16/26) + = ASU 2-5	-	-	$\chi2 = 0.201$ df = 1 P = 0.654
Mesial marginal accessory tubercles (16/26) + = Scott and Turner (1997) +	-	-	$\chi2 = 0.275$ df = 1 P = 0.600

Table 4.3.1. (Continued.)

Trait and tooth (FDI)	Female grade frequencies	Male grade frequencies	Pearson's *chi*-square
Enamel extensions (16/26) + = ASU 1-3	0: 95.3% (304/319) 1: 1.9% (6/319) 2: 0.3% (1/319) 3: 2.5% (8/319)	0: 98.5% (259/263) 1: 0.0% (0/263) 2: 0.8% (2/263) 3: 0.8% (2/263)	χ2 = 4.620* df = 1 P = 0.032
C4 (17/27) + = ASU 3-5	-	-	χ2 = 1.057 df = 1 P = 0.304
Enamel extensions (17/27) + = ASU 1-3	-	-	χ2 = 2.110 df = 1 P = 0.146
Enamel extensions (18/28) + = ASU 1-3	0: 90.9% (149/164) 1: 4.3% (7/164) 2: 4.3% (7/164) 3: 0.6% (1/164)	0: 96.5% (165/171) 1: 0.0% (0/171) 2: 2.9% (5/171) 3: 0.6% (1/171)	χ2 = 4.528* df = 1 P = 0.033
Parastyle (18/28) + = ASU 1-6	-	-	χ2 = 0.225 df = 1 P = 0.635
Shoveling (31/41) + = ASU 2-6	-	-	N/A
Shoveling (32/42) + = ASU 2-6	-	-	N/A
Distal accessory ridge (33/43) + = ASU 1-5	0: 68.1% (301/442) 1: 22.6% (100/442) 2: 7.7% (34/442) 3: 1.6% (7/442)	0: 61.0% (255/418) 1: 17.5% (73/418) 2: 17.0% (71/418) 3: 4.5% (19/418)	χ2 = 5.182* df = 1 P = 0.023
Odontome (34/44) + = ASU 1	-	-	N/A
Lingual cusp number (34/44) + = ASU 2-9	-	-	χ2 = 0.018 df = 1 P = 0.894
Odontome (35/45) + = ASU 1	-	-	χ2 = 2.227 df = 1 P = 0.136
Lingual cusp number (35/45) + = ASU 2-9	-	-	χ2 = 0.254 df = 1 P = 0.614
Deflecting wrinkle (36/46) + = ASU 1-3	0: 92.3% (274/297) 1: 4.4% (13/297) 2: 2.4% (7/297) 3: 1.0% (3/297)	0: 97.1% (335/345) 1: 1.4% (5/345) 2: 1.4% (5/345) 3: 0.0% (0/345)	χ2 = 7.580** df = 1 P = 0.006
Anterior fovea (36/46) + = ASU 1-4	-	-	χ2 = 0.681 df = 1 P = 0.409
Groove pattern (36/46) + = ASU Y	Y: 89.9% (303/337) X: 10.1% (34/337)	Y: 94.0% (358/381) X: 6.0% (23/381)	χ2 = 3.929* df = 1 P = 0.047
Distal trigonid crest (36/46) + = ASU 1	0: 96.7% (323/334) 1: 3.3% (11/334)	0: 98.9% (376/380) 1: 1.1% (4/380)	χ2 = 4.293* df = 1 P = 0.038
Protostylid (36/46) + = ASU 1-7	-	-	χ2 = 0.180 df = 1 P = 0.671
MMPT (36/46) + = Weets (2009) [adpt.] 1-'3+'	-	-	χ2 = 1.356 df = 1 P = 0.244
Cusp number (36/46) + ~= ASU 5	-	-	χ2 = 0.445 df = 1 P = 0.505
C5 (36/46) + = ASU 1-5	-	-	χ2 = 0.284 df = 1 P = 0.594

Table 4.3.1. (Continued.)

Trait and tooth (FDI)	Female grade frequencies	Male grade frequencies	Pearson's *chi*-square
C6 (36/46) + = ASU 1-5	-	-	$\chi^2 = 0.004$ df = 1 P = 0.951
C7 (36/46) + = ASU 1-4	-	-	$\chi^2 = 3.436$ df = 1 P = 0.064
Groove pattern (37/47) + = ASU +/X	Y: 31.1% (127/408) X: 68.9% (281/408)	Y: 23.3% (98/421) X: 76.7% (323/421)	$\chi^2 = 6.456^*$ df = 1 P = 0.011
Distal trigonid crest (37/47) + = ASU 1	0: 95.4% (392/411) 1: 4.6% (19/411)	0: 98.3% (415/422) 1: 1.7% (7/422)	$\chi^2 = 6.050^*$ df = 1 P = 0.014
Protostylid (37/47) + = ASU 1-7	0: 90.8% (385/424) 1: 6.4% (27/424) 2: 2.1% (9/424) 3: 0.0% (0/424) 5: 0.2% (1/424) 7: 0.5% (2/424)	0: 85.2% (363/426) 1: 9.2% (39/426) 2: 2.1% (9/426) 3: 3.1% (13/426) 5: 0.5% (2/426) 7: 0.0% (0/426)	$\chi^2 = 6.546^*$ df = 1 P = 0.011
MMPT (37/47) + = Weets (2009) [adpt.] 1-'3+'	-	-	$\chi^2 = 1.651$ df = 1 P = 0.199
Cusp number (37/47) + ~= ASU 4	-	-	$\chi^2 = 2.590$ df = 1 P = 0.108
C5 (37/47) + = ASU 1-5	-	-	$\chi^2 = 2.412$ df = 1 P = 0.120
C6 (37/47) + = ASU 1-5	-	-	$\chi^2 = 0.130$ df = 1 P = 0.718
C7 (37/47) + = ASU 1-4	-	-	$\chi^2 = 1.972$ df = 1 P = 0.160
Groove pattern (38/48) + = ASU Y	-	-	$\chi^2 = 0.357$ df = 1 P = 0.550
Distal trigonid crest (38/48) + = ASU 1	-	-	$\chi^2 = 0.425$ df = 1 P = 0.514
Protostylid (38/48) + = ASU 1-7	-	-	$\chi^2 = 0.225$ df = 1 P = 0.635
MMPT (38/48) + = Weets (2009) [adpt.] 1-'3+'	0: 69.7% (186/267) 1: 20.2% (54/267) 1-2: 2.2% (6/267) 2: 3.7% (10/267) 2-3: 1.9% (5/267) 3: 0.7% (2/167) 3+: 1.5% (4/267)	0: 83.7% (242/289) 1: 13.5% (39/289) 1-2: 1.7% (5/289) 2: 0.7% (2/289) 2-3: 0.3% (1/289) 3: 0.0% (0/289) 3+: 0.0% (0/289)	$\chi^2 = 15.512^{**}$ df = 1 P = 0.000
Cusp number (38/48) + ~= ASU 4	-	-	$\chi^2 = 0.351$ df = 1 P = 0.553
C5 (38/48) + = ASU 1-5	-	-	$\chi^2 = 1.759$ df = 1 P = 0.185
C6 (38/48) + = ASU 1-5	-	-	$\chi^2 = 2.937$ df = 1 P = 0.087
C7 (38/48) + = ASU 1-4	-	-	$\chi^2 = 1.131$ df = 1 P = 0.288

Table 4.3.1. (Continued.)

Trait and tooth (FDI)	Female grade frequencies	Male grade frequencies	Pearson's *chi*-square
Foramina mentales + = 2+	-	-	χ2 = 0.270 df = 1 P = 0.603
Mylohyoid bridge + = Incomplete-Complete bridge	-	-	χ2 = 2.212 df = 1 P = 0.137
Mandibular *torus* (ASUDAS) + = 1-3	0: 77.7% (233/300) 1: 18.7% (56/300) 2: 3.7% (11/300)	0: 85.6% (256/299) 1: 11.4% (34/299) 2: 3.0% (9/299)	χ2 = 6.317* df = 1 P = 0.012
Mandibular *torus* (Galera *et al.*, 1995) + = Débil-Fuerte	Ausente (Absent): 77.7% (233/300) Débil (Weak): 16.7% (50/300) Medio (Medium): 5.3% (16/300) Fuerte (Strong): 0.3% (1/300)	Ausente (Absent): 85.6% (256/299) Débil (Weak): 10.4% (31/299) Medio (Medium): 4.0% (12/299) Fuerte (Strong): 0.0% (0/300)	χ2 = 6.317* df = 1 P = 0.012
Maxillary *torus* (ASUDAS) + = 1-4	-	-	χ2 = 0.135 df = 1 P = 0.713
Maxillary *torus* (Galera *et al.*, 1995) + = Débil (inc.)-Fuerte (compl.)	-	-	χ2 = 0.322 df = 1 P = 0.570

*: P <= 0.05; **: P <= 0.01.

nonmetric traits is demonstrated, and Kondo and Townsend's (2006) advice seems unwarranted.

Positive (cusp-like) manifestations of Carabelli's trait are more likely to be expressed in larger teeth, since their greater formation time allows for the fifth enamel knot to produce the infolding of the inner enamel epithelium, thus forming the cusp. Smaller teeth may present only the reduced form of the trait, such as pits or grooves. This may explain the difference in frequencies and expression between male and female individuals of the same population (Kondo and Townsend, 2006). Besides the probable meaninglessness of the exclusion of this (or any other) trait for sexual dimorphism, this find may be due to a choice of breakpoint, as stated by the authors themselves.

In the present author's opinion, it is random and unwise to proceed to elimination of results or separation of sexes. The inclusion of all traits in the analysis of biological relationships between populations using dental morphology seems justified, since this variability allows for biological identification of populations or groups, as a part of it, expressed in the pooled sexes' frequency for each sample. The fact that the present sample is balanced, with 300 individuals of each sex, makes for a better representation of the population as a whole. But, if an uneven number of individuals of each sex were used, the error margin would not be large and the statistical comparison

of biological relatedness would most likely cluster the sexes together, if they were separated. Despite the occasionally significant difference between the sexes, when compared to other, clearly distinct populations, the frequencies' disparity is meaningless.

The same population was studied for metric trait sexual dimorphism by Galera and Cunha (1993), who found some dimorphism in several dental pieces. This dimorphism has little expression, as found for the dental discrete characters, which show only negligible differences. Contemporary Portuguese, however, show statistically significant dimorphism in metric traits recorded on upper incisors and canines, with 3.4% dimorphism for UI1, 5.7% for UI2 and 5.3% for UC (Pereira *et al.*, 2010b).

Deciduous nonmetric traits of Pima Indians' teeth seem to not display evidence of sexual dimorphism, which was not statistically detected within a 95% confidence level. The most dimorphic trait (C7 on the second lower deciduous molar) displayed a difference of 13.8%, which was not detected due to small sample size, most likely. The present sample's most dimorphic trait is not included in the ASUDAS method and will not be included on biological affinity analyses when using other authors' data (LM3 MMPT), and displayed a difference of 14.0% ($P < 0.01$). The most dimorphic trait included in ASUDAS was UP4 accessory crest. It was not recorded with the aid of the most recently introduced ASUDAS methodology (Burnett *et al.*, 2010), unavailable to the author at the time of the observations, which could have affected results due to the exclusion of truncated crests as present in the current analysis. The following dimorphisms found correspond to differences of 7.8% (LM2 groove patter) and 7.9% (mandibular *torus*) between the sexes. Despite the sample sizes allowing dimorphism to be statistically detectable, this illustrates the small degree to which it is present and the lack of biological importance it has when a large battery of traits are compared.

It is standard ASUDAS protocol to pool the sexes (Irish and Guatelli-Steinberg, 2003), since sexual dimorphism is generally low and varies throughout populations (as mentioned above) and is thus expected to be representative of their biological identity.

4.3.2. Trait correlations

The existence of correlations between trait pairs are known as a hindrance in the study of biological affinities that use a set of traits, since statistical tests (particularly

MMD) assume traits are not correlated (Edgar, 2004; Irish, 2010). Berry (1976) described dental morphological traits as useful in the measure of distance between populations, though only when variants are not correlated and the effects of a single variant do not compress the whole of the variation.

Correlation between trait expression on a tooth and its expression on other teeth of the same type (and so with the potential to express said trait) is expected and has been found across populations (Scott and Turner, 1997). The teeth of mice and voles displayed gene controlled positioning of cusp tips, from the original enamel knots, since a very early developmental stage. Evolution of a different cusp spatial organization occurs by changing the position of the signaling genes coordinating cusp formation, which may consequently alter the formation of such discrete variables as crests or patterns (Jernvall *et al.*, 2000). If this is valid for *H. sapiens*, the occurrence of some traits may be the catalyst needed for the formation of others.

Later research addressed this issue in modern humans, primates and other hominins. Carabelli's trait expression is possibly correlated to small intercuspal distances, when related to tooth size, in Ohio individuals (Hunter *et al.*, 2010). Results found by Moormann and colleagues (2013), comparing Carabelli's trait, hypocone and upper molar accessory cusps, suggest dental traits could be correlated. Findings related the presence of C6 on the lower molars of chimpanzees with smaller intercuspal distances (Skinner and Gunz, 2010).These results are in line with the patterning cascade model of odontogeny (Jernvall and Jung, 2000; Salazar-Ciudad and Jernvall, 2010). This predicts interplay between genotype and phenotype, and the importance of morphology during development to a tooth's definitive shape, is explained through a morphodynamic model. According to it, intercuspal distances define the possibility of the formation of new enamel knots, and generate new dental nonmetric traits (Salazar-Ciudad and Jernvall, 2002; 2010). See Guatelli-Steinberg and colleagues (2013) for a review of the authors' contribution on the study of the patterning cascade model influence on Carabelli's trait expression and intertrait correlation.

Various other associations have also been described (see below). So, in order to allow for the best biological affinity analyses possible, correlations from all possible trait pairs were investigated, with 1830 comparisons made (results not shown), using the rank correlation coefficient Kendall's *tau*.

From these comparisons, only five produced *tau* values above 0.4, showing moderate to strong associations. Four of these were expected, since they involve related

traits. LM2 cusp number and C5 were very strongly correlated (*tau* = 0.927; P = 0.000; n = 491), as were these traits on LM3 (*tau* = 0.719; P = 0.000; n = 367). These same traits were associated with a *tau* coefficient nearing 0.4 on LM1 as well (*tau* = 0.393; P = 0.000; n = 423). Cusp number and C6 were strongly associated on LM1 (*tau* = 0.427; P = 0.000; n = 424) and LM3 (*tau* = 0.606; P = 0.000; n = 367). Evidently, the number of cusps present in a tooth correlate with the presence of cusps which are independently scored as well, because of their greater variability. In fact, the presence of these cusps (C5 and C6) in a molar in any of the grades of presence (grades 1-5) causes a change in the cusp number of said molar.

The presence of a UP3 odontome is very strongly correlated with the presence of the same trait on UP4 (*tau* = 0.706; P = 0.000; n = 430). This is due to the fact this trait only presents itself twice in 487 individuals on the UP3, and once on the UP4 (in 489 individuals), and a single individual presents the trait in both upper premolars, displaying two of the total three trait presences. Due to the small presence of this trait throughout the world (Scott and Turner, 1997), and the reasonable likelihood of the genotype with the potential to express odontomes generating two phenotypically identical teeth in the same field, this situation does not seem able to provoke statistical inaccuracies.

The only unexpected weak to moderate correlation was found between UP3 accessory cusps and the LM2 C6 (*tau* = 0.309; P = 0.000; n = 407). Since the accessory cusps different locations (mesial or distal) or location combinations (mesial/distal) are coded with digits, this correlation may be accidentally caused by a correlation between the grades (0-5) composing the distribution of C6 and these digits (0-3). This artifact should not affect biological affinity analyses.

There is trait association between several instances of shoveling, suggesting the use of only one key tooth in evaluating this trait, so as to not disturb statistical analysis (Tocheri, 2002). The only Coimbra sample's moderately correlated pair is shoveling on the lower incisors (*tau* = 0.384; P = 0.000; n = 340). Associations between shoveling on UI1 and LI1 (*tau* = 0.270; P = 0.000; n = 192) and LI2 (tau = 0.155; P = 0.023; n = 212) are much weaker. These results do not justify the removal of any of these traits, since *tau* values are lower than a relatively conservative 0.4 and much lower than a very strong association of 0.6, for example.

Scott (1977) found correlation between upper and lower canine distal accessory ridges in 7 out of 8 samples, but considered Kendall's *tau* of between 0.2 and 0.4 as a

sufficiently strong association. The present author only considers those yielding *tau* values above 0.4 as relevant associations, and the result for the correlation between these traits is only 0.206 (P = 0.000; n = 415).

Pechenkina and Benfer (2002) state there is some correlation between lingual mandibular exostoses and buccal maxillary exostoses and both are correlated to temporomandibular joint pathology. The association between mandibular *torus* and palatine *torus* is very weak in the Coimbra sample (*tau* = 0.123; P = 0.02; n = 595). This indicates that these exostoses may in fact be independently formed, either resulting from different gene control or differently influenced by environment (or a combination of these factors, in the likely case these are other quasicontinuous, threshold traits).

The UM1 and UM2 hypocone and Carabelli's trait were found to correlate across six Southwest American Indian samples, mainly the hypocone on either molar and UM1 Carabelli's trait (Scott, 1979a). Carabelli's trait reveals a slight correlation with intercuspal distances in upper first molars, and an indication of the same trend on upper second molars. In the latter tooth, correlations could be hindered by tooth size and shape. In this study, UM1 Carabelli's trait also correlates with hypocone, since larger expressions of the latter cusp are associated with greater expressions of Carabelli (Moormann *et al.*, 2013).

In the present sample, only UM1 Carabelli's trait and the UM2 hypocone were scored. The association between them is weak (*tau* = 0.179; P = 0.000; n = 443). This hampers the suggestion underlined by Scott (1979a) that the progressive reduction of molar sizes was represented and paralleled by these traits. The hypocone is present (+ = ASU 3-5) in 58.4% and expressed on 87.2% (ASU 1-5) of this Portuguese sample, and the Carabelli's trait is present on 22.5% (+ = ASU 2-7; if + = ASU 5-7: 6.1%) and expressed in 51.1% of the individuals (ASU 1-7).

UM1 Carabelli's trait was found to correlate to upper molar accessory cusps, when a moderate number of these are present. The associations found (this one and the correlation between Carabelli's trait and hypocone, mentioned above) by Moormann and colleagues (2013) are explained by the patterning cascade model: cusp ontogeny is possible due to an approximation of enamel knots, but the formation of a great number of new knots can hinder the formation of Carabelli's trait; on the other hand, the latter may be associated with a few number of extra cusps or with large hypocone expressions if their development still allows the formation of that mesiolingual enamel knot (Moormann *et al.*, 2013).

The present sample yielded a very weak correlation (*tau* = 0.021; P = 0.619; *n* = 457) between Carabelli's trait and mesial marginal accessory tubercles, yet it was non-significant and the number of tubercles found was not considered (the most found were the protoconule and the mesial accessory tubercle). Kangas and colleagues (2004) also found a single protein can affect several dental morphologic traits, relating to intercuspal distance and exuberance in tooth morphology. According to them, this brings to question the independence of dental traits, mainly when used in phylogenetic classification (see also Skinner and Gunz, 2010). The authors, however, recognized the potential for individual traits to be independently affected by other gene activities, and merely advised caution in assuming independence of traits when comparing different species (Kangas *et al.*, 2004).

Images provided alongside the work of Skinner and colleagues (2008, 2009) and their consideration of protostylid as a crest or a set of crests that involve not only the protoconid, but also the hypoconid, seem to include the MMPT as a part of a protostylid complex trait, present in several taxa. Hlusko (2004) considers a more mesial cingular remnant to not covary with the protostylid, and therefore to be a different trait. The MMPT (proposed by Weets [2009]) is described and its variation divided by grades that record this most mesial cingular derivative. These protostylid and MMPT crests as seen either on the outer enamel surface or the enamel-dentine junction, are not visibly connected (see images provided by Skinner and colleagues [2008, 2009]). This suggests the MMPT is a physically independent trait.

Table 4.3.2. displays the Kendall's *tau* correlation values for the MMPT and the protostylid. With the exceptions of the protostylid on LM1 and LM3 and the MMPT and protostylid on LM2, the correlations are lower between these traits than among

Table 4.3.2. Correlations between and among the MMPT and Protostylid on lower molars. Kendall's *tau* values are above the divide and P and n (number of individuals) values are under it.

	LM1 MMPT	LM2 MMPT	LM3 MMPT	LM1 Protostylid	LM2 Protostylid	LM3 Protostylid
LM1 MMPT		0.157	0.119	0.061	0.077	0.065
LM2 MMPT	P = 0.002 n = 384		0.107	0.021	0.101	0.020
LM3 MMPT	P = 0.048 n = 257	P = 0.052 n = 306		0.063	0.046	0.020
LM1 Protostylid	P = 0.213 n = 419	P = 0.683 n = 385	P = 0.289 n = 259		0.199	0.043
LM2 Protostylid	P = 0.124 n = 383	P = 0.023 n = 484	P = 0.396 n = 304	P = 0.000 n = 386		0.192
LM3 Protostylid	P = 0.301 n = 252	P = 0.719 n = 301	P = 0.697 n = 342	P = 0.493 n = 254	P = 0.001 n = 300	

them, when they are compared from one tooth to the next. In general, all correlations are very weak to moderately weak. This suggests these are independent traits and should be treated as such. More research must be conducted before the MMPT can be introduced into a method as the ASUDAS. Nonetheless, its correlation with protostylid, at least from what is gathered from this sample, seems not be an issue of concern.

In conclusion, it must be remarked this is a sample with very low correlations throughout, since only about a dozen correlations are remotely notable within 1830 paired traits tested. This allows for the use of most variation to be regarded as unique and expressing, through phenotype, a different aspect of the genotype of the Portuguese population. Biological affinity analyses benefitted from this, as it allow for a greater expression of diversity to be found between this and other population groups.

4.4.Dental and oral nonmetric traits

4.4.1.Introduction to dental traits

Dental nonmetric traits have been deeply contextualized, through a review of their research history and their importance (see 1.Introduction). The first part of the present chapter will be devoted to the reproduction of the present study's results for each dental morphological trait, and to the *ad hoc* comparison of each result to a set of results from other populations which are somewhat similar. This exercise means to show each trait's specificity in the identification of the present sample's biological origin, and unveil the occasionally wide spread of similar trait frequencies.

4.4.2.Dental nonmetric traits

Winging

Table 4.4.1. Frequencies of winging in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 1a-1b	1.9% (385)
	Coimbra (Portugal)	1a: 0.3% 1b: 1.6% 2: 1.8% 3: 91.4% 4: 4.9%
Scott and Turner, 1997 + = ASU 1a-1b	Western Europe	7.2% (180)
	Northern Europe	4.7% (150)
	North Africa	7.5% (460)
	South Africa	4.2% (496)
	New Guinea	7.6% (170)

1a: bilateral winging >20º; 1b: bilateral winging <20ª; 2: unilateral winging; 3: straight; 4: counter-winging.

Winging, or "bilateral mesial rotation", can occur because of crowding but is primarily found in dentitions that display sufficient space (Dahlberg, 1963). Because of its potential relation to crowding, it is considered taxonomically less valuable and useful only in intra-group, and not in inter-group, comparisons by Rodríguez (2003). Counter-winging and unilateral winging, on the other hand, are often related to overcrowding (Scott, 2008), which justifies their consideration as trait absence.

It is present in only 1.9% of the Coimbra sample, and similar frequencies are still much higher in frequency (Table 4.4.1.). The ones nearest this Portuguese

population are South Africa (4.2%) and Northern Europe (4.7%). The remaining close samples (Western Europe, North Africa and New Guinea) are all above 7.0%.

Shoveling (upper central incisor and lower incisors)

Table 4.4.2. Frequencies of shoveling in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UI1 + = ASU 2-6	2.3% (262)
	Coimbra (Portugal) UI1 + = ASU 3-6	0.0% (262)
	Coimbra (Portugal) LI1 + = ASU 2-6	0.0% (363)
	Coimbra (Portugal) LI1 + = ASU 1-6	2.5% (363)
	Coimbra (Portugal) LI2 + = ASU 2-6	0.0% (434)
	Coimbra (Portugal) UI1	0: 85.9% 1: 11.8% 2: 2.3%
	Coimbra (Portugal) LI1	0: 97.5% 1: 2.5%
	Coimbra (Portugal) LI2	0: 96.8% 1: 3.2%
Scott and Turner, 1997 UI1: + = ASU 3-6	Western Europe	2.7% (186)
	Northern Europe	2.2% (46)
	New Guinea	0.0% (30)
Willermet and Edgar, 2009 LI1: + = ASU 1-6	Western European (3rd-18th century)	3.4% (276)

Lasker (1950) deemed shoveling a genetically determined trait for incisors, with other morphological variables from these teeth (such as ridges and tubercles) lacking sufficient research at the time. Family studies have shown high heritability for shoveling (Hillson, 1996). It can occur only in the distal or the mesial margin of an incisor, and so can be treated as two different variables (Scott, 2008).

Mizoguchi (2013), who proposes world frequency variation of dental traits to be due to natural selection, found shoveling to portray a positive association with latitude and a negative association with temperature and subsistence strategies focusing on milking.

Shoveling on the lower lateral incisors is one of the few dental discrete variables which are correlated between deciduous and permanent dentitions (Edgar and Lease, 2007).

This trait is considered an anomaly in Caucasian populations, alongside several other traits or expressions thereof, which renders it useful in kinship studies (Alt and Türp, 1998). Despite that, its usefulness in forensic context is limited when the trait is used on its own (Edgar, 2009a).

In the Portuguese presently studied the trait is rare, always below 3.0% on every incisor analyzed (see Table 4.4.2.). Only European and New Guinean samples display similar frequencies. Upper central incisor frequency for the Coimbra sample is 0.0% (+ = ASU 3-6), equivalent to New Guinea and near Western Europe (2.7%) and Northern Europe (2.2%) samples. The lower central incisor (+ = ASU 1-6) presents frequencies of 2.5% on Portuguese individuals, comparable to historic Western Europeans (3.4%).

Double shoveling (upper central incisors)

Table 4.4.3. Frequencies of double shoveling in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 2-6	0.8% (250)
	Coimbra (Portugal)	0: 97.6% 1: 1.6% 3: 0.4% 4: 0.4%
Scott and Turner, 1997 + = ASU 2-6	Western Europe	3.8% (184)
	Northern Europe	5.0% (100)
	West Africa	2.6% (39)
	South Africa	1.8% (282)
	Khoikhoi	0.0% (79)
	Jomon	1.4% (138)
	Polynesia	4.5% (287)
	Australia	4.2% (261)
	New Guinea	0.0% (32)

Double shoveling is the formation of prominent marginal ridges on the labial surface of incisors and canines (Hillson, 1986). It can also be divided into mesial and distal manifestations, since they can occur independently (Scott, 2008).

Double shoveling is very rare among the Coimbra sample, occurring only on 0.8% of the individuals (Table 4.4.3.). Despite there are some relatively low frequencies

from Europeans populations (Western and Northern Europe), the nearest are from Khoikhoi and New Guinea (0.0%), and the Japanese Jomon (1.4%).

Midline diastema

Table 4.4.4. Frequencies of midline diastema in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = Irish (1998b) > 0.5 mm	10.6% (218)
Irish, 1998b + = Irish (1998b) > 0.5 mm	Chad	12.5% (24)
	Nigeria/Cameroon	9.1% (44)
	San	10.3% (87)
	Togo/Benin	10.5% (19)
	Tukulor	10.3% (29)
	Bedouin	8.8% (34)
	Kabyle (Algeria)	12.0% (25)
	Meroitic (Nubia)	10.0% (20)

The midline diastema is not a physiological primate space, as the ones displayed by pongides, although it is an anomaly when present for life (after the eruption of canines) and is hereditary (Alt and Türp, 1998).

The maxillary midline diastema decreased in frequency from ages 6 (64.6%) to 12 years (14.3%) in Taiwanese children. The decrease with age was more accentuated in female individuals, since it is connected to the eruption of lateral incisors and canines, which is faster in girls (Liu *et al.*, 2013). This underlines the possibility its remainder for life is genetically determined.

In Portuguese individuals from the 19th and 20th centuries, this trait was present 10.6% of the time. This figure is comparable to several of the African populations reported on by Irish (1998b; see Table 4.4.4.), particularly San (10.3%), Togo/Benin (10.5%) and Tukulor (10.3%).

Table 4.4.5. Frequencies of interruption grooves in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UI1 + = ASU 1	4.3% (358)
	Coimbra (Portugal) UI2 + = ASU 1	17.3% (452)
	Coimbra (Portugal) UI1	0: 95.7% Mesial: 2.0% Distal: 0.6% Mesial/Distal: 0.3% Medial: 2.5%
	Coimbra (Portugal) UI2	0: 82.7% Mesial: 4.6% Distal: 9.5% Mesial/Distal: 0.4% Medial: 2.7%
Scott and Turner, 1997 UI2: + = ASU 1	Khoikhoi	15.7% (83)
	Australia	18.2% (357)
	New Guinea	15.1% (56)
	Melanesia	18.8% (165)

The interruption groove is a crown-root groove (Hillson, 1986). It may be a facilitator of periodontal disease, due to allowing food to be captured and bacteria to penetrate the radicular surfaces (Soto *et al.*, 2010).

It is present on 4.3% of Portuguese individuals on upper central incisors and on 17.3% on upper lateral incisors (Table 4.4.5.). The latter frequency resembles those found on the UI2 of Khoikhoi (15.7%), Australians (18.2%), New Guineans (15.1%) and Melanesians (18.8%).

Peg-shaped upper second incisor

Peg-shaped incisors are microdonts (notably small teeth; Alt and Türp, 1998). A peg is the result of a progressive reduction of the lateral incisor, which probably culminates in tooth agenesis (Turner *et al.*, 1991).

Table 4.4.6. Frequencies of peg-shaped second incisors in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 1-2	3.5% (492)
	Coimbra (Portugal)	0: 96.5% 1: 2.3% 2: 1.2%
Manzi *et al.*, 1997 + = ASU 1-2	*Lucus Feroniae* (Roman Empire Italy)	1.7% (58)
	Portus (Roman Empire Italy)	0.0% (33)
Pereira, 2009 + = ASU 1-2	Lisbon (18th century; tooth count method)	5.3% (76)
Al Oumaoui, 2009 + = ASU 1-2	Bronze Age and Medieval Spain (12 sites)	0.0% - 8.2%
Pacelli and Márquez-Grant, 2010 + = ASU 1-2	Islamic Medieval (Molí de Can Fonoll, Ibiza)	3.2% (189)

It occurs in 3.5% of the Portuguese individuals studied, a figure comparable to a Spanish Islamic Medieval necropolis (3.2%) and in the interval of Bronze Age and Medieval Spanish samples (see Table 4.4.6.).

Distal accessory ridge (canines)

Observable in both upper and lower canines, the distal accessory ridge is located lingually, between the medial lingual ridge and the distal marginal ridge, but closer to the latter (Scott, 1977).

Table 4.4.7. Frequencies of distal accessory ridge in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UC + = ASU 1-5	77.6% (469)
	Coimbra (Portugal) UC + = ASU 2-5	58.8% (469)
	Coimbra (Portugal) LC + = ASU 1-5	41.1% (511)
	Coimbra (Portugal) UC	0: 32.4% 1: 18.8% 2: 32.6% 3: 14.9% 4: 1.3%
	Coimbra (Portugal) LC	0: 58.9% 1: 23.5% 2: 13.7% 3: 3.9%

Table 4.4.7. (Continued.)

Source	Sample	Frequencies (*n* [when available])
Irish, 1998b UC: + = ASU 2-5	Chad	55.6% (9)
	Gabon	58.3% (12)
	Ghana	62.5% (16)
	Nguni (South Africa)	55.6% (9)
	Nigeria/Cameroon	57.9% (19)
	Pygmy	57.1% (7)
	Sotho (South Africa)	57.3% (171)
	Togo/Benin	61.5% (13)
Willermet and Edgar, 2009 UC: + = ASU 2-5	African American (1650-1850)	53.3% (34)

This trait occurs in up to 77.6% of upper canines and 41.1% of lower canines on the Portuguese sample (+ = ASU 1-5, see Table 4.4.7.). The upper canine frequency of 58.8% on the same sample (+ = ASU 2-5) is most similar to Gabon (58.3%) and Nigeria/Cameroon (57.9%).

Upper premolars mesial and distal accessory cusps

Small distal and mesial cusps can appear on the occlusal surface of upper premolars, at each end of the sagittal groove, and clearly separated from the buccal and lingual cusps (Turner *et al.*, 1991; Scott and Turner, 1997).

Table 4.4.8. Frequencies of mesial and distal accessory cusps in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UP3 + = ASU 1	1.1% (455)
	Coimbra (Portugal) UP4 + = ASU 1	3.2% (466)
	Coimbra (Portugal) UP3	0: 98.9% Mesial: 0.7% Distal: 0.4%
	Coimbra (Portugal) UP4	0: 96.8% Mesial: 1.3% Distal: 1.7% Mesial/Distal: 0.2%
Al Oumaoui, 2009 + = ASU 1	La Navilla (Bronze Age; Granada, Spain)	UP3: 9.1% UP4: 18.8%

Table 4.4.8. (Continued.)

Source	Sample	Frequencies (*n* [when available])
García Sívoli, 2009 + = ASU 1	Son Real (6th-2nd century B.C.)	UP3: 0.0% (29)
		UP4: 4.0% (25)
Pereira, 2009 + = ASU 1	Lisbon (18th century; tooth count method)	All [P]: 2.1% (94)
Hanihara, 2008 + = ASU 1	Europe	UP3 M: 4.2% (406) F: 3.4% (176)
		UP4 M: 5.4% (389) F: 3.1% (163)
	North Africa	UP3 M: 2.5% (79) F: 0.0% (48)
		UP4 M: 2.6% (77) F: 0.0% (52)
	Sub-Saharan Africa	UP3 M: 4.6% (346) F: 5.0% (140)
		UP4 M: 9.8% (338) F: 3.7% (136)

These occur on 1.1% of the Coimbra sample individuals for the third upper premolar and 3.2% for the fourth (Table 4.4.8.). The Son Real (UP3: 0.0%; UP4: 4.0%), Europe (M – UP3: 4.2%, UP4: 5.4%; F – UP3: 3.4%, UP4: 3.1%) and North Africa (M – UP3: 2.5%, UP4: 2.6%; F – UP3: 0.0%; UP4: 0.0%) samples are the most similar frequencies.

Upper premolars accessory ridges

Ridges can be present on the mesial and distal accessory lobe segments of the buccal cusp of upper premolars. Most commonly, the distal ridge is present, although the presence of either ridge is not considered independent. Despite occurring at greater frequencies than most premolar traits and being useful in population studies, they are largely ignored (Scott and Turner, 1997; Burnett *et al.*, 2010).

The presence of accessory ridges on the premolars of the Coimbra sample was not scored using the plaque supplied to ASUDAS plaques' owners after the publication of Burnett and colleagues' (2010) work. So, the results should not be entirely compatible. The exclusion of truncated ridges on the present study renders comparisons with the mentioned work's results difficult (see Table 4.4.9.). Individuals of European

ancestry seem to be the ones with least frequency of these ridges, which suggests biological proximity to the Portuguese (UP3: 5.3%; UP4: 25.6%).

Table 4.4.9. Frequencies of accessory ridges in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UP3 + = 1 (truncated ridges excluded)	5.3% (453)
	Coimbra (Portugal) UP4 + = 1 (truncated ridges excluded)	25.6% (469)
	Coimbra (Portugal) UP3	0: 94.7% Mesial: 0.7% Distal: 4.0% Mesial/Distal: 0.7%
	Coimbra (Portugal) UP4	0: 74.4% Mesial: 5.3% Distal: 12.8% Mesial/Distal: 7.2% Medial: 0.2%
Burnett *et al.*, 2010 + = ASU 2-4	Papago	UP3 Mesial: 36.0% (75) UP3 Distal: 80.2% (86) UP4 Mesial: 76.7% (90) UP4 Distal: 92.6% (94)
	Alaskan Inuit	UP3 Mesial: 50.0% (46) UP3 Distal: 40.4% (47) UP4 Mesial: 89.4% (47) UP4 Distal: 95.7% (47)
	Pima	UP3 Mesial: 25.8% (89) UP3 Distal: 57.0% (93) UP4 Mesial: 83.9% (93) UP4 Distal: 91.4% (93)
	American Chinese	UP3 Mesial: 40.8% (49) UP3 Distal: 64.6% (48) UP4 Mesial: 70.6% (51) UP4 Distal: 77.1% (48)
	Solomon Islanders	UP3 Mesial: 30.2% (53) UP3 Distal: 52.9% (51) UP4 Mesial: 66.7% (54) UP4 Distal: 63.5% (52)
	South African Bantu	UP3 Mesial: 7.4% (94) UP3 Distal: 25.3% (99) UP4 Mesial: 59.6% (94) UP4 Distal: 66.7% (96)
	European American	UP3 Mesial: 9.8% (92) UP3 Distal: 33.0% (91) UP4 Mesial: 47.8% (90) UP4 Distal: 67.8% (90)
	South African Indian	UP3 Mesial: 2.2% (93) UP3 Distal: 26.6% (94) UP4 Mesial: 48.4% (91) UP4 Distal: 71.0% (93)
	European South African	UP3 Mesial: 5.3% (94) UP3 Distal: 23.4% (94) UP4 Mesial: 62.1% (95) UP4 Distal: 66.7% (84)

Tricuspid upper premolars

Table 4.4.10. Frequencies of tricuspid upper premolars in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UP3 + = ASU 1	0.2% (493)
	Coimbra (Portugal) UP4 + = ASU 1	0.2% (496)
Manzi *et al.*, 1997 + = ASU 1	*Lucus Feroniae* (Roman Empire Italy)	UP3: 4.1% (49)
		UP4: 0.0% (37)
	Portus (Roman Empire Italy)	UP3: 0.0% (88)
		UP4: 0.0% (62)
García Sívoli, 2009 + = ASU 1	Epipaleolithic to Late Medieval Spain (8 samples)	UP3: 0.0% UP4 : 0.0%
Pereira, 2009 + = ASU 1	Lisbon (18th century; tooth count method)	All UP: 0.0% (94)

An extra lingual cusp is very rarely present on upper premolars (Turner *et al.*, 1991; Scott and Turner, 1997), which are therefore named tricuspid premolars. It occurs on 0.2% of the Coimbra individuals analyzed, for either upper premolar (Table 4.4.10.). The most similar samples (*Portus*, Epipaleolithic to Medieval Spain and 18th century Lisbon) display no occurrence of this trait on either premolar (0.0%).

Odontome (upper and lower premolars)

Odontomes are small enamel and dentine projections which are rarely expressed on the occlusal surface of any premolar (Turner *et al.*, 1991; Scott e Turner, 1997). Due to their rarity, evaginated odontomes can be considered dental anomalies (Soames and Southam, 2005).

This trait is present only on 0.5% of the individuals studied, considering all premolars (Table 4.4.11.). The closest samples are Jomon, from Japan (0.4%) and South Siberia (0.6%), but Western Europe (0.8%) also displays a comparable frequency.

Table 4.4.11. Frequencies of odontomes in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UP3 + = ASU 1	0.4% (487)
	Coimbra (Portugal) UP4 + = ASU 1	0.2% (489)
	Coimbra (Portugal) LP3 + = ASU 1	0.0% (535)
	Coimbra (Portugal) LP4 + = ASU 1	0.2% (511)
	Coimbra (Portugal) all P + = ASU 1	0.5% (592)
Scott and Turner, 1997 All P: + = ASU 1	Western Europe	0.8% (246)
	Northern Europe	0.0% (111)
	North Africa	0.2% (545)
	West Africa	0.0% (56)
	Khoikhoi	0.0% (86)
	Jomon	0.4% (260)
	South Siberia	0.6% (155)
	New Guinea	0.0% (119)

Carabelli's trait (first upper molar)

Carabelli's trait is found on the mesiolingual cusp of upper molars (particularly the first), and varies from a small ridge, pit or furrow to a very large cusp, rivaling the main cusps in size (Hillson, 1996). Georg Carabelli, the dentist of the Austrian Emperor Franz, first described his *tuberculus anomalus* in 1842 (Hillson, 1996). The heredity of Carabelli's trait has long been accepted, and as early as 1951, Kraus studied eight families of Mexicans and Papago Indians and found a biallelic mode of inheritance for the trait. The overall distribution of Carabelli's trait on most major ethnic groups shows the trait is most frequently expressed in Caucasians (between 75.0% and 85.0%), then on Africans, Native Americans, Indians, Inuit and Pacific Islanders (Scott, 1980). Its usefulness in ancestry estimation on forensic contexts is limited, when the trait is used on its own (Edgar, 2009a). Carabelli's trait has been named in various ways in the literature across time. It has been found in primates and hominins, which suggests its relevance in phylogenetic studies (Correia and Pina, 2002). A recent review of the trait can be found in Marado and Campanacho (2013).

Table 4.4.12. Frequencies of Carabelli's trait in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 2-7	22.5% (479)
	Coimbra (Portugal) + = ASU 3-7	15.9% (479)
	Coimbra (Portugal) + = ASU 5-7	6.1% (479)
	Coimbra (Portugal)	0: 48.9% 1: 28.6% 2: 6.7% 3: 6.3% 4: 3.5% 5: 2.9% 6: 1.3% 7: 1.9%
Hanihara, 2008 + = ASU 3-7	Southeast Asia	M: 16.0% (656) F: 12.9% (263)
	Pacific	M: 13.8% (457) F: 14.2% (373)
	Melanesia	M: 16.8% (471) F: 13.5% (386)
	Sub-Saharan Africa	M: 18.6% (570) F: 13.8% (261)
Scott and Turner, 1997 + = ASU 5-7	Northeast Siberia	5.3% (172)
	Northwest America	5.5% (388)
	North and South Amerindian	5.6% (2054)

According to Mizoguchi (2013), Carabelli's trait is found on buccolingually smaller molars, and in people relying on a subsistence strategy focusing on milking who live in dry and moderately cold environments. Smaller teeth may be connected to the metabolic advantage of developing them, facilitated by a lack of need for big teeth, through a greater consumption of wheat and eggs that provide a rich nutrition (Mizoguchi, 2013). However, in Croatia, Carabelli's trait is only weakly correlated with the tooth dimensions of UM1, for example (Vodanovic *et al.*, 2013).

This trait can be useful in the study of population movements. In Croatia, the Late Antiquity and Medieval periods display similar frequencies of Carabelli's trait on UM1, but these are significantly different from early modern period and 21st century samples. This corroborates the archaeological and historical hypothesis that suggests the Croatian population was partially replaced between the aforementioned periods (Vodanovic *et al.*, 2013).

Carabelli's trait may be more frequently present on the deciduous dentition, which can be caused by reduced penetrance, resulting from environmental factors intervening during the long developmental period of permanent teeth (Bermúdez de

Castro, 1989). However, Edgar and Lease (2007) found correlation in trait presence between the second primary molar and the first permanent molar.

Carabelli's trait is phylogenetically very old, and has been well studied from very early on. So, frequencies are known for most populations, the trait has been shown to be independent, and not sexually dimorphic. Its presence is proportionately smaller on the second and third molars and its degree of asymmetry varies (Kolakowski *et al.*, 1980). The models tested by Kolakowski and colleagues (1980) for inheritance of this trait could not be fitted for all samples tested, which could be due to the irregular influence of environmental factors and the uncertain genetic influence of a major locus.

The above considerations have been more recently put into question, and Kolakowski and colleagues' difficulties have been put into perspective. Results found by Moormann and colleagues (2013), comparing Carabelli's trait, hypocone and upper molar accessory cusps, suggest these dental traits could be correlated, in line with the patterning cascade model of odontogeny (Jernvall and Jung, 2000; Salazar-Ciudad and Jernvall, 2002). Carabelli's trait reveals slight correlation with intercuspal distances in upper first molars, and an indication of the same trend on upper second molars. In the latter tooth, correlations could be hindered by tooth size and shape. Carabelli's trait on UM1 also correlates with hypocone, since larger expressions of the latter cusp are associated with greater expressions of Carabelli. Finally, Carabelli's trait on UM1 correlates to this upper molar's accessory cusps, when a moderate number of these are present. These associations are explained by the patterning cascade model: cusp ontogeny is possible due to an approximation of enamel knots, but the formation of a great number of new knots can hinder the formation of Carabelli's trait. On the other hand, the latter may be associated with a few number of extra cusps or with large hypocone expressions if their development still allows the formation of that mesiolingual enamel knot (Moormann *et al.*, 2013).

Guatelli-Steinberg and colleagues (2013) review their contribution on the study of the patterning cascade model's influence on Carabelli's trait expression and intertrait correlations. The model accurately justifies the presence of Carabelli's cusp, since it is related to intercuspal distances in relation to crown area (the smaller the intercuspal distances and the bigger the crown area, most likely was the presence of Carabelli's cusp). It also is able to justify antimeric (asymmetries), metameric (differences in frequencies across molars), population and sex differences, which correspond to differences in intercuspal distances. The authors also found some correlation between

intercuspal distances and the expression of other supernumerary cusps, such as the hypocone, cusp 5, or the mesial marginal accessory tubercles.

Kangas and colleagues (2004) found a single protein can affect several dental morphologic traits, relating to intercuspal distance and exuberance in tooth morphology. This brings to question the independence of dental traits, mainly when used in phylogenetic classification. The authors, however, recognized the potential for individual traits to be independently affected by other gene activities, and merely suggest care in assuming independence of traits when comparing different species (Kangas *et al.*, 2004).

Kondo and Townsend (2006) advise caution when using standardized observations to compare Carabelli's trait between groups, since Australians have been found to differ in the frequency and degree of expression among sexes. Positive (cusp-like) manifestations of Carabelli's trait are more likely to be expressed in larger teeth, since their greater formation time allows for the fifth enamel knot to produce the infolding of the inner enamel epithelium, thus forming the cusp (according to these authors). Smaller teeth may present only the reduced form of the trait, such as pits or grooves. This may explain the difference in frequencies and expression between male and female individuals of the same population (Kondo and Townsend, 2006).

Carabelli's trait expression is possibly correlated to small intercuspal distances, when related to tooth size, in Ohio individuals. This is again in agreement with the patterning cascade model and suggests Carabelli's as homoplastic (Hunter *et al.*, 2010). Guatelli-Steinberg and Irish (2005) had also proposed the trait as homoplastic, after finding frequencies analogous to those of *Paranthropus* in *A. afarensis*, differentiating this taxon from both *A. africanus* and early *Homo*.

Morphological variability in the mesiolingual cusp of humans and chimpanzees were compared in the outer enamel surface (OES) and enamel-dentine junction (EDJ). Despite the occasional occurrence of Carabelli's trait in chimpanzees (which could be a developmental anomaly in *Pan*), the trait present in the mesiolingual cusp of these primates is different from the variability measured by ASUDAS, either on the OES or the EDJ. It is a shelf-like structure with no cusp development, called lingual *cingulum*. This analysis, besides clarifying the distinction between traits in the same locus in *H. sapiens* and *Pan*, suggests the same distinction can divide *Australopithecus* and *Paranthropus* sp. from *Homo* sp. The morphology as determined by the *membrana praeformativa*, which later is mineralized as the EDJ, seems to be very important in

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determining OES morphology, mainly in chimpanzees, since in humans the greater enamel thickness hinders association between grade classification of EDJ and OES morphology (Ortiz *et al.*, 2012).

As Carabelli's cusp can be dichotomized through several breakpoints, it is present on the first upper molars of the Portuguese population in 22.5% (+ = ASU 2-7), 15.9% (+ = ASU 3-7) and 6.1% (+ = ASU 5-7; see Table 4.4.12.) of individuals. The geographically closest population to display similar trait frequency to the Coimbra sample is Northeast Siberia (5.3%; + = ASU 5-7).

Metaconule (cusp 5 on the first upper molar)

Table 4.4.13. Frequencies of cusp 5 (metaconule) in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 2-5	3.3% (478)
	Coimbra (Portugal) + = ASU 1-5	8.8% (478)
	Coimbra (Portugal)	0: 91.2% 1: 5.4% 2: 3.1% 3: 0.2%
Scott and Turner, 1997 + = ASU 1-5	Western Europe	11.8% (238)
	Northeast Siberia	10.4% (106)

The metaconule, the fifth cusp of the upper molars, is located between cusps 3 and 4, in the distal marginal ridge (Turner *et al.*, 1991; Scott and Turner, 1997). This trait has been shown as highly heritable through family studies (Hillson, 1996).

Bermúdez de Castro and Martínez (1986) illustrated the confusion in scoring the metaconule before the establishment of ASUDAS (and cited ways to identify the metaconule in the absence of the hypocone). This trait can be homoplastic in *Homo* sp., since it is one of the traits differentiating *A. afarensis* from *A. africanus* and early *Homo*, while approximating it to *Paranthropus* sp (Guatelli-Steinberg and Irish, 2005).

Portuguese individuals (mainly from Coimbra) display UM1 C5 at a frequency of 8.8%, which is relatively near to Western Europe (11.8%) and Northeast Siberia (10.4%; see Table 4.4.13.).

Table 4.4.14. Frequencies of mesial marginal accessory tubercles in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = Scott and Turner (1997) 1	4.6% (457)
	Coimbra (Portugal)	0: 95.4% MPT: 2.0% PL: 1.1% MAT: 1.3% PL/MAT: 0.2%
Kanazawa *et al.*, 1990	Japanese	PL: 19.6% MAT: 66.1% MPT: 64.3% LPT: 37.5% (56)
	Inuit	PL: 43.2% MAT: 58.0% MPT: 64.2% LPT: 59.3% (81)
	Bantu	PL: 33.3% MAT: 16.7% MPT: 30.0% LPT: 46.7% (30)
	Bushman	PL: 40.0% MAT: 26.7% MPT: 23.3% LPT: 60.0% (30)
	Australian Aborigines	PL: 18.2% MAT: 20.0% MPT: 36.4% LPT: 78.2% (55)
	Dutch	PL: 23.1% MAT: 46.2% MPT: 50.0% LPT: 50.0% (26)
	Indian	PL: 15.6% MAT: 28.1% MPT: 37.5% LPT: 37.5% (32)

PL – protoconule; MAT: mesial accessory tubercle; MPT: mesial paracone tubercle; LPT: lingual paracone tubercle.

These four tubercles on the upper first molar were clearly defined through moiré contourography, studied across several populations and proposed to be phylogenetically significant, because of their variation throughout population samples (Kanazawa *et al.*, 1990). The frequencies found are generally higher than those reported in records using visual observation, because moiré contourography may be a more sensitive, objective method (Kanazawa *et al.*, 1990). This explains the differences found between the

present research and the other results reported on Table 4.4.14. Only 4.6% of all individuals studied presented any of these tubercles. This suggests Indians are most similar, due to their low frequencies (PL: 15.6%; MAT: 28.1%; MPT: 37.5%; LPT: 37.5%) when compared to the other populations.

Hypocone (C4 on the second upper molar)

Table 4.4.15. Frequencies of cusp 4 (hypocone) in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 0-1	26.4% (530)
	Coimbra (Portugal) + = ASU 3-5	58.4% (530)
	Coimbra (Portugal)	0: 12.8% 1: 13.6% 2: 15.3% 3: 13.6% 3.5: 14.2% 4: 21.5% 5: 9.1%
Scott and Turner, 1997 + = ASU 0-1	Western Europe	24.7% (308)
	Northeast Siberia	21.8% (192)
	American Arctic	30.6% (569)
Hanihara, 2008 + = ASU 3-5	West Asia	M: 79.7% (172) F: 72.0% (75)
	Europe	M: 77.0% (655) F: 72.2% (241)

M – male individuals; F – female individuals.

The distolingual cusp in upper molars has tended to diminish in size in hominin evolution, after having been the last cusp added to the upper molars in primate evolution (Turner *et al.*, 1991; Scott and Turner, 1997).

In the individuals who died in Portugal in the late 19th and early 20th century, housed in Coimbra, the trait was absent 26.4% of the time, and clearly expressed in 58.4% of scorable individuals (Table 4.4.15.). The most similar frequency for this trait's absence is found in Western Europe (24.7%).

Parastyle (third upper molar)

Table 4.4.16. Frequencies of parastyle in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 1-6	3.4% (296)
	Coimbra (Portugal)	0: 96.6% 1: 1.7% 3: 1.0% 4: 0.3% 5: 0.3%
Irish, 1998b + = ASU 1-5	Congo	5.3% (19)
	Gabon	4.0% (25)
	Kenya	2.7% (73)
	Togo/Benin	4.5% (22)
	El Hesa (Egypt)	2.7% (37)

Parastyle ranges from a pit in the buccal groove of upper molars to a cusp in the mesiobuccal side of those teeth (Hillson, 1986). Dahlberg (1945) describes the stylar cusps of opossums and other animals and suggests the upper form of the paramolar tubercle be called parastyle, accordingly. Bolk did not find any evidence of the paramolar tubercle (the protostylid on the mandible and the parastyle on the maxilla) on the first molar, attributing such absence to the inexistence of supernumerary teeth between the premolars and the first molar. Bolk thought his paramolar tubercle was the reminiscent of such teeth, now rare due to their elimination from the dentition on account of evolutionary processes (Dahlberg, 1945). The cusp form of parastyle on first molars seems to be rarer due to the greater stability of those teeth. Nonetheless, it does appear rarely on the first molar, and Dahlberg (1945) describes three bilateral cases from the literature, thus suggesting genetic influence on the trait's genesis.

Nabeel and colleagues (2012) report two cases of parastyle with associated caries from India (where these tubercles are common). They also convey a treatment for such ailments that produces good results. They recommend general caries treatment and that dental medicine practitioners refrain from the removal of the cusps (since they sometimes interfere with orthodontic treatments), so as to conserve a potentially meaningful dental morphological trait.

A large, two cusped parastyle tubercle in a maxillary right second molar was analyzed and found to have two roots with separate pulp chambers and root canals,

despite fusing with mesiobuccal and distobuccal roots. This finding is contrary to most cases, where root canals are usually shared (Nayak *et al.*, 2013).

The parastyle is rare on the Coimbra sample, with 3.4% of the individuals displaying any form of the trait (Table 4.4.16.). El Hesa and Kenya (2.7%), and Gabon (4.0%) have the most similar frequencies.

Enamel extensions (upper molars)

Table 4.4.17. Frequencies of enamel extensions in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) UM1 + = ASU 1-3	4.0% (353)
	Coimbra (Portugal) UM1 + = ASU 2-3	3.1% (353)
	Coimbra (Portugal) UM2 + = ASU 1-3	18.4% (419)
	Coimbra (Portugal) UM3 + = ASU 1-3	7.2% (221)
	Coimbra (Portugal) UM1	0: 96.0% 1: 0.8% 2: 0.8% 3: 2.3%
	Coimbra (Portugal) UM2	0: 81.6% 1: 3.1% 2: 5.3% 3: 10.0%
	Coimbra (Portugal) UM3	0: 92.8% 1: 1.8% 2: 4.5% 3: 0.9%
Scott and Turner, 1997 UM1: + = ASU 2-3	Western Europe	3.8% (371)
	Northern Europe	2.2% (229)
	North Africa	6.8% (502)
	New Guinea	5.0% (240)
	Melanesia	3.5% (289)

Enamel extensions are extrusions of enamel from the cervical crown margin, that range from a small lobe to a long tongue dividing the roots of molars (and, occasionally, premolars; Hillson, 1986). Enamel extensions and pearls may be genetically determined, according to population studies and research on enamel defects (Lasker, 1950). These variations of enamel distribution may also be involved in facilitating periodontal disease, since that extra enamel strip does not allow for the

correct attachment of the periodontal ligament (like what occurs on the surrounding cement), and accumulates plaque (Soto *et al.*, 2010).

Enamels extensions are present in 4.0% (UM1), 18.4% (UM2) and 7.2% (UM3) of individuals from the present sample (+ = ASU 1-3). The 3.1% frequency found for first upper molars (+ = ASU 2-3) is most similar to those found in Melanesia (3.5%), Western (3.8%) and Northern (2.2%) Europe (Table 4.4.17.).

Lingual cusp variation (lower premolars)

Table 4.4.18. Frequencies of lower premolar lingual cusp variation in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LP3 + = ASU 2-9	25.1% (526)
	Coimbra (Portugal) LP4 + = ASU 2-9	64.3% (502)
	Coimbra (Portugal) LP3	0: 74.5% 1: 0.4% 2: 11.2% 3: 4.6% 4: 0.8% 5: 1.7% 6: 4.2% 7: 0.4% 8: 2.1% 9: 0.2%
	Coimbra (Portugal) LP4	0: 35.5% 1: 0.2% 2: 40.0% 3: 12.5% 4: 2.8% 5: 0.8% 6: 5.0% 7: 0.2% 8: 2.8% 9: 0.2%
Irish, 1998b LP4: + = ASU 2-9	Chad	62.5% (8)
	Nguni (South Africa)	66.7% (18)
	San	67.5% (83)
	Bedouin	64.3% (28)
	El Hesa	61.5% (62)
	Kharga (Egypt)	62.5% (8)
	Lisht (Egypt)	66.7% (12)

Lower premolars can vary between none and three lingual cusps (Turner *et al.*, 1991; Scott and Turner, 1997). A family study as shown high heritability for this trait (Hillson, 1996).

The Portuguese present 25.1% of individuals with two or three cusps on UP3 and 64.3% on UP4 (Table 4.4.18.). This latter frequency is identical to a Bedouin (64.3%) sample and similar to Kharga and Chad (62.5%), for example.

Deflecting wrinkle (lower first molar)

Table 4.4.19. Frequencies of deflecting wrinkle in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 1-3	7.0% (384)
	Coimbra (Portugal) + = ASU 2-3	3.7% (384)
	Coimbra (Portugal) + = ASU 3	0.8% (384)
	Coimbra (Portugal)	0: 93.0% 1: 3.4% 2: 2.9% 3: 0.8%
Scott and Turner, 1997 + = ASU 3	Western Europe	5.2% (154)
	Jomon	4.5% (162)
	New Guinea	3.8% (52)
Hanihara, 2008 + = ASU 2-3	West Asia	M: 9.7% (31) F: 9.1% (11)
	Europe	M: 16.8% (358) F: 9.2% (141)

M – male individuals; F – female individuals.

The deflecting wrinkle is the distal folding of the mesiolingual cusp on lower first molars, forming an 'L' shape (Hillson, 1986). It is one of the traits found by Edgar and Lease (2007) to correlate between the primary (lower second deciduous molar) and secondary (lower first permanent molar) dentitions.

It is found on 7.0% of individuals of the current sample (+ = ASU 1-3; see Table 4.4.19.). New Guinea (3.8%) has the most similar frequency, when only grade 3 is included (0.8%). Europeans (M: 16.8%; F: 9.2%) and West Asians (M: 9.7%; F: 9.1%) display higher frequencies, which are however the most similar frequencies, when grades 2 and 3 are included (3.7% of Coimbra individuals).

Anterior fovea (lower first molar)

Table 4.4.20. Frequencies of anterior fovea in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 1-4	17.7% (417)
	Coimbra (Portugal) + = ASU 2-4	11.3% (417)
	Coimbra (Portugal)	0: 82.3% 1: 6.5% 2: 7.7% 3: 3.1% 4: 0.5%
Irish, 1998b + = ASU 2-4	Canary Islands	23.5% (34)
	Carthage	20.0% (10)
Willermet and Edgar, 2009 + = ASU 2-4	European American (1650-1850)	20.0% (37)
	European American (1825-1910)	17.9% (90)
	European American (1920-1980)	20.1% (173)

Anterior fovea is a groove located in the mesial area of the occlusal surface of lower first molars (Turner *et al.*, 1991; Scott and Turner, 1997). Present in 11.3% of individuals in the Coimbra collections (+ = ASU 2-4; see Table 4.4.20.), its frequency is most similar on European Americans from various periods (17.9% to 20.1%) and Carthage (20.0%).

Groove pattern (lower molars)

The groove pattern is determined by how the cusps contact in the lower molar central fossa (Turner *et al.*, 1991; Scott and Turner, 1997). Dahlberg (1963) found the groove pattern variation is dependent on the relative sizes of cusps. For instance, a Y pattern is obtained when cusp 2, the metaconid, is relatively large when compared with the entoconid, cusp 4. Crown traits such as cusp pattern on molars are pointed out as genetically determined (Lasker, 1950).

Gregory's 1916 (*in* Biggerstaff, 1968) work that defined the *Dryopithecus* (Y) pattern is contested, since it does not take into account the point of contact between the second and third cusps, as described later by Hellman (1928 *in* Biggerstaff, 1968).

Table 4.4.21. Frequencies of groove pattern in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + = ASU Y	89.9% (426)
	Coimbra (Portugal) LM2 + = ASU +/X	79.8% (480)
	Coimbra (Portugal) LM2 + = ASU Y	20.2% (480)
	Coimbra (Portugal) LM3 + = ASU Y	19.5% (369)
	Coimbra (Portugal) LM1	Y: 89.9% X: 10.1%
	Coimbra (Portugal) LM2	Y: 20.2% X: 79.8%
	Coimbra (Portugal) LM3	Y: 19.5% X: 80.5%
Willermet and Edgar, 2009 LM1: + = ASU Y	Eastern European (8th-18th century)	88.9% (189)
	West African (early)	92.7% (185)
Scott and Turner, 1997 LM2: + = ASU Y	Northern Europe	21.0% (319)
	Northeast Siberia	18.6% (245)
	South Siberia	22.2% (270)
	American Arctic	20.0% (529)
	Micronesia	21.2% (160)

Besides, neither of these works explains how the distal fovea and the marginal ridge are considered integrant to the pattern, but are not present on some examples they display. These earlier authors were writing in a period when an association with *Dryopithecus* would be welcomed in the scientific community, since it put the modern human on a different branch of evolution, apart from apes. Several authors found different results and diverse types of groove patterns, as of yet unexplained because of the inflexibility of the earlier concept of the Y pattern (Biggerstaff, 1968).The association between cusp number and pattern had been disproved recently, by Garn (1966 *in* Biggerstaff, 1968).

The Y pattern is present on Portuguese individuals at a frequency 89.9% in LM1, 20.2% in LM2 and 19.5% in LM3 (Table 4.4.21.). The first of these frequencies is comparable to historic Eastern Europeans (88.9%) and early West Africans (92.7%). The lower second molar frequency is similar to American Arctic (20.0%) and Northern Europe (21.0%) samples, for instance.

Table 4.4.22. Frequencies of distal trigonid crest in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + = ASU 1	2.6% (424)
	Coimbra (Portugal) LM2 + = ASU 1	4.2% (481)
	Coimbra (Portugal) LM3 + = ASU 1	21.0% (376)
Scott and Turner, 1997 LM1: + = ASU 1	Northern Europe	2.4% (200)
	North Africa	3.3% (276)
Hanihara, 2008 LM1: + = ASU 1	East-Northeast Asia	M: 1.9% (209) F: 2.3% (89)
	North America	M: 2.2% (274) F: 1.8% (229)
	South America	M: 1.5% (130) F: 2.5% (81)

M – male individuals; F – female individuals.

The distal trigonid crest is a ridge that unites the mesiobuccal and mesiolingual cusps and isolates the mesial fossa (Hillson, 1986). The distal trigonid crest (as part of the trigonid crest pattern) corresponds between the EDJ and the OES morphologies in several taxa (including *H. sapiens;* Skinner *et al.*, 2008). However, further research revealed true distal trigonid crests, with origin in both sides of the distal portion of the trigonid, seem very rarely expressed or not expressed at all at the EDJ (Bailey *et al.*, 2011). This may indicate only enamel variation constitutes this trait, which contributes to the difficulty in detecting it on worn teeth, as noted by Turner and colleagues (1991).

In the Coimbra sample, 2.6% (LM1), 4.2% (LM2) and 21.0% (LM3) of the individuals displayed this crest feature (Table 4.4.22.). Northern Europe (2.4%) is the most similar sample for the lower first molar.

Protostylid (lower molars)

Protostylid is a feature of the mesiobuccal cusp, and presents itself as a pit, a furrow or even a cusp of varying sizes (Hillson, 1986). Bolk did not find evidence of the presence of paramolar tubercles (protostylid) on lower first molars, and hypothesized its

Table 4.4.23. Frequencies of protostylid in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + = ASU 1-7	19.6% (429)
	Coimbra (Portugal) LM1 + = ASU 2-7	0.5% (429)
	Coimbra (Portugal) LM2 + = ASU 1-7	16.1% (490)
	Coimbra (Portugal) LM3 + = ASU 1-7	6.9% (346)
	Coimbra (Portugal) LM1	0: 80.4% 1: 19.1% 2: 0.5%
	Coimbra (Portugal) LM2	0: 83.9% 1: 10.4% 2: 2.9% 3: 2.0% 5: 0.4% 7: 0.4%
	Coimbra (Portugal) LM3	0: 93.1% 1: 3.8% 2: 1.2% 3: 1.2% 5: 0.3% 7: 0.6%
Hanihara, 2008 LM1: + = ASU 2-7	Melanesia	M: 3.8% (238) F: 2.3% (218)
	West Asia	M: 0.0% (49) F: 0.0% (15)
	Europe	M: 2.2% (402) F: 4.4% (158)
	North Africa	M: 1.3% (75) F: 2.1% (47)
	Sub-Saharan Africa	M: 2.1% (292) F: 0.0% (107)

M – male individuals; F – female individuals.

absence was due to the lack of supernumerary teeth between the LP4 and the LM1 (Dahlberg, 1945). Cusp forms of the protostylid (like parastyle on the upper arch) on lower first molars are most likely rare due to a greater stability of those teeth. Dahlberg (1945), however, describes three bilateral cases, and this rare presence of this form suggests genetic influence as the trait's origin. It was this author who suggested the lower form of the paramolar tubercle be called protostylid.

Trait frequencies including protostylid data show an analogy between *A. afarensis* and *Paranthropus* sp., and separate the latter taxon from *A. africanus* and *Homo* sp. The protostylid may be homoplastic, according to these results (Guatelli-Steinberg and Irish, 2005). Protostylid is presented as a crest along the mesiobuccal cusp or both buccal cusps on hominin lower molars, when observed at the EDJ. This surface also suggests this trait not to be a cusp, at least on *A. africanus* and *P. robustus*, since there are no dentine horns to demarcate it (Skinner *et al.*, 2009).

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The use of protostylid's grade 1 in population frequencies is questionable (Scott, 2008). However, according to images from the EDJ of hominins (Skinner *et al.*, 2009), the pit described as ASUDAS grade 1 is related to the trait, which hints at its correct inclusion. Aguirre and colleagues (2006) consider *foramen caecum* (common in American populations) as protostylid grade 1.

Exclusion of grade 1 from the data recorded on the Coimbra sample alters frequencies substantially from 19.6% (+ = ASU 1-7) to 0.5% (+ = ASU 2-7) on the first lower molar (Table 4.4.23.). The second molar has a frequency of 16.1% and the third one of 6.9% (+ = ASU 1-7). West Asia (0.0%) and Sub-Saharan Africa (M: 2.1%; F: 0.0%) have the frequencies nearer the current sample, if the grade 1 is not considered as trait presence.

MMPT (lower molars)

Table 4.4.24. Frequencies of MMPT (mandibular molar pit/tubercle) in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + = Weets (2009) [adpt.] 1 – '3+'	2.1% (424)
	Coimbra (Portugal) LM2 + = Weets (2009) [adpt.] 1 – '3+'	3.5% (491)
	Coimbra (Portugal) LM3 + = Weets (2009) [adpt.] 1 – '3+'	30.3% (353)
	Coimbra (Portugal) LM1	0: 97.9% 1: 1.9% 3: 0.2%
	Coimbra (Portugal) LM2	0: 96.5% 1: 2.4% 1-2: 0.2% 2: 0.4% 3: 0.4%
	Coimbra (Portugal) LM3	0: 69.7% 1: 21.2% 1-2: 2.8% 2: 2.8% 2-3: 1.7% 3: 0.6% 3+: 1.1%
Marado, 2010 + = Weets (2009) 1-3	Porto (Portugal) LM1	0.0% (85)
	Porto (Portugal) LM2	6.0% (100)
	Porto (Portugal) LM3	31.4% (86)
Weets, 2009 + = Weets (2009) 1-3	Ireland (Neolithic-Early Christian) LM1	L: 0.0% (170) R: 2.1% (151)
	Ireland (Neolithic-Early Christian) LM2	L: 1.7% (178) R: 3.4% (179)
	Ireland (Neolithic-Early Christian) LM3	L: 27.6% (131) R: 31.2% (126)

L – left side; R – right side.

The mandibular molar pit-tubercle (MMPT; see Figure 4.4.1., p. 234) was described by Weets (2009) and previously recorded by Marado (2010) in a presumably Northern Portuguese sample (see 4.5.Dental variation and historical migrations).

Hlusko (2004) identifies a more mesial cingular remnant which does not covary with the protostylid, and therefore should be a different trait. Images provided alongside the work of Skinner and colleagues (2008, 2009) and their consideration of protostylid as a crest or a set of crests including the hypoconid seem to include MMPT as a part of a protostylid complex trait, present in several taxa. Despite this consideration, these protostylid and (as here suggested) MMPT crests as seen either on the OES or EDJ, are not directly connected. Differences in middle crown and anterior expressions of this cingular crest in *Australopithecus afarensis* and *Paranthropus robustus* (Skinner *et al.*, 2009) suggest to the present author that different genomic factors may originate each form. Skinner and colleagues (2008, 2009) consider that if cingular expressions on the buccal cusps are developmentally related, they should not be considered different traits. More research is needed to understand the relation between protostylid and MMPT (see 4.3.Sexual dimorphism and intertrait correlations).

The results found for the present sample are relatively similar to those found for another Portuguese sample and the Irish sample where MMPT was first detected, with a pattern of low presence on the first lower molar (from 0.0% to 2.1%), intermediate results on LM2 (from 1.7% to 6.0%) and higher on LM3 (27.6% to 31.4%), as seen on Table 4.4.24.

Cusp number (lower molars)

Variation in cusp number, between 3 and 6 cusps, is due to the evolutionary trend in teeth reduction, which affects second lower molars the most (Turner *et al.*, 1991; Scott and Turner, 1997). When a Chalcolithic Portuguese population's frequencies are compared with the results found among Neolithic and Mesolithic Portuguese populations, a reduction in the number of cusps found on second lower molars demonstrated the mentioned trend (Silva, 2000).

Table 4.4.25. Frequencies of cusp number variation in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + ~= ASU 5	9.7% (424)
	Coimbra (Portugal) LM1 + = ASU 6+	1.7% (424)
	Coimbra (Portugal) LM2 + ~= ASU 4	21.4% (491)
	Coimbra (Portugal) LM2 + = ASU 5+	21.0% (491)
	Coimbra (Portugal) LM3 + ~= ASU 4	56.7% (367)
	Coimbra (Portugal) LM1	4: 8.0% 5: 90.3% 6: 1.7%
	Coimbra (Portugal) LM2	3: 0.4% 4: 78.6% 5: 20.0% 6: 1.0%
	Coimbra (Portugal) LM3	3: 3.0% 4: 43.3% 5: 39.2% 6: 14.4%
Irish, 1998b LM1: + = ASU 6+	Chad	0.0% (17)
	Khoikhoi	0.0% (16)
	Pygmy	0.0% (9)
	San	4.7% (85)
	Canary Islands	4.7% (64)
	Carthage	0.0% (11)
	El Hesa	1.9% (53)
	Pharonic Nubia	0.0% (8)
Irish, 1998b LM2: + = ASU 5+	Carthage	16.7% (12)
	Kharga (Egypt)	15.4% (13)
	Lisht (Egypt)	20.8% (24)
	Pharonic Nubia	26.7% (15)

Six cusps are found in 1.7% of the Coimbra individuals on LM1, which is comparable to El Hesa (Table 4.4.25.). Five or more cusps on second lower molars are found on 21.0% of this sample, which is most similar to Lisht (20.8%). More than half (56.7%) of this Portuguese sample displays other than 4 cusps on LM3.

Table 4.4.26. Frequencies of cusp 5 (hypoconulid) in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + = ASU 1-5	91.3% (423)
	Coimbra (Portugal) LM1 + = ASU 0	8.7% (423)
	Coimbra (Portugal) LM2 + = ASU 1-5	20.4% (491)
	Coimbra (Portugal) LM2 + = ASU 0	79.6% (491)
	Coimbra (Portugal) LM3 + = ASU 1-5	53.3% (368)
	Coimbra (Portugal) LM1	0: 8.7% 2: 3.5% 3: 15.4% 4: 45.4% 5: 27.0%
	Coimbra (Portugal) LM2	0: 79.6% 1: 1.0% 2: 2.4% 3: 9.2% 4: 5.5% 5: 2.2%
	Coimbra (Portugal) LM3	0: 46.7% 1: 0.5% 2: 4.1% 3: 6.5% 4: 15.5% 5: 26.7%
Scott and Turner, 1997 LM1: + = ASU 0	Western Europe	7.8% (217)
	Northern Europe	10.0% (170)
	North Africa	10.0% (250)
Scott and Turner, 1997 LM2: + = ASU 0	Western Europe	71.1% (284)
	Northern Europe	84.4% (225)
	North Africa	66.4% (381)

Cusp 5 or hypoconulid is a cusp placed on the distal side of the occlusal surface of lower molars, between cusps 3 and 4 (Turner *et al.*, 1991; Scott and Turner, 1997). It is present on 91.3% of the LM1, 20.4% of the LM2 and 53.3% of the LM3 of the Coimbra sample (Table 4.4.26.). The trait's absence (LM1: 8.7%; LM2: 79.6%) is between the frequencies found for Western (LM1: 7.8%; LM2: 71.1%) and Northern (LM1: 10.0%; LM2: 84.4%) Europe, and relatively near those from North Africa (LM1: 10.0%; LM2: 66.4%).

Table 4.4.27. Frequencies of cusp 6 (entoconulid) in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + = ASU 1-5	1.6% (424)
	Coimbra (Portugal) LM2 + = ASU 1-5	1.0% (491)
	Coimbra (Portugal) LM3 + = ASU 1-5	14.4% (368)
	Coimbra (Portugal) LM1	0: 98.4% 1: 0.7% 2: 0.9%
	Coimbra (Portugal) LM2	0: 99.0% 2: 1.0%
	Coimbra (Portugal) LM3	0: 85.6% 1: 0.8% 2: 7.6% 3: 2.2% 4: 2.4% 5: 1.4%
Scott and Turner, 1997 LM1: + = ASU 1-5	Western Europe	8.3% (217)
	North Africa	7.7% (352)
	Khoikhoi	4.7% (85)
Hanihara, 2008 LM1: + = ASU 1-5	Europe	M: 5.7% (383) F: 6.5% (154)
	North Africa	M: 8.8% (80) F: 4.3% (47)
Hanihara, 2008 LM2: + = ASU 1-5	India	M: 4.2% (119) F: 0.0% (68)
	West Asia	M: 2.3% (43) F: 0.0% (13)
	Europe	M: 1.2% (403) F: 1.2% (161)
	North Africa	M: 1.1% (94) F: 1.5% (68)

M – male individuals; F – female individuals.

Cusp 6, or entoconulid, is a cusp located lingually to C5 (Turner *et al.*, 1991; Scott and Turner, 1997).

C6 corresponds between the EDJ and the OES morphologies in several taxa (including *H. sapiens*; Skinner *et al.*, 2008). The C6 is expressed in several ways at the EDJ in the taxa analyzed by Skinner and colleagues (2008). It may be expressed as two dentine horns or a single dentine horn on the shoulder of either the hypoconulid dentine horn, or between this latter cusp's dentine horn and the entoconid's.

C6 is only considered when C5 is present, but it has occasionally been considered even when there were only five cusps, if the distal one was positioned distolingually in relation to the central groove (see Townsend *et al.*, 1990).

The entoconulid and its frequencies (on the second deciduous molar and all permanent molars as well) in an Australian aboriginal population seem to demonstrate a quasicontinuous variation affected by environmental factors. Its frequencies are more prominent as the time of odontogenesis is delayed (less on the deciduous molars and increasingly more present on the permanent ones; Townsend *et al.*, 1990).

Associations between C6 and the metaconule are suggested, like those between Carabelli's cusp and protostylid (Scott, 1978 *in* Townsend *et al.*, 1990), as evolutionarily advantageous (Townsend *et al.*, 1990).

Findings related with the presence of C6 on the lower molars of chimpanzees corroborate the patterning cascade model's predictions, since in molars of the same size, smaller intercuspal distances are associated with C6. This prompts the authors to advise caution in the use of dental morphologic traits in taxonomic or phylogenetic research, since they are dependent on tooth size and cusp morphology (Skinner and Gunz, 2010). The presence of a distolingual root on lower first permanent and lower second deciduous molars is correlated with greater intercuspal distances and buccolingual width. On the other hand, it is not correlated to C6 (Kim *et al.*, 2013). These apparently contradicting results suggest the role of interplay between genome and environment portrayed by the patterning cascade model may need further research before the phylogenetic usefulness of C6 (and other traits) is ruled out. Guatelli-Steinberg and Irish's (2005) work suggests its usefulness, by demonstrating how C6 (and other traits) allow for *A. afarensis* to be deemed closer to *Paranthropus* sp. than *A. africanus* or early *Homo*. Besides, the traits (including C6) are proposed as a homoplasy in the latter taxa.

C6 is present in 1.6% (LM1), 1.0% (LM2) and 14.4% (LM3) of the Coimbra individuals (Table 4.4.27.). The most similar LM1 frequencies are higher, and are found on Khoikhoi (4.7%) and Europe (M: 5.7%; F: 6.5%). For LM2, Europe (1.2%) and North Africa (M: 1.1%; F: 1.5%) are the most similar.

Cusp 7 (metaconulid on lower molars)

C7, metaconulid or *tuberculum intermedium*, is a cusp located in the lingual area of the occlusal surface of lower molars, between cusps 2 and 4 (Turner *et al.*, 1991; Scott and Turner, 1997; see Figure 4.4.2.).

Table 4.4.28. Frequencies of cusp 7 (metaconulid) in the present sample and similar frequencies found in the literature.

Source	Sample	Frequencies (*n* [when available])
Present study	Coimbra (Portugal) LM1 + = ASU 1-4	5.1% (432)
	Coimbra (Portugal) LM2 + = ASU 1-4	0.2% (492)
	Coimbra (Portugal) LM3 + = ASU 1-4	1.1% (376)
	Coimbra (Portugal) LM1	0: 93.3% 1a: 1.6% 1: 0.2% 2: 1.6% 3: 1.9% 4: 1.4%
	Coimbra (Portugal) LM2	0: 99.8% 3: 0.2%
	Coimbra (Portugal) LM3	0: 98.7% 1a: 0.3% 1: 0.3% 2: 0.5% 3: 0.3%
Scott and Turner, 1997 LM1: + = ASU 1-4	Western Europe	4.5% (291)
	Northern Europe	5.0% (179)
	North Africa	9.4% (414)
	China-Mongolia	7.9% (285)
	Japan	5.7% (382)
	Northeast Siberia	6.0% (151)
	American Arctic	8.5% (565)
	Northwest America	6.8% (473)
	North and South Amerindians	8.5% (2756)
	Southeast Asia (early)	7.5% (370)
	Southeast Asia (recent)	7.3% (588)
	Polynesia	7.1% (495)
	Micronesia	5.8% (175)
	Australia	5.3% (294)
	New Guinea	7.0% (100)
Willermet and Edgar, 2009 LM2: + = ASU 1-4	European American (1650-1850)	8.6% (37)
	European American (1825-1910)	9.7% (90)
	European American (1920-1980)	6.0% (173)

Although this trait is sometimes considered useful for forensic ancestry estimation, its sole application is limited (Edgar, 2009a).

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Figure 4.4.1. Detail of the lower right third molar of individual 31 of the Internacional Trades collection (ITC; 19 year-old female) with a grade 3+ MMPT.

Figure 4.4.2. Detail of the lower left posterior dental arch of individual 187 ITC (38 year-old male). In the center of the image, a grade 4 cusp 7 can be seen on the lower left first molar.

It was found as one of the possibly homoplastic traits which approximate *A. afarensis* and *Paranthopus* sp., and distinguish the former taxon from early *Homo* and *A. africanus*, due to frequency distinctions (Guatelli-Steinberg and Irish, 2005).

Cusp 7, in correspondence between the EDJ and OES morphologies in several taxa (including *H. sapiens*), may be expressed as a slight elevation on the shoulder of the metaconid's dentine horn (grade 1a), or between this and the entoconid, with an inclination towards one or the other (Skinner *et al.*, 2008).

The frequencies for this trait on the Portuguese studied sample are 5.1% (LM1), 0.2% (LM2) and 1.1% (LM3). Table 4.4.28. shows some comparable samples, the closest of which are Northern Europe (5.0%) and Australia (5.3%) for LM1. As for the lower second molar, the European Americans of historic and contemporary periods provide relatively close, but higher frequencies (between 6.0% and 9.7%).

4.4.3. Conclusions on discrete dental traits

Recently, Scott and colleagues (2013) proposed a definition of Eurodont pattern. This Eurodonty is characterized by a set of typically low and high frequency traits, mostly crown traits. The present results can be compared to the expectations of correspondence to this pattern, if only in what respects crown traits and enamel extensions (root traits were not scored on the present sample; a new such trait, the reduction of upper central incisor roots, has recently been proposed for Iberian samples

by Cunha and colleagues [2012]). The results reported for worldwide (Scott and Turner, 1997) and Spanish samples (Scott *et al.*, 2013) are used as reference for the considerations below.

Winging, shoveling and double shoveling on the upper central incisors appear in very low frequency on the Portuguese population, as sampled in the present study (see Tables 4.4.1., 4.4.2. and 4.4.3.). Enamel extensions on upper first molars are also of low frequency, as expected (see Table 4.4.17.). The Y pattern on lower second molars can also be considered of low frequency (Table 4.4.21.), like cusp 7 on lower first molars (Table 4.4.28.). Cusp 6 (Table 4.4.27.), protostylid (+ = ASU 2-7; Table 4.4.23.) and deflecting wrinkle (+ = ASU 3; Table 4.4.19.) on lower first molars are present at very low frequencies as well.

High frequencies are found for two or more lingual cusps on the lower third premolar (Table 4.4.18.), and for mass-reducing traits like three-cusped upper second molars (Table 4.4.15.) and four-cusped lower first and second molars (Table 4.4.25.). The only discrepancy is found in the frequency of upper first molars Carabelli's cusp or tubercle forms, which are expected to be high as well, but are very low on the Portuguese sample housed in Coimbra. The frequency found for this sample (6.1%; see Table 4.4.12.) is placed among the low frequency groups, the groups with the lowest trait frequency for Carabelli's, from four groups defined by Scott and Turner (1997).

So, despite the discrepancy with Carabelli's cusp and the lack of data for root traits, the Portuguese results from the Coimbra sample suggest the Portuguese are a fairly typical Eurodont population. The biological proximity to other European, and particularly Iberian, samples will be further explored on 4.5.Dental variation and historical migrations.

The data from this large sample characterize the Portuguese (particularly from Coimbra) population's dental crown morphological variables, and allow for comparison with data from many other sources, collected using the same scoring method (ASUDAS) and many of the same traits.

4.4.4.Introduction to oral traits

The orofacial skeleton and its nonmetric traits are of great interest. The development and evolution of such structures may be directly or indirectly related to

important functions such as speech, walking and, more obviously, eating (see, for example, Coquerelle *et al.*, 2013). Each of the four traits analyzed will be introduced below, and their respective relevance in population movements and biological affinity analyses will be discussed.

4.4.5.Oral nonmetric traits

Foramina mentales

The mandibular canal, which begins in the mandibular *foramen* and ends in the mental *foramen*, transports the inferior alveolar nerves and blood vessels. It can bifurcate, separate itself in several ramifications and originate accessory *foramina mentales*. Occasionally, two ramifications can enter the mandible through two *foramina*

Table 4.4.29. Frequencies (individual and side count methods) of *foramina mentales* in the present sample and similar frequencies found in the literature. Presence is considered when there is one or more accessory *foramen*.

Source	Sample	Frequency (*n* [when available])
Present study	Coimbra (Portugal) §	4.7% (600)
	Coimbra (Portugal) *	2.8% (1198)
	Coimbra (Portugal) §	1: 95.3% 2: 4.5% 3: 0.2%
Hauser and De Stefano, 1989	French (medieval) *	3.7%
	Native Americans (Northwest; undefined period) *	3.7%
	Indians (modern) §	4.7%
	Australian (pre-history) *	4.1%
Sawyer *et al.*, 1998	French *	2.6% (800)
	Native Americans (Northwest coast) *	3.3% (607)
	Hungarians *	3.0% (989)
	Greeks *	3.3% (928)
Hanihara and Ishida, 2001b	Peruvians §	5.4% (93)
	Torres Strait (Melanesia) §	5.5% (73)
	East Europe §	4.4% (68)
	Ensay (UK) §	3.9% (104)
	Poundbury (UK) §	4.4% (160)
	Spitalfields-2 (UK) §	4.5% (112)

* - side count method; § - individual count method.

mandibulares, and converge in the mandibular body. There is also the rare possibility of the formation of two mandibular canals, with corresponding *foramina mandibulares* and *foramina mentales* (Zeze *et al.*, 1996). As stated in the description of the methodology (3.Methods) these *foramina mentales* are located externally in the mandible, under the premolars. Variation in number, position, size, shape and relative distance is expected. Asymmetry, some sexual dimorphism and variation in frequency between age groups is possible (Hauser and De Stefano, 1989).

Table 4.4.29. presents the frequencies for the present samples (individual and side count methods) and compares them with similar frequencies found in other sources (Hauser and De Stefano, 1989; Sawyer *et al.*, 1998; Hanihara and Ishida, 2001b).

The frequencies most similar to the ones from the present Portuguese sample are European, predictably. These frequencies are low, when compared to values from other continents, usually (see above, for dental nonmetric traits). There are some exceptions, even within the most similar samples. French samples (2.6%; 3.7%) and a Hungarian sample (3.0%) are the most similar to the Portuguese frequency when the side count method (2.8%) is applied. Outside Europe, the Native American samples from the Northwest (3.3%; 3.7%) are also similar. As for the individual count method (4.7%), modern Indians have the same proportion (4.7%) and compose the most similar exception (from outside of Europe). As for European samples, East Europeans (4.4%) and two archaeological British samples are very similar (Poundbury: 4.4%; Spitalfields-2: 4.5%). Other frequencies found within the cited sources confirm these are among the lowest for this trait, worldwide. This suggests the Portuguese sample is typically European, when concerning *foramina mentales*.

Mylohyoid bridge

As stated in the methodological description (see 3.Methods), the visceral face of the mandibular ramus has a diagonal groove (traversed by the muscular branch of the inferior alveolar nerve and the blood vessels that accompany it) that crosses it posteroanteriorly. The mylohyoid bridge (the possible ossification of a ligament or of periosteum) can cover it, either completely or partially, at one or several points with varying positions. This trait also most likely develops with age (it may only be present from adolescence onwards), varies among different populations and may display sexual dimorphism (Hauser and De Stefano, 1989).

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Ossenberg (1974) dissected the mandible of 36 cadavers so as to identify the membrane which covers the mylohyoid nerve and artery and, consequently, the mylohyoid groove. A membrane contiguous to the spheno-mandibular ligament and inferior to the mandibular *foramen* was found. In six individuals this membrane was partially ossified. It connects to the periosteum, and envelops the bone that contains the mylohyoid groove. Both structures envelop the aforementioned mylohyoid nerve and artery (Ossenberg, 1974).

The mylohyoid bridge is useful in population studies because of its genetic origin and of its variability among human groups (Ossenberg, 1974; Hauser and De

Table 4.4.30. Frequencies (individual and side count methods) of mylohyoid bridge in the present sample and similar frequencies found in the literature. Any expression, complete or incomplete, of the trait is considered trait presence.

Source	Sample	Frequency (*n* [when available])
Present study	Coimbra (Portugal) §	17.6% (591)
	Coimbra (Portugal) *	8.6% (1111)
	Coimbra (Portugal) §	0: 82.4% Incomplete: 6.3% 1: 11.3%
Ossenberg, 1974	Ainu (recent; Japan) *	6.7% (104)
	Inuit (Greenland; AD 1400-1800) *	8.0% (288)
Hauser and De Stefano, 1989	Inuit (Alaska) §	15.5%
	Australian (pre-history) *	7.5%
	African Americans (modern) *	10.4%
	European Americans (modern) *	11.2%
	Melanesians (recent) *	6.5%
Hanihara and Ishida, 2001a	Ainu (Hokkaido) §	17.8% (191)
	Inuit (Greenland) §	17.1% (76)
	German §	19.6% (51)
	Spitalfields-2 (UK) §	17.0% (112)
	Naqada §	16.2% (99)
	Gizeh §	18.3% (126)
	Nubia-2 §	16.7% (42)
	Nigeria-2 §	16.7% (24)
	South Africa §	18.0% (61)
Turan-Ozdemir and Sendemir, 2006	Late Byzantine period *	9.0% (89)
	Ainu (Hokkaido) *	11.1%
	Jomon (Neolithic) *	10.3%

* - side count method; § - individual count method.

Stefano, 1989). Hanihara and Ishida (2001a) state the variability expressed in the mylohyoid bridge suggests genetic drift as responsible for some of it, when it comes to the loss, retention or increment of trait presence, when compared to its prevalence in earlier human populations. Thus, genetic processes seem to mediate this trait's frequency.

Table 4.4.30. has the mylohyoid bridge frequencies found in the present sample, for individual and side count methods, as well as similar frequencies found in the literature.

As testified by Table 4.4.30., no European sample has a similar frequency, either to the side or the individual count method. Samples from the Late Byzantine period (9.0%) and Greenland Inuit (8.0%) come closest to the side count method (8.6%; some Southeast Asian and Oceania samples reported by Hanihara *et al.* [2012] are also close). As for the individual count method (17.6%), South Africans (18.0%), again Greenland Inuit (17.1%) and the Ainu from Hokkaido (17.8%) are closest. Ainu are demonstrated as relatively similar by two other sources (side count methods: 6.7%; 11.1%). The Alaskan Inuit (individual count method: 15.5%) are also relatively close, in a third occasion for Inuit samples. European Americans display a side count method frequency of 11.2% and Germans an individual count method frequency of 19.6% (and a small sample: 51 individuals). These are the closest frequencies for populations of European origin.

The apparent biological diversity of samples with similarity to the Portuguese, and the almost complete absence of Europeans (only two relatively close populations) allow the questioning of this trait as useful in measuring biological affinities between populations.

Palatine torus

The *torus palatinus* is a hamartoma; a benign, sessile, nodular, osseous growth on the midline of the palate (Gorsky *et al.*, 1998; Morrison and Tamimi, 2013). It involves both cancellous and compact bone, but not the nasal layer of compact bone (Sisman *et al.*, 2012). Idiopathic *torus palatinus* is suggested to be transmitted as an autosomal dominant trait by results from an Israeli contemporaneous population. Families (along two or three generations) were observed for *torus palatinus* and some parents are suspected of being homozygotic carriers and others unaffected nonpenetrant

carriers, since the frequency of their children with this trait was higher than expected (Gorsky *et al.*, 1998). Even so, the relative importance of genes and environment in the development of *torus palatinus* is still controversial (Halffman and Irish, 2004), and oral *tori* are thought to be caused by both environmental and genetic factors (Galera *et al.*, 2003/2004).

The Guanches (pre-Hispanic Canary Islanders) are originally from Northwest Africa, according to most evidence. The frequency of *torus palatinus* (23.8%) is however much higher than the one found in that geographical area (which is averaged at 4.2% and at most is 13.3%; Northeast Africa mean: 6.1%; maximum expression: 14.7%) and more similar to Northern Europe. Gene flow and genetic drift probably are not the explanation for this phenomenon, since other traits are not affected. This may instead be due to environmental factors, such as heavy chewing or high intake of marine resources. The latter hypothesis is interesting, because it suggests that micronutrients such as omega-3, omega-6 and vitamin D may be involved in the growth of bony traits, like this threshold trait, the palatine *torus* (Halffman and Irish, 2004; see also García-García *et al.*, 2010).

In a 2010 review of the literature, García-García and colleagues found *torus palatinus* in living contemporary individuals from various geographical and ethnical origins to vary in terms of population frequency and shape, and generally display a small size more frequently. This trait grows during life, and is largest during the second or third decade. It can, however, be present from an early age onwards (García-García *et al.*, 2010).

End-stage renal disease patients who suffer from renal osteodystrophy display greater frequency of TP (with a different shape) than the general population. Those who underwent longer periods of peritoneal dialysis present longer TP (Sisman *et al.*, 2012).

Table 4.4.31. displays *torus palatinus* frequencies for the present sample (both methods and two different presence characterizations for ASUDAS) and compares it to the frequency found from individuals from the same population and to other similar frequencies found in the literature.

The variation (8.7%) found between this study's result and the one determined by Galera and colleagues (1995) and Garralda and colleagues (1997) for the same population may result from different sensitivities from the observers or from a random variation in presence of each sample.

When the ASUDAS method frequencies with presence from grades 2 to 4 are compared, the Portuguese frequency (6.7%) is similar to the North African (4.1% and 6.2%) and Southern European (7.5%) frequencies. In terms of full presence of the trait, the most similar are the Thai (61.7%). The highest frequencies that follow the ones found for Portuguese and Thai are from Spain (44.3%), Norway (36.1%) and African Americans (36.0%).

Table 4.4.31. Frequencies (individual count method; both observation methods) of palatine *torus* in the present sample and similar frequencies found in the literature. Trait presence is determined for each situation.

Source	Sample	Frequency (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 1-4	79.9% (596)
	Coimbra (Portugal) + = ASU 2-4	6.7% (596)
	Coimbra (Portugal) + = Galera *et al.* (1995) Débil (inc.)-Fuerte (compl.)	79.5% (596)
	Coimbra (Portugal) ASU	0: 20.1% 1: 73.2% 2: 6.7%
	Coimbra (Portugal) Galera *et al.* (1995)	Ausente: 20.5% Débil Inc.: 47.1% Débil Compl.: 20.5% Medio Inc.: 9.9% Medio Compl.: 1.8% Fuerte Compl.: 0.2%
Galera *et al.*, 1995; Garralda *et al.*, 1997	Coimbra (Portugal) + = Galera *et al.* (1995) Débil (inc.)-Fuerte (compl.)	88.2% (476)
Galera *et al.*, 2003/2004	Contemporary Spanish + = *torus palatinus* presence	44.3% (278)
Halffman and Irish, 2004 + = ASU 2-4	Northwest Africa (pre-historic to contemporary)	4.2% (167)
	Northeast Africa (pre-historic to contemporary)	6.1% (327)
	Southern Europe (historic to modern)	7.5% (147)
García-García *et al.*, 2010 + = *torus palatinus* presence	Thai (contemporary)	61.7% (609)
	Norwegian (contemporary)	36.1% (2010)
	African American (contemporary)	36.0%

As concluded by the review of García-García and colleagues (2010), the weakest expression of the trait (grade 1 = 73.2%; Débil inc.+compl. = 77.6%) is the most common. When included in the total trait frequency, it is very high in comparison with most samples, and much higher than European samples (see García-García *et al.*, 2010). This may be partly due to a lack of adequate samples for comparison, since the samples from the living may not yield an accurate total frequency, for difficulties in the identification of the weakest expression through the soft tissue of the palate (García-

García *et al.*, 2010). The weakest manifestation of palatine *torus* may also be more susceptibly brought upon by environmental factors, which would explain why, at least for this sample, the only presence-absence dichotomy which obtained a value closer to the predictable samples (North Africans and Southern Europeans) excluded the slightest trait expression.

The influence of environmental factors in this trait's expression needs to be further studied, as suggested by what was said above and the differences between Portuguese (79.5%) and Spanish (44.3%) frequencies. This difference can, again, be caused by problems with detecting this trait in the living.

Mandibular torus

The mandibular *torus* is an osseous excrescence in the visceral facet of the mandible, usually under the second premolar and with variable shape and size, of unknown function and environmental effect relevance (Hauser and De Stefano, 1989; Silva, 2002; Richter and Eliasson, 2012; Morrison and Tamimi, 2013; see 3.Methods). The *torus mandibularis* can also be defined as a hamartoma, a benign nodular growth in the cortical tissue of the alveolar bone of the mandible, located always above the mylohyoid ridge (Rouas and Midy, 1997; Morrison and Tamimi, 2013). García-García and colleagues (2010) propose these congenital osseous protuberances are formed due to the excessive effort of osteoblasts, which originate an osseous accumulation in the mandibular hemi-arch.

The development of the mandibular *torus* is explained through the threshold model, since its predisposition is genetic, but environmental cues (such as masticatory hyperfunction) are involved in triggering it, according to Pechenkina and Benfer (2002) and Ihunwo and Phukubye (2006). This trait is more common in individuals in the middle of their life cycle (20 to 40 years old), which may be related to the increased masticatory function during this period (Ihunwo and Phukubye, 2006; see also García-García *et al.*, 2010). Galera and colleagues (2003/2004) state all oral *tori* are thought to be caused by multiple factors that include genetic and environmental interactions. García-García and colleagues (2010) review the literature and discuss the possibility of both genetic and environmental factors, with masticatory function and diet (consumption of omega-3 and vitamin D; see also Halffman and Irish, 2004) playing a

part. So, despite an unknown contribution from environmental causes, there is some genetic intervention that molds the presence of mandibular *torus*.

Although unlikely, unilateral fracture of mandibular *torus* has been reported, due to a fall from a mountain bike where the forearm and carpal area sustained the impact on the chin, possibly causing the fracture. Paraesthesia was occasioned in part of the lower lip, possibly derived from affected anterior most mental nerve from the fracture and its consequent swelling (Saura-Ingles *et al.*, 2005).

Table 4.4.32. Frequencies (individual count method; both observation methods) of mandibular *torus* in the present sample and similar frequencies found in the literature. Trait presence is determined for each situation.

Source	Sample	Frequency (*n* [when available])
Present study	Coimbra (Portugal) + = ASU 1-3	18.4% (599)
	Coimbra (Portugal) + = Galera *et al.* (1995) Débil-Fuerte	18.4% (599)
	Coimbra (Portugal) ASU	0: 81.6% 1: 15.0% 2: 3.4%
	Coimbra (Portugal) Galera *et al.* (1995)	Ausente: 81.6% Débil: 13.5% Medio: 4.7% Fuerte: 0.2%
Galera *et al.*, 1995; Garralda *et al.*, 1997	Coimbra (Portugal)	Left side Ausente: 45.2% Débil: 46.7% Medio: 8.0% Right side Ausente: 44.9% Débil: 47.1% Medio: 8.0% (195)
Ihunwo and Phukubye, 2006	Finns	14.0% (400)
	Inuit (Alaska)	20.0% (86)
	European American females	16.0% (300)
	North Norway	12.7% (1181)
	Native Americans	13.6% (2000)
	European South Africans (living)	16.0% (436)
	Native South Africans	21.5% (284)
García-García *et al.*, 2010	Norwegian (contemporary)	18.8% (2010)
	European American 1 (contemporary)	24.8% (254)
	European American 2 (contemporary)	16.0%
	Ghanan (contemporary)	12.1% (926)

Table 4.4.32. shows the frequencies found for each method used to ascertain the expression of the mandibular *torus* on the Coimbra sample. Besides this, other frequencies similar to the one found for the Portuguese are reported, as well as their sources.

Galera and colleagues (1995) and Garralda and colleagues (1997) found, in the same population, frequencies per side (left = 54.8%; right = 55.1%) that differ greatly from the individual frequencies of this study (18.4%). The use of different individuals can justify this divergence, but differences in the detection of the trait should account for some variation. The use of the ASUDAS simultaneously by the present author may have conditioned the observation. The ASUDAS is, however, more objective, since it considers the relative dimension of the bone growth. The "Débil" (weak) grade of the method adaptation proposed by Galera and colleagues (1995) was only recorded when a *torus* was clearly palpable, so as not to confuse it with some other variation, either of morphological or pathological origin. Neither of these methods obtained a good intra-observer error, as seen on chapter 4.1. Although that should not account for such a great variation on its own, it could certainly enhance it.

The frequencies nearer the Portuguese proportion (18.4%) of individuals with mandibular *torus* presence are the contemporary Norwegian (18.8%). Most other samples with similar frequencies are of European origin or ancestry. Some (namely Ghanans, Native Americans, South Africans and Alaskan Inuit) are clearly distinct biologically, but are the exception. The proximity with some Northern samples (Norwegians, Finns, Alaskans) is somewhat bewildering, since those are usually near the maximum frequencies for this trait (see Richter and Eliasson, 2012), and again suggest the importance of genetic predisposition in inter-population variability. Within the sources mentioned in Table 4.4.32. there are other, more divergent, European samples.

Hassett (2006) studied eight widely varying, in chronology and geography, archaeological samples for mandibular *torus*, in order to determine if the variation found corresponded to that of a predominantly genetic trait or a predominantly environmentally defined trait. Variation between groups is large and opens the possibility of either genetic or environmental etiology. Sexual dimorphism exists in some groups and varies between them, which can be due to cultural differences in gender role or may be a random biological phenomenon. Variation with age exists, since *tori* rarely appear in juvenile individuals. Significant variation is only present

within each group, and not in the overall sample. Age might not be directly correlated to mandibular *torus* expression, but may covariate with stimuli enhancing its frequency.

Temporomandibular disorder (but see Pechenkina and Benfer [2002] and below), mandibular robusticity and maxillary *torus* did not correlate with mandibular *torus*. Greater tooth wear was correlated with mandibular *torus*, which suggests functional stress may be related to its formation and decrease (since it apparently decreases or is reabsorbed when the first molar is lost, and it is greater at a relatively lower level of wear). Results are best explained in the light of the threshold model, since the genetic potential is necessary alongside the environmental factor (functional stress) to allow the formation of mandibular *torus*. This is not explained by robusticity, joint disorder, or solely by genetic factors, but by an interaction of masticatory activity and genetic potential. Therefore, a bias could exist when environmental factors are not identical for every population in a biodistance analysis, requiring caution (Hassett, 2006).

Morrison and Tamimi (2013), using a test and a control group, compared the prevalence of mandibular and palatine *tori* to dental wear and temporomandibular dysfunction. They also controlled for the use of pharmacological substances known to potentiate bone growth, the presence of diseases such as hypothyroidism and diabetes, and smoking. Clear associations were found between *tori* presence and wear as well as temporomandibular dysfunction, which may be an indirect correlation between the *tori* and bruxism. The use of antihypertension medications was also connected to palatine *torus*. A slighter association was found between hypothyroidism and palatine *torus*, which may be because this condition leads to decreased bone resorption. The use of certain medication due to penicillin allergy was associated with presence of mandibular *torus*, by potentiating bone growth (Morrison and Tamimi, 2013).

In light of the finds reported by Hassett (2006) and Morrison and Tamimi (2013), the correlations between palatine and mandibular *tori* and (a) individual age, (b) individual *ante mortem* tooth loss (AMTL; sum of teeth lost per individual), (c) AMTL on molars, (d and e) AMTL on molars for each dental arcade, (f) individual mean wear, (g) mean molar wear, and (h and j) mean molar wear per each dental arch were calculated using Kendall's *tau*-b. The results are found on Tables 4.4.33., 4.4.34. and 4.4.35.

These calculations demonstrated consistently weak correlations, showing neither palatine (TP) nor mandibular *tori* (TM) to be associated with age (MT = 0.147; TP =

0.170), AMTL (TM = 0.062; TP = 0.151), AMTL for all molars (TM = 0.068; TP = 0.151), AMTL for upper molars (TM = 0.107; TP = 0.151), and AMTL for lower molars (TM = 0.042; TP = 0.136).

Table 4.4.33. Kendall's *tau*-b correlations between mandibular and palatine *tori* and *ante-mortem* tooth loss (AMTL, sum of all teeth loss in life) and individual age. Coefficients are above the divide, P-values and *n* values are below.

	Mandibular *torus*	Palatine *torus*	AMTL	Age
Mandibular *torus*		0.123	0.062	0.147
Palatine *torus*	P = 0.002 n = 595		0.151	0.170
AMTL	P = 0.074 n = 599	P = 0.000 n = 596		0.523
Age	P = 0.000 n = 599	P = 0.000 n = 596	P = 0.000 n = 600	

The weak correlations found here display some positive association nonetheless, which precludes the influence of tooth loss in the resorption of either of these *tori*. Decreased functionality of the masticatory apparatus seems to be unlinked to the diminishment of these traits. It seems to even be connected to their slight enhancement (Tables 4.4.33. and 4.4.34.).

Table 4.4.34. Kendall's *tau*-b correlations between mandibular and palatine *tori*, *ante-mortem* tooth loss (AMTL, sum of the teeth loss in life) on molars and AMTL on upper and lower molars. Coefficients are above the divide, P-values and *n* values are below.

	Mandibular *torus*	Palatine *torus*	AMTL (all molars)	AMTL (upper molars)	AMTL (lower molars)
Mandibular *torus*		0.123	0.068	0.107	0.042
Palatine *torus*	P = 0.002 n = 595		0.151	0.146	0.136
AMTL (all molars)	P = 0.52 n = 599	P = 0.000 n = 596		0.749	0.820
AMTL (upper molars)	P = 0.004 N = 599	P = 0.000 n = 596	P = 0.000 n = 600		0.483
AMTL (lower molars)	P = 0.245 n = 599	P = 0.000 n = 596	P = 0.000 n = 600	P = 0.000 n = 600	

Excessive masticatory activity, on the other hand, is commonly associated with the occurrence of bony exostoses (Pechenkina and Benfer, 2002; Ihunwo and Phukubye, 2006; García-García *et al.*, 2010; Morrison and Tamimi, 2013). The present sample does not reflect that premise, since individual mean wear (TM = 0.094; TP = 0.136), mean molar wear (TM = 0.096; TP = 0.143), mean upper molar wear (TM = 0.077; TP = 0.089) and mean lower molar wear (TM = 0.048; TP = 0.070) are weakly associated with either *tori* studied here (see Table 4.4.35.).

The increase in frequency of mandibular and palatine *tori* are only very slightly associated to dental wear rates, which is another contribution to their potential genetic origin as the most important source of their variation. The differences between the present results and those of Morrison and Tamimi (2013) may be caused by the different origins of dental wear and temporomandibular dysfunction between populations. The Canadian contemporary populations, as suggested by the mentioned authors, derives increased wear and joint disorder to bruxism, as the turn of the 19th century Portuguese most likely wore their teeth during mastication, and during a more prolonged period of time. This difference in dynamic intensity of the masticatory activity may justify the lack of a correlation between *tori* and dental wear.

Table 4.4.35. Kendall's *tau*-b correlations between mandibular and palatine *tori*, mean wear and mean molar wear (all molars, upper and lower molars only). Coefficients are above the divide, p-values and *n* values are below.

	Mandibular *torus*	Palatine *torus*	Mean wear	Mean molar wear	Mean upper molar wear	Mean lower molar wear
Mandibular *torus*		0.123	0.094	0.096	0.077	0.048
Palatine *torus*	P = 0.002 n = 595		0.136	0.143	0.089	0.070
Mean wear	P = 0.004 n = 599	P = 0.000 n = 596		0.713	0.321	0.239
Mean molar wear	P = 0.005 n = 595	P = 0.000 n = 592	P = 0.000 n = 596		0.291	0.190
Mean upper molar wear	P = 0.022 n = 599	P = 0.008 n = 596	P = 0.000 n = 600	P = 0.000 n = 596		0.388
Mean lower molar wear	P = 0.154 n = 599	P = 0.034 n = 596	P = 0.000 n = 600	P = 0.000 n = 596	P = 0.000 n = 600	

Despite these finds, it should be noted Bocquet-Appel (1984) found cranial morphological traits vary, in male skulls from the Coimbra collections, throughout the 19th century (when analyzed in generations twenty years apart), in accordance with the variation of the price of wheat, which is interpreted as an environmental factor impacting cranial nonmetric traits. The same cause could not be identified in the female variation.

This evidence, together with the report by Halffman and Irish, 2004 (see above) and that reviewed by García-García and colleagues (2010), shows the potential relevance of nutrition (with some nutrients possibly more influential than others) in the frequency of cranial traits. Morrison and Tamimi (2013) alert to the intervention of diseases or conditions such as hypertension (or rather its treatment), hypothiroidism and penicillin allergy (the immune system), which can trigger *tori* development.

4.4.6.Concluding thoughts on oral traits

The frequencies of *foramina mentales*, mylohyoid bridge, mandibular *torus* and palatine *torus* were reported for the sample of Coimbra, Portugal. This European sample was found to be placed among geographically and (presumably) biologically near and distant populations alike, in most occasions. This situation may be due to phenomena as diversified as observational errors, sample sizes, genetic differences, nutritional and cultural variability and differences brought about by the differences in the observations of live or dissected individuals, casts or skeletal samples.

Care is recommended by many when it comes to using osseous nonmetric variables in population biological comparisons, since the plasticity of bones and the influence of environmental factors cannot be eluded (for example, see Turan-Ozdemir and Sendemir, 2006). When used alongside a battery of phenotypically stable dental nonmetric traits, their variability will probably be of use in biological affinities studies. This is due to the genetic mediation that seems to affect their frequencies, which should be taken into account and valued, particularly when resources are scarce.

4.5.Dental variation and historical migrations

Several analyses will attempt to demonstrate the biological affinities and relations of the Portuguese sample with other samples, which frequencies were found in the literature. These analyses will compare diversified samples from different authors and use the battery of traits available, which varies widely according to the availability and compatibility of the dichotomizations (or breakpoints) found for each trait in said sources. Scott and colleagues (2013) state a common difficulty in comparing data from dental morphology studies is the application of different traits and breakpoints. Through family studies, dental crown trait variables were found to be most likely polygenic, exhibiting threshold dichotomies on a quasicontinuous form (Scott, 1974). This allows for several requisites to be implemented in establishing trait presence/absence. The following chapter has many such examples.

Scott and Turner (1997) and Scott (1977, 1980) advocate the use of the individual count method, because it allows for the sample to be used to an almost full potential, at the same time reflecting the strongest genotype. This count method was used for the present sample, but in cases when other samples' frequencies were obtained via the tooth count method (for example), they were adopted nonetheless. The effects of this are broached in 4.7.Count method.

Some traits were occasionally removed from analysis, due to the nullity of their variation across samples. There is trait association between several instances of shoveling, suggesting the use of only one key tooth in evaluating this trait, so as to not disturb statistical analysis (Tocheri, 2002). Scott and Turner (1997) also recommend the use of a key tooth, with the same end. In order to allow for the most comprehensive analysis, since there are no trait correlations in the Coimbra sample and because this did not perturb the quantitative test used (see below), traits were often compared in more than one tooth.

As stated in the chapter 3.Methods, all analyses will be conducted using principal components analysis (PCA) to extract the most information available in the variability between samples. Only principal components with *eigenvalues* above one will be considered, and only the principal components encompassing the most variance (usually the first three) will be analyzed, so as not to confound the interpretation with the inclusion of less meaningful components, and those including the least variation.

4.5.1. Why use principal components analysis (PCA)? Its advantages and disadvantages in relation with statistical resources

Biological and evolutionary research has long been interested in the contribution of genetic variation between populations, or in how the biologic interaction between populations enhances genetic variability. This originated a search for the best methodologies available, including that for the best tests that allow a representation of the biological relations between samples.

Nei's (1972) work is an example of such search, as are many there cited. This author uses DNA sequence data to detect genetic distance between several types of geographically distant populations (local populations, island-bound populations, populations subjected to founder-effect, etc.). The need for accurate measurement of biological affinities is illustrated as a relatively old concern, even in the branch of genetics.

The referred search resulted in numerous advances in the representation of genetic relations between samples. Tests such as the MMD, Mahalanobis D^2 (both are distance statistics) and PCA (a quantitative reduction of data) will be briefly introduced, to better contextualize choosing the latter.

The Mean Measure of Divergence (MMD) was developed by Smith and Grewal, who studied cranial nonmetric variables in lab mice. Berry and Berry popularized the test's use in anthropology, through the measure of biological distances using skeletal discrete traits (Harris and Sjovold, 2004).

The MMD is the most typically used statistical test in the inference of biological relations between populations through dental morphological data. It works with nominal data, is easily computed and allows for the comparison of data between researchers. The independence of variables is assumed, which means variables should be removed in case of correlation (Edgar, 2004; Harris and Sjovold, 2004). The test derives its results from the divergence between mean trait frequencies in several discrete variables from any number of samples. It measures lack of similarity, so results near 0 reveal high similarity, and those nearing 1 mean greater difference. A statistically significant MMD is greater than twice the standard deviation calculated between the samples using a specific formula (Tyrrell, 2000).

As an example of the application of MMD and some complementary analysis, see Vargiu and colleagues (2009). These researchers compared nine population groups from Copper Age Italy, and found little distance between them. This was considered as related to technological development, which most likely allowed for greater population mobility and, therefore, greater gene flow. Notable exceptions were found for Sardinia Island and Lorenza, samples which revealed greater distance from the remaining seven. MMD was used with standardized distances and the Freeman and Tukey angular transformation, and multidimensional scaling (MDS) was applied to it, as well as a minimum spanning tree (MST). Spearman rank-order correlation was also used to test the relation between standardized MMD and geographic distances.

Mahalanobis D^2 was originally conceived to measure biological distances through metric uncorrelated data. Later, it was adapted to nonmetric continuous correlated data by the same author. This test is a measure of divergence, like MMD (Irish, 2010).

D^2 is relatively difficult to compute, can be limited in the analysis of variables with little or no correlation and demands multiple observations per individual, yet allows the use of a greater number of variables (Edgar, 2004). Harris (2008) considers D^2 as the answer to most problems in measuring phenetic distance. Its requirement of entire sets of data, without missing information, is particularly problematic in dental morphology, since it is very common to have missing or destroyed teeth in a sample.

The application of both MMD and D^2 was used to compare African Americans and European Americans from three distinct periods. Results were relatively similar in both statistical analyses (Edgar, 2004).

The application of Mahalonobis D^2 allows the application of other statistical tests to measure the relations between populations through the analysis of allelic frequencies. The R-matrix is one of them. It was initially projected to use with allelic frequency data (Hanihara, 2010). The R-matrix produces mean kinship coefficients; positive results attest greater likeness, and negative results express less proximity than average. Values nearer the centroid demonstrate greater genetic variability, while those further from it are more homogeneous, due to lower migration and genetic drift rates (Irish, 2010).

The Ainu, an indigenous people from Northern Japan, were studied with the objective of inferring the biological contribution of geographically close populations they interacted with. Besides applying the MMD and D^2, Hanihara (2010) used the R-

matrix to understand the inherent population structure through dental morphology. In order to do so, the author also used the number of sampled individuals, the individuals composing the population (according to a census from 1875) and estimated the heritability rate as 0.5.

Bernal and colleagues (2010) also applied D^2 and the R-matrix to dental morphometrics. Seventeen South American samples contributed to state the hypothesis this sub-continent was originally populated by a single (most likely hunter-gatherer) population. This population's genetic variability might have been progressively reduced through serial founder effect (due to a constant subdivision of the original population, as they advanced into southern South America), like suggested by these tests' results.

The other example of the application of statistical tests commonly used with genetic data to dental morphology is F_{ST}. It considers each variable through the difference between the means of a sample pair. These means are reduced when necessary, in cases that analyze small samples, traits displaying little heritability or correlated traits (Harris, 2008). F_{ST} is a measure of population differentiation; the value obtained through the test is the percentage of biological difference between populations in allelic frequency (Irish, 2010).

Principal components analysis (PCA; see 3.Methods for a more complete explanation) is a procedure which reduces data, by re-expressing trait frequency variation along composite axes, factors that translate the interrelations between variables. These components may be expressed graphically, and simplify interpretation. Since the PCA generates the correlations between the original variables and the resulting components, those dental nonmetric characteristics most connected to the distribution attained for the sample on each component are easily identifiable, through their listed loadings (Irish and Guatelli-Steinberg, 2003; Delgado-Burbano, 2007b; Harris, 2008). Variables of little use are virtually eliminated, since their variation is not loaded into the final components (Delgado-Burbano, 2007b). The variation among samples previously analyzed for dental morphology can be extracted by applying PCA to the frequency/percentage of each nonmetric trait (Irish and Guatelli-Steinberg, 2003; Delgado-Burbano, 2007a).

Coppa and colleagues (2008) provide an example of the use of PCA, applied to the study of several pre-conquest Central and South American samples. Six circum-Caribbean areas (Florida, Cuba, Dominican Republic, Puerto Rico, US Virgin Islands, Guadalupe) and Venezuela, were studied using PCA, MMD (and its results' MDS) and

Maximum Likelihood. All methods used provided comparable results. These show two different pre-conquest migrations into the Caribbean, one of hunter-gatherers and a later one of agriculturalists (Coppa *et al.*, 2008).

Therefore, PCA yields graphical representations of biological relations of the same nature as the MDS of MMD or D^2 results, as illustrated by the example above. It has the added advantage of not being affected by intertrait correlations, and informing on each variable's relevance to establish sample distribution. The use of a methodology that allows for the use of the most nonmetric traits possible is essential to the following analyses. To know the variability the results correspond to, and which variables interrelate to condense that variability are also valuable tools.

4.5.2. From reptiles to humans: dental evolution, biological relations and migrations

Therapsids, known as "mammal-like reptiles", started to differentiate teeth, initially showing derivations akin to canines. Their surviving lineage, mammals, introduced heterodonty, differentiated teeth with multiple functions, apart from the conic and pointed teeth of reptiles, mainly (homodonty). From synapsids (the class that originated the therapsid order) to mammalian heterodonty, the change was gradual, with increasing cups and cingula (Pérez-Pérez *et al.*, 2010).

Polyphyodonty (several generations of teeth) was gradually suppressed to a diphyodonty (a decidual and a permanent set of teeth). The mesial and distal cusps that complemented the original conic tooth were set linearly. The next evolutionary step was the formation of a triangular shape, in which upper molars' distal and mesial cusps drifted towards the buccal side and the lower molars' cusps towards the lingual. Through the addition of an extra talon (upper molars) or talonid (lower molars), distal structure was also increased, and this differentiation of teeth made the mammalian dentition much more versatile and uniquely varied (Pérez-Pérez *et al.*, 2010).

The original mammalian dental formula is 3-1-4-3: three incisors, one canine, four premolars and three molars. Many mammals have since evolved from this ancestral form, due to adaptive needs. The current *H. sapiens* dental formula is 2-1-2-3 and "our" dentition is bunodont (of low, rounded cusps) with a cusp pattern close to the primitive

state (although it tends to alter, as the cusp number and the groove pattern is less predictably Y5 for M1's and X/+4 for M2's; Pérez-Pérez *et al.*, 2010).

At a much smaller scale, teeth presently continue to alter. The resulting morphologic alterations are diminutive, but can have a major role in the distinction among and within human, hominoid and hominid populations. The following analyses only compare small population-wide frequency differences among human groups, due to micro-evolution and population genetic processes. Their aim is to clarify the biological relations and origins of Coimbra's late 19th and early 20th century Portuguese population, and to illustrate how this large sample can help explain the population history of other related samples as well.

4.5.3. Portuguese biological affinities to worldwide samples

The initial comparisons will be derived from data available from Scott and Turner (1997) and Hanihara (2008), and pertain to the affinities between the Portuguese and the samples representative of the main geographical and ethnical divisions of mankind. The objective is to confirm this sample's close relationship with European samples and to infer the biological relation between the Portuguese and the North African sample superficially (since this will be further analyzed below).

The first comparison was drawn from the data published by Scott and Turner (1997), and the data from the present sample was dichotomized according to it (see Table 4.5.1.). Figure 4.5.1. shows the Portuguese sample very near Western European, North European and North African samples, with the remaining samples clearly more distant. This portrays the results of the first two components (summing 68.6% of the total variance).

The factor loading of principal component 1 (PC1: 49.0% of the total variance; see Table 4.5.1.) shows the strongest positive loadings to be located mainly on the upper arch and on the anterior dentition. The traits with loadings above 0.7 are UI1 shoveling, UM1 enamel extensions, UI1 double shoveling, odontome on all premolars, UI1 winging, LM1 deflecting wrinkle and UI2 interruption grooves. Other very high loadings (> 0.5) are LM1 cusp 6 and LM1 distal trigonid crest. The highest scoring

Table 4.5.1. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and world-wide samples reported in Scott and Turner (1997).

Trait (tooth)	PC 1	PC 2	PC 3
Winging (11/21) + = ASU 2-6	**<u>0.806</u>**	0.315	0.064
Shoveling (11/21) + = ASU 3-6	**<u>0.972</u>**	0.020	0.087
Double Shoveling (11/21) + = ASU 2-6	**<u>0.880</u>**	-0.034	0.157
Interruption Grooves (12/22) + = ASU 1	**<u>0.761</u>**	-0.393	-0.045
Odontome (all premolars) + = ASU 1	**<u>0.853</u>**	0.064	-0.178
Hypocone (17/27) + = ASU 0-1	0.295	**-0.800**	0.096
Carabelli's trait (16/26) + = 5-7	**-0.561**	0.316	-0.487
C5 (16/26) + = ASU 1-5	-0.347	**<u>0.817</u>**	-0.292
Enamel Extensions (16/26) + = ASU 2-3	**<u>0.911</u>**	-0.097	-0.023
C5 (36/46) + = ASU 0	**-0.649**	**-0.556**	0.134
C5 (37/47) + = ASU 0	**-0.654**	**-0.603**	-0.287
Groove Pattern (37/47) + = ASU Y	**-0.630**	0.166	**<u>0.622</u>**
C6 (36/46) + = ASU 1-6	**<u>0.674</u>**	**<u>0.524</u>**	-0.301
C7 (36/46) + = ASU 1-4	-0.349	**<u>0.556</u>**	**<u>0.602</u>**
Deflecting Wrinkle (36/46) + = ASU 3	**<u>0.775</u>**	0.251	0.285
Distal Trigonid Crest (36/46) + = ASU 1	**<u>0.627</u>**	-0.344	0.020
Eigenvalue	7.843	3.142	1.424
Variance	49.0%	19.6%	8.9%
Total variance	49.0%	68.6%	77.5%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

samples along PC1 also display the highest frequencies for these traits; so, these traits account for most the variation in each sample's relative position along this axis. Traits with strong negative loadings (<-0.5) are UM1 Carabelli's trait, the lack of expressive LM1 and LM2 cusp 5 and LM2 groove pattern. The highest scoring samples along PC1 tend to have lower frequencies of these traits.

As for PC2 (19.6% of the variance), its strongest positive loadings are UM1 C5, LM1 C6 and LM1 C7. Negative strong loadings occur on the following traits: LM1 an LM2 C5. Therefore, the highest scorers in this component tend to have highest frequencies of the former traits and lowest of the latter.
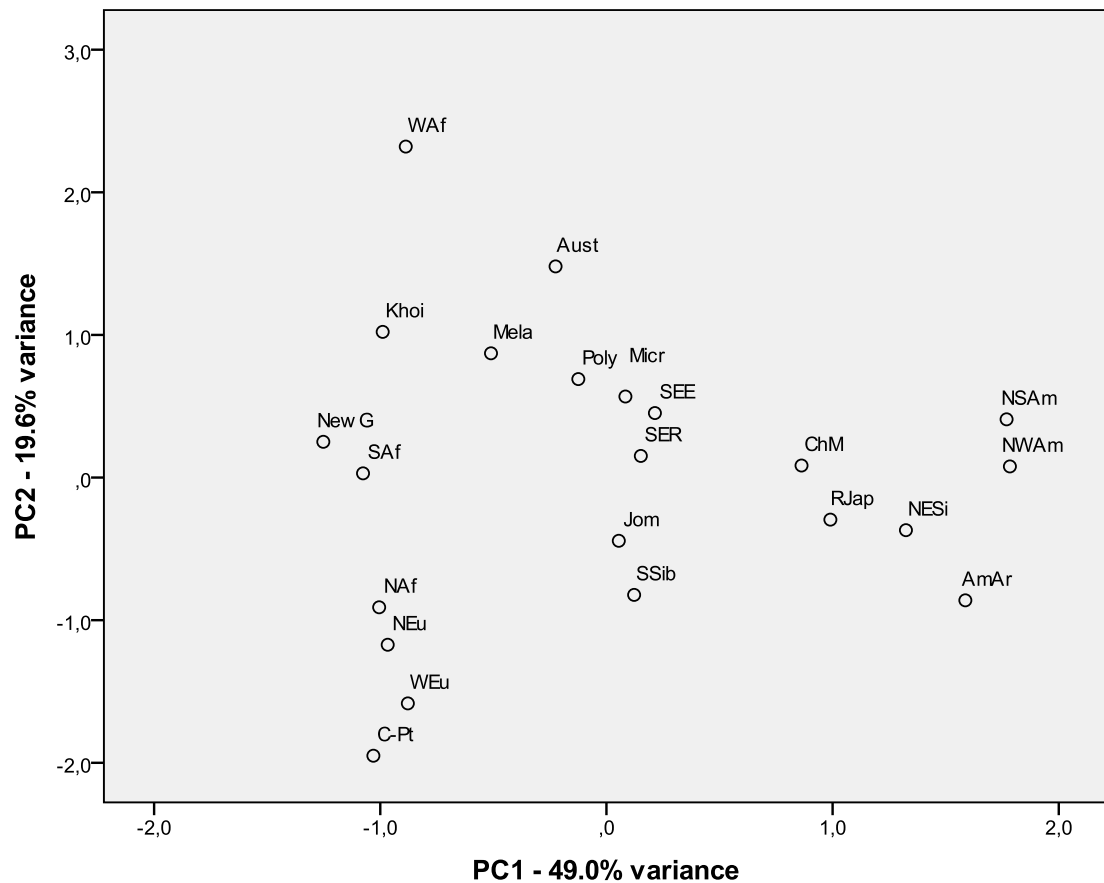
Figure 4.5.1. Scatterplot of the first two components in the comparison between Coimbra and world-wide samples reported in Scott and Turner (1997).
AmAr: American Arctic; Aust: Australia; ChM: China-Mongolia; C-Pt: Coimbra (Portugal); Jom: Jomon; Khoi: Khoisan; Mela: Melanesia; Micr: Micronesia; NAf: North Africa; NESi: Northeast Siberia; NEu: Northern Europe; NewG: New Guinea; NSAm: North and South Native Americans; NWAm: Northwest North America; Poly: Polynesia; RJap: Recent Japan; SAf: South Africa; SEE: Southeast Asia (Early); SER: Southeast Asia (Recent); SSib: South Siberia; WAf: West Africa; WEu: Western Europe.

Figure 4.5.2. displays the relative position of the samples along both PC1 and PC3 (8.9% of the variance), so as to allow the third dimension of this comparison to be taken into account without the visual confusion of displaying a tri-dimensional graph with this many samples. PC3 separates the Coimbra Portuguese from both European samples and places it among North Africans, West Africans, Southern and Northeastern Siberian populations, Jomon Japanese and Native Americans (American Arctic natives, Northwest North American natives and North and South American natives). The proximity towards North Africans is once again notorious, particularly along these two PC's. The strongest positive loadings are LM2 groove pattern and LM1 C7 and there are no strong negative loadings (<-0.5). These trait's frequencies follow the scoring trend for each sample, increasing as scores increase along PC3.
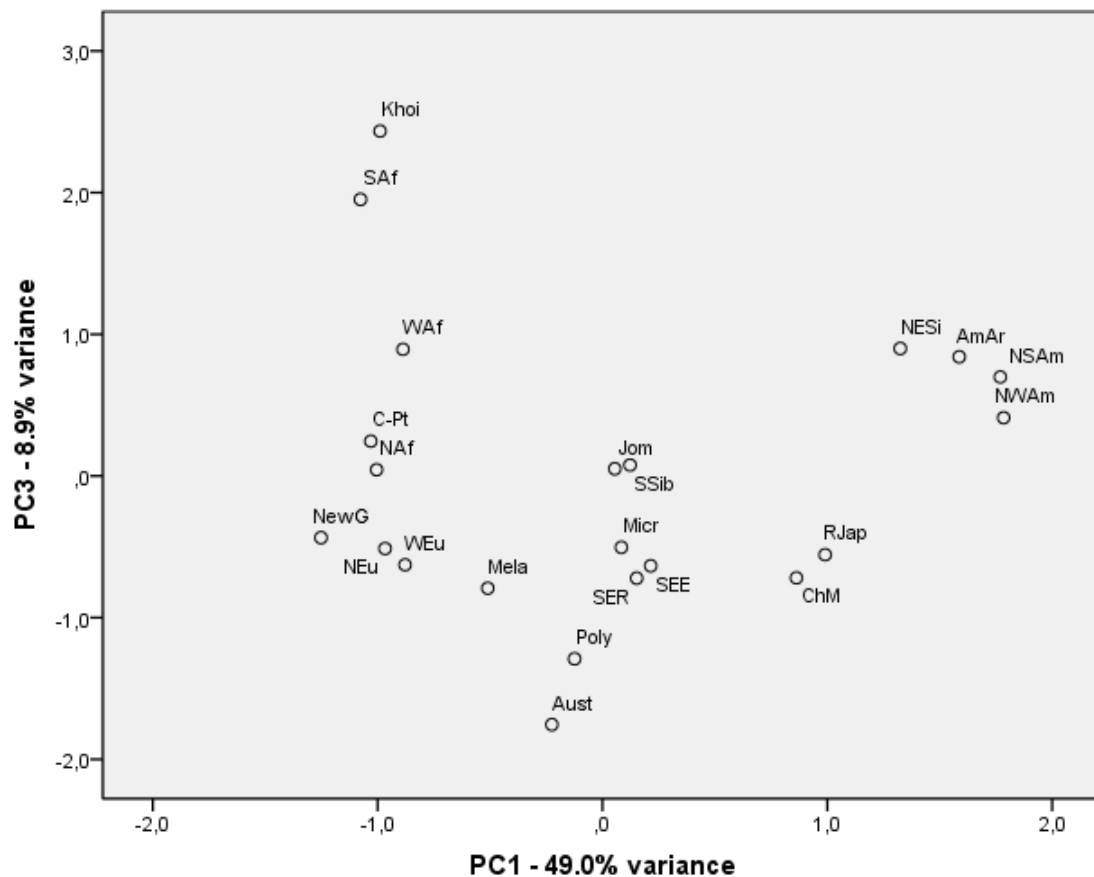
Figure 4.5.2. Scatterplot of the first and third components in the comparison between Coimbra and world-wide samples reported in Scott and Turner (1997).
AmAr: American Arctic; Aust: Australia; ChM: China-Mongolia; C-Pt: Coimbra (Portugal); Jom: Jomon; Khoi: Khoisan; Mela: Melanesia; Micr: Micronesia; NAf: North Africa; NESi: Northeast Siberia; NEu: Northern Europe; NewG: New Guinea; NSAm: North and South Native Americans; NWAm: Northwest North America; Poly: Polynesia; RJap: Recent Japan; SAf: South Africa; SEE: Southeast Asia (Early); SER: Southeast Asia (Recent); SSib: South Siberia; WAf: West Africa; WEu: Western Europe.

This first PCA shows the close biological relationship between the European and North African samples. The Portuguese in particular are closer to North Africans along PC1 and PC3. Most of the variation encompassing PC 1 and PC2 places the Portuguese closer to North and Western European samples.

The second comparison used data from Hanihara (2008). Both sexes from this source's samples were pooled. The dichotomization used by this author for each trait was applied to the Coimbra sample results (see Table 4.5.2.). Figure 4.5.3. shows the tight closeness between the European and the North African samples and Coimbra, along the PC1 (54.6% of the variance). West Asians and Indians were also close. PC2 (12.9% variance) adds samples from the Pacific and North America particularly, but

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Table 4.5.2. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and world-wide samples found in Hanihara (2008).

Trait (tooth)	PC 1	PC 2	PC 3
Shoveling (11/21) + = ASU 3-6	**<u>0.852</u>**	-0.265	0.219
Double Shoveling (11/21) + = ASU 2-6	**<u>0.669</u>**	-0.469	-0.305
Accessory Cusps (14/24) + = ASU 1	**<u>0.769</u>**	-0.394	-0.009
Accessory Cusps (15/25) + = ASU 1	**<u>0.663</u>**	0.380	-0.420
Carabelli's trait (16/26) + = ASU 3-7	**-0.865**	0.147	0.155
Hypocone (17/27) + = ASU 3-5	**<u>0.673</u>**	0.311	**<u>0.593</u>**
C6 (36/46) + = ASU 1-5	**<u>0.862</u>**	0.319	0.196
C7 (36/46) + = ASU 1-4	-0.390	**<u>0.621</u>**	0.100
Deflecting Wrinkle (36/46) + = ASU 2-3	**<u>0.864</u>**	0.448	0.102
Protostylid (36/46) + = ASU 2-7	**<u>0.831</u>**	-0.359	0.216
Distal Trigonid Crest (36/46) + = ASU 1	0.353	-0.081	**<u>0.553</u>**
C5 (37/47) + = ASU 1-5	**-0.746**	-0.221	0.363
C6 (37/47) + = ASU 1-5	**<u>0.825</u>**	0.302	-0.344
Eigenvalue	7.099	1.673	1.356
Variance	54.6%	12.9%	10.4%
Total variance	54.6%	67.5%	77.9%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

also Southeast Asia, and keeps the former samples relatively close. Figure 4.5.4. is a tridimensional representation, displaying the PC3 (10.4% variance) as well. Along that axis, the closest sample is North America, followed by Australia and Sub-Saharan Africa, and only then by West Asians, and finally Europeans and South Americans.

PC1's strongest positive loadings (> 0.6) are in UI1 shoveling and double shoveling, UP3 and UP4 accessory cusps, UM2 hypocone, LM1 and LM2 C6, LM1 deflecting wrinkle and protostylid (see Table 4.5.2.). The strongest negative loadings (<-0.7) are found in LM2 C5 and UM1 Carabelli's trait. The former increase, and the latter decrease, in frequency as the scores of each sample augment along PC1, contributing to their relative position.

The strongest positive loading on PC2 is LM1 C7 (0.621). On PC3, the UM2 hypocone and the LM1 distal trigonid crest display strong loadings (>0.5). These traits contribute the most to determine the relative sample position along those axes.
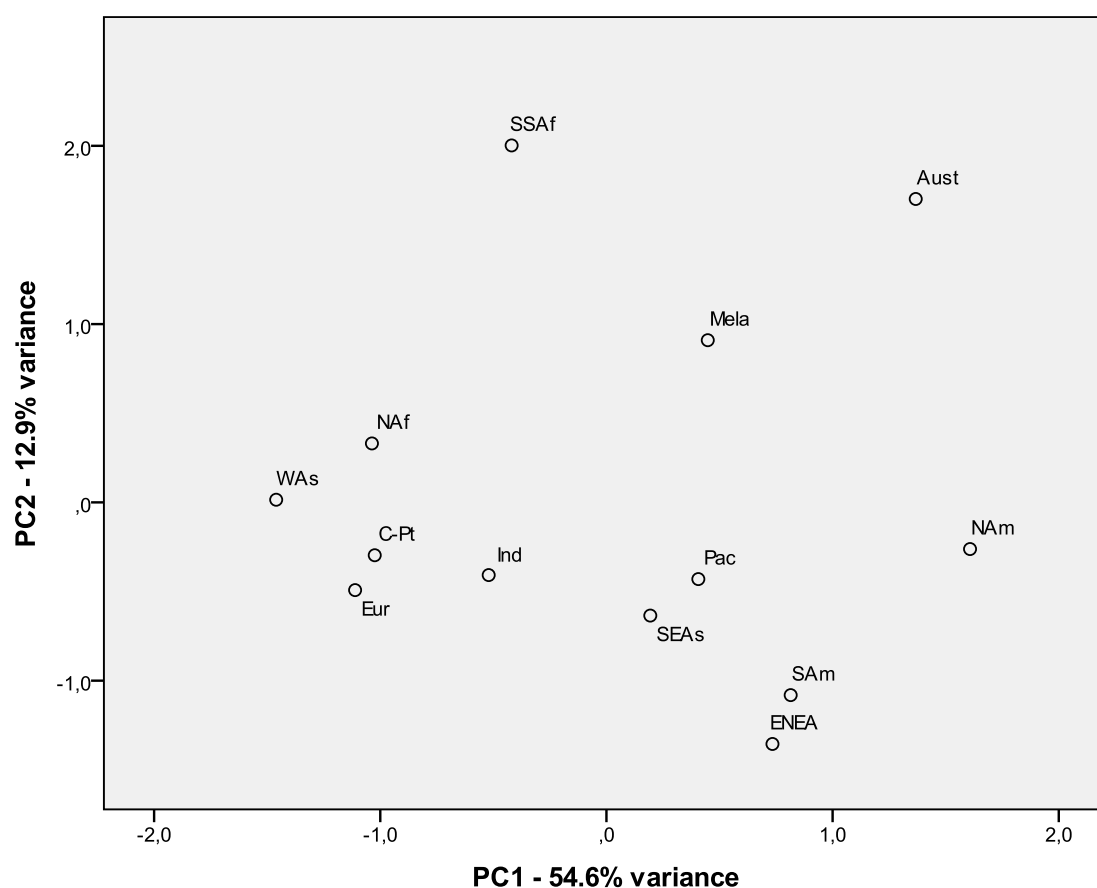
Figure 4.5.3. Scatterplot of the first two components in the comparison between Coimbra and world-wide samples reported in Hanihara (2008).
Aust: Australia; C-Pt: Coimbra (Portugal); ENEA: East/Northeast Asia; Eur: Europe; Ind: India; Mela: Melanesia; NAf: North Africa; NAm: North America; Pac: Pacific; SAm: South America; SEAs: Southeast Asia; SSAf: Sub-Saharan Africa; WAs: West Asia.

The closest overall samples are Europeans, West Asians and North Africans. All sub-samples that compose "West Asians" were drawn from the Near to Middle Orient, explaining their biological relatedness to Europe (and, indirectly, the Portuguese). "North Africans" are composed mainly of ancient Egyptians and Nubians, which might explain their further distance when compared to the homonymous sample from Scott and Turner (1997), with data compiled from Joel D. Irish (see, for example: Irish, 1998b). Despite this, along the axis that represents the most variance (PC1: 54.6% variance), North Africans are positioned almost in the same position as the Portuguese. This will be further analyzed and discussed below.
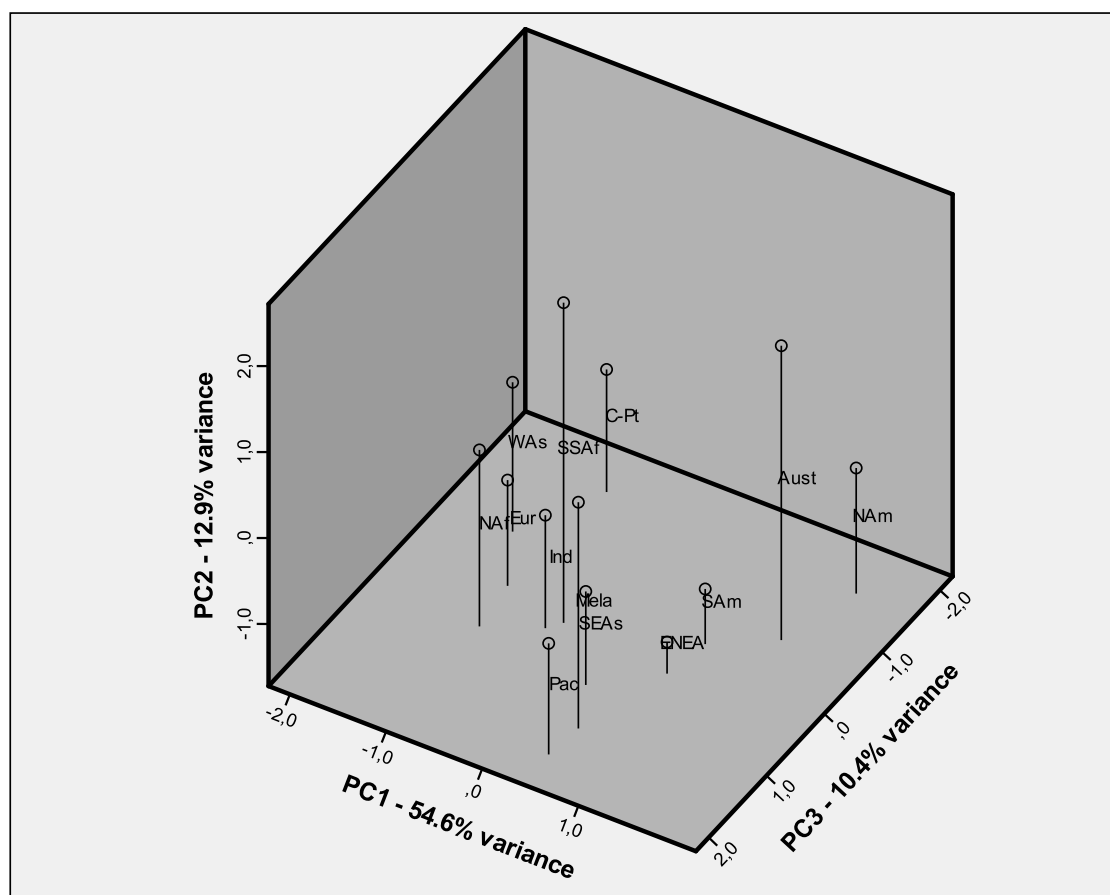
Figure 4.5.4. Scatterplot of the first and third components in the comparison between Coimbra and world-wide samples reported in Hanihara (2008).
Aust: Australia; C-Pt: Coimbra (Portugal); ENEA: East/Northeast Asia; Eur: Europe; Ind: India; Mela: Melanesia; NAf: North Africa; NAm: North America; Pac: Pacific; SAm: South America; SEAs: Southeast Asia; SSAf: Sub-Saharan Africa; WAs: West Asia.

4.5.4. Portuguese biological affinities to Iberian samples

So as to understand the placement of the Coimbra 19th/20th century population within a diachronic set of Iberian samples (from Spain), several morphologically well documented samples were used, alongside two world samples (North Africa and North and South Native Americans). The theses of Al Oumaoui (2009) and García Sívoli (2009) were consulted for the Spanish samples, as well as Scott and Turner's (1997) iconic work for the world samples. The inclusion of these two world samples provide a much needed contrast, due to their biological diversity when compared to what is expected from the other samples, presumably very similar. Since PCA extracts as much information as possible from the available data to differentiate the samples, the

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Table 4.5.3. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and several prehistoric and historic Spanish archaeological samples.

Trait (tooth)	PC 1	PC 2	PC3
Double Shoveling (11/21) + = ASU 2-6	**<u>0.876</u>**	0.183	-0.021
Interruption Grooves (12/22) + = ASU 1	0.057	**-0.573**	-0.032
Carabelli's trait (16/26) + = ASU 5-7	0.332	**-0.594**	0.436
C5 (16/26) + = ASU 1-5	-0.080	0.091	**<u>0.773</u>**
Hypocone (17/27) + = ASU 0-1	0.174	**-0.563**	0.461
Groove Pattern (37/47) + = ASU Y	-0.308	0.350	**<u>0.567</u>**
C5 (36/46) + = ASU 0	**-0.660**	0.180	0.335
C5 (37/47) + = ASU 0	**-0.891**	0.203	-0.119
C6 (36/46) + = ASU 1-5	**<u>0.618</u>**	**<u>0.562</u>**	0.186
C7 (36/46) + = ASU 1-4	0.280	**<u>0.843</u>**	0.112
Eigenvalue	2.703	2.263	1.497
Variance	27.0%	22.6%	15.0%
Total variance	27.0%	49.6%	64.6%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

comparison of biologically very similar samples without any such contrast would provide more detailed results, but hinder the exploration of all the available variability and force separation between samples. This could result in an erroneous interpretation of the real biological relations, which are much clearer when foreign samples are included.

Table 4.5.3. presents the data resultant from the PCA. Figure 4.5.5. shows a major cluster, which can be divided into at least three layers. The central portion clusters Coimbra very near the prehistoric Cerro de la Virgen, but is enlarged by prehistoric Motilla del Azuer, Son Real and S'Illot des Porros (both from the island of Mallorca), Late Roman Can Reines (Mallorca) and Roman Vila d' Madrid (Catalunia), Late Roman to Medieval Sant Pere and the smaller cluster of the prehistoric Son Maimó and Cerro de la Encina.

The first outer layer includes only the Majorcan pre-Talaiotic S'Aigua Dolça to one side, and the medieval Sahl ben Malik to the other. The second outer layer, further apart the central cluster, aligns the Medieval samples of Villanueva de Soportilla, El
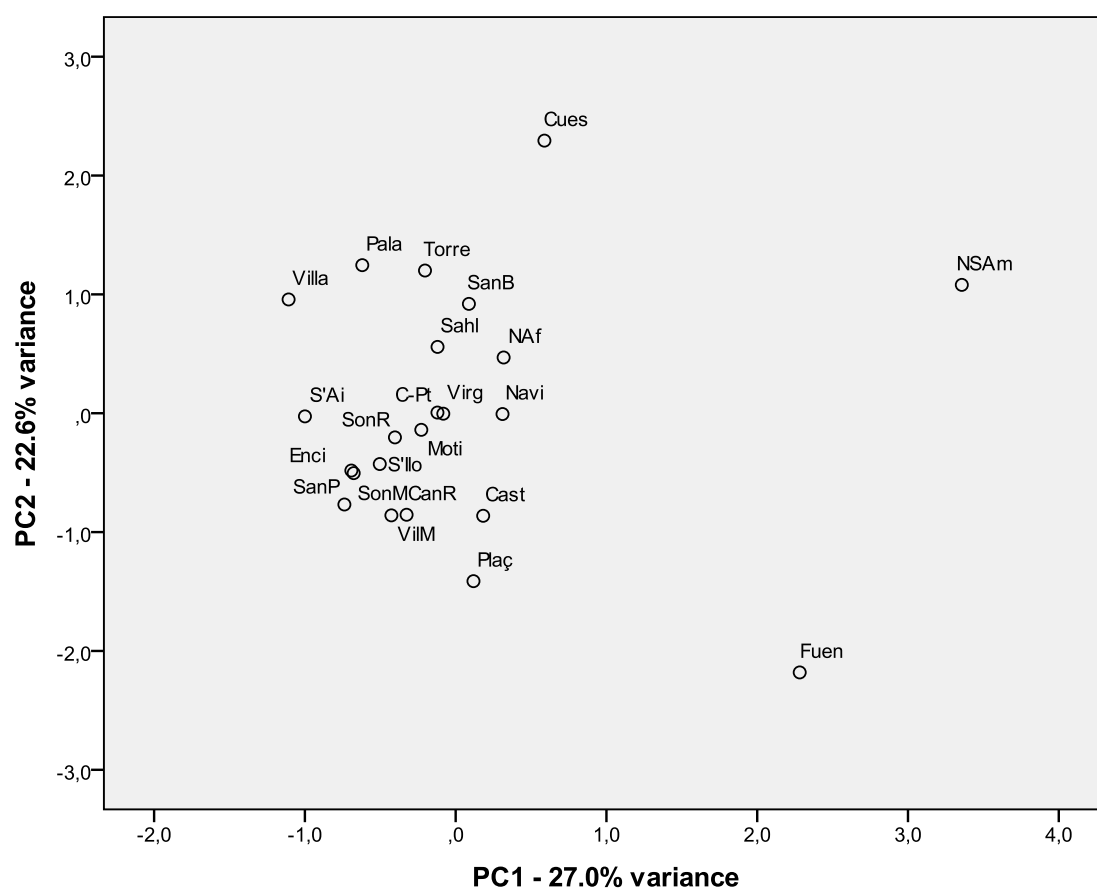
Figure 4.5.5. Scatterplot of the first two components in the comparison between Coimbra, other Iberian and world-wide samples reported in Al Oumaoui (2009) and García Sívoli (2009), and Scott and Turner (1997), respectively.
CanR: Can Reines; Cast: El Castellón Alto; C-Pt: Coimbra (Portugal); Cues: Cuesta del Negro; Enci: Cerro de la Encina; Fuen: Fuente Amarga; Moti: Motilla del Azuer; NAf: North Africa; Navi: La Navilla; NSAm: North and South Native Americans; Pala: El Castillo (Palacios de la Serra); Plaç: Plaça Vella; Sahl: Sahl ben Malik; S'Ai: S'Aigua Dolça; SanB: San Baudelio de Berlanga; SanP: Sant Pere; S'Ilo: S'Ilot des Porros; SonM: Son Maimó; SonR: Son Real; Torre: La Torrecilla; Villa: Villanueva de Soportilla; VilM: Vila d' Madrid; Virg: Cerro de la Virgen.

Castillo (Palacios de la Sierra), La Torrecilla (Islamic necropolis) and San Baudelio de Berlanga along the x axis, and aligns North Africa, the prehistoric sites of La Navilla and El Castellón Alto, and the modern sample of Plaça Vella along the y axis.

A third, much more distant layer, is very loosely formed by both disperse prehistoric samples of Cuesta del Negro and Fuente Amarga. North and South Native Americans are also distant, as expected.

Figure 4.5.6. shows the Coimbra sample roughly aligned with S'Illot des Porros, Can Reines, El Castillo (Palacios de la Sierra) and North and South American Natives along PC3, the z axis. The Portuguese sample is aligned and very near Plaça Vella, the Modern Spanish sample.

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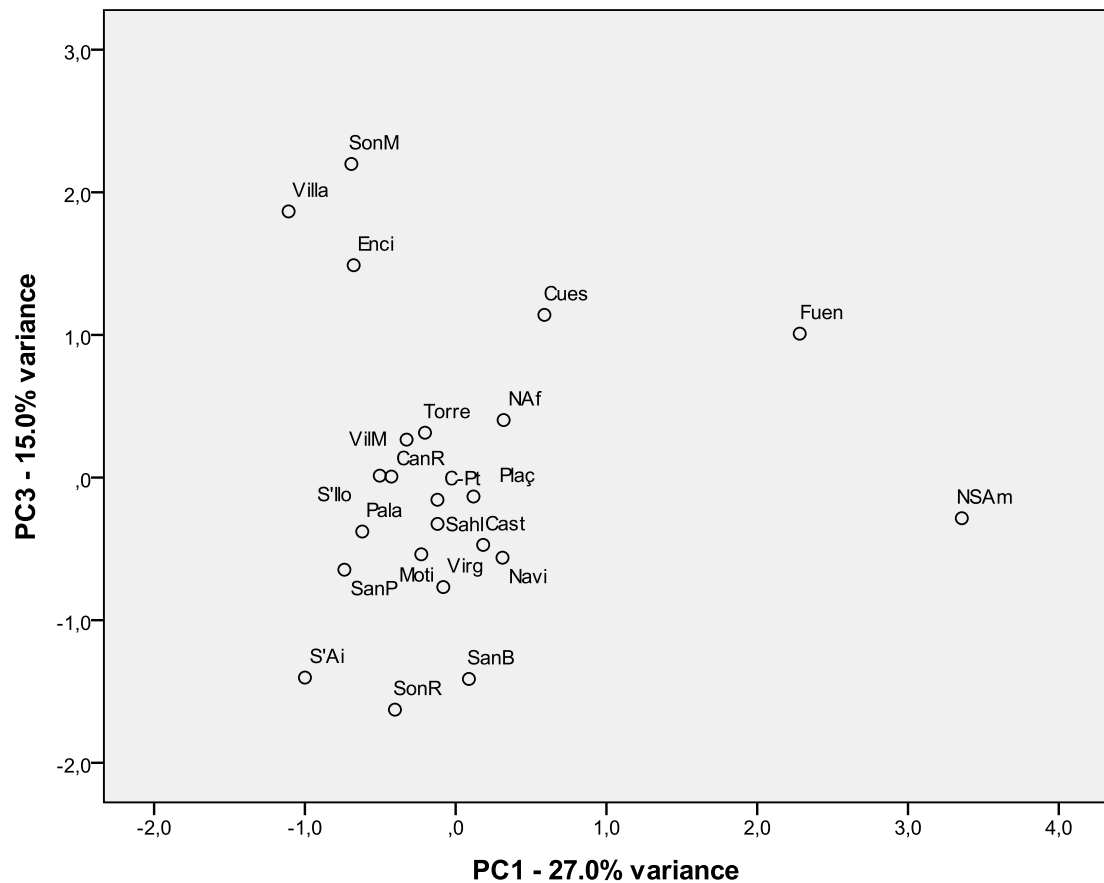
Figure 4.5.6. Scatterplot of the first and third components in the comparison between Coimbra, other Iberian and world-wide samples reported in Al Oumaoui (2009) and García Sívoli (2009), and Scott and Turner (1997), respectively.
CanR: Can Reines; Cast: El Castellón Alto; C-Pt: Coimbra (Portugal); Cues: Cuesta del Negro; Enci: Cerro de la Encina; Fuen: Fuente Amarga; Moti: Motilla del Azuer; NAf: North Africa; Navi: La Navilla; NSAm: North and South Native Americans; Pala: El Castillo (Palacios de la Serra); Plaç: Plaça Vella; Sahl: Sahl ben Malik; S'Ai: S'Aigua Dolça; SanB: San Baudelio de Berlanga; SanP: Sant Pere; S'Ilo: S'Ilot des Porros; SonM: Son Maimó; SonR: Son Real; Torre: La Torrecilla; Villa: Villanueva de Soportilla; VilM: Vila d' Madrid; Virg: Cerro de la Virgen.

The traits whose trend is most relevant to define the distribution of PC1's (27.0% of the variance) scores are UI1 double shoveling and LM1 C6, with strong positive loadings, as well as the lack of LM1 and LM2 C5, with strong negative loadings.

Strong positive loadings on PC2 (22.6% variance) were found for LM1 C6 and C7. Strong negative loadings were found for UI1 interruption grooves, UM1 Carabelli's trait and UM2 hypocone.

PC3 (15.0% variance) is characterized by the strong positive loadings found for UM1 C5 and LM2 groove pattern.

The PCA results demonstrate it is difficult to differentiate much of the samples, since the variability extracted from the data was limited, with the first three PC's

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amounting to only 64.6% of the variation. The disparity found for the Cuesta del Negro and Fuente Amarga Argaric (Bronze Age) samples shows the likeness of there being some influence of small sample size in their frequencies. The fact that only eleven traits could be included into this comparison may also contribute to this.

The Coimbra sample seems to be integrated within the Spanish samples, suggesting close biological proximity. North Africans are not biologically very distant, despite there being some closer populations. The Plaça Vella Modern sample is relatively close to Coimbra as well.

Both Roman samples of Can Reines and Vila d' Madrid seem closely related, through all three PC's analyzed. Medieval samples of Villanueva de Soportilla, El Castillo (Palacios de la Sierra), La Torrecilla (Islamic necropolis) and San Baudelio de Berlanga are close together in Figure 4.5.5., but are dispersed along PC3. La Torrecilla and Sahl ben Malik, Islamic cemeteries, are relatively close to both Coimbra and North Africans. This, as will be analyzed below, may indicate gene flow between North Africa and the Iberian Peninsula, through the Berber and Arabic invasion and their eight centuries long stay.

Some of the prehistoric and post-Romanization samples (Motilla de Azuer, Cerro de la Virgen, Can Reines, Vila d' Madrid, Sant Pere and S'Illot des Porros) seem to cluster together in all three components. This suggests some biological continuity in Bronze Age to Late Roman Iberian (or, at least, Spanish) samples. The overall analysis, excluding the major outliers of Cuesta del Negro and Fuente Amarga, also shows a relative proximity between the Iberian and the North African samples, and suggests gene flow between the latter and the former and shared ancestry within the former.

An MMD analysis comparing the Argaric culture sites of Castellón Alto and Fuente Amarga and the megalithic site of La Navilla (Granada, Spain) found similarities between the three samples. Divergent trait frequencies should correspond to endogamy or genetic drift, since the biological source of all three populations is historically considered to be East Andalucians from the Copper Age (Esquivel *et al.*, 2004). This, alongside the few traits considered, may explain the distance found between both Castellón Alto and La Navilla, and Fuente Amarga, for the present analysis.

Figure 4.5.7. compares the Coimbra sample to the averages of Bronze Age (Cuesta del Negro, Cerro da le Encina, La Navilla, El Castellón Alto, Cerro de la Virgen, Motilla del Azuer and Fuente Amarga) and Medieval (Sahl ben Malik, La Torrecilla, San Baudelio de Berlanga, Villanueva de Soportilla and El Castillo de

Palacios de la Sierra) samples in Al Oumaoui's (2009) work and the averages of Majorcan (S'Aigua Dolça, Son Maimó, Son Real, S'Illot des Porros and Can Reines) and Catalonian (Vila d' Madrid, Sant Pere and Plaça Vella) samples in García Sívoli's (2009) thesis, using 35 dental nonmetric traits (instead of the 10 used in the previous comparison, so as to allow inclusion of world-wide samples for contrast).

This bi-dimensional representation of the variation between these samples encompassed in PC1 (40.0%) and PC2 (26.0%) shows an overall equidistant position that only excludes the proximity between the Bronze Age sample and Coimbra.

Figure 4.5.8., on the other hand, with the introduction of the third PC (21.1% of the variance), allows for the distribution of the samples throughout the graphic.

Strong positive loadings (>0.5) for PC1 (see Table 4.5.4.) were: UI1 double shoveling, UP3 and UP4 accessory cusps, LP3 and UP4 odontome, LP3 and LP4 lingual cusp variation, LM2 and LM3 groove pattern, LM1 protostylid, LM3 C5, LM2 and LM3 C6, and LM1 and LM3 C7. Strong negative loadings (<-0.5) were: UI1 and

Table 4.5.4. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and Spanish samples.

Trait (tooth)	PC 1	PC 2	PC3
Double Shoveling (11/21) + = ASU 2-6	**<u>0.585</u>**	-0.489	0.647
Shoveling (11/21) + = ASU 2-6	-0.346	0.113	-0.348
Interruption Grooves (11/21) + = ASU 1	**-0.951**	-0.277	-0.056
Interruption Grooves (12/22) + = ASU 1	**-0.990**	-0.126	0.053
Distal Accessory Ridge (13/23) + = ASU 1-5	0.331	**<u>0.534</u>**	**-0.658**
Accessory Cusps (14/24) + = ASU 1	**<u>0.609</u>**	-0.334	0.716
Accessory Cusps (15/25) + = ASU 1	**<u>0.624</u>**	-0.362	0.686
Odontome (14/24) + = ASU 1	**-0.730**	-0.313	0.088
Odontome (15/25) + = ASU 1	**<u>0.678</u>**	**-0.714**	-0.141
Carabelli's trait (16/26) + = ASU 5-7	-0.219	0.313	0.903
Hypocone (17/27) + = ASU 0-1	-0.281	**<u>0.869</u>**	0.054
Parastyle (18/28) + = ASU 3-5	0.161	**<u>0.653</u>**	0.176
Distal Accessory Ridge (33/43) + = ASU 1-5	0.111	**<u>0.829</u>**	0.042
Lingual Cusp Variation (34/44) + = ASU 2-9	**<u>0.741</u>**	**<u>0.519</u>**	-0.231
Lingual Cusp Variation (35/45) + = ASU 2-9	**<u>0.769</u>**	-0.298	-0.273
Odontome (34/44) + = ASU 1	**<u>0.634</u>**	**-0.767**	-0.084

Table 4.5.4. (Continued.)

Trait (tooth)	PC 1	PC 2	PC3
Odontome (35/45) + = ASU 1	0.273	0.365	0.869
Deflecting Wrinkle (36/46) + = ASU 1-3	**-0.959**	-0.135	-0.109
Anterior Fovea (36/46) + = ASU 1-4	0.106	**-0.826**	0.363
Distal Trigonid Crest (36/46) + = ASU 1	0.287	0.460	**-0.840**
Groove Pattern (36/46) + = ASU X	**-0.723**	**-0.621**	-0.237
Groove Pattern (37/47) + = ASU Y	**0.924**	0.378	0.017
Groove Pattern (38/48) + = ASU Y	**0.909**	-0.330	-0.169
Protostylid (36/46) + = ASU 1-7	**0.893**	0.101	-0.404
Protostylid (37/47) + = ASU 1-7	0.248	0.147	**-0.908**
Protostylid (38/48) + = ASU 1-7	0.482	-0.204	-0.489
C5 (36/46) + = ASU 0	0.169	**0.867**	0.458
C5 (37/47) + = ASU 0	0.431	**0.783**	0.247
C5 (38/48) + = ASU 0	**0.783**	0.444	0.314
C6 (36/46) + = ASU 1-5	0.330	0.154	0.843
C6 (37/47) + = ASU 1-5	**0.580**	**-0.766**	-0.176
C6 (38/48) + = ASU 1-5	**0.984**	-0.075	0.139
C7 (36/46) + = ASU 1a-4	**0.923**	-0.019	-0.124
C7 (37/47) + = ASU 1a-4	0.281	**0.648**	**-0.511**
C7 (38/48) + = ASU 1a-4	**0.734**	**-0.598**	-0.284
Eigenvalue	14.012	9.103	7.378
Variance	40.0%	26.0%	21.1%
Total variance	40.0%	66.0%	87.1%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

UI2 interruption grooves, UP3 odontome, and LM1 deflecting wrinkle and groove pattern.

For PC2, there were strong positive loadings from UC and LC distal accessory ridge, UM2 hypocone, UM3 parastyle, UP4 lingual cusp variation, LM1 and LM2 C5, and LM2 C7. Strong negative loadings were found in UP4 and LP3 odontome, LM1 anterior fovea and groove pattern, LM2 C6 and LM3 C7.

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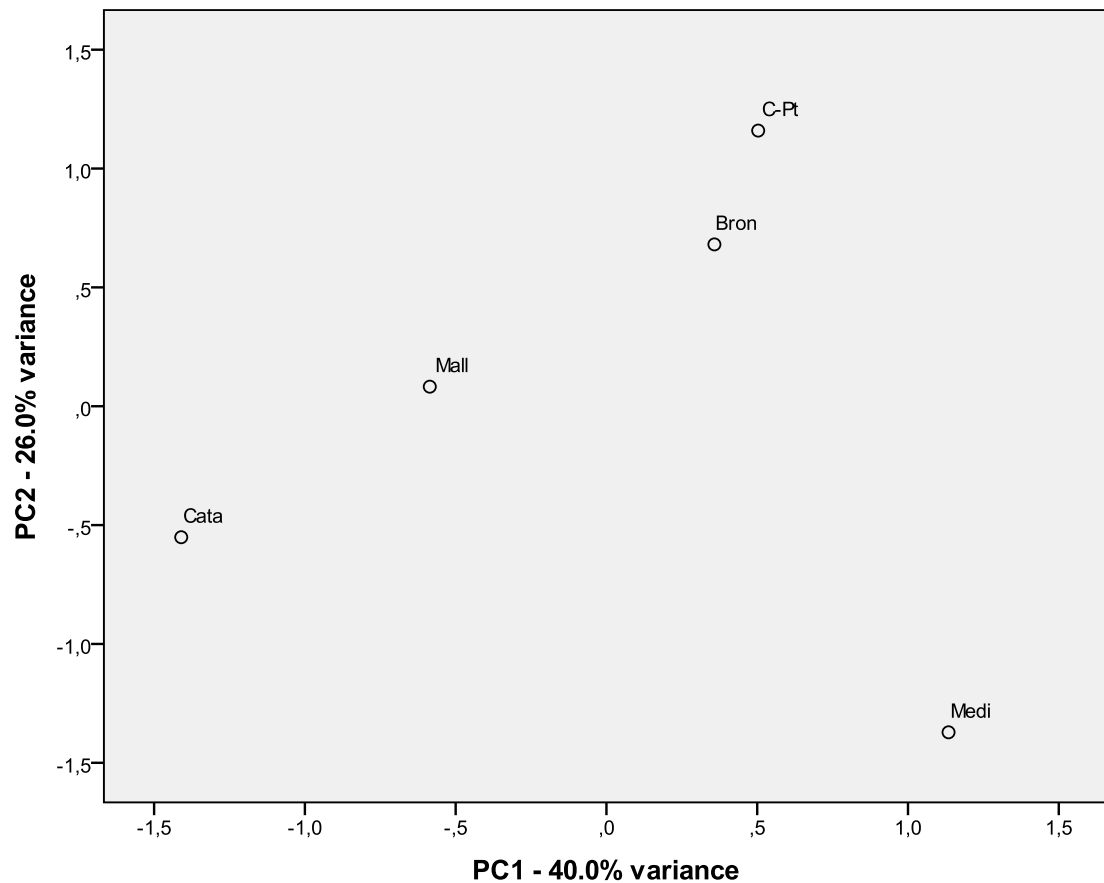
Figure 4.5.7. Scatterplot of the first two components in the comparison between Coimbra and averaged chronological and geographical Iberian samples reported in Al Oumaoui (2009) and García Sívoli (2009). Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Mall: Mallorca; Medi: Medieval.

PC3 is characterized by strong positive loadings from UI1 double shoveling, UP3 and UP4 accessory cusps, UM1 Carabelli's trait, LP4 odontome and LM1 C6; and by strong negative loadings from UC distal accessory ridge, LM1 distal trigonid crest, and LM2 protostylid and C7.

PCA translates variation in the samples' scores for each component, so the factor loadings demonstrate how each variable contributes to the score of each sample. If a loading is strong and positive, it indicates the highest sample scores for that PC correspond roughly to the highest variable frequency. The strong negative ones indicate the highest scores are connected to the lower trait frequencies.

The positioning of the Bronze Age samples' average trait frequencies near Coimbra in the first two PC's (66.0% of the total variance) could suggest this Portuguese population to be biologically derived from these protohistoric populations, and to have had little gene flow or genetic drift. However, two major outliers from the

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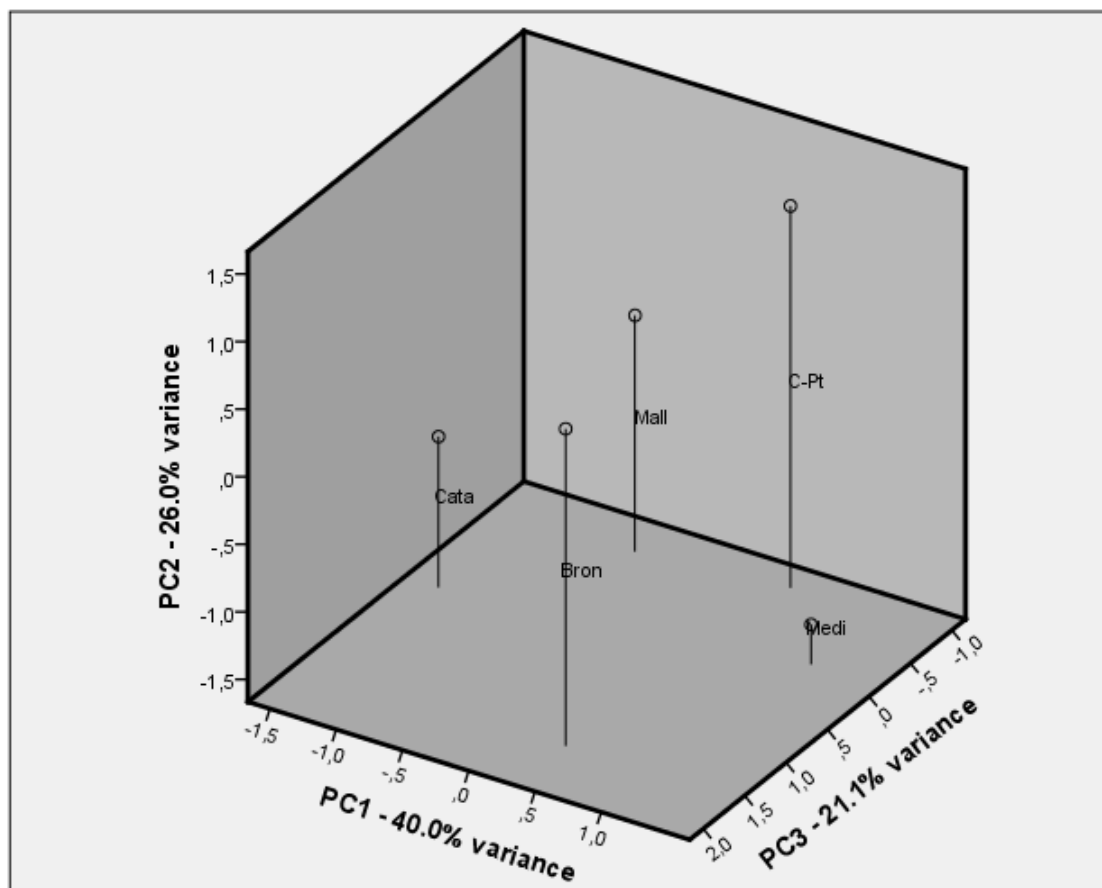
Figure 4.5.8. Scatterplot of the first three components in the comparison between Coimbra and averaged chronological and geographical Iberian samples reported in Al Oumaoui (2009) and García Sívoli (2009). Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Mall: Mallorca; Medi: Medieval.

previous PCA (Fuente Amarga and Cuesta del Negro) are considered within this average, which may have distorted the final results. The tridimensional graph (87.1% variance) also contradicts this hypothesis, since PC3 places the Bronze Age samples very far from Coimbra.

The relative equidistant distribution of the samples in Figure 4.5.8. shows these samples to be very biologically close to each other. The most distant to Coimbra seem to be the Catalonian and Medieval samples, which is probably caused by their heterogeneity. The Catalonians are represented by a Roman Age sample (Vila d' Madrid), a Late Roman to Medieval sample (Sant Pere) and a Modern sample (Plaça Vella) and the Medieval samples include Southern (with potentially heavy Islamic influence) and Northern populations.

So, and once again not excluding gene flow, Iberian samples seem to be derived from a common ancestor.

Table 4.5.5. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and several prehistoric Portuguese archaeological samples.

Trait (tooth)	PC 1	PC 2	PC 3
Carabelli's trait (16/26) + = ASU 5-7	-0.342	**_0.727_**	0.034
Hypocone (17/27) + = ASU 0-1	**-0.865**	-0.107	0.288
Lingual Cusp Variation (35/45) + = ASU 2-9	**_0.820_**	-0.084	0.205
Groove Pattern (37/47) + = ASU Y	**-0.827**	-0.032	0.390
C5 (37/47) + = ASU 1-5	0.444	-0.089	0.128
C6 (37/47) + = ASU 1-5	0.241	**_0.899_**	-0.267
C6 (36/46) + = ASU 1-5	0.471	-0.025	**_0.568_**
C7 (36/46) + = ASU 1-4	0.269	0.482	**_0.645_**
C7 (37/47) + = ASU 1-4	**-0.691**	0.077	-0.293
C5 (16/26) + = ASU 1-5	**_0.844_**	-0.052	-0.261
Eigenvalue	3.960	1.606	1.258
Variance	39.6%	16.1%	12.6%
Total variance	39.6%	55.7%	68.3%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The visual representation of the results from the next PCA is found on Figures 4.5.9. and 4.5.10. The prehistoric (Neolithic and Chalcolithic) and contemporary (drawn from the same set of collections as the present sample) Central Portuguese samples from Silva (2002, 2012) were compared to the data from Al Oumaoui (2009) and García Sívoli (2009), as summarized in the previous analysis (providing contrast), and the present Coimbra sample. Chronologically, the oldest samples dated by Silva (2002; see also Jackes *et al.*, 2001) are Dólmen de Ansião and Serra da Roupa (4600 BP), followed by Hipogeu de Monte Canelas I (4400 BP) and Paimogo I (4200 BP; except the oldest occupation, which would be grouped with the former chronological group), then Cova da Moura (again, the oldest occupation, presumably a minority, is much older) and São Paulo II (3900 BP; henceforth, for brevity, the Roman numeral identifying the chronological stage of some samples - *eg*. Paimogo I - will be omitted). Geographically, all samples hail from the Lisbon Peninsula, except Dólmen de Ansião (from Leiria, to the north), Hipogeu de São Paulo (from the Setúbal Peninsula, to the South) and Hipogeu de Monte Canelas (from Algarve, Southern Portugal).
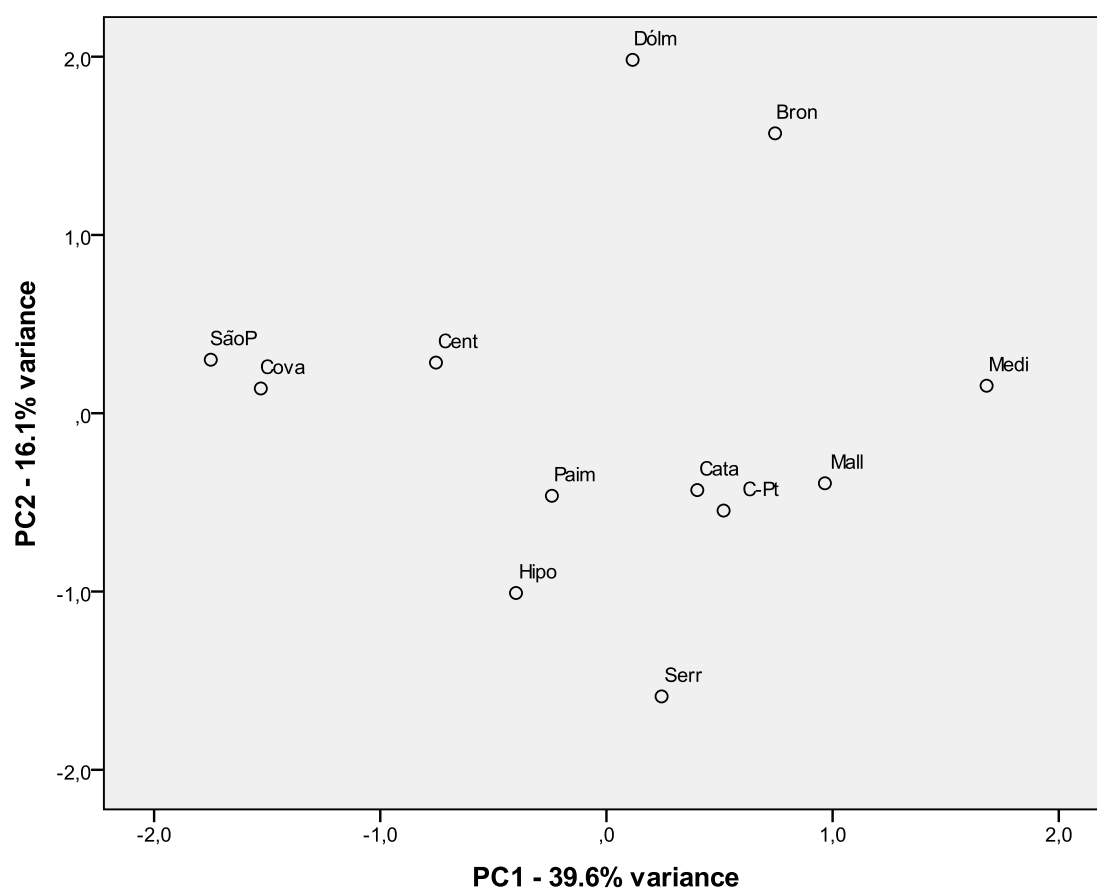
Figure 4.5.9. Scatterplot of the first two components in the comparison between Coimbra, other Portuguese prehistoric and contemporary samples (Silva, 2002, 2012) and averaged Spanish samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; Cent: Central Portugal; Cova: Cova da Moura; C-Pt: Coimbra (Portugal); Dólm: Dólmen de Ansião; Hipo: Hipogeu de Monte Canelas; Mall: Mallorca; Medi: Medieval; Paim: Paimogo; SãoP: Hipogeu de São Paulo; Serr: Serra da Roupa.

Figure 4.5.9. shows a distribution predicted by the statistical analyses' results reported by Silva (2002), separating São Paulo and Cova da Moura from Dólmen de Ansião, Paimogo and Serra da Roupa along the x axis (PC1: 39.6% variance). The exception is the positioning of Hipogeu de Monte Canelas, nearer Paimogo and further from São Paulo and Cova da Moura, contrarily to what was found by Silva (2002). The y axis (PC2: 16.1% variance) puts Dólmen de Ansião further apart from the other Portuguese prehistoric samples. The present Coimbra sample is very close to the Catalonian and Majorcan samples. After these, the Medieval sample, Paimogo, Serra da Roupa, Hipogeu of Monte Canelas and Central Portugal are the closest samples.

Figure 4.5.10. defines two loosely established clusters determined by PC3 (12.6% variance), the z axis. The first one concentrates Dólmen de Ansião, Cova da Moura, Paimogo, Hipogeu of Monte Canelas, Central Portugal, the Medieval Spanish

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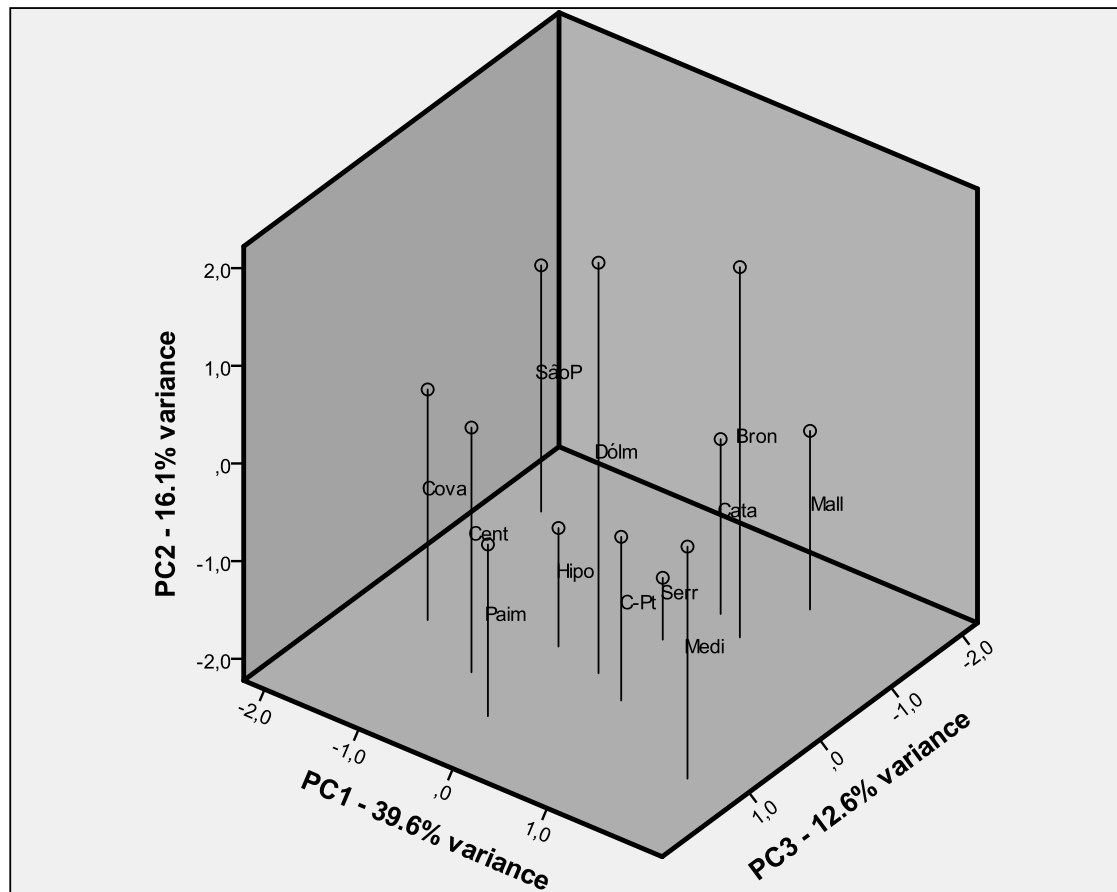
Figure 4.5.10. Scatterplot of the first three components in the comparison between Coimbra, other Portuguese prehistoric and contemporary samples (Silva, 2002, 2012) and averaged Spanish samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; Cent: Central Portugal; Cova: Cova da Moura; C-Pt: Coimbra (Portugal); Dólm: Dólmen de Ansião; Hipo: Hipogeu de Monte Canelas; Mall: Mallorca; Medi: Medieval; Paim: Paimogo; SãoP: Hipogeu de São Paulo; Serr: Serra da Roupa.

sample and Coimbra. The second concentrates São Paulo, Catalonian, Majorcan and Bronze Age samples. These "clusters" are interposed by Serra da Roupa. Central Portugal and the Coimbra sample are very near each other.

These positions are determined by the strongest loadings from ten dental non-metric traits on three PC's (see Table 4.5.5.). PC1 has strong positive loadings (>0.5) for LP4 lingual cusp variation and UM1 C5. Strong negative loadings (<-0.5) are yielded by UM2 hypocone absence, and LM2 groove pattern and C7.

PC2 displays strong positive loadings for UM1 Carabelli's trait and LM1 C6; and no strong negative loadings. PC3 is characterized by strong positive loadings for LM2 C6 and LM1 C7. Strong negative loadings are also absent.

The Medieval Spanish and most prehistoric Portuguese samples are more distant than the remaining less diachronic samples of Catalonia, Mallorca, and the

contemporary Portuguese. Serra da Roupa unexpectedly falls near this latter cluster. The Bronze Age Spanish and Medieval Spanish samples are relatively isolated from the other clusters, according to the y and z axes.

Figure 4.5.9. seems to see Central Portugal placed in the center of a loose circle composed of São Paulo, Dólmen de Ansião, Bronze Age Spain, Catalonia, Paimogo, Hipogeu de Monte Canelas and Cova da Moura. The present Coimbra sample, presumably extremely close to Central Portugal, since they were drawn from the same chronological and geographical context, is again at the center of a semi-circle formed by Serra da Roupa, Paimogo, Hipogeu de Monte Canelas, Mallorca and Catalonia, with the Bronze Age sample nearby (along PC1). Without the further separation between prehistoric and Medieval (including Medieval Islamic) and protohistoric and Roman, Medieval, Modern and contemporary provided by PC3, the other two components (55.7% variance) suggest the contemporary late 19th/early 20th century Portuguese are biologically influenced by all these samples. Even on Figure 4.5.10., these samples (Central Portugal and Coimbra-Portugal) seem to be the most central in relation to the Portuguese Neolithic, corroborating this suggestion, based on the data available for these twelve samples and ten traits.

Another factor indicating proximity between all samples is the most peripheral samples according to PC2 are central in PC3 distribution, and *vice versa* (except Bronze Age Spain). São Paulo (along PC's 1 and 3) and Medieval Spain (along PC's 1) seem to be the most distant samples, since Bronze Age Spain is near Coimbra along PC 1 (which variance is, by far, the most relevant).

Dental morphological data indicate biological homogeneity between Portuguese Mesolithic and Neolithic (Jackes *et al.*, 1997). The above data also demonstrate some continuity between all Late Neolithic/Chalcolithic populations, which corroborates the possibility that no sudden replacement of the population originated the introduction of a new biological entity into the Portuguese territory in the late prehistory/early protohistory. First molar occlusal area did not change between Late Neolithic (Paimogo) and Modern Portuguese (Coimbra) populations, while the area of the polygon formed by first molar cusp tips augmented between the same time periods, which testifies to a derivation of cusp tips to a more peripheral area of the crown's occlusal surface, which probably reflects evolutionary adaption and not biological discontinuity (Fernandes *et al.*, 2013).

Table 4.5.6. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and several diachronic Iberian samples.

Trait (tooth)	PC 1	PC 2	PC 3
Lingual Cusp Variation (35/45) + = ASU 2-9	**<u>0.776</u>**	0.286	-0.161
Groove Pattern (37/47) + = ASU Y	**-0.654**	-0.151	0.440
C5 (37/47) + = ASU 1-5	**<u>0.675</u>**	-0.334	-0.341
C6 (36/46) + = ASU 1-5	0.069	**<u>0.857</u>**	-0.107
C6 (37/47) + = ASU 1-5	**<u>0.615</u>**	-0.090	**<u>0.570</u>**
C7 (36/46) + = ASU 1-4	0.363	0.369	**<u>0.700</u>**
C7 (37/47) + = ASU 1-4	-0.305	**<u>0.765</u>**	-0.152
Eigenvalue	2.093	1.680	1.184
Variance	29.9%	24.0%	16.9%
Total variance	29.9%	53.9%	70.8%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The same samples used on the previous PCA are again compared in the present analysis, now including the sample described by Silva and colleagues (2006a) of another Late Neolithic/Chalcolithic population, from Praia da Samarra (Samarra Beach). The inclusion of this sample mandates that only seven lower dental discrete traits be used, and that justifies its exclusion from the former analysis and the realization of this one.

Figures 4.5.11. and 4.5.12. show the spatial distribution of the samples along two and three axes, respectively. PC1 (29.9% variance) and PC2 (24.0% variance) provide 53.9% of the variation. When PC3 (16.9%) is included, 70.8% of the variation is represented (see Table 4.5.6.).

Strong positive loadings (>0.5) characterizing PC1 are found for LP4 lingual cusp variation, LM2 C5 and C6. A strong negative loading (<-0.5) is provided by LM2 groove pattern.

PC2 presents strong positive loadings for LM1 C6 and LM2 C7. Strong negative loadings are absent.

The strongest positive loadings on PC3 are for LM2 C6 and LM1 C7.

The relations among the samples also found on the previous analysis are not fundamentally altered. The Central Portuguese sample is not surrounded by the mentioned samples, but it is closer to them. Coimbra is still the center of a semi-circle,
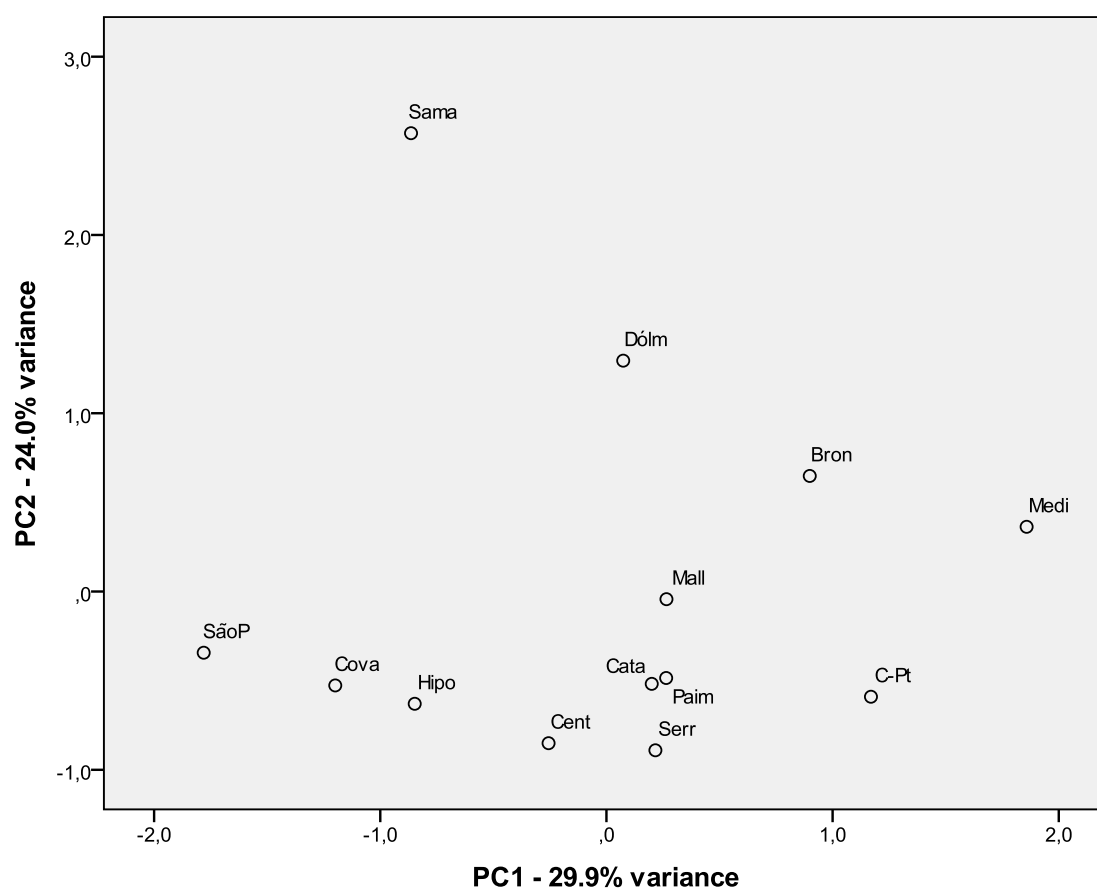
Figure 4.5.11. Scatterplot of the first two components in the comparison between Coimbra, other Portuguese prehistoric and contemporary samples (Silva, 2002, 2012; Silva *et al.*, 2006a) and averaged Spanish samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; Cent: Central Portugal; Cova: Cova da Moura; C-Pt: Coimbra (Portugal); Dólm: Dólmen de Ansião; Hipo: Hipogeu de Monte Canelas; Mall: Mallorca; Medi: Medieval; Paim: Paimogo; Sama: Praia da Samarra; SãoP: Hipogeu de São Paulo; Serr: Serra da Roupa.

which is now completed by the Bronze Age sample. São Paulo and Dólmen de Ansião are now apparently closer than before.

The changes in position found on Figure 4.5.11. are derived from the introduction of the Samarra sample, which seems to be biologically distinct from the other Iberian samples. The third dimension (the z axis, PC3) places this sample in the middle of the clusters formed from the coordinates for PC1 a PC3, akin Coimbra. Samarra is only relatively related to Dólmen de Ansião, and seems to be at least as distinct from this sample as it is distinct from the other samples. Thus, Samarra seems, from the present analysis, to be a far from direct biological influence towards the contemporary Portuguese populations.

In the Mehrgarh site (South Asia) there does not seem to be biological continuity
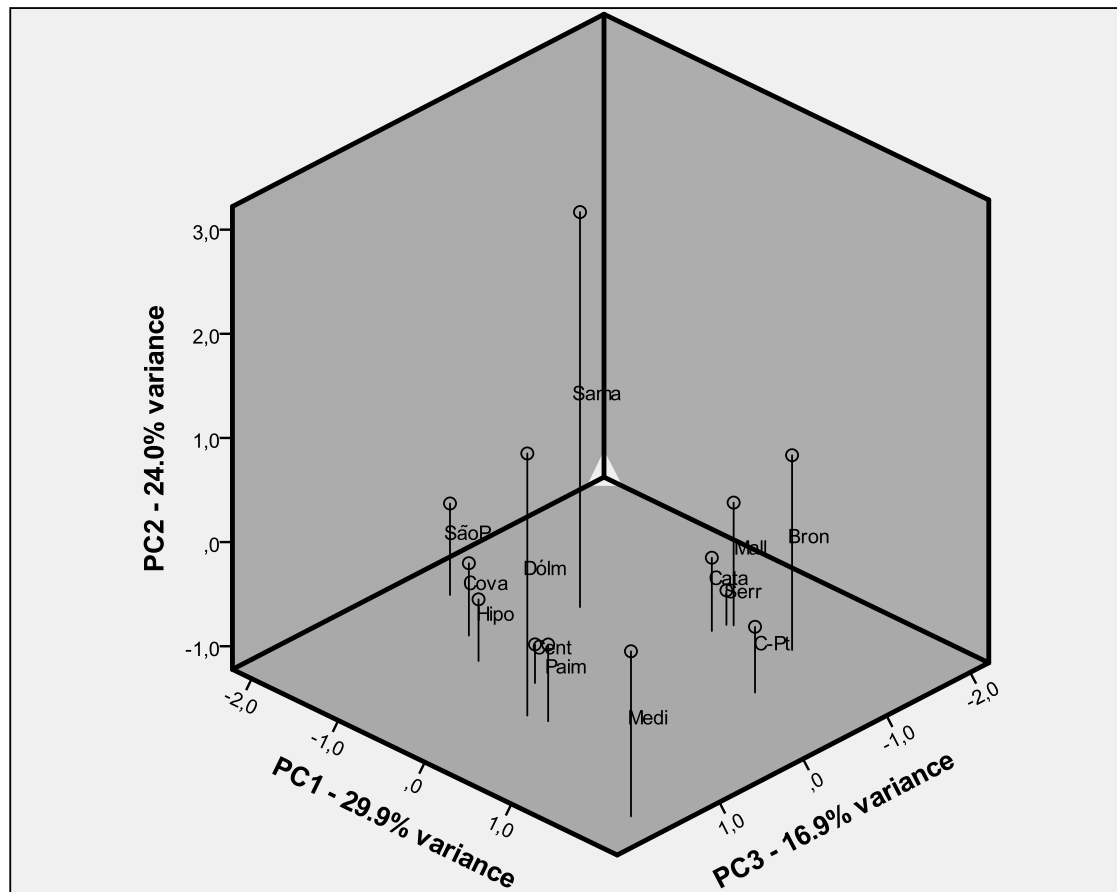
Figure 4.5.12. Scatterplot of the first three components in the comparison between Coimbra, other Portuguese prehistoric and contemporary samples (Silva, 2002, 2012; Silva *et al.*, 2006a) and averaged Spanish samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; Cent: Central Portugal; Cova: Cova da Moura; C-Pt: Coimbra (Portugal); Dólm: Dólmen de Ansião; Hipo: Hipogeu de Monte Canelas; Mall: Mallorca; Medi: Medieval; Paim: Paimogo; Sama: Praia da Samarra; SãoP: Hipogeu de São Paulo; Serr: Serra da Roupa.

between the Neolithic and the Chalcolithic occupations. In fact, the Neolithic group seems to be connected to other Chalcolithic sites, suggesting gene flow into the Mehrgarh site in between these chronological periods, despite the cultural continuity testified by archaeology (Lukacs and Hemphill, 1991). Dental morphology was used to determine if the Bell Beaker culture (Chalcolithic) found in Switzerland was of Southern influence (from Spain and France) or Eastern influence (from the Czech Republic and Hungary). Biologically, since the Final Neolithic and through the Bell Beaker phase, the influence came from Southern Europe (Desideri and Besse, 2010). In Portugal, these biological discontinuities are hard to postulate, since the relations between the samples compared in the two last PCA's do not seem to justify a rupture between two separate populations.

The complex biological relations between prehistoric and contemporary populations in Portugal need further research in order to be fully understood, but there seems to have been differentiation processes in genetic diversity, such as gene flow and genetic drift, both expected phenomena when interpreting the biological relations of such diachronic populations. The affinities between Bronze Age Spain and Neolithic/Chalcolithic Portugal seem distant, but only more research can shed light into population movements in Iberia.

The same average results from Al Oumaoui (2009) and García Sívoli (2009) are used as Iberian contrast to another analysis, now including a Menorcan diachronic sample (from the prehistory to the Romanization in Menorca Island) and a Medieval sample from the river basins of Ebro and Douro (or, in Spanish, Duero), which include samples that are part of the set used to produce the average results represented as Medieval Spain. The sample from the island of Menorca is comprised of 49 individuals from between the 15th century BC and the Roman Period. The second is from the Alto Ebro and Alto Duero river basins and is comprised of 88 individuals from between the 9th and 13th centuries. These groups were considered genetically similar, according to

Table 4.5.7. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and several diachronic Spanish samples.

Trait (tooth)	PC 1	PC 2	PC 3
Parastyle (18/28) + = ASU 3-5	**0.665**	-0.332	**0.505**
Anterior Fovea (36/46) + = ASU 1-4	**0.615**	-0.277	0.150
Groove Pattern (36/46) + = ASU X	**-0.946**	0.265	0.088
Groove Pattern (37/47) + = ASU Y	**0.986**	-0.125	-0.065
Protostylid (36/46) + = ASU 1-7	0.372	**0.921**	0.085
Protostylid (38/48) + = ASU 1-7	-0.077	**0.683**	0.444
C7 (36/46) + = ASU 1a-4	**0.706**	**0.629**	-0.229
C7 (37/47) + = ASU 1a-4	-0.434	**0.671**	0.496
Cusp Number (36/46) + = ASU 4	0.460	-0.172	**0.796**
Cusp Number (37/47) + = ASU 5+	**0.650**	**0.619**	-0.411
Eigenvalue	4.154	2.846	1.595
Variance	41.5%	28.5%	16.0%
Total variance	41.5%	70.0%	86.0%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

the 42 observed traits, and biologically proximate to both North European and North African populations (Souich, 2001).

Ten dental morphologic traits were used (Table 4.5.7.). The ones that yielded stronger positive loadings (>0.5) on PC1 (41.5% variance) are UM3 parastyle, LM1 anterior fovea and C7, and LM2 groove pattern and cusp number. The only strong negative loading (<-0.5) is LM1 groove pattern.

PC2 (28.5% variance) shows strong positive loadings for LM1 and LM3 protostylid, LM1 and LM2 C7, and LM2 cusp number. Strong positive loadings on PC3 (16.0% variance) are found on UM3 parastyle and LM1 cusp number.

Contrarily to what was expected, both the Spanish Medieval samples and the samples from the major Balearic Islands did not cluster together. On Figure 4.5.13. and Figure 4.5.14., AEAD and Medieval samples are far apart, like Menorca and Mallorca
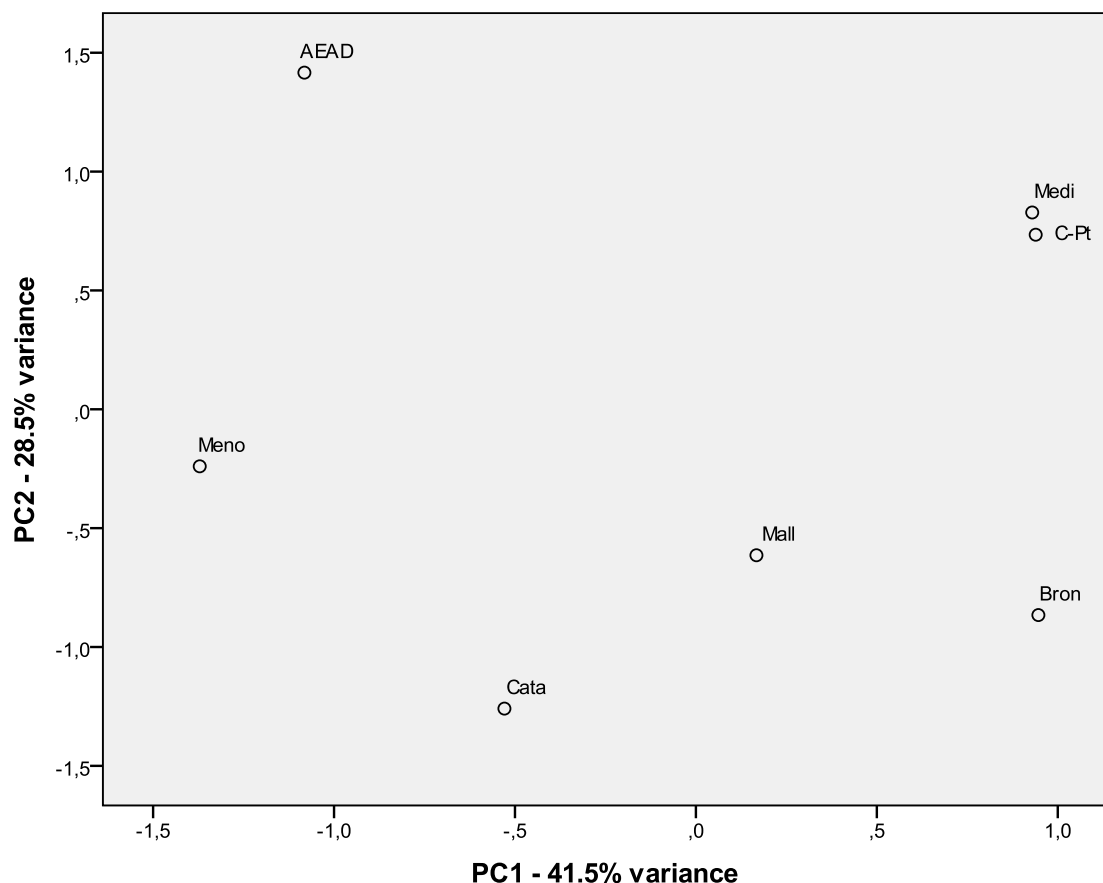
Figure 4.5.13. Scatterplot of the first two components in the comparison between Coimbra, Menorca, Ebro and Douro (Souich, 2001) and averaged chronological and geographical Iberian samples reported in Al Oumaoui (2009) and García Sívoli (2009).
AEAD: Alto Ebro and Alto Douro; Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Mall: Mallorca; Medi: Medieval; Meno: Menorca.

islands' samples. Only along PC2 (y axis) do these sets of samples approximate. The only clustering samples are Coimbra and Medieval Spain. All remaining samples are spread in two- and three-dimensional space. This dispersion of the samples may again testify their relative closeness, and also be a product of their heterogeneity, either in terms of geography or of chronology.

The fact that the Medieval samples from Spain derived from data reported by Al Oumaoui (2009) include Islamic cemeteries can account for its proximity to Coimbra and distance from the other Medieval sample from Northern Spain (AEAD). As will be further tested and discussed below, there probably was gene flow between North Africa and the Iberian Peninsula during most of the Middle Age, which left a long lasting biological effect. The Spanish Medieval sample is mixed with Islamic populations, more heavily influenced by North African gene flow than Northern populations, almost
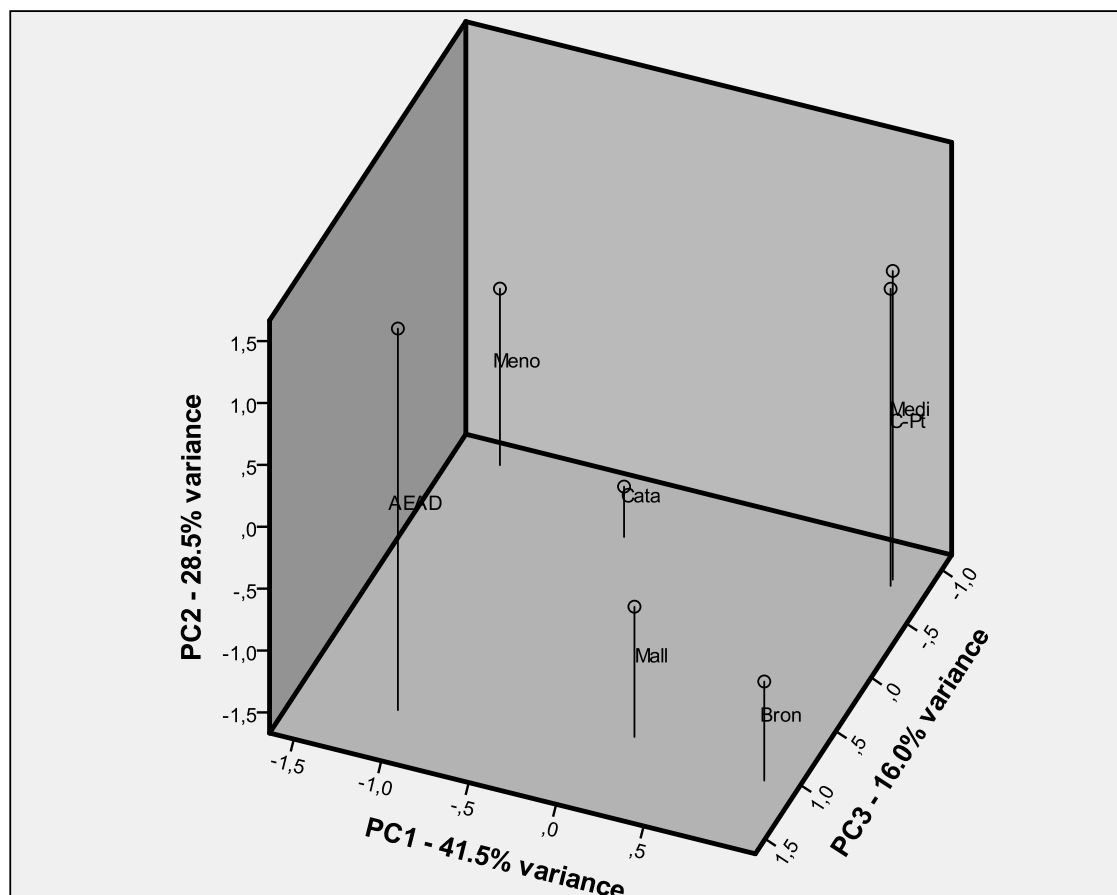
Figure 4.5.14. Scatterplot of the first three components in the comparison between Coimbra, Menorca, Ebro and Douro (Souich, 2001) and averaged chronological and geographical Iberian samples reported in Al Oumaoui (2009) and García Sívoli (2009).
AEAD: Alto Ebro and Alto Douro; Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Mall: Mallorca; Medi: Medieval; Meno: Menorca.

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not affected by it. This mixture can mimic the biological variation found on contemporary central Portugal, in Coimbra.

Most traits originating separation between samples are related to a greater morphologic complexity, and that mostly places the Medieval Spanish and the Coimbra sample with a high score (except on PC3), which again suggests the importance of North African gene flow.

The comparison of several relatively small samples of Portuguese origin, but of different historical periods and/or involving different population movements is interesting because it allows the effects of those differences in their dental morphology, as a correlate to genetic diversity, to be compared.

Besides of the Portuguese sample from Coimbra, five others were included in the subsequent analysis: an ossuary which should correspond to a secondary burial from São Julião church in Figueira da Foz, probably from the 17th to 19th centuries (Pinto, 2012); another three ossuaries from the Romanic church of S. João de Almedina (12th to 17th centuries), from Medieval Coimbra (Jesus, 2012, personal communication); a sample from the church of Santa Maria da Vitória, in Batalha, Leiria (15th to 18th

Table 4.5.8. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Almedina, Batalha, Figueira da Foz, Miranda do Corvo and Shantarin samples.

Trait (tooth)	PC 1	PC 2	PC 3
Foramina Mentales + = > 2	-0.422	0.137	**-0.679**
Lingual Cusp Variation (35/45) + = ASU 2-9	**<u>0.799</u>**	0.104	-0.296
Cusp Number (36/46) + = ASU 5	-0.102	**<u>0.818</u>**	0.497
Groove Pattern (36/46) + = ASU Y	0.336	**<u>0.802</u>**	0.455
C6 (36/46) + = ASU 1-5	**-0.747**	**<u>0.555</u>**	0.320
C7 (36/46) + = ASU 1-4	**<u>0.739</u>**	**<u>0.561</u>**	-0.316
Cusp Number (37/47) + = ASU = 4	**-0.904**	0.324	-0.095
Groove Pattern (37/47) + = ASU X	**<u>0.677</u>**	0.071	-0.037
Cusp Number (38/48) + = ASU = 4	0.102	**-0.784**	**<u>0.564</u>**
Groove Pattern (38/48) + = ASU X	**<u>0.812</u>**	-0.215	0.471
C6 (38/48) + = ASU 1-5	**<u>0.852</u>**	0.337	-0.211
Eigenvalue	4.713	2.850	1.800
Variance	42.9%	25.9%	16.4%
Total variance	42.9%	68.8%	85.2%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

centuries), studied by Marques (2007); a secondary burial from a church bell tower (an adapted tower in the defensive wall of the locality), which consisted of an ossuary most likely from the 18th century Miranda do Corvo, near Coimbra, an important military outpost in the defense of the region (Coelho, 2013); 45 individuals from Medieval Santarém (8th/9th to 12th centuries), also known as Shantarin, its Muslim denomination, which funerary practices indicate the sample was most likely of the Islamic faith (Rodrigues, 2013).

The PCA used eleven dental and oral non-metric traits (Table 4.5.8.), the ones available on all five samples and on the Coimbra sample studied by the present author which presented variation between them. Table 4.5.8. yields each trait's component loadings, the components' *eigenvalues* and variances, as well as the traits and breakpoints used, and the cumulative variances.
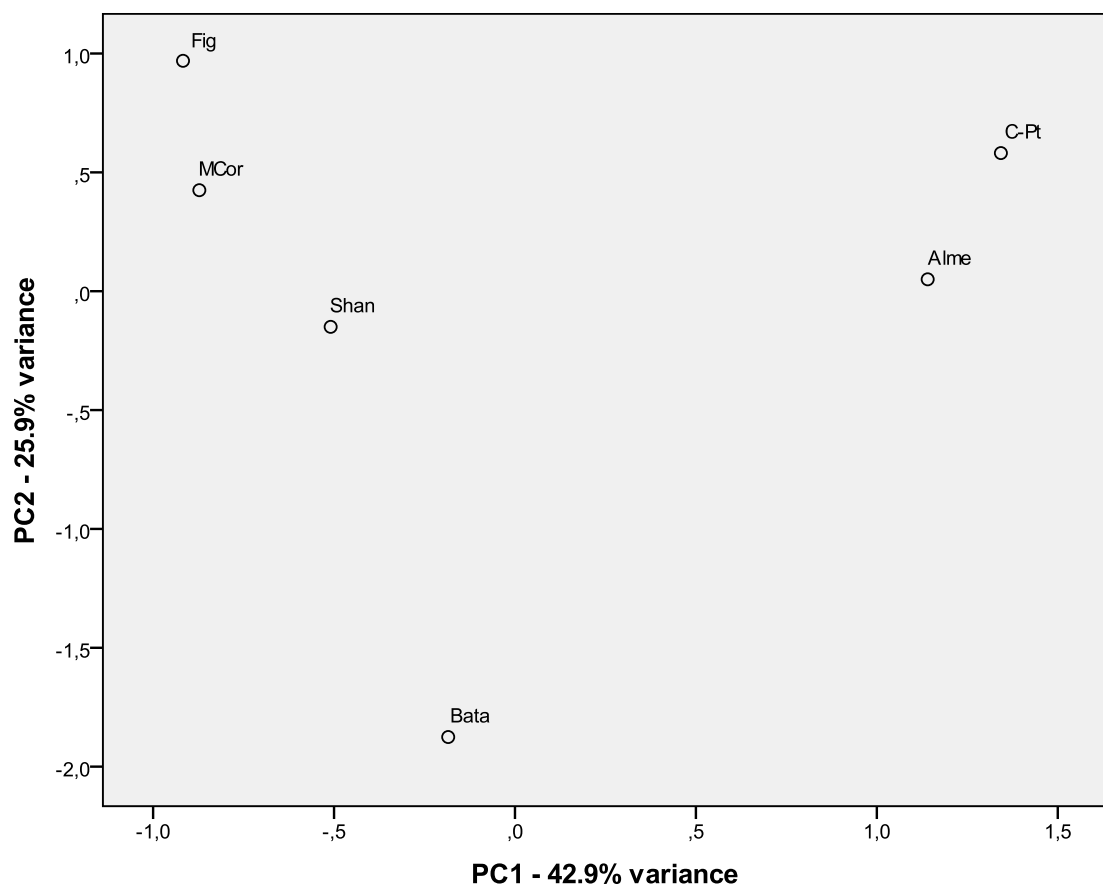
Figure 4.5.15. Scatterplot of the first two components in the comparison between Coimbra and several Medieval to Modern central Portuguese samples (Marques, 2007; Jesus, 2012; Pinto, 2012; Coelho, 2013; Rodrigues, 2013).
Alme: São João de Almedina church (Coimbra); Bata: Santa Maria da Vitória church (Batalha); C-Pt: Coimbra (Portugal); Fig: São Julião church (Figueira da Foz); MCor: Miranda do Corvo; Shan: Shantarin (Muslim Medieval Santarém).

PC1 (42.9% variance) is characterized by strong positive loadings (>0.5) from LP4 lingual cusp variation, LM1 C7, LM2 and LM3 groove pattern, and LM3 C6; and by strong negative loadings (<-0.5) in the LM1 C6 and LM2 cusp number.

The second PC, which expresses 25.9% of the variation between the samples, graphically demonstrates strong positive loadings from LM1 cusp number, groove pattern, C6 and C7. Its sole strong negative loading is found on LM3 cusp number.

The strong positive loading that contributes to the distribution of the samples along PC3 (16.4% variance) is from LM3 cusp number, while the strong negative loading is from *foramina mentales*.
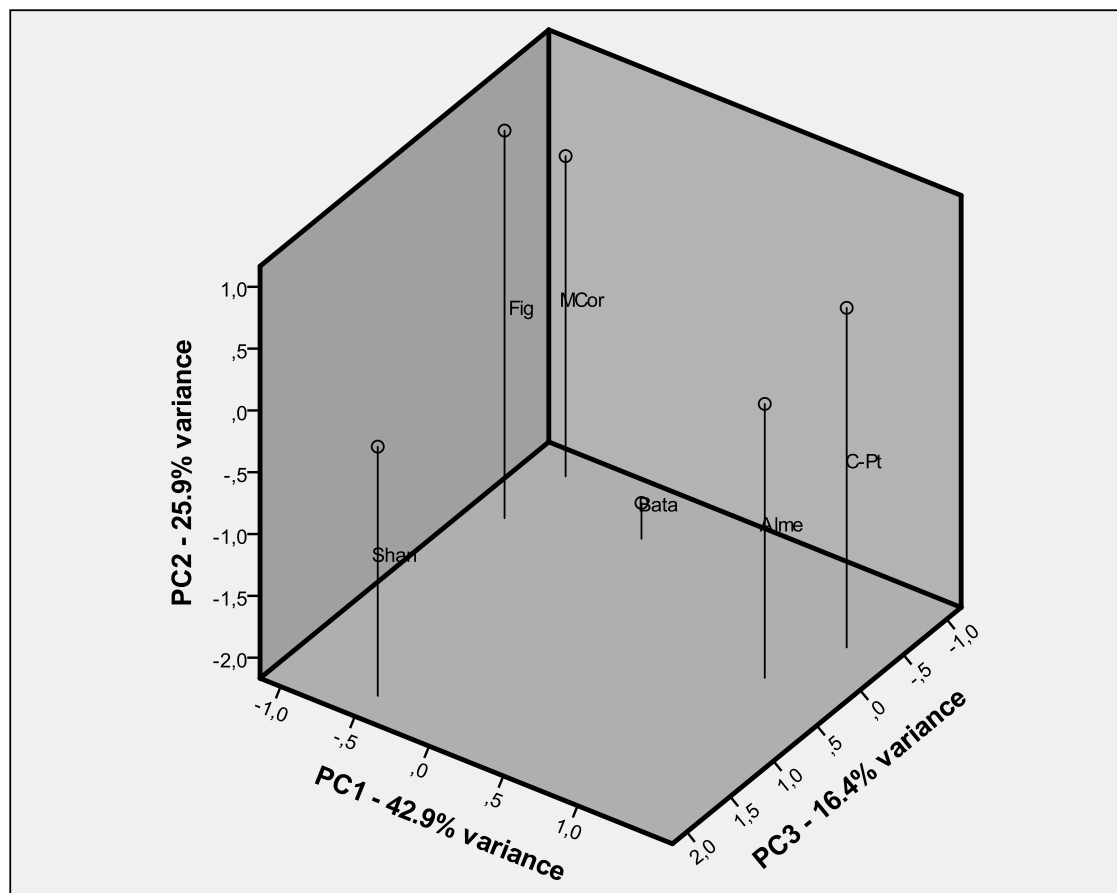
Figure 4.5.16. Scatterplot of the first three components in the comparison between Coimbra and several Medieval to Modern central Portuguese samples (Marques, 2007; Jesus, 2012; Pinto, 2012; Coelho, 2013; Rodrigues, 2013).
Alme: São João de Almedina church (Coimbra); Bata: Santa Maria da Vitória church (Batalha); C-Pt: Coimbra (Portugal); Fig: São Julião church (Figueira da Foz); MCor: Miranda do Corvo; Shan: Shantarin (Muslim Medieval Santarém).

Figure 4.5.15. expresses 68.8% of the total variation among the samples. Along PC1, Coimbra and S. João de Almedina (also in Coimbra) are separated from a cluster

that contains Figueira da Foz, Miranda do Corvo, Shantarin and Batalha. As for PC2, Batalha is separated from a wide cluster which includes all five remaining samples (Coimbra, Almedina, Figueira da Foz, Miranda do Corvo and Shantarin).

Figure 4.5.16. is the three-dimensional representation of approximately 85.2% of the variation among the samples, along all three PC's. Shatarin is separated from the remaining samples along the newly added axis, PC3.

These distributions, along the components derived from the PCA, denote three different separations: S. João de Almedina (in Coimbra) and the Portuguese sample mainly from Coimbra are separated from other samples by the x axis, PC1; Batalha is separated from the remaining samples by PC2; like Shantarin is by the z axis (PC3).

S. João de Almedina and Coimbra display the highest or near the highest values for the traits with strong positive loadings on PC1 (LP4 lingual cusp variation, LM1 C7, LM2 and LM3 groove pattern, and LM3 C6) and the lowest or among the lowest values for its strong negative loadings (LM1 C6 and LM2 cusp number).

Batalha presents the lowest or among the lowest frequencies for the traits with strong positive loading on PC2 (LM1 cusp number, groove pattern, C6 and C7) and the second highest frequency of four-cusped LM3's, PC2's strong negative loading.

Shantarin has the highest frequency of four-cusped LM3's, the sole strong positive loading on PC3, and the second lowest percentage of two or more *foramina mentales*, the only strong negative loading on the z axis.

Given the generally very small samples and the few morphological characters examined, the relationships demonstrated by these data are not without question. However, they allow for preliminary considerations. The first of which pertains to the lack of major consistent biological distinctions among the samples.

The two samples that are separated from the rest within the most important component, PC1, are both from the city of Coimbra. This proximity and the chronological broadness encompassed by both samples (12th to 17th centuries for Almedina, and 19th/20th centuries for Coimbra) suggest the city did not undergo severe biological or genetic alterations from the Late Middle Ages to the 20th century.

The two other samples that cluster with Almedina and Coimbra in PC's 2 and 3, Miranda do Corvo (18th century) and Figueira da Foz (17th to 19th century), are both from the Portuguese district of Coimbra, and are near the aforementioned samples. Despite the separation occasioned by the distribution of the x axis, these four samples do not differ in a great degree, apparently. This suggests some diversity within the

Coimbra region, but still supports continuity within the geographical and chronological boundaries alluded to in the previous paragraph.

Batalha is in Leiria, a district just to the South of Coimbra. This sample is from the Late Medieval period and early Modern Age (15th to 18th centuries). There is very little chronological gap between this and the remaining samples, so the relatively small distance found between them along PC2 is most likely derived from the (albeit small) geographical distance between them.

Shantarin is located in the Santarém district, in the South of the Central region of Portugal, and the oldest sample in the present group. The biological relation suggested by the distribution of PC3, the less representative component obtained in the present analysis, can be due to the distance in both space and time that separated this to most other samples. The likelihood of an Islamic biological presence among the individuals of Medieval Shantarin can also provide the source of the biological relation between this and the remainder of the samples. This distance is, however, very small. That renders unlikely the existence of cumulative effects of time, space and genetic differences.

The present analysis underlines, above all, the possibility of a lack of discontinuity brought about by processes common in population genetics, which suggest no major migrations into Portugal or long term separation between the populations inhabiting that country took place from the 9th to the 20th century.

The next analyses will include a sample of mandibles of unknown origin, kept at the Museu de História Natural da Faculdade de Ciências da Universidade do Porto (MHNP; the Museum of Natural History of the Faculty of Sciences of the University of Oporto). This sample, previously studied by the present author (Marado, 2010, 2012), was once identified, or at least of known origin. Those records have since been lost and, despite remarks from Santos Júnior (1969) regarding a since lost indentified skeletal sample that could be MHNP (presumably collected from Oporto cemeteries by Professor Mendes Corrêa, on the first half of the 20th century), dental and mandibular nonmetric traits were the only secure source of information, which can shed a light on the biological origins of this sample.

In order for the most possible traits to be included and to have some contrast, the MHNP was compared not only to Coimbra, but also to the means from the dissertations

of Al Oumaoui (2009: Bronze Age and Medieval Spain) and García Sívoli (2009: Mallorca and Catalonia).

Table 4.5.9. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, MHNP and Spanish diachronic samples.

Trait (tooth)	PC 1	PC 2	PC 3
Lingual Cusp Variation (34/44) + = ASU 2-9	**0.773**	-0.047	**-0.544**
Lingual Cusp Variation (35/45) + = ASU 2-9	**0.620**	-0.109	**0.615**
Odontome (34/44) + = ASU 1	**0.598**	0.146	**0.756**
Odontome (35/45) + = ASU 1	0.125	**-0.805**	-0.157
Deflecting Wrinkle (36/46) + = ASU 1-3	**-0.788**	0.499	-0.229
Anterior Fovea (36/46) + = ASU 1-4	0.094	0.367	**0.518**
Distal Trigonid Crest (36/46) + = ASU 1	0.274	-0.075	-0.018
Groove Pattern (38/48) + = ASU X	**-0.689**	0.211	**0.679**
Groove Pattern (37/47) + = ASU Y	**0.859**	0.045	-0.477
Groove Pattern (36/46) + = ASU Y	**0.900**	0.001	0.381
Protostylid (38/48) + = ASU 1-7	**0.687**	**0.544**	-0.470
Protostylid (37/47) + = ASU 1-7	0.356	**0.661**	-0.226
Protostylid (36/46) + = ASU 1-7	**0.510**	**0.612**	0.044
C5 (36/46) + = ASU 1-5	0.183	-0.183	**-0.926**
C5 (37/47) + = ASU 1-5	0.279	**-0.854**	-0.281
C5 (38/48) + = ASU 1-5	**0.547**	**-0.811**	0.017
C6 (36/46) + = ASU 1-5	0.167	**-0.709**	0.066
C6 (37/47) + = ASU 1-5	**0.533**	0.117	**0.774**
C6 (38/48) + = ASU 1-5	**0.882**	-0.381	0.269
C7 (36/46) + = ASU 1-4	**0.896**	0.255	-0.156
C7 (37/47) + = ASU 1-4	0.193	**0.662**	**-0.645**
C7 (38/48) + = ASU 1-4	**0.728**	**0.594**	0.190
Eigenvalue	7.811	5.166	4.789
Variance	35.5%	23.5%	21.8%
Total variance	35.5%	59.0%	80.8%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

Figure 4.5.17. Scatterplot of the first two components in the comparison between Coimbra, a sample of unknown origin (Marado, 2010, 2012) and Iberian samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Mall: Mallorca; Medi: Medieval; MHNP: Museu de História Natural da Universidade do Porto.

Figure 4.5.17. shows Coimbra nearer Bronze Age and Medieval Spanish samples, but nearly aligned with MHNP in the x axis (PC1: 35.5% variance). Catalonia and Mallorca are relatively near and MHNP is almost equally distant to Medieval Spain, Mallorca and Coimbra, with the major separation from this latter sample caused by their different positions along the y axis (PC2: 23.5% variance).

Figure 4.5.18., including PC3 (21.8% variance) shows the closest samples to be Coimbra and MHNP, followed by Bronze Age southern Spain.

The loadings for each trait on every analyzed component are found on Table 4.5.9. The strongest positive loadings (>0.5) found on PC1 were from LP3 and LP4 lingual cusp variation, LP3 odontome, LM2 and LM3 groove pattern, LM1 and LM3 protostylid, LM3 C5, LM2 and LM3 C6 and LM1 and LM3 C7. Strong negative loadings (<-0.5) were from LM1 deflecting wrinkle and groove pattern.

PC2 derived its scores from strong positive loadings for protostylid on all lower molars and LM2 and LM3 C7. Strong negative loadings are present for LP4 odontome, LM2 and LM3 C5 and LM1 C6.

Strong positive loadings on PC3 were produced on LP4 lingual cusp variation, LP3 odontome, LM1 anterior fovea and groove pattern, and LM2 C6. Strong negative loadings are present on LP3 lingual cusp variation, LM1 C5 and LM2 C7.
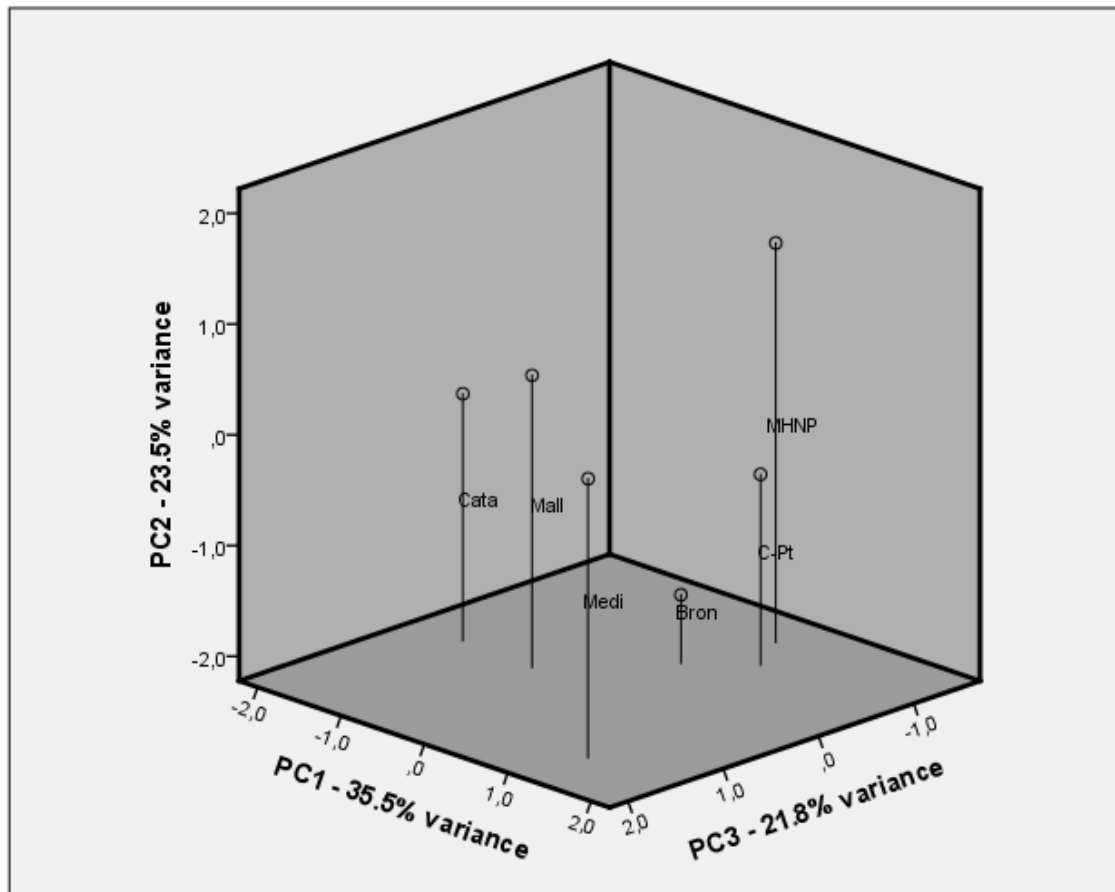
Figure 4.5.18. Scatterplot of the first three components in the comparison between Coimbra, a sample of unknown origin (Marado, 2010, 2012) and Iberian samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Mall: Mallorca; Medi: Medieval; MHNP: Museu de História Natural da Universidade do Porto.

MHNP was expected to be a sample from Iberian, particularly Portuguese origin, probably from the same chronology as Coimbra (late 19th/early 20th century). These results, indicating an immediate proximity between both samples, in a context of biologically and geographically close samples, seems to corroborate the hypothesis. The only separation, along the y axis (PC2) is mainly justified by the differences in protostylid and C7 frequencies (MHNP has higher frequencies) and C5 and C6

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frequencies (due to greater frequencies from Coimbra). PC1 and PC3 (57.3% of the variation) reveal close biological proximity between these (presumably) Portuguese samples. The greater distance found for the other Iberian samples, shown above to be biologically close, clarifies the likeliness that these samples were drawn from the same Portuguese population, which seems high. This will be further tested, alongside other samples, in the subsequent analyses.

Table 4.5.10. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Modern Lisbon and Spanish samples.

Trait (tooth)	PC 1	PC 2	PC 3
Groove Pattern (36/46) + = ASU X	**-0.633**	-0.163	0.455
Groove Pattern (37/47) + = ASU Y	**0.895**	0.134	-0.383
Groove Pattern (38/48) + = ASU Y	-0.216	**0.905**	-0.081
C5 (36/46) + = ASU 1-5	**0.673**	-0.464	-0.432
C5 (37/47) + = ASU 1-5	**0.838**	-0.214	0.395
C5 (38/48) + = ASU 1-5	**0.773**	0.213	0.492
C6 (36/46) + = ASU 1-5	**0.514**	-0.082	0.448
C6 (37/47) + = ASU 1-5	0.442	**0.546**	0.273
C6 (38/48) + = ASU 1-5	**0.798**	**0.544**	0.244
C7 (36/46) + = ASU 1a-4	**0.854**	-0.106	-0.045
C7 (37/47) + = ASU 1a-4	**0.617**	-0.326	**-0.555**
C7 (38/48) + = ASU 1a-4	-0.053	**0.816**	**-0.554**
Eigenvalue	5.212	2.555	1.897
Variance	43.4%	21.3%	15.8%
Total variance	43.4%	64.7%	80.5%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The former analysis (comparison between Coimbra, Spanish samples and MHNP) was repeated with fewer traits (twelve), in order to include another Portuguese sample from Lisbon (17th/18th century), composed of individuals exhumed from the cemetery and ossuaries of the College of Santo Antão-o-Novo in Lisbon, from the 17th to 18th centuries. In total, 163 individuals were counted, but the totality of the necropolis was not exhumed. Sixty-two skeletons were studied by Godinho (2008).

Despite Lisbon seeming distant from Coimbra when looking at the graph displaying bi-dimensional distribution (including PC1: 43.4% variance; and PC2: 21.3%

variance; see Table 4.5.10. and Figure 4.5.19.), the most distant sample is Medieval Spain. Coimbra, Lisbon, MHNP and Bronze Age Spain form a broad cluster, while Catalonia groups with Mallorca, on the tridimensional graph (Figure 4.5.20.), including PC3 (15.8% variance).
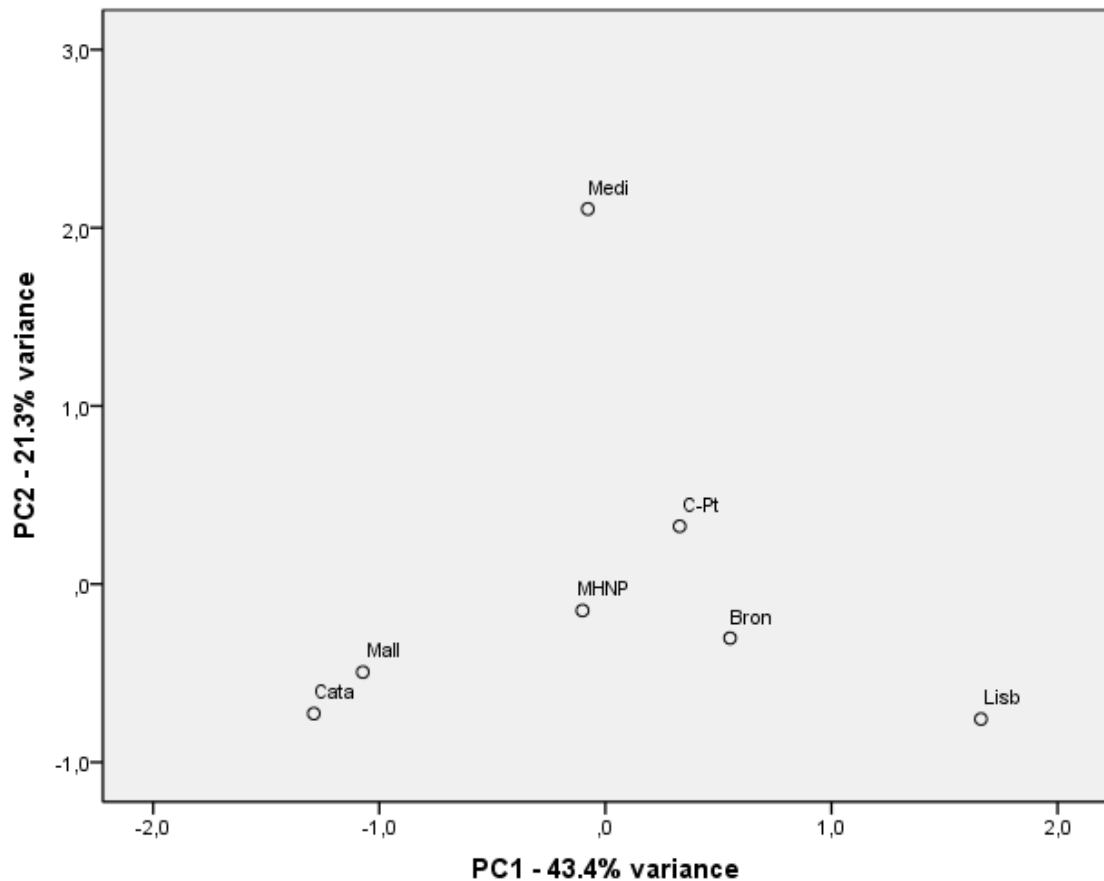
Figure 4.5.19. Scatterplot of the first two components in the comparison between Coimbra, Lisbon (Godinho, 2008), a sample of unknown origin (Marado, 2010, 2012) and Iberian samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Lisb: College of Santo Antão-o-Novo (Lisbon); Mall: Mallorca; Medi: Medieval; MHNP: Museu de História Natural da Universidade do Porto.

PC1's strongest positive loadings (>0.5) are from LM2 groove pattern, C5 on all lower molars, LM1 and LM3 C6, and LM1 and LM2 C7. A strong negative loading (<-0.5) hails from LM1 groove pattern.

Strong positive loadings were produced on PC2 for LM3 groove pattern, LM" and LM3 C6, and LM3 C7.

Strong negative loadings for PC3 were derived from LM2 and LM3 C7.

No clearly close relationships are established, with the possible exception of the closeness between MHNP and Coimbra, already understood by the former analyses.

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The traits available for this analysis only show that, through what was already suggested before (the biological affinity between all samples except Lisbon, newly introduced), all
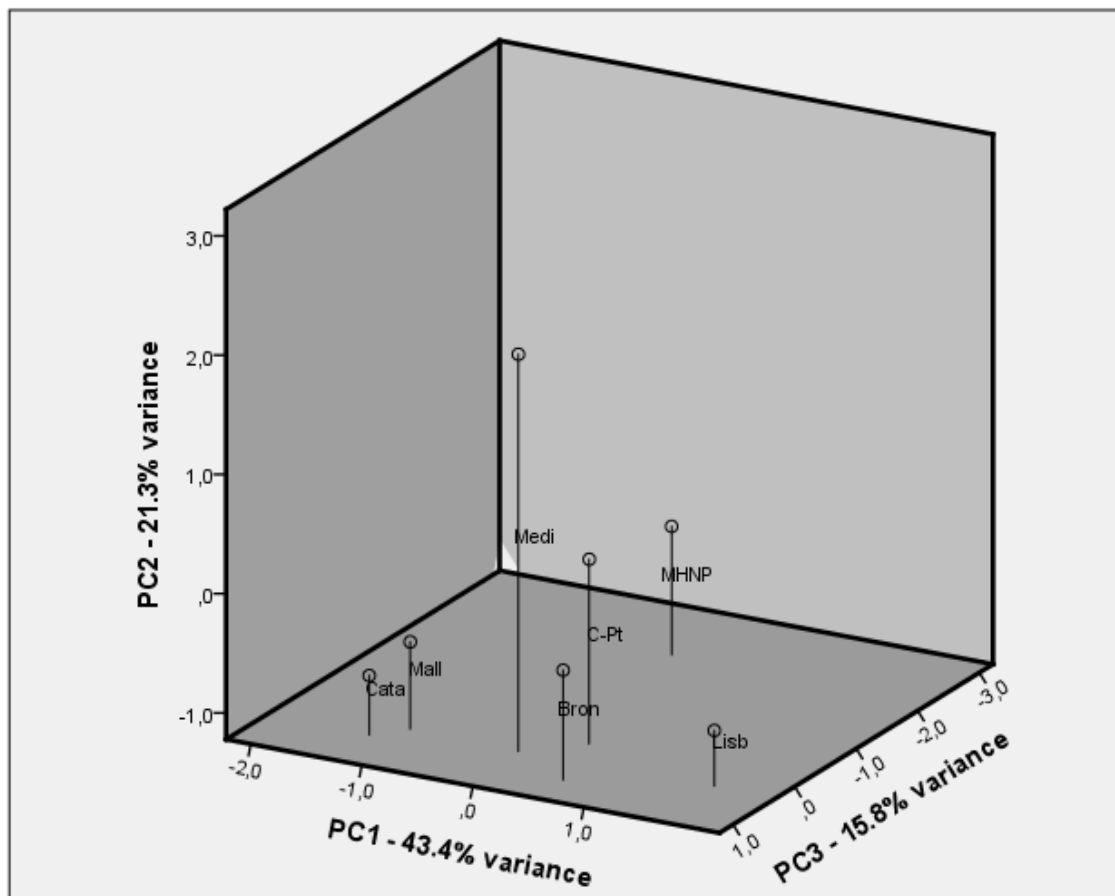
Figure 4.5.20. Scatterplot of the first three components in the comparison between Coimbra, Lisbon (Godinho, 2008), a sample of unknown origin (Marado, 2010, 2012) and Iberian samples (Al Oumaoui, 2009; García Sívoli, 2009).
Bron: Bronze Age; Cata: Catalonia; C-Pt: Coimbra (Portugal); Lisb: College of Santo Antão-o-Novo (Lisbon); Mall: Mallorca; Medi: Medieval; MHNP: Museu de História Natural da Universidade do Porto.

samples are biologically close to each other. The distance between Coimbra/MHNP and Lisbon is not great, but is in the same order as the distance between the former and the samples from Catalonia, Mallorca and Medieval Spain. Bronze Age Spain is even closer than those samples.

The suggested biological relation between early Modern Lisbon and Coimbra may be derived from the set of traits (only four traits considered for each of the three molars) and the small sample of the former. Even so, this analysis is sufficient to understand these samples are not dissimilar and can be considered relatively close. Only with a broader analysis, using more traits from a larger sample, can the definite nature of this biological relation clarified.

The next PCA was calculated using not only dental, but also mandibular nonmetric traits. This precluded the inclusion of any samples foreign to the Portuguese territory to provide contrast. Two Portuguese samples were included, besides the present sample (Coimbra) and MHNP. These are a sample from Oporto, from Hospital de Santo António (HSA) that hails from the Hospital's gardens and spans a chronology from the 17th to the 20th century (Costa, 2006; Pinto, 2006; Costa, 2007); and a sample from Modern Santarém, originating from a 18th century necropolis from Rua dos Barcos (Gomes, 2005; Rodrigues, 2005; Simão, 2005; Pombal, 2006) and a Largo de Cândido Reis chronologically similar sample (Tereso, 2009; Gonçalves, 2010; Graça, 2010). Tereso (2009) researched material from several interments and an ossuary; Gonçalves

Table 4.5.11. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing the Coimbra, HSA, MHNP and Santarém samples.

Trait (tooth)	PC 1	PC 2	PC 3
Lingual Cusp Variation (35/45) + = ASU 2-9	**<u>0.938</u>**	0.311	0.150
Groove Pattern (36/46) + = ASU X	**<u>0.958</u>**	-0.096	-0.269
Groove Pattern (37/47) + = ASU Y	**<u>0.914</u>**	-0.320	-0.248
Groove Pattern (38/48) + = Y	**<u>0.901</u>**	-0.054	-0.431
C5 (36/46) + = ASU 1-5	-0.242	0.251	**<u>0.937</u>**
C5 (37/47) + = 1-5	**<u>0.588</u>**	**<u>0.618</u>**	**-0.522**
C5 (38/48) + = ASU 1-5	-0.323	**<u>0.926</u>**	0.196
C6 (36/46) + = ASU 1-5	**<u>0.857</u>**	0.097	**<u>0.507</u>**
C6 (37/47) + = ASU 1-5	0.459	**<u>0.879</u>**	-0.127
C6 (38/48) + = ASU 1-5	**<u>0.820</u>**	**<u>0.558</u>**	-0.131
C7 (36/46) + = ASU 1-4	**<u>0.966</u>**	-0.208	0.152
C7 (37/47) + = ASU 1-4	**<u>0.604</u>**	-0.492	**<u>0.627</u>**
C7 (38/48) + = ASU 1-4	**<u>0.777</u>**	**-0.586**	0.229
Mandibular *Torus* + = ASU 1-3	**<u>0.706</u>**	0.280	**<u>0.650</u>**
Mylohyoid Bridge + = +	**<u>0.938</u>**	0.168	0.302
Foramina Mentales + = > 2	**-0.860**	0.241	0.450
Eigenvalue	9.593	3.401	3.007
Variance	60.0%	21.3%	18.8%
Total variance	60.0%	81.3%	100.0%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

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(2010) analyzed 20 interments and an associated ossuary; Graça (2010) studied 24 interments and associated avulse bones and teeth.

From the sixteen traits used (thirteen from lower teeth and three from the mandibular bone) from these four samples, three PC's were produced (Table 4.5.11.). Strong positive loadings (>0.5) on PC1 were derived from LP4 lingual cusp variation, groove pattern on all lower molars, LM2 C5, LM1 and LM3 C6, C7 on all lower molars, mandibular *torus* and mylohyoid bridge. A strong negative loading was established for *foramina mentales* (-0.737).

PC2 is characterized by strong positive loadings for LM2 and LM3 C5, and LM2 and LM3 C6. There is also a strong negative loading from LM3 C7.

Strong positive loadings on PC3 are determined for LM1 C5, LM1 C6, LM2 C7 and mandibular *torus*. A strong negative loading (<-0.5) is present for LM2 C5.

PC1 concentrates a great deal of the variance found (60.0%) and approximates Coimbra and MHNP. Santarém is also relatively close. PC2 (21.3% of the total variance) approximates MHNP to Santarém and places HSA between them and Coimbra. PC3 (18.8% variance) locates Coimbra between Santarém as well as MHNP and HSA. So, all axes form different associations; clearly this is a testimony to the lack of overall biological distinctions between these samples (when using these variables for comparison).

Apparently the strongest connections are the ones derived from the x axis, since PC1 comprises more than half the variation and is related to the frequencies of most variables. Focusing on Figure 4.5.21., this suggests a slight gradation along this axis, related to chronological differences, separating Santarém from more recent (Coimbra and MHNP) populations. This assumes MHNP is in fact contemporary to Coimbra, which is suggested by the results of this and the last two PCA's. HSA, however, possibly due to either its wider chronological spread or to the small sample size, is relatively isolated.
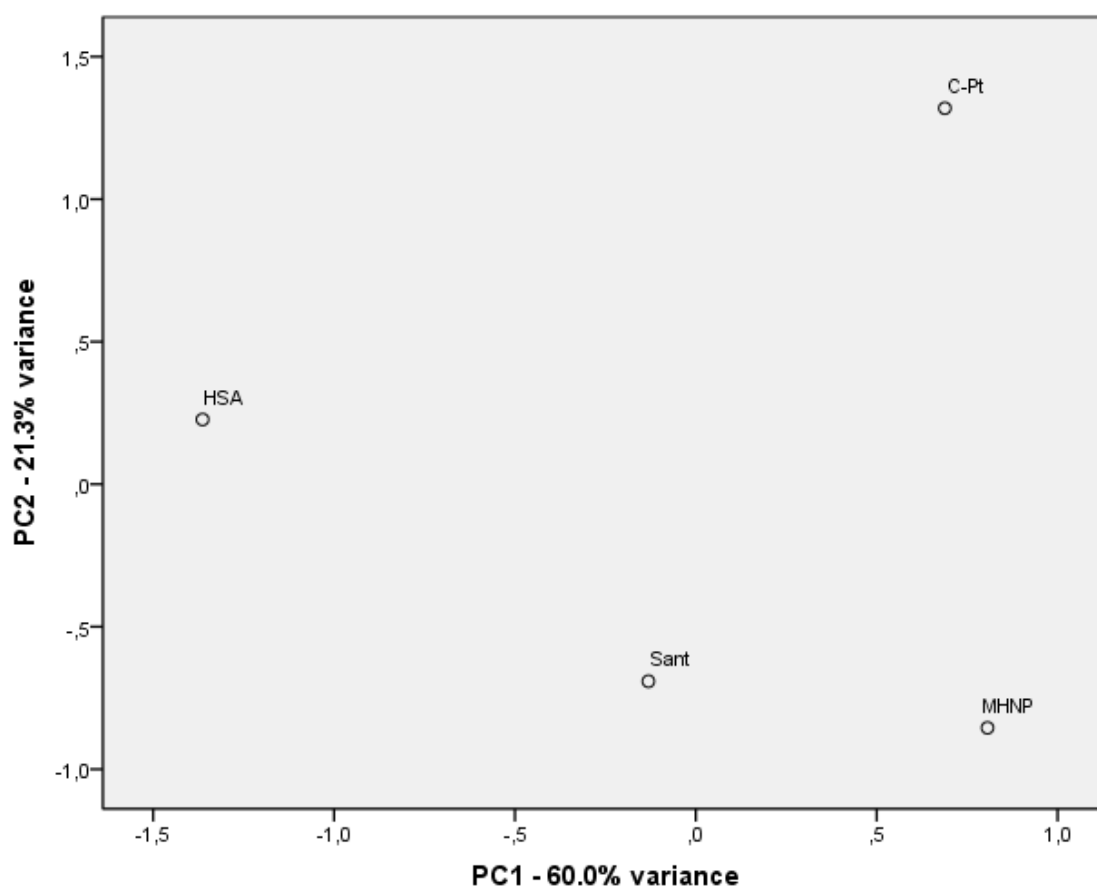
Figure 4.5.21. Scatterplot of the first two components in the comparison between Coimbra, Santo António Hospital (Costa, 2006; Pinto, 2006; Costa, 2007), Santarém (Gomes, 2005; Rodrigues, 2005; Simão, 2005; Pombal, 2006; Tereso, 2009; Gonçalves, 2010; Graça, 2010) and a sample of unknown origin (Marado, 2010, 2012).
C-Pt: Coimbra (Portugal); HSA: Modern period Hospital of Santo António; MHNP: Museu de História Natural da Universidade do Porto; Sant: Modern Santarém.

On the other hand, PC2 (y axis) seems to be rather random, approximating samples supposed to be from different chronologies and known to be from different regions in Portugal. Coimbra (Northern Centre of Portugal) and HSA (Oporto, Northern Portugal) are separated by about 120 km, and are here closely placed. MHNP (also from Oporto) and Santarém (Southern Centre of Portugal) are also placed together, despite their difference in chronology and space (these cities are separated by about 240 km). So, PC2 corroborates the proximity amongst all samples.

PC3, on the other hand, suggests a geographic gradation, by approximating both Oporto samples and both Central Portuguese samples, the furthest being Santarém (more to the South). Figure 4.5.22. displays a graphic representation of all the variation
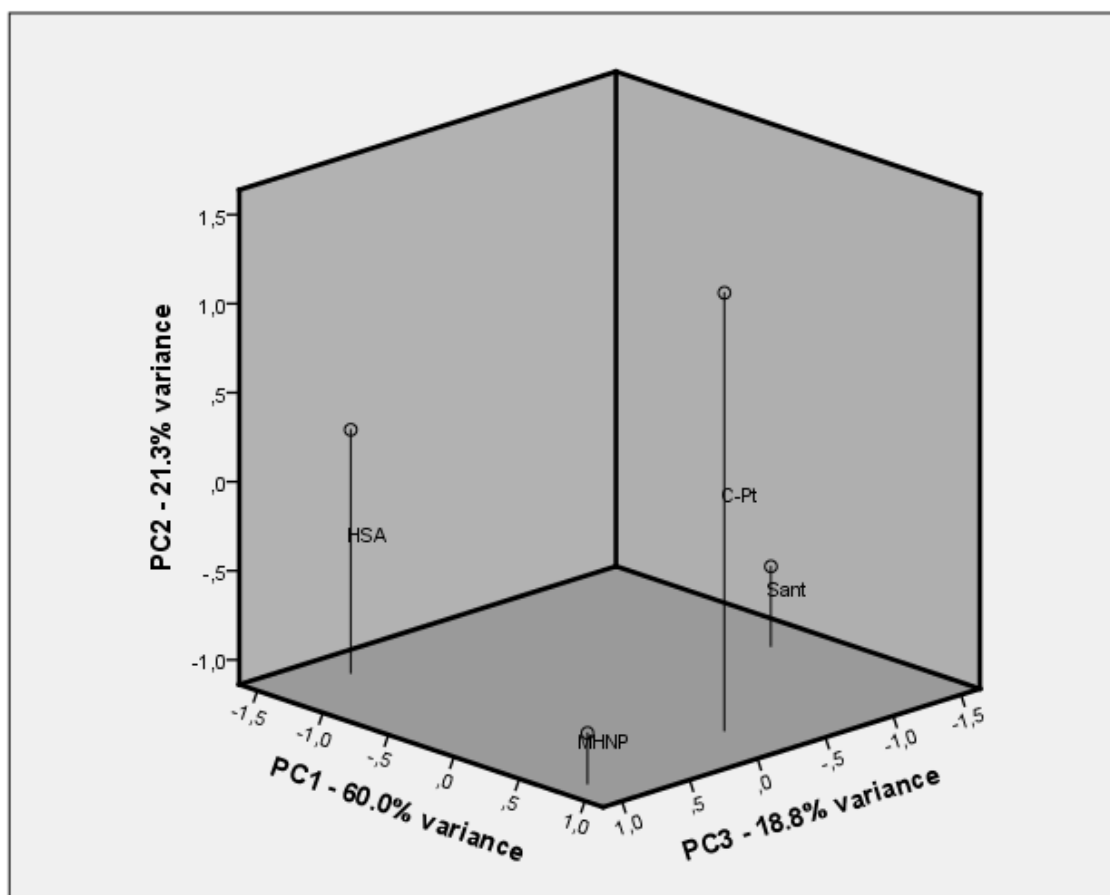
Figure 4.5.22. Scatterplot of the first three components in the comparison between Coimbra, Santo António Hospital (Costa, 2006; Pinto, 2006; Costa, 2007), Santarém (Gomes, 2005; Rodrigues, 2005; Simão, 2005; Pombal, 2006; Tereso, 2009; Gonçalves, 2010; Graça, 2010) and a sample of unknown origin (Marado, 2010, 2012).
C-Pt: Coimbra (Portugal); HSA: Modern period Hospital of Santo António; MHNP: Museu de História Natural da Universidade do Porto; Sant: Modern Santarém.

of the three components (100%). This evidence underlines the utility of dental (and oral) morphology and the ASUDAS in detecting biological relations, even between samples from very close geographical and chronological positions, and even with a limited amount of traits. On the other hand, if used to determine the origin of MHNP (which is uncertain), this PCA demonstrates the usefulness of the mentioned scientific theory and method to unveil its biological relations with other, very close, samples.

These praises can only be entirely meaningful if these results can be properly reproduced using a larger battery of nonmetric traits and better contextualized in a global comparison. The latter of these needs will be approached in the next analyses.

The establishment of the biological relations between the former four samples (Coimbra; MHNP, the unknown origin sample from Oporto; HSA, the Modern sample

Table 4.5.12. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, other Portuguese and world-wide samples.

Trait (tooth)	PC 1	PC 2
C5 (36/46) + = ASU 1-5	**<u>0.602</u>**	-0.446
C5 (37/47) + = ASU 1-5	**<u>0.932</u>**	0.263
Groove Pattern (37/47) + = ASU Y	**-0.614**	**<u>0.735</u>**
C6 (36/46) + = ASU 1-5	**<u>0.981</u>**	0.076
C7 (36/46) + = ASU 1-4	0.477	**<u>0.839</u>**
Eigenvalue	2.796	1.517
Variance	55.9%	30.4%
Total variance	55.9%	86.3%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

from an Hospital in Oporto; and Santarém, another Portuguese Modern sample) was attempted through the introduction of North African and North and South Native American (NSAm) data collected from Scott and Turner (1997), to provide contrast. Unfortunately, only five lower dental discrete characters were available and compatible on all these samples, which can hinder conclusions.

Two PC's were produced by the PCA (Table 4.5.12.). These add up to approximately 86.3% of the variation (PC1: 55.9%; PC2: 30.4%). PC1 is characterized by strong positive loadings (>0.5) from LM1 and LM2 C5, and LM1 C6; a strong negative loading (<-0.5) is present for LM2 groove pattern. PC2's sample scores were derived from strong positive loadings from LM2 groove pattern and LM1 C7.

The visual representation of the variation is found on Figure 4.5.23. Coimbra groups with MHNP, with Santarém close by. HSA is separated from them along PC2 (y axis), but clusters with North Africa, Coimbra and MHNP along PC1 (x axis). North Africa is also separated from the Portuguese samples along PC2, although the most isolated sample is, as expected, NSAm. This sample clusters with Santarém, Coimbra and MHNP along the y axis, which separates North Africa to one side and HSA to the other. These separations are due to the elevated frequency of LM2 Y groove pattern and LM1 C7 found for North Africans, which contrasts with the low frequencies on HSA. NSAm displays the lowest groove pattern frequency, but has a relatively high C7 frequency, and is thus placed among the remaining Portuguese samples. These latter samples have moderate (to high, in the case of the C7) frequencies of these traits.
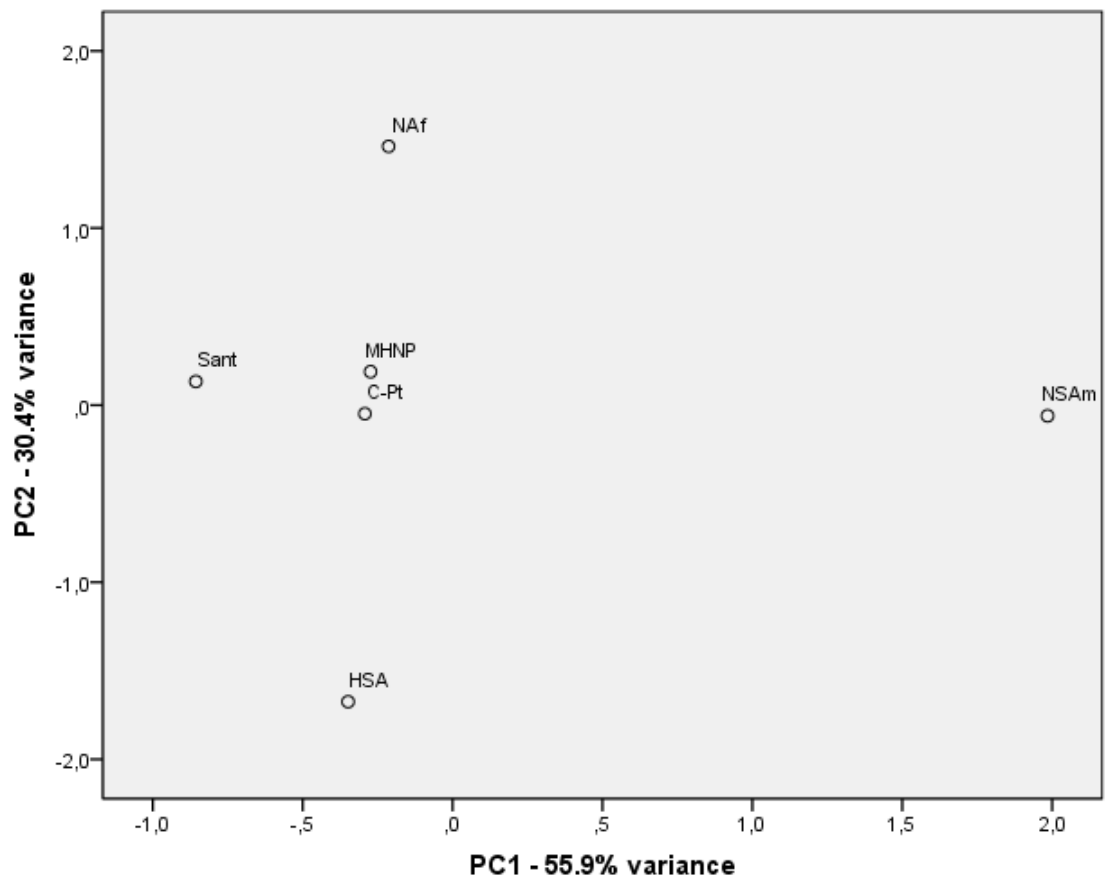
Figure 4.5.23. Scatterplot of the first two components in the comparison between Coimbra, Santo António Hospital (Costa, 2006; Pinto, 2006; Costa, 2007), Santarém (Gomes, 2005; Rodrigues, 2005; Simão, 2005; Pombal, 2006; Tereso, 2009; Gonçalves, 2010; Graça, 2010), a sample of unknown origin (Marado, 2010, 2012) and two world-wide samples (Scott and Turner, 1997).
C-Pt: Coimbra (Portugal); HSA: Modern Hospital de Santo António; NAf: North Africa; NSAm: North and South Native Americans; MHNP: Museu de História Natural da Universidade do Porto; Sant: Modern Santarém.

The x axis, on the other hand, puts Portuguese samples and North Africa on a tight cluster, when compared to NSAm. This must reflect the biological relations between these populations better, which will have to be further tested, using more traits and, perhaps, more samples. High to very high frequencies of supernumerary cusps (C5, C6 and, with less analytical relevance, C7) and low LM2 Y groove pattern clearly distinguish North and South American Natives from the Portuguese and North Africa.

Once again, North Africans are placed in close biological relation to Portuguese samples.

This PCA, limited as it may be, allows for the Portuguese samples to be placed together, underlining their biological proximity.

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Table 4.5.13. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, MHNP and world-wide samples.

Trait (tooth)	PC 1	PC 2	PC 3
Deflecting Wrinkle (36/46) + = ASU 3	**<u>0.830</u>**	-0.321	0.301
Distal Trigonid Crest (36/46) + = ASU 1	-0.183	**-0.656**	**<u>0.645</u>**
Groove Pattern (37/47) + = ASU Y	-0.051	**<u>0.893</u>**	0.423
C5 (36/46) + = ASU 1-5	**<u>0.724</u>**	-0.280	**-0.541**
C5 (37/47) + = ASU 1-5	**<u>0.937</u>**	0.103	0.285
C6 (36/46) + = ASU 1-5	**<u>0.976</u>**	-0.184	0.043
C7 (36/46) + = ASU 1-4	**<u>0.659</u>**	**<u>0.725</u>**	-0.042
Eigenvalue	3.514	1.979	1.063
Variance	50.2%	28.3%	15.2%
Total variance	50.2%	78.5%	93.7%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The need to better discern the biological affinity between MHNP and Coimbra can only by as satisfied as possible when these two samples are compared, using as many dental nonmetric traits as possible, to some (close and distant) world samples. This was attempted by comparing them with Western Europe, Northern Europe, North Africa (closer worldwide samples) and West Africa, South Africa and North and South Native Americans (frequencies from Scott and Turner, 1997).

Table 4.5.13. describes the data related to this PCA, whereas Figures 4.5.24. and 4.5.25. show the graphic results and project the three components, totaling 93.7% of the variance.

The strongest positive loadings (>0.5) on PC1 (50.2% variance) are for LM1 deflecting wrinkle, C5, C6 and C7, and LM2 C5.

PC2 (28.3% variance) is derived from strong positive loadings for LM2 groove pattern and LM1 C7, and from a strong negative loading (<-0.5) for LM1 distal trigonid crest.

Strong positive loadings on PC3 (15.2% variance) hail from the LM1 distal trigonid crest. The only strong negative loading is for LM1 C5.

Figure 4.5.24. reports the cluster formed by Coimbra, MHNP, Western Europe, Northern Europe and North Africa. MHNP is placed between North Africa and
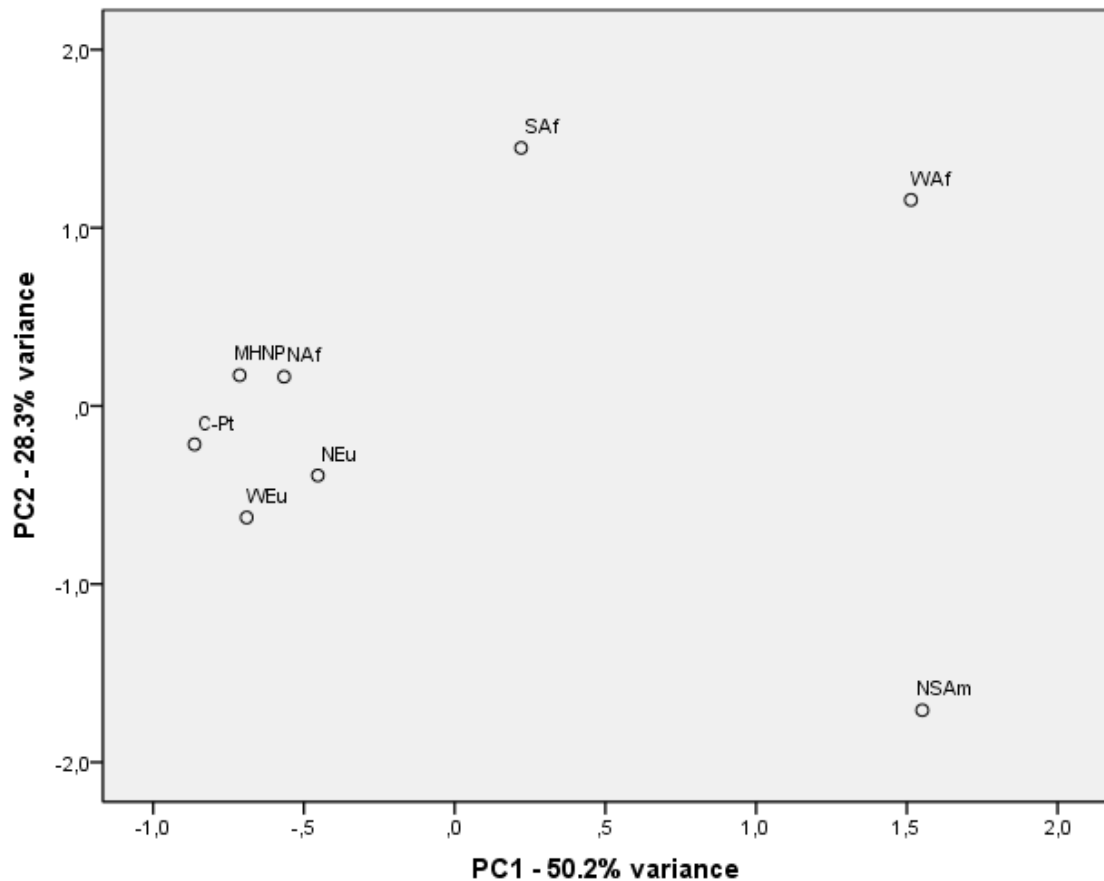
Figure 4.5.24. Scatterplot of the first two components in the comparison between Coimbra, a sample of unknown origin (Marado, 2010, 2012) and six world-wide samples (Scott and Turner, 1997).
C-Pt: Coimbra (Portugal); MHNP: Museu de História Natural da Universidade do Porto; NAf: North Africa; NEu: Northern Europe; NSAm: North and South Native Americans; SAf: South Africa; WAf: West Africa; WEu: Western Europe.

Coimbra. This latter sample is located between the former and the European populations (Western and Northern). Western Africa, South Africa and particularly NSAm are isolated and further apart.

Figure 4.5.25. shows the same cluster previously described, but without MHNP. This sample was furthered by the z axis, which visually represents the component comprising the least variation (PC3). MHNP is still followed most closely by West Africa and Coimbra along the z axis. In this graph where almost all variance is represented (93.7%, as stated above), MHNP is still closest to Coimbra.

When observing the samples most likely to cluster together, we can see that Coimbra is very closely related to North Africa and Northern Europe, just followed by the slightly more distant Western Europe and MHNP, which are only clearly separated along the z axis (PC3). This last component derives relations from a small amount of
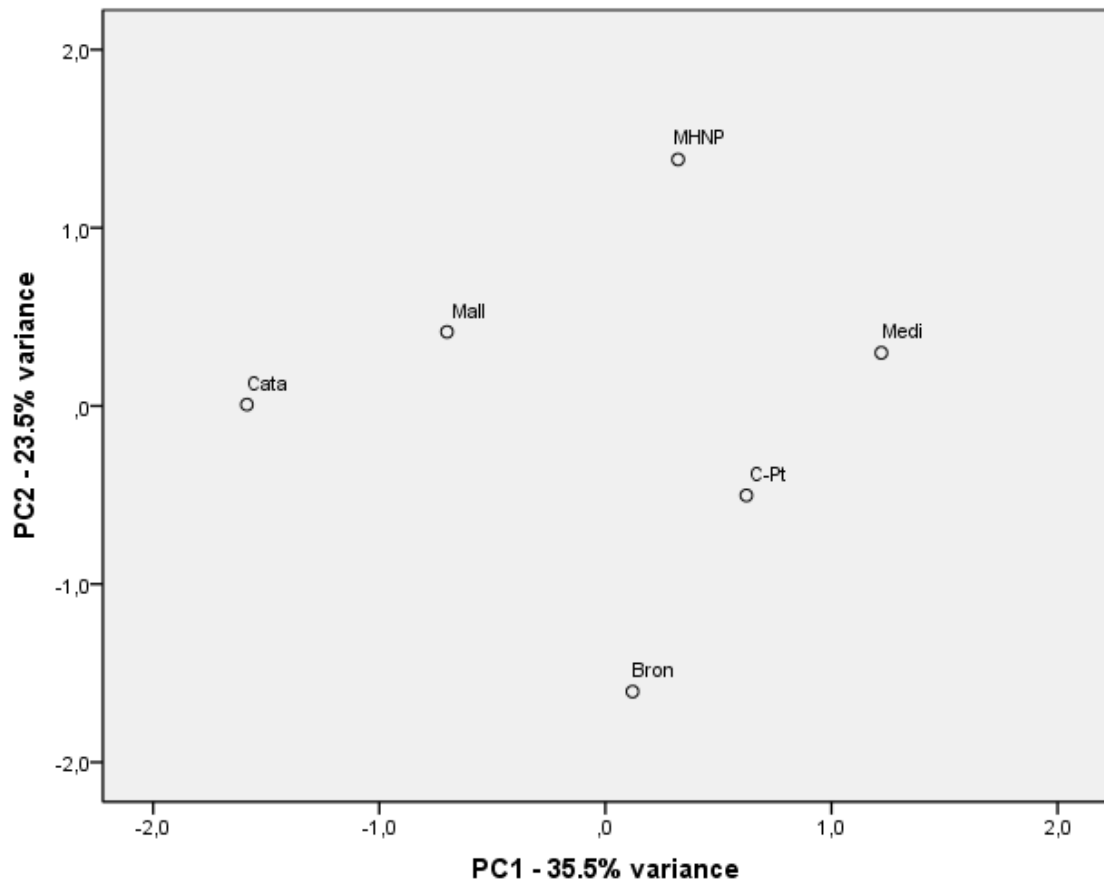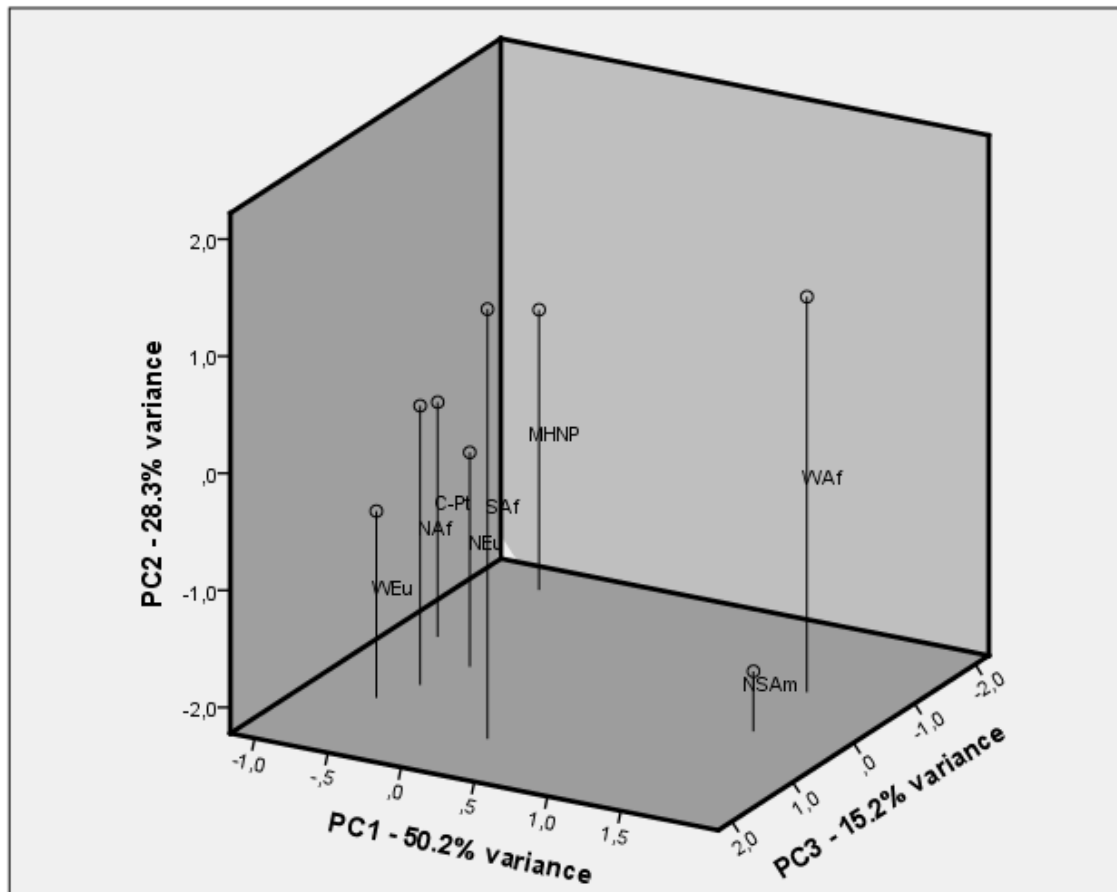
Figure 4.5.25. Scatterplot of the first three components in the comparison between Coimbra, a sample of unknown origin (Marado, 2010, 2012) and six world-wide samples (Scott and Turner, 1997).
C-Pt: Coimbra (Portugal); MHNP: Museu de História Natural da Universidade do Porto; NAf: North Africa; NEu: Northern Europe; NSAm: North and South Native Americans; SAf: South Africa; WAf: West Africa; WEu: Western Europe.

variation with distal trigonid crest as the only trait clearly responsible for such difference. Since this trait is not frequent anywhere in the world and varies only between 0% and 10% within the chosen samples, this diversity may be random or result from a sampling error.

MHNP sample constraints (lack of maxillae) and the traits reported on by Scott and Turner (1997) limited the number of usable traits for this analysis. Still, it demonstrated the biologically close affinity between Coimbra and MHNP, and the elevated likeliness of the latter sample being of Portuguese and late 19th/early 20th century, as was presumed. Another conclusion is the likely contribution of North African gene flow towards the Iberian Peninsula to the present genetic variability found on Portugal and Spain (see below).

Table 4.5.14. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Spanish, Europeans and North African samples.

Trait (tooth)	PC 1	PC 2	PC 3
Shoveling (11/21) + = ASU 3-6	0.263	-0.100	**0.709**
Lingual Cusp Variation (35/45) + = ASU 2-9	0.259	**-0.688**	-0.317
Hypocone (17/27) + = ASU 0-1	-0.404	0.331	0.184
C5 (16/26) + = ASU 1-5	**0.536**	**0.563**	**-0.525**
C5 (37/47) + = ASU 0	**-0.737**	0.286	-0.260
Groove Pattern (37/47) + = ASU Y	**0.688**	-0.130	0.304
C6 (36/46) + = ASU 1-5	**0.732**	0.489	-0.187
C7 (36/46) + = ASU 1-4	-0.029	**0.719**	0.408
Eigenvalue	2.141	1.766	1.275
Variance	26.8%	22.1%	15.9%
Total variance	26.8%	48.9%	64.8%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

Recently, a book chapter by Scott and colleagues (2013) compared (through cluster analysis), the biological affinities of two Basque samples, alongside several European samples, two North African samples and two South Asian samples (early and late India/Sri Lanka), all of wide chronological origins.

Using eight of the dental nonmetric traits reported therein, a PCA was produced to include Coimbra. The results from this information extraction are divulged on Table 4.5.14. PC1 (26.8% variance) heeds to the strong positive loadings (>0.5) from UM1 C5, LM2 groove pattern and LM1 C6; and to the strong negative loading (<-0.5) from LM2 C5.

As for the PC2 (22.1% of the variance), its variation in sample scores is derived from strong positive loadings for UM1 C5 and LM1 C7, and from a strong negative loading for LP4 lingual cusp variation.

Lastly, PC3 (15.9% variance) is characterized by the strong positive loading of UI1 shoveling, and the strong negative loading of UM1 C5.

Figure 4.5.26. corresponds to the distribution of the samples concerning 48.8% of the variance. A total approximating 64.8% of the variation is represented in Figure 4.5.27. This relatively small amount of graphically represented variation demonstrates the difficulty in reducing the amount of information retained by these samples. Their

geographic proximity and their chronological heterogeneity are most likely responsible for their relative closeness, but also for their randomly patterned variation, respectively.
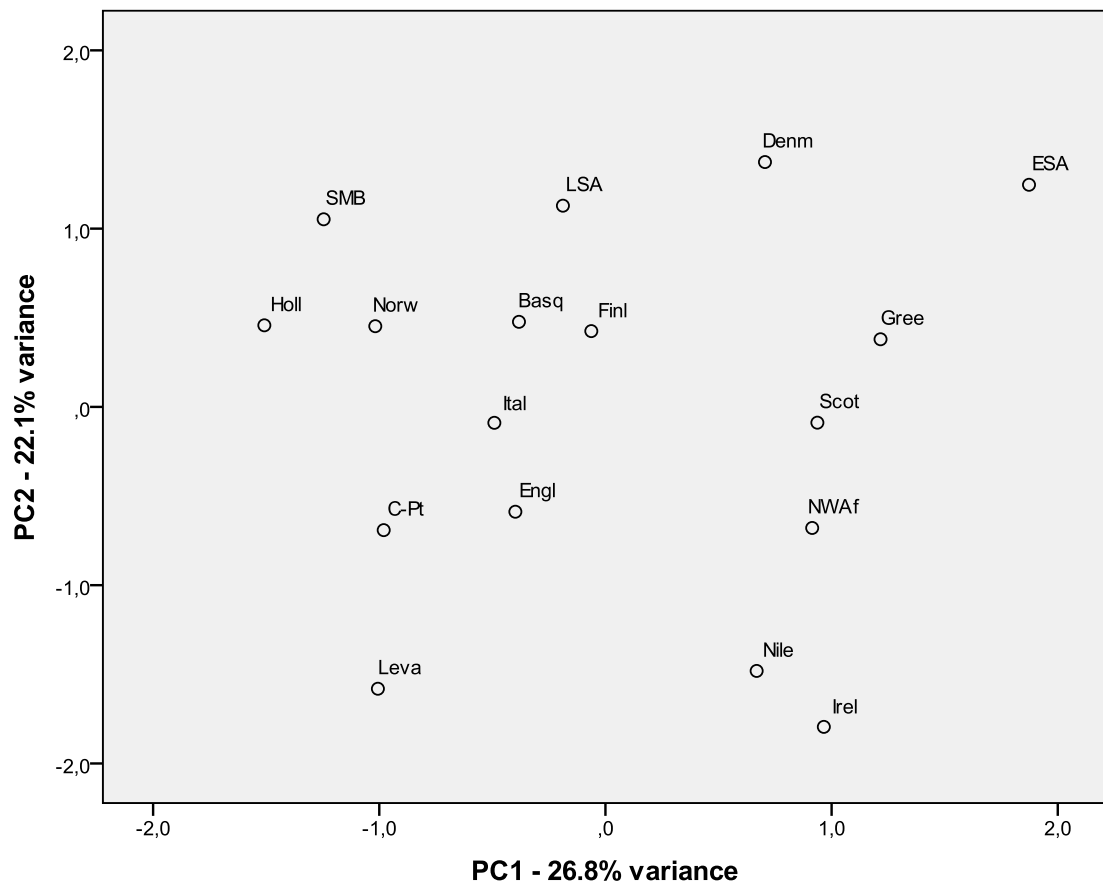
Figure 4.5.26. Scatterplot of the first two components in the comparison between Coimbra and several Iberian, European and North African samples (Scott *et al.*, 2013).
Basq: Basques; C-Pt: Coimbra (Portugal); Denm: Denmark; Engl: England; ESA: Early South Asia; Finl: Finland; Gree: Greece; Holl: Holland; Irel: Ireland; Ital: Italy; Leva: Levant; LSB: Late South Asia; Nile: Nile Valley; Nor: Norway; NWAf: Northwest Africa; Scot: Scotland; SMB: Santa Maria Basques.

These difficulties are expressed in Figure 4.5.26., which does not form clear associations between any of the samples. Coimbra is near Holland, the Santa Maria Basques, the Levant and Norway along the x axis (PC1) and near England, Northwest Africa, Italy and Scotland along PC2 (the y axis). The closest samples overall are Holland, Norway, Italy, England and Levant, with both Basque samples not much further.

Figure 4.5.27. aligns Coimbra with Holland, Santa Maria, Levant, Italy, England, Ireland and ESA along the z axis (PC3). The Portuguese sample thus clusters very closely with Holland, and forms a looser cluster with Holland, Levant, both

Basque samples, Italy, England and Norway. All other most distant samples are non-European or Northern European. Ireland and ESA seem to be the most isolated samples.
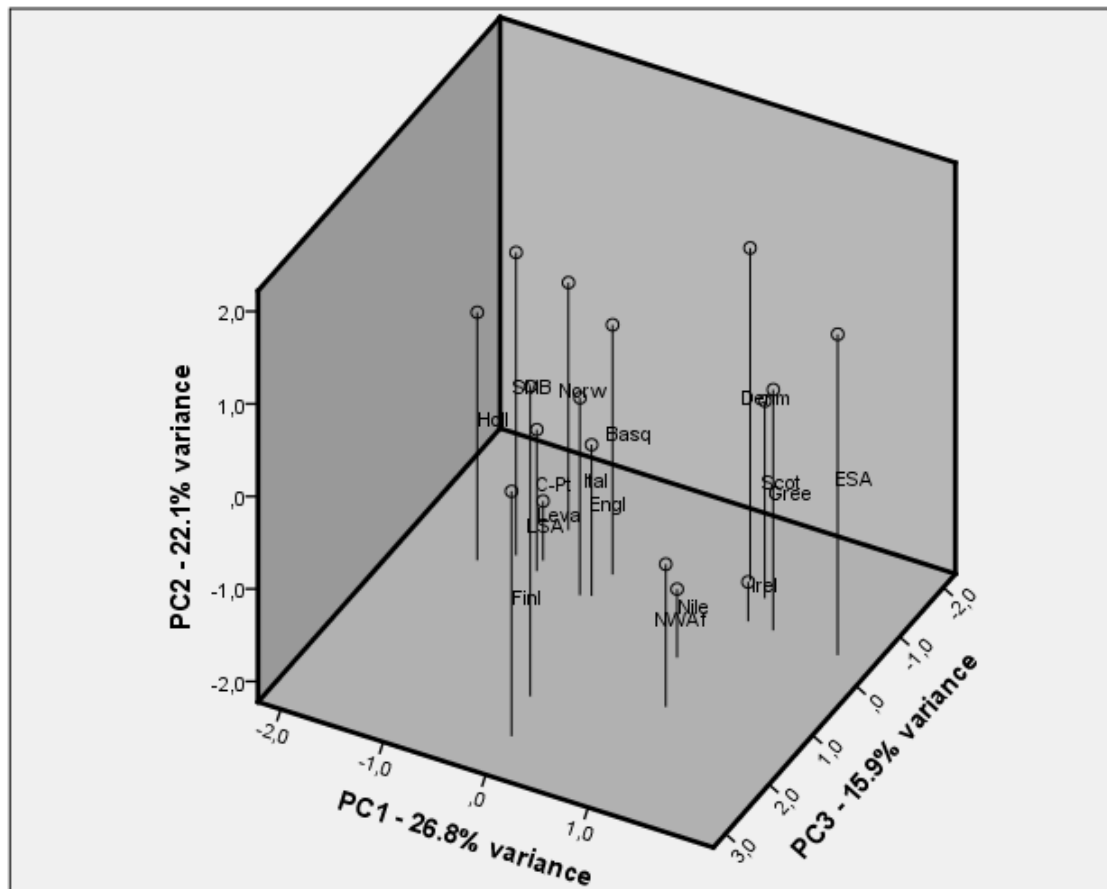
Figure 4.5.27. Scatterplot of the first three components in the comparison between Coimbra and several Iberian, European and North African samples (Scott *et al.*, 2013).
Basq: Basques; C-Pt: Coimbra (Portugal); Denm: Denmark; Engl: England; ESA: Early South Asia; Finl: Finland; Gree: Greece; Holl: Holland; Irel: Ireland; Ital: Italy; Leva: Levant; LSB: Late South Asia; Nile: Nile Valley; Nor: Norway; NWAf: Northwest Africa; Scot: Scotland; SMB: Santa Maria Basques.

These affinities towards samples as disparate as Holland, Norway (7th to 12th centuries: Salo, 2005), pre-historic Italy (see for example Coppa *et al.* [2007] and Vargiu *et al.* [2009]), England, Levant and even the Basques, particularly those from the Cathedral of Santa Maria (due to its diversity, since up to 25.0% of this sample could be foreign), are a testimony to the varied biological influences affecting Coimbra and the Portuguese gene pool, but can also testify to the inadequacy of this little battery of traits in establishing the most accurate biological relations.

A great deal of research needs to be conducted in order to fully understand the intricacy of the population movements that occurred across Europe in the course of time. Those studies will help clarify or nullify these results, and better understand the

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placement of Coimbra as the centre of yet another semi-circle, this one of diverse samples, many of which with no direct historical contact with Portugal, or no noticeable shared population movements. Genetic markers indicate Iberian isolation in relation to other European populations, with a low number of common ancestors in the last 1500 to 2500 years. This may be justified by isolation by distance or due to the Pyrenees, since Iberian samples have many common ancestors among themselves (Ralph and Coop, 2013).

For example, "Italy" includes several samples of continental Italy, Sicily and Sardinia from the Copper Age, which demonstrates homogeneity during this period, primarily among the continental regions. Sicily is the most divergent group, which is due to the island's distance from Italy and the possibility that their original population is biologically different, besides the island's greater contact with Aegean populations, through commerce. Biological relation is correlated with geographical distance when the Southernmost group of Laterza and Sicily are removed, since the former also had close ties to the Aegean Sea. This underlines the greater genetic homogeneity of the North and Central Italian groups from the Copper Age (Vargiu *et al.*, 2009). "Italy" also includes results from a transversal study of the dental anthropology of several populations from the Italian peninsula, from the ancient pre-History to the Middle Ages, showing the tendency for a replacement of the hunter-gatherer populations with migrating farmers (Coppa *et al.*, 2007).

The results reported by Salo (2005) refer to material from the Merovingian, Viking and Crusade periods (7th to 12th century) from Finland, mainly Viking material.

These two samples reassembled by Scott and colleagues (2013) exemplify the diversity found within and between these European samples, and how they increase the difficulty in interpreting this analysis' results.

According to Levy-Coffman (2005), contemporary Europeans are not descendants of Paleolithic or even Neolithic populations. Due to gene flow, founder effect, genetic drift, bottlenecks and evolution, Europeans are a new genetic mix resulting from these phenomena across time (Levy-Coffman, 2005). The Portuguese sample of Coimbra is here shown as a product of that process, with relations with many other samples.

Phenotype and allotype frequencies for the GM and KM genetic systems were analyzed in the Galician population. These show Galicia as genetically proximate to Portugal and both these populations in the center of the European genetic landscape,

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accounting for their shared histories and reflecting their importance in receiving historic European population movements (Calderón *et al.*, 2007). This illustrates the present results as reflecting a part of this centrality towards the genetic landscape of Europe, which is also an interesting avenue for further research.

Table 4.5.15. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Spanish, Basque, Spanish-Basque and Santa Maria Basque samples.

Trait (tooth)	PC 1	PC 2	PC 3
Winging (11/21) + = ASU 1a-1b	**0.961**	-0.108	-0.185
Shoveling (11/21) + = ASU 2-6	**0.774**	**-0.588**	-0.019
Double Shoveling (11/21) + = ASU 2-6	-0.012	-0.210	**-0.828**
Interruption Grooves (11/21) + = ASU 1	**0.751**	0.217	**0.612**
Interruption Grooves (12/22) + = ASU 1	**0.898**	-0.098	0.111
Distal Accessory Ridge (13/23) + = ASU 1-5	**-0.755**	**0.521**	-0.226
Distal Accessory Ridge (33/43) + = ASU 1-5	-0.481	**0.874**	0.062
Lingual Cusp Variation (34/44) + = ASU 2-9	**-0.992**	0.122	-0.012
Lingual Cusp Variation (35/45) + = ASU 2-9	**-0.685**	-0.018	**0.711**
Hypocone (17/27) + = ASU 3-5	-0.304	-0.393	**-0.760**
Carabelli's trait (16/26) + = ASU 2-7	-0.107	**-0.948**	0.117
C5 (16/26) + = ASU 2-5	**0.794**	-0.485	-0.242
Cusp Number (36/46) + = ASU 5	**0.818**	0.334	-0.055
Cusp Number (37/47) + = ASU ~= 4	0.456	**0.861**	0.048
Groove Pattern (36/46) + = ASU Y	0.491	0.274	-0.259
Groove Pattern (37/47) + = ASU Y	**-0.893**	0.253	-0.370
C6 (36/46) + = ASU 1-5	**-0.643**	**-0.737**	0.034
C7 (36/46) + = ASU 1-4	-0.305	**-0.627**	**0.598**
Protostylid (36/46) + = ASU 1-7	0.031	**0.950**	0.171
Protostylid (37/47) + = ASU 1-7	0.215	**0.925**	0.242
Deflecting Wrinkle (36/46) + = ASU 1-3	-0.159	**-0.622**	**0.642**
Eigenvalue	8.380	6.869	3.385
Variance	39.9%	32.7%	16.1%
Total variance	39.9%	72.6%	88.7%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

To better clarify the biological relations between the contemporary Spanish and Portuguese populations, another PCA was conducted, using only original data from this study and Scott and colleagues' (2013) work. These researchers report thoroughly on the frequencies found for many traits, mostly crown nonmetric variables, on samples from Spain, the Basque Country (those used in the previous analysis) and another of interbred Spanish and Basques. This allowed for an analysis including twenty two variables, which compares Coimbra to the mentioned Iberian samples.

Table 4.5.15. holds all details of this PCA. The strongest positive loadings (>0.5) on PC1 (39.9% variance) are UI1 winging and shoveling, UI1 and UI2 interruption grooves, UM1 C5 and LM1 cusp number. Strong negative loadings (<-0.5) hail from UC distal accessory ridge, LP3 and LP4 lingual cusp variation, LM2 groove pattern and LM1 C6.

PC2 (32.7% variance) is characterized by strong positive loadings from UC and LC distal accessory ridge, LM1 and LM2 protostylid, and LM2 cusp number. Strong negative loadings are reported for UI1 shoveling, UM1 Carabelli's trait, C6 and C7, and LM1 deflecting wrinkle.

Strong positive loadings on PC3 (16.1% variance) are presented for UI1 interruption grooves, LP4 lingual cusp variation, LM1 C7 and deflecting wrinkle. Strong negative loadings are also expressed for UI1 double shoveling and UM2 hypocone.

Figure 4.5.28. shows the Spanish-Basques, the Basques and the Spanish contemporaries to cluster together, while the samples of Santa Maria (slightly closer to the cluster) and Portugal (slightly closer to the Spanish) remain isolated.

The x axis (PC1) separates a cluster of Coimbra, Spanish-Basques, Basques and Spanish from Santa Maria, slightly separated from the middle sample (Spanish) than any other sample. Coimbra is nearer the Spanish sample.

The y axis (PC2) unites, once again, Spanish-Basques, Basques and Spanish, but this time also the Santa Maria sample, while the Portuguese sample are more isolated, and nearer the Spanish.

The introduction of PC3, through the z axis (Figure 4.5.29.), places Basques and Spanish in opposite ends of the distribution, divided by a cluster of Coimbra, Santa Maria and Spanish-Basques.

This relatively wide distribution of all samples suggests an amplification of the differences on what is really a set of samples with little biological variation. The late
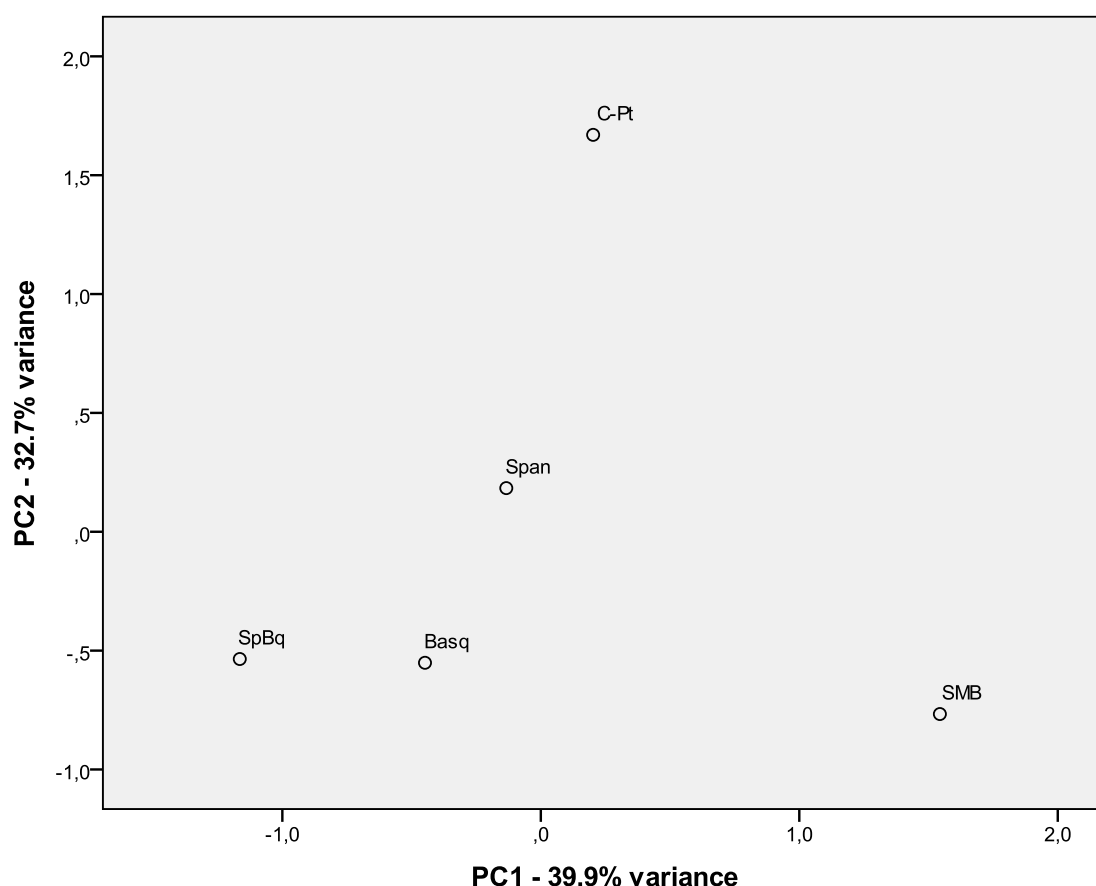
Figure 4.5.28. Scatterplot of the first two components in the comparison between Coimbra and contemporary Spanish samples (Scott *et al.*, 2013).
Basq: Basques; C-Pt: Coimbra (Portugal); SMB: Santa Maria Basques; Span: Spanish; SpBq: Spanish Basques.

19th/early 20th century Coimbra is the most disparate sample, followed by Santa Maria. Both have been (and Coimbra will continue to be; see below) shown as samples with diverse sources of biological variation, which can account for their greater distinction. Coimbra is, nonetheless, relatively closer to the contemporary Spanish than any other sample, which enlightens their biological, geographical and chronological proximity.

The Basques are very close to the Spanish along the most relevant axis (PC1, representing 39.9% of the variation). They are separated from each other and have the Spanish-Basque sample put between them along PC2 and 3 (representing 48.8% of the variation). Santa Maria is closer to the other samples influenced by the Basque genetic diversity, particularly the Basques.

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The Basque people (Northern Spain and Southern France) have long been supposed to be from a different genetic background from the remaining Iberian and Western European populations. This is due to a hypothesized better resistance to
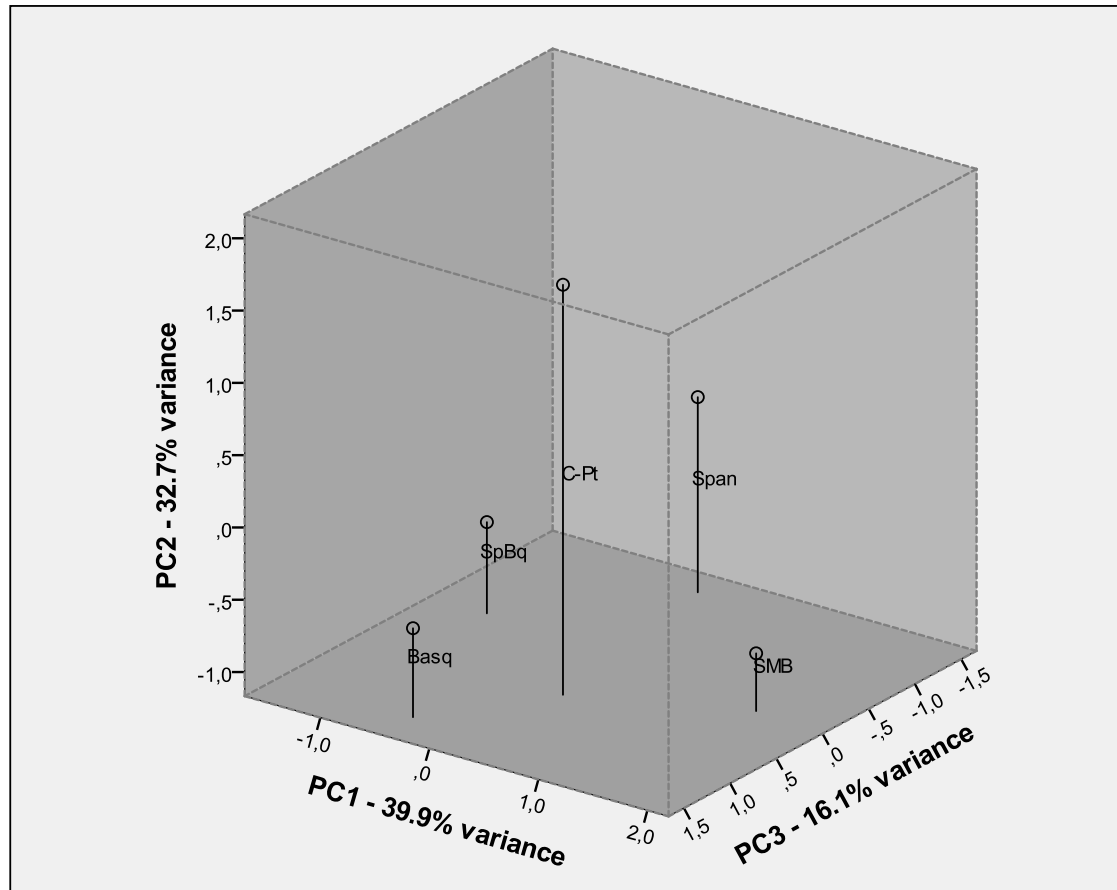
Figure 4.5.29. Scatterplot of the first three components in the comparison between Coimbra and contemporary Spanish samples (Scott *et al.*, 2013).
Basq: Basques; C-Pt: Coimbra (Portugal); SMB: Santa Maria Basques; Span: Spanish; SpBq: Spanish Basques.

Neolithic farmers from the Near East, who theoretically repopulated or interbred with the remainder of Europe, but not with Basques, who retained their Upper Paleolithic genetic patrimony. The study of this hypothesis is reviewed by Scott and colleagues (2013). These researchers' results show the Basque samples are outliers within the distribution of European samples, but do not display a clear and distinct characteristic that diverges from European frequencies, nor are isolated from European samples, since they cluster with them (Scott *et al.*, 2013).

Despite the hypothesis stating the Basques as an outlier in European biological variation, present results show this people's variation is mostly enclosed within the

Iberian genetic variability, since only one sample (with foreign influence) is more clearly separated from the cluster of Spanish samples. When compared to this sample, the Portuguese seem to be more of an outlier (despite being inserted within the same Iberian genetic variability) and have a more direct biological affinity with the Spanish, as was expected. In the previous analysis, the Basque samples were only marginally separated from the main cluster, with other European samples being much further. This analysis could have been severely limited due to the low number of traits and the low variability expressed tri-dimensionally (as explored above), which could have accidentally valued the diversity of other samples more than that of the Basques.

Levy-Coffman (2005) states the use of contemporary DNA results without comparison with ancient DNA has been found as misleading, since it assumes the haplogroup frequencies found are directly derived from the other populations whence they are found today. The case of the Basques is particular in the fact that this population is considered as directly descendant of Paleolithic hunter-gatherers, maybe the sole such example in Europe. However, ancient mitochondrial DNA has demonstrated the contemporary haplogroup frequencies found for the Basques are different from those of past Basques, indicating they probably were admixed with other populations across time, and that their differentiation is most likely due to the consanguinity promoted by their culture and to language barriers.

Both previous analyses displayed some proximity between the Basque and the present Portuguese sample, underlining the possibility that their variation is enclosed in the predictable variability of the Iberian gene pool. The relative closeness to both Spanish and Portuguese samples suggests Basques hail from the same genetic background as the other Iberian samples, and have genetically diverged from them through consanguinity. Their particular mountainous geographic locations, their particular culture and their outlier, non-Indo-European language, seem to be the causes of such process.

The analyses comparing these several Iberian samples, albeit informative, are limited. The samples compared are rarely divergent, and their relations are relatively diffuse. This underlines the need for continued research on the dental morphology of Iberian diachronic and geographically diverse populations, as well as on those that most likely influence the biological variation of this Peninsula's current gene pool.

Asturian population groups are distinguished genetically by markers of both mtDNA and Y-chromosomes. These distinctions are compatible with historical pre-Roman and Roman territory divisions and with geographical barriers to gene flow and illustrate the complexity of the history of biological variation in Iberia (Pardiñas *et al.*, 2012).

Four Ukrainian Mesolithic groups are heterogeneous and seemingly biologically related to Caucasus Paleolithic populations. Yet, the analysis of their biological proximity in the region shows the possible influence of many micro-evolutionary events contributing to their biological diversity (Haeussler, 1998). This example shows the susceptibility of a place of population convergence, with a relevant part in many population movements, due to its geographically advantageous position. Land and sea routes put Portugal and the Iberian Peninsula in contact with all European, Mediterranean, and Atlantic peoples across history, and ultimately, with the whole world. Population history and genetics are forcefully rich and attention worthy. Internal comparisons are necessary, but need proper contrast and to be related to other origins of diversity. An approach to such needs will therefore follow.

4.5.5. Portuguese biological affinities to North African samples

Having established Coimbra's biological relatedness to European and North African samples on a worldwide scale and shown these Portuguese sample's proximity to most other Iberian samples available, the next step is an inspection of the North African contribution to Iberian populations. History suggests it to be important, and will mediate these analyses.

After Islam's creation earlier in the 7th century, the caliph Abd al-Malik starts to define the rule of Arabia and their ever-expanding territories as an organized empire, instead of a tribal diffuse tradition, and got as far as the Iberian Peninsula, establishing hold of North Africa in the meantime (Silverstein, 2010). The Mediterranean was controlled by the Islamic empire by early 8th century, and the first incursions into Iberia were carried out by Berber allies, with a full conquest of al-Andalus accomplished by 712 (Zakrzewski, 2011).

This was achieved through the establishment of Arabic as the institutionalized language, the minting of coins and the definition of an Islamic and Arabic identity. This process was furthered by the Abbasid dynasty that followed. These caliph rulers were internationalists, and promoted the role of non-Arabian peoples, introducing the concept of the caravan, of Persian origin, as the mode of travel of excellence. The use of paper, a much cheaper medium than parchment or papyrus, created a wave of literacy and Islamic culture (Silverstein, 2010).

The conquest of Iberia by the Islamists took only roughly two years (Wyse, 2011). During the conquest, Syrian soldiers were also involved, and migrated there. Afterwards, a continuous flow of Arabs, but mainly Berbers and slaves (from the Islamic empire in North Africa, but also from other regions such as Eastern Europe and Ireland), the latter of which were traded frequently during the Islamic occupation of Iberia, was kept. Berbers, although mostly converted to Islamism, had different cultural practices and funerary rites than Arabs (Zakrzewski, 2011).

The first Berber incursion into Iberia was in July 710, and the riches found justified a larger invasion to these North African Islamic populations. The Visigoths had been menaced by plague and war and had wavering populations (as shown by a decrease from 6 to 4 million inhabitants of Iberia since Roman rule). After the readily accomplished conquest, the Arab ruling dynasty, the Umayyads, sent an army of Yemenite Arabs to avoid the excessive power of the Berber Islamists. From early on, attrition was found within the Islamic rule of al-Andalus. This was furthered when Berbers started revolting against the Arabs, after relegation to the mountainous regions, as the Arabs settled in the more fertile lowlands (Arabs traditionally avoided mountain environments: Silverstein, 2010). A new army was sent from Arabia to control the region. These Egyptian and Syrian men decided to stay in al-Andalus. The fall of the Umayyads left the Abbasids in power, and the tie between the Arabian caliphate and Iberia was broken. Ummayad influence rose in the Iberian Peninsula, and a new caliphate was created there in the 10th century, after a 9th century marked by internal division (Wyse, 2011). So, al-Andalus was established as an independent state, in the midst of a crashing Islamic Empire, limited by the time's lack of efficient communication in such a great length (Silverstein, 2010).

Al-Mansur was regent from the late 10th century onwards, and created a system of fiefs, whereby a new military class (mainly Berber tribes from Tunisia and Morocco and Slavic slaves) held control of the agricultural production. The early 11th century saw

new conflict between the Berber and Arab communities, with intervention from the Christians, resulting in loss of territory to the Islamic populations. Al-Mansur's son and successor alienated ethnicities other than Berbers, and was removed from power by the Umayyads. They, on the other hand, alienated the Berbers and were definitely removed from power of Cordova in 1031, after years of tumults. The Islamic territory in Iberia was divided in Taifas, whose "kings" were not much more than war-lords, some trying to get legitimacy out of false claims of connection to the Umayyads and the Abbasids (Wyse, 2011).

Christians in the North and West of the Iberian Peninsula resisted the Islamic presence since the 8th century, and the "Reconquest" (or "Reconquista", in both Spanish and Portuguese) was a very long war (more than seven centuries). As demonstrated, the 11th century was a turning point, since Islamic political disorganization helped regain territory. The fall of the independent caliphate of the Peninsula in 1031 left the territory fragmented and belligerent (Silverstein, 2010). Only the opportunism of the Reconquista forced some unity in the war-lords of the Taifa al-Andalus, who agreed to summon Berber allies from North Africa, the Almoravids, who ended the Taifa chapter of the history of the Islamic presence in Iberia. From then on, they took control of the Muslim "kings" and these war-lords became dependent on them and on Christian kings (Wyse, 2011).

The Berber dynasties of the Almoravids, succeeded by the Almohads (both religious orthodox, and threatening both Muslims residing in the Peninsula and Christians or Jews), did not keep Christian kingdoms from recuperating the hegemony over Iberia (Silverstein, 2010). This was finally accomplished only in 1492 (Gonçalves *et al.*, 2005).

During the Islamic stay in Iberia, cultural and even religious exchanges between the ethnicities present was notable, with Muslims described as sharing gifts in Christmas and with the new, indigenous, embracers of Islam and even indigenous people of Jewish faith being part of the ruling hierarchy (Wyse, 2011).

Zakrzewski (2011) studied an Islamic skeletal sample from Écija, Andalucía, Spain, from the 8th to 11th centuries. This maqbara (cemetery) probably contained not only Arabs, but also converted Berbers, slaves and early local converts, thus exhibiting genetic variation, placing itself between European and North African populations (Zakrzewski, 2011). This was to be expected, when the previous brief historic review is taken into consideration.

The mention of members of the Jewish faith should not be neglected. Sephardic Jews have been present in Portugal since the 3rd century. Genetically, it was found that a haplogroup of likely Jewish origin is present, with frequencies diminishing from the South of Portugal northward. Its presence may have explanations other than the Sephardic Jews, since this haplogroup seems to have variation justifying a longer presence in the Portuguese territory and it could have reached Portugal from other, more unlikely, sources, or through more than one wave of Middle Eastern populations (Gonçalves *et al.*, 2005). The Sephardic group could have arrived as slaves to the Roman Empire after the defeat of Judea in 70 AD (Adams *et al.*, 2008).

Berber haplogroups are found in Portugal and the Atlantic archipelagos at a frequency higher than the rest of Europe, suggesting the relevance of the gene flow between Northwest Africans and Iberia. This may also justify the presence of Middle Eastern haplogroups in Portuguese territory (Gonçalves *et al.*, 2005).

Historical sources indicate Arab and Berber populations got as far North as Galicia (the northwestern most region), in the Iberian Peninsula (Amorim, 2005).

Uniparental genetic markers are easier to use in detecting a given lineage, but any lineage may extinguish itself across time, since it may not be passed to any offspring at any given time. As for biparental markers, they do not represent a lineage in such a direct way, but are much less likely to be lost across generations, because they are not passed exclusively, but recombine in the offspring (Amorim, 2005). The latter markers are very similar, in Portugal and Galicia, and contrast with matrilineages and patrilineages found across this region. The former demonstrate Sub-Saharan African lineages throughout Portugal and North African lineages concentrating in Northern Portugal and Galicia only, when they were expected to be located towards the South, where the Muslim occupation was far more lasting. The origins of both these matrilineages are recent in the genetic pool of this Iberian population, since geographic distance within this territory is not correlated with genetic distance. They seem to derive from female slavery from both Sub-Saharan and North Africans. On the other hand, Sub-Saharan male slave reproduction seemed to have been at least frowned upon. There are no male lineages from this origin. North African patrilineages are much more in accord with historical facts, with frequencies gradually descending from South of Portugal to Galicia. Genetic mobility of matrilineages seems to be greater than patrilineage mobility, since genetic difference in markers is steeper for Y-chromosome markers than mtDNA (Amorim, 2005).

The concern with Sub-Saharan African gene flow into Portuguese and Galician territory is justified by the Portuguese Empire's role in the commercialization and employment of slaves.

Sub-Saharan African slaves composed up to 10% of the population of Lisbon in the period of slavery, from the 15th century onwards (Gonçalves *et al.*, 2005). A lack of Y-chromosome evidence of the sub-Saharan African presence in Iberia and the North Atlantic archipelagos (Canary Islands, Madeira and Azores) is most likely related to the lack of sexual contact and production of offspring between slave males and European women (Gonçalves *et al.*, 2005). This had also been underlined by Amorim (2005).

To trace a historical parallel, the peopling of the United States of America is a good example. Its widely varied biological contributions project an expectation of admixture far beyond cultural perceptions of "race". Through dental morphology, observing European and African Americans (from three periods) and comparing them to Europeans (several groups) and West Africans, Edgar (2009b) found that biological distances tended to diminish between early European Americans (derived mostly from Western Europe) and Eastern or Southern Europeans (initially discriminated). African Americans, despite their much longer contact with European Americans, have only a slight approximation to the latter, and mainly between the early and middle periods. This may be due to the social perception of race, which changed much more rapidly within Europeans, due to sociopolitical factors, than towards African Americans. The present author views the steepest transition between early and middle African Americans to be related to the somewhat accepted sexual access Caucasian men had to African women during slavery, pointed out by Edgar (2009b).

The historical and genetic approaches allow the present author to expect some North African (including Jewish) gene flow, approximating Coimbra and some North African contemporary and historical populations. Proximity with Sub-Saharan Africans is not likely, and has been demonstrated as that in both previous PCA's.

The first step into the understanding of the genetic inflow from North Africa and its current biological influence in the Iberian Peninsula is the introduction of Coimbra into the comprehensive comparison made by Irish (1998b) between several samples from North and Sub-Saharan Africa. The results are patent on Table 4.5.16. and on Figures 4.5.30. and 4.5.31.

Coimbra was occupied, during Islamic rule, by North African Berbers, recently converted to Islam, and therefore not strong enforcers of cultural or urban traditions. Besides, for most of the Islamic occupation, Coimbra was one of the most important mozarab centers (Christians under Islamic rule), reflecting the continuity of the city's

Table 4.5.16. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and several diachronic African samples.

Trait (tooth)	PC 1	PC 2	PC 3
Winging (11/21) + = ASU 2-6	0.184	0.041	**-0.577**
Palatine *Torus* + = ASU 2-4	-0.152	0.090	-0.295
Shoveling (11/21) + = ASU 2-6	0.446	0.449	**-0.570**
Double Shoveling (11/21) + = ASU 2-6	**-0.560**	0.375	-0.187
Interruption Grooves (12/22) + = ASU 1	**-0.569**	<u>0.506</u>	0.224
Distal Accessory Ridge (13/23) + = ASU 2-5	<u>0.795</u>	0.102	-0.051
Hypocone (17/27) + = ASU 3-5	<u>0.644</u>	0.300	0.331
C5 (16/26) + = ASU 2-5	<u>0.674</u>	0.154	0.062
Carabelli's trait (16/26) + = ASU 2-7	0.142	0.459	<u>0.694</u>
Enamel Extensions (16/26) + = ASU 1-3	0.414	<u>0.593</u>	-0.407
Peg Incisors (22/22) + = ASU 1-2	<u>0.514</u>	**-0.548**	0.268
Midline Diastema + = > 0.5 mm	0.496	-0.120	0.144
Lingual Cusp Variation (35/45) + = ASU 2-9	0.138	<u>0.812</u>	0.154
Anterior Fovea (36/46) + = ASU 2-4	<u>0.829</u>	-0.043	0.151
Groove Pattern (37/47) + = ASU Y	<u>0.633</u>	-0.469	-0.021
Cusp Number (36/46) + = ASU 6+	<u>0.571</u>	<u>0.538</u>	0.117
Cusp Number (37/47) + = ASU 5+	<u>0.860</u>	-0.226	-0.165
Deflecting Wrinkle (36/46) + = ASU 2-3	<u>0.635</u>	0.279	0.019
Protostylid (36/46) + = ASU 1-7	-0.010	0.003	<u>0.576</u>
C7 (36/46) + = ASU 1-4	<u>0.614</u>	-0.186	-0.127
Parastyle (18/28) + = ASU 1-6	0.003	0.201	-0.065
Eigenvalue	6.049	2.984	2.127
Variance	28.8%	14.2%	10.1%
Total variance	28.8%	43.0%	53.1%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

population (Trindade, 2007). However, the strong presence of North African and Arab populations in Iberia presumably allowed for a diffusion of their genetic variability, possibly reaching the presently considered Coimbra sample.
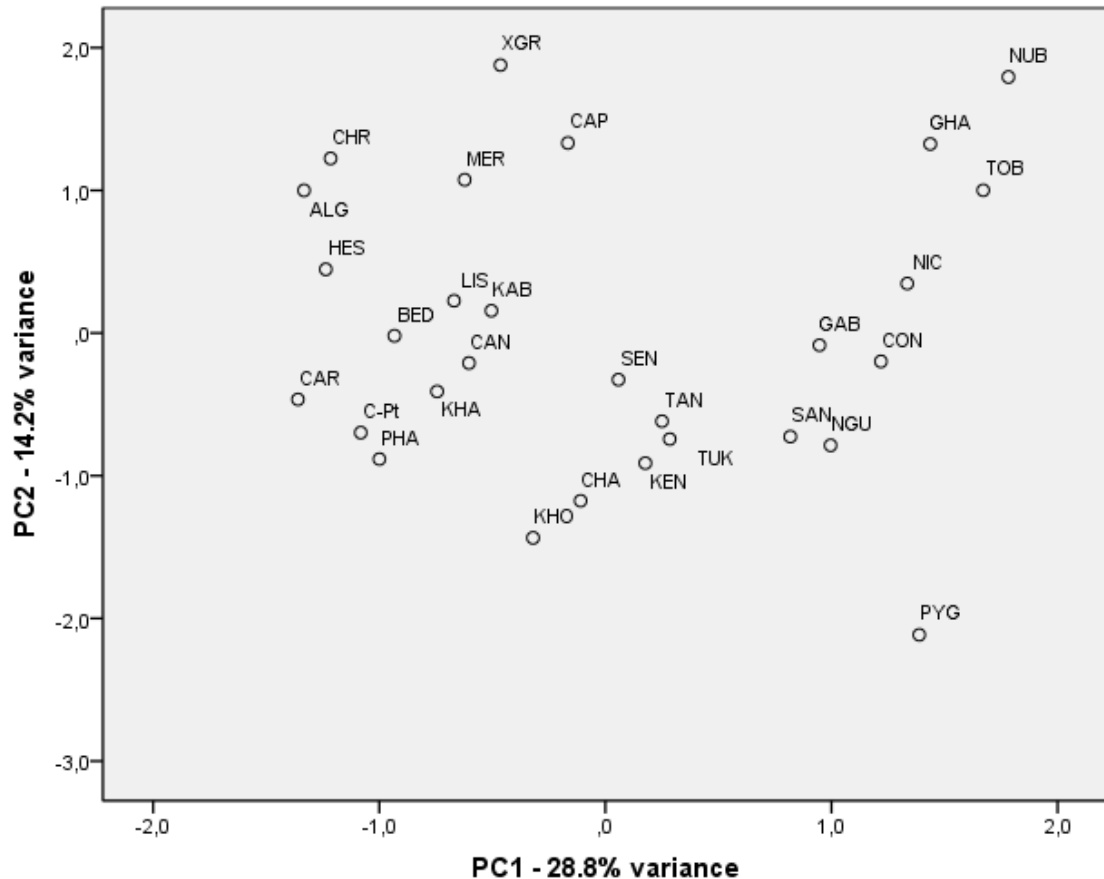
Figure 4.5.30. Scatterplot of the first two components in the comparison between Coimbra and diachronic African samples (Irish, 1998b).
ALG: Algeria; BED: Bedouin; CAN: Canary Islands; CAP: Capsian; CAR: Carthage; CHA: Chad; CHR: Christian Nubia; CON: Congo ; C-Pt: Coimbra (Portugal); GAB: Gabon; GHA: Ghana; HES: El Hesa; KAB: Kabyle; KEN: Kenya; KHA: Kharga; KHO: Khoikhoi; LIS: Lisht; MER: Meroitic Nubia; NGU: Nguni; NIC: Nigeria/Cameroon; NUB: Mesolithic Nubia; PHA: Pharonic Nubia; PYG: Pygmy; SAN: San; SEN: Senegambia; TAN: Tanzania; TOB: Togo/Benin; TUK: Tukulor; XGR: X-Group Nubia.

Table 4.5.16. underlines the influence of each of the 21 dental and oral nonmetric traits used in the production of each component. PC1 (28.8% of the variance) is defined by strong positive loadings (>0.5) from UC distal accessory ridge, UM2 hypocone, UM1 C5, peg-shaped UI2, LM1 anterior fovea, deflecting wrinkle, cusp number and C7, and LM2 groove pattern and cusp number. Strong negative loadings (<-0.5) are present for UI1 double shoveling and UI2 interruption grooves.

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PC2 (14.2% variance) is characterized by strong positive loadings for UI2 interruption grooves, UM1 enamel extensions, LP4 lingual cusp variation and LM1 cusp number. A strong negative loading is evinced for peg-shaped UI2.

Strong positive loadings on PC3 (10.1% variance) are reported for UM1 Carabelli's trait and LM1 protostylid. UI1 winging and shoveling contribute with strong negative loadings.
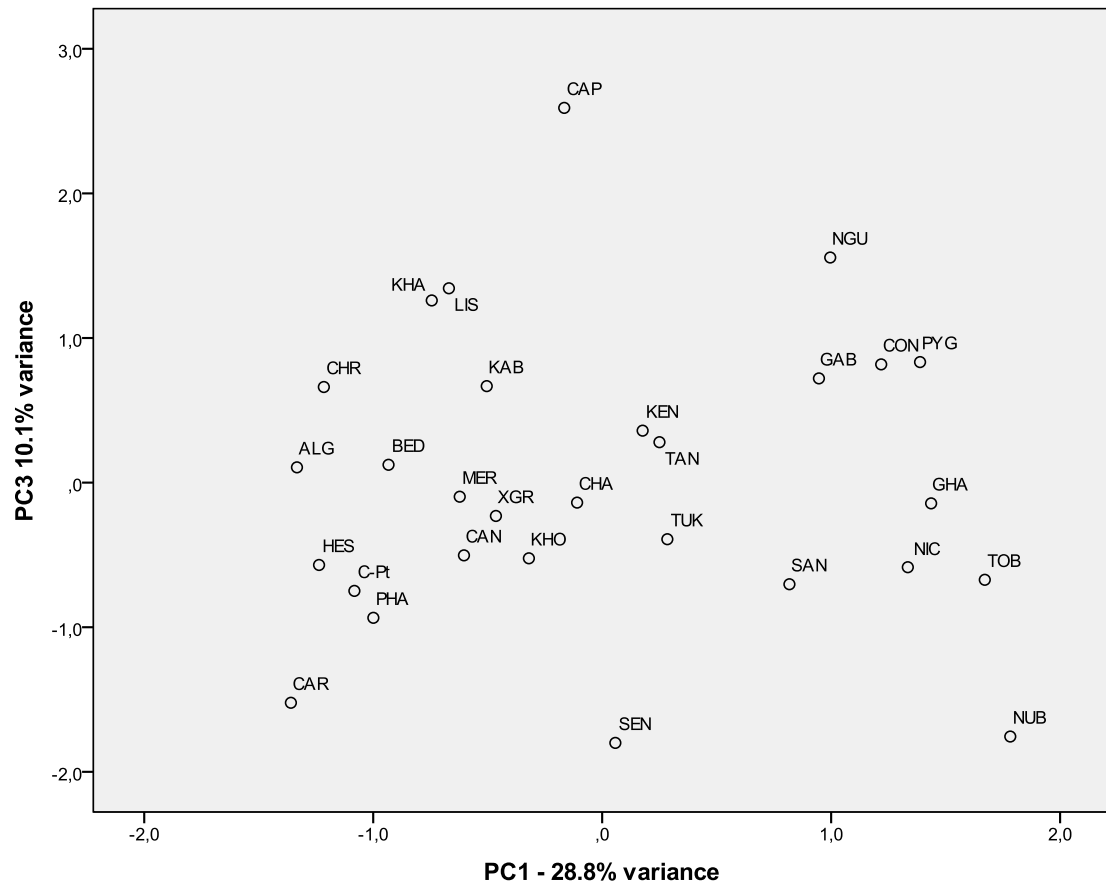
Figure 4.5.31. Scatterplot of the first and third components in the comparison between Coimbra and diachronic African samples (Irish, 1998b).
ALG: Algeria; BED: Bedouin; CAN: Canary Islands; CAP: Capsian; CAR: Carthage; CHA: Chad; CHR: Christian Nubia; CON: Congo ; C-Pt: Coimbra (Portugal); GAB: Gabon; GHA: Ghana; HES: El Hesa; KAB: Kabyle; KEN: Kenya; KHA: Kharga; KHO: Khoikhoi; LIS: Lisht; MER: Meroitic Nubia; NGU: Nguni; NIC: Nigeria/Cameroon; NUB: Mesolithic Nubia; PHA: Pharonic Nubia; PYG: Pygmy; SAN: San; SEN: Senegambia; TAN: Tanzania; TOB: Togo/Benin; TUK: Tukulor; XGR: X-Group Nubia.

Figure 4.5.30. reveals a pattern of distribution akin the one found by Irish (1998b) in his statistical analysis of the data (using more traits and including Sotho, a sample here excluded because of the lack of some of the used traits; naturally, Coimbra was not included in Irish's analysis). A marked division separates Sub-Saharan (including Mesolithic Nubia) from North African samples. Coimbra is included within

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the latter. The placement of this Portuguese sample nears that of Pharonic Nubians (16th to 14th centuries BC), Chartage (8th to 2nd centuries BC Punic Phoenicians), Kharga (6th/7th century Byzantine Egyptians) and, at a relatively further distance, of Canary Islands (probably 5th to 10th centuries) and Bedouins Arabs (19th/20th century).

Figure 4.5.31. (including PC3 as the y axis, instead of PC2; tridimensional representation of such an amount of samples proved, once again, confusing) reveals a slightly more diffuse, but still clear division between the same major clusters defined above. El Hesa (6th to 14th century Roman/Byzantine Egyptians) is nearer Coimbra, as Bedouins and Carthage are slightly further, and Kharga is much more distant.

This tridimensional (albeit constrained by a two phased approach to its construction and by a total of 53.1% of the variance visually represented) suggests clear and specific contribution of North African genes to the variation of the late 19th/early 20th century Portuguese gene pool. This genetic influence approximates Carthaginians, Canary islanders, Moroccan, Tunisian and Libyan Bedouins, Byzantine, Roman and Pharonic Egyptians to each other and to Coimbra. It should be noted Canary islanders are related to Northwest Africans and biologically homogeneous before European conquest (Guatelli-Steinberg *et al.*, 2001). Shawia Berbers (Algeria sample; 19th century) and Kabyle Berbers (also from Algeria; 19th/20th century) are distant, in spite of the Berber importance in the Islamic presence in Iberia, throughout eight centuries, and the genetic influence of Arabic, Carthaginian, Roman, Greek, French and Turkish influence, for example, in Shawia (Irish, 2000). Kabyle, however, experienced little genetic admixture, contrarily to most Berbers (Irish, 2000), which can explain its position further from Coimbra.

Capelli and colleagues (2009) found Portugal has a North African Y-chromosome marker frequency of 7.1%, which when compared to other Iberian and Italian samples is only lower than Cantabria (18.6%) and Sicily (7.5%).

Y-chromosome haplogroup frequencies in Northwest Africa (Berber and Islamic groups) and Iberia (Andalucía, Basques and Catalans) show there is small contribution of patrilineages from one area to the other (5% from North Africa in Iberia, and 4% from Iberia in North Africa). The remainder of the haplogroups for both areas is mostly of Upper Paleolithic and Neolithic origin, mainly the former. North Africa also displays around 8% Sub-Saharan African haplogroups (Bosch *et al.*, 2001). This analysis puts into question whether the Iberomaurusians were a part of the genetic makeup of Upper

Paleolithic Iberia, despite their relative proximity to these North African samples (Irish, 2000), and these samples' proximity to Coimbra.

Some Y-chromosome haplogroups identified in Huelva (Andalucía, Spain) originate (1) in the Eastern Mediterranean, due to commercial relations and, later, the Visigoth settling; (2) in Egypt, since people from that area were brought to Iberia to fight the Berber insurgency against the Arabs and settled, in part, in Beja (Portugal, near Huelva); (3) in the Arab occupants, who were relatively few, but were polygamists; (4) in Jewish communities, settled in Andalucía since at least the Roman Empire; and, to a lesser extent, (5) in Berbers, whose genetic influence in Huelva is, interestingly, less relevant in this area than on the remaining Iberian Peninsula, probably due to the particular relations between Huelva and the Balkans or Eastern North Africa (Ambrosio *et al.*, 2010).

These genetic findings also enlighten the present results, since the Berber influence is distant, when compared to some Egyptian samples and to other North African sources.

The genetic patrimony of these populations influences each other or shares common ancestry. Empires, eras and thousands of miles are crossed between these peoples, but genes and dental morphology alike seem to suggest they are biologically relatively close.

Irish (1998b) also found North Africans are phenotypically proximate to Europeans and Western Asians, showing a mass-reduced pattern of dental morphological frequencies. Across all North Africa, populations are very similar to one another, despite the large geographical and temporal gaps analyzed (Irish, 1998d).

Nonetheless, the distinction found between Mesolithic, - the only North African group clustering with Sub-Saharan groups -, and Pharonic Nubians was predicted. Dental nonmetric traits show Nubian post-Paleolithic discontinuity, when compared to Late Paleolithic Nubia (Irish, 1998c).

Greene (1982) demonstrated biological continuity across historical periods in Nubia, namely Meroitic, X-Group and Christian. Turner and Markowitz (1990) also corroborated it. They found continuity between late Holocene and recent Nubians, but a marked difference between late Pleistocene and recent Nubians, which can be justified by population replacement or admixture. This prompted Irish and Turner (1990) to try to explain the biological proximity between Pleistocene Nubians and contemporary

West Africans, contributing to the evolutionary and population histories of the South Nile region and West Africa.

The phenotypic similarity between Egyptian groups (Lisht, El Hesa and Kharga) and Nubian ones (Pharaonic Nubia, Meroitic, X-Group and Christian period) show gene flow from North Africa. Historically, this trend is also observed; culturally there are many influences, since the documented relations between the Mediterranean and Nubia are varied and almost constant until the 7th century AD invasion of Egypt by Arabs. Pharonic Egyptian depictions of Nubians are increasingly whiter, contrasting to the early darker (sub-Saharan African) paintings (Irish, 1998c).

Biological interactions between North and Sub-Saharan Africans, or those between North Africans and Europeans are not exclusively in one direction, as testified by four Bedouin tribes from South Sinai. These were compared, and one did not cluster with the others, possibly because of the varied biological origins, with a mix of Caucasoid, Mongoloid and Negroid influences. Still, all of them presented high frequencies of shoveling of the central incisor (characteristic of Mongoloids) and Carabelli's cusp on the first upper molar (typical of Caucasoids), which is an example of how interbreeding may cause amplification or disappearance of genes/traits. These tribes are strongly encouraged to breed within their own group (Moskona *et al.*, 1997).

These varied influences and other examples of diversity, even within sites, demonstrate the North African gene pool as heteregoneous. For example, dental morphology has demonstrated biological differences between cemeteries of different grave goods in predynastic Egypt, suggesting inbreeding and biological separation between a ruling or royal class and the general population. Although different temporal periods might justify this, the biological distance attained in a short time is unlikely (Johnson and Lovell, 1994). But not only dental data were used to delve into the question of the heterogeneity within North African populations. Nonmetric cranial traits were recently used to distinguish biological distances between North African Late Holocene populations, demonstrating the effect of the Sahara Desert in such relations (Nikita *et al.*, 2012).

The Mediterranean both separates and unites populations. Some biological relatedness was found between Late Bronze Age Northeast Cyprus and Middle Bronze Age Greece, although neither of these cultural groups is biologically homogeneous. On the other hand, Chalcolithic Southwest Cyprus is homogeneous, besides showing some biological proximity towards the Late Bronze Age sample from the same island and

some relation to Syria as well (Parras, 2004; Harper and Fox, 2008). Southern Europe and North Africa maintained contact through sea, as testified here. This underlines the already mentioned diversity of the North African gene pool and furthers the need to understand population movements to and from this area of the world.

In order to better comprehend the relations of some of closer samples portrayed in the previous analysis, most of the Sub-Saharan and some of the North African samples were removed. From the remaining nine samples (Mesolithic Nubia was kept to provide contrast), five were amongst the ones more consistently close to Coimbra (El Hesa, Bedouin, Carthage, Pharonic Nubian and Canary Island) and the Berbers (Algeria and Kabyle) were kept so as to clarify their biological relation with the Portuguese.

Table 4.5.17. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and selected North African samples.

Trait (tooth)	PC 1	PC 2	PC 3
Winging (11/21) + = ASU 2-6	**0.858**	-0.191	0.450
Palatine *Torus* + = ASU 2-4	0.401	**-0.722**	-0.070
Shoveling (11/21) + = ASU 2-6	**0.731**	0.123	0.456
Double Shoveling (11/21) + = ASU 2-6	-0.313	**0.874**	0.152
Interruption Grooves (12/22) + = ASU 1	**-0.564**	**0.580**	0.471
Distal Accessory Ridge (13/23) + = ASU 2-5	**0.760**	0.007	-0.232
Hypocone (17/27) + = ASU 3-5	**0.712**	-0.199	0.489
C5 (16/26) + = ASU 2-5	**0.940**	-0.043	0.220
Carabelli's trait (16/26) + = ASU 2-7	0.303	**0.734**	-0.295
Enamel Extensions (16/26) + = ASU 1-4	**0.906**	-0.012	0.316
Peg Incisors (22/22) + = ASU 1-2	0.370	-0.231	**-0.790**
Midline Diastema + = > 0.5 mm	**0.862**	0.045	-0.258
Lingual Cusp Variation (35/45) + = ASU 2-9	**0.565**	0.360	-0.333
Anterior Fovea (36/46) + = ASU 2-4	**0.754**	0.235	-0.111
Groove Pattern (37/47) + = ASU Y	**0.639**	-0.321	0.295
Cusp Number (36/46) + = ASU 6	**0.728**	0.367	-0.463
Cusp Number (37/47) + = ASU 5+	**0.957**	0.084	0.048
Deflecting Wrinkle (36/46) + = ASU 2-3	**0.838**	0.313	0.191
Distal Trigonid Crest (36/46) + = ASU 1	-0.304	0.250	0.109

Table 4.5.17. (Continued.)

Trait (tooth)	PC 1	PC 2	PC 3
Protostylid (36/46) + = ASU 1-7	0.380	-0.031	**-0.604**
C7 (36/46) + = ASU 1-4	<u>**0.572**</u>	0.486	0.068
Eigenvalue	9.619	3.137	2.724
Variance	45.8%	14.9%	13.0%
Total variance	45.8%	60.7%	73.7%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The three PC's visually projected (see Figures 4.5.32. and 4.5.33.) and analyzed below comprise 73.7% of the total variation among these samples. Table 4.5.17. reports on each trait's contribution to each component.

The strongest positive loadings (>0.5) on PC1 (45.8% variance) are from midline diastema, UI1 winging and shoveling, UC distal accessory ridge, UM1 C5 and
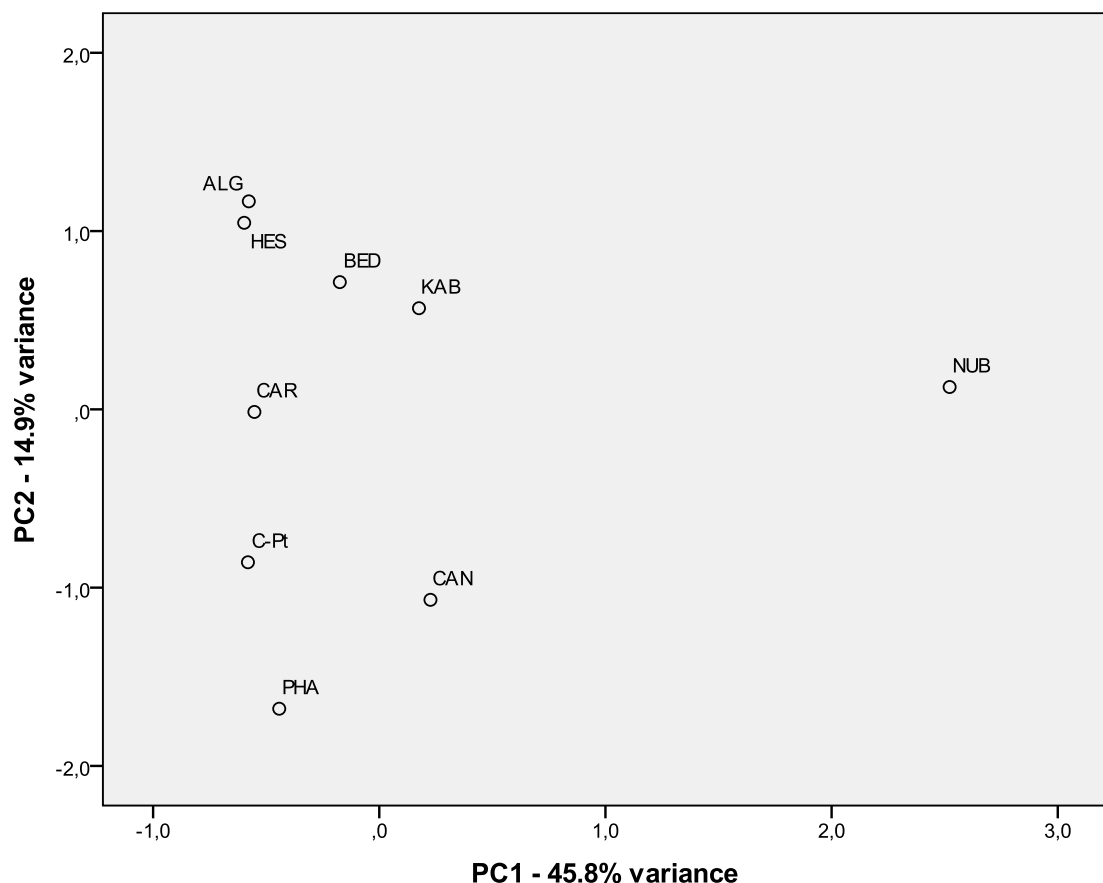
Figure 4.5.32. Scatterplot of the first two components in the comparison between Coimbra and selected diachronic African samples (Irish, 1998b).
ALG: Algeria; BED: Bedouin; CAN: Canary Islands; CAR: Carthage; C-Pt: Coimbra (Portugal); HES: El Hesa; KAB: Kabyle; NUB: Mesolithic Nubia; PHA: Pharonic Nubia.

enamel extensions, UM2 hypocone, LP4 lingual cusp variation, LM1 anterior fovea, cusp number, deflecting wrinkle and C7, and LM2 groove pattern and cusp number. A strong negative loading (<-0.5) was associated with UI2 interruption grooves.

Strong positive loadings contributing to the variation found on PC2 (14.9% variance) are from UI1 double shoveling, UI2 interruption grooves and UM1 Carabelli's traits. The single strong negative loading is from palatine *torus*.

PC3 (13.0% variance) is characterized by strong negative loadings from peg-shaped UI2 and LM1 protostylid.

Figure 4.5.32. places Coimbra in the center of a semi-circle formed by Pharonic Nubia, Carthage and Canary Islands, suggesting some major contribution from these populations to the constitution of this gene pool. Algeria, El Hesa, the Bedouin sample and Kabyle are close to each other and placed beyond Carthage. Mesolithic Nubia is far from every other sample.
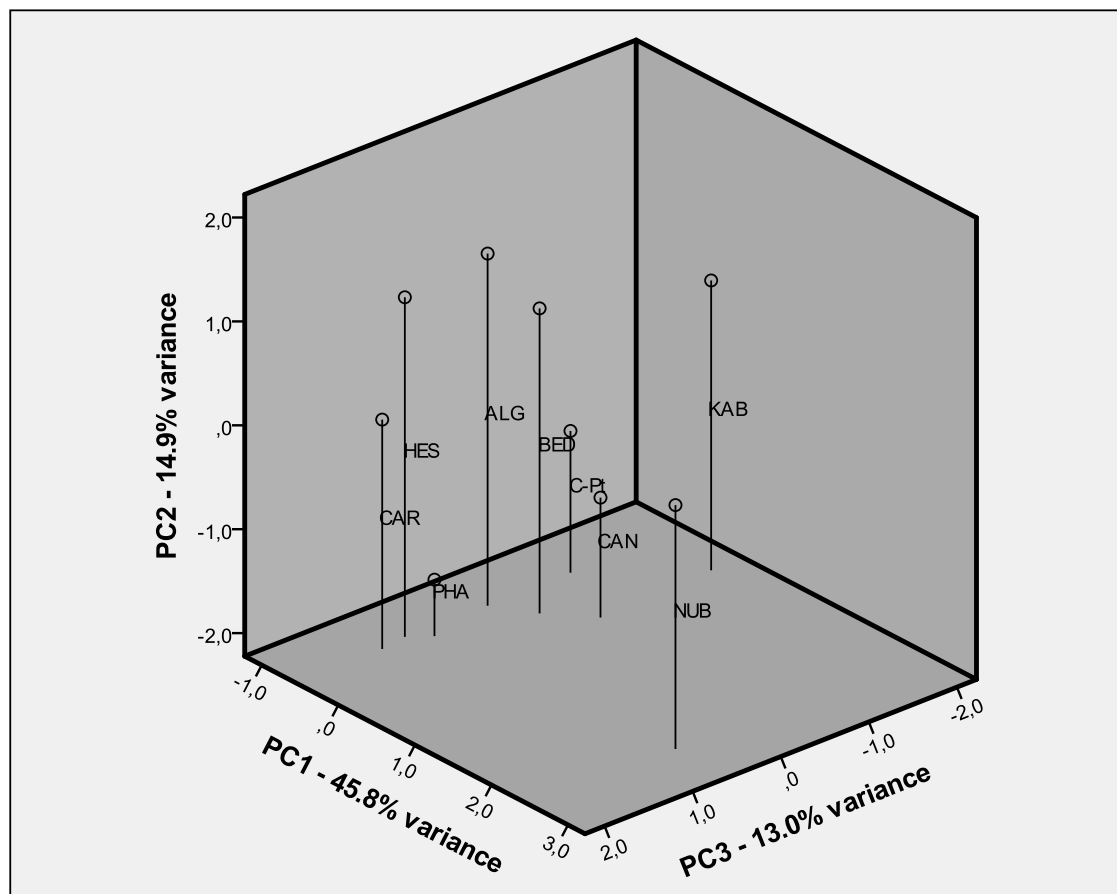
Figure 4.5.33. Scatterplot of the first three components in the comparison between Coimbra and selected diachronic African samples (Irish, 1998b).
ALG: Algeria; BED: Bedouin; CAN: Canary Islands; CAR: Carthage; C-Pt: Coimbra (Portugal); HES: El Hesa; KAB: Kabyle; NUB: Mesolithic Nubia; PHA: Pharonic Nubia.

Figure 4.5.33. aligns Mesolithic Nubia and Pharonic Nubia, but these samples from the same geographical area remain clearly separated. Coimbra, contrarily to what was just narrated for Figure 4.5.32., is surrounded by Algeria, Bedouins and Kabyle. Canary Islands is, however, even closer. The other closest samples (Carthage and Pharonic Nubia) are separated along the z axis (PC3).

The x axis (PC1), accumulating most of the graphically projected variation (45.8%), places Coimbra very near Pharonic Nubia, Carthage, Algeria, El Hesa, and relatively close to Bedouin, Kabyle and Canary Islands. This latter sample is subsequently nearer Coimbra along the y and z axes, PC2 and 3 respectively.

The only consistently distant sample, as evidenced by Figure 4.5.33., is Mesolithic Nubia. The remaining samples form a relatively close affinity either along PC2 (Carthage, Pharonic Nubia and Canary Islands) or PC3 (Algeria and Bedouin), besides PC1 (described above). El Hesa and Kabyle are somewhat of an exception, since they mainly approximate Coimbra in the PC1.

Carthage, Pharonic Nubians, Bedouin, Algeria and particularly Canary Islands and Coimbra are biologically close. This further demonstrates population genetics phenomena such as gene flow or genetic drift allowed for these samples from different geographic, and mainly chronologic, backgrounds to share genetic variation.

Another population movement worthy of interest and associated with North Africa is the Jewish Diaspora, which also influenced Iberia, and Portugal in particular. In order to check for the presence of genetic contribution of Jewish origin, data from Sofaer and colleagues (1986) were used in a PCA. For contrast, other North African and Broadbeach (Australian aboriginals) were included by the authors in the original analysis, and kept here.

The authors found, despite differences in some morphological and anthropometric variables, that tooth morphology of five Jewish populations (four modern and Mount Zion, from 3000 BP) showed biological proximity between three of the modern samples and the skeletal samples. Five other populations, much less wide-spread, were shown to be biologically more diverse than the Jewish groups. This demonstrates the capacity of dental morphology in evaluating biological distances even when selective pressures and population history create difficulties, resulting in the uselessness of other resources (Sofaer *et al.*, 1986).

Table 4.5.18. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra and several diachronic North African samples.

Trait (tooth)	PC 1	PC 2	PC 3
Hypocone (17/27) + = ASU 3-5	0.211	**0.673**	-0.093
Cusp Number (36/46) + = ASU 5	0.265	**-0.830**	0.040
C6 (36/46) + = 1-5	**0.617**	**0.515**	0.388
C7 (36/46) + = 1-4	-0.174	-0.065	**0.742**
Protostylid (37/47) + = ASU 1-7	**0.786**	-0.114	**0.559**
Carabelli's trait (16/26) + = ASU 2-7	**-0.861**	0.281	0.126
Shoveling (11/21) + = ASU 1-6	**-0.727**	-0.059	**0.594**
Interruption Grooves (12/22) + = ASU 1	0.042	**0.880**	0.009
Eigenvalue	2.415	2.280	1.392
Variance	30.2%	28.5%	17.4%
Total variance	30.2%	58.7%	76.1%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

PC1 (30.2% variance) is defined through strong positives loadings (>0.5) of LM1 C6 and LM2 protostylid, and strong negative loadings (<-0.5) of LM1 Carabelli's trait and UI1 shoveling (see Table 4.5.18.).

Strong positive loadings characterizing PC2 (28.5% variance) were from UM2 hypocone, LM1 C6 and UI2 interruption grooves. The strong negative loading of LM1 cusp number is also reported.

The strongest positive loadings on PC3 (17.4% variance) hail from LM1 C7, LM2 protostylid and UI1 shoveling.

In Figure 4.5.34., Coimbra is relatively isolated, although not as much as Broadbeach and Habbanite Jews. The sample closest to Coimbra is that of Mount Zion, constituted of Jews from the 10th century BC in Jerusalem. The non-Jewish samples of Broadbeach, Samaritans (religious sect separated from Judaism on the 5th century BC) and Israel Bedouin nomads are the next closest samples. Bedouin are also close to
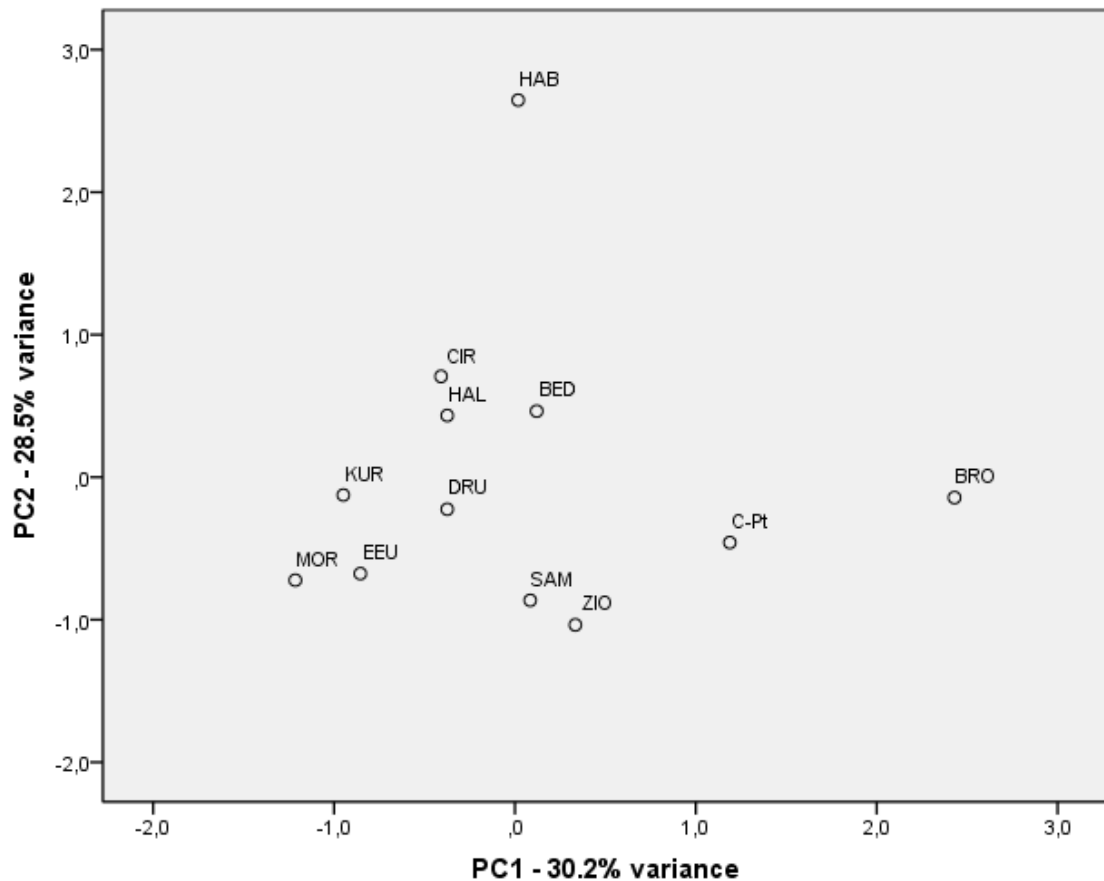
Figure 4.5.34. Scatterplot of the first two components in the comparison between Coimbra, Jewish, North African and Australian aboriginal samples (Sofaer *et al.*, 1986).
BED: Bedouins; BRO: Broadbeach (Australian natives); CIR: Circassians; C-Pt: Coimbra (Portugal); DRU: Druse; EEU: Eastern European Jews; HAB: Habbanite Jews; HAL: Wadi Halfa Nubians; KUR: Kurdish Jews; MOR: Moroccan Jews; SAM: Samaritans; ZIO: Mount Zion.

Circassians (Muslims originally from the Caucasus) and to Wadi Halfa Nubians. The Eastern European Jews are placed relatively far from Coimbra, near Moroccan and Kurdish Jews, and also Druse (an ethnic and religious entity from Israel). The Moroccan Jews are thought to be partly composed by exiles from Spain, from the 15th century, but are one of the samples furthest to Coimbra.

In Figure 4.5.35., Broadbeach is confirmed as the main outlier. Coimbra is once again nearest Mount Zion Jews. Eastern European, Moroccan and Kurdish Jews clearly cluster together. Habbanite Jews are still relatively isolated, and now Samaritans seem distant from the remaining samples as well. Wadi Halfa is placed between Samaritans and the Jewish cluster. The Bedouin are relatively close to Mount Zion, Circassians and Druse. They are also the second closest sample to Coimbra.

This result is interesting, since the samples placed nearest to Coimbra are Mount
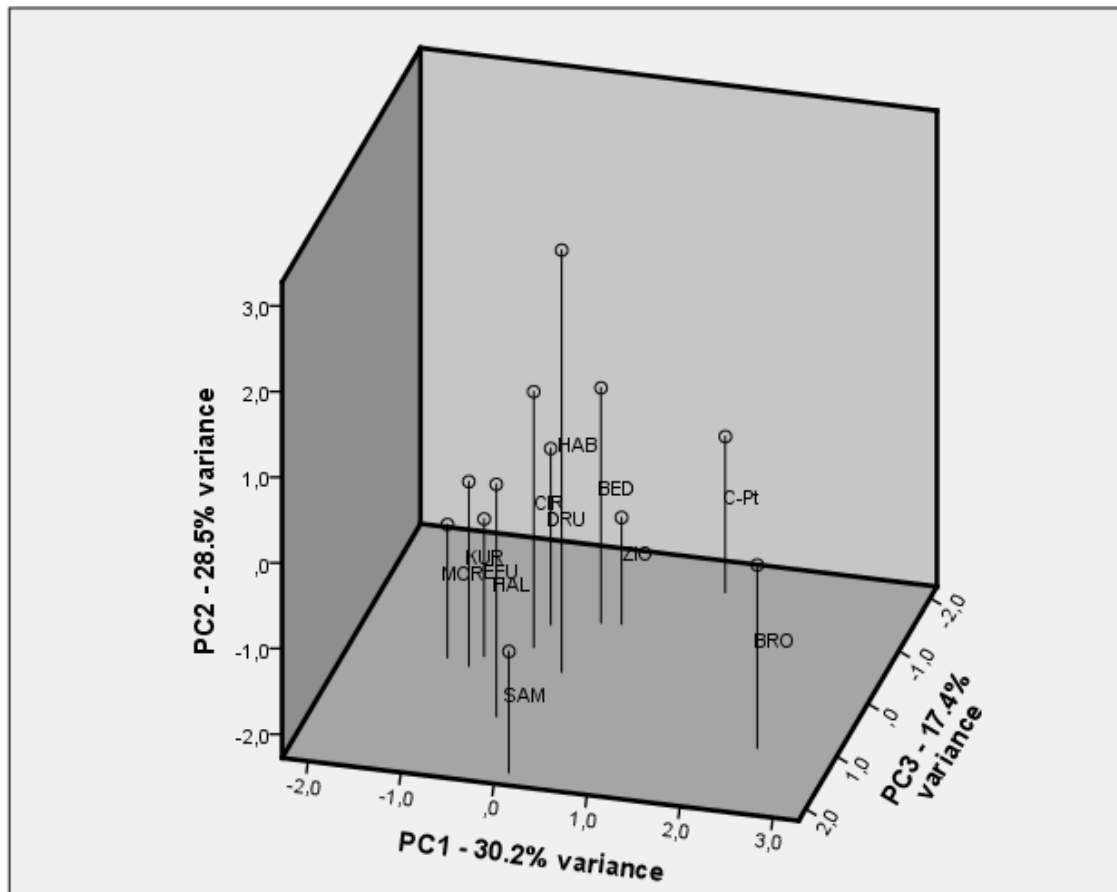
Figure 4.5.35. Scatterplot of the first three components in the comparison between Coimbra, Jewish, North African and Australian aboriginal samples (Sofaer *et al.*, 1986).
BED: Bedouins; BRO: Broadbeach (Australian natives); CIR: Circassians; C-Pt: Coimbra (Portugal); DRU: Druse; EEU: Eastern European Jews; HAB: Habbanite Jews; HAL: Wadi Halfa Nubians; KUR: Kurdish Jews; MOR: Moroccan Jews; SAM: Samaritans; ZIO: Mount Zion.

Zion, the oldest sample representing the original Jewish gene pool, and Bedouins, North African nomads. It may confirm the Jewish contribute towards the Portuguese, or even the Iberian, genetic variation; it may also testify to the contribution of nomadic peoples in the population of Iberia, when it was under Islamic rule.

Y-chromosome analysis found Sephadic Jewish ancestry in Portugal to ascend to 10.0% to the North of the Mondego River (which crosses Coimbra) and approximately 15.0% to the South of it (Adams *et al.*, 2008). Dental morphology data seem to corroborate this finding, through the approximation of an early Jewish sample with that of Coimbra.

Figures 4.5.36. and 4.5.37. place eight heterogeneous samples along bi- and tridimensional space, respectively, in accordance to the results of a PCA including ten dental nonmetric variables, five from each dental arcade. The samples included hail

mostly from the Iberian Peninsula. These are Coimbra, La Torrecilla and Sahl ben Malik (two Islamic Medieval cemeteries from Andalucía, Spain: Al Oumaoui, 2009) and three samples from different chronological contexts (Neolithic, Late Roman and Medieval Islamic) from the cemetery of Tossal de les Basses, Catalonia (Laguillo *et al.*, 2009).

Table 4.5.19. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, diachronic Spanish, North African and North and South American Native samples.

Trait (tooth)	PC 1	PC 2	PC 3
Double Shoveling (11/21) + = ASU 2-6	**_0.917_**	-0.271	-0.138
Interruption Grooves (12/22) + = ASU 1	**_0.910_**	0.054	0.065
Carabelli's trait (16/26) + = ASU 5-7	-0.211	0.427	0.307
C5 (16/26) + = ASU 1-5	-0.342	**-0.722**	0.281
Hypocone (17/27) + = ASU 2-5	0.108	0.398	**_0.799_**
Groove Pattern (37/47) + = ASU Y	0.159	**_0.766_**	-0.374
C5 (36/46) + = ASU 1-5	**_0.781_**	0.103	0.437
C5 (37/47) + = ASU 1-5	**_0.898_**	-0.287	-0.032
C6 (36/46) + = ASU 1-5	**_0.822_**	-0.316	-0.044
C7 (36/46) + = ASU 1-4	**_0.586_**	**_0.538_**	-0.129
Eigenvalue	4.302	2.008	1.185
Variance	43.0%	20.1%	11.9%
Total variance	43.0%	63.1%	75.0%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

Two worldwide samples were also included (data from Scott and Turner, 1997). North Africa was included in order to inspect its biological relations with the Medieval samples (with presumed gene flow from North Africa) and with Coimbra. North and South American Native Americans (NSAm) were included so as to provide contrast and better put into scale the proximity of the relations between the other samples.

Table 4.5.19. displays the proportion of variance each component reflects, as well as the traits' loadings into such components. PC1 (43.0% variance) presents strong positive loadings (>0.5) for UI1 double shoveling, UI2 interruption grooves, LM1 C5, C6 and C7, and LM2 C5.

The strongest positive loadings on PC2 (20.1% variance) are derived from LM2 groove pattern and LM1 C7. A strong negative loading (<-0.5) is patent for LM1 C5.

A strong positive loading of UM2 hypocone characterizes PC3 (11.9% variance).

Figure 4.5.36. clusters Coimbra and North Africa with the Medieval Islamic samples. Relatively near, the Islamic phase of the cemetery of Tossal de les Basses (CBI) is found. The Late Roman phase (CBT) and the Neolithic phase (CBN) are
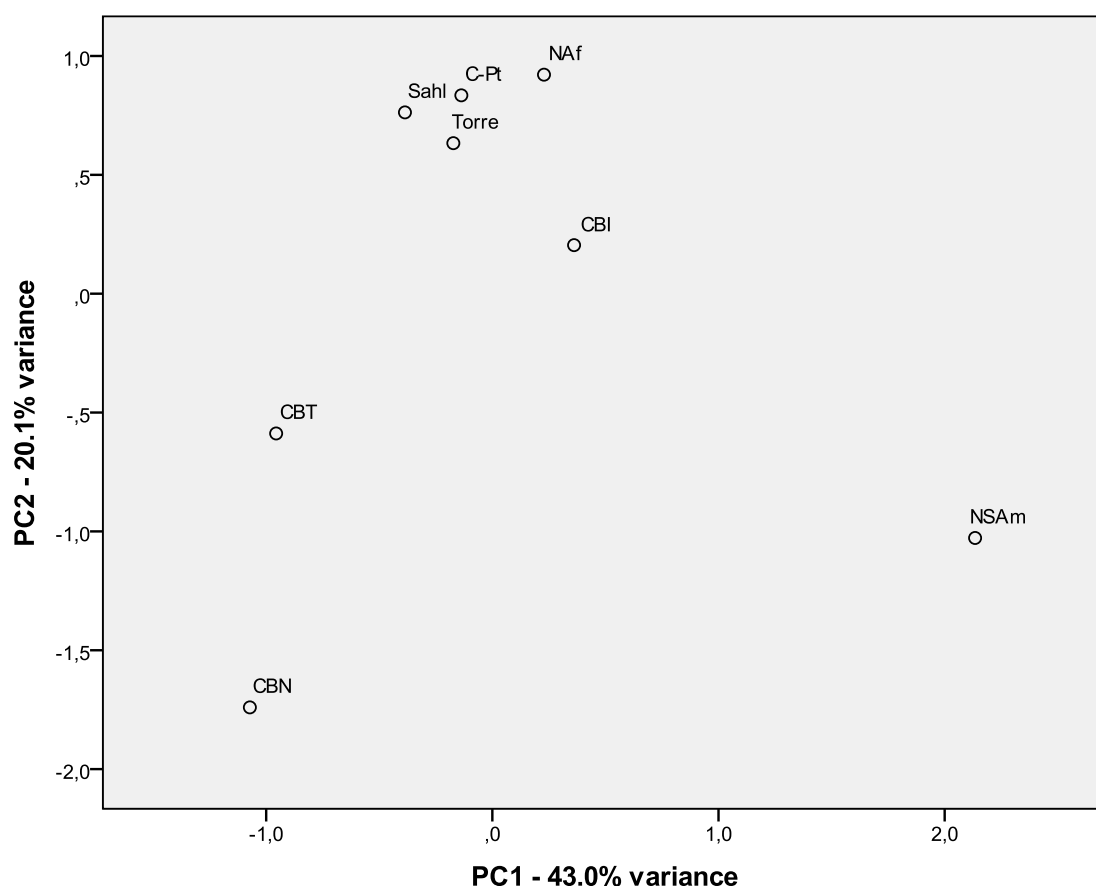
Figure 4.5.36. Scatterplot of the first two components in the comparison between Coimbra, Neolithic, Late Roman and Islamic Iberian (Al Oumaoui, 2009; Laguillo *et al.*, 2009) samples.
CBI: Cemetery of Tossal de les Basses (Islamic phase); CBN: Cemetery of Tossal de les Basses (Neolithic phase); CBT: Cemetery of Tossal de les Basses (Late Roman phase); C-Pt: Coimbra (Portugal); NAf: North Africa; NSAm: North and South Native Americans; Sahl: Sahl ben Malik; Torre: La Torrecilla.

increasingly further, mainly along the y axis (PC2). NSAm is, as expected, the furthest sample, separated along both axes.

Figure 4.5.37. approximates North Africa and the Medieval Islamic cemeteries of La Torrecilla and Sahl ben Malik. CBN is also closer along the z axis (PC3). NSAm divides these samples from Coimbra, along the same axis. Coimbra is now closer to CBI and more distant to the cluster originally formed on the previous representation. CBT remains fairly isolated.

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It should be remarked that the samples from Tossal de les Basses present a severe hindrance to analysis: the samples are all exceedingly small (from two to twelve teeth, depending on the sample and the trait analyzed), particularly that from the Neolithic phase. This is probably the main cause for the widespread distribution of these samples in both graphs, but still allows for some rough interpretation of the biological relations between the considered samples.
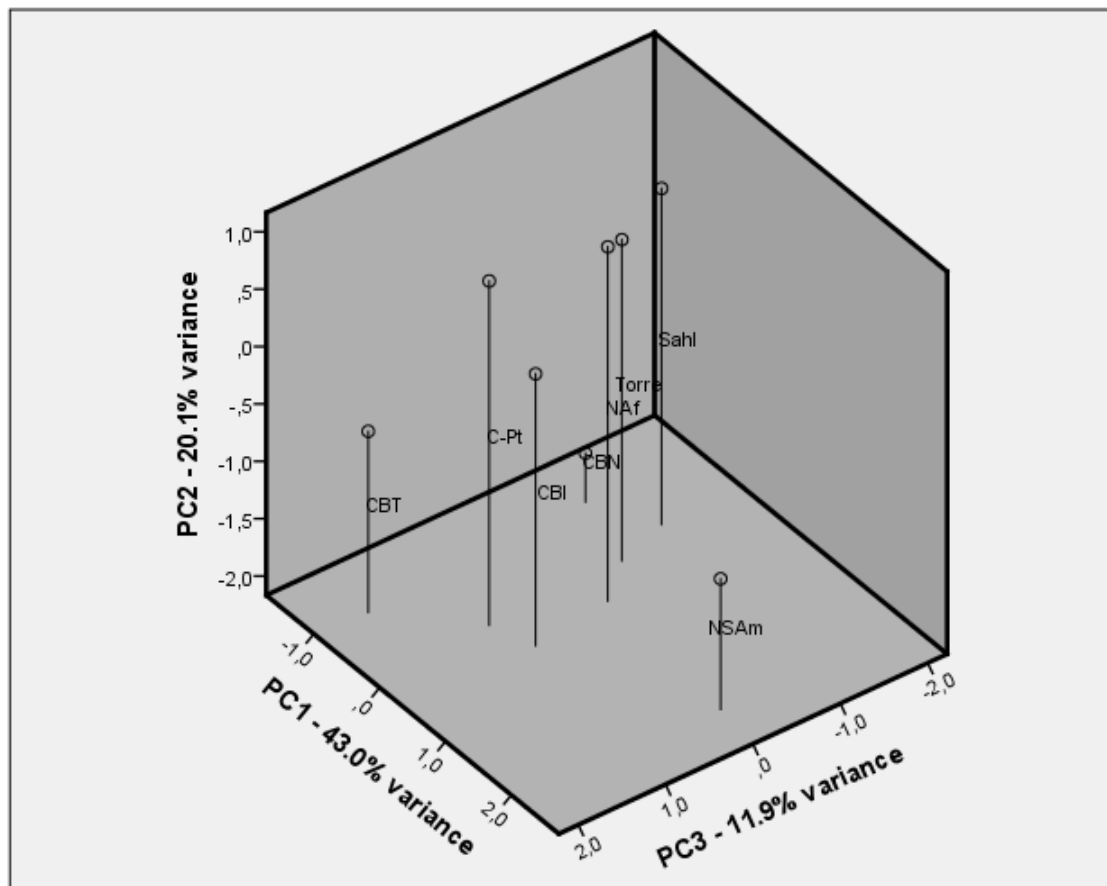
Figure 4.5.37. Scatterplot of the first three components in the comparison between Coimbra, Neolithic, Late Roman and Islamic Iberian (Al Oumaoui, 2009; Laguillo *et al.*, 2009) samples.
CBI: Cemetery of Tossal de les Basses (Islamic phase); CBN: Cemetery of Tossal de les Basses (Neolithic phase); CBT: Cemetery of Tossal de les Basses (Late Roman phase); C-Pt: Coimbra (Portugal); NAf: North Africa; NSAm: North and South Native Americans; Sahl: Sahl ben Malik; Torre: La Torrecilla.

There seems to be an influence of North African gene flow on the Medieval Islamic populations, according to these results. This influence is apparently reflected on the Coimbra sample, the main focus of attention in this analysis. The Portuguese sample is the closest to North Africa along the y axis (PC2) and is the second closest along the x axis (PC1). PC3 (z axis) separates these two samples, but it represents a much smaller part of the variation (11.9%). CBI shows the influence of North African genes through

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its position along PC1, despite a slight deviation on PC2 and approximately the same distance as Coimbra along PC3. La Torrecilla and Sahl ben Malik are consistently close to North Africa, particularly the former. This suggests a long lasting effect in biological diversity on the Iberian Peninsula, going back from the Medieval occupation of al-Andalus by Arabians and Berbers, mostly.

The Muslim population of Tossal de les Basses (CBI) was shown to be of mainly Iberian biological background, including influence of North African groups and sub-Saharan African populations, to a lesser extent (Laguillo *et al.*, 2009). This was not thoroughly supported by the present analysis, since the sample was portrayed as more distant from North Africans than the other Medieval Islamic sites in Spain. Even so, the small sample used still is relatively close to North Africa, suggesting a possible relation that should be further investigated.

The study of nonmetric dental variables in a medieval population from Ibiza, constituted of 167 Muslims from the 10th to the 13th centuries, showed this sample to be possibly influenced be gene flow from North Africa (Pacelli and Márquez-Grant, 2010). Unfortunately, the results were not compatible with the analyses developed within the present research.

The fact that there is proximity between three southern Spanish Medieval Islamic sites (at least, since CBI and the above mentioned Ibiza sample are not considered), North Africa and Coimbra supports a continuity of shared genetic diversity among North African and Iberian populations through time.

Iberians from Northeast Spain (pre-Roman proto-historic population), when ancient mtDNA was compared to other Iberian, European and African samples, showed greater proximity to contemporary samples from the same geographical location. Distinctions between the Portuguese, Andalucians and North Africans suggest gene flow between North Africa and Iberia was only effective from the 8th century onwards and differentiates the Portuguese and Andalucians from the Iberians. Even so the authors, Sanpietro and colleagues (2005), suggest the Roman, Visigoth, Vandal and North African (Berber and Arab) presence in Iberia did not alter the genetic substrate much. The Iberians could have little genetic variation due to the small and biased sample used in their study or due to endogamic, tribal mating practices.

Y-chromosome haplogroups from North Africa correspond to a mean 10.6% ancestry from that origin. In western Iberia (including Portugal and Galicia), these patrilineages are detected in greater proportion, when compared to the eastern part of

the Peninsula. In Northern Portugal (North of the Mondego River), the contribution seems to have been of over 20%. As for the Southern part of the country, approximately 35% of patrilineages include North African genetic markers (Adams *et al.*, 2008). Coimbra is crossed by the Mondego River and there are several people born to the North (and South, although less commonly) of that city in the sample. This suggests the frequency of North African haplogroups for the Coimbra sample to be between those cited before (20.0% and 35.0%).

Dental morphological data, as suggested through this analysis, place the contemporary Portuguese, the Medieval Islamic and the North African samples relatively very close to each other, clearly suggesting some biological proximity between them. This influence hardly seems to account for a small contribution of genetic diversity from the North African gene flow, as reported for mtDNA markers (Sanpietro *et al.*, 2005). It seems to reflect the greater contribution attested for by Y-chromosome haplogroups (Adams *et al.*, 2008), which underline the biological importance of the eight centuries North African presence in Iberia.

Biological affinities between Bronze and Iron Age Lachish and Dothan, from the Levant region (Near East), were studied by Ullinger and colleagues (2005), and compared to other Levantine, an Egyptian and an Italian sample. There is absence of historical evidence pointing to any direct biological relations (gene flow) between these chronologically and geographically remote samples and Coimbra, or any Portuguese or Iberian population. Some authors postulate the transition from Mesolithic to Neolithic was brought upon by the movement of Eastern Mediterranean peoples from the Levant. mtDNA and Y-chromosome genetic markers were recently used to discern the role of the Levant in the Out of Africa migration and the population movement in the Neolithic transition (Badro *et al.*, 2013). This, however, is not supported by dental morphology in Portugal, which suggests biological homogeneity between the Mesolithic and Neolithic samples (Jackes *et al.*, 2001). Despite this, the biological proximity inferred from a PCA including 15 variables was thought to benefit the search for affinities between North African/Near Eastern and Iberian (and particularly, Portuguese) genetic variability. Comparison between samples from before and after the time that encompasses the direct biological interaction between North African, Near Eastern and Arabian peoples, and Iberian peoples can be useful. If any relation is to be established, that could demonstrate the effect of the gene flow verified between each point in time.

Table 4.5.20. reveals strong positive loadings (>0.5) pertinent to PC1 (34.8% variance) are from UI1 double shoveling, UM2 hypocone, UM1 Carabelli's trait, LM2 groove pattern and LM1 C6. Strong negative loadings (<-0.5) derive from UM3 parastyle and LM2 cusp number.

Table 4.5.20. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Iron Age Italy and diachronic Levantine samples.

Trait (tooth)	PC 1	PC 2	PC 3
Shoveling (11/21) + = ASU 3-6	-0.260	**0.618**	0.126
Double Shoveling (11/21) + = ASU 2-6	**0.678**	0.264	-0.386
Interruption Grooves (12/22) + = ASU 1	0.238	**0.856**	0.102
Distal Accessory Ridge (13/23) + = ASU 1-5	-0.021	0.402	-0.456
Hypocone (17/27) + = ASU 2-5	**0.970**	0.058	0.185
C5 (16/26) + = ASU 1-5	0.365	**0.816**	0.175
Carabelli's trait (16/26) + = ASU 2-7	**0.834**	0.381	0.008
Parastyle (18/28) + = ASU 1-6	**-0.681**	**0.588**	-0.291
Lingual Cusp Variation (35/45) + = ASU 2-9	0.471	-0.403	**0.517**
Protostylid (36/46) + = ASU 1-7	-0.134	**0.757**	**0.594**
Groove Pattern (37/47) + = ASU Y	**0.855**	-0.100	0.494
C6 (36/46) + = ASU 1-5	**0.921**	0.027	-0.307
Cusp Number (37/47) + = ASU 4	**-0.743**	-0.059	**0.625**
Deflecting Wrinkle (36/46) + = ASU 3	-0.198	**0.870**	0.138
C7 (36/46) + = ASU 1-4	-0.005	**0.963**	-0.137
Eigenvalue	5.227	4.941	1.920
Variance	34.9%	32.9%	12.8%
Total variance	34.9%	67.8%	80.6%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

PC2 (32.9% variance) is characterized by strong positive loadings from UI1 shoveling, UI2 interruption grooves, UM1 C5, UM3 parastyle, and LM1 protostylid, deflecting wrinkle and C7.

The strongest positive loadings on PC3 (12.8% variance) hail from LP4 lingual cusp variation, LM1 protostylid and LM2 cusp number.

The results represented on Figures 4.5.38. and 4.5.39. reflect the relations observed by Ullinger and colleagues (2005) between the samples they analyzed. Dothan
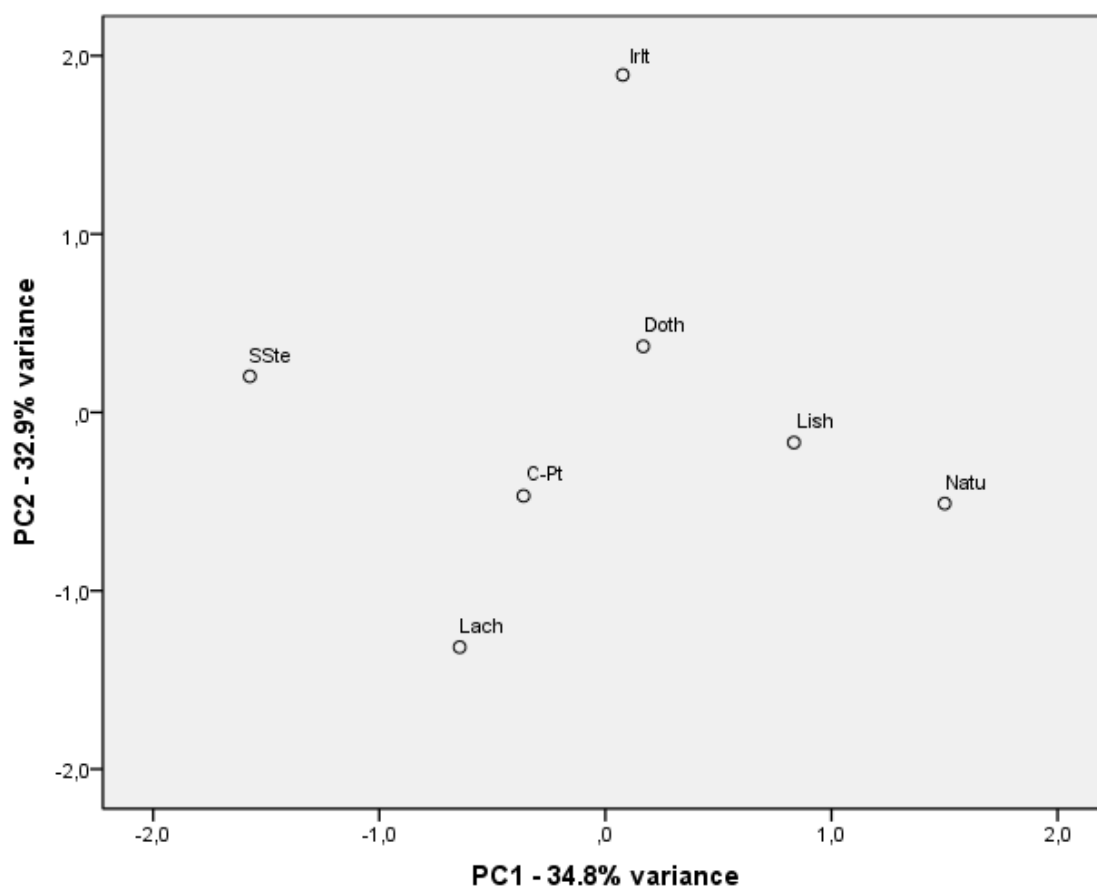
Figure 4.5.38. Scatterplot of the first two components in the comparison between Coimbra, Levantine, Egyptian and Italian samples (Ullinger *et al.*, 2005).
C-Pt: Coimbra (Portugal); Doth: Dothan; IrIt: Iron Age Italy; Lach: Lachish; Lish: Lisht; Natu: Natufian; SSte: St. Stephen's Byzantine monastery.

(15th to 11th centuries BC) and Lachish (4th millennia to 4th century BC) are relatively close, but the latter is more isolated. Lisht (Egyptian Middle Kingdom, 20th to 18th centuries BC) and St. Stephen's (Byzantine Jerusalem monastery, 5th to 7th centuries) are not very disparate, contrarily to Iron Age Italy (10th to 1st centuries BC) and Natufian (Jordan Epipaleolithic, 11th to 9th millennia BC).

Coimbra is placed between Dothan and Lachish, along both the x (PC1) and y (PC2) axes. Coimbra and Lisht were already compared before, amidst many other North African and Sub-Saharan samples (see Figures 4.5.30. and 4.5.31.). Then, these samples were placed within the same major group of North African origin, but had merely a fleeting proximity. If, despite differences among PCA's, this distance can be transposed to this interpretation, it is easy to associate this fleeting proximity to Dothan and

Lachish, and one akin it to St. Stephen's. Coimbra is placed in the center of these samples in Figure 4.5.38., suggesting similar affinities to each, and separated from Iron Age Italy and St. Stephen's, not to mention the Natufians, the most distant sample. A
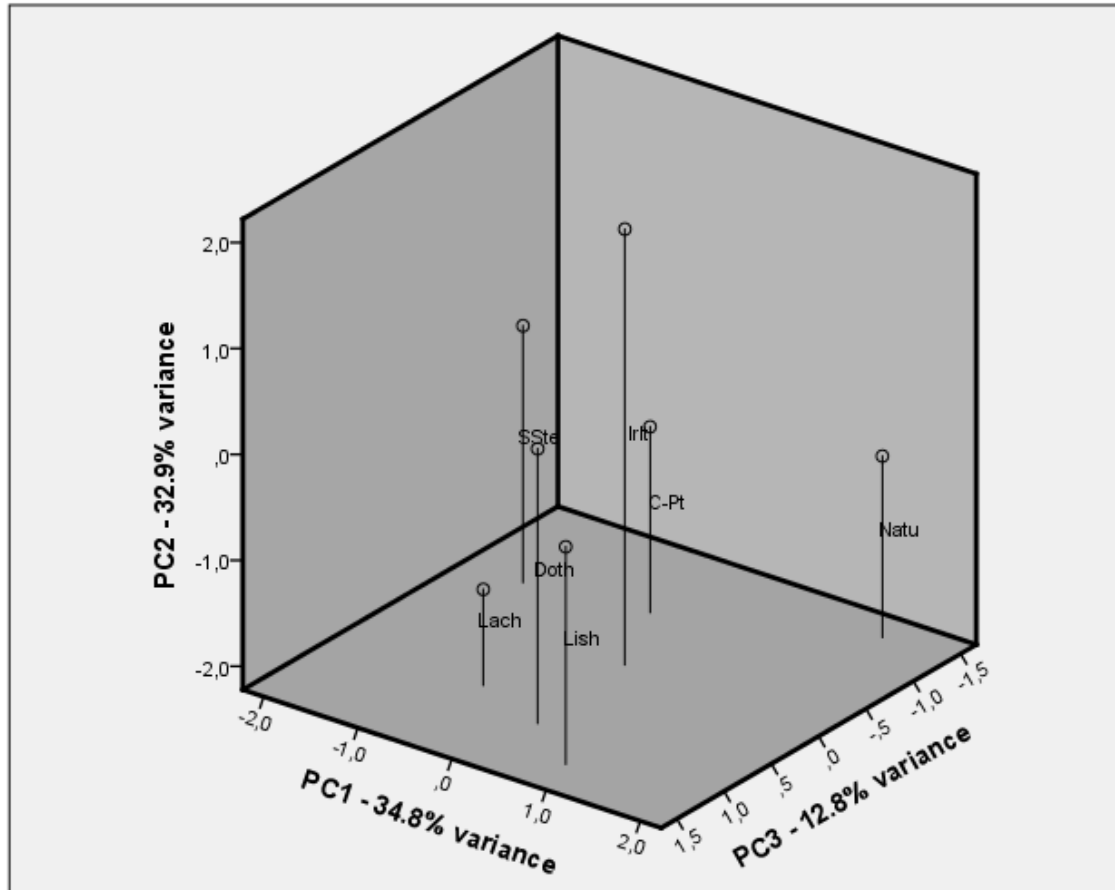
Figure 4.5.39. Scatterplot of the first three components in the comparison between Coimbra, Levantine, Egyptian and Italian samples (Ullinger *et al.*, 2005).
C-Pt: Coimbra (Portugal); Doth: Dothan; IrIt: Iron Age Italy; Lach: Lachish; Lish: Lisht; Natu: Natufian; SSte: St. Stephen's Byzantine monastery.

greater proximity between Coimbra and Iron Age Italy (the sole European sample), and St. Stephen's (a sample with some European admixture; see Ullinger, 2002) is only found along the z axis, through the influence of PC3, the least relevant component analyzed (only 12.9% of the variation; Figure 4.5.39. comprises 66.8% of the variation). Even so, Figure 4.5.39. proposes St. Stephen's as the sample with a greater biological affinity to Coimbra, due to its closeness. The Byzantine monastery of St. Stephen's population is shown by dental morphology to be most similar to Historic North Europeans and other people from the Near East (Early Near East and Early Egypt), and disparate when compared to the contemporaneous and geographically close group of

Ein Gedi (Ullinger, 2002). Some proximity with Coimbra was, therefore, to be expected.

These results suggest Coimbra is biologically influenced by similar factors as St. Stephen's, an ethnically diversified monastery of the early Middle Ages. Once again, the genetic patrimony found in North Africa apparently contributed to the Portuguese genetic diversity. The fact that these ancient populations, separated from Coimbra by millennia in many cases, share remote connections to it (demonstrated in particular through PC2), allows the suggestion of notorious and long lasting gene flow from North Africa to present Portuguese and, possibly, Spanish territories.

The only studies dealing with the dental morphology of a Portuguese Medieval sample of Islamic influence focus on Mértola, Lower Alentejo. Leandro (2011) studied 30 individuals from this origin, from Late Medieval chronology (14th to 16th centuries, after the Christian "Reconquista"). Cunha (2011) also describes another 30 individuals from this same archaeosite. Despite the funerary evidences denoting a clear religious affiliation with the Christian faith, a coin was placed in the hands of the interred, in order to allow for the payment of Charon, which is a pagan tradition (Leandro, 2011). Mértola profited from the use of the Guadiana River as a means of communication. Around 60km of this river are crossable, from the river mouth to the city, allowing its connection with the Mediterranean Sea. This made the city an important port for Phoenicians, Carthaginians, Romans and Arabs alike (Cunha, 2011).

Although Mértola was not Islamic at the time the mentioned individuals were interred, the Islamic biological influence, if there ever was one, should still be present. Another sample, that of Shantarin (Islamic Medieval Santarém), was studied by Rodrigues (2013). Although it was recovered in Largo Cândido dos Reis, in Santarém, as the previous sample from Santarém (mentioned above), this sample of 45 individuals was from an anterior period, from the 8th/9th to the 12th centuries, and they were mostly buried according to Muslim customs.

These samples from Mértola and Shantarin were analyzed alongside the Coimbra Portuguese sample, two Spanish Islamic necropolises (La Torrecilla and Sahl ben Malik) and two prehistoric samples (Cuesta del Negro and Fuente Amarga) reported on by Al Oumaoui (2009). The latter samples provided the contrast to better infer the relationship between these samples. The aim of this comparison was to understand the proximity of the Portuguese Islamic, Medieval and Modern samples to

each other and to Spanish Islamic samples, shown above as affected by gene flow from North African populations.

Table 4.5.21. provides the *eigenvalues* and trait loadings of the PCA. Figures 4.5.40. and 4.5.41. present the graphic representation of the variation among the samples in the eleven traits considered, in two and three dimensions, respectively. The PC's represented account for 69.4% (Figure 4.5.40.) and 83.7% (Figure 4.5.41.) of the variation among samples.

Table 4.5.21. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, two Portuguese Medieval, two Spanish Islamic, and two Spanish prehistoric samples.

Trait (tooth)	PC 1	PC 2	PC3
Lingual Cusp Variation (35/45) + = ASU 2-9	0.342	**0.569**	**0.736**
Groove Pattern (36/46) + = ASU X	0.377	**-0.709**	0.202
Groove Pattern (37/47) + = ASU Y	**0.898**	-0.107	-0.392
Groove Pattern (38/48) + = ASU Y	**0.511**	**-0.714**	-0.176
C5 (36/46) + = ASU 1-5	**-0.726**	**0.551**	-0.336
C5 (37/47) + = ASU 1-5	**-0.807**	0.260	0.414
C5 (38/48) + = ASU 1-5	0.492	**0.560**	0.127
C6 (36/46) + = ASU 1-5	**0.665**	**0.588**	-0.294
C6 (38/48) + = ASU 1-5	**0.747**	0.482	0.106
C7 (36/46) + = ASU 1-4	**0.862**	0.359	0.016
C7 (38/48) + = ASU 1-4	0.383	**-0.503**	**0.639**
Eigenvalue	4.639	2.992	1.573
Variance	42.2%	27.2%	14.3%
Total variance	42.2%	69.4%	83.7%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

PC1 (42.2% variance) is resultant of strong positive loadings (> 0.5) from LM2 and LM3 groove pattern, LM1 and LM3 C6, and LM1 C7. The strong negative loadings (< -0.5) for that PC are LM1 and LM2 C5.

The strong positive loadings for PC2 are LP4 lingual cusp variation, LM1 and LM3 C5, and LM1 C6. LM1 and LM3 groove pattern are the corresponding strong negative loadings.

As for PC3, there are only strong positive loadings, from LP4 lingual cusp variation and LM3 C7.

In Figure 4.5.40., La Torrecilla, Mértola and Sahl ben Malik cluster together. Coimbra is near them in the x axis, while Shantarin is among them in the y axial distribution. Fuente Amarga and Cuesta del Negro are the either end of the spectrum
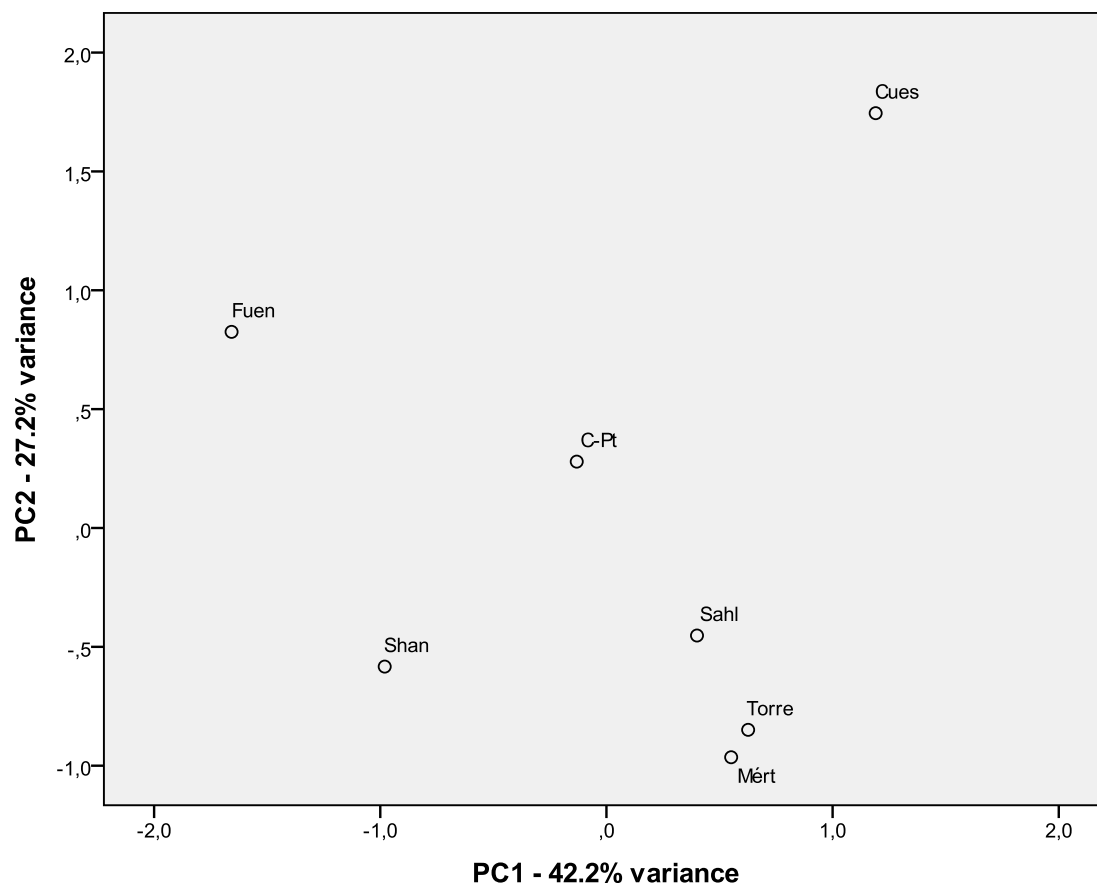
Figure 4.5.40. Scatterplot of the first two components in the comparison between Coimbra, Cuesta del Negro, Fuente Amarga, La Torrecilla, Sahl ben Malik (Al Oumaoui, 2009), Mértola (Cunha, 2011; Leandro, 2011) and Shantarin (Rodrigues, 2013).
C-Pt: Coimbra (Portugal); Cues: Cuesta del Negro; Fuent: Fuente Amarga; Mért: Mértola; Sahl: Sahl ben Malik; Shan: Shantarin (Islamic Medieval Santarém); Torre: La Torrecilla.

along the x axis. Coimbra is in the centre of the overall distribution. The Portuguese Modern individuals are between Fuente Amarga and Shantarin (on the negative side), and Cuesta del Negro, Sahl ben Malik, La Torrecilla and Mértola (on the positive side) along the x axis. The y axis, on the other hand, places Coimbra between the prehistoric samples (Fuente Amarga and Cuesta del Negro), in the positive side, and the remaining samples on the negative side.

Figure 4.5.41. adds PC3, which again sees Coimbra as the middle sample. It is closer to Mértola and Cuesta del Negro (in the positive side) and La Torrecilla and

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Fuente Amarga (in the negative side). The distribution is ended by the further samples, Shantarin (the furthest one) and Sahl ben Malik, each at one end of the distribution.

This analysis seems easily interpretable. Coimbra is the centre of the distribution on all axes. The samples of Islamic period all cluster together, except Shantarin, which
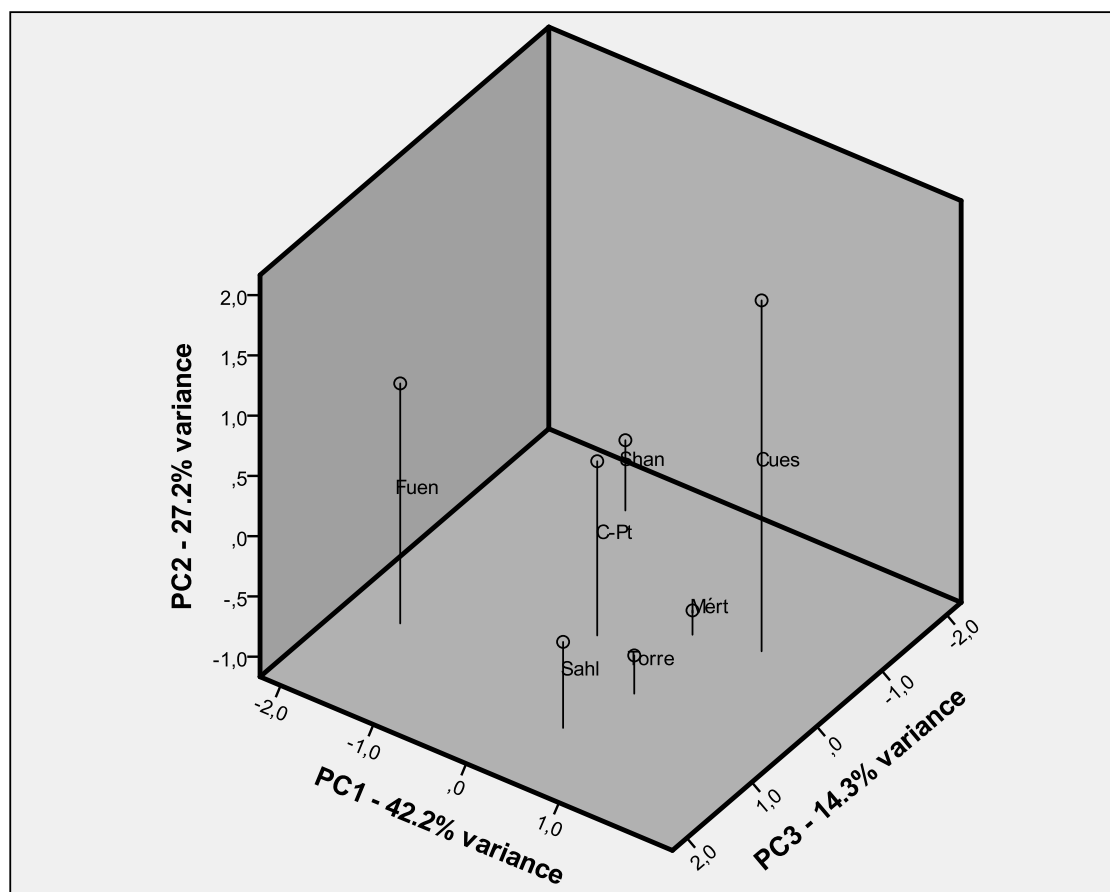
Figure 4.5.41. Scatterplot of the first three components in the comparison between Coimbra, Cuesta del Negro, Fuente Amarga, La Torrecilla, Sahl ben Malik (Al Oumaoui, 2009), Mértola (Cunha, 2011; Leandro, 2011) and Shantarin (Rodrigues, 2013).
C-Pt: Coimbra (Portugal); Cues: Cuesta del Negro; Fuent: Fuente Amarga; Mért: Mértola; Sahl: Sahl ben Malik; Shan: Shantarin (Islamic Medieval Santarém); Torre: La Torrecilla.

is further apart, despite still among them in PC2. The prehistoric samples are furthest from Coimbra. This suggests Coimbra is related to all of these samples, which are neither very close nor very different from this Modern sample. The prehistoric samples provide a good contrast, and again seem relatively disparate from the remainder of the populations. The Medieval samples are all relatively close to each other, despite the greater distance of Shantarin. This latter sample could not be as heavily influenced by North African genes as the other samples, despite its timeline and ritual interments in line with the Islamic faith.

These samples are mostly small, except Coimbra. Yet, from this analysis, it seems all of them share some biological relation with Coimbra. The Modern Portuguese people seem to be, one more time, a "melting pot" of the populations that anteceded it, and still related to those populations that contributed to the history of the Iberian Peninsula.

The next analysis is undertaken to clarify the relationship between the Portuguese Modern Coimbra and other Portuguese Medieval and Modern samples, as well as their relation with North Africa. The samples of Shantarin (Rodrigues, 2013), Mértola (Cunha, 2011; Leandro, 2011), Santarém (Gomes, 2005; Rodrigues, 2005; Simão, 2005; Pombal, 2006; Tereso, 2009; Gonçalves, 2010; Graça, 2010), Hospital de Santo António (Costa, 2006; Pinto, 2006; Costa, 2007), Museum of Natural History of the University of Oporto (MHNP; Marado, 2010, 2012), Coimbra (present sample), Miranda do Corvo (Coelho, 2013), North Africa and North and South Native Americans (Scott and Turner, 1997). The latter sample was included, once again to provide contrast.

Table 4.5.22. provides the loadings for the two PC's with *eigenvalues* above 1 (also conveyed), the variances for each PC and the cumulative variance, as well as the five lower crown non-metric traits available for this comparison and their breakpoints.

Table 4.5.22. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing the Coimbra, HSA, MHNP, Santarém, Mértola, Shantarin, Miranda do Corvo, North Africa and North and South America Natives samples.

Trait (tooth)	PC 1	PC 2
C5 (36/46) + = ASU 1-5	0.424	**-0.734**
C5 (37/47) + = ASU 1-5	**0.957**	0.151
Groove Pattern (37/47) + = ASU Y	-0.493	**0.551**
C6 (36/46) + = ASU 1-4	**0.940**	0.060
C7 (36/46) + = ASU 1-5	**0.609**	**0.626**
Eigenvalue	2.594	1.260
Variance	51.9%	25.2%
Total variance	51.9%	77.1%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The first component (51.9% of the variation) is marked by strong positive loadings (>0.5) from LM1 C6 and C7, and LM2 C5. PC2 (25.2% variance) is mostly defined by strong positive loadings from LM1 C7 and LM2 groove pattern, and a strong negative loading (<-0.5) from LM1 C5.

Figure 4.5.42. expresses a total of 77.1% of the variation found among the samples via two axes. North and South American Natives are clearly separated from the remaining samples along PC1. The latter are only disaggregated into two clusters along PC2, which separates HSA and Shantarin from the other samples.
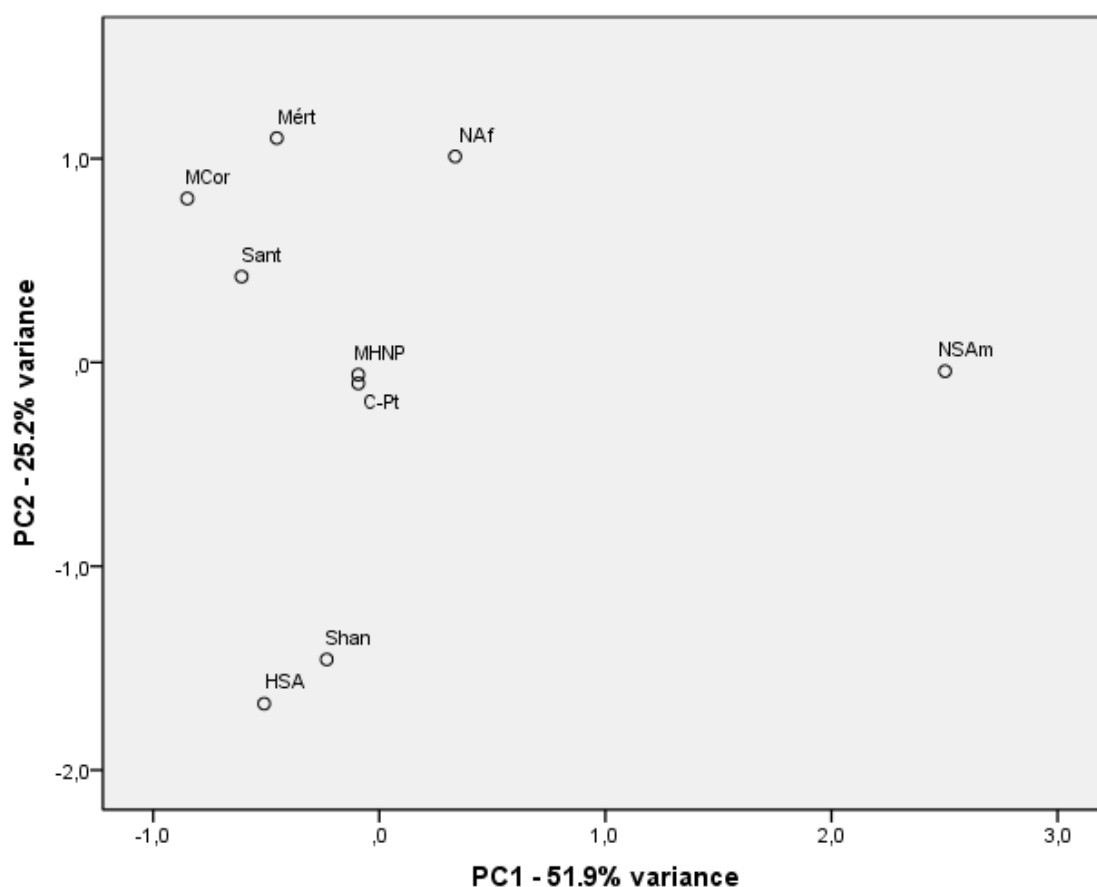
Figure 4.5.42. Scatterplot of the first two components in the comparison between Coimbra, other Portuguese (Gomes, 2005; Rodrigues, 2005; Simão, 2005; Costa, 2006; Pinto, 2006; Pombal, 2006; Costa, 2007; Tereso, 2009; Gonçalves, 2010; Graça, 2010; Cunha, 2011; Leandro, 2011; Coelho, 2013; Rodrigues, 2013), world-wide samples (Scott and Turner, 1997) and a sample of unknown origin (Marado, 2010, 2012).
C-Pt: Coimbra (Portugal); HSA: Modern period Hospital of Santo António; Mért: Mértola; MCor: Miranda do Corvo; MHNP: Museu de História Natural da Universidade do Porto; NAf: North Africa; NSAm: North and South Native Americans; Sant: Modern Santarém; Shan: Shantarin (Muslim Medival Santarém).

MHNP and Coimbra are closer to North Africa than any other sample along PC1. However, these samples are equally close to Mértola, Santarém and, to a lesser

extent, to Miranda do Corvo. The latter three references are closer to North Africa than Coimbra and MHNP along PC2.

The very few traits available and the scarcity that characterizes most samples does not allow for profound conclusions to be drawn. The clear separation between Santarém and Shantarin (both samples from Medieval and Modern Santarém) and HSA and MHNP (both from Oporto and presumably of similar chronology) are most likely artifacts from the noted drawbacks of the samples available, and cannot therefore be interpreted otherwise.

The general conclusion to be drawn is the close biological affinity between North Africa and the Portuguese samples, all of which could have been affected by the genetic inflow from North Africa that accompanied the Islamic presence in Iberia from the 8th to the 15th century. The overlying position of Coimbra and MHNP again suggest their great proximity, which underlines the possibility of a chronological parallelism among the samples. The relationships between these and the other Portuguese samples appear to be of general closeness, since the limited statistical data cannot discern any further.

There are examples of reports concerning Islamic Medieval sites in Portugal other than Shantarin and Mértola (see, for example, Cunha *et al.* [2001-2002], who studied a Loulé Islamic necropolis, where dental morphology was not studied, however the teeth from the 43 individuals provided data related to hypoplasias, dental calculus, wear and carious activity; and Ferreira *et al.* [2005], containing the morphological description of an individuals' lower dentition), but unfortunately there are none other reporting the frequencies of dental morphological traits in a sample.

Comparing contemporary Parsis and Sanjan Zoroastrians (the genetic origin of Parsis in India, composed of refugees from Persia) with data from other Indian groups reported by Lukacs and colleagues (1998), the contemporary sample seemed integrated within Indian populations, showing admixture and a lack of biological continuity through time. The unavailable Iranian and Cujarat (where Zoroastrians first settled in India) data make further analysis difficult (Jonnalagadda *et al.*, 2011). This example illustrates the difficulty in deriving clear conclusions from the previous PCA: other Portuguese samples from the early presence of Islamists in the territory would be most informative, by providing context (not to mention again the need for more comprehensive dental morphology data).

The relative genetic closeness between Iberian, European and North African populations has been the focus of some studies. According to Alu insertions, Galicians are placed between Iberian and other European populations, and are integrated in the expected genetic variability of the European. This should be the result of gene flow into Iberia since Neolithic times, mostly through the invasions by Germanic peoples (Celts) and, to a lesser degree, pilgrimage to Santiago de Compostela since the Middle Ages (Varela *et al.*, 2008).

The Human Leukocyte Antigen (HLA) genetic system was analyzed using high resolution techniques in three Portuguese populations, from North (46 individuals), Center (50) and South (49) Portugal (Spínola *et al.*, 2005). HLA allele frequencies position Portugal between European and North African populations. When analyzed separately, the North and the South of Portugal cluster with North Africans, and Central Portuguese people cluster with Europeans. This could be due to a bipolar distribution of ancient Portuguese to the North and North African influence to the South, resulting in a gradient with less contribution from each gene pool in the Center of Portugal, approximating it to the rest of Europe due to the lack of common markers with the remaining Portuguese (Spínola *et al.*, 2005).

The dental morphological data analyzed via seven PCA's suggests a biological relatedness between Portuguese individuals (mainly from Coimbra, in Central Portugal) from the 19th and 20th century, as well as other Iberian samples, and North African populations. The Portuguese, unlike the Galicians studied by Varela and colleagues (2008), seem to share genetic background with samples north of the Sahara desert. The population from the Northern Central Portugal, in Coimbra, contributes to that biological proximity and does not seem to reflect the bipolarity suggested by Spínola and colleagues (2005), as suggested by dental morphology and PCA.

History, as has been noted, suggested this proximity of Iberian populations to North African and Arabian ones, which was therefore predictable. The full extent of that proximity and the population movements that underline it can be further investigated through dental morphology, by the study of larger samples deriving from populations coeval to the Islamic control, and of the subsequent inhabitants of those regions. Future research in this field in Portugal and Iberia should attempt this reconstruction, which would clarify the biological and further enlighten the cultural and social repercussions of this contact between different religious and geographical entities.

4.5.6.Portuguese biological affinities to Roman Empire samples

The Roman Empire controlled, at its summit, vast territories that encompassed must of the then known world. The Iberian Peninsula was one of such territories, Hispania, and was conquered during the Roman Republic, in the late 3rd century BC (Tsarkin, 1989; Sanpietro *et al.*, 2005). Cultural influence, religious and territorial reorganization were part of the six centuries of Roman occupation. Biologically, the contribution of the Romans towards the present genetic variation of Iberia seems relatively difficult to ascertain from historical sources (Carreras, 1996; Edmondson, 2006; Klein, 2007-2008).

The distribution of the population of Hispania (around 4.1 million people) was mostly rural, and cities (concentrating over one million people) were associated with the presence of Italics, who developed urbanism as increased civility, opposed to the predominance of rural settlements. The Peninsular Northwest was scarcely urbanized, as was Southern Portugal (Carreras, 1996). The present author infers a lesser presence of Italians in these areas, affecting Portugal. The cult of indigenous divinities in the current territory of Portugal seems to suggest a division: it was public and is present throughout the rural portion, but is replaced by Imperial cult in the urban centers (Encarnação, 1981; see also Klein, 2007-2008). This suggests again a greater control, and perhaps presence, of Italics in the cities. This control constricted and gave pagan characteristics to early Christian Counsels in Iberia, which still followed some pagan social and structural precepts (Sotomayor, 1981).

Colonies were initially settled by soldiers, usually. The poorer social strata of Rome were used to populate them, as well as some of the locals. However, many Roman cities replaced previous settlements. See Conimbriga, created where an Iron Age settlement used to be, in Condeixa-a-Velha, near Coimbra, in the northern Lusitania. It was remodeled during the Augustan and Flavian rules, by initiative of the local elite. Local elites were the link between the provinces and Roman rulers, and these elements sometimes even kept the traditional titles of their city or region, keeping also high status roles in the communities (Edmondson, 2006; Klein, 2007-2008). Even so, the power warranted to provincial elites was very limited (Edmondson, 2006).

It must be noted that one hundred thousand Roman citizens were living in Hispania by the latter half of the 1st century BC, mainly in the Baetica region (Andalucía). More Italics (not Roman citizens) were also there. After this, colonies began to be settled, and Roman veterans were placed in Hispania at least during the 1st century AD. Since then, veterans would prefer to settle away from their regions of service, so they settled in Tarraco (Tarrogona), or more to the South or the East, where they could relax in a fully Romanized city (Tsirkin, 1989). Portugal does not seem to have been a usually selected destination.

When discussing mtDNA influence on the Iberian people (Southeast and Northeast Spain), Sanpietro and colleagues (2005) postulate the Roman biological influence was likely limited to the initial military occupations, and that these people's presence in Iberia could have merely contributed to a greater genetic variability.

Dental morphology may be used to shed light into this question. Two Roman Empire samples, from the 2nd century, were studied by Manzi and colleagues (1997). These samples, – *Lucus Feroniae* and *Portus Romae*, both located approximately 30 km away from Rome, the capital of the Empire –, were compared with three Roman and Late Roman to Medieval Spanish samples reported on by García Sívoli (2009): Late Roman (5th to 7th centuries) Can Reines, Mallorca; Roman (1st to 3rd centuries) Vila d' Madrid, Catalonia; and Late Roman to Medieval (5th to 12th century) Sant Pere, Catalonia. Coimbra was naturally added to these samples, thus investigating the influence of the Roman Imperial samples to the Coimbra gene pool.

Table 4.5.23. informs on strong positive loadings (>0.5) for PC1 (36.8% variance) yield from UC and LC distal accessory ridge, UM3 parastyle, C5 on all lower

Table 4.5.23. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Spanish and Italian Roman samples.

Trait (tooth)	PC 1	PC 2	PC 3
Shoveling (11/21) + = ASU 3-6	0.166	**-0.688**	0.216
Double Shoveling (11/21) + = ASU 2-6	0.261	**-0.696**	-0.074
Interruption Grooves (11/21) + = ASU 1	**-0.646**	-0.466	<u>**0.566**</u>
Interruption Grooves (12/22) + = ASU 1	**-0.901**	-0.203	-0.119
Distal Accessory Ridge (13/23) + = ASU 1-5	<u>**0.992**</u>	-0.077	0.002
Tricuspid premolars (14/24) + = ASU 1	0.239	**-0.707**	-0.073
Carabelli's trait (16/26) + = ASU 5-7	-0.129	**-0.686**	<u>**0.637**</u>

Table 4.5.23. (Continued.)

Trait (tooth)	PC 1	PC 2	PC 3
C5 (16/26) + = ASU 0-1	-0.084	**0.881**	-0.381
Hypocone (17/27) + = ASU 0-1	0.395	**-0.892**	-0.036
Parastyle (18/28) + = ASU 1-6	**0.657**	0.286	0.301
Distal Accessory Ridge (33/43) + = ASU 1-5	**0.676**	**0.657**	0.286
Lingual Cusp Variation (34/44) + = ASU 2-9	0.156	**0.577**	**0.785**
Lingual Cusp Variation (35/45) + = ASU 2-9	-0.022	**0.911**	0.317
C5 (36/46) + = ASU 1-5	**0.653**	-0.204	0.369
C6 (36/46) + = ASU 1-5	-0.469	**0.514**	**0.678**
C7 (36/46) + = ASU 1a-4	**0.851**	0.017	-0.053
Groove Pattern (36/46) + = ASU Y	**0.797**	-0.286	-0.110
Groove Pattern (37/47) + = ASU X	**0.870**	0.281	0.352
C5 (37/47) + = ASU 1-5	**0.862**	0.328	0.196
C6 (37/47) + = ASU 1-5	-0.077	0.380	**-0.919**
C7 (37/47) + = 1a-4	0.262	**-0.695**	-0.074
Deflecting Wrinkle (36/46) + = 1-3	**-0.765**	**0.601**	-0.108
Distal Trigonid Crest (36/46) + = ASU 1	0.096	**0.518**	0.457
Protostylid (36/46) + = ASU 1-7	**0.830**	0.443	-0.017
Protostylid (37/47) + = ASU 1-7	**0.862**	-0.004	-0.397
Protostylid (38/48) + = ASU 1-7	0.354	**-0.924**	0.083
Groove Pattern (38/48) + = ASU Y	0.273	0.165	**-0.846**
C5 (38/48) + = ASU 1-5	**0.870**	-0.006	0.191
C6 (38/48) + = ASU 1-5	**0.803**	0.368	-0.292
Eigenvalue	10.669	8.483	4.680
Variance	36.8%	29.3%	16.1%
Total variance	36.8%	66.1%	82.2%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

molars, LM1 C7, LM1 and LM2 groove pattern and protostylid, and LM3 C6. Strong negative loadings (<-0.5) are present for UI1 and UI2 interruption grooves and LM1 deflecting wrinkle.

PC2 (29.3% variance) is characterized by strong positive loadings for UM1 C5, LC distal accessory ridge, LP3 and LP4 lingual cusp variation, and LM1 C6, deflecting

wrinkle and distal trigonid crest. Strong negative loadings are evident for UI1 shoveling and double shoveling, tricuspid UP3, UM1 Carabelli's trait, UM2 hypocone, LM2 C7 and LM3 protostylid.

Strong positive loadings on PC3 (16.1% variance) are reported for UI1 interruption grooves, UM1 Carabelli's trait, LP3 lingual cusp variation and LM1 C6. Strong negative loadings are present for LM2 C6 and LM3 groove pattern.
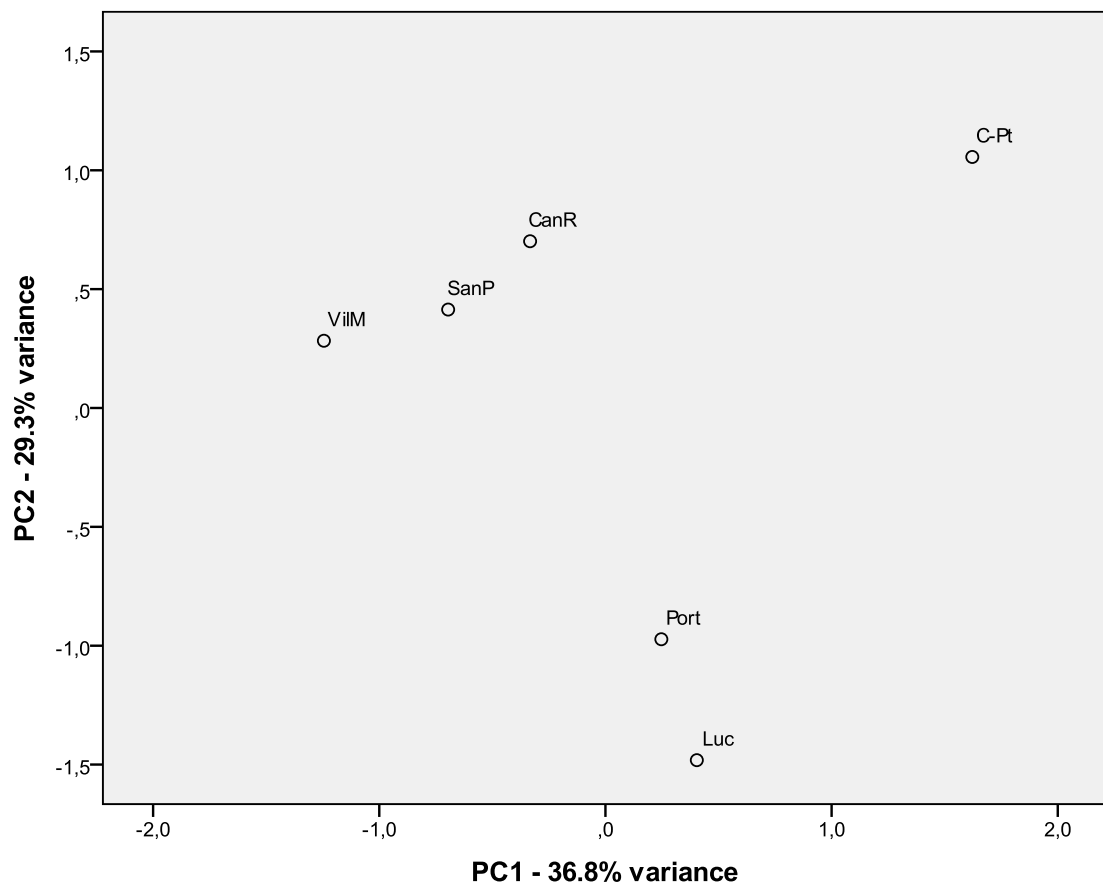
Figure 4.5.43. Scatterplot of the first two components in the comparison between Coimbra, two Imperial Roman (Manzi *et al.*, 1997) and three Iberian post-Romanization samples (García Sívoli, 2009).
CanR: Can Reines; C-Pt: Coimbra (Portugal); Luc: *Lucus Feroniae*; Port: *Portus Romae*; SanP: Sant Pere; VilM: Vila d' Madrid.

Figure 4.5.43. displays an isolated Coimbra and two clusters, one grouping the Spanish Roman/Medieval samples and the other grouping the Italian Roman samples. Along the x axis (PC1), the Roman samples are placed between the Spanish and the Portuguese samples. The y axis (PC2), on the other hand, places the Spanish samples between the Portuguese and the Roman samples. Along this axis, Spanish and Portuguese samples are very near.

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The introduction of PC3 (z axis) on Figure 4.5.44. separates Sant Pere from the remaining samples. Coimbra and the Roman samples of *Lucus Feroniae* and *Portus Romae* are close together along this axis, with the Portuguese sample placed between the Italian ones. The Spanish samples of Vila d' Madrid and Can Reines are close by, on the opposite end from Sant Pere.

Despite these samples not differing much from one another in the biological and genetic senses, the Spanish Roman samples seem to be closer to the Portuguese one
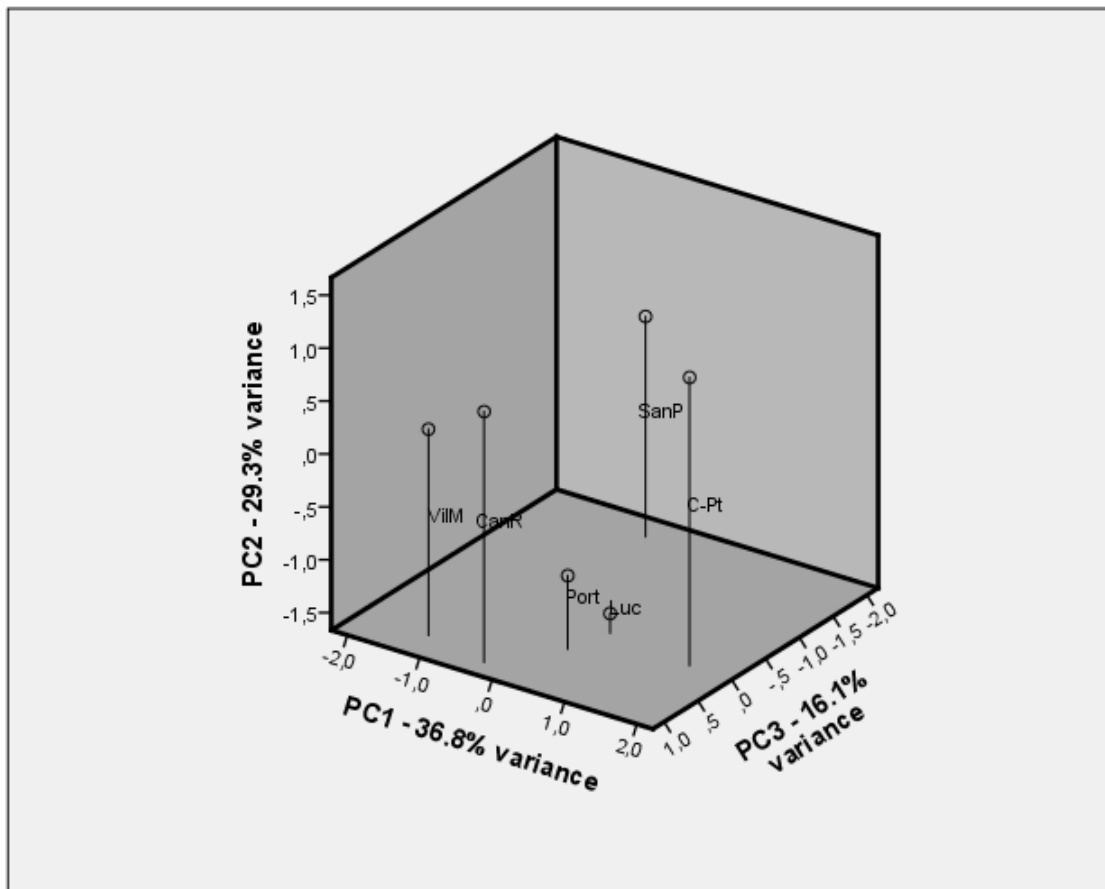
Figure 4.5.44. Scatterplot of the first three components in the comparison between Coimbra, two Imperial Roman (Manzi *et al.*, 1997) and three Iberian post-Romanization samples (García Sívoli, 2009).
CanR: Can Reines; C-Pt: Coimbra (Portugal); Luc: *Lucus Feroniae*; Port: *Portus Romae*; SanP: Sant Pere; VilM: Vila d' Madrid.

than the Italian ones, but are still drawn closer to the latter. From the Spanish samples, Sant Pere is the furthest from *Lucus Feroniae* and *Portus Romae*, probably due to gene flow of Visigoth and Islamic origin, in Medieval times. Still, it retains proximity to the Romans. Vila d' Madrid is the second furthest sample of Spanish Roman origin, which can be derived from its relatively early chronology. This timeline possibly did not allow

for as much gene flow from the Lazio as it did for Can Reines (of Late Roman chronology), the most similar sample to the ones from Rome's surroundings.

The Portuguese population, here sampled, is mainly separated from the Roman samples by the y axis (PC2), representing almost a third of the variation (29.3%), and more than a third of the variation graphically represented (approximately 82.2%). The relative proximity allowed by PC1 and the clustering on PC3 (summing 52.9% of the variation) underlines the possibility of some shared genetic variability, between the centre of Portugal in late 19th century and 2nd century Rome. However, these biological relations seem to have been diluted on account of the population movements that followed the Roman control of Hispania, and possibly lessened by the weaker presence of Romans in the Northwest Iberia and Southern Portugal (see above).

The main suggestion these results provide is the likely biological influence of the Roman presence in Iberia, according to the relative affinity between Spanish Roman and Italian Roman samples.

Table 4.5.24. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, diachronic Spanish and Roman Italian samples.

Trait (tooth)	PC 1	PC 2	PC 3
Shoveling (11/21) + = ASU 3-6	**0.831**	0.309	-0.093
Double Shoveling (11/21) + = ASU 2-6	-0.149	**0.841**	0.302
Interruption Grooves (12/22) + = ASU 1	**0.689**	-0.202	-0.326
Carabelli's trait (16/26) + = ASU 5-7	**0.537**	0.118	**0.795**
C5 (16/26) + = ASU 2-5	**0.812**	0.229	0.320
Hypocone (17/27) + = ASU 2-5	**-0.831**	-0.456	-0.032
C5 (36/46) + = ASU 1-5	0.153	**0.804**	-0.040
C6 (36/46) + = ASU 1-5	-0.064	**-0.602**	**0.675**
C7 (36/46) + = ASU 1a-4	-0.443	**0.847**	0.064
Groove Pattern (36/46) + = ASU Y	**0.726**	0.064	-0.469
C5 (37/47) + = ASU 1-5	**-0.633**	**0.716**	-0.082
Eigenvalue	3.976	3.362	1.630
Variance	36.1%	30.6%	14.8%
Total variance	36.1%	66.7%	81.5%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The previous PCA was produced from the variation between the samples in twenty nine dental nonmetric traits. In order for the use of such an amount of traits to be possible, the amount of samples could not be any greater. This reason justifies the completion of two other PCA's, each with a different set of eleven variables (each also incompatible with one another). Both analyses include the samples from the present study and those from Manzi and colleagues (1997) and García Sívoli (2009), as the previous analysis.

The first one of these comparisons once again incorporates the data from Tossal de les Basses (Laguillo *et al.*, 2009). The difference between this PCA and the one previously including these data (besides different samples) is the inclusion of UI1 shoveling. Its objective is to better understand the biological affinities among Iberian samples and between these and the Roman population. The main difficulty is the small
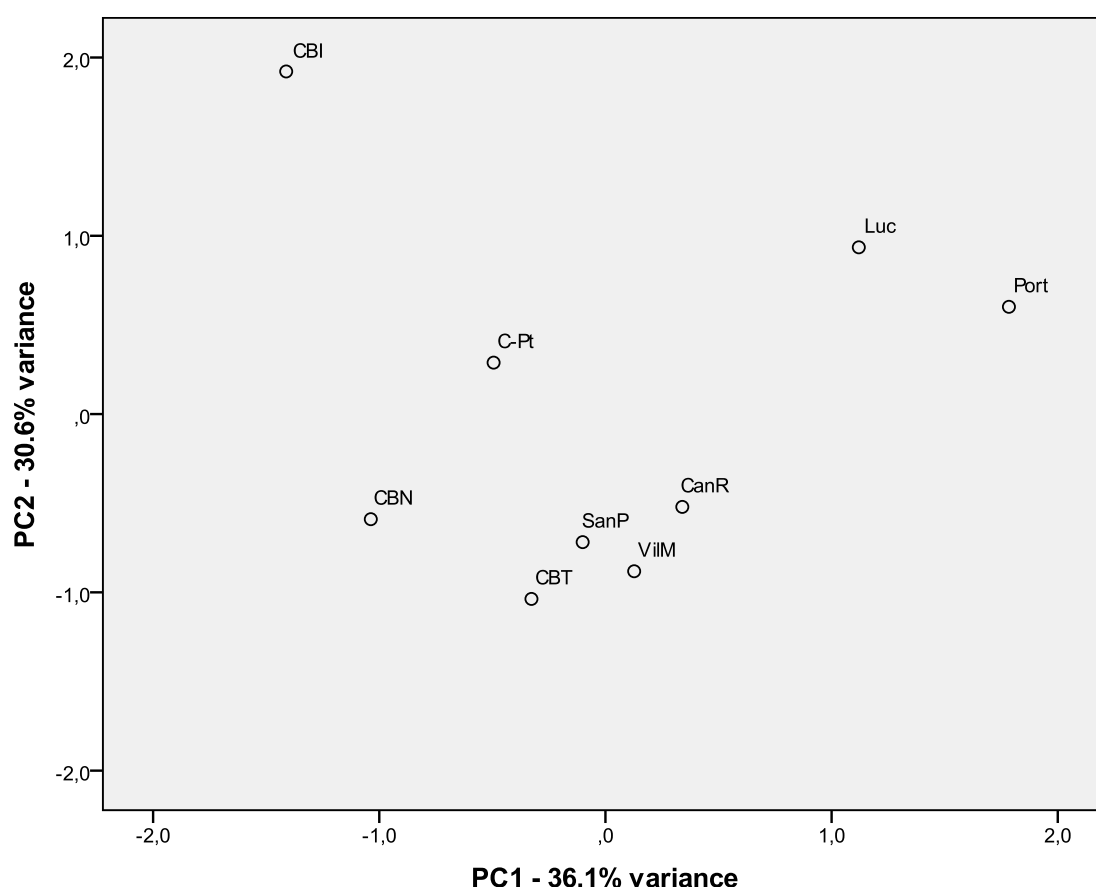
Figure 4.5.45. Scatterplot of the first two components in the comparison between Coimbra, two Imperial Roman (Manzi *et al.*, 1997), three Iberian post-Romanization (García Sívoli, 2009) and the Cemetery of Tossal de les Basses (Laguillo *et al.*, 2009) samples.
CanR: Can Reines; CBI: Cemetery of Tossal de les Basses (Islamic phase); CBN: Cemetery of Tossal de les Basses (Neolithic phase); CBT: Cemetery of Tossal de les Basses (Late Roman phase); C-Pt: Coimbra (Portugal); Luc: *Lucus Feroniae*; Port: *Portus Romae*; SanP: Sant Pere; VilM: Vila d' Madrid.

samples provided from all Tossal de les Basses chronological phases (Neolithic, Late Roman and Islamic).

The strongest positive loadings (>0.5) on PC1 (36.1% variance) are derived from UI1 shoveling, UI2 interruption grooves, UM1 Carabelli's trait and C5 and LM1 groove pattern on M_1 (see Table 4.5.24.). Strong negative loadings (<-0.5) hail from UM2 hypocone and LM2 C5.

PC2 (30.6% variance) is characterized by strong positive loadings for UI1 double shoveling, LM1 and LM2 C5, and LM1 C7. A single strong negative loading is evident for LM1 C6.

Strong positive loadings on PC3 (14.8% variance) originate from UM1 Carabelli's trait and LM1 C6.

Figure 4.5.45., when compared to Figure 4.5.43. (from the last PCA) shows roughly the same relations between the samples represent on both graphs, albeit
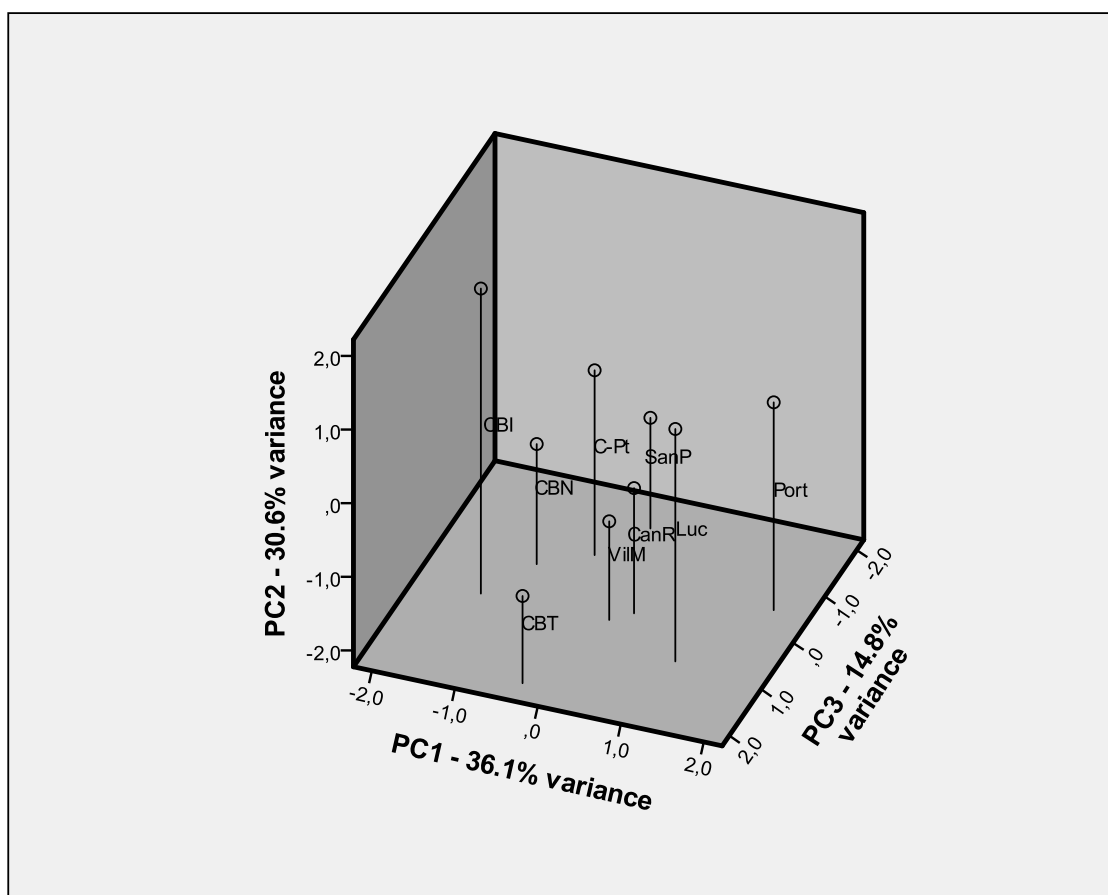
Figure 4.5.46. Scatterplot of the first three components in the comparison between Coimbra, two Imperial Roman (Manzi *et al.*, 1997), three Iberian post-Romanization (García Sívoli, 2009) and the Cemetery of Tossal de les Basses (Laguillo *et al.*, 2009) samples.
CanR: Can Reines; CBI: Cemetery of Tossal de les Basses (Islamic phase); CBN: Cemetery of Tossal de les Basses (Neolithic phase); CBT: Cemetery of Tossal de les Basses (Late Roman phase); C-Pt: Coimbra (Portugal); Luc: *Lucus Feroniae*; Port: *Portus Romae*; SanP: Sant Pere; VilM: Vila d' Madrid.

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expressed through different axes. This is probably due to the importance almost all of the traits with strong loadings share between the present analysis and the former, on PC1 and PC2.

On the other hand, when compared to Figure 4.5.36. (which also includes the Tossal de les Basses samples), differences are notorious. This is most likely due to the lack of UI1 shoveling and the weak loadings on PC1 and PC2 of UM2 hypocone and UM1 Carabelli's cusp, which are here valued by the PCA and contribute to the current sample scores.

Figure 4.5.46. demonstrates the addition of PC3 on both cases (compare with Figure 4.5.43. and Figure 4.5.44. from the previous analysis) contributes much the same. The previous PCA is different from the present one (along PC3) mainly in displaying the samples more closely and in separating the two Roman samples. This testifies to the closeness between all analyzed samples, which amplify the biological differences between these Roman peripheral populations. *Portus Romae* is of an urban middle-class social backdrop, whereas *Lucus Feroniae* is more rural lower-class social status (including slaves; see Manzi *et al.*, 1997). As for the PCA previously including Tossal de les Basses, it shows these samples distributed in much the same way along PC3 (Figure 4.5.37.).

Figure 4.5.45. shows the relations among samples somewhat as expected, when the previous PCA's including these samples are considered. The samples with some North African influence (CBI, from Tossal de les Basses) and the samples from around Rome are the ones furthest from the other Iberian samples. All Spanish samples with Roman influence are clustered together (including CBT, Late Roman Tossal de les Basses). CBN (Neolithic Tossal de les Basses) is relatively near these and Coimbra. The Portuguese sample is placed almost at the middle of this irregular circle, closer to CBN and the Spanish Roman samples.

Figure 4.5.46. provides a loose cluster formed by Coimbra, Can Reines, Vila d' Madrid and CBN. CBT is furthered from these samples along PC3 (z axis). CBI, *Lucus Feroniae* and *Portus Romae* form a second layer centered in Coimbra, but cluster with the Spanish samples along PC3.

If the small amount of total biological divergence between the Roman and the Iberian samples had not been demonstrated in the previous analysis, it apparently is by the present one. All Tossal de les Basses samples have little reliability, due to these small samples being unlikely representatives of the total biological variation of their

populations. CBT and CBN were previously shown distant from samples sharing North African genetic variation. They are still shown here as relatively distant to one another and provide the much needed contrast, which allows the identification of the affinities between samples. The separation between *Lucus Feroniae* and *Portus Romae*, considered two biologically similar Roman samples (Manzi *et al.*, 1997) are another good source of scale, permitting the evaluation of the distances between the other samples and themselves.

Coimbra is placed at the center of this distribution, with direct proximity to Neolithic and Romanized samples, mostly, and indirect influence from Roman and Islamic Iberia. The placement of CBI as an outlier affected by North African gene flow, and the placement of *Lucus Feroniae* and *Portus Romae* as the other most distant samples, because of their foreign status, does not prevent the interpretation that their genetic influence is patent, and ultimately represented by Coimbra. Neolithic Tossal de les Basses, the sole representative of a pre-Hispania Iberian gene pool is not far from Coimbra either, indicating the prevalence of this genetic variability in the contemporary gene pool.

Clearly not all processes of progressive, population-wide, genetic differentiation are due to population replacement. For example, four samples from Bactria, in Central Asia, were heterogeneous in dental morphology, particularly when both earlier were compared to both later samples. Their biological relationship with Harappan and post-Harappan populations from the Indus Valley in South Asia were analyzed. While the earlier samples were not close to Harappans, there was some convergence between later Bactrian samples and post-Harappans, suggesting bidirectional gene flow (Hemphill *et al.*, 1998). The Coimbra population, like the more recent Bactrian populations, results from an amalgam of contributions from different populations. These graphs (Figure 4.5.45. and 4.5.46.) are probably among the most representative. They underline the contribution of Neolithic peoples; of Romanized Iberian populations, alongside the contribution from Romans themselves; and that of Islamized Iberian populations. Bidirectional gene flow is not represented. But gene flows from diachronic, successive and disperse origins into the Iberian Peninsula are apparent.

Two southern Portuguese Romanized samples (from Beja and Faro) were compared to the Roman samples and the Spanish Romanized samples already analyzed. The biological effect of the Roman presence on southern Portugal will thus be inferred.

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The main difficulty in the subsequent analysis is the availability of exclusively lower arch dental morphological characters and the very small samples available for the *Villa* of Monte da Cegonha (Beja; Fernandes, 2006) and the *Villa/Vicus* of Cerro da Vila (Faro; Lucas, 2006).

Table 4.5.25. shows strong positive loadings (>0.5) on PC1 (44.4% variance) are present for LP4 lingual cusp variation, LM1 cusp number, LM2 C5 and C6, and LM3 C5, C6 and C7.

Table 4.5.25. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Portuguese, Spanish and Italian samples of Roman Period.

Trait (tooth)	PC 1	PC 2	PC 3
Lingual Cusp Variation (35/45) + = ASU 2-9	**<u>0.536</u>**	-0.413	-0.255
Cusp Number (36/46) + = ASU 5+	**<u>0.607</u>**	-0.484	0.483
C7 (36/46) + = ASU 1-4	0.034	**<u>0.702</u>**	**<u>0.620</u>**
Groove Pattern (37/47) + = ASU X	0.231	**-0.538**	**<u>0.767</u>**
C5 (37/47) + = ASU 1-5	**<u>0.943</u>**	0.259	-0.001
C6 (37/47) + = ASU 1-5	**<u>0.883</u>**	0.001	-0.242
C7 (37/47) + = ASU 1-4	-0.240	**<u>0.776</u>**	0.377
Groove Pattern (38/48) + = ASU Y	-0.458	-0.448	**<u>0.580</u>**
C5 (38/48) + = ASU 1-5	**<u>0.840</u>**	0.055	0.308
C6 (38/48) + = ASU 1-5	**<u>0.836</u>**	0.354	0.165
C7 (38/48) + = ASU 1-4	**<u>0.914</u>**	0.009	-0.196
Eigenvalue	4.887	2.186	1.970
Variance	44.4%	19.9%	17.9%
Total variance	44.4%	64.3%	82.2%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The strongest positive loadings on PC2 (19.9% variance) emanate from LM1 and LM2 C7. A strong negative loading (<-0.5) is evinced for LM2 groove pattern.

PC3 (17.9% variance) is characterized by strong positive loadings for LM1 C7 and LM2 and LM3 groove patterns.

The differences of distribution of the previously analyzed samples of Spain, Italy and Coimbra between Figures 4.5.47. and 4.5.48. and Figures 4.5.43. and 4.5.44. (from the first PCA on the Roman biological influence on the Iberian Peninsula) are caused by the different strong loadings of some traits. These are LP4 lingual cusp variation and

LM2 C6 along PC1, and LM1 C7 and LM2 groove pattern along PC2, besides the addition of LM1 cusp number and the removal of several traits between these different PCA's.

PC1, expressing almost half the variation, clearly separated Beja from Faro, *Lucus Feroniae*, *Portus Romae*, Can Reines, Vila d' Madrid and Sant Pere, placing Coimbra between Beja and this cluster. PC2, comprising less than half of the variation patented by PC1, separates Faro from *Lucus Feroniae*, leaving the remaining samples
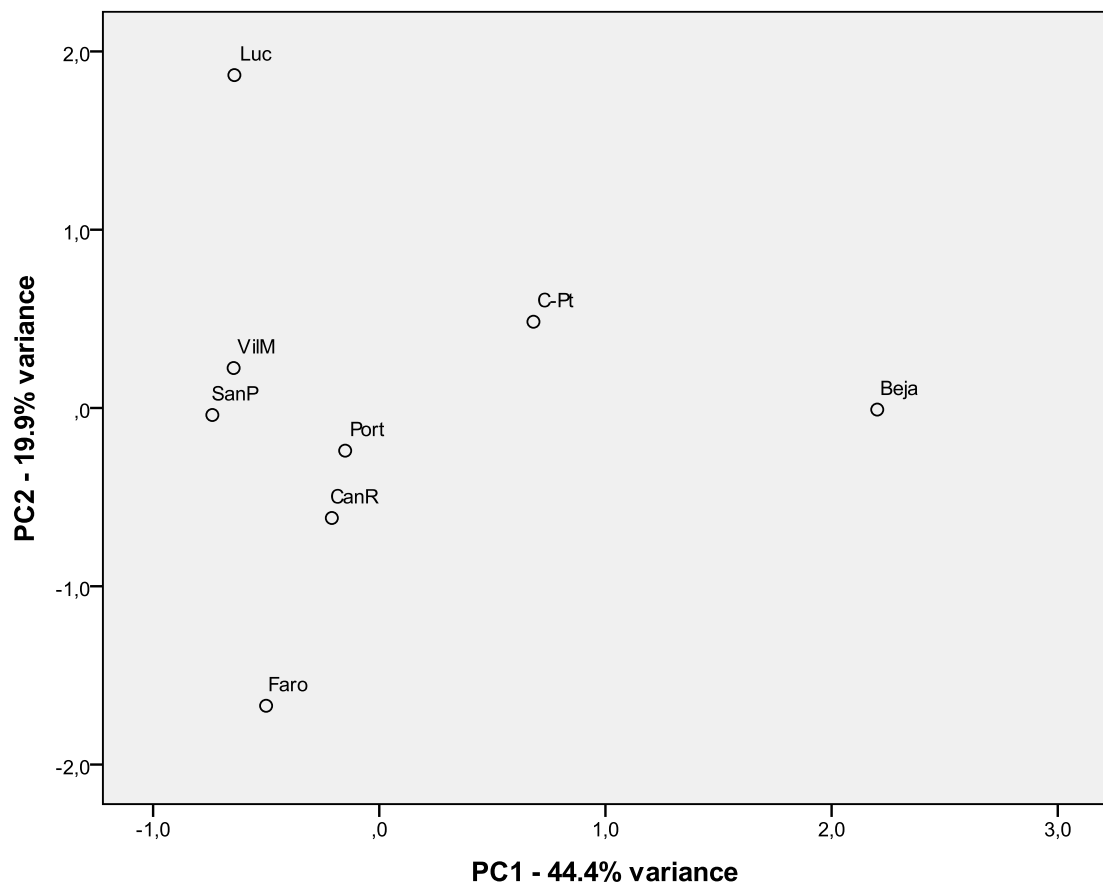
Figure 4.5.47. Scatterplot of the first two components in the comparison between Coimbra, two Imperial Roman (Manzi *et al.*, 1997), three Iberian post-Romanization (García Sívoli, 2009), Beja (Fernandes, 2006) and Faro (Lucas, 2006) samples.
Beja: *Villa* of Monte da Cegonha (Beja); CanR: Can Reines; C-Pt: Coimbra (Portugal); Faro: *Villa/Vicus* of Cerro da Vila (Faro); Luc: *Lucus Feroniae*; Port: *Portus Romae*; SanP: Sant Pere; VilM: Vila d' Madrid.

clustered between them. PC3, representing a variation comparable to that of PC2, forms two clusters: Coimbra, Faro and *Lucus Feroniae* compose one of them and Beja, Can Reines, Sant Pere and *Portus Romae* the other. These clusters are relatively close to one another and Vila d' Madrid is close to the latter one.

The low amount of traits and the small samples included (Beja and Faro) do not seem to leave room for much interpretation. Yet, Faro and Beja seem to be the outliers, having little relation to the remaining samples. At this scale, where biological proximity among sample seems to be generalized (for example, see the graphical distance between *Lucus Feroniae* and *Portus Romae*, two biologically close samples), the meaning of this is blurred. This testifies mainly to the biological variability in southern Portugal at the time of the Roman occupation. Interbreeding between previous populations and Roman
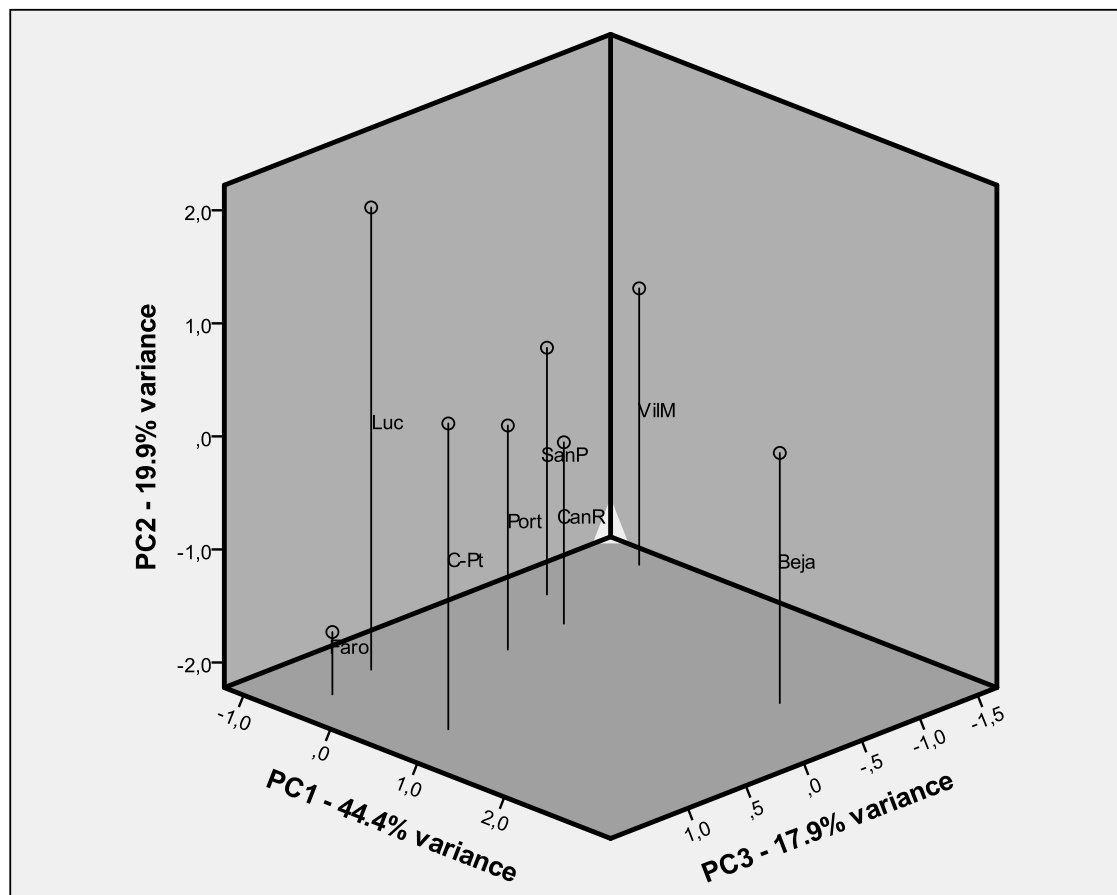
Figure 4.5.48. Scatterplot of the first three components in the comparison between Coimbra, two Imperial Roman (Manzi *et al.*, 1997), three Iberian post-Romanization (García Sívoli, 2009), Beja (Fernandes, 2006) and Faro (Lucas, 2006) samples.
Beja: *Villa* **of Monte da Cegonha (Beja); CanR: Can Reines; C-Pt: Coimbra (Portugal); Faro:** *Villa/Vicus* **of Cerro da Vila (Faro); Luc:** *Lucus Feroniae***; Port:** *Portus Romae***; SanP: Sant Pere; VilM: Vila d' Madrid.**

peoples seems to have been more scarce in this region, since the positions of Faro and Beja are the most distant from *Portus Romae*, the sample nearest the centre of the distribution for both Figure 4.5.47. and 4.5.48.

Notable are the proximity of Portus Romae and the Romanized samples of Vila d' Madrid, Can Reines and Sant Pere, and the position of Coimbra, equidistant to Lucus

Feroniae, Portus Romae, and the southern Portuguese samples. These facts demonstrate once again the influence of Roman genetic variability to the populations of their contemporary Hispania and of the modern Portuguese.

Unfortunately, these conclusions should be very cautiously viewed, since the inclusion of very small samples might have distorted the results.

The study of pre-Roman and Roman influence in the present Iberian gene pool needs more data, and will benefit from a thorough research on the population movements associated with it along space and time. This analysis is an indicative that Roman genetic variability contributes to the present biological variation of the Portuguese people, besides having most likely contributed to those of the population coeval to the Roman Empire. The inclusion of Medieval and more prehistoric samples into an analysis with more dental discrete traits could unveil the complexity of gene flow and other genetic phenomena contributing to the human biological diversity of the Portuguese and the Spanish. The clarification of the differences in proportion of cultural and biological influences from the peoples that controlled the peninsula would follow suit.

4.5.7.Coimbra's biological affinities to Brazil

Portugal was, from the Late Middle Ages onwards, the centre of its own empire, after its territories had been a part of other Empires and domains. Brazil was a part of this, since it was discovered and claimed by Portugal in 1500. The biological influence of the Portuguese affluence into the present territory of Brazil is expected to be somewhat large, due to its dimension before and after the country lost its political control over the colony.

Brazil is one of the most genetically diversified countries in the world. It was originally populated around 21000 years BP by Amerindians, who were the sole inhabitants (with around 2.5 million people) until 1500 AD, when the Portuguese colonization brought about half a million Europeans (between the late 15th and the early 19th century), mostly men, and around 3.5 to 4 million African slaves, from the mid-16th to the late 19th centuries. This trihybrid population is characterized by the interbreeding of Portuguese (and other European) males and African and Amerindian females (Alves-Silva *et al.*, 2000; Carvalho-Silva *et al.*, 2001; Abe-Sandes *et al.*, 2004; Marrero *et al.*,

2005; Silva *et al.*, 2006b). Migration into Brazil continued the gene flow from Europe, Africa and, particularly in recent times, Asia (Abe-Sandes *et al.*, 2004).

Admixture between Europeans and the Amerindians was encouraged so as to enable population growth. Amerindians suffered population decline from confrontation with the colonizers and inability to fight diseases their immune-systems were not adapted to (Alves-Silva *et al.*, 2000).

Bartolomucci (2006) studied the biological affinities between several fluvial and littoral settlements related to Sambaquieiros (shell mounds), describing a fluvial archaeosite (Moraes) biologically closer to a littoral site (Matinhos), possibly due to the geographical proximity, despite diachronic distance. The same fluvial site is more similar to most littoral sites. Interregional comparisons also showed continuity between some of the fluvial (from Vale do Ribeira, São Paulo) and the littoral sites (Paraná). The three littoral regions diverge from each other, suggesting biological diversity among these settlements (Bartolomucci, 2006). Unfortunately, the data provided by this author was insufficient to allow comparison with the Coimbra sample.

Despite this, some characteristics of the Brazilian native and general Native American dentition are known. Brazilian natives are proximate to other North and South American natives, according to dental morphology analyses (Turner and Machado, 1983). So, other dental data may be used to infer the proximity of Native Americans to the Coimbra population. Argentinean aboriginals from Pampa Grande were characterized as probably belonging to a Sinodont dental complex, thus descending from the original inhabitants of the Americas (Bollini *et al.*, 2010). The dental morphology of three Amazonian populations from Colombia was analyzed, both on deciduous and permanent dentitions, demonstrating the close relationship between them, their Sinodont ancestry and the biological influence of Caucasoid and African origin (Aragón *et al.*, 2008). The Calchaquí (native Northwest Argentineans), on the other hand, are characterized and described as not strictly adherent to the Sinodont dental complex, contrarily to what was expected (Bollini *et al.*, 2009b).

Obviously, dental nonmetric variables are also useful in inferring pre-Conquest population movements. A study of pre-Hispanic Petén, Guatemala, where dental morphology is used to assess the affinities between settlements (Tiesler and Cucina, 2008); the search of biological continuity between pre-contact and European-contact period Taino culture people for El Soco, in Hispaniola (Coppa *et al.*, 1995); and the exploration of the effects of gene flow versus cultural exchanges in an archaeological

context of the Southwestern US (LeBlanc *et al.*, 2008) are some examples. However, the typical presence of a Sinodont dental complex permits the use of a general proxy in establishing the relations between Native Brazilians and a Brazilian contemporary sample.

The PCA conducted here to test for the affinities between Coimbra and Brazil uses a sample of 130 Brazilians of Brazilian descent (at least two generations) of the Rio de Janeiro metropolitan area, studied by Tinoco (2010), who concluded they

Table 4.5.26. **Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing Coimbra, Rio de Janeiro and world-wide samples.**

Trait (tooth)	PC 1	PC 2
Shoveling (11/21) + = ASU 3-6	**<u>0.911</u>**	-0.237
Carabelli's trait (16/26) + = ASU 5-7	**-0.642**	**<u>0.558</u>**
C5 (16/26) + = ASU 1-5	0.087	**<u>0.939</u>**
Hypocone (17/27) + = ASU 0-1	-0.392	-0.448
C6 (36/46) + = ASU 1-5	**<u>0.937</u>**	0.180
C5 (37/47) + = ASU 1-5	**<u>0.837</u>**	0.176
Eigenvalue	2.982	1.512
Variance	49.7%	25.2%
Total variance	49.7%	74.9%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

resembled Europeans and Sub-Saharan Africans and were genetically placed between these populations. To clarify the biological relations of the Rio de Janeiro sample, world data from Scott and Turner (1997) provide contrast and an array of samples needed for comparison. The main hindrance to this analysis is the small number of dental nonmetric characters reported by Tinoco (2010).

This inference of biological relations between present South American populations and Europeans has been attempted before, like in Colombia, for example, where Mongoloid and Caucasoid characteristics were found (Aguirre *et al.*, 2006) and the biological connection between a population of slave-descendant Colombians with West and Central-West Africa was demonstrated through discrete dental traits (Delgado-Burbano, 2007a).

The PCA resulted on two components with an *eigenvalue* above 1 (74.9% of the variation; see Table 4.5.26.). PC1 (49.7% variance) is characterized by strong positive

loadings (>0.5) from UI1 shoveling, LM1 C6 and LM2 C5. A strong negative loading (<-0.5) is reported for UM1 Carabelli's trait. The strongest loadings on PC2 (25.2% variance) are positive and hail from UM1 Carabelli's trait and C5.

This information is translated visually in Figure 4.5.49. The sample closest to Coimbra is Rio de Janeiro. The Brazilian sample has North Africa and Northern Europe as the closest samples, but Coimbra follows suit. There is a loose cluster formed between the European samples, North Africa and Rio. South Africa is almost as close to
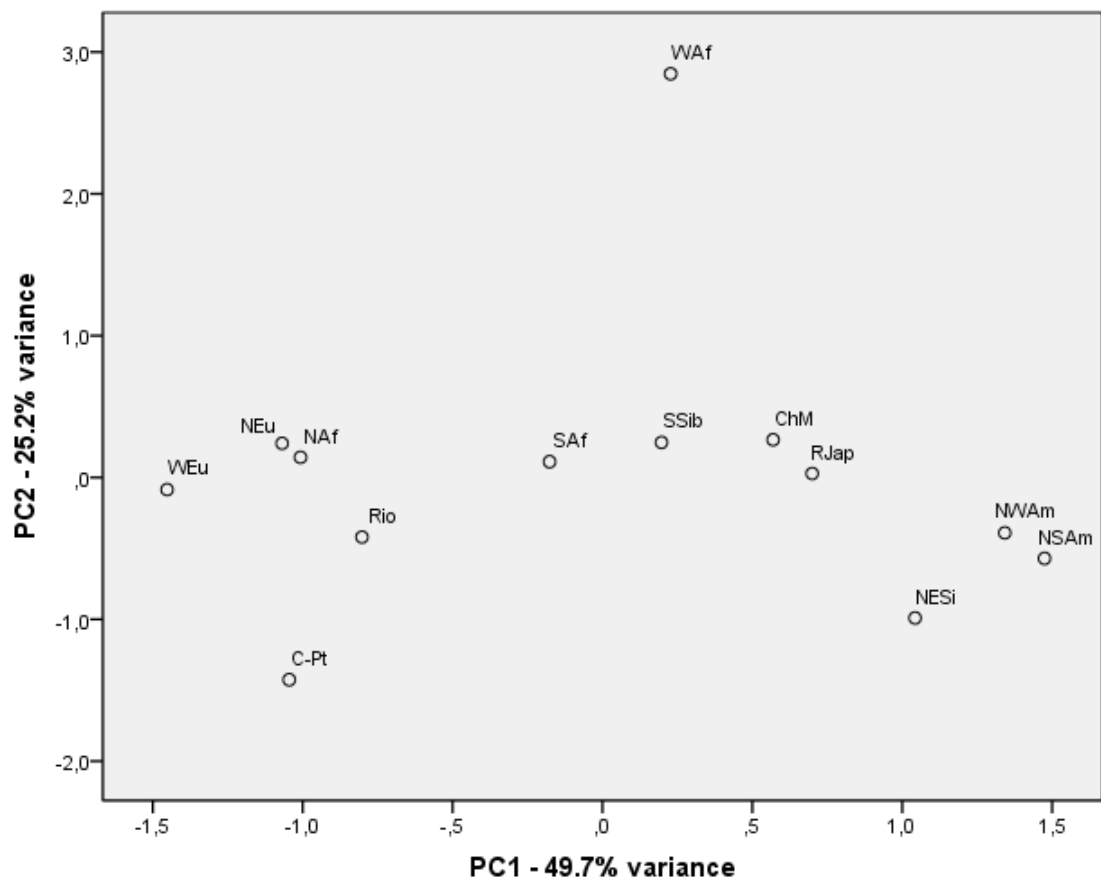
Figure 4.5.49. Scatterplot of the first two components in the comparison between Coimbra, Rio de Janeiro (Tinoco, 2010) and world-wide samples (Scott and Turner, 1997).
ChM: China-Mongolia; C-Pt: Coimbra, Portugal; NAf: North Africa; NESi: Northeast Siberia; NEu: Northern Europe; NSAm: North and South Native Americans; NWAm: Northwest North America; Rio: Rio de Janeiro; RJap: Recent Japan; SAf: South Africa; SSib: South Siberia; WAf: West Africa; WEu: Western Europe.

Rio de Janeiro as Western Europe. Along PC2, the sample closest to Rio is Northwest North Americans and North and South Native Americans. Yet, they are the furthest sample along PC1 (x axis). West Africans are the most distant and the only isolated sample along PC2 (y axis). PC2 brings Coimbra close to Northeast Siberia, followed by the cluster of Rio, Northwest North Americans and North and South Native Americans.

These results, - if not binding, due to the scarceness of variables available -, are interesting and suggest Coimbra is only separated from Rio due to this sample's proximity to African samples. It should be noted that both North and South African samples proceed from data collected by Irish (see Irish, 1998b), according to Scott and Turner (1997). The samples composing South Africa are from Sub-Saharan Africa, from West Africa, Southern African and even include a sample from East Africa. Using metric and nonmetric dental data, two southern African groups were distinguished and separation was estimated at about 12000 to 14000 years (Haeussler *et al.*, 1989), which explains the importance of the variability found in this South African sample. Rio is, thus, relatively close to South Africa because of Sub-Saharan slave gene flow. This (together with the Portuguese biological affinity with these populations) is most likely the reason that the sample closest to Rio is North Africa: the admixture between European, mainly Portuguese, and some Sub-Saharan African genetic variability produced such a relationship with North Africans.

The search for biological results attesting the Sub-Saharan African gene flow to South America was also conducted. For example, Fejerman and colleagues (2005) found 2.2% of the expression of 12 unlinked autosomal DNA markers from 90 random donors from a private hospital in Buenos Aires (Argentina) was of African descent. This proportion originated from 10% of the individuals in the sample. Afro-Argentines in the city were up to 30% during most of the 19th century.

Dental morphology testifies to the heterogeneity between North American and South American African descendants, suggesting different origins in Africa for each population. In the Colombian Pacific coast, African Americans are mainly from West African and Central-West African descendants (Delgado-Burbano, 2007b). Most African slaves in Brazil were Bantu speakers (Silva *et al.*, 2006b), which suggests a similar origin to Colombian slaves. The wide origin of Sub-Saharan African slaves in America, though, probably helps justify the relative proximity of the "South Africans" used for comparison, since these are composed of many populations throughout Sub-Saharan Africa.

Coimbra is closer to Rio than any other sample, including Europeans and North Africans. This is a great testimony to the shared human biological diversity found in these populations, which is most likely due to the heavy gene flow from Portugal into this South American country.

Rio's clustering with Native Americans along PC2, noted above, is also important. It reveals some influence of the Native American genetic patrimony into the present Brazilian gene pool, albeit a relatively small one. As was pointed out above, Native Americans are considered Sinodonts, a dental complex derived from Asia.

The population of Asia is dentally divided between Sinodonts (Northeast Asia) and Sundadonts (Southeast Asia, from the Sunda Shelf, previously above water, uniting what now are islands to the continent), each with their own dental complex, characterized by differences in eight discrete crown and root variables: maxillary central incisor shoveling, maxillary central incisor double shoveling, single-rooted maxillary first premolars, maxillary first molars enamel extensions, peg/reduced/congenital absence of maxillary third molars, mandibular first molar deflecting wrinkle, three-rooted mandibular first molar and four-cusped mandibular second molar (Turner, 1990). Sundadonts have evolved from Late Pleistocene peoples from the Sunda Shelf, according to the hypothesis Turner's (1990) results seem to corroborate. For an example of contemporary Sundadonty, see Artaria's (2007) data on the Javanese, from Indonesia.

Several samples influenced by Sinodonty are relatively close to Rio along PC2 (China-Mongolia, Northeast Siberia, Recent Japan, and particularly Northwest North American Natives and North and South Native Americans). This marks the slight influence of Native Americans into the current dental traits' frequencies of the Rio de Janeiro Brazilians, which should be further investigated using local samples for comparison.

Silva and colleagues (2006b) studied Y-chromosomes markers of 127 unrelated individuals from the Rio de Janeiro state. Despite the expected variability in this Brazilian state (the homonymous main city was the port of entry to most individuals travelling from the other side of the Atlantic Ocean), 88.1% of the patrilineages come from European contribution (mainly Portuguese, with one haplogroup in particular being traceable to a pre-Neolithic Iberian origin). African contributions amounted to 8.7% and Amerindian to 1.6%. The differences between the Portuguese and Rio de Janeiro European Y-chromosome gene pool is null and only contribution from Spain cannot be disregarded as another main contributor to this setup (others, like Italian, German, Syrian, Lebanese and Japanese, can). The patrilineages are mainly Portuguese, with some other European and Sub-Saharan African contributions, but no Amerindian participation, supporting the asymmetry in contribution from paternal and maternal lineages to the Brazilian gene pool found in previous research as well (Silva *et al.*,

2006b). Genetic data suggest the findings described by the present analysis to be correct.

Among 200 Brazilian white males, Y-chromosomes display markers from Europe mostly, and all the patrilineages could have come from Portugal, since there is no statistical difference between the Brazilian and the Portuguese (93 unrelated individuals from the North of Portugal were analyzed). Other major contributes could have come from the Italian, Dutch, Portuguese and Moroccan Jewish immigration. No Amerindian and very little Sub-Saharan African contribution was detected, even when poor rural white individuals from Brazil where compared to the middle-class and upper middle-class original sample. The four studied regions did not vary between them, variation mostly occurred within each of them (Carvalho-Silva *et al.*, 2001).

Two hundred and forty seven Brazilian (mainly white, middle-class, from four regions) unrelated individuals were analyzed for their mtDNA (Alves-Silva *et al.*, 2000). Amerindians (33.0%) and Africans (28.0%) have major contributions to the matrilineages found. This could be a minimal value, due to the bias introduced by the middle-class social standing of the participants (Alves-Silva *et al.*, 2000).

Rio Grande do Sul has a particular history within Brazil, since its colonization only started in the 18th century and its control successively altered between the Portuguese and the Spanish. This region was a preferred destination to German and Italian immigrants, who came to Brazil mainly after 1808. One hundred and nineteen white Brazilian individuals from Rio Grande do Sul (88 from Veranópolis, the others comprising the "general white sample") were tested for Y-chromosome and mtDNA variation. Y-chromosomes show patrilineage to derive from European populations (with few exceptions of Amerindian and African origin on the "general white sample") and mtDNA shows matrilineages, although mostly European (particularly for the Veranópolis sample: 97.0%; "general white sample": 48.0%), to be also from Amerindian (36.0%) and African (16.0%) haplogroups, detected for the "general white sample" studied (Marrero *et al.*, 2005).

The encouragement of interbreeding with the natives (mentioned above) and the probable free access European males had to African female slaves originated the inclusion of African and Native American mtDNA into the Caucasian genetic variation. Only Veranópolis seems to be an exception, and yet it is not by a greater inclusion of non-European mtDNA, but for an almost exclusively European genetic variation. Y-chromosomes, on the other hand, reflect that Native and African males had close to no

access to European females. That seems to be a continued habit of "racial" separation (also suggested above; see Edgar, 2009b), since it is still reflected in the present genetic variation.

A genetic study of Y-chromosome haplogroups from six Brazilian samples, four of African descent (two urban and two isolated), one of European descent and one of Japanese descent showed genetic diversity, mainly on the urban African-Brazilians and the European-Brazilians. The patrilinearity of European origin was more important for Afro-Brazilians, when compared to the Amerindian influence, relatively very small. Heterogeneity in diversity is hindered by preferential marriages, within the same ethnicity (Abe-Sandes *et al.*, 2004).

Ancient informative genetic markers from ten rural quilombos (communities of individuals of African descent) populations showed 39.7% African, 39.0% European and 21.3% Amerindian mean genetic contribution (Kimura *et al.*, 2013). Araújo Silva and colleagues (2006) conducted a genetic study focusing on mtDNA from both African (Cameroon and Congo) and African-Brazilian (mainly rural quilombos' samples, originally established by escaped slaves, and an urban sample). The presence of European matrilineage is non-existent in rural samples, as opposed to some evidence of Amerindian matrilineage, probably due to the greater amount of male slave escapees. The urban sample only demonstrates 5% European matrilineage (despite reporting only African ascendency). African descendents also show a pattern of matrilineages suggesting influence of ethnic-specific sex bias in the slave trade, where West-Central Bantu Africans are less represented through matrilineage than West Africans (Araújo Silva *et al.*, 2006).

These latter studies reiterate the importance of European male access to female African slaves, which heavily contrasts with the absence of European female access to males of African origin. This is expected to have been the case across America. Yet, African slaves in the Barbados presented greater frequencies of Carabelli's cusp and *tuberculum dentale* in younger generations, which might testify admixture in generations born on Barbados (Corruccini *et al.*, 1982). This explains that, because of the generalized lack of sexual dimorphism in dental discrete characters, independently of the sex most involved in ethnic interbreeding, that process bares some results in dental morphology.

This brief review of the genetic diversity in Brazil accounts for the results found for the present analysis. The closeness to the Portuguese sample of Coimbra is justified

not only by the heavy migration towards that Southern American country but also by the lack of generalized ethnic admixture. The admixture that is found, allowed for by the contact between European males and African or Native American females is also portrayed in Figure 4.5.49., which approximates Rio to North Africa and South Africa, and to North and South Native Americans along PC2.

Despite these six dental discrete characters co-variation suggesting this distribution of the compared samples, much more research is necessary before the influence of the presence of the Natives, African slaves, Spanish, Dutch, Italian and mainly Portuguese colonialists and immigrants, into the human biological diversity portrayed in every region of Brazil and South America is understood. The study of dental morphology from samples across time and space is necessary to understand the interplay of these diverse contributions. Yet, this interesting start explains the variation found in light of the population movements historically narrated.

4.5.8. Final thoughts on biological affinities and historical migrations that involve 19th and 20th centuries' Portugal

Dental morphology obviously is not the only scientific methodology apt to study biological affinities between populations. For example, relationships between Inuit groups in Alaska suggested by linguistic, archaeological and ethnographic research were attested through genetics (Schurr *et al.*, 2012), and the population history of the Portuguese Gypsies was analyzed in light of genetic drift and admixture, through genetic markers (Pereira *et al.*, 2012a). Yet, dental morphology is useful, even when dealing with living individuals. The phenetic proximity between different ethnic groups in Malaysia was established, corroborating historical patterns (Khamis *et al.*, 2006), through dental morphological data from present populations.

Dental morphological data can be easily, cheaply and reliably gathered from any skeletal sample, as long as teeth are conserved. Sample size is important, so as to allow any conclusion to be confidently stated.

A group of researchers with access to the appropriate material can help clarify some of the history of population movements in a region, analyzing samples from any time period, in a matter of years. See the work of Y. Manabe, Y. Kitagawa, J. Oyamada, A. Rokutanda, K. Kato, and other colleagues (1997, 2003, 2008, 2011), for example:

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(1) These researchers and their colleagues helped understand Sinodont incursions into Sundadont territory (Manabe *et al.*, 1997): (a) the Thai tribe, the main population in Northern Thailand, is Sundadont; (b) the Aka and Yao tribes, on the other hand, reveal clear influence from Sinodonty. An analysis of this find reveals that this is an example of an exception, since in Southeast Asia there are few incursions of Sinodonty, as Sundadonty evolved there without Northern influence;

(2) They used dental morphological evidence from the Neolithic population of Dawenkou (North China) to demonstrate continuity from the Sinodont pattern found in the Paleolithic Zhoukoudian Cave, underlining the possibility that the origin of this pattern was this region of China. The discontinuity between the Jomon (Sundadonts) and the Yayoi (Sinodonts) cultures of Japan suggests gene flow into the Japanese islands. Dawenkou cannot be ruled out as one of the sources, despite the fact that the coexistence between Dawenkou and Jomon cultures for 3000 years demonstrates the detriment to gene flow caused by the Japan and East China seas (Manabe *et al.*, 2003);

(3) They attested the gene flow direction and chronology into the Nansei Islands, from the main Japanese islands to the North. Migrant Japanese populations increasingly spread their biological influence throughout the Nansei Islands, which is testified by the gradation indicating lesser influence on each step towards the southern part of the archipelago (Manabe *et al.*, 2008);

(4) They compared data derived from 106 individuals from the Early Modern population of Okuma, in the Nansei Islands, with several other Japanese and Asian sample frequencies in order to clarify the origin of the population of the archipelago. The results again suggest the presence of Jomon influence, but the reduction of that influence from South to North and with time. The biological influence causing a Sinodont dental morphology in the Nansei Islands may come both from the North, the main islands of Japan where Yayoi culture and biological origin prevail, but also from China, since the archipelago held good relations with those populations from the 14th to the early 17th centuries (Manabe *et al.*, 2011).

These few examples of how these workers could contribute to the understanding of the Sinodont and Sundadont distribution across Asia, and the population movements within the regions of the Japan and China seas, are very illustrative of how this sub-field, dental anthropology (and, particularly, dental morphology), can help resolve questions of archaeological, historical and anthropological origin.

Another example regarding an anthropological issue was reported on by Lukacs and colleagues (2008): the Mahars (a low-status caste) claimed to be the representatives of the autochthonous inhabitants of Maharashtra (in India), but dental discrete variables show the Marathas (a high-status caste) to be closer to Inamgaon, a prehistoric sample from Maharashtra. A tribal sample, Madia Gonds, is placed closer to the prehistoric sample as well. So, although all samples from Maharashtra are similar, the Mahars have the least biological affinity to the autochthonous population (Lukacs *et al.*, 2008). Hemphill (2013) has also worked with Indian dental traits to better understand the peopling of India and the subsequent population movements into that sub-continent, in light of various models.

As pointed out in the first chapter (1.Introduction), the historical view on the Portuguese biological patrimony from the turn of the 20th century garnered heated discussions, reviewed by Sobral (2004). From the differences between northern and southern Portuguese, which ones were considered superior and which population (Celts, Visigoths, Arabs, Jews, Romans, Lusitanians, etc.) was the predominant contributor to the genetic and cultural makeup of the Portuguese, the mid-20th century settled on a unity that expressed biological continuity from the Lusitanians (see 1.Introduction and Sobral, 2004).

McMillan and Boone (1999) also report that, according to conservative Iberian views, Hispano-Roman populations were biologically almost unaltered, either adopting some cultural habits from the varied imperial occupants (Romans, Visigoths and Islamists) or integrating their few individuals within the local customs and families. More extremely, some have proposed an indigenous population adopted Islamic customs, instead of a degrading Visigoth tradition yielding centuries of famine and disease.

A different thesis on the Islamization of Iberia purports the importance of the endogamic mating patterns of the invaders, which would signify the Peninsula was mostly peopled by Arabs and Berbers within centuries. This theory fails in establishing actual basis towards this endogamic practice (McMillan and Boone, 1999).

According to cranial traits, those interred in a Paleo-Christian basilica from Mértola and those from the Medieval Islamic cemetery in the same site were most likely drawn from different gene pools, demonstrating a peopling of the locality by Arab and Berber groups (McMillan and Boone, 1999).

The purpose of the several analyses described above was to enlighten, through the use of dental morphological characteristics, which populations influenced (and to what extent) the biological patrimony of the population of Coimbra, thought of as a good proxy for the Portuguese population of the time (late 19th/early 20th century), given its relatively central position within the country and the diverse origin of about a third of the individuals included. Historic narrative, describing the successive occupations of the territory by numerous populations; anthropological and genetic data suggesting their relative importance; and archaeological evidence, questioning whether local populations would have accepted subjection to new habits, drove the necessity of these analyses. On the other hand, they were fed by the bibliographically available data, which were compared to one another and to the most versatile sample available, that on which the interpretation was centered: Coimbra.

The most general conclusion obtained was the identification of Coimbra as a European sample with possible genetic influx from North Africa. Further analyses demonstrated Coimbra's close relation to most Iberian samples, and connected the diverse degrees of relative biological proximity to historical and geographical justifications. The Portuguese sample's apparently clear close biological relationship to the populations from North Africa and Arabia was also further attested through several PCA's, which consistently corroborated it. Finally, two historical Empires that affected the presently Portuguese territory in different manners were also analyzed. Those studies enabled the identification of a potential gene flow of Roman origin into Portuguese populations, with a lasting effect, or of a previous biological proximity between the Italian and Iberian Peninsulas; and a possibly very important contribute of Portuguese genetic patrimony to the Brazilian biological makeup.

Several interpretations allowed some light and many shadows to be shed across the vast prehistory and history of Portugal, yet consist only of a minor contribution of this work to the dental morphology of that country. A point of access and departure from mainland Europe by land and sea, Portugal was the scenario of many relevant population movements throughout time. Increased effort is demanded of dental anthropologists, in the quest for the unveiling of the human biological history of one of the most important regions in Western Europe.

4.6.Dental wear

Wear is a function of teeth since their inception, so this mechanism has been instrumental in shaping and characterizing the qualities of teeth and their materials (Kaidonis, 2008). Since their eruption, teeth wear. Through the contact with other teeth (either those of the opposing dental arcade, or those next to it, on the same jaw – approximal wear), with food, and with tongue and cheeks, teeth are progressively worn. Attrition is the type of wear defined by contact with other teeth, and abrasion is defined by contact with food and the soft tissues, so it is more diffuse (Alt and Pichler, 1998; Kieser *et al.*, 2001; Hillson, 2005; Soames and Southam, 2005; Kaidonis, 2008). Erosion is the chemical dissolution of tooth tissue (without bacterial mediation), and normally results in dentinal scooping, by the elimination of the occlusal surface and the continuous undermining of the underlying dentine (Soames and Southam, 2005; Kaidonis, 2008).

Attrition may be caused, besides mastication, by bruxism (the tapping or grinding of teeth) or by other occasions when teeth are brought together. Abrasion occurs through the transport of abrasive particles on the cheeks, tongue and food. These contact teeth and reduce surface detail, eliminating edges and producing a glossy look. Contemporarily this is more common, because of tooth brushing with abrasive paste. Microscopically, Tomes' process pits and perikymata (part of the structural composition of enamel) are abraded away and are not visible as when the tooth first erupted (Hillson, 1996). Erosion can be occasioned by diet (acidic foods or beverages), occupation (exposure to airborne acids), or (usually) pathological regurgitation and vomiting (Soames and Southam, 2005). Interproximal wear produces vertical furrows, which appear to "interdigitate" with the adjacent tooth's furrows. This suggests vertical movement is the main source of this phenomenon, since horizontal movement (such as the mesial drift) would not produce this effect (Kaidonis *et al.*, 1992). This type of wear may be one of the factors involved in the retromolar space displayed by Neanderthals, since this tends to augment with the increase of attrition between adjacent teeth (Nara *et al.*, 1998). In the earlier stages of occlusal wear (up to 35% exposure of dentine) there is a positive correlation between occlusal wear and approximal wear. In later stages, on the other hand, the obliteration of occlusal surfaces reduces approximal wear facets, producing a negative correlation between occlusal and approximal wear (Deter, 2012).

A tooth's wear pattern is determined by each of the phenomena behind wear, in combination. Kaidonis (2008) states that abrasion is the most pervasive one, since contact with food is very common. Attrition, on the other hand, is more uncommon,

since it has been shown such wear facets are not related to mastication (Kaidonis, 2008). The heavy wear detected in the Maori (pre-contact New Zealand aboriginals) dentition was partially caused by mechanical forces and erosion, since the latter contributed to 30% of the wear detected (Kieser *et al.*, 2001). Even when dental wear is mainly caused by attrition, as suggested by Soames and Southam (2005), the complementation of such process with erosion and abrasion cannot be denied. Soames and Southam advocate that, in such cases, individuals be diagnosed as showing "tooth wear with a major component of attrition" (Soames and Southam, 2005: 36). These examples justify the use of the wider term "wear", instead of "attrition" or any other describing the loss of mineral material from teeth, in the present text.

In the late 19th century, dental wear was first studied by Mummery, who hypothesized the involvement of grit in the severe wear of Egyptian dentitions. Despite this, the early focus of dental wear was not diet reconstruction, but ageing. Several methods were developed across the 20th century. They were predominantly population-specific, although they were nonetheless used by researchers across the world to age different samples (Rose and Ungar, 1998).

Tooth wear is difficult to use in the estimation of age at death, as many techniques and ameliorations on those have demonstrated. Wear rates vary with age, the most objective techniques are very time consuming or require many calculations which can adulterate the data, and age estimating techniques that can be used for comparison have high error margins (Walker *et al.*, 1991). Dental attrition is not directly correlated with age, even when trying to age individuals from a reference population, because variables such as social status and health care access alter the observed attrition rate from the expected pattern (Boldsen, 2005). For example, in a 19th century European sample of known age at death, advanced molar wear is rare, occurring only on 14.0% of the teeth, despite the age distribution including older individuals (Mays, 2002). A two year study, measuring wear rates by volume, by area and by thickness of enamel loss, registered a small wear rate overall, and demonstrates that the loss of volume is constant in each year period, but a each year a less thick amount of enamel is removed on a greater area, proportionately (Pintado *et al.*, 1997). This demonstrates the difficulty in relating age with dental wear, since the loss of crown height is progressively lessened.

Still, the Miles method, for example, is widely applied and recognized as a valid method in aging skeletal remains. The recent modification proposed by Gilmore and Grote (2012) needs further testing, but appears as accurate as skeletal based estimations

and does not rely on establishing rate of wear from immature individuals (Gilmore and Grote, 2012). Other authors have claimed some success using dental attrition and alveolar resorption, like Constandse-Westermann (1997), who correctly aged 80% of the individuals of an early 19th century population from The Netherlands. Besides, overlaps on the age classes (better distributed across the adult life cycle) were only of five years and discrepancies were of the same level for female and less frequent for male individuals, when compared with other commonly used methods (Constandse-Westermann, 1997).

Dental wear can be considered a part of the recent subfield of dental ecology (Cuozzo *et al.*, 2012). Diet is correlated with many diseases (such as cancer and oral ailments, like caries and periodontal disease), affecting either the mouth and teeth or the whole body. So, the study of dietary habits in the past may be important in the comprehension of paleoepidemiology and paleopathology (Moynihan, 2005).

Since the beginning, dental wear was also studied to reconstruct diet, particularly among observation of fossil hominids, but without systematization. The first attempt at this tried to use a wear gradient to avoid the issue of ageing the analyzed skeletal samples, and preceded the advent of Bioarchaeology (which resulted from the relation between the New Archaeology and the New Physical Anthropology of the 1960's and 70's, as both aimed to integrate scientific method and multidisciplinary practices). Analyses of dental wear to infer diet became more of a focus, and originated more complex systems, which took into account the direction and shape of wear. The relevance of interstitial wear was also reviewed, since it is related to the force and duration of mastication. Wear evaluation fit into the 1980's trend on the study of the transition between hunter-gatherer subsistence systems and agriculture, by contributing to distinguish such groups and providing further information on the effects of diet. Further on, the perceived need to apply statistical parametric tests on data originated different techniques, which measured the area of exposed dentine, or the relation between the buccolingual and mesiodistal sizes of teeth and their height. These were, once again, time consuming, and did not originate the expected results because of the nonlinearity of tooth wear. Microwear analysis was the next advance in the study of dental wear, which demanded research to fully exploit the potential of determination of dietary particularities in human archaeological, fossil and primate samples (Rose and Ungar, 1998).

Another application for the study of dental wear is to uncover particular habits and the use of teeth as tools. For example, "Lingual surface attrition of the maxillary anterior teeth" is a dental wear pattern specifically associated with manioc consumption, through its processing, that uses the upper front teeth. This was found in a hunter-gatherer group from Brazil, thought therefore to be the first to consume manioc in great quantities, because of their widespread, early onset of a very particular dental wear and caries development pattern. The latter occurred in very high frequencies, analog to agriculturalists, despite this being a hunter-gatherer settlement from the archaeosite of Carondó, Brazil (3000-4200 BP) (Turner and Machado, 1983). LSAMAT also occurred in Senegalese historic populations after the introduction of manioc by the Portuguese, although this may not be the only reason for the elevated caries and LSAMAT rates, which are not as high as in Carondó (Irish and Turner, 1997).

Tooth wear of greater proportions than those observed on contemporary western populations is recorded in human populations from the past or from traditional cultures, as well as from mammals (including extant and extinct primates). This difference is attributed to the heavily processed foods that compose the current western diet, when compared to coarser foods and inclusion of mineral particles in the production of food in the past (Mays, 2002; Kaifu *et al.*, 2003).

This originated Begg's theory, since this author observed that the "normal" occlusion present in modern industrialized populations was negatively affected by a lack of wear. Worn teeth, in an attrition occlusion, affecting the occlusal but also the approximal surfaces, would prevent some of today's ailments on teeth (anterior crowding, rotation of teeth, impaction, bimaxillary protrusion), since it corresponds to the natural process of oral development (Kaifu *et al.*, 2003). Begg's suggested implications for low wear rates are not easily confirmed, seeming rather exaggerated, as are the claims that masticatory efficiency (akin to other mammals) is only attained when the cusps (as mere guides to correct occlusion) are worn off (Kaifu *et al.*, 2003).

Even so, teeth wear effectively diminishes progressively across historical periods. During the Paleolithic, hominins' dentitions were subjected to a great deal of stress, so as to justify their greater degree of wear. This stress was generated from eating hard foods, not cooking or improperly cooking fish and bones, and cracking nuts with their teeth, for example. Wear (mainly attrition and abrasion) was still greatly present during the Neolithic, since hard particles were still present in foods, like collagen from animal and fish bones and grain from the processing of cereal. Only since the Industrial

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Revolution have the processing of foods and dietary changes greatly diminished dental wear (Wasterlain, 2006).

In the hunter-gatherer/agricultural transition in Levant, the tooth wear in early Neolithic groups occurs to a lesser extent than in a Paleolithic sample, particularly in the anterior teeth. The exception is a population with access to marine resources, which still relied on hunting and fishing, besides agriculture. This and the use of teeth as a third hand probably justify the maintained high levels of attrition (Eshed *et al.*, 2006). Comparisons of wear rates between Mesolithic and Neolithic peoples show the former to be much faster. When the M3 erupts, M1 wear is already advanced in the Mesolithic, which contrasts with the Neolithic. The Mesolithic populations are characterized by a flatter wear, as opposed to the Neolithic populations' cupped wear (Lubell *et al.*, 1994). This difference in wear type is probably due to differential wear rates of enamel and dentine in relation to the loading they are exposed to. Enamel shows slow wear rates when exposed to smaller loadings, but rates are enhanced when it is exposed to a greater loading, probably due to the hardness and brittleness of the material. Dentine, on the other hand, demonstrated significantly higher wear rates when exposed to the lesser loadings; however comparable, it showed smaller, wear rates when exposed to the highest loading (Burak *et al.*, 1999).

4.6.1.Present sample

Dental wear *per se* was thoroughly studied in this population by Wasterlain (2006). This author compared degrees of wear between males and females in the occlusal and interproximal aspects, between each arcade and side of the dentition. It was concluded wear occurs in a small degree, with a mean of 2.6 (+- 1.2) in the scale proposed by Smith (1984). The present subsample from the same collections averages 3.0 (+- 0.7), which should be caused by a difference in age distribution (Wasterlain worked with a sample of the same number of individuals, 600, 300 of each sex; however, this author selected her individuals so as to divide the sample in six equal adult age ranges, whereas the present one was randomly picked in terms of age). This is lesser wear than that observed for Mesolithic, Neolithic/Chalcolithic, and Middle Age individuals in Portugal (Wasterlain, 2006). When compared with Medieval individuals

from Coimbra, the difference in dental wear is evident: the wear average was 3.86 (Carvalho, 2013).

These facts can only be explained by the already mentioned better processing of food stuffs, since the individuals from older populations were, on average, younger than the age-stratified sample chosen by Wasterlain (2006). Flour would have been better ground, fish would have been better washed and prepared and, probably, the dentition was less used as a third hand in professional or other contexts. Dental wear of grade 2 was the most frequently recorded, in 49.0% of the teeth (Wasterlain, 2006). In the present sample, only 14.9% (1898/12710) of teeth were graded 2 in the Smith (1984) scale, whereas 67.1% (8527/12710) were characterized with grade 3 (when only 17.8% of the teeth observed by Wasterlain were described thusly). The third most frequent grade was 4 (13.6%; 1724/12710) for the present study (all other grades were present with frequencies under 2.5%), whereas Wasterlain (2006) found the third greater frequency in grade 1 (12.7%). This shows a shift in the wear distribution between these samples taken from the same population, which may be caused by the difference in age distribution or between each author's sensitivity to the grading scheme. However, the conclusions drawn by Wasterlain (2006) are thought of as perfectly applicable to, - if not more representative of, - the Portuguese population (because of the mentioned balance in age distribution).

Recording dental wear in the present study had the objective to investigate the relations between dental wear and intra-observer error, and between dental wear and dental morphology. Berry (1976) stated the most severe limitations to the use of dental morphology are dental wear and caries. As an example, Formicola (1986) found dental wear to be very advanced in a Paleolithic Italian sample, making it very difficult to score nonmetric dental traits. Considerations such as these prompted the present author to investigate, using this vast and well documented Portuguese sample, the importance of dental wear in the reliability of the scoring of dental nonmetric variables.

4.6.2.Relationship between dental wear rate and intra-observer error

Table 4.6.1. compares overall precision between teeth with low (under grade 4) and high (grades 4 and above) wear rates and reports rank correlations (Kendall's *tau*-b and Spearman's *rho*) between each wear rate level (low and high) and the intra-observer error. Contrarily to what was expected, a majority of the 58 traits (35 traits, or 60.3%) shows a greater precision when measured on high wear rate teeth. Evidently, the same proportion of traits shows negative associations between rate level and observational error. No correlation, either positive or negative, reports a value which exceeds weak association.

The highest correlation value (both *tau* and *rho*) is 0.118 (P < 0.01; low wear rate overall precision (L): 95.5%, high wear rate overall precision (H): 81.8%), and is found on a trait poorly affected by wear rate, enamel extensions on UM3's. Despite the P-value indicative of reliable coefficients for both tests, this may still be better explained as a random event. The other relatively high coefficients were found for the groove pattern on LM1 (both coefficients: 0.115, P < 0.01, L: 95.7%, H: 89.8%), as severe dentine exposure (found on Smith's [1984] grades 4 and above) can disturb the scoring of this trait. The relationship found was, however, low.

As for the lowest correlations (under -0.1), these were found for six traits, also showing reasonably notorious differences in precision. The highest negative association was -0.172 on both tests (P < 0.01; L: 90.7%, H: 98.9%), found for LM1 deflecting wrinkle. It probably reflects a greater care in scoring traits when dealing with high wear, to eliminate dubious observations from consideration, a conscious effort from the present author, as recommended in the ASUDAS (see Turner *et al.* [1991] and Scott and Turner [1997]). The same reasoning can be taken for four other traits: LM1 anterior fovea (both coefficients: -0.168, P < 0.01, L: 74.1%, H: 87.5%), UM1 C5 (both coefficients: -0.117, P < 0.01, L: 92.4%, H: 98.6%) and mesial marginal accessory tubercles (both coefficients: -0.101, P < 0.01, L: 95.3%, H: 99.5%), and the UC distal accessory ridge (both coefficients: -0.115, P < 0.01, L: 55.8%, H: 78.7%). This may also justify the difference in precision and the high negative association found for UM1 Carabelli's trait (both coefficients: -0.147, P < 0.01, L: 66.2%, H: 81.2%),

Table 4.6.1. Comparison between the overall precisions of teeth with lower wear (up to grade 3) and higher wear (from grade 4 to 8), and correlations between wear level (low/high) and observation error.

Tooth (FDI)	Trait	Overall precision – Low wear (*n*)	Overall precision – High wear (*n*)	Kendall's *tau*-b	Spearman's *rho*
11/21	Winging	95.2% (319/335)	93.8% (211/225)	0.031	0.031
	Shoveling	84.7% (227/268)	91.7% (88/96)	-0.090	-0.090
	Double shoveling	95.6% (258/269)	95.5% (105/110)	0.010	0.010
	Diastema	99.2% (121/122)	100.0% (75/75)	-0.056	-0.056
	Interruption grooves	97.4% (301/309)	96.8% (180/186)	0.019	0.019
12/22	Interruption grooves	91.9% (519/565)	93.4% (71/76)	-0.019	-0.019
	Tuberculum dentale	39.8% (238/598)	32.4% (22/68)	0.046	0.046
	Peg incisors	96.7% (591/611)	93.3% (84/90)	0.060	0.060
13/23	Distal accessory ridge	55.8% (375/672)	78.7% (37/47)	-0.115**	-0.115**
14/24	Accessory cusps	98.6% (695/705)	100.0% (39/39)	-0.027	-0.027
	Accessory crests	96.4% (693/719)	100.0% (22/22)	-0.033	-0.033
	Tricuspid premolars	99.9% (761/762)	100.0% (72/72)	-0.011	-0.011
	Odontome	100.0% (756/756)	100.0% (61/61)	N/A	N/A
15/25	Accessory cusps	97.7% (681/697)	100.0% (28/28)	-0.030	-0.030
	Accessory crests	87.3% (613/702)	89.3% (25/28)	-0.011	-0.011
	Tricuspid premolars	99.7% (745/747)	100.0% (58/58)	-0.014	-0.014
	Odontome	99.7% (737/739)	100.0% (53/53)	-0.013	-0.013
16/26	Carabelli's trait	66.2% (389/588)	81.2% (181/223)	-0.147**	-0.147**
	C5	92.4% (545/590)	98.6% (213/216)	-0.117**	-0.117**
	Mesial marginal accessory tubercles	95.3% (525/551)	99.5% (202/203)	-0.101**	-0.101**
	Enamel extensions	96.0% (388/404)	98.5% (135/137)	-0.061	-0.061
17/27	C4	60.6% (526/868)	47.8% (22/46)	0.057	0.057
	Enamel extensions	88.4% (528/597)	96.8% (30/31)	-0.057	-0.057
18/28	Enamel extensions	95.5% (275/288)	81.8% (9/11)	0.118*	0.118*
	Parastyle	98.1% (418/426)	100.0% (16/16)	-0.026	-0.026
31/41	Shoveling	96.4% (402/417)	96.2% (175/182)	0.006	0.006
32/42	Shoveling	96.6% (570/590)	91.8% (90/98)	0.084*	0.084*
33/43	Distal accessory ridge	72.8% (565/776)	81.8% (45/55)	-0.051	-0.051
34/44	Odontome	100.0% (864/864)	100.0% (57/57)	N/A	N/A

Table 4.6.1. (Continued.)

Tooth (FDI)	Trait	Overall precision – Low wear (*n*)	Overall precision – High wear (*n*)	Kendall's *tau*-b	Spearman's *rho*
34/44	Lingual cusp number	81.3% (681/838)	80.0% (40/50)	0.007	0.007
35/45	Odontome	99.8% (813/815)	100.0% (50/50)	-0.012	-0.012
	Lingual cusp number	68.8% (548/797)	66.7% (28/42)	0.010	0.010
36/46	Deflecting wrinkle	90.7% (332/366)	98.9% (266/269)	-0.172**	-0.172**
	Anterior fovea	74.1% (277/374)	87.5% (279/319)	-0.168**	-0.168**
	Cusp/groove pattern	95.7% (355/371)	89.8% (307/342)	0.115**	0.115**
	Distal trigonid crest	97.0% (359/370)	97.9% (331/338)	-0.029	-0.029
	Protostylid	89.0% (332/373)	86.3% (297/344)	0.041	0.041
	MMPT	98.4% (366/372)	98.8% (331/335)	-0.018	-0.018
	Cusp number	96.3% (361/375)	96.2% (325/338)	0.003	0.003
	C5	71.1% (266/374)	62.5% (210/336)	0.092*	0.092*
	C6	97.9% (367/375)	99.4% (336/338)	-0.065	-0.065
	C7	95.8% (363/379)	94.4% (323/342)	0.031	0.031
37/47	Cusp/groove pattern	89.6% (666/742)	94.7% (72/76)	-0.049	-0.049
	Distal trigonid crest	94.9% (710/748)	100.0% (73/73)	-0.069*	-0.069*
	Protostylid	84.0% (642/764)	90.4% (66/73)	-0.050	-0.050
	MMPT	97.4% (750/770)	100.0% (68/68)	-0.046	-0.046
	Cusp number	95.8% (735/767)	93.2% (69/74)	0.036	0.036
	C5	89.7% (688/767)	93.2% (69/74)	-0.033	-0.033
	C6	99.1% (760/767)	100.0% (75/75)	-0.029	-0.029
	C7	99.0% (764/772)	98.8% (81/82)	0.005	0.005
38/48	Cusp/groove pattern	86.7% (450/519)	77.1% (27/35)	0.067	0.067
	Distal trigonid crest	84.9% (461/545)	97.2% (35/36)	-0.086*	-0.086*
	Protostylid	91.4% (449/491)	97.0% (32/33)	-0.049	-0.049
	MMPT	88.9% (447/503)	94.1% (32/34)	-0.041	-0.041
	Cusp number	86.5% (466/539)	90.6% (29/32)	-0.028	-0.028
	C5	77.2% (416/539)	78.1% (25/32)	-0.005	-0.005
	C6	95.2% (512/538)	93.8% (30/32)	0.015	0.015
	C7	98.5% (538/546)	94.6% (35/37)	0.074	0.074

*: P <= 0.05; **: P <= 0.01.

notwithstanding its apparent independence of occlusal wear (because of its lingual position). All of these errors in corresponding one observation with the other may diminish within teeth with high wear rates because of an apparent lesser grade variability within them, which allows for a lesser margin of error.

From the several traits that are apparently independent of occlusal wear rate, due to their position, most (UI1 winging, UI1 and UI2 interruptions grooves, UI2 peg incisors, UM1 enamel extensions, UM3 parastyle, LI1 shoveling and LM1 protostylid) show reasonably equivalent precision between wear rates and coefficient values near zero (no relation between wear rate level and intra-observer error). The remaining traits seem to illustrate the random effect of this comparison, and therefore show there is an unlikely real relationship between wear rate level and scoring error: UI1 shoveling (both coefficients: 0.090, $P > 0.05$, L: 84.7%, H: 91.7%) and LI2 shoveling (both coefficients: 0.084, $P < 0.05$, L: 96.6%, H: 91.8%); the mentioned case of Carabelli's trait; UM2 enamel extensions (both coefficients: -0.057, $P > 0.05$, L: 88.4%, H: 96.8%) and the mentioned situation of UM3 enamel extensions; and finally LM2 protostylid (both coefficients: -0.050, $P > 0.05$, L: 84.0%, H: 90.4%) and LM3 protostylid (both coefficients: -0.049, $P > 0.05$, L: 91.4%, H: 97.0%).

From these results, showing usually higher overall precision for teeth with heavy wear and displaying only low associations between wear rate type and observation error, it seems safe to underline the reliability of the ASUDAS (at least when the evaluated traits are concerned), which is composed of dental traits that "most[ly] persist for many years in dentally harsh lifeways" (Turner *et al.*, 1991: 13). The MMPT was scored using a method adapted from Weets (2009), which seems to be reproducible in any wear rate stage. The midline diastema, which is recorded as suggested by Irish (1998b), as was foreseeable, is also reliable independently of wear rate.

4.6.3. Relationship between individual mean wear and dental morphology frequencies

Table 4.6.2. displays frequencies of dental morphological trait presence for individuals with wear rate mean under grade 3 (low mean wear) and individuals with wear rate mean of grade 3 and above (high mean wear). The rank correlation

Table 4.6.2. Comparison of trait frequencies between low (under grade 3) and high mean wear (grade 3 and above), and correlations between trait grade and mean wear level (low/high).

Tooth (FDI)	Trait	Low mean wear (below 3)	High mean wear (3 and above)	Kendall's *tau*-b	Spearman's *rho*
11/21	Winging + = ASU 1a-1b	1.5% (3/191)	2.1% (4/194)	-0.013	-0.013
	Shoveling + = ASU 2-6	2.6% (4/153)	1.8% (2/109)	-0.031	-0.031
	Double shoveling + = ASU 2-6	1.4% (2/146)	0.0% (0/104)	-0.027	-0.027
	Diastema + = Irish (1998) > 0.5 mm	6.9% (7/102)	13.8% (16/116)	0.113	0.113
	Interruption grooves + = ASU 1	3.9% (7/180)	6.7% (12/178)	0.066	0.066
12/22	Interruption grooves + = ASU 1	18.7% (46/246)	15.5% (32/206)	-0.041	-0.041
	Tuberculum dentale + = ASU 1-6	91.0% (232/255)	86.9% (183/213)	-0.086*	-0.086*
	Peg incisors + = ASU 1-2	3.8% (10/260)	3.0% (7/232)	-0.024	-0.024
13/23	Distal accessory ridge + = ASU 1-5	79.0% (203/257)	53.8% (114/212)	-0.258**	-0.282**
14/24	Accessory cusps + = ASU 1	0.8% (2/258)	1.5% (3/197)	0.035	0.035
	Accessory crests + = 1 (truncated ridges excluded)	7.2% (19/264)	2.6% (5/189)	-0.101*	-0.101*
	Tricuspid premolars + = ASU 1	0.4% (1/271)	0.0% (0/222)	-0.041	-0.041
	Odontome + = ASU 1	0.7% (2/270)	0.0% (0/217)	-0.058	-0.058
15/25	Accessory cusps + = ASU 1	4.2% (11/260)	1.9% (4/206)	-0.063	-0.063
	Accessory crests + = 1 (truncated ridges excluded)	33.6% (88/262)	15.5% (32/262)	-0.196**	-0.204**
	Tricuspid premolars + = ASU 1	0.0% (0/267)	0.4% (1/229)	0.049	0.049
	Odontome + = ASU 1	0.4% (1/265)	0.0% (0/224)	-0.042	-0.042
16/26	Carabelli's trait + = ASU 2-7	29.1% (79/272)	14.0% (29/207)	-0.154**	-0.166**
	C5 + = ASU 2-5	3.3% (9/269)	3.4% (7/209)	-0.119**	-0.120**

Table 4.6.2. (Continued.)

Tooth (FDI)	Trait	Low mean wear (below 3)	High mean wear (3 and above)	Kendall's *tau*-b	Spearman's *rho*
16/26	Mesial marginal accessory tubercles + = Scott and Turner (1997) +	6.8% (18/264)	1.6% (3/193)	-0.124**	-0.125**
	Enamel extensions + = ASU 1-3	4.3% (9/211)	3.5% (5/142)	-0.018	-0.019
17/27	C4 + = ASU 3-5	63.2% (182/288)	52.4% (127/242)	-0.134**	-0.153**
	Enamel extensions + = ASU 1-3	20.5% (48/234)	15.7% (29/185)	-0.058	-0.060
18/28	Enamel extensions + = ASU 1-3	10.4% (11/106)	4.3% (5/110)	-0.116	-0.117
	Parastyle + = ASU 1-6	4.8% (7/147)	2.0% (3/149)	-0.076	-0.076
31/41	Shoveling + = ASU 2-6	0.0% (0/192)	0.0% (0/171)	-0.044	-0.044
32/42	Shoveling + = ASU 2-6	0.0% (0/230)	0.0% (0/230)	-0.094	-0.094
33/43	Distal accessory ridge + = ASU 1-5	44.9% (119/265)	37.0% (91/246)	-0.077	-0.081
34/44	Odontome + = ASU 1	0.0% (0/276)	0.0% (0/276)	N/A	N/A
	Lingual cusp number + = ASU 2-9	29.0% (79/273)	20.9% (53/253)	-0.092*	-0.097*
35/45	Odontome + = ASU 1	0.4% (1/256)	0.0% (0/255)	-0.044	-0.044
	Lingual cusp number + = ASU 2-9	69.4% (175/252)	59.2% (148/250)	-0.110**	-0.119**
36/46	Deflecting wrinkle + = ASU 1-3	10.2% (23/225)	2.5% (4/159)	-0.146**	-0.147**
	Anterior fovea + = ASU 1-4	25.9% (60/232)	7.6% (14/185)	-0.243**	-0.250**
	Cusp/groove pattern + = ASU Y	90.0% (206/229)	89.8% (177/197)	0.002	0.002
	Distal trigonid crest + = ASU 1	3.9% (9/231)	1.0% (2/193)	-0.090	-0.090
	Protostylid + = ASU 1-7	19.4% (45/232)	19.8% (39/197)	0.003	0.003
	MMPT + = Weets (2009) [adpt.] 1-'3+'	3.4% (8/232)	0.5% (1/192)	-0.101*	-0.101*
	Cusp number + ~= ASU 5	10.8% (25/231)	8.3% (16/193)	-0.025	-0.025
	C5 + = ASU 1-5	90.4% (208/230)	92.2% (178/193)	-0.001	-0.001
	C6 + = ASU 1-5	2.6% (6/231)	0.5% (1/193)	-0.081	-0.081

Table 4.6.2. (Continued.)

Tooth (FDI)	Trait	Low mean wear (below 3)	High mean wear (3 and above)	Kendall's *tau*-b	Spearman's *rho*
36/46	C7 + = ASU 1-4	6.0% (14/234)	4.1% (8/198)	-0.043	-0.043
37/47	Cusp/groove pattern + = ASU +/X	79.3% (211/266)	80.4% (172/214)	0.013	0.013
	Distal trigonid crest + = ASU 1	6.3% (17/269)	1.4% (3/212)	-0.122**	-0.122**
	Protostylid + = ASU 1-7	17.5% (47/268)	14.4% (32/222)	-0.044	-0.045
	MMPT + = Weets (2009) [adpt.] 1-'3+'	5.5% (15/271)	0.9% (2/220)	-0.126**	-0.126**
	Cusp number + ~= ASU 4	23.3% (63/270)	19.0% (41/221)	-0.038	-0.038
	C5 + = ASU 1-5	21.5% (58/270)	19.0% (41/221)	-0.029	-0.030
	C6 + = ASU 1-5	1.5% (4/270)	0.5% (1/221)	-0.051	-0.051
	C7 + = ASU 1-4	0.4% (1/270)	0.0% (0/226)	-0.041	-0.041
38/48	Cusp/groove pattern + = ASU Y	18.3% (35/191)	20.8% (37/178)	-0.031	-0.031
	Distal trigonid crest + = ASU 1	26.0% (51/196)	15.6% (28/180)	-0.128*	-0.128*
	Protostylid + = ASU 1-7	8.5% (14/165)	5.5% (10/181)	-0.058	-0.059
	MMPT + = Weets (2009) [adpt.] 1-'3+'	32.3% (54/167)	28.5% (53/186)	-0.052	-0.054
	Cusp number + ~= ASU 4	62.0% (116/187)	51.1% (92/180)	-0.106*	-0.112*
	C5 + = ASU 1-5	58.3% (109/187)	48.1% (87/181)	-0.080	-0.087
	C6 + = ASU 1-5	17.6% (33/187)	11.0% (20/181)	-0.088	-0.090
	C7 + = ASU 1-4	0.5% (1/190)	1.6% (3/186)	0.071	0.071

*: P <= 0.05; **: P <= 0.01.

coefficients (Kendall's *tau*-b and Spearman's *rho*) between trait grade and mean wear level are also reported. Seventeen out of the 58 traits compared (29.3%) show coefficients above 0.1 or below -0.1, and most show high differences between the presence frequencies among these two groups.

From the aforementioned 17 traits, only one, the midline diastema (*tau*: 0.113, *rho*: 0.113, P > 0.05, low mean wear frequency (LF): 6.9%, high mean wear frequency (HF): 13.8%), had a correlation between the increase of frequency accompanying the increase in mean wear. This may be due to the fact teeth are spread further apart on the midline with increasing wear, since approximal wear seems to be related with the force

and duration of the mastication (Rose and Ungar, 1998), but also with occlusal wear (Hillson, 2005). Mesial drift is the process by which teeth do not allow approximal wear to keep them apart, and has been observed throughout the world. It may be caused by the traction of the transeptal fibers which connect teeth (Kaifu *et al.*, 2003). This process should keep a midline diastema from appearing, but this trait may be the realization of a genetic potential for such space to occur at the midline, not affected by the mesial drift; dental wear may be necessary to bring it about.

All other 16 traits display coefficients under -0.1, negative association between trait grade frequencies and mean wear level. This means individuals with low wear display greater trait frequencies.

Three traits display moderate correlation. The UC distal accessory ridge (*tau*: -0.258, *rho*: -0.282, P < 0.01, LF: 79.0%, HF: 53.8%) has a 25.2% difference in presence frequencies. The UP4 accessory crests (*tau*: -0.196, *rho*: -0.204, P < 0.01, LF: 33.6%, HF: 15.5%) show a 18.1% difference in trait presence frequency, which can be due to a larger presence of mere truncated ridges (excluded from the present sample's observation), instead of full crests, and can therefore be due to not using the most appropriate and recent method (Burnett *et al.*, 2010). The LM1 anterior fovea (*tau*: -0.243, *rho*: -0.250, P <0.01, LF: 25.9%, HF: 7.6%) displays an 18.3% difference, which is probably due to the fact this trait can be removed by heavy wear (Turner *et al.*, 1991).

UP3 accessory crests (*tau*: -0.101, *rho*: -0.101, P < 0.05, LF: 7.2%, HF: 2.6%) also occur with different expressions according to mean wear level (see possible explanation above, for this same trait on UP4). Although not directly affected by occlusal wear, the same processes can obscure the presence of the least expressive grade of Carabelli's trait on UM1 (*tau*: -0.154, *rho*: -0.166, P < 0.01, LF: 29.1%, HF: 14.0%), apparently. UM1 C5 (*tau*: -0.119, *rho*: -0.120, P < 0.01, LF: 3.3%, HF: 3.4%) is present on nearly the same frequency for both mean wear levels, but is less expressed when wear is higher, according to the rank correlation coefficients that show a weak negative association. The small UM1 mesial marginal accessory tubercles (*tau*: -0.124, *rho*: -0.125, P < 0.01, LF: 6.8%, HF: 1.6%) appear to also be obscured by wear. The same happens when analyzing results for the UM2 hypocone (*tau*: -0.134, *rho*: -0.153, P < 0.01, LF: 63.2%, HF: 52.4%). LP4 lingual cusp number (*tau*: -0.110, *rho*: -0.119, P < 0.01, LF: 69.4%, HF: 59.2%) shows variation due to wear level, which probably hinders the discrimination of smaller extra cusps. LM1 deflecting wrinkle (*tau*: -0.146, *rho*: -0.147, P < 0.01, LF: 10.2%, HF: 2.5%) is known for its difficulty in scoring when some

wear is present (Turner *et al.*, 1991). LM1 MMPT (*tau*: -0.101, *rho*: -0.101, P <0.05, LF: 3.4%, HF: 0.5%) and LM2 MMPT (*tau*: -0.126, *rho*: -0.126, P <0.01, LF: 5.5%, HF: 0.9%) were expected to have some differences, since the smaller expressions are easily worn off indentations. Distal trigonid crests are considered difficult to observe when molars are somewhat worn, and so differences on LM2 (*tau*: -0.122, *rho*: -0.122, P < 0.01, LF: 6.3%, HF: 1.4%) and LM3 (*tau*: -0.128, *rho*: -0.128, P < 0.05, LF: 26.0%, HF: 15.6%) were predictable. The LM3 cusp number (*tau*: -0.106, *rho*: -0.112, P < 0.05, LF: 62.0%, HF: 51.1%) displays some differences, derived mainly from the lesser frequency of LM3 C5 (*tau*: -0.080, *rho*: -0.087, P > 0.05, LF: 58.3%, HF: 48.1%) and LM3 C6 (*tau*: -0.088, *rho*: -0.090, P > 0.05, LF: 17.6%, HF: 11.0%), which can be difficult to detect if less expressive.

Some other frequency differences are notable, despite the small relation between grade expression and level of wear, as underlined to coefficients of correlation nearing zero. UI2 *tuberculum dentale* (*tau*: -0.086, *rho*: -0.086, P < 0.05, LF: 91.0%, HF: 86.9%), a trait dismissed from biological affinity analyses due to high intra-observer error, displays some distinction depending on the wear level, but this could be random. The LC distal accessory ridge (*tau*: -0.077, *rho*: -0.081, P > 0.05, LF: 44.9%, HF: 37.0%) displays a difference proportional to that found for the more frequent upper canine version of the trait. LP3 lingual cusp number (*tau*: -0.092, *rho*: -0.097, P < 0.05, LF: 29.0%, HF: 20.9%), despite the slightly lower difference, reflects the results found for the trait on LP4. LM2 cusp number (*tau*: -0.038, *rho*: -0.038, P > 0.05, LF: 23.3%, HF: 19.0%) displays a susceptibility to wear level paired to its propensity to reduced or absent cusps 5 and 6.

UM2 enamel extensions (*tau*: -0.058, *rho*: -0.060, P > 0.05, LF: 20.5%, HF: 15.7%) and UM3 enamel extensions (*tau*: -0.116, *rho*: -0.117, P > 0.05, LF: 10.4%, HF: 4.3%), traits that have no relation to wear that the present author can establish, are diminished in presence and expression in individuals with increased wear rate means. This may mean that some of this variability is caused not by a real difficulty in scoring traits when wear is increased, but by a biological difference between these groups of individuals.

The data on Table 4.6.3., describing the correlation between individual mean wear (all teeth and molars only), the sum of teeth lost *ante-mortem* (AMTL; all teeth and molars only) and age, show this biological difference may be caused by the

Table 4.6.3. Kendall's *tau*-b correlations between mean wear (for all teeth, and for molars only), *ante-mortem* tooth loss (for all teeth, and for molars only), and individual age. All P-values are 0.000. Above the divide are *tau* values and below are *n* values.

	Mean wear (all teeth)	Mean wear (molars)	Total AMTL (all teeth)	Total AMTL (molars)	Age
Mean wear (all teeth)		0.713	0.403	0.390	0.558
Mean wear (molars)	596		0.296	0.280	0.505
Total AMTL (all teeth)	600	596		0.899	0.523
Total AMTL (molars)	600	596	600		0.498
Age	600	596	600	600	

presence of different generations, since wear rates correlate with age (*tau*: 0.558). However, secular trends on dental morphology should be seen. Chapter 4.8.Intrasample biological relations, where sample variation is analyzed, shows that there are scarce differences between generations. This dismisses the unlikely possibility of definite biological differences between high and low wear samples. The differences found for enamel extensions, for example, may be related to genetic or evolutionary processes like stabilizing selection or random sampling.

The correlation between mean wear and AMTL on all teeth (*tau*: 0.403) also points to a possible relation between wear and loss of teeth that might have trait presence, therefore diminishing the trait frequency. In fact, enamel extensions have been associated with periodontal disease (Soto *et al.*, 2010) Table 4.6.3. also denotes high correlations between age and all other variables, moderate correlations between mean molar wear and AMTL (on all teeth and molars), moderate to high correlations between individual mean wear and AMTL (on all teeth and molars), and very high correlations between AMTL for molars and all teeth and between mean wear on molars and all teeth, as expectable.

According to research by Burnett and colleagues (2013), wear may influence trait frequencies, since they tend to diminish with increasing wear on UI1 shoveling, UC distal accessory ridge, UM2 hypocone and LM2 cusp number. This may be due to a downgrading of the trait with increasing wear (a trait may look smaller or of less expression than what it presumably was) or to violations of the "missing completely at random" supposition, which states missing data are random if they are not related to the trait's value or to the influence of other trait(s). The authors conclude by suggesting there should be more research on the subject, since there are some faults with their results. These are due to the relative inexperience of the observers and to the size and

nature of the sample (small archaeological samples are not ideal for this type of research, as would be longitudinal data on dental morphology), besides the small amount of traits studied.

The great deal of successful research conducted on the field of dental morphology, which results were able to mimic migration patterns suggested by other scientific fields, are a reminder of the small potential for real confusion brought by dental wear. However, future research should measure wear using Smith's (1984) method and, when possible, populations with highly different wear rates should not be compared (Burnett *et al.*, 2013).

Despite this, what the overall trend of diminished trait presence in individuals with higher wear rate means seems to indicate is an important difficulty with worn teeth that may cause a bias in biological affinity analyses, if this factor is not considered. As seen above, differences in intra-observer error are not responsible for this difference, but denote more care in scoring (or not scoring, more likely) heavily worn teeth. This necessary care and teeth wear may originate a sub-representation of the genotype. If this effect is diluted within large and diversified samples (in terms of wear rates), it should be corrected for in heavily worn samples of teeth. Apparently no amount of care can avoid error caused by tooth wear, since even not scoring dubious situations (which was evidenced by higher precision on more heavily worn teeth) does not prevent notable differences between trait frequencies.

4.7.Count method

4.7.1.Comparison between count methods

In terms of ASUDAS application, symmetry can allow for the tooth count method to be used, instead of the individual count method, which enhances the sample *n*. The latter method counts only a grade for each trait per individual. A specific side, the strongest, or the weaker expression, can be chosen to represent each individual (usually the strongest). If the tooth count method has the merit of considering all data, it can create a statistical or a genetic bias. Therefore, the need to ensure symmetry is imposed, so as to avoid the adulteration of results. The individual count method is more conservative, nevertheless it may mean giving up meaningful information, when samples display scarce tooth conservation (Scott and Turner, 1997). Scott (1980) argues that if tooth count is used, *n* should be the number of individuals from whom observations were made (not tooth number), in order not to inflate the numbers due to large symmetry. Scott (1980) also describes the two forms of unilateral count, the strict one (observing teeth from one side only) and the one where the loss of the observed side allows the observation of the other, if the tooth is present.

Usually the method used to calculate the frequency of morphological dental (and oral) traits is the individual count method, and the most expressive antimere is valued. With this approach, few data are lost and each individual's genetic information is better translated, using the most marked phenotype, instead of opting for the least expressive side or accounting for both, as if an individual could portray two different genotypes (Scott, 1977; Scott and Turner, 1997). The individual count method allows for the genotype to be better expressed when there is presence-absence asymmetry (Scott, 1980).

Turner (1985), after describing the other count methods, proposes a different one (the "expression count method") which allows for a better representation of a population through a smaller sample and enables comparisons between very similar samples, which values the differences in the several grades that describe most traits. It assumes polygenic inheritance and lack of dominance or sex influence (Turner, 1985). A major difficulty involving this method is the impossibility of comparisons with other data where different methods were used. There is also a lack of the necessary information (frequencies for each grade), that would allow for the needed calculations, in most

studies. This method, while not included here for a lack of comparability, will be used in the next chapter (4.8.Intrasample biological relations).

The present study applies the individual count method on the Portuguese sample, when it is compared to other samples. However, the present author acknowledges that some situations warrant the use of the tooth count method. In a previous study (Marado, 2010, 2012) that method was used in order to record as much data as possible. Samples from archaeological origin (like many of the ones used for statistical comparisons: Sofaer *et al.*, 1986; Manzi *et al.*, 1997; Irish, 1998b; Souich, 2001; Silva, 2002; Rodrigues, 2005; Simão, 2005; Costa, 2006; Fernandes, 2006; Lucas, 2006; Pinto, 2006; Pombal, 2006; Silva *et al.*, 2006a; Costa, 2007; Godinho, 2008; Al Oumaoui, 2009; García Sívoli, 2009; Pereira, 2009; Tereso, 2009; Gonçalves, 2010; Graça, 2010; Pacelli and Márquez-Grant, 2010; Laguillo *et al.*, 2011; Leandro, 2011; Ullinger *et al.*, 2005) are often forced to use the tooth count method due to small sample size, and the need to use as much of the available information as possible, once again. The current chapter intends to explore the data available for this study to the full extent, and compare the effect of the tooth count method, the individual count method and either side of the (strict) unilateral count method (see Table 4.7.1.) in biological affinity analysis. The differences between sexes and sides (see 4.2.Fluctuating asymmetry and 4.3.Sexual dimorphism and intertrait correlations), between different dental wear stages (see 4.6.Dental wear) and between different generations sampled (see 4.8.Intrasample biological relations), as well as the correlations between different nonmetric variables (see 4.3.Sexual dimorphism and intertrait correlations) are available and allow for the consideration of this battery of traits using any method. This exercise of comparison will allow an estimate of the degree of error expected when samples using different count methods are compares.

Table 4.7.1. displays the frequencies obtained for the studied Portuguese sample using the tooth count method, both strict unilateral counts (left and right) and the individual count method. The sampled *n* for each situation, as well as the frequencies for each grade, can be verified in Table 4.2.1. (in the chapter 4.2.Fluctuating asymmetry) and Table 4.7.1. Sixteen out of 58 traits (27.6%; midline diastema, mandibular torus and palatine torus were recorded as individual, not lateralized traits, and so are not included) display at least a 4.0% difference within the individual count

Table 4.7.1. Percentages of presence of tooth, side (left and right) and individual count methods for all bilaterally recorded nonmetric dental and oral traits.

	Tooth/side count (%)	Left side count (%)	Right side count (%)	Individual count (%)
Winging (11/21) + = ASU 1a-1b	1.9	1.6	2.2	1.9
Shoveling (11/21) + = ASU 2-6	2.5	2.0	3.0	2.3
Double shoveling (11/21) + = ASU 2-6	0.9	1.0	0.5	0.8
Interruption grooves (11/21) + = ASU 1	3.8	3.7	3.8	4.3
Interruption grooves (12/22) + = ASU 1	12.7	12.9	12.5	17.3
Peg incisors (12/22) + = ASU 1-2	3.4	3.2	3.6	3.5
Distal accessory ridge (13/23) + = ASU 1-5	64.2	65.5	62.9	77.6
Accessory cusps (14/24) + = ASU 1	0.7	1.3	0.0	1.1
Accessory crests (14/24) + = 1 (truncated ridges excluded)	3.8	3.9	3.7	5.3
Tricuspid premolars (14/24) + = ASU 1	0.1	0.2	0.0	0.2
Odontome (14/24) + = ASU 1	0.2	0.2	0.2	0.4
Accessory cusps (15/25) + = ASU 1	2.4	2.1	2.8	3.2
Accessory crests (15/25) + = 1 (truncated ridges excluded)	20.3	20.8	19.8	25.6
Tricuspid premolars (15/25) + = ASU 1	0.1	0.2	0.0	0.2
Odontome (15/25) + = ASU 1	0.1	0.2	0.0	0.2
Carabelli's trait (16/26) + = ASU 2-7	19.2	19.4	19.0	22.5
C5 (16/26) + = ASU 2-5	2.6	3.5	1.7	3.3
Mesial marginal accessory tubercles (16/26) + = Scott and Turner (1997) +	3.0	1.6	4.4	4.6
Enamel extensions (16/26) + = ASU 1-3	3.3	3.1	3.4	4.0
C4 (17/27) + = ASU 3-5	55.6	54.9	56.3	58.4
Enamel extensions (17/27) + = ASU 1-3	16.2	15.5	16.9	18.4

Table 4.7.1. (Continued.)

	Tooth/side count (%)	Left side count (%)	Right side count (%)	Individual count (%)
Enamel extensions (18/28) + = ASU 1-3	6.3	6.7	5.9	7.2
Parastyle (18/28) + = ASU 1-6	2.4	2.9	1.8	3.4
Shoveling (31/41) + = ASU 2-6	0.0	0.0	0.0	0.0
Shoveling (32/42) + = ASU 2-6	0.0	0.0	0.0	0.0
Distal accessory ridge (33/43) + = ASU 1-5	35.3	37.0	33.6	41.1
Odontome (34/44) + = ASU 1	0.0	0.0	0.0	0.0
Lingual cusp number (34/44) + = ASU 2-9	21.3	19.8	22.5	25.1
Odontome (35/45) + = ASU 1	0.2	0.2	0.2	0.2
Lingual cusp number (35/45) + = ASU 2-9	58.0	53.0	63.0	64.3
Deflecting wrinkle (36/46) + = ASU 1-3	5.1	2.8	7.5	7.0
Anterior fovea (36/46) + = ASU 1-4	17.4	16.9	18.0	17.7
Groove pattern (36/46) + = ASU Y	92.1	93.4	90.6	89.9
Distal trigonid crest (36/46) + = ASU 1	2.1	1.6	2.6	2.6
Protostylid (36/46) + = ASU 1-7	16.1	16.1	16.3	19.6
MMPT (36/46) + = Weets (2009) [adpt.] 1-'3+'	1.3	1.6	0.9	2.1
Cusp number (36/46) + ~= ASU 5	10.8	10.4	11.3	9.7
C5 (36/46) + = ASU 1-5	89.8	90.7	88.9	91.3
C6 (36/46) + = ASU 1-5	1.5	1.9	1.1	1.6
C7 (36/46) + = ASU 1-4	4.4	4.6	4.2	6.7
Groove pattern (37/47) + = ASU +/X	72.9	74.5	71.2	79.8
Distal trigonid crest (37/47) + = ASU 1	3.1	2.7	3.6	4.2
Protostylid (37/47) + = ASU 1-7	12.0	11.2	12.8	16.1
MMPT (37/47) + = Weets (2009) [adpt.] 1-'3+'	2.6	2.8	2.3	3.5
Cusp number (37/47) + ~= ASU 4	17.8	19.3	16.2	21.4

Table 4.7.1. (Continued.)

	Tooth/side count (%)	Left side count (%)	Right side count (%)	Individual count (%)
C5 (37/47) + = ASU 1-5	16.9	18.1	15.8	20.4
C6 (37/47) + = ASU 1-5	0.8	0.7	0.9	1
C7 (37/47) + = ASU 1-4	0.2	0.2	0.2	0.2
Groove pattern (38/48) + = ASU Y	24.8	28.2	21.4	19.5
Distal trigonid crest (38/48) + = ASU 1	17.1	17.1	17.1	21.0
Protostylid (38/48) + = ASU 1-7	4.5	5.1	4.0	6.9
MMPT (38/48) + = Weets (2009) [adpt.] 1-'3+'	23.0	21.1	24.9	30.3
Cusp number (38/48) + ~= ASU 4	53.7	53.8	53.5	56.7
C5 (38/48) + = ASU 1-5	49.0	50.0	48.0	53.3
C6 (38/48) + = ASU 1-5	11.2	12.4	10.0	14.4
C7 (38/48) + = ASU 1-4	0.6	0.6	0.6	1.3
Foramina mentales + = > 1	2.8	2.0	3.5	4.7
Mylohyoid bridge + = > 0	13.4	11.8	15.0	17.6

method and either of the other frequencies. This difference threshold level of 4.0% was established so as to filter large differences from the smaller ones, more likely to be caused by random variation.

Only two traits (included in the 16 traits mentioned) display a 4.0% difference between sides (LP4 lingual cusp number − tooth count (T): 58.0%, left side count (L): 53.0%, right side count (R): 63.0%, individual count (I): 64.3%; LM3 groove pattern − T: 24.8%, L: 28.2%, R: 21.4%, I: 19.5%), and only one of which (the lingual cusp number) displays such a difference between the tooth count and either unilateral count. Neither of these most different proportions among sides yielded a moderate or high Kendall's rank correlation coefficient (*tau*-b) between sides (see 4.2.Fluctuating asymmetry), which allows the likely supposition that the difference between count methods is small enough to detect statistically, on these and on every other trait.

The reason why the remaining differences above 4.0% are always found between the individual method and one of the others compared is indirectly stated above, and fairly evident: fluctuating asymmetry. The unilateral counts are very similar

and statistically correlated, and the tooth count is a mean of the former. Even so, the individual count method evinces the differences in fourteen other traits.

The maximum difference in UI2 interruption grooves (T: 12.7%, L: 12.9%, R: 12.5%, I: 17.3%) amounts to 4.8% and is consistently above 4.0%, but these values all correspond to low frequency samples (according to Scott and Turner, 1997), and should therefore be comparable. The canine distal accessory ridge (UC – T: 64.2%, L: 65.5%, R: 62.9%, I: 77.6%; LC – T: 35.3%, L: 37.0%, R: 33.6%, I: 41.1%) has maximum differences of 14.7% (upper canine) and 7.5% (lower canine), which keeps the UC in the high frequencies for the trait, independently of the method used, according to data provided by Irish (1998a); the lower canine has a lower difference, particularly when comparing the most used methods (tooth count and individual count: 5.8%). The UP4 accessory crests (T: 20.3%, L: 20.8%, R: 19.8%, I: 25.6%) have a 5.8% maximum difference which should be taken into account, but more data from different samples are needed to allow further comments. The LP3 lingual cusp number (T: 21.3%, L: 19.8%, R: 22.5%, I: 25.1%) displays a 5.3% maximum difference which can be sensitive, but does not seem to be sufficient to confuse any comparisons if included in a large battery of traits, when compared to data from Al Oumaoui (2009) and García Sívoli (2009). The LM1 deflecting wrinkle (T: 5.1%, L: 2.8%, R: 7.5%, I: 7.0%) has a relatively large difference of 4.9%, but only if a comparison with the left side only were to be used, since the difference between the main methods is merely 1.9%. The LM2 groove pattern (T: 72.9%, L: 74.5%, R: 71.2%, I: 79.8%) differs by 8.6% at most, and by 6.9% within tooth and individual counts; this is a relatively small overall margin, and maintains this trait near the low frequency Y-pattern populations. The maximum difference of 4.9% obtained for LM2 protostylid (T: 12.0%, L: 11.2%, R: 12.8%, I: 16.1%) is relatively large, but again most likely not enough to disrupt a statistical analysis comprising several traits. When LM2 cusp number (T: 17.8%, L: 19.3%, R: 16.2%, I: 21.4%) is considered, the largest difference amounts to 5.2%, but the divergence between total and individual count methods is merely 3.6%, a seemingly minimal margin. The same pattern is, naturally, evident for LM2 C5 as well (T: 16.9%, L: 18.1%, R: 15.8%, I: 20.4%). The 7.3% discrepancy between tooth and individual count method for LM3 MMPT (T: 23.0%, L: 21.1%, R: 24.9%, I: 30.3%) is relatively large, as is the largest difference (9.2%), but more data must be gathered before any conclusions are taken, since this trait is not part of the ASUDAS. The LM3 C5 (T: 49.0%, L: 50.0%, R: 48.0%, I: 53.3%) has a maximum difference of 5.3%, which seems reasonably small

when compared to the wide variability in geographically proximate samples (see Al Oumaoui [2009] and García Sívoli [2009]. A 3.2% difference between tooth and individual count methods seems to weaken the 4.4% maximum difference for LM3 C6 (T: 11.2%, L: 12.4%, R: 10.0%, I: 14.4%). The only oral nonmetric trait with a relatively large difference is mylohyoid bridge (T: 13.4%, L: 11.8%, R: 15.0%, I: 17.6%), with 5.8% difference between the left side and the individual count methods, and more importantly a 4.2% difference between the latter and the tooth count. This is a reasonably small difference and consistently places this sample as one of highest presences for this trait (when compared to Ossenberg, 1974; Hauser and De Stefano, 1989; Corruccini *et al.*, 1982; Hanihara and Ishida, 2001a; Turan-Ozedemir and Sendemir, 2006; Marado, 2010).

Scott (1980) finds the differences in frequencies for the Carabelli's trait when different count methods (tooth count: 33.4%, unilateral count: 32.5%, individual count: 37.4%) are used to be small, with a negligible bias. These 4.9% (between individual and unilateral count) and 4.0% (between individual and tooth count) differences are near or above most of the differences found for this sample's traits. The present author agrees these differences are small and provide a small bias, and therefore are a guarantee of reliable results when comparing samples, even if from populations of relatively similar biological backgrounds. The pattern of frequencies from a subset of these traits is the same, even if sharing slight deviations, and therefore is likely to produce a similar result when compared. The use of either tooth count or individual count methods is considered recommendable, despite the use of the individual count method being preferable, so as to value the "truest" expression of the genotype possible. The use of the unilateral count method, be it the "strict" version or the version compensating tooth loss with teeth from the other side (when available), seems to deviate further from the genotype's expressed potential.

4.7.2.Biological relations between count methods

Forty seven of the 59 traits considered in the count method differentiation analysis have sufficient variability to perform a PCA (see Table 4.7.2.). This analysis was able to capture 99.8% of the variance among the results for each count method and side included (see Figure 4.7.1.). PC1 (62.9% variance) displays a clear separation

between the tooth/side count, left and right side count, and the individual count method results. The traits with strongest loadings are those on which the individual count

Table 4.7.2. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing differences between each count method applied to the Coimbra sample.

Trait (tooth)	PC 1	PC 2
Winging (11/21)	0.050	**-0.998**
Shoveling (11/21)	-0.189	**-0.981**
Double Shoveling (11/21)	-0.045	**<u>0.953</u>**
Interruption Grooves (11/21)	**<u>0.992</u>**	-0.099
Interruption Grooves (12/22)	**<u>0.993</u>**	0.120
Peg Incisor (12/22)	0.340	**-0.940**
Distal Accessory Ridge (13/23)	**<u>0.979</u>**	0.205
Accessory Cusps (14/24)	0.332	**<u>0.943</u>**
Accessory Crests (14/24)	**<u>0.988</u>**	0.157
Accessory Cusps (15/25)	**<u>0.829</u>**	**-0.558**
Accessory Crests (15/25)	**<u>0.980</u>**	0.201
Carabelli's trait (16/26)	**<u>0.989</u>**	0.147
C5 (16/26)	0.385	**<u>0.923</u>**
Mesial Marginal Accessory Tubercles (16/26)	**<u>0.613</u>**	**-0.790**
Enamel Extensions (16/26)	**<u>0.962</u>**	-0.267
Hypocone (17/27)	**<u>0.943</u>**	-0.332
Enamel Extensions (17/27)	**<u>0.909</u>**	-0.416
Enamel Extensions (18/28)	**<u>0.779</u>**	**<u>0.626</u>**
Parastyle (18/28)	**<u>0.721</u>**	**<u>0.693</u>**
Distal Accessory Ridge (33/43)	**<u>0.879</u>**	0.476
Lingual Cusp Variation (34/44)	**<u>0.894</u>**	-0.447
Lingual Cusp Variation (35/45)	**<u>0.649</u>**	**-0.760**
Deflecting Wrinkle (36/46)	0.481	**-0.876**
Anterior Fovea (36/46)	0.331	**-0.943**
Groove Pattern (36/46)	**-0.717**	**<u>0.697</u>**
Distal Trigonid Crest (36/46)	**<u>0.564</u>**	**-0.826**
Protostylid (36/46)	**<u>0.999</u>**	0.001
MMPT (36/46)	**<u>0.795</u>**	**<u>0.606</u>**
Cusp Number (36/46)	**-0.811**	**-0.585**
C5 (36/46)	**<u>0.679</u>**	**<u>0.734</u>**
C6 (36/46)	0.102	**<u>0.994</u>**
C7 (36/46)	**<u>0.982</u>**	0.189
Groove Pattern (37/47)	**<u>0.913</u>**	0.408
Distal Trigonid Crest (37/47)	**<u>0.850</u>**	**-0.526**
Protostylid (37/47)	**<u>0.967</u>**	-0.256
MMPT (37/47)	**<u>0.894</u>**	0.446
Cusp Number (37/47)	**<u>0.791</u>**	**<u>0.611</u>**
C5 (37/47)	**<u>0.854</u>**	**<u>0.519</u>**
C6 (37/47)	**<u>0.805</u>**	**-0.593**
Groove Pattern (38/48)	**-0.726**	**<u>0.688</u>**
Protostylid (38/48)	**<u>0.916</u>**	0.400
MMPT (38/48)	**<u>0.939</u>**	-0.345
Cusp Number (38/48)	**<u>0.991</u>**	0.130
C5 (38/48)	**<u>0.916</u>**	0.401
C6 (38/48)	**<u>0.826</u>**	**<u>0.563</u>**
Foramina Mentales	**<u>0.870</u>**	-0.492
Mylohyoid Bridge	**<u>0.874</u>**	-0.485
Eigenvalue	29.542	17.338
Variance	62.9%	36.9%
Total variance	62.9%	99.8%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

method registered a higher frequency than the other counts employed. PC2 (36.9% of the variation) places tooth/side count and individual count in the middle of the distribution, and left and right side counts on either side. Accordingly, the stronger the loading of a trait, the wider apart are the frequencies for each side and the more average are the frequencies for the tooth/side and the individuals counts.

This, despite the PCA's statistical amplification of the difference between samples, places the individual count and the tooth count methods as the most similar, and underlines their preference. The fact the individual count method is the most disparate (Figure 4.7.1.) merely testifies to its consideration of the highest trait expression, which clearly separates it from the "diluted" tooth/side and, particularly, left or right single side count.
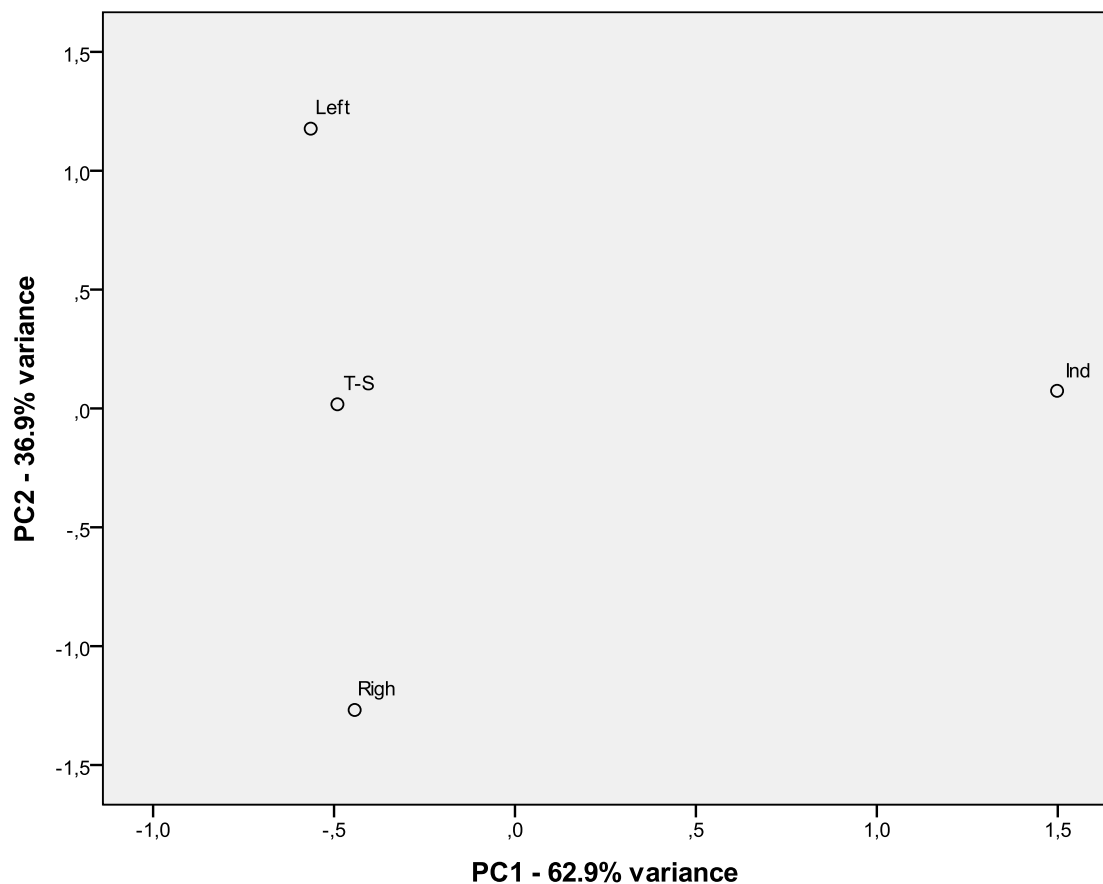
Figure 4.7.1. Scatterplot of the two components among the left and right sides, individual (Ind), and tooth/mandibular side count (T-S) methods. A total of 99.8% of the variation is represented.

4.8.Intrasample biological relations

4.8.1.Sample heterogeneity

The large sample analyzed in this text, composed of 600 individuals, is divisible in more categories than sex. As described above (see 2.Sample), the individuals from this Portuguese sample were born between the early 19th and the early to mid-20th centuries; the sample comprises individuals from several districts (almost all Portuguese continental districts are represented) and regions of the country; and it has individuals with several degrees of dental morphology fluctuating asymmetry.

Dental morphology has demonstrated biological differences between cemeteries of different grave goods in predynastic Egypt, which suggests inbreeding and biological separation between a ruling or royal class and the general population. Although different temporal periods might justify this, such biological distance as attained in a short period of time is unlikely (Johnson and Lovell, 1994). In Portugal, biological differences that derive from different social strata are not expected, and this example deems different chronologies as unlikely to produce biological variation.

However, cranial morphological traits vary, in male skulls from the Coimbra collections, throughout the 19th century (when analyzed in generations twenty years apart), in accordance with the variation of the price of wheat, which is interpreted as an environmental factor impacting cranial nonmetric traits. The same cause could not be identified in the female variation (Bocquet-Appel, 1984).

There are also secular trends in tooth crown size (Scott and Potter, 1984). Although typically the secular trend is for teeth to decrease in size, there are examples otherwise. In coastal Peru, tooth crowns were continuously enhanced between 10000BP and 1000 BP. This could be related to genetic processes, such as gene flow, inbreeding or natural selection, or unknown environmental factors (Scott, 1979b). A positive trend in dental dimensions was found for South African blacks, which teeth presented greater mesiodistal and buccolingual diameters in a later sample. Genetic drift is suggested as the most likely cause of this effect (Kieser and Cameron, 1987).

These same genetic processes could potentially affect dental nonmetric trait frequencies. This seems to be, however, unlikely, since despite showing differences in some other morphologic and anthropometric variables, the tooth morphology of five widespread Jewish populations (four modern and one skeletal, from 3000 BP) showed biological proximity between three of the modern samples and the skeletal samples.

Five other populations, much less widespread, were shown to be biologically more diverse than the Jewish groups. This demonstrates the capacity of dental morphology in evaluating biological affinities even when selective pressures and population history create difficulties, resulting in the uselessness of other resources (Sofaer *et al.*, 1986). In light of the Portuguese sample's characteristics (drawn from a very large and biologically diverse population), processes leading to genetic differentiation, typical in population genetics, are not likely.

Despite the likeliness that the aforementioned divisions within the Portuguese sample will not reflect clear biological distinctions, that hypothesis will be tested. The "expression count method", suggested by Turner (1985; and described in the previous chapter, 4.7.Count method), will be used. This count method values the grade of expression of each trait (as long as it is divided in a quasicontinuous expression and graded as such through the plaques or the descriptions in ASUDAS), and the frequency of each grade. That is accomplished by attributing a different and crescent weight to each grade. So for example, suppose UI1 shoveling frequency is 100%, but its presence is distributed along 6 positive grades. Each one of those grades is attributed a proportional weight. That is determined by (1) dividing the total proportion by the number of positive grades (1/6 = 0.167), and (2) multiplying the result by the grade number (e.g., Grade 4: 0.167*4 = 0.667); then, (3) the percentage of individuals in the sample for each grade is multiplied by the weighting factor (e.g., Grade 4: 0.667*20% = 13.3%). The sample's frequency is the sum of all weighted grade frequencies (Turner, 1985). This allows for the comparison of smaller and very similar samples, and was thus the most appropriate method for the ensuing comparisons.

4.8.2.Biological relations between "generations"

As seen in chapter 4.2.Fluctuating asymmetry, the individuals in the Portuguese sample were divided into four groups according to their year of birth. These groups were called "generations". The intervals of time that comprise each generation have a maximum of 28 years, according to Fenner's (2005) overall human generation interval.

The following comparison intends to understand the biological relations between Portuguese groups along time, a secular trend through a short time span of just over one century (the individuals were born between 1820 and 1924).

The sample was divided into four "generations": G1 (1820-1847), G2 (1848-1875), G3 (1876-1903) and G4 (1904-1924). The expression count method trait frequencies were calculated for each generation, and are patent on Table 4.8.1. They were then compared using a PCA (principal components analysis), to infer their biological relatedness. Only 36 traits were used, since the remaining traits presented too little variation to be included.

Table 4.8.2. presents the *eigenvalues* and variances for each of the three principal components (PC's) obtained from the PCA, as well as the loadings of each trait onto every component.

The three PC's comprise the complete variation found between the samples (see Table 4.8.2.). The first component (PC1; 69.6% variance) is characterized by strong positive loadings (> 0.5) from 25 traits and strong negative loadings (< -0.5) from eight other traits. PC2 (22.6% variance) comprises strong positive loadings from nine traits and strong negative loadings from seven traits. Finally, PC3 (7.5% variance) is the product of generally weak loadings, with the strong positive loading of LM1 cusp number on as the exception.

These components are graphically expressed in Figures 4.8.1. and 4.8.2. Figure 4.8.1. presents the first two components (92.5% variance). G2 and G3 are the generations closest to each other along the horizontal axis. G4 is also relatively close. G1 and G4 are very close to each other on the vertical axis. G2 and G3 are also relatively close to one another along the same component (PC2).

Figure 4.8.2. introduces PC3, which separates G3 from the other samples, with G1, G2 and G4 closer together along the z axis. Overall, G2 and G3 are the closest samples. G3 and G4 are relatively close, as are G2 and G4. The most distant "generation" is G1, only relatively close to G4 along the y and z axes.

As has been noted and tested before (see 4.2.Fluctuating asymmetry) the "generations" have significantly different mean ages at death, since when the "generation" numbers advance, the ages at death of the individuals included diminish. This suggests the root of the differences found between these samples may be derived from wear rate differences, at least partly. This is difficult to interpret, since some relatively strong negative correlations were found between wear level and grade frequencies in traits unrelated to the occlusal surface (like enamel extensions; see 4.6.Dental wear).

Table 4.8.1. Trait frequencies for each "generation".

Trait		G1	G2	G3	G4	Trait		G1	G2	G3	G4
		\	Generations		\			\	Generations		\
Distal Accessory Ridge (13/23)	%	15,0%	15,2%	24,4%	35,1%	Groove Pattern (36/46)	%	77.8%	87.5%	88.9%	92.3%
	n	8	66	227	167		n	9	56	190	168
Distal Accessory Ridge (33/43)	%	8.0%	9.9%	13.3%	13.0%	Distal Trigonid Crest (36/46)	%	0.0%	1.8%	1.6%	4.1%
	n	10	79	241	179		n	7	56	189	170
Winging (11/21)	%	12.5%	3.9%	2.6%	4.0%	Protostylid (36/46)	%	1.8%	3.7%	3.1%	2.6%
	n	8	57	185	132		n	8	54	195	169
Shoveling (11/21)	%	0.0%	1.9%	2.1%	3.9%	Cusp Number (36/46)	%	14.3%	5.6%	10.2%	8.3%
	n	4	26	129	103		n	7	54	192	168
Midline Diastema (11/21)	%	0.0%	32.3%	9.2%	4.1%	C7 (36/46)	%	0.0%	3.9%	5.6%	2.7%
	n	3	31	109	73		n	8	56	194	171
Interruption Grooves (12/22)	%	28.6%	19.3%	12.2%	22.7%	Groove Pattern (37/47)	%	70.0%	78.1%	81.9%	78.0%
	n	7	57	213	172		n	10	64	221	182
Accessory Crests (14/24)	%	0.0%	0.0%	2.8%	10.2%	Distal Trigonid Crest (37/47)	%	0.0%	0.0%	1.8%	8.7%
	n	7	53	215	176		n	9	63	223	183
Accessory Cusps (15/25)	%	0.0%	0.0%	2.3%	5.6%	Protostylid (37/47)	%	0.0%	2.2%	4.7%	3.7%
	n	7	63	216	177		n	10	65	230	182
Accessory Crests (15/25)	%	22.2%	3.3%	23.0%	36.3%	C5 (37/47)	%	0.0%	6.9%	12.3%	10.4%
	n	9	61	217	179		n	9	64	232	183
Carabelli's trait (16/26)	%	5.7%	9.7%	15.3%	18.7%	Groove Pattern (38/48)	%	12.5%	21.7%	20.0%	17.6%
	n	10	59	226	183		n	8	46	195	119
C5 (16/26)	%	0.0%	0.7%	2.6%	3.1%	Distal Trigonid Crest (38/48)	%	0.0%	17.8%	18.1%	28.5%
	n	11	56	227	182		n	8	45	199	123
Mesial Marginal Accessory Tubercles (16/26)	%	0.0%	0.0%	1.9%	9.4%	C5 (38/48)	%	28.6%	33.2%	46.3%	47.2%
	n	10	57	208	181		n	7	47	197	116
Hypocone (17/27)	%	31.5%	43.7%	49.2%	56.0%	C6 (38/48)	%	0.0%	4.3%	8.7%	8.3%
	n	9	66	264	188		n	7	47	197	116
Enamel Extensions (18/28)	%	0.0%	2.5%	3.3%	8.5%	C7 (38/48)	%	2.9%	0.0%	1.2%	0.0%
	n	1	27	133	59		n	7	46	203	119
Lingual Cusp Variation (34/44)	%	6.7%	9.5%	10.7%	10.5%	*Foramina Mentales*	%	0.0%	6.3%	4.1%	5.2%
	n	10	83	253	177		n	13	96	294	194
Lingual Cusp Variation (35/45)	%	25.9%	21.6%	19.1%	23.2%	Mylohyoid Bridge	%	23.1%	19.3%	16.0%	9.0%
	n	9	77	247	166		n	13	96	291	188
Deflecting Wrinkle (36/46)	%	0.0%	1.6%	3.4%	5.0%	Mandibular *Torus*	%	20.5%	10.5%	7.6%	4.1%
	n	5	43	166	167		n	13	95	294	194
Anterior Fovea (36/46)	%	0.0%	4.2%	6.2%	12.3%	Maxillary *Torus*	%	23.1%	23.9%	22.9%	18.4%
	n	6	53	186	169		n	13	94	292	194

This confounding factor should be taken into account nonetheless. Its consideration probably implies that G1, the most distant "generation", should be dismissed from analysis, since conclusions should not be drawn on the oldest aged, and

Table 4.8.2. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing the four Portuguese sample "generations".

Trait (tooth)	PC 1	PC 2	PC 3
Distal Accessory Ridge (13/23)	**0.940**	0.002	0.340
Distal Accessory Ridge (33/43)	**0.855**	**0.515**	0.060
Winging (11/21)	**-0.875**	0.482	-0.033
Shoveling (11/21)	**0.966**	0.121	-0.226
Midline Diastema (11/21)	0.098	**-0.869**	-0.484
Interruption Grooves (12/22)	**-0.595**	**0.646**	-0.478
Accessory Crests (14/24)	**0.796**	**0.594**	-0.114
Accessory Cusps (15/25)	**0.839**	**0.544**	0.014
Accessory Crests (15/25)	0.416	**0.862**	0.289
Carabelli's trait (16/26)	**0.975**	0.189	0.121
C5 (16/26)	**0.944**	0.204	0.260
Mesial Marginal Accessory Tubercles (16/26)	**0.767**	**0.616**	-0.181
Hypocone (17/27)	**0.999**	0.033	-0.034
Enamel Extensions (18/28)	**0.906**	0.355	-0.232
Lingual Cusp Variation (34/44)	**0.954**	-0.276	0.116
Lingual Cusp Variation (35/45)	**-0.615**	**0.673**	-0.410
Deflecting Wrinkle (36/46)	**0.977**	0.206	0.055
Anterior Fovea (36/46)	**0.952**	0.267	-0.147
Groove Pattern (36/46)	**0.984**	-0.137	-0.116
Distal Trigonid Crest (36/46)	**0.910**	0.227	-0.347
Protostylid (36/46)	0.477	**-0.853**	-0.212
Cusp Number (36/46)	**-0.616**	**0.563**	**0.551**
C7 (36/46)	**0.674**	**-0.663**	0.325
Groove Pattern (37/47)	**0.826**	**-0.501**	0.257
Distal Trigonid Crest (37/47)	**0.769**	**0.615**	-0.177
Protostylid (37/47)	**0.909**	-0.211	0.359
C5 (37/47)	**0.933**	-0.246	0.264
Groove Pattern (38/48)	**0.612**	**-0.781**	-0.127
Distal Trigonid Crest (38/48)	**0.973**	-0.047	-0.225
C5 (38/48)	**0.932**	0.140	0.334
C6 (38/48)	**0.962**	-0.101	0.253
C7 (38/48)	**-0.804**	0.327	0.498
Foramina Mentales	**0.760**	**-0.510**	-0.403
Mylohyoid Bridge	**-0.941**	-0.327	0.091
Mandibular *Torus*	**-0.994**	0.092	0.050
Maxillary *Torus*	**-0.657**	**-0.728**	0.194
Eigenvalue	25.058	8.248	2.693
Variance	69.6%	22.6%	7.5%
Total variance	69.6%	92.5%	100.0%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

more worn, sample. However, this mean age difference is of increasingly lesser magnitude. That should result in smaller differences between G2 and G3, and G3 and G4. The fact the latter "generation", G4, is the most different of the most recent three may be an indication of some unforeseen biological phenomenon. In general, the
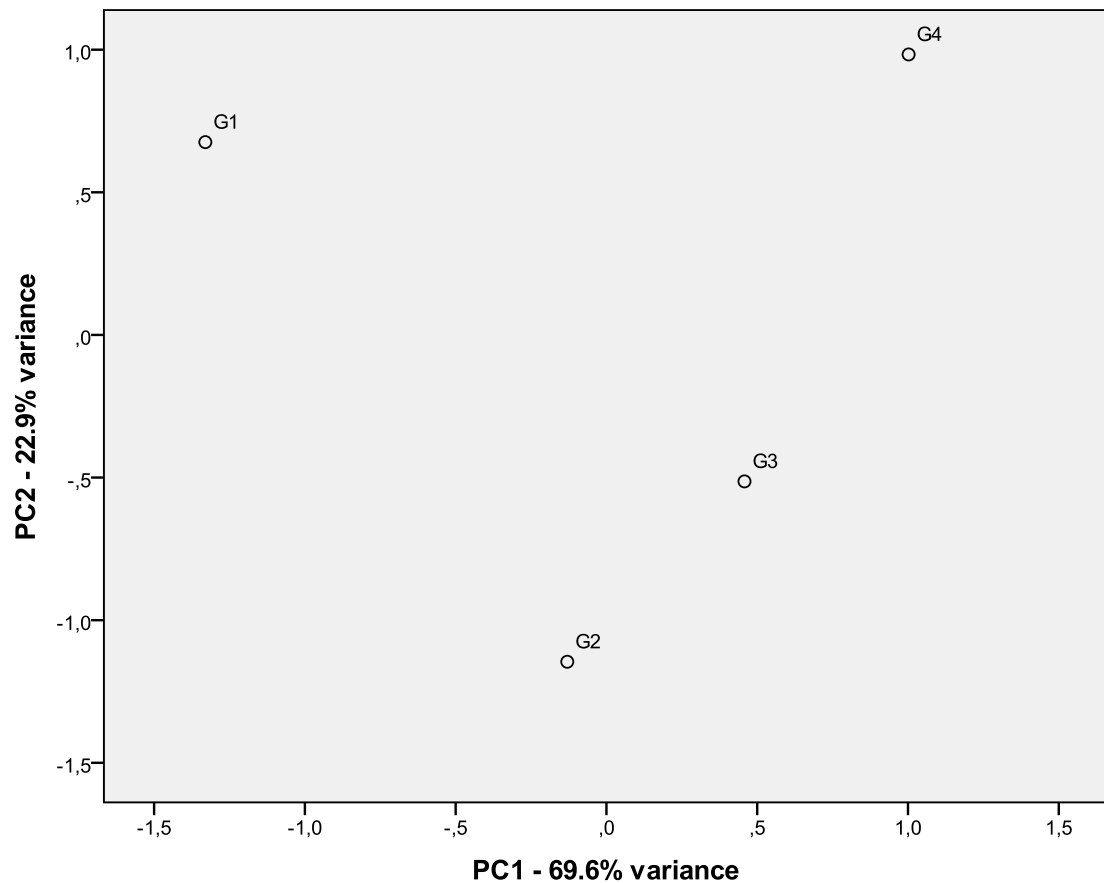
Figure 4.8.1. Scatterplot of the two first components among "generations". A total of 92.5% of the variation is represented.
G1: Generation 1; G2: Generation 2: G3: Generation 3; G4: Generation 4.

relative overall closeness and distance between the four "generations" indicate the variation is small, and these individuals were most likely biologically similar, whatever their year of birth.

Khudarverdyan (2011) used some dental nonmetric traits to test the effect of selection on teeth. The author concluded there is biological continuity between Bronze Age and contemporary Armenians, and the changes verified in the trait frequencies reflect the preeminence of stabilizing selection, since no evolutionary or outside genetic influences are detected. The present sample is much more chronologically constrained, and no such conclusions are easily approached. Although the proximity between the latter three "generations" suggests a lack of evolutionary or exterior influences in the biological variation of the Portuguese during the period between early 19th and early to mid-20th century.
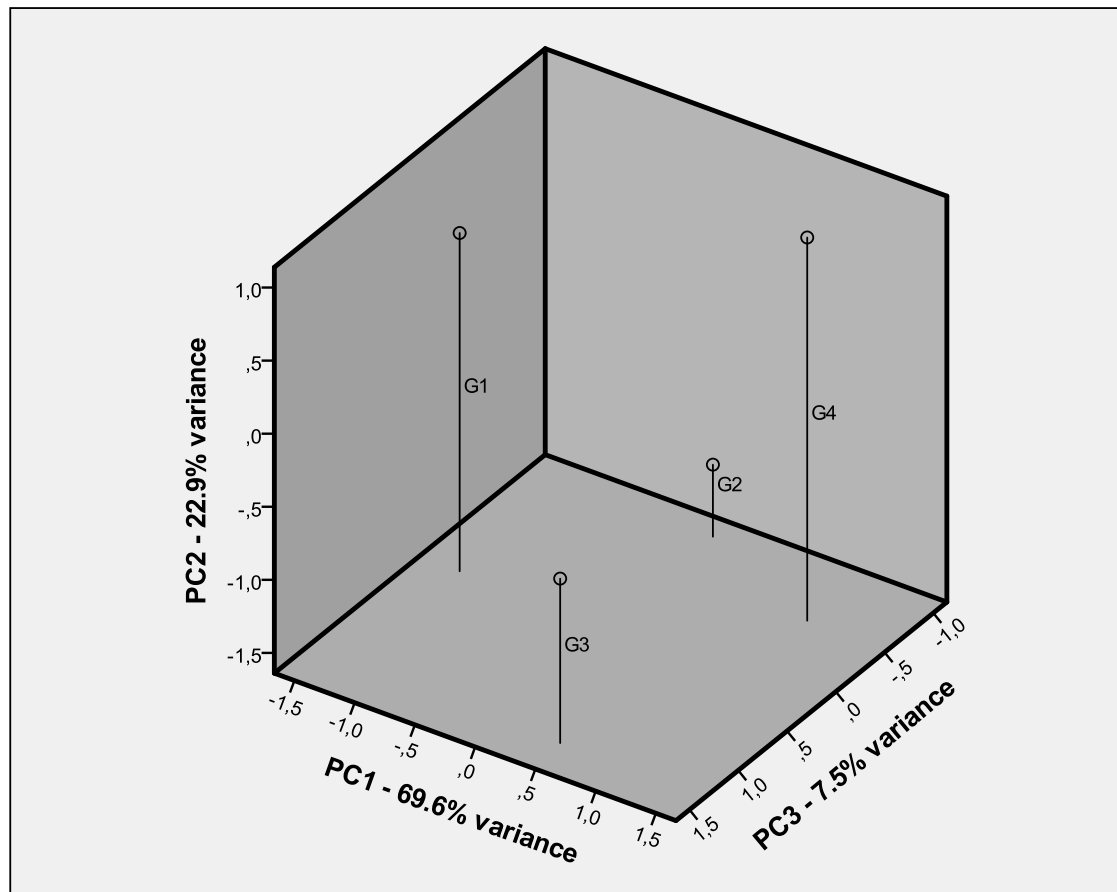
Figure 4.8.2. Scatterplot of the three components among "generations". The total 100% of the variation is represented.
G1: Generation 1; G2: Generation 2: G3: Generation 3; G4: Generation 4.

4.8.3.Biological relations between districts

The Portuguese sample analyzed contains individuals from overseas, from the Madeira archipelago, and from 16 districts in Portugal. The estimation of the biological relation between the groups born in different administrative areas of continental Portugal is interesting. It can demonstrate an overlap of biological diversity or biological distinctions among the Portuguese districts, which could be the result of historical migration patterns. Unfortunately, most districts are represented by very small samples (see Table 2.4., on 2.Sample). Therefore, only nine districts were included in the following analysis.

The comparison of these nine districts (Aveiro, Castelo Branco, Coimbra, Guarda, Leiria, Lisboa, Porto, Vila Real and Viseu), with samples between nine (Castelo Branco) and 402 individuals (Coimbra), was accomplished through a PCA. This statistical test compared frequencies obtained through the expression count method

(see above) for all traits whose frequencies varied among the samples, as shown on Table 4.8.3.

Table 4.8.3. Trait frequencies for each district.

Trait		Districts								
		Aveiro	Castelo Branco	Coimbra	Guarda	Leiria	Lisboa	Porto	Vila Real	Viseu
Winging (11/21)	%	2.3%	0.0%	3.9%	0.0%	6.5%	7.1%	0.0%	3.1%	1.7%
	n	11	5	265	22	23	7	5	8	15
Shoveling (11/21)	%	2.8%	0.0%	2.5%	3.3%	3.3%	4.2%	0.0%	0.0%	6.7%
	n	6	2	183	15	20	4	3	3	10
Interruption grooves (11/21)	%	0.0%	0.0%	4.5%	13.6%	8.7%	33.3%	20.0%	0.0%	0.0%
	n	8	4	246	22	23	6	5	7	14
Interruption grooves (12/22)	%	0.0%	16.7%	19.1%	10.7%	13.8%	0.0%	0.0%	22.2%	21.7%
	n	13	6	304	28	29	6	6	9	23
Peg incisors (12/22)	%	3.3%	8.3%	2.1%	1.6%	4.7%	0.0%	0.0%	5.0%	2.2%
	n	15	6	331	31	32	7	8	10	23
Distal accessory ridge (13/23)	%	20.0%	28.6%	28.0%	18.3%	32.3%	15.0%	22.2%	31.4%	22.6%
	n	14	7	319	24	26	8	9	7	23
Accessory cusps (15/25)	%	10.0%	0.0%	3.2%	7.1%	3.2%	0.0%	10.0%	0.0%	0.0%
	n	10	6	317	28	31	7	10	7	21
Accessory crests (15/25)	%	9.1%	16.7%	27.1%	11.5%	35.5%	28.6%	40.0%	0.0%	18.2%
	n	11	6	317	26	31	7	10	7	22
Tricuspid premolars (15/25)	%	0.0%	0.0%	0.3%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
	n	12	6	335	30	31	8	10	8	23
Odontome (15/25)	%	0.0%	0.0%	0.0%	3.3%	0.0%	0.0%	0.0%	0.0%	0.0%
	n	10	6	330	30	31	8	10	8	23
Carabelli's trait (16/26)	%	10.2%	5.7%	17.1%	13.8%	14.8%	10.2%	6.5%	16.1%	16.8%
	n	14	5	324	27	30	7	11	8	23
Enamel extensions (16/26)	%	2.8%	0.0%	2.8%	10.0%	0.0%	0.0%	0.0%	0.0%	5.6%
	n	12	5	237	20	24	3	7	6	18
Hypocone (17/27)	%	42.2%	43.7%	50.1%	54.3%	64.3%	35.0%	40.0%	50.0%	54.5%
	n	15	8	353	31	35	10	10	8	26
Enamel extensions (17/27)	%	21.2%	12.5%	14.8%	15.3%	15.1%	14.3%	12.5%	28.6%	13.3%
	n	11	8	277	24	31	7	8	7	20
Enamel extensions (18/28)	%	6.7%	0.0%	3.7%	9.5%	5.0%	13.3%	0.0%	0.0%	12.1%
	n	5	3	144	14	20	5	4	5	11
Distal accessory ridge (33/43)	%	7.7%	13.3%	12.7%	11.0%	16.8%	11.1%	5.7%	6.0%	14.5%
	n	13	9	347	29	31	9	7	10	22
Lingual cusp number (34/44)	%	5.1%	0.0%	11.0%	15.3%	10.1%	9.7%	0.0%	6.7%	4.3%
	n	13	6	354	32	33	8	8	10	26
Lingual cusp number (35/45)	%	20.6%	29.2%	20.4%	19.3%	20.4%	13.9%	36.1%	19.7%	20.4%
	n	14	8	340	30	30	4	8	9	25
Deflecting wrinkle (36/46)	%	5.6%	0.0%	4.3%	0.0%	2.8%	5.6%	0.0%	0.0%	0.0%
	n	12	4	257	21	24	6	6	6	19
Anterior fovea (36/46)	%	11.5%	0.0%	9.3%	6.0%	3.4%	3.6%	12.5%	0.0%	2.5%
	n	13	4	278	21	29	7	8	6	20
Groove pattern (36/46)	%	92.3%	75.0%	90.5%	81.8%	82.1%	85.7%	87.5%	100.0%	85.7%
	n	13	4	284	22	28	7	8	6	21
Protostylid (36/46)	%	2.4%	0.0%	3.0%	3.7%	3.1%	4.1%	3.6%	2.0%	1.4%
	n	12	4	287	23	28	7	8	7	21
C5 (36/46)	%	58.3%	75.0%	74.7%	75.5%	71.1%	71.4%	72.5%	71.4%	76.2%
	n	12	4	284	22	27	7	8	7	21
C7 (36/46)	%	1.5%	15.0%	4.1%	3.5%	3.4%	0.0%	10.0%	0.0%	4.8%
	n	13	4	289	23	29	7	8	6	21

Table 4.8.3. (Continued.)

Trait		Districts								
		Aveiro	Castelo Branco	Coimbra	Guarda	Leiria	Lisboa	Porto	Vila Real	Viseu
Groove pattern (37/47)	%	78.6%	80.0%	78.5%	83.3%	80.0%	71.4%	100.0%	62.5%	83.3%
	n	14	5	325	24	30	7	10	8	24
Distal trigonid crest (37/47)	%	0.0%	20.0%	4.0%	8.3%	3.4%	14.3%	0.0%	0.0%	0.0%
	n	14	5	327	24	29	7	10	8	24
Protostylid (37/47)	%	2.2%	8.6%	3.8%	6.2%	3.8%	6.1%	0.0%	0.0%	6.3%
	n	13	5	334	23	30	7	10	9	25
C5 (37/47)	%	4.6%	0.0%	14.3%	19.2%	12.7%	0.0%	4.0%	8.9%	9.6%
	n	13	4	336	25	30	7	10	9	25
Groove pattern (38/48)	%	14.3%	60.0%	18.1%	20.8%	25.0%	12.5%	0.0%	33.3%	17.6%
	n	7	5	254	24	20	8	7	6	17
Distal trigonid crest (38/48)	%	14.3%	20.0%	22.1%	25.0%	26.3%	33.3%	14.3%	0.0%	11.8%
	n	7	5	262	24	19	9	7	7	17
Protostylid (38/48)	%	0.0%	2.9%	1.8%	0.7%	0.0%	1.6%	0.0%	16.3%	0.0%
	n	7	5	236	22	18	9	7	7	15
MMPT (38/48)	%	8.2%	17.1%	11.1%	9.9%	15.9%	19.1%	10.2%	4.1%	20.5%
	n	7	5	241	23	18	9	7	7	16
C5 (38/48)	%	40.0%	72.0%	46.4%	37.4%	37.9%	11.1%	22.9%	25.7%	58.7%
	n	7	5	257	23	19	9	7	7	15
C6 (38/48)	%	11.4%	0.0%	8.7%	3.5%	2.1%	4.4%	0.0%	0.0%	12.0%
	n	7	5	257	23	19	9	7	7	15
Foramina mentales	%	6.3%	0.0%	4.5%	2.8%	10.8%	0.0%	9.1%	0.0%	3.4%
	n	16	9	402	36	37	10	11	10	29
Mylohyoid bridge	%	9.4%	33.3%	16.3%	7.1%	2.8%	15.0%	0.0%	10.0%	16.1%
	n	16	9	396	35	36	10	11	10	28
Mandibular *torus*	%	8.3%	7.4%	6.9%	4.6%	11.7%	0.0%	9.1%	6.7%	4.6%
	n	16	9	402	36	37	10	11	10	29
Maxillary *torus*	%	23.4%	25.0%	21.1%	21.5%	24.3%	22.2%	18.2%	20.0%	22.4%
	n	16	9	400	36	37	9	11	10	29

The results obtained are expressed in Table 4.8.4. and Figures 4.8.3., 4.8.4. and 4.8.5. Table 4.8.4. exposes the *eigenvalues*, the proportions of variance, the trait loadings and the total variance expressed through the six further analyzed PC's obtained.

PC1 (22.7% variance) is determined by strong positive loadings (> 0.5) from the UC distal accessory ridge, UI2 peg incisors, LM1 C5, LM2 distal trigonid crest and protostylid, LM3 groove pattern, MMPT and C5, mylohyoid bridge and maxillary *torus*. It presents strong negative loadings (< -0.5) for UP4 accessory cusps and LM1 groove pattern.

PC2 (21.2% variance) expresses strong positive loadings from UI1 shoveling and interruption grooves, UP4 accessory crests, UM3 enamel extensions, LM3 distal trigonid crest and MMPT; and strong negative loadings from LC distal accessory ridge, UI2 interruption grooves and peg incisors, UM2 enamel extensions, and LM3 groove pattern and protostylid were also expressed.

Table 4.8.4. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing nine Portuguese districts.

Trait (tooth)	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Distal Accessory Ridge (13/23)	**0.739**	0.324	0.131	0.448	0.262	0.241
Distal Accessory Ridge (33/43)	-0.066	**-0.721**	0.095	0.331	**0.591**	0.031
Winging (11/21)	-0.004	0.371	0.489	-0.247	**0.549**	0.489
Shoveling (11/21)	0.233	**0.688**	0.453	0.298	0.022	-0.218
Interruption Grooves (11/21)	-0.197	**0.710**	-0.197	-0.488	-0.161	0.374
Interruption Grooves (12/22)	0.477	**-0.515**	0.438	0.374	-0.236	0.175
Peg Incisor (12/22)	**0.558**	**-0.735**	-0.027	0.066	0.329	-0.003
Accessory Cusps (15/25)	**-0.696**	0.156	-0.414	0.296	0.060	-0.302
Accessory Crests (15/25)	-0.086	**0.531**	**-0.548**	0.153	0.181	**0.523**
Carabelli's trait (16/26)	-0.036	0.017	**0.838**	0.445	-0.118	0.161
Enamel Extensions (16/26)	0.076	0.316	0.287	0.481	**-0.527**	-0.439
Hypocone (17/27)	0.189	-0.134	0.383	**0.799**	0.028	0.350
Enamel Extensions (17/27)	-0.420	**-0.599**	**0.603**	-0.234	0.094	-0.077
Enamel Extensions (18/28)	0.184	**0.803**	0.430	-0.027	-0.062	-0.256
Lingual Cusp Variation (34/44)	-0.025	0.433	**0.658**	0.174	-0.112	0.221
Lingual Cusp Variation (35/45)	-0.158	-0.358	**-0.884**	0.162	-0.157	0.029
Deflecting Wrinkle (36/46)	-0.187	0.480	0.246	-0.272	**0.688**	-0.141
Anterior Fovea (36/46)	-0.709	0.331	-0.370	0.222	0.111	-0.287
Groove Pattern (36/46)	**-0.713**	-0.318	**0.523**	-0.175	0.003	-0.073
C5 (36/46)	**0.505**	0.053	-0.064	0.163	**-0.675**	0.442
C7 (36/46)	0.422	-0.268	**-0.838**	0.138	-0.128	-0.035
Groove Pattern (37/47)	-0.201	0.294	**-0.787**	0.449	-0.199	-0.064
Distal Trigonid Crest (37/47)	**0.741**	0.132	-0.263	-0.474	-0.008	0.058
Protostylid (37/47)	**0.910**	0.339	-0.036	-0.005	-0.071	-0.179
C5 (37/47)	-0.112	0.075	0.462	**0.711**	-0.319	0.166
Groove Pattern (38/48)	**0.749**	**-0.607**	0.001	-0.103	0.092	0.019
Distal Trigonid Crest (38/48)	0.340	**0.780**	-0.142	-0.084	0.206	0.233
Protostylid (38/48)	-0.120	**-0.730**	0.456	-0.393	-0.206	0.217
MMPT (38/48)	**0.693**	**0.541**	-0.163	0.008	0.117	0.076
C5 (38/48)	**0.683**	-0.331	-0.178	0.475	0.060	-0.373
C6 (38/48)	-0.026	0.386	0.373	0.317	0.213	**-0.654**
Foramina Mentales	-0.471	0.189	-0.338	**0.634**	0.392	0.244
Mylohyoid Bridge	**0.815**	-0.228	-0.065	-0.295	0.030	-0.310
Mandibular *Torus*	-0.239	-0.480	-0.341	**0.593**	0.431	0.222
Maxillary *Torus*	**0.720**	0.038	0.067	0.108	**0.599**	-0.174
Eigenvalue	7.962	7.410	6.614	4.615	3.248	2.624
Variance	22.7%	21.2%	18.9%	13.2%	9.3%	7.5%
Total variance	22.7%	43.9%	62.8%	76.0%	85.3%	92.7%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The distribution along PC3 (18.9% variance) was influenced by strong positive loadings from UM1 Carabelli's trait, UM2 enamel extensions, LP3 lingual cusp variation and LM1 groove pattern; and by strong negative loadings from UP4 accessory crests, LP4 lingual cusp variation, LM1 C5 and LM2 groove pattern.

PC4 (13.2% variance) results from the strong positive loadings of UM2 hypocone, LM2 C5, *foramina mentales* and mandibular *torus*.

The traits that contribute strong loadings to PC5 (9.3% variance) are LC distal accessory ridge, UI1 winging, LM1 deflecting wrinkle, and maxillary *torus*, with positive loadings; and UM1 enamel extensions and LM1 C5, with negative loadings.
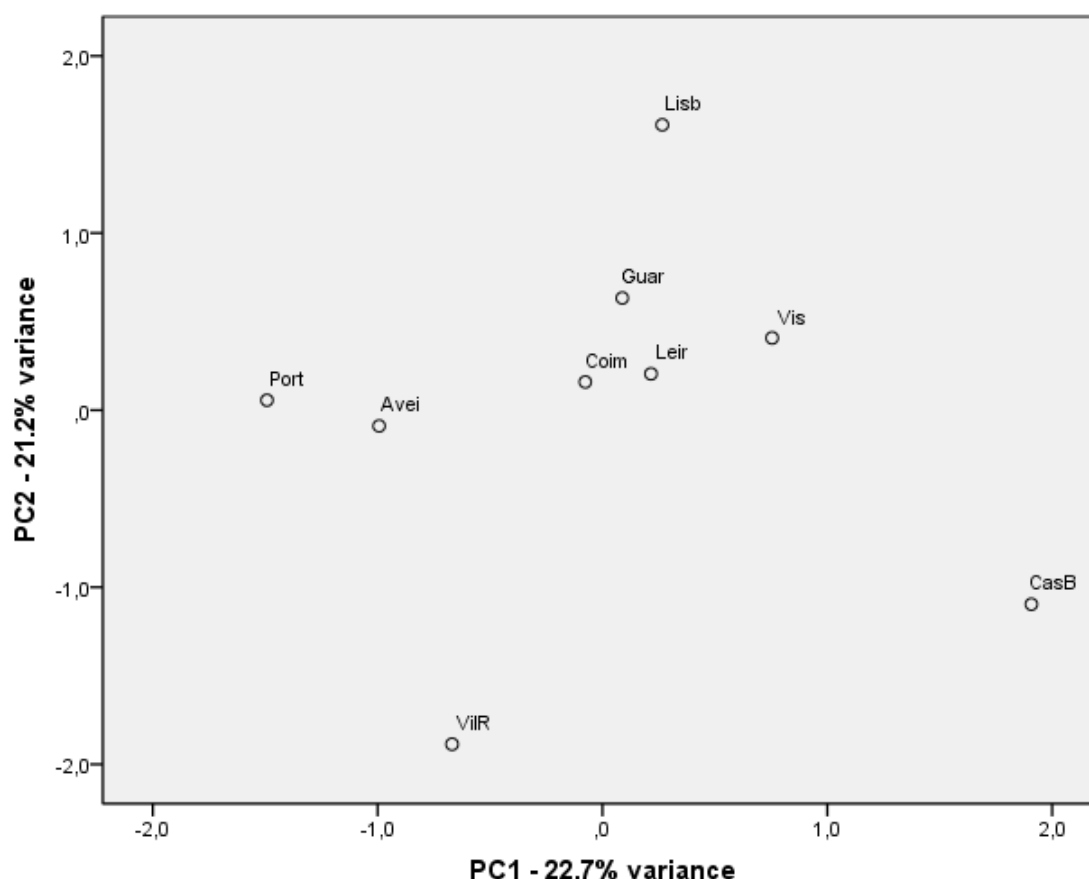
Figure 4.8.3. Scatterplot of the two first components among districts. A total of 43.9% of the variation is represented.
Avei: Aveiro; CasB: Castelo Branco; Coim: Coimbra; Guar: Guarda; Leir: Leiria; Lisb: Lisbon; Port: Porto; VilR: Vila Real; Vis: Viseu.

Finally, PC6 (7.5% variance) is organized through a strong positive loading from UP4 accessory crests and a strong negative loading from LM3 C6.

Figure 4.8.3. exposes the first two components' distribution (which amount to 43.9% variance). Guarda, Coimbra, Leiria and Viseu are grouped in the centre of both axial distributions. Porto, Aveiro and Vila Real derived towards the negative side of the x axis, while Castelo Branco is placed in the opposite direction. Lisbon, while aligned with the central cluster along PC1, is distanced toward the more positive part of the distribution along PC2. Vila Real and Castelo Branco are both placed in the negative area of the y axis.

Figure 4.8.4. shows the distribution along PC's 3 and 4 (32.1% variance). Once again, Guarda, Coimbra, Leiria and Viseu cluster together. Aveiro and Lisbon are aligned with this group along PC3, but are placed in the negative spectrum of variation
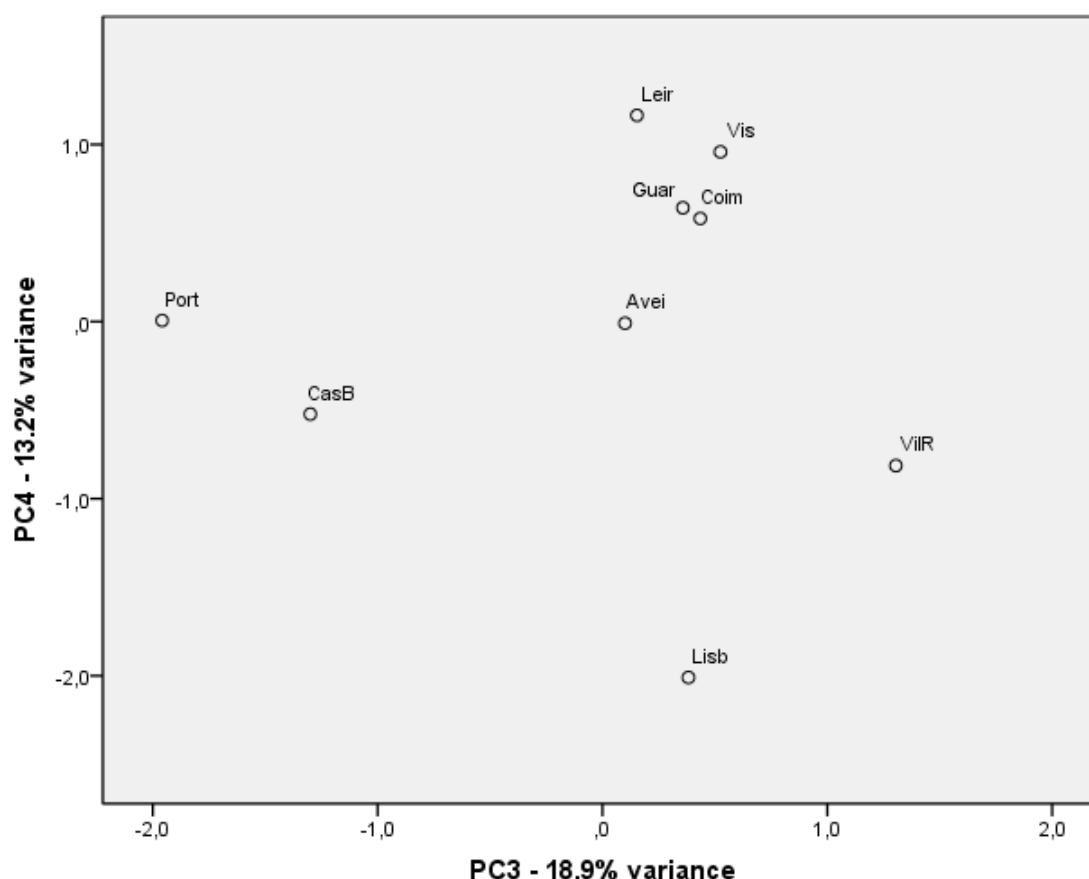
Figure 4.8.4. Scatterplot of PC3 and PC4 among districts. A total of 32.1% of the variation is represented. Avei: Aveiro; CasB: Castelo Branco; Coim: Coimbra; Guar: Guarda; Leir: Leiria; Lisb: Lisbon; Port: Porto; VilR: Vila Real; Vis: Viseu.

on PC4, alongside the remaining samples (Porto, Castelo Branco and Vila Real). Porto and Castelo Branco are placed in the negative range of variation along PC3, while Vila Real is on the more positive side, when related to the aforementioned cluster.

Figure 4.8.5. graphically expresses PC's 5 and 6 (16.9% variance). The samples are relatively widely spread on both axes, but there is a large cluster encompassing most samples: Vila Real, Porto, Lisboa, Coimbra, Castelo Branco, Viseu and Guarda. Leiria and Aveiro are placed in the positive end of the PC5 range, and are positioned on the extreme positive and negative ends of the PC6 spectrum, respectively.

These six components express 92.7% of the variation found among the samples. The four most expressive PC's suggest a cluster of the Coimbra, Guarda, Viseu and Leiria samples. These samples are the biggest (Coimbra = 402; Leiria = 37; Guarda = 36; Viseu = 29). This suggests the main differences found may have been caused not by real biological distance between these samples, though by a difference in sample size that could not be corrected by the use of the expression count method.

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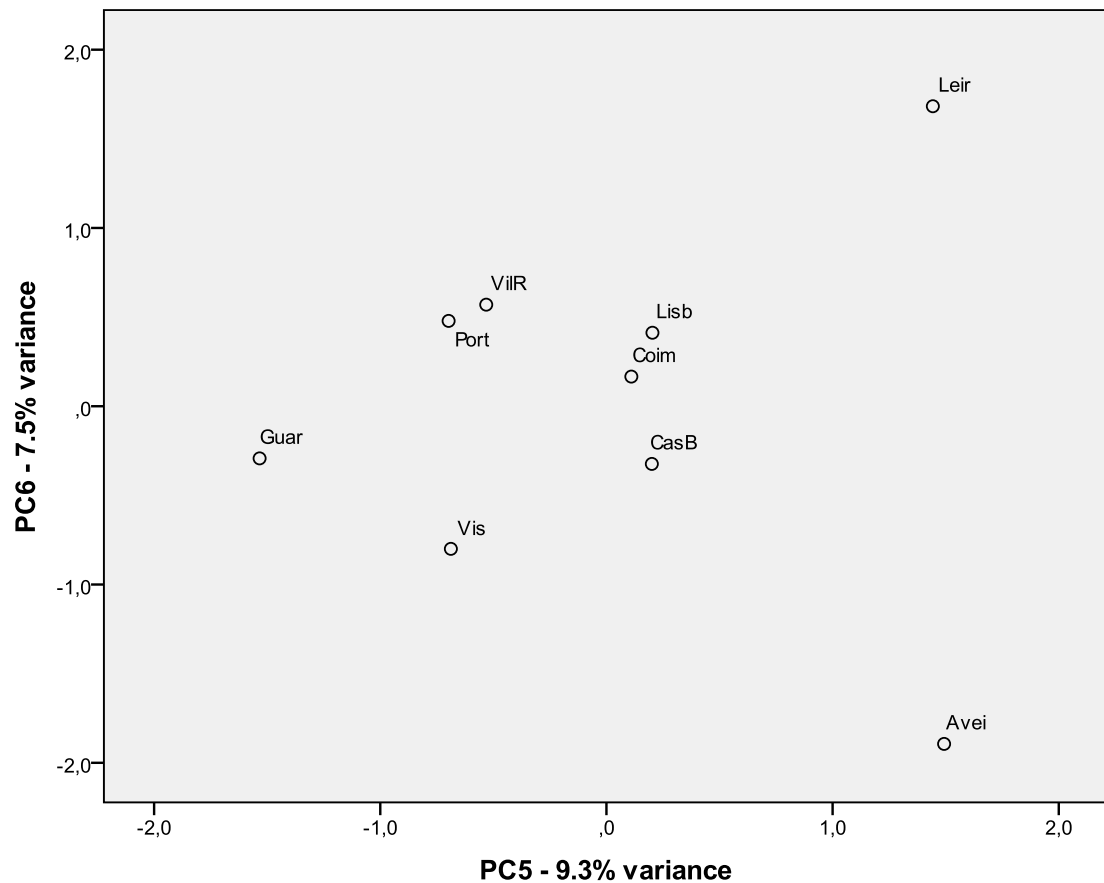
Figure 4.8.5. Scatterplot of PC5 and PC6 among districts. A total of 16.8% of the variation is represented.
Avei: Aveiro; CasB: Castelo Branco; Coim: Coimbra; Guar: Guarda; Leir: Leiria; Lisb: Lisbon; Port: Porto;
VilR: Vila Real; Vis: Viseu.

The small samples for the Aveiro (n = 16), Castelo Branco (n = 9), Lisboa (n = 10), Porto (n = 11) and Vila Real (n = 10) districts may have originated the expression frequency differences that enabled the noted distinctions. That seems to account for the random dispersion of the smaller samples along the first four PC's (Figures 4.8.3. and 4.8.4.). The latter two, less expressive PC's, on the other hand, display the bigger samples as relatively widely distributed, mainly along PC5. This small portion of the variation may hide the real biological distances among the samples, which are possibly generally small. Coimbra, the largest sample by far (n = 402), is located at the centre of the distribution, and also splits the remaining samples in half along PC5 and PC6 alike. The bigger samples besides Coimbra, which are Guarda, Viseu and Leiria, are among the furthest from Coimbra, particularly Leiria (which is geographically close and the second largest sample). This may mean that the strong loading traits for PC's 5 and 6 (see above) may be the ones hiding the variation among the Portuguese 19th and 20th century districts, which is likely to be very small.

4.8.4. Biological relations between regions

The Portuguese born in continental districts of the country were also divided into regions of birth. Most of the sample was born in the Centre of Portugal (n = 466), while the North is also well represented (n = 107), and the South contributed few individuals (n = 12). The expression count method was again used to determine the trait frequencies for these samples, presented on Table 4.8.5. The 29 traits that varied the most between these samples were analyzed in a PCA.

Table 4.8.5. Trait frequencies for each region.

Trait		North	Centre	South
Distal Accessory Ridge (13/23)	%	21.5%	28.2%	26.7%
	n	79	368	9
Distal Accessory Ridge (33/43)	%	10.0%	13.2%	14.0%
	n	84	402	10
Winging (11/21)	%	1.2%	4.0%	6.3%
	n	63	308	4
Shoveling (11/21)	%	3.5%	2.6%	11.1%
	n	38	213	3
Double Shoveling (11/21)	%	0.0%	0.8%	5.6%
	n	37	203	3
Interruption Grooves (11/21)	%	6.9%	5.2%	0.0%
	n	58	287	4
Midline Diastema (11/21)	%	6.9%	10.6%	0.0%
	n	29	179	3
Interruption Grooves (12/22)	%	12.3%	17.8%	40.0%
	n	81	353	5
Accessory Crests (14/24)	%	1.3%	6.2%	0.0%
	n	80	357	7
Accessory Cusps (15/25)	%	5.1%	3.0%	0.0%
	n	79	367	10
Accessory Crests (15/25)	%	16.0%	27.7%	30.0%
	n	81	368	10
Odontome (15/25)	%	1.2%	0.0%	0.0%
	n	86	382	10
Carabelli's trait (16/26)	%	12.8%	16.4%	20.6%
	n	87	373	9
C5 (16/26)	%	1.2%	2.7%	4.4%
	n	86	374	9
Mesial Marginal Accessory Tubercles (16/26)	%	1.2%	5.3%	0.0%
	n	83	357	9

Trait		North	Centre	South
Enamel Extensions (16/26)	%	5.3%	2.8%	0.0%
	n	63	275	7
Enamel Extensions (17/27)	%	16.4%	14.7%	8.3%
	n	71	330	8
Enamel Extensions (18/28)	%	7.7%	4.0%	0.0%
	n	39	177	2
Deflecting Wrinkle (36/46)	%	2.0%	4.3%	0.0%
	n	66	299	8
Anterior Fovea (36/46)	%	7.0%	8.4%	9.4%
	n	71	326	8
Groove Pattern (36/46)	%	87.8%	89.7%	100.0%
	n	74	331	9
Distal Trigonid Crest (36/46)	%	1.4%	3.0%	0.0%
	n	74	329	9
C5 (36/46)	%	72.2%	74.3%	68.9%
	n	72	330	9
C7 (36/46)	%	3.8%	4.4%	8.9%
	n	74	337	9
Groove Pattern (37/47)	%	83.5%	78.9%	88.9%
	n	85	374	9
Cusp Number (37/47)	%	16.3%	22.7%	0.0%
	n	86	384	8
Distal Trigonid Crest (38/48)	%	15.6%	22.2%	0.0%
	n	64	302	3
C5 (38/48)	%	41.0%	45.1%	66.7%
	n	60	297	3
C6 (38/48)	%	5.7%	8.1%	0.0%
	n	60	297	3

Table 4.8.6. describes the two generated components, by stating their *eigenvalues*, variances and trait loadings. PC1 (76.2% variance) is characterized by strong positive loadings (>0.5) from 15 traits and strong negative loadings from 13 others. Strong positive loadings from LC and UC distal accessory ridges, UP3 and UP4

Table 4.8.6. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing three Portuguese regions.

Trait (tooth)	PC 1	PC 2
Distal Accessory Ridge (13/23)	**-0.745**	**0.667**
Distal Accessory Ridge (33/43)	-0.422	**0.907**
Winging (11/21)	**-0.899**	0.438
Shoveling (11/21)	**-0.975**	-0.222
Double Shoveling (11/21)	**-1.000**	0.005
Interruption Grooves (11/21)	**0.994**	-0.112
Midline Diastema (11/21)	**0.888**	0.460
Interruption Grooves (12/22)	**-0.998**	0.062
Accessory Crests (14/24)	**0.562**	**0.827**
Accessory Cusps (15/25)	**0.957**	-0.291
Accessory Crests (15/25)	**-0.720**	**0.694**
Odontome (15/25)	**0.606**	**-0.796**
Carabelli's trait (16/26)	**-0.939**	0.345
C5 (16/26)	**-0.936**	0.353
Mesial Marginal Accessory Tubercles (16/26)	**0.576**	**0.817**
Enamel Extensions (16/26)	**0.934**	-0.356
Enamel Extensions (17/27)	**0.997**	-0.073
Enamel Extensions (18/28)	**0.931**	-0.365
Deflecting Wrinkle (36/46)	**0.771**	**0.637**
Anterior Fovea (36/46)	**-0.881**	0.473
Groove Pattern (36/46)	**-1.000**	0.018
Distal Trigonid Crest (36/46)	**0.772**	**0.636**
C5 (36/46)	**0.866**	0.499
C7 (36/46)	**-1.000**	-0.019
Groove Pattern (37/47)	**-0.823**	**-0.568**
Cusp Number (37/47)	**0.920**	0.393
Distal Trigonid Crest (38/48)	**0.913**	0.408
C5 (38/48)	**-1.000**	0.022
C6 (38/48)	**0.913**	0.407
Eigenvalue	22.110	6.890
Variance	76.2%	23.8%
Total variance	76.2%	100.0%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

accessory crests, UM1 mesial marginal accessory tubercles, and LM1 deflecting wrinkle and distal trigonid crest contribute to PC2 distribution. Alongside these, strong negative loadings from UP4 odontome and LM2 groove pattern are also related to PC2 variation (23.8% of the total variance).

Figure 4.8.6. reports on the distributions along PC1 and PC2, which reflect the whole variation between the samples (100.0%). The x axis (PC1) only clearly separates the South from Centre and North, which are clearly very near. PC2, on the other hand, places those two samples further apart, with the Southern sample in the middle, nearer the North.

The placement of the South as clearly disparate from the other two regions along the most relevant axis, PC1 (76.2% variance), is most likely due to its very small
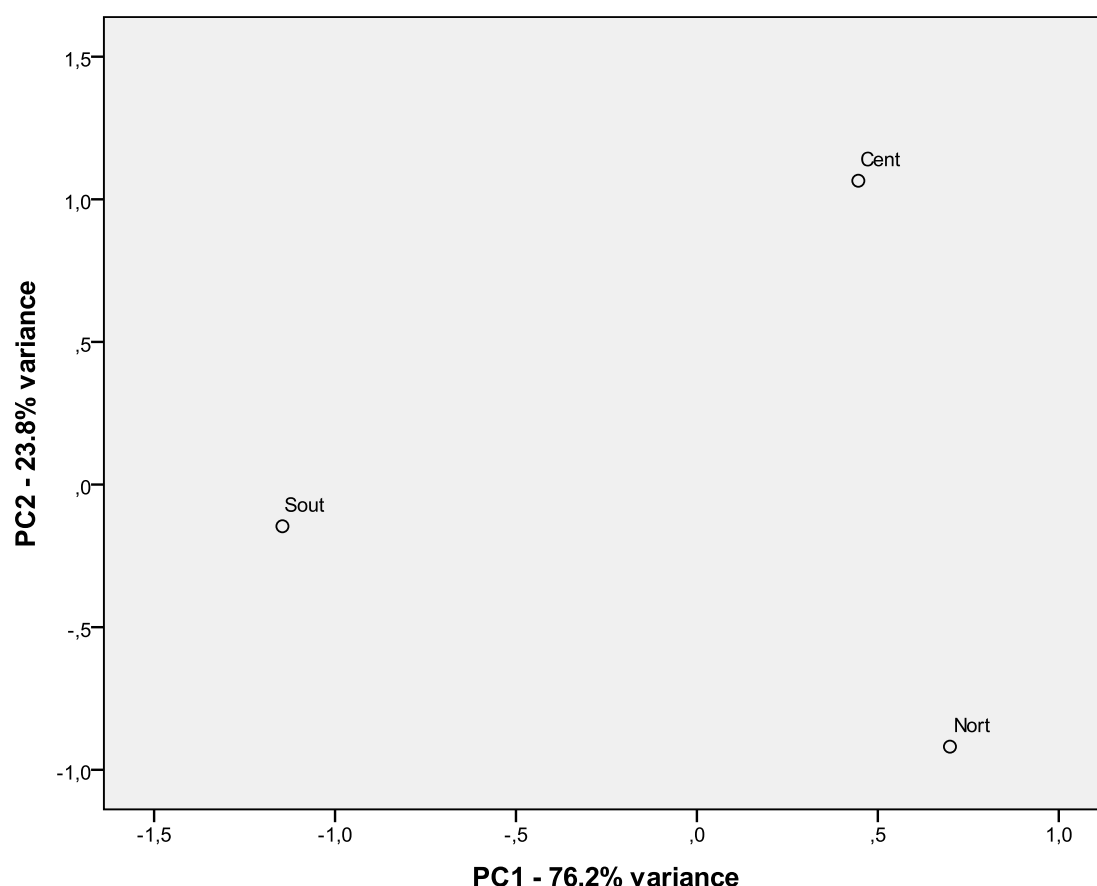
Table 4.8.6. Scatterplot of the two components among regions. The total 100% of the variation is represented. Cent: Central Portugal; Nort: North Portugal; Sout: South Portugal.

sample size (n=12), once again. Noteworthy is the closeness between the Centre and North regions along the same relevant axis, which suggests the biological distance between the two Portuguese samples is small, and characterized by PC2. Some of the traits that originate the distance found on that axis were also among the ones which contributed to the separation between the most well represented districts in the previous analysis. So, the LC distal accessory ridge and the LM1 deflecting wrinkle may be either very sensitive to small genetic distinctions or more susceptible to small environmental differences, because they reflect the main biological distinctions within the Portuguese 19th and 20th century regional populations. The other traits with strong loadings on PC2 are also relevant and can also be more sensitive to small genomic or environmental changes.

Human Leukocyte Antigen (HLA) genetic system was analyzed using high resolution techniques in three Portuguese populations, from North (46 individuals), Center (50) and South (49) Portugal (Spínola *et al.*, 2005). HLA allele frequencies position Portugal between European and North African populations. When analyzed

separately, the North and the South of Portugal cluster with North Africans, and Central Portuguese people cluster with Europeans. This could be due to a bipolar distribution of ancient Portuguese to the North and North African influence to the South, resulting in a gradient with less contribution from each gene pool in the Center of Portugal, approximating it to the rest of Europe due to the lack of common markers with the remaining Portuguese (Spínola *et al.*, 2005).

This distribution is not mimicked by the results drawn from the analysis of the dental morphological traits of the Portuguese. More data, especially if pertaining to the South of Portugal, could allow for the endorsement of the hypothesis advanced by Spínola and colleagues (2005). However, the North and Centre of Portugal seem to show a relative cohesion, with a small subset of traits originating the difference found.

4.8.5. Biological relations between high and low FA groups

Riga and colleagues (2013) suggest the presence and expression of several upper molar supernumerary cusps could be influenced by stress level, since individuals with high linear enamel hypoplasias (LEH) displayed greater frequencies of those traits, when compared to individuals with no LEH.

Exposure to developmental instability (DI), through susceptibility to stress, was inferred in this sample, in an attempt to analyze the dental ecology (see a definition in Cuozzo *et al.*, 2012) of the sample through the observation of absolute and relative frequencies of fluctuating asymmetry (FA; see 4.2.Fluctuating asymmetry). The hypothesis that different levels of FA could result in different expressions of some traits was tested. This was done by comparing expression count method frequencies of several traits of individuals with high and low FA levels through a PCA. Individuals with low level of FA are those with "individual comparable FA" percentage under 25%, while high FA level was considered when "individual comparable FA" was over 60%. Furthermore, only individuals who had four or more sites where traits could be bilaterally scored and were at least unilaterally present were included. This eliminated uninformative bilaterally absent trait sites and individuals which low trait site presence could provide excessive weight to each FA occurrence found. The aim was to consider only those individuals with clearly informative and clearly high or low FA percentages, so as to obtain valid results. Seventy-two individuals were included in the "low FA

level" category, and 95 were included as "high FA level" (in a sample with 167 individuals overall). Their expression count method trait frequencies are on Table 4.8.7.

Table 4.8.7. Trait frequencies for Low and High FA levels.

Trait		FA level		Trait		FA level	
		Low	High			Low	High
Distal Accessory Ridge (33/43)	%	13.0%	16.3%	Distal Trigonid Crest (36/46)	%	0.0%	3.0%
	n	60	80		n	63	67
Interruption Grooves (11/21)	%	6.0%	12.1%	C5 (36/46)	%	3.2%	3.3%
	n	50	58		n	62	70
Midline Diastema (11/21)	%	3.7%	8.6%	Groove Pattern (37/47)	%	86.2%	82.4%
	n	27	35		n	65	85
Interruption Grooves (12/22)	%	6.8%	26.3%	Distal Trigonid Crest (37/47)	%	3.1%	8.2%
	n	59	80		n	65	85
Accessory Cusps (15/25)	%	0.0%	6.0%	Protostylid (37/47)	%	1.6%	4.3%
	n	54	83		n	64	90
Accessory Crests (15/25)	%	20.0%	26.8%	MMPT (37/47)	%	0.0%	1.6%
	n	55	82		n	63	89
Carabelli's trait (16/26)	%	15.0%	18.6%	Distal Trigonid Crest (38/48)	%	15.4%	25.3%
	n	62	80		n	39	75
C5 (16/26)	%	2.0%	3.8%	MMPT (38/48)	%	5.3%	13.9%
	n	61	80		n	38	66
Mesial Marginal Accessory Tubercles (16/26)	%	1.7%	6.4%	C5 (38/48)	%	40.0%	50.0%
	n	60	78		n	39	72
Hypocone (17/27)	%	49.5%	55.7%	C6 (38/48)	%	4.6%	9.4%
	n	64	87		n	39	72
Enamel Extensions (17/27)	%	11.8%	21.5%	C7 (38/48)	%	0.0%	1.9%
	n	51	73		n	39	75
Enamel Extensions (18/28)	%	2.9%	7.0%	*Foramina Mentales*	%	1.4%	7.4%
	n	23	38		n	72	95
Parastyle (18/28)	%	0.0%	2.0%	Mylohyoid Bridge	%	13.2%	10.9%
	n	32	49		n	72	92
Lingual Cusp Variation (35/45)	%	10.1%	10.6%	Mandibular *Torus*	%	4.6%	7.4%
	n	65	86		n	72	95
Anterior Fovea (36/46)	%	11.5%	7.5%	Maxillary *Torus*	%	19.1%	21.3%
	n	63	67		n	72	95
Groove Pattern (36/46)	%	98.4%	82.9%				
	n	62	70				

The analysis was undertook using the trait frequencies of the three continental Portuguese districts (North, Centre and South) as contrast, so the biological relations and the traits that contributed the most to it could be found. The 31 traits included were the ones most divergent between the low and high FA level samples. The PCA resulted in three PC's (which represent 94.2% variance). Table 4.8.8. reports the loading factors of each trait, as well as the *eigenvalues* and variances of each component. Figures 4.8.7. and 4.8.8. demonstrate the distribution of the samples along the first two and all PC's, respectively.

Table 4.8.8. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing differences between high and low FA groups in the Coimbra sample.

Trait (tooth)	PC 1	PC 2	PC 3
Distal Accessory Ridge (33/43)	0.145	**0.705**	**0.684**
Interruption Grooves (11/21)	**0.897**	-0.024	0.184
Midline Diastema (11/21)	**0.930**	-0.036	-0.065
Interruption Grooves (12/22)	-0.404	**0.910**	-0.081
Accessory Cusps (15/25)	**0.865**	0.212	-0.392
Accessory Crests (15/25)	-0.198	**0.834**	0.346
Carabelli's trait (16/26)	-0.360	**0.866**	0.347
C5 (16/26)	-0.288	**0.898**	0.333
Mesial Marginal Accessory Tubercles (16/26)	**0.854**	0.323	0.349
Hypocone (17/27)	**0.686**	**0.626**	0.283
Enamel Extensions (17/27)	**0.946**	0.153	-0.043
Enamel Extensions (18/28)	**0.864**	-0.171	-0.354
Parastyle (18/28)	**0.878**	0.449	0.069
Lingual Cusp Variation (35/45)	**0.768**	0.326	0.124
Anterior Fovea (36/46)	**-0.590**	-0.398	**0.699**
Groove Pattern (36/46)	**-0.935**	-0.225	0.241
Distal Trigonid Crest (36/46)	**0.883**	0.352	-0.059
C5 (36/46)	**0.850**	0.463	-0.198
Groove Pattern (37/47)	**-0.851**	0.022	0.074
Distal Trigonid Crest (37/47)	**0.939**	0.157	0.245
Protostylid (37/47)	0.443	**0.700**	**-0.543**
MMPT (37/47)	**0.906**	0.222	-0.321
Distal Trigonid Crest (38/48)	**0.973**	-0.086	0.193
MMPT (38/48)	-0.490	**0.814**	-0.312
C5 (38/48)	**-0.600**	**0.799**	-0.033
C6 (38/48)	**0.985**	-0.016	0.143
C7 (38/48)	**0.757**	**0.569**	0.320
Foramina Mentales	**-0.587**	**0.796**	-0.139
Mylohyoid Bridge	**0.693**	**-0.557**	0.209
Mandibular *Torus*	**-0.715**	**0.677**	-0.169
Maxillary *Torus*	**-0.521**	**0.730**	-0.425
Eigenvalue	17.099	9.161	2.951
Variance	55.2%	29.5%	9.5%
Total variance	55.2%	84.7%	94.2%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

The characterization of PC1 (55.2% variance) is made by strong positive loadings (>0.5) from 17 traits and strong negative loadings (<-0.5) from seven others.

PC2 (29.5% variance) is defined by strong positive loadings from 13 traits and strong negative loadings from the mylohyoid bridge.

As for PC3 (9.5% variance), the strong positive loadings from LC distal accessory ridge and LM1 anterior fovea, and the strong negative loading from LM2 protostylid, are the main justifications for its sample distribution.

Figure 4.8.7. shows both PC1 and PC2 distribution (84.7% variance). Low FA and High FA derive little from the Centre and North samples, which characterize most of the samples' diversity, along PC1. PC2's distribution allows for a wider distribution of these samples, placed each at one end of the spectrum.
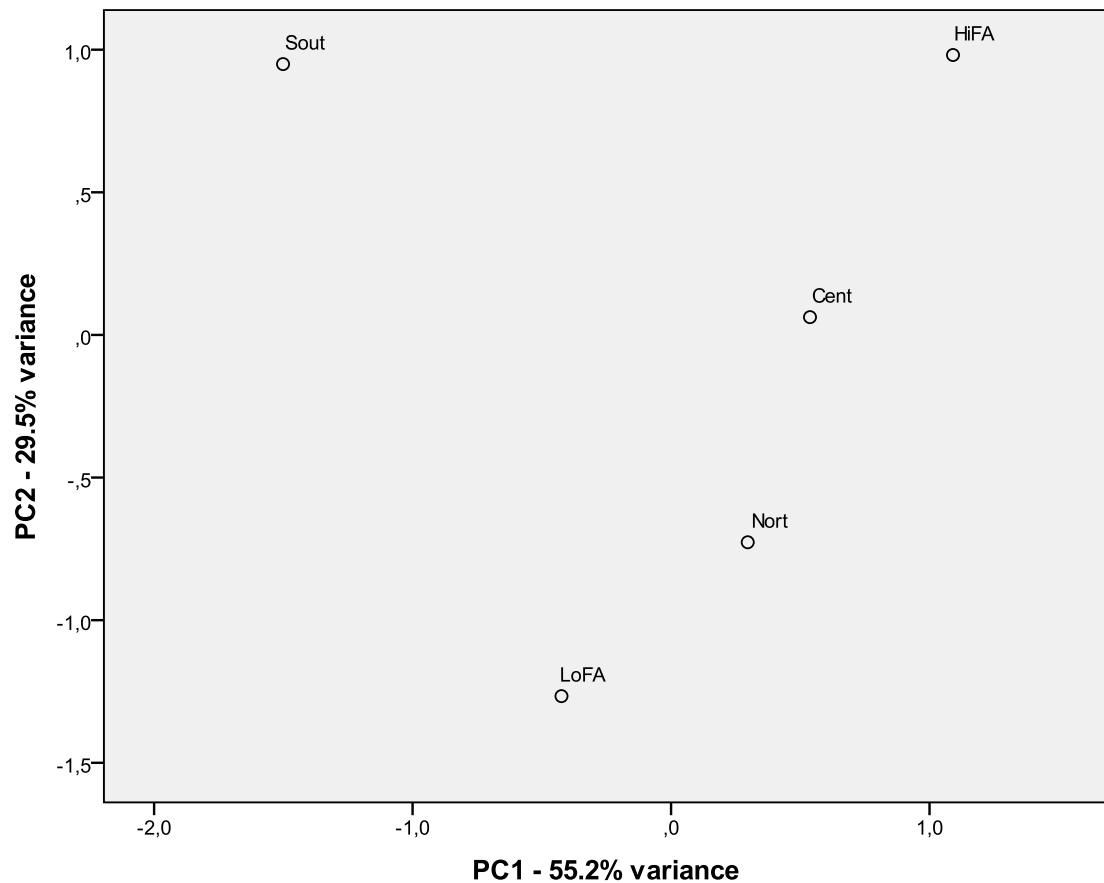
Figure 4.8.7. Scatterplot of the first two components among FA levels and regions. A total of 84.7% of the variation is represented.
Cent: Central Portugal; HiFA: High FA; LoFA: Low FA; Nort: North Portugal; Sout: South Portugal.

Figure 4.8.8. adds PC3 and provides a general view of the biological relations between the samples. PC3 does not distinguish between Low FA and High FA samples, which are close together along the z axis.

As seen on Tables 4.8.7. and 4.8.8., the biological relation found between Low and High FA for PC1 and PC2 is due to the fact that almost all traits present greater expression count frequencies for the High FA sample, which places them far apart, when compared to the similar regional samples. Between these two PC's, all traits present strong, either positive or negative, loadings at least once.

This difference between these two opposed levels of FA percentage can be due to a number of reasons: (1) wear rate, AMTL, or any kind of degenerative elimination of dental morphology data could simultaneously reduce trait frequencies and expressions, and reduce the level of FA, (2) a greater likeliness of FA occurrence the greater the potential for trait expression, (3) biological distinctions between the two
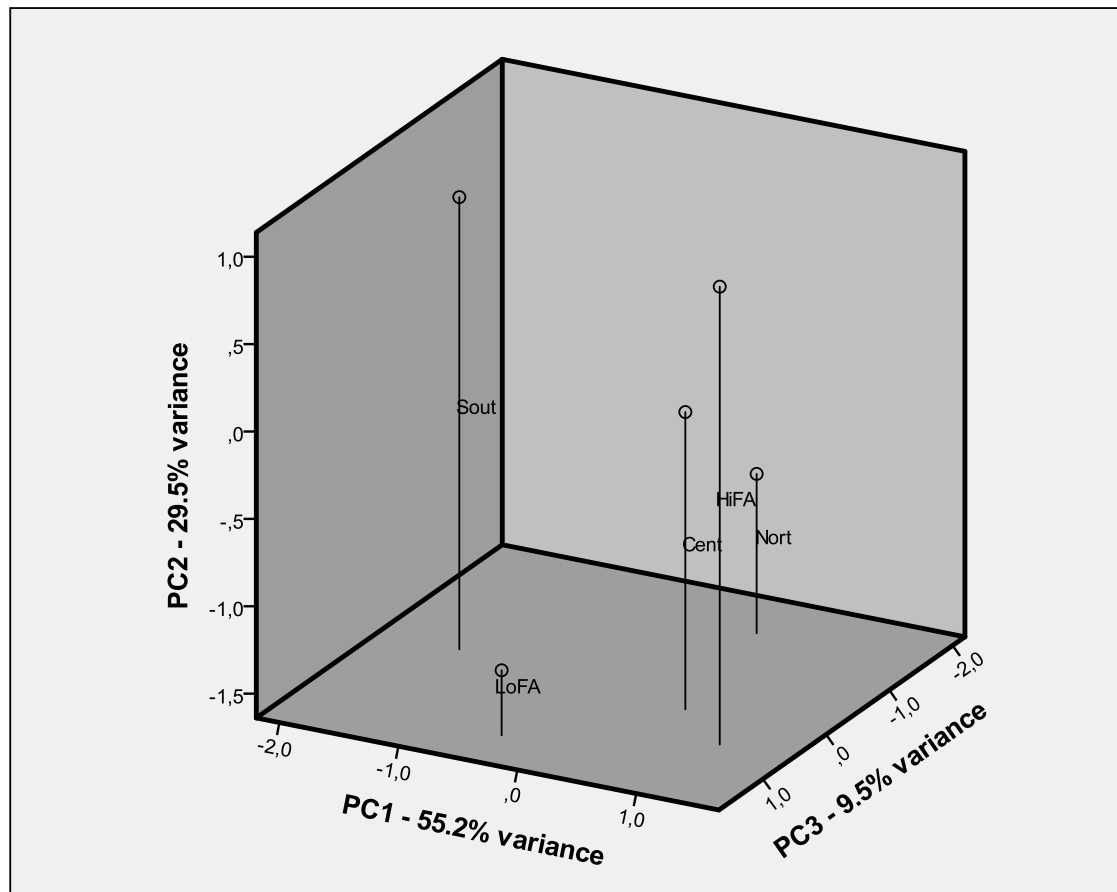
Figure 4.8.8. Scatterplot of the three components among FA levels and regions. A total of 94.2% of the variation is represented.
Cent: Central Portugal; HiFA: High FA; LoFA: Low FA; Nort: North Portugal; Sout: South Portugal.

groups, causing a difference in FA levels and a difference on trait expression, (4) exposure to greater levels of DI could prompt some traits to develop, as a form of developmental plasticity, which places the tooth development beyond a genetic threshold.

The developmental origins of health and disease (DOHaD) seem to be related to developmental plasticity, a phenomenon in a timescale between that of homeostasis (short-term adaptability) and evolution (generations-long adaptation). That phenomenon, developmental plasticity, consists on the ability of the unborn organism to detect nutritional hints to the most likely environmental conditions of his future life, as mediated by the mother's nutritional intake, health status and biological characteristics. This adaptation to the environmental constraints has the biological functions to promote survival and enable gene transmission into future generations. On the other hand, it may consist in trade-offs that enable the susceptibility to certain non-communicable diseases (Gluckman *et al.*, 2010). It is unclear how this phenomenon could promote changes in

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dental nonmetric trait frequencies and to what effect that would serve. Mizoguchi (2013) proposes that dental metric and nonmetric traits may provide environmental advantages and may be geographically distributed according to evolutionary needs of adaptations. The presence of higher frequencies of dental nonmetric traits in individuals presenting high FA levels may be connected to such a hypothesis, since environmental limitations as signaled by nutritional or endocrinal hints may trigger the development of traits that can increase the individual's potential of alternate nutritional resources exploration.

While Riga and colleagues (2013) seem to support the latter hypothesis [see (4), above], it is very difficult to demonstrate it empirically. There is, however, a clearly demonstrated difference between these relatively large samples of individuals affected by diverse levels of developmental stress, or FA as a measure of DI.

Table 4.8.9. displays individual count method grade frequencies for the same 31 traits used in the previous analysis, and compares those of low and high level FA using a Mann-Whitney U test. This was carried out with the intention to test the significance of the difference of distributions between these two opposite groups.

Only five of the 31 dental nonmetric traits analyzed produce statistically highly confident differences. Two of them, UI2 interruption grooves (U = 1902; P = 0.004) and LM1 groove pattern (U = 1833; P = 0.003), display differences with a degree of confidence over 99.0%. The remaining three, - UM2 hypocone (U = 2240; P = 0.038), LM2 protostylid (U = 2500.5; P = 0.027) and LM3 MMPT (U = 1011; P = 0.037) -, show a degree of confidence over 95.0%.

These results suggest that for 26 of the traits, the differences could be due to sampling error. The five traits yielding significant differences mostly present the directional differences found above. Four traits display greater expression on the high FA level group. However, LM1 groove pattern reduces Y pattern expression on high level FA individuals. However, because this trait cannot be characterized as growing into a given direction, this can be seen from the opposite perspective, which shows a greater expression of the X and + patterns on high FA level group individuals.

None of the hypothesis stated above are more easily proposed as the most likely by the latter results. Further studies should shed light on the matter, particularly if using very large and complete samples. The existence of a relation between FA and greater trait expression seems clear, even if limited to some traits. It underlines a connection between genetic potential and environment and may be useful in the socio-cultural

characterization of past populations. Despite this, it may also hinder some of the biological affinity analysis produced using dental morphology. Most likely, this effect

Table 4.8.9. Grade frequencies (individual count method; grade 0 and absent grades omitted) for Low and High FA individuals and Mann-Whitney U test. P-values under 0.05 are in bold.

Trait		FA level		Mann-Whitney	
		Low	High		
Distal Accessory Ridge (33/43)	%	1: 31.7% 2: 11.7% 3: 3.3%	1: 27.5% 2: 25.0% 3: 1.3%	U	2146
	n	60	80	P	0.245
Interruption Grooves (11/21)	%	1: 6.0%	1: 12.1%	U	1364
	n	50	58	P	0.292
Midline Diastema (11/21)	%	1: 3.7%	1: 8.6%	U	449.5
	n	27	35	P	0.443
Interruption Grooves (12/22)	%	1: 6.8%	1: 26.2%	U	1902
	n	59	80	P	**0.004**
Accessory Cusps (15/25)	%	1: 0.0%	1: 6.0%	U	2106
	n	54	83	P	0.067
Accessory Crests (15/25)	%	20.0%	26.8%	U	2106.5
	n	55	82	P	0.384
Carabelli's trait (16/26)	%	1: 27.4% 2: 8.1% 3: 3.2% 4: 4.8% 5: 0.0% 6: 1.6% 7: 3.2%	1: 27.5% 2: 8.8% 3: 7.5% 4: 5.0% 5: 5.0% 6: 0.0% 7: 2.5%	U	2230.5
	n	62	80	P	0.272
C5 (16/26)	%	1: 3.3% 2: 3.3% 3: 0.0%	1: 5.0% 2: 5.0% 3: 1.3%	U	2323.5
	n	61	80	P	0.334
Mesial Marginal Accessory Tubercles (16/26)	%	1: 1.7%	1: 6.4%	U	2227
	n	60	78	P	0.170
Hypocone (17/27)	%	1: 17.2% 2: 17.2% 3: 21.9% 3.5: 6.3% 4: 23.4% 5: 6.3%	1: 11.5% 2: 18.4% 3: 13.8% 3.5: 19.5% 4: 19.5% 5: 11.5%	U	2240
	n	64	87	P	**0.038**
Enamel Extensions (17/27)	%	1: 2.0% 2: 2.0% 3: 9.8%	1: 5.5% 2: 6.8% 3: 15.1%	U	1618
	n	51	73	P	0.086
Enamel Extensions (18/28)	%	1: 0.0% 2: 4.3% 3: 0.0%	1: 2.6% 2: 5.3% 3: 2.6%	U	410
	n	23	38	P	0.398
Parastyle (18/28)	%	3: 0.0%	3: 4.1%	U	752
	n	32	42	P	0.250
Lingual Cusp Variation (35/45)	%	2: 43.5% 3: 9.7% 4: 4.8% 5: 0.0% 6: 6.5% 8: 1.6% 9: 0.0%	2: 37.0% 3: 13.6% 4: 2.5% 5: 2.5% 6: 7.4% 8: 3.7% 9: 1.2%	U	2327.5
	n	62	81	P	0.431

Table 4.8.9. (Continued.)

Trait		FA level		Mann-Whitney	
		Low	High		
Anterior Fovea (36/46)	%	1: 7.9% 2: 11.1% 3: 3.2% 4: 1.6%	1: 3.0% 2: 4.5% 3: 6.0% 4: 0.0%	U	1906.5
	n	63	67	P	0.160
Groove Pattern (36/46)	%	Y: 98.4%	Y: 82.9%	U	1833
	n	62	70	P	**0.003**
Distal Trigonid Crest (36/46)	%	1: 0.0%	1: 3.0%	U	2047.5
	n	63	67	P	0.169
C5 (36/46)	%	2: 0.0% 3: 17.7% 4: 46.8% 5: 19.4%	2: 7.1% 3: 12.9% 4: 45.7% 5: 28.6%	U	1874.5
	n	62	70	P	0.151
Groove Pattern (37/47)	%	X/+: 86.2%	X/+: 82.4%	U	2657.5
	n	65	85	P	0.531
Distal Trigonid Crest (37/47)	%	1: 3.1%	1: 8.2%	U	2620
	n	65	85	P	0.189
Protostylid (37/47)	%	1: 4.7% 2: 3.1% 3: 0.0%	1: 15.6% 2: 2.2% 3: 3.3%	U	2500.5
	n	64	90	P	**0.027**
MMPT (37/47)	%	1: 0.0% 2: 0.0%	1: 3.4% 2: 1.1%	U	2677.5
	n	63	89	P	0.089
Distal Trigonid Crest (38/48)	%	1: 15.4%	1: 25.3%	U	1317
	n	39	75	P	0.225
MMPT (38/48)	%	1: 10.5% 1-2: 5.3% 2: 0.0% 2-3: 0.0% 3+: 0.0%	1: 24.2% 1-2: 1.5% 2: 4.5% 2-3: 3.0% 3+: 1.5%	U	1011
	n	38	66	P	**0.037**
C5 (38/48)	%	1: 0.0% 2: 5.1% 3: 5.1% 4: 17.9% 5: 20.5%	1: 1.4% 2: 8.3% 3: 8.3% 4: 8.3% 5: 34.7%	U	1204
	n	39	72	P	0.190
C6 (38/48)	%	1: 0.0% 2: 5.1% 3: 0.0% 4: 0.0% 5: 2.6%	1: 1.4% 2: 8.3% 3: 1.4% 4: 2.8% 5: 2.8%	U	1279
	n	39	72	P	0.194
C7 (38/48)	%	1a: 0.0% 2: 0.0%	1: 1.3% 2: 2.7%	U	1404
	n	39	75	P	0.208
Foramina Mentales	%	2: 1.4%	2: 7.4%	U	3215.5
	n	72	95	P	0.074
Mylohyoid Bridge	%	Inc.: 4.2% 1: 11.1%	Inc.: 8.7% 1: 6.5%	U	3287
	n	72	92	P	0.895
Mandibular *Torus*	%	1: 13.9% 2: 0.0%	1: 11.6% 2: 5.3%	U	3294
	n	72	95	P	0.518
Maxillary *Torus*	%	1: 68.1% 2: 4.2%	1: 70.5% 2: 7.4%	U	3155
	n	72	95	P	0.288

will be negligible, since genetic potential should still play a major part in trait expression.

4.8.6. Biological relations between individuals born in Portugal and in foreign countries

Nine of the 600 individuals included in the Coimbra sample studied here were born in foreign countries (five in Spain, two in Brazil, one in France, and another in the Príncipe Island, in the Gulf of Guinea, West Africa). Their inclusion was decided upon the realization that the Portuguese gene pool at the time, the gene pool that had the potential to contribute to the future biological diversity of Portuguese generations to come, included such individuals. Removing them would, therefore, be artificial and random. Other individuals who were born in Portugal had foreign surnames, indicating their potential genetic diversity. Migration, the very process behind the presence of foreign nationals and Portuguese individuals with foreign names, is in the essence of this work, since one of its aims is to understand how migration and the transmission of cultural heritage affected the biological composition of the successive populations inhabiting Portugal. As that phenomenon, migratory travel, was relatively common by the early 20th century, its effect on any particular gene pool should be accepted as predictable.

So as to understand if such foreign nationals in the sample affect the results,

Table 4.8.10. Trait frequencies for individuals born in foreign countries, those born in Portugal, and the total sample.

Trait		Birth country			Trait		Birth country		
		Foreign	Portugal	Total			Foreign	Portugal	Total
Distal Accessory Ridge (33/43)	%	8.9%	12.6%	12.5%	Lingual Cusp Variation (35/45)	%	6.9%	9.4%	9.3%
	n	9	502	511		n	8	494	502
Distal Accessory Ridge (13/23)	%	31.4%	26.7%	26.8%	Deflecting Wrinkle (36/46)	%	5.6%	3.8%	3.8%
	n	7	462	469		n	6	378	384
Shoveling (31/41)	%	0.0%	0.4%	0.4%	Anterior Fovea (36/46)	%	14.3%	8.2%	8.3%
	n	7	356	363		n	7	410	417
Winging (11/21)	%	0.0%	3.6%	3.6%	Groove Pattern (36/46)	%	100%	89.7%	89.9%
	n	6	379	385		n	7	419	426
Shoveling (11/21)	%	0.0%	2.8%	2.7%	Distal Trigonid Crest (36/46)	%	0.0%	2.6%	2.6%
	n	6	256	262		n	7	417	424
Double Shoveling (11/21)	%	0.0%	0.7%	0.7%	Protostylid (36/46)	%	2.0%	2.9%	2.9%
	n	5	245	250		n	7	422	429
Interruption Grooves (11/21)	%	0.0%	5.4%	5.3%	MMPT (36/46)	%	0.0%	0.8%	0.7%
	n	6	352	358		n	7	417	424

Table 4.8.10. (Continued.)

Trait		Birth country			Trait		Birth country		
		Foreign	Portugal	Total			Foreign	Portugal	Total
Midline Diastema (11/21)	%	20.0%	10.3%	10.6%	C5 (36/46)	%	82.9%	73.8%	73.9%
	n	5	213	218		n	7	416	423
Interruption Grooves (12/22)	%	22.2%	17.2%	17.3%	C6 (36/46)	%	2.9%	0.5%	0.5%
	n	9	443	452		n	7	417	424
Peg Incisor (12/22)	%	5.6%	2.3.%	2.3%	C7 (36/46)	%	0.0%	4.3%	4.3%
	n	9	483	492		n	7	425	432
Accessory Cusps (14/24)	%	0.0%	1.1%	1.1%	Groove Pattern (37/47)	%	71.4%	79.9%	79.8%
	n	6	449	455		n	7	473	480
Accessory Crests (14/24)	%	20.0%	5.1%	5.3%	Distal Trigonid Crest (37/47)	%	0.0%	4.2%	4.2%
	n	5	448	453		n	7	474	481
Tricuspid Premolars (14/24)	%	0.0%	0.2%	0.2%	Protostylid (37/47)	%	1.8%	3.9%	3.9%
	n	7	486	493		n	8	482	490
Odontome (14/24)	%	0.0%	0.4%	0.4%	MMPT (37/47)	%	0.0%	1.4%	1.4%
	n	6	481	487		n	8	483	491
Accessory Cusps (15/25)	%	0.0%	3.3%	3.2%	C5 (37/47)	%	25.7%	13.1%	13.3%
	n	7	459	466		n	7	484	491
Accessory Crests (15/25)	%	16.7%	25.7%	25.6%	C6 (37/47)	%	0.0%	0.4%	0.4%
	n	6	463	469		n	7	484	491
Tricuspid Premolars (15/25)	%	0.0%	0.2%	0.2%	C7 (37/47)	%	0.0%	0.2%	0.2%
	n	7	489	496		n	6	490	496
Odontome (15/25)	%	0.0%	0.2%	0.2%	Groove Pattern (38/48)	%	20.0%	19.5%	19.5%
	n	7	482	489		n	5	364	369
Carabelli's trait (16/26)	%	19.1%	15.7%	15.8%	Distal Trigonid Crest (38/48)	%	25.0%	21.0%	21.0%
	n	6	473	479		n	4	372	376
C5 (16/26)	%	8.0%	2.4%	2.5%	Protostylid (38/48)	%	0.0%	2.2%	2.1%
	n	5	473	478		n	5	341	346
Mesial Marginal Accessory Tubercles (16/26)	%	25.0%	4.4%	4.6%	MMPT (38/48)	%	21.4%	11.6%	11.7%
	n	4	453	457		n	4	349	353
Enamel Extensions (16/26)	%	0.0%	3.2%	3.1%	C5 (38/48)	%	40.0%	44.7%	44.7%
	n	5	348	353		n	4	364	368
Hypocone (17/27)	%	31.5%	50.9%	50.6%	C6 (38/48)	%	30.0%	7.6%	7.8%
	n	9	521	530		n	4	364	368
Enamel Extensions (17/27)	%	0.0%	14.8%	14.6%	C7 (38/48)	%	0.0%	0.7%	0.7%
	n	6	413	419		n	3	373	376
Enamel Extensions (18/28)	%	0.0%	4.5%	4.5%	*Foramina Mentales*	%	0.0%	4.7%	4.7%
	n	1	220	221		n	9	591	600
Parastyle (18/28)	%	0.0%	1.3%	1.3%	Mylohyoid Bridge	%	27.8%	14.3%	14.5%
	n	2	294	296		n	9	582	591
Shoveling (32/42)	%	0.0%	0.5%	0.5%	Mandibular *Torus*	%	11.1%	7.2%	7.2%
	n	8	426	434		n	9	590	599
Lingual Cusp Variation (34/44)	%	12.5%	6.3%	6.4%	Maxillary *Torus*	%	22.2%	21.6%	21.6%
	n	8	518	526		n	9	587	596
Odontome (35/45)	%	0.0%	0.2%	0.2%					
	n	8	503	511					

these individuals were compared with the remaining 591 and the regional samples (providing contrast). The expression count method frequencies for foreign born individuals, Portuguese born individuals and the total sample are in Table 4.8.10.

Those frequencies were used to produce a PCA, which loadings, PC *eigenvalues* and variances are available on Table 4.8.11.

Strong positive (> 0.5) and negative (< -0.5) variable loadings are very common

Table 4.8.11. Matrix of the component loadings, *eigenvalues* and variances of the PCA analyzing differences between foreign born, Portuguese born individuals and the whole Coimbra sample.

Trait (tooth)	PC 1	PC 2	PC 3
Distal Accessory Ridge (13/23)	0.174	**0.784**	**0.596**
Distal Accessory Ridge (33/43)	**-0.515**	**-0.502**	**0.694**
Shoveling (31/41)	**0.709**	-0.041	**0.704**
Winging (11/21)	-0.003	**0.869**	0.494
Shoveling (11/21)	-0.360	**0.932**	-0.027
Double Shoveling (11/21)	**-0.539**	**0.821**	0.187
Interruption Grooves (11/21)	**0.976**	0.009	-0.219
Midline Diastema (11/21)	-0.032	**-0.986**	0.159
Interruption Grooves (12/22)	**-0.787**	**0.566**	0.246
Peg Incisor (12/22)	-0.154	**-0.988**	-0.031
Accessory Cusps (14/24)	**0.708**	-0.041	**0.705**
Accessory Crests (14/24)	-0.399	**-0.897**	0.192
Tricuspid Premolars (14/24)	**0.692**	-0.040	**0.709**
Odontome (14/24)	**0.665**	0.039	**-0.744**
Accessory Cusps (15/25)	**0.923**	0.018	-0.383
Accessory Crests (15/25)	0.047	**0.679**	**0.733**
Tricuspid Premolars (14/24)	**0.692**	-0.040	**0.709**
Odontome (14/24)	0.429	0.048	**-0.902**
Carabelli's trait (16/26)	**-0.868**	0.149	0.474
C5 (16/26)	**-0.853**	-0.480	0.203
Mesial Marginal Accessory Tubercles (16/26)	-0.485	**-0.867**	0.113
Enamel Extensions (16/26)	**0.897**	0.022	-0.442
Hypocone (17/27)	**0.660**	**0.746**	0.092
Enamel Extensions (17/27)	**0.902**	0.421	-0.093
Enamel Extensions (18/28)	**0.891**	0.022	-0.453
Parastyle (18/28)	**0.899**	-0.027	0.436
Shoveling (32/42)	**0.890**	0.023	-0.451
Lingual Cusp Variation (34/44)	**-0.686**	-0.300	0.077
Odontome (35/45)	**0.692**	-0.040	**0.709**
Lingual Cusp Variation (35/45)	0.149	**0.632**	-0.329
Deflecting Wrinkle (36/46)	0.180	**-0.921**	0.345
Anterior Fovea (36/46)	**-0.774**	**-0.608**	0.173
Groove Pattern (36/46)	**-0.989**	-0.005	0.146
Distal Trigonid Crest (36/46)	**0.924**	-0.024	0.382
Protostylid (36/46)	-0.307	**0.922**	0.236
MMPT (36/46)	**0.703**	-0.040	**0.706**
C5 (36/46)	-0.262	**-0.959**	0.105
C6 (36/46)	-0.499	**-0.853**	0.154
C7 (36/46)	-0.042	**0.991**	0.129

Table 4.8.11. (Continued.)

Trait (tooth)	PC 1	PC 2	PC 3
Groove Pattern (37/47)	0.033	**0.975**	-0.221
Distal Trigonid Crest (37/47)	**0.990**	-0.010	0.138
Protostylid (37/47)	**0.745**	**0.664**	0.049
MMPT (37/47)	**0.998**	-0.006	0.065
C5 (37/47)	0.020	**-0.999**	-0.013
C6 (37/47)	**0.983**	0.007	-0.184
C7 (37/47)	**0.714**	-0.041	**0.683**
Groove Pattern (38/48)	**-0.670**	**0.739**	0.066
Distal Trigonid Crest (38/48)	0.424	-0.884	0.198
Protostylid (38/48)	**-0.581**	**0.812**	0.046
MMPT (38/48)	**-0.990**	0.134	0.030
C5 (38/48)	-0.491	**0.847**	0.204
C6 (38/48)	-0.387	**-0.921**	0.036
C7 (38/48)	**0.707**	-0.041	**0.706**
Foramina Mentales	-0.352	**0.928**	0.123
Mylohyoid Bridge	-0.142	**-0.982**	0.123
Mandibular *Torus*	**-0.865**	0.487	0.122
Maxillary *Torus*	**-0.760**	**0.645**	0.074
Eigenvalue	24.742	22.082	9.179
Variance	43.4%	38.8%	16.1%
Total variance	43.4%	82.2%	98.3%

* Highlighted figures represent strong positive (> 0.5; boldface and underline) and strong negative (< -0.5; boldface only) loadings within each component; PC – principal component.

along all three PC's. PC1 represents almost half of the variation (43.4%), while PC2 is still very important (38.8%) in comparison with PC3 (16.1%), which is nonetheless instrumental in expressing the almost complete variation within these samples.

Figure 4.8.9. represents 82.2% of the total variance, while the three-dimensional Figure 4.9.10. represents 98.3% of the variation found among Foreign individuals, Portuguese individuals, the Coimbra sample, and the regional samples analyzed.

The first image (Figure 4.8.9.) illustrates how the North and Centre regions, the Portuguese individuals and the complete Coimbra sample cluster together, while the South region and the Foreign individuals are in the opposite side of the PC1 (z axis) distribution, and spread to either side of that cluster along PC2 (y axis).

The addition of PC3 (see Figure 4.8.10.) confirms the almost total superimposition of the Portuguese individuals with the full Coimbra sample. That same

axis aligns the foreign and the South individuals with the mentioned samples. The North region is, however, set apart from the remaining ones along PC3.

This PCA illustrates how the smaller samples, the Foreign individuals (9
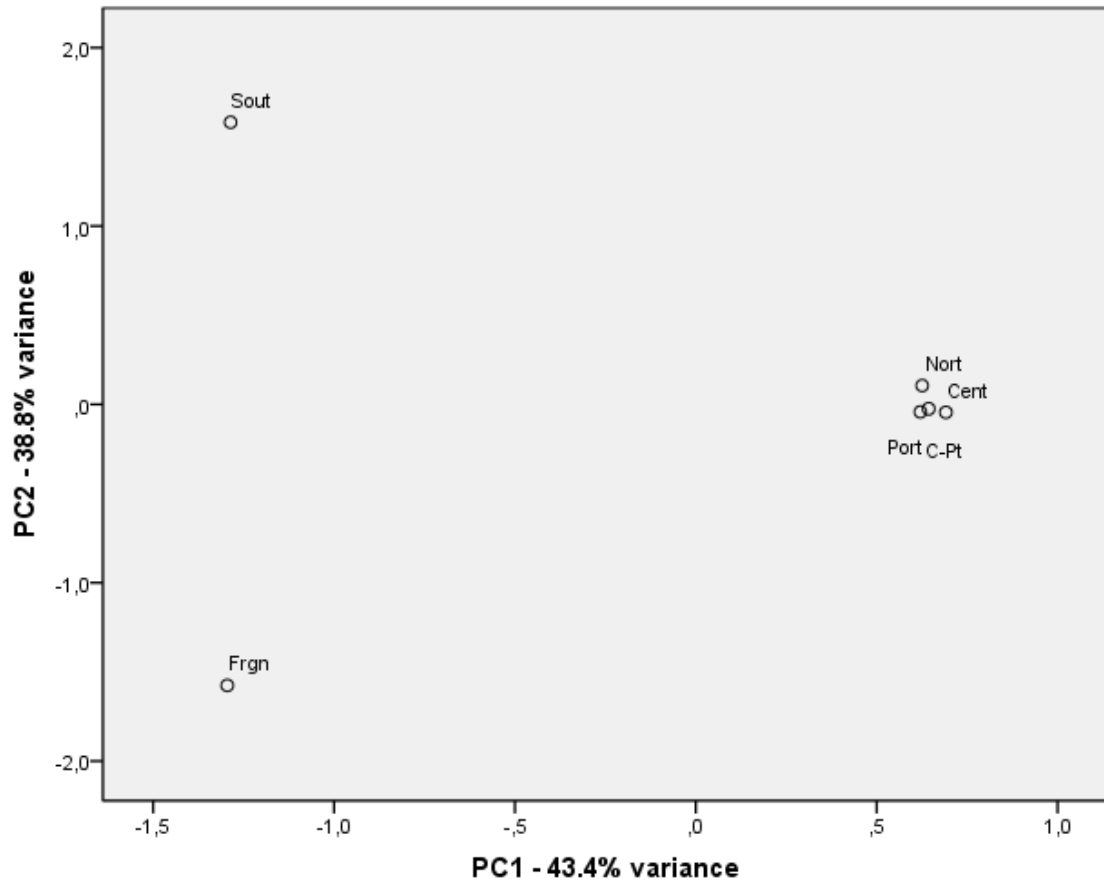
Figure 4.8.9. Scatterplot of the first two components among Portuguese born individuals, foreign born individuals, the complete Coimbra sample and the Portuguese regions.
Cent: Central Portugal; C-Pt: Coimbra (Portugal) full sample; Frgn: Individuals born in foreign countries; Nort: North Portugal; Port: Portuguese born individuals; Sout: South Portugal.

individuals) and the South region (12 individuals), are set apart from the cluster of the most representative samples (Coimbra: 600; Portuguese: 591; North: 107; Centre: 466), most likely because of their very low numbers. The most relevant fact, however, is how the inclusion of the 9 foreign born individuals from the sample does not alter that sample's position in the distribution. This is evidenced by the superposition between the Coimbra (all individuals included) and the Portuguese (that included only the 591 individuals born in Portugal) samples. Therefore, it is demonstrated that the foreign born individuals included in the present sample do not bias any analyses or hinder their conclusions.

To further test the possible incompatibility of the Portuguese and foreign individuals, a Mann-Whitney U test was applied to every trait, in order to better classify the statistical significance of the differences between them. The results can be seen in Table 4.8.12.
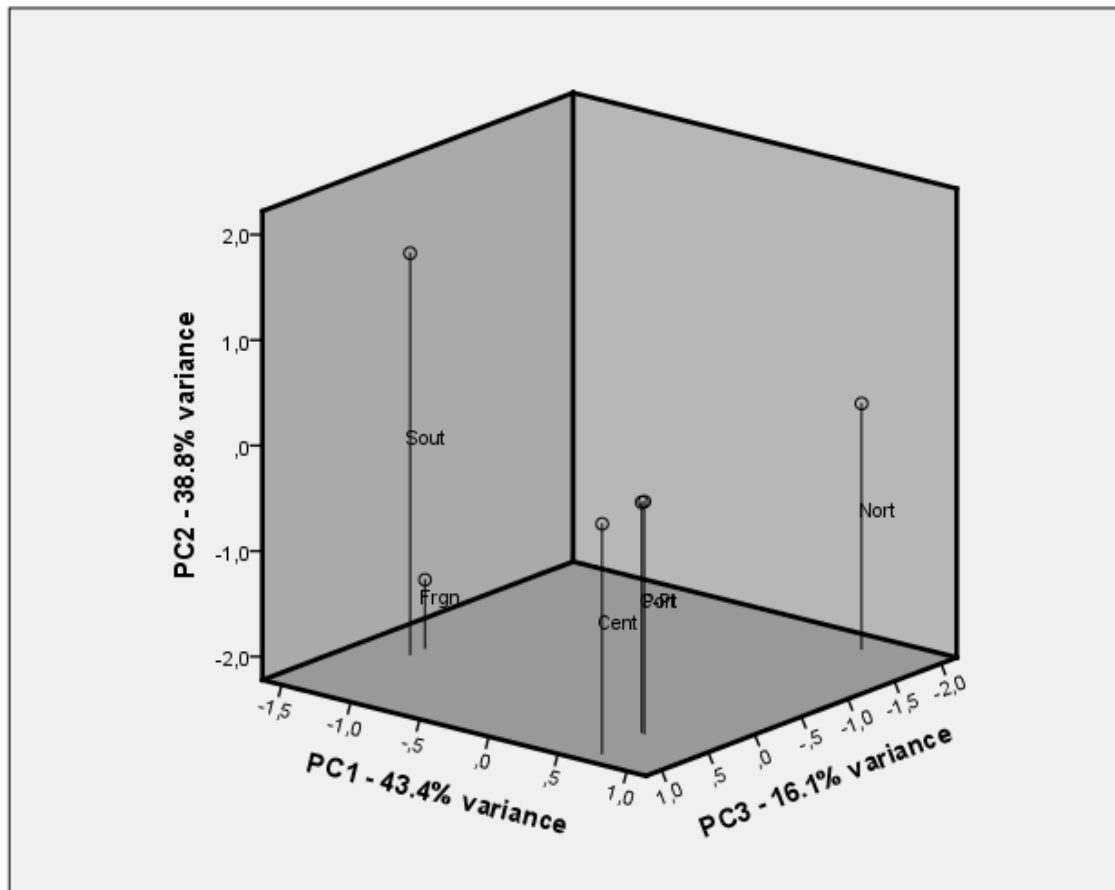
Figure 4.8.10. Scatterplot of the first three components among Portuguese born individuals, foreign born individuals, the complete Coimbra sample and the Portuguese regions.
Cent: Central Portugal; C-Pt: Coimbra (Portugal) full sample; Frgn: Individuals born in foreign countries; Nort: North Portugal; Port: Portuguese born individuals; Sout: South Portugal.

From the 57 dental and oral nonmetric traits analyzed, only two were significantly different between foreign and Portuguese individuals within the Coimbra sample. LM1 cusp 6 (U = 1274; P = 0.009) and LM3 cusp 6 (U = 458.5; P = 0.037) present significantly different variances between foreign and Portuguese individuals. Said differences were, however, diminished in the expression count method (see Table 4.8.10.), particularly for LM1 C6 (Foreign: 2.9%; Portuguese: 0.5%). LM3 C6 (Foreign: 30.0%; Portuguese: 7.6%) did not produce much close frequencies when using the

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Table 4.8.12. Grade frequencies (individual count method; grade 0 and absent grades omitted) for foreign born and Portuguese born individuals and Mann-Whitney U test. P-values under 0.05 are in bold.

Trait		Birth country		Mann-Whitney	
		Foreign	Portugal		
Distal Accessory Ridge (33/43)	%	1: 44.4% 2: 0.0% 3: 0.0%	1: 23.1% 2: 13.9% 3: 4.0%	U	2156
	n	9	502	P	0.791
Distal Accessory Ridge (13/23)	%	1: 14.3% 2: 28.6% 3: 28.6% 4: 0.0%	1: 18.8% 2: 32.7% 3: 14.7% 4: 1.3%	U	1421.5
	n	7	462	P	0.567
Shoveling (31/41)	%	1: 0.0%	1: 2.5%	U	1214.5
	n	7	356	P	0.671
Winging (11/21)	%	1a: 0.0% 1b: 0.0% 2: 0.0% 4: 0.0%	1a: 0.3% 1b: 1.6% 2: 1.8% 4: 5.0%	U	1038
	n	6	379	P	0.451
Shoveling (11/21)	%	1: 0.0% 2: 0.0%	1: 12.1% 2: 2.3%	U	657
	n	6	256	P	0.317
Double Shoveling (11/21)	%	1: 0.0% 3: 0.0% 4: 0.0%	1: 1.6% 2: 0.4% 3: 0.4%	U	597.5
	n	5	245	P	0.724
Interruption Grooves (11/21)	%	1: 0.0%	1: 5.4%	U	999
	n	6	352	P	0.559
Midline Diastema (11/21)	%	1: 20.0%	1: 10.3%	U	481
	n	5	213	P	0.488
Interruption Grooves (12/22)	%	1: 22.2%	1: 17.2%	U	1885.5
	n	9	443	P	0.672
Peg Incisor (12/22)	%	1: 11.1% 2: 0.0%	1: 2.1% 2: 1.2%	U	2007
	n	9	483	P	0.213
Accessory Cusps (14/24)	%	1: 0.0%	1: 1.1%	U	1332
	n	6	449	P	0.795
Accessory Crests (14/24)	%	1: 20.0%	1: 5.1%	U	953.5
	n	5	448	P	0.141
Tricuspid Premolars (14/24)	%	0.0%	0.2%	U	1697.5
	n	7	486	P	0.904
Odontome (14/24)	%	0.0%	0.4%	U	1437
	n	6	481	P	0.874
Accessory Cusps (15/25)	%	1: 0.0%	1: 3.3%	U	1554
	n	7	459	P	0.627
Accessory Crests (15/25)	%	1: 16.7%	1: 25.7%	U	1258.5
	n	6	463	P	0.605
Tricuspid Premolars (15/25)	%	0.0%	0.2%	U	1708
	n	7	489	P	0.905
Odontome (15/25)	%	0.0%	0.2%	U	1683.5
	n	7	482	P	0.904
Carabelli's trait (16/26)	%	1: 0.0% 2: 0.0% 3: 0.0% 4: 33.3% 5: 0.0% 6: 0.0% 7: 0.0%	1: 29.0% 2: 6.8% 3: 6.3% 4: 3.2% 5: 3.0% 6: 1.3% 7: 1.9%	U	1333
	n	6	473	P	0.783
C5 (16/26)	%	1: 0.0% 2: 20.0% 3: 0.0%	1: 5.5% 2: 3.0% 3: 0.2%	U	1036
	n	5	473	P	0.331

Table 4.8.12. (Continued.)

Trait		Birth country		Mann-Whitney	
		Foreign	Portugal		
Mesial Marginal Accessory Tubercles (16/26)	%	1: 25.0%	1: 4.4%	U	725.5
	n	4	453	P	0.058
Enamel Extensions (16/26)	%	1: 0.0% 2: 0.0% 3: 0.0%	1: 0.9% 2: 0.9% 3: 2.3%	U	835
	n	5	348	P	0.648
Hypocone (17/27)	%	1: 11.1% 2: 11.1% 3: 22.2% 3.5: 22.2% 4: 0.0% 5: 0.0%	1: 13.6% 2: 15.4% 3: 13.4% 3.5: 14.0% 4: 21.9% 5: 9.2%	U	1845
	n	9	521	P	0.267
Enamel Extensions (17/27)	%	1: 0.0% 2: 0.0% 3: 0.0%	1: 3.1% 2: 5.3% 3: 10.2%	U	1008
	n	6	413	P	0.245
Enamel Extensions (18/28)	%	1: 0.0% 2: 0.0% 3: 0.0%	1: 1.8% 2: 4.5% 3: 0.9%	U	102
	n	1	220	P	0.780
Parastyle (18/28)	%	1: 0.0% 3: 0.0% 4: 0.0% 5: 0.0%	1: 1.7% 3: 1.0% 4: 0.3% 5: 0.3%	U	284
	n	2	294	P	0.791
Shoveling (32/42)	%	1: 0.0%	1: 3.3%	U	1648
	n	8	426	P	0.603
Lingual Cusp Variation (34/44)	%	1: 0.0% 2: 0.0% 3: 25.0% 4: 0.0% 5: 0.0% 6: 12.5% 7: 0.0% 8: 0.0% 9:0.0%	1: 0.4% 2: 11.4% 3: 4.2% 4: 0.8% 5: 1.7% 6: 4.2% 7: 0.4% 8: 2.1% 9: 0.2%	U	1765
	n	8	518	P	0.347
Odontome (35/45)	%	0.0%	0.2%	U	2008
	n	8	503	P	0.900
Lingual Cusp Variation (35/45)	%	1: 0.0% 2: 62.5% 3: 12.5% 4: 12.5% 5: 0.0% 6: 0.0% 7: 0.0% 8: 0.0% 9: 0.0%	1: 0.2% 2: 39.7% 3: 12.6% 4: 2.6% 5: 0.8% 6: 5.1% 7: 0.2% 8: 2.8% 9: 0.2%	U	1636
	n	8	494	P	0.376
Deflecting Wrinkle (36/46)	%	1: 16.7% 2: 0.0% 3: 0.0%	1: 3.2% 2: 2.9% 3: 0.8%	U	1030
	n	6	378	P	0.384
Anterior Fovea (36/46)	%	1: 0.0% 2: 28.6% 3: 0.0% 4: 0.0%	1: 6.6% 2: 7.3% 3: 3.2% 4: 0.5%	U	1265
	n	7	410	P	0.419
Groove Pattern (36/46)	%	Y: 100%	Y: 89.7%	U	1316
	n	7	419	P	0.372

Table 4.8.12. (Continued.)

Trait		Birth country		Mann-Whitney	
		Foreign	Portugal		
Distal Trigonid Crest (36/46)	%	1: 0.0%	1: 2.6%	U	1421
	n	7	417	P	0.664
Protostylid (36/46)	%	1: 14.3% 3: 0.0%	1: 19.2% 3: 0.5%	U	1396.5
	n	7	422	P	0.719
MMPT (36/46)	%	1: 0.0% 3: 0.0%	1: 1.9% 3: 0.2%	U	1428
	n	7	417	P	0.695
C5 (36/46)	%	2: 0.0% 3: 14.3% 4: 57.1% 5: 28.6%	2: 3.6% 3: 15.4% 4: 45.2% 5: 26.9%	U	1268
	n	7	416	P	0.533
C6 (36/46)	%	1: 14.3% 2: 0.0%	1: 0.5% 2: 1.0%	U	1274
	n	7	417	P	**0.009**
C7 (36/46)	%	1a: 0.0% 1: 0.0% 2: 0.0% 3: 0.0% 4: 0.0%	1a: 1.6% 1: 0.2% 2: 1.6% 3: 1.9% 4: 1.4%	U	1386
	n	7	425	P	0.475
Groove Pattern (37/47)	%	X/+: 71.4%	X/+: 79.9%	U	1515
	n	7	473	P	0.579
Distal Trigonid Crest (37/47)	%	1: 0.0%	1: 4.2%	U	1589
	n	7	474	P	0.579
Protostylid (37/47)	%	1: 12.5% 2: 0.0% 3: 0.0% 5: 0.0% 7: 0.0%	1: 10.4% 2: 2.9% 3: 2.1% 5: 0.4% 7: 0.4%	U	1843
	n	8	482	P	0.738
MMPT (37/47)	%	1: 0.0% 1-2: 0.0% 2: 0.0% 3: 0.0%	1: 2.5% 1-2: 0.2% 2: 0.4% 3: 0.4%	U	1864
	n	8	483	P	0.590
C5 (37/47)	%	1: 0.0% 2: 0.0% 3: 42.9% 4: 0.0% 5: 0.0%	1: 1.0% 2: 2.5% 3: 8.7% 4: 5.6% 5: 2.3%	U	1339
	n	7	484	P	0.175
C6 (37/47)	%	2: 0.0%	2: 1.0%	U	1676.5
	n	7	484	P	0.787
C7 (37/47)	%	3: 0.0%	3: 0.2%	U	1467
	n	6	490	P	0.912
Groove Pattern (38/48)	%	Y: 20.0%	Y: 19.5%	U	905.5
	n	5	364	P	0.978
Distal Trigonid Crest (38/48)	%	1: 25.0%	1: 21.0%	U	714
	n	4	372	P	0.844
Protostylid (38/48)	%	1: 0.0% 2: 0.0% 3: 0.0% 5: 0.0% 7: 0.0%	1: 3.8% 2: 1.2% 3: 1.2% 5: 0.3% 7: 0.6%	U	792.5
	n	5	341	P	0.539

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Table 4.8.12. (Continued.)

Trait		Birth country		Mann-Whitney	
		Foreign	Portugal		
MMPT (38/48)	%	1: 0.0% 1-2: 0.0% 2: 0.0% 2-3: 0.0% 3: 25.0% 3+: 0.0%	1: 21.5% 1-2: 2.9% 2: 2.9% 2-3: 1.7% 3: 0.3% 3+: 1.1%	U	687
	n	4	349	P	0.946
C5 (38/48)	%	1: 0.0% 2: 0.0% 3: 25.0% 4: 0.0% 5: 25.0%	1: 0.5% 2: 4.1% 3: 6.3% 4: 15.7% 5: 26.6%	U	684
	n	4	364	P	0.824
C6 (38/48)	%	1: 0.0% 2: 25.0% 3: 0.0% 4: 25.0% 5: 0.0%	1: 0.8% 2: 7.4% 3: 2.2% 4: 2.2% 5: 1.4%	U	458.5
	n	4	364	P	**0.037**
C7 (38/48)	%	1a: 0.0% 1: 0.0% 2: 0.0% 3: 0.0%	1a: 0.3% 1: 0.3% 2: 0.5% 3: 0.3%	U	552
	n	3	373	P	0.840
Foramina Mentales	%	2: 0.0% 3: 0.0%	2: 4.6% 3: 0.2%	U	2533.5
	n	9	591	P	0.504
Mylohyoid Bridge	%	Inc.: 11.1% 1: 22.2%	Inc.: 6.2% 1: 11.2%	U	2197
	n	9	582	P	0.210
Mandibular *Torus*	%	1: 11.1% 2: 11.1%	1: 15.1% 2: 3.2%	U	2516
	n	9	590	P	0.688
Maxillary *Torus*	%	1: 66.7% 2: 11.1%	1: 73.3% 2: 6.6%	U	2599.5
	n	9	587	P	0.916

expression count method. Still, the morphological variability found in the lower third molar may partly explain this difference between the subsamples.

The presence of only two significantly different variances seems to suggest these are random occurrences, and that the samples are, summarily, biologically identical. Their differences are, apparently, almost wholly derived from random sampling, and are expected not to have affected any analyses or conclusions.

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4.9. *Ad hoc* observations

The present chapter is not composed of systematic and methodologically approached registry. These observations were made extemporaneously, with the aim to better understand and characterize the dental morphology, and occasionally peruse paleopathological issues, of the current sample.

In such a large sample, there were many cases which caught the observer's eye. While not systematic, these observations can help guide future researchers who come across similar findings. The reading of this chapter should be particularly critical, and aware of the lack of time of the present author, which prevented the collection of better images, of radiographic insight into the situations that required it, as well as thorough and wide reaching differential diagnoses and bibliographical research. Future works will attempt to diminish the effect of these limitations and correctly assess most cases.

Each abnormality or pathology that was deemed important will be addressed individually or within a specific group. These cases will be further grouped into general divisions to help guide the reader.

4.9.1. Morphological abnormalities

Central cusp (lower third molar)

The male individual with the number 520 from the International Trades Collections (henceforth referred to as ITC), who died in 1930 at 23 years of age and was originally from Coimbra, presented a retained left LM3 (retention occurs when a tooth partially erupts, however is constrained from further eruption and correct occlusion by an obstacle: Alt and Türp, 1998) with expected size and morphology, with the exception of an abnormal central cusp (Figure 4.9.1.). This evagination of the enamel can be characterized as a molar form of odontome or an occlusal enamel pearl. (The very large distolingual cusp, cusp 5, is not an abnormal finding. Some irregularities in proportion or shape of third molars are to be expected.)

An occlusal enamel pearl is identified as a central supernumerary cusp on permanent molars. These central cusps in molars can be exuberant in individuals with lobodontia. In a sample of 500 Hungarian individuals, occlusal enamel pearls of the molars were not found (Kocsis *et al.*, 2002), which suggests their rarity. A case was detected in Portugal, from the Chalcolithic (São Paulo II, in Silva, 2002). In the present

Figure 4.9.1. Detail of the left lower third molar of individual 520 ITC, with a central occlusal cusp.

Figure 4.9.2. Detail of the right upper lateral incisor of individual 517 ITC, with a talon cusp.

sample, the LM3's of 367 individual were analyzed, and only this case of central occlusal cusp was detected (0.3%).

Talon cusp (upper lateral incisor)

The individual 517 ITC was a male from Coimbra of 23 years at his death, in 1925. His right UI2 presents with a V-shaped tubercle in the palatal facet, which originated in the cingulum, near the cement-enamel junction, and is slightly larger than half the cemento-incisal height of the tooth (Figure 4.9.2.).

Between 0.06% and 7.7% of the individuals in a population can present this alteration, which is more common in maxillary permanent lateral incisors of male individuals (Dankner *et al.*, 1996; Hattab and Hazza'a, 2001). *Dens evaginatus* of the anterior dentition, which can occur in the occlusal surface (odontome) or on the lingual facet (talon cusp), was first identified as early as in 1892 (Dankner *et al.*, 1996). The talon cusp is an accessory cusp-like structure on the tooth crown, which incisal shape will assume a T or Y-form (Alt and Türp, 1998). The talon cusp (*dens evaginatus*) occurs as a cusp-like projection from the cingulum or the cement-enamel junction which can have a pulp, besides normal enamel and dentine. It is polymorphic, yet is mostly recognized by the exuberant forms that resemble an eagle's talon. These cusps are etiologically poorly understood, and can be conditioned by both environmental and genomic factors. They are formed during the morpho-differentiation stage of tooth formation, and involve the folding of the inner enamel epithelium and protrusion of the cells in the dental papilla (Hattab and Hazza'a, 2001).

Another instance of talon cusp as been reported for a Portuguese sample, namely that of a talon cusp and possible simultaneous double tooth in a three year old Portuguese Medieval child (Silva and Subtil, 2009).

A literature review and a survey of radiographs from 15000 individuals revealed *dens evaginatus* is most commonly found in upper teeth, and mainly on permanent lateral incisors (Dankner *et al.*, 1996). In the present sample, 492 individuals kept at least one UI2, and only this case of talon cusp was found (0.2%). No other such cusps were found on other anterior teeth.

Perturbations in occlusal relations, displacement of the involved tooth, tongue irritation related to speech and mastication, caries, pulp necrosis, excessive wear of opposing teeth, difficulties during breast-feeding, esthetic issues, temporomandibular joint pain, problems in the interpretation of radiographic evidence, and periodontal issues caused by exaggerated occlusal forces are among the complications related to large talon cusps (Dankner *et al.*, 1996; Hattab and Hazza'a, 2001; Tulunoglu *et al.*, 2007). Issues like pulp necrosis and periapical inflammation are susceptible if certain cases remain untreated. The lack of generalized dental care in the Portuguese population of the turn of the 19th century (see, for example, Wasterlain [2006] and below) could thus have presented other cases which, because of these or other of the mentioned subsequent alterations, resulted in lost teeth or fractured cusps/crowns.

Macrodont teeth

The individual number 114 of the Medical Schools Collection (henceforth referred to as MSC), a female from Coimbra of 29 years when she died, in 1896, presents a rotated and enlarged left LP4, which is a molarized or molariform premolar. The tooth (see Figure 4.9.3.) is rotated mesially, with its buccal side mesially directed. It presents two well defined buccal cusps, and a mesiobuccal cusplet. Lingually, it presents two well developed cusps. The largest is the mesiolingual cusp. This individual is the only, out of 511 individuals with scorable LP4's, to present this anomaly, which is thus prevalent in 0.2% of this sample.

Another individual, number 976 ITC, a 26 years old female who died in 1934, has a macrodont right UP3. The molarized premolar is irregular in crown shape, and apparently has an enlarged root structure supporting it. The irregular crown is mostly derived from the enlarged medial ridge that buccolingually crosses the occlusal surface

Figure 4.9.3. Detail of the lower left second premolar of individual 114 MSC, a macrodont or molarized premolar.

Figure 4.9.4. Upper dental arcade of individual 976 ITC. The right first premolar is macrodont or molarized.

and the enlarged mesial and distal marginal ridges. Besides the aforementioned medial ridge, the lingual surface presents a distolingual cusp, which is a part of the alluded distal marginal ridge. Two buccal cusps are distinguished besides the terminal end of the medial ridge. Each of them is part of the mesial and distal marginal ridges, and is further complemented by other cusplets without free apices (Figure 4.9.4.). The prevalence of molarized UP3 in the present sample is 0.2%, since only one individual in 487 presented it.

In human evolution, progressive dental size reduction on lower second premolars took place, and was accompanied by morphological alterations in the distances between occlusal structures and proportional differences between buccal and lingual halves. If Pliocene to Middle Pleistocene individuals presented large crowns with greater distances between occlusal structures, which resulted in quadrangular teeth, Late Pleistocene specimens compensated the reduction in distances between occlusal structures through an enlarged talonid that resulted in a distolingual bulge. Modern *Homo sapiens* usually present small crowns with oval shapes, and reduced lingual structures (Martinón-Torres *et al.*, 2006). Despite this, additional cusps may be present in *H. sapiens* on either upper or lower premolars, in a feature called molarization (Alt and Türp, 1998). Molarization of a mandibular second premolar results in the increase in the number of buccal cusps, from one to three, and the presence of one to three lingual cusps, besides tooth enlargement (Canut and Arias, 1999).

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The presently reported cases correspond to female individuals. Even so, macrodont lower second premolars occur with equivalent frequency in both male and female individuals (Fuentes and Borie, 2011). The feature seems to be rare in maxillary premolars, since it is highly uncommon in the literature, only mentioned in passing by Alt and Türp (1998).

Molarized or macrodont lower premolars are found in the literature. For example: there is report of a case where molarized lower second premolars perturbed occlusal relations (Canut and Arias, 1999), or of a 22 year old Chilean male with bilateral macrodont LP4 (Fuentes and Borie, 2011).

A single case of macrodontia in an individual's dentition is uncommon. It is characterized by enlarged occlusal area, as a result of greater mesiodistal and buccolingual dimensions (Fuentes and Borie, 2011).

Macrodontia, the designation of abnormally large teeth, which can affect one, some or all teeth of an individual (Alt and Türp, 1998), affected another tooth from the individuals of the present Portuguese sample. Wasterlain (2006) recorded a left mandibular second molar with an enlarged and possibly more complex crown, which was also found in the present sample, although the present author considers it may be a third molar, since it is highly irregular, which migrated mesially due to mesial drift (Figure 4.9.5.).

Peg-shape (upper third molar)

Alterations in normal size are not limited to enlarged teeth. Peg-shaped UI2 were systematically scored using the ASUDAS (Turner *et al.*, 1991) and are presented in "4.4.Dental and oral nonmetric traits", for instance. In Figure 4.9.6., a peg-shaped UM3 is seen, as an example of the several not scored microdont or peg-shaped UM3's. Two peg-shaped and four microdont UM3 were also noted by Wasterlain (2006) in the same population.

The reduction of size or peg-shaped teeth can be regarded as diminished manifestations of aplasia, or absence of a tooth (Alt and Türp, 1998). The agenesis of third molars has long been considered as related to the agenesis of other teeth in the dental arcade, and to delays in the development of teeth (Garn *et al.*, 1963). Reduced or peg-shaped third molars were not scored because of the impossibility of furthering the insight into their agenesis by performing radiographic inquiries. This note intends to

Figure 4.9.5. Detail of the mandible of individual 253 ITC, with an enlarged left molar.

Figure 4.9.6. Detail of the upper dental arch of individual 372 ITC, with a peg-shaped left third molar.

underline the importance of these manifestations, which should be duly reported, especially when the use of radiography is facilitated by time and financial resources.

Paramolar tubercles

The female individual 424 ITC, who was born in Viseu and died at the age of 30 in 1930, has a paramolar tubercle on the mesiobuccal cusp of the right LM2, which is apparent mainly through its most representative feature, a prominent paramolar root which descends for more than half of the buccal surface of the aforementioned cusp (Figure 4.9.7.).

Another female individual, 399 ITC, who was born in Coimbra and died in 1929 at 24 years, presents a bulgier and irregular paramolar tubercle with root involvement also on the right LM2 (Figure 4.9.8.). Of the 491 individuals with at least one LM2 present, this anomaly was found on 0.4% (two individuals, both female).

The fusion of two teeth can occur at any stage of odontogeny. It involves fusion of dentine, and can involve that of pulp chambers and canals. It can be of genetic etiology and its frequencies vary among populations. However, the fusion of molars and supernumerary teeth is unusual. It can contribute to caries formation, periodontal disease and crowding (Ghoddusi *et al.*, 2006). Even so, there are examples: a supernumerary paramolar with independent root and root canal was fused with a lower second molar in the clinical case reported by Ballal and colleagues (2007); a mandibular second molar and paramolar tooth fusion with carious lesions (Ghoddusi *et al.*, 2006).

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Figure 4.9.7. Detail of the mandible of individual 424 ITC, with a paramolar tubercle mainly represented by its *radix paramolaris* (paramolar root).

Figure 4.9.8. Detail of the mandible of individual 399 ITC, with a large and irregular paramolar tubercle with an apparent *radix paramolaris* (paramolar root).

Radix paramolaris is a root formed under a paramolar tubercle, next to the regular mesiobuccal root (Alt and Türp, 1998).

A 42-year-old woman from Viseu, individual 636 ITC, who died in 1931, has a morphological anomaly patent in the buccal surface of the left UP4. This anomaly is a paramolar tubercle (Figure 4.9.9.). Besides the supernumerary tubercle, the premolar seems normal, albeit the moderate to considerable wear that affected it (and did not affect the paramolar tubercle perceivably). Its dimensions are seemingly as expected. The paramolar tubercle does not reach the cemento-occlusal height of the buccal cusp, and is not as wide as it is. However, the supernumerary cusp is buccolingually relatively thick.

Accessory cusps like the paramolar tubercle can be present on premolars, mostly in maxillary teeth (Alt and Türp, 1998). Bilateral paramolar tubercles originate from the buccal cingula of each UP4 of an individual with (presumably unrelated) palatally impacted canine (Turner and Harris, 2004). Both teeth are of an expected buccolingual dimension, with the tubercles as a part of their normal mass. It does not seem to have a functional adaptive origin, since it does not present any occlusal relationship with the lower dentition, and should not contact it even in the presence of advanced wear. The free apices of these cusps denote their origin was an independent enamel knot (Turner and Harris, 2004).

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Figure 4.9.9. Detail of the left upper hemiarcade of individual 636 ITC, with a paramolar tubercle on the second premolar.

Figure 4.9.10. Detail of the mandible of individual 481 ITC, with an apparently mineralized mass of unknown etiology.

The present case is relatively similar to the one presented above, with the exception of the tooth dimensions, which seem to be enlarged when the tubercle is considered in the Portuguese tooth.

Mineralized mass

A 47 year old male individual from Coimbra who died in 1930, 481 ITC, presents an unusual formation in the mandibular bone (Figure 4.9.10.), on the right molar area (all these molars were lost *ante-mortem*). This apparently mineralized substance is slightly irregular in the occlusal facet, but seems to be of well defined margins otherwise. The bone surrounding this unidentified object is cortically widened, although it seems to otherwise envelop it. Radiographic imagery is essential to further understand this finding. However, some tentative differential diagnostics will be attempted.

Odontomas are benign tumors formed within alveolar bone. When differentiated epithelial and mesenchymal cells generate ameloblasts and odontoblasts in abnormal locations, an odontogenic tumor, the odontoma, is created. When these tumors form structures that resemble normal teeth, they are called compound odontomas. When, on the other hand, irregular shaped structures are formed, their name is complex odontoma (Oliveira *et al.*, 2001).

Odontomas can be caused by trauma or infection, are generally asymptomatic and grow slowly. When they are large, which is rare, they can produce a bulge on the

cortical bone. Usually, they are intraosseous and even associated with an impacted secondary tooth, but it is possible for them to erupt (Oliveira *et al.*, 2001).

Other possible diagnoses are more unlikely. Ameloblastic fibro-odontomas are tumors which can present neoplastic behavior and occur mostly in the posterior region of the mandible. They tend to be intraosseous, painless and slow growing. They are well circumscribed and usually easily separated from the bone (Oliveira *et al.*, 2001).

Ameloblastic fibrosarcomas are malignant tumors that can occur as the recurrence of an ameloblastic fibroma or an ameloblastic fibro-odontoma. They are characterized by pain, swelling, and rapid growth. They are not well circumscribed and show a destructive relation with bone (Oliveira *et al.*, 2001).

Odontoameloblastomas are very rare odontogenic tumors that occur more frequently in the mandibles of young individuals, producing a destructive process that can present miniature tooth-like formations or large masses of calcified tissues (Oliveira *et al.*, 2001).

Both of these latter hypotheses are very unlikely, due to the macroscopic superficial characteristics of the potential lesion. Many other possible conditions are likewise unlikely (see Kay [1971] for an example of differential diagnosis).

4.9.2.Superficial alterations

The male 26 year old 36 ITC from Coimbra, who died in 1927, presents superficial alterations to the crowns of his teeth, mainly the molars. His teeth are opaque, present chipped enamel, removed enamel near the cement-enamel junction, fractures (mainly *post-mortem* in the posterior teeth, and *ante-mortem* in the anterior ones, mainly UI1's), and heavy cupping of the dentinal surfaces where the enamel had been previously worn/chipped away (Figure 4.9.11.).

Number 340 ITC, a 43-year-old female individual, also from Coimbra, who perished in 1929, shows heavy pitting of the buccal surfaces of every tooth, more exuberantly so in the anterior dentition (Figure 4.9.12.). The general appearance of the tooth crowns is normal, besides some brownish coloration, mostly found on lower molars, which may be a *post-mortem* artifact or a part of the normal color variation of teeth.

Figure 4.9.11. Occlusal view of the complete maxillary dentition of individual 36 ITC, with discoloration and chipping of the enamel.

Figure 4.9.12. Detail of the labial surfaces of the upper anterior teeth of individual 340 ITC, with widespread enamel pitting.

These cases are two examples of the apparently superficial alterations, due to the quality of the enamel's mineralization. There is at least one other case, that of individual 31 ITC, a Coimbra female of 19 years at death, which occurred in 1927, that poses doubt. There are superficial alterations in some teeth, mainly through loss of enamel in the buccal facets, near the cement-enamel junction. There is no discoloration and no consistent degradation of the enamel on, or nearly on, every tooth. This can be due to the youth of this particular individual. Only radiographic inspection can further the knowledge in this, or any of these cases. However, the differential diagnosis conducted by Wasterlain and Dias (2009) on similar cases from the same population provided some helpful perspective on what these alterations may be.

In these similar cases found in the Coimbra collections, fluorosis was dismissed because of the low fluoride level on the soils in Centre Portugal and the absence of fluoridation. The areas affected and the types of lesions did not correspond to regurgitation erosion, which was also dismissed. Both cases where then diagnosed as hypocalcified amelogenesis imperfecta (or AI; Wasterlain and Dias, 2009).

The distinction of the second case as hypomaturation AI was accomplished mainly through correct and precise radiography (that had to be repeated), since it could have been confounded with dentinogenesis imperfecta (Wasterlain and Dias, 2009).

Hypocalcified AI corresponds to a lack of calcification of the enamel deposited on the tooth, which results in the gradual loss of occlusal enamel early on. The enamel

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can be stained dark, from brown to black (Alt and Türp, 1998; Wasterlain and Dias, 2009).

Dentinogenesis imperfecta (DI) evinces a blue-grey or yellow-brown discoloration of enamel due to poor development of the structure and composition of the underlying dentine. The enamel tends to fracture in the incisal or occlusal surfaces despite its normal state, possibly because of an abnormal enamel-dentine junction (Alt and Türp, 1998; Wasterlain and Dias, 2009).

There are other forms of AI, which were considered by Wasterlain and Dias (2007) in their differential diagnosis. Hypoplastic AI presents teeth with pinpoint- to pinhead-sized pits that interrupt normal enamel deposition, mainly on the buccal side (Alt and Türp, 1998; Wasterlain and Dias, 2009).

Hypomaturation AI is characterized by normally deposited enamel and mineralization where maturation of the enamel crystal structure is absent or incomplete. A mottled opaque and white to brown discoloration is evident in such teeth, which enamel is soft and chips easily, and presents a radiographic density akin that of dentine (Alt and Türp, 1998; Wasterlain and Dias, 2009).

The case of 36 ITC should not be related to airborne erosive materials, since his profession was woodworking craftsmanship, which should not involve such materials. It could be a case of DI or hypocalcified AI, particularly the latter.

The second case, 340 ITC, is most likely one of hypoplastic AI, since the buccal surfaces of teeth are pitted in pinpoint- to pinhead-sized little holes, and the remaining enamel seems relatively normal.

As for the 31 ITC case (not shown), there is insufficient data to provide further comments, since this could represent any of the diagnoses hypothesized above or other, more localized, condition.

4.9.3. Ectopia

Ectopic teeth are those located remotely from their usual eruption site (Alt and Türp, 1998). The female individual 917 ITC, a 17 year old born in Leiria who died in 1934, reveals an ectopic left UM3, which has reabsorbed a part of the posterior alveolar bone, in the left palatine bone (Figure 4.9.13.).

Figure 4.9.13. Detail of the upper posterior alveolar bone of individual 917 ITC, with an ectopic left third molar.

Figure 4.9.14. Occlusal view of the upper dentition of individual 343 ITC, with an ectopic right canine in the palate and a retained decidual right canine.

A female individual of 18 years at death (in 1929), who originated from Figueira da Foz (Coimbra), 343 ITC, presents an ectopic canine which is visible in the palatal process of the right maxillary bone, since it caused the resorption of some of the cortical bone. Besides, the deciduous canine in the same side is still kept (Figure 4.9.14.).

A similar, however bilateral case, is found on the palate of the 934 ITC individual from Coimbra, a female of 16 years when she died in 1934 (Figure 4.9.15.).

These are merely examples, since this ectopia of the canine occurs in ten individuals (1.7% of the 600 individuals in this Portuguese sample; includes bilateral cases), and bilaterally in two (0.3%). Six female individuals are affected (60% of the cases), while only four men are (40%).

One case of buccally displaced canines was also found, in the male individual 330 ITC, born in Figueira da Foz (Coimbra) and dead in 1929, at the age of 21. That individual presented the left canines from both dental arches tipped buccally and deprived of normal occlusion, but at a relatively normal place of eruption.

Maxillary canines are palatally displaced from around 1% to 3% of individuals in a population (Peck *et al.*, 1994). Occurrence of this displacement is always more common in female individuals, according to data cited by Peck and colleagues (1994). Europeans show much more incidence of palatal displacement of the upper canines than individuals of African and Asian descent. In cases of canine displacement, palatal cases are much more common in Europeans than in Asians (Peck *et al.*, 1994). The ectopic

eruption or position of a canine can develop into pathological conditions (see, for example, Dwivedi *et al.*, 2013). Therefore, they should be treated, as the cases reported by Liu and colleagues (in press), of bilaterally impacted canines that achieved correct occlusion after treatment. One of the canines was transposed, while on the other side there was a retained deciduous canine.

Canine impaction occurs in rates between 0.2-2.8% of a population, according to works cited by Delli and colleagues (2013), who evaluated 1636 young adult male individuals from the Greek military. They found impacted canines in 0.8% of the sample, which were mostly in the maxilla and in the right side. It was bilateral in only one of the 14 individuals. Eleven individuals presented retained decidual canines (Delli *et al.*, 2013).

This phenomenon can occur because of retained decidual canines, malformed or absent second incisors, dental crowding or delayed eruptive pathways, among other factors (Peck *et al.*, 1994). The etiological reasons for this displacement of the canine were fervently debated, mainly by Peck and colleagues (1994) and Becker (*in* Becker *et al.*, 1995).

Peck and colleagues (1994) argued the palatal displacement of the maxillary canines is of polygenic inheritance because of the differences in frequencies between the sexes, the co-occurrence within families and the ancestry-related differences. Along with these arguments, they put aside the mechanical hypothesis, or "guidance theory", which correlates this phenomenon with alterations in the size of the crown and/or root, or absence, of the lateral incisor. They see it as disproven because of the relatively low co-occurrence of the alterations, and the apparent dissociation between canine and lateral incisor in the maxillary canine/first premolar transposition. The retained deciduous canine is also dismissed as a cause, and is thought of as a consequence, of the palatal displacement of the canine (Peck *et al.*, 1994).

The first author in Becker and colleagues (1995), a special article providing Becker's response to Peck and colleagues (1994) and their subsequent rebuttal, disagrees with his cited colleagues (Peck, Peck and Kataja). He starts by stating there is no positional anomaly in palatally displaced canines, since their long axes indicate from whence the tooth came, developmentally. Since their long axes indicate they developed in the correct position, there should be the lack of control of the tooth's direction that caused its palatal displacement (Becker *et al.*, 1995).

Becker then explains how the co-occurrence of palatally displaced canines with other dental anomalies of genetic origin can be caused by them, since they influence the environment involving the occlusion of the canine. He also dismisses his colleagues' argument that sex differences are evidence of genetic origin (see Peck *et al.*, 1994), since females are more affected by the dental anomalies that can condition the environmental positioning of the canine. Family occurrence can be either of genetic or environmental origin, as can the ancestral population differences. The author does not assume the guidance theory can explain all the instances of palatal displacement of canines, but it cannot be dismissed since it is behind a part of these cases (Becker *et al.*, 1995).

In their rebuttal, the remaining authors (Peck, Peck and Kataja) explain how the guidance theory is based on methodologically flawed studies with young samples and how the dismissal of genetic factors by Becker seems to be precipitated (Becker *et al.*, 1995).

The results of the study of Yan and colleagues (2013) may help understand this conundrum. Cases of buccally and palatally ectopic canines were compared to each other and to those of other individuals in a Chinese population. Different etiologies were found for both situations. Palatal displacements were associated with reduced mesiodistal dimension of second incisors, while buccal displacements were not associated with any of the anterior teeth mesiodistal dimensions. Narrow anterior dental arch and skeletal width was associated with buccal displacements, but not with palatal ones, which might justify the greater prevalence of the former condition in Chinese people, who tend to present this narrowing more often. The fact that only lateral incisor anomalies directly affected the frequency of palatal displacements of upper canines seems to agree with the guidance theory. Since other aplasias or anomalies of other teeth are associated with displaced canines, but not specifically with palatal canines, this suggests the genetic theory may be wrong.

Incisor impaction may be associated with buccal canine displacements. Differences in the position of the canine cusp tips of buccally (distal to the long axis of the lateral incisor) and palatally (mesial to the long axis of the lateral incisor) displaced canines in the mesiodistal plane may provide an etiological explanation for these displacements. If developing and erupting canines derive mesiopalatally and occlusally, they normally should be limited in their movement by an adequately and timely developed lateral incisor root that points them to the centre of the alveolar bone for

Figure 4.9.16. Detail of the maxilla of individual 489 ITC, with a supernumerary distal molar.

Figure 4.9.15. Occlusal view of the maxillary dentition of individual 934 ITC, with bilateral ectopic canines in the palate.

normal occlusion. In the case there is radicular crowding or an impacted incisor, that obstruction can drive the canine buccally. In the case there is only a small root or a root limited in size by late development, the lack of a block can open way for a palatal displacement. The relative rate of this migration can further affect the canine's positional outcome: if the tooth derives towards the occlusal direction with greater speed than towards the mesiopalatal direction, it can still occlude normally, despite of the lack of guidance from the second incisor root (Yan *et al.*, 2013).

In the Coimbra population, this displacement of canines could therefore be caused by smaller UI2 or their smaller roots, since no cases of agenetic or peg-shaped UI2 were detected in association with these occurrences.

4.9.4. Supernumerary teeth

The individual 489 ITC, a 16-year-old male individual who died in 1930 and was originally from Coimbra, displays a supernumerary reduced molar in the distal end of the upper right molar area, partially covered in a brownish glue, probably used to conserve the teeth in place sometime in the past (Figure 4.9.16.).

There are other possible supernumerary teeth in the present sample, involving seven individuals (1.2% of the 600 individuals), but the remaining six cases are mostly comprised of empty alveolar sockets that may have held supernumerary teeth or retained decidual teeth. One other case is doubtful, since there is an apparent socket

with mineralized material of a relatively irregular shape, which can be a fractured supernumerary tooth or a neoplasia (radiography should clarify the finding). Four of the empty alveoli are located in the medial line of the maxillary arcade, and so were probably mesiodentes.

Wasterlain (2006) also found two extra alveoli that could be occupied by either supernumerary or retained decidual teeth in a sample from the same populations, with some overlap with the present sample.

Permanent supernumerary teeth are those teeth that surpass the usual 32 dental pieces present in the permanent dentition, and can be eumorph or heteromorph (Alt and Türp, 1998). The three preferred regions for supernumerary teeth are the anterior maxilla, the molar region of the maxilla, and the premolar region of the mandible. Mesiodentes, paramolars and distomolars are the most common types, from most to least frequent. These are irregularly shaped, usually, while the lower premolar region tends to present anatomically correct supplemental teeth (Alt and Türp, 1998). Supernumerary teeth can be uni- or bilateral, mandibular or maxillary, single or multiple. The phenomenon involving these supernumerary teeth is called hypodontia, and they can erupt around 25.0% of the time (Corrêa *et al.*, 2009). They develop mostly in the first two decades of life and are present in 0.1 to 3.5% of individuals (Alt and Türp, 1998; Corrêa *et al.*, 2009; Delli *et al.*, 2013).

It is more frequent in males, in the maxilla, and on the anterior portion. Etiologically, its origin is uncertain. It may be caused by an extra tooth germ from the dental lamina and be of autosomic dominant transmission, without penetrance in some generations. It is also associated with some pathologies of genetic etiology (Corrêa *et al.*, 2009).

A mesiodens can be present in the permanent dentition in between 0.15% and 3.8% of individuals. It can cause crowding, delays in eruption, midline diastemas, rotations, cysts and the resorption of adjacent teeth (Vautier *et al.*, 2012).

Resulting damage to an individual's health is manifested through such conditions as crowding (and other occlusal maladies), impaction of permanent teeth, retarded or ectopic eruption, dental rotation, diastemas, permanent tooth resorption, etc. (Corrêa *et al.*, 2009).

In the Greek army, 1.5% of the 1636 males observed presented non-syndromic supernumerary teeth, mostly in the maxilla. Distomolars were more common in the

maxilla and supernumerary premolars were more common in the mandible (Delli *et al.*, 2013).

In Brazil, 843 individuals, aged 12 to 20 years, were analyzed for hypodontia, and 2.5% (24 individuals) had the condition, presenting several related complications: lessened arch integrity, impaction, crowding, pain, tooth rotation, resorption, a cyst, a composed odontome, and inadequate positioning of the three permanent teeth. Only three cases had no symptoms associated with hyperdontia (Corrêa *et al.*, 2009).

The Portuguese population of the 19th and 20th centuries should be further analyzed, preferably with radiographic imagery, so as to better characterize the prevalence of supernumerary teeth in that population. It seems from this study that around 1.2% of individuals presented supranumerary teeth, and mesiodentes were more than 50% of those.

4.9.5. Retained decidual teeth

Figure 4.9.17. shows a decidual right second molar in the place of a LP4, which may be congenitally missing or impacted underneath. Figure 4.9.14., mentioned above because of the palatally displaced permanent canine, shows a deciduous canine in its occlusal place.

In 9 of the 600 individuals studied there were retained primary teeth (1.5%). Two are upper canines (22.2%; one from each side) and the remaining seven are second molars (77.8%). Wasterlain (2006) reported two (one upper and one lower) retained decidual second molars in a sample drawn from the same population (with some overlap).

Retained decidual teeth can occur because of tooth aplasia, because of the agenesis of the permanent tooth or its diminished size and delayed ontogeny (Alt and Türp, 1998). Decidual dentition is resorbed and exfoliated only in the presence of the permanent successor (Sletten *et al.*, 2003).

When healthy, decidual second molars are likely to be retained in adult age for many years; when they are eventually lost, there is a great likelihood they will have survived for as long as prosthetic substitutes. Their roots are scarcely shortened over many years, and their submergence is not altered either. Sletten and colleagues (2003)

Figure 4.9.17. Detail of the mandible of individual 306 MSC, with a retained deciduous right second molar.

Figure 4.9.18. Detail of the mandible of individual 388 ITC, with a reconstructed right second molar and a possibly treated right second premolar.

therefore conclude the maintenance of these teeth is recommended as a valid clinical option.

The Portuguese individuals of the present sample in this situation, with retained deciduous second molars, were likely to have been favored by it, since they kept occlusal proficiency in mastication.

4.9.6.Dental treatments

Albeit their rarity, evidences of dental treatments were found in the present sample, as had been noted in Wasterlain's (2006) dissertation. A dental amalgam seems to have been used in the right LM2 seen in Figure 4.9.18. (and possibly in LP4, which could also have been pivoted) and in the right UM2 seen in Figure 4.9.19. A lighter reconstructive filling was apparently used in the left LM3 seen in Figure 4.9.20., which Wasterlain (2006) hypothesizes could be silicate cement. These types of reconstructions were found on eleven individuals of this 600 individual sample (1.8%).

Dental treatments were rare in the period which encompasses the present sample (19th to mid-20th centuries), presumably because they were expensive and there were only two dentists practicing in Portugal. Besides, minor treatments like dental removals were often done by unqualified individuals (Wasterlain *et al.*, 2009).

Figure 4.9.19. Detail of the upper dental arch of individual 507 ITC, with a reconstructed (fractured *post-mortem)* left second molar.

Figure 4.9.20. Detail of the mandible of individual 739 ITC, with the left third molar reconstructed with a light filling.

Dental fillings at this time were predominantly made of tin. Gold was recommended as the ideal material; however the cheaper alternative lay with tin (Glenner *et al.*, 1996). Tin and silicate cement were thought as the materials potentially used in reconstructions reported on by Wasterlain (2006), for the same population. In an 18th century French reconstruction, the dental filling was made of a dental amalgam mainly made of tin (Bertrand *et al.*, 2009). Besides tin, thorium, led and tungsten were found on the dental amalgams used in United States Civil War veterans (Glenner *et al.*, 2006).

The present findings are coherent with their coeval and earlier counterparts, and demonstrate by their proportion the lack of dental treatment available at an affordable price at the time.

4.9.7. Bone changes

Maxillary bone erosion

The differences between apical granulomas and apical periodontal cysts, two common types of periapical inflammations, are described for skeletonized material by Dias and colleagues (2007). One of the exampled used was also included in the present sample, 21 ITC, and was diagnosed by the authors as affected by a large periapical periodontal cyst. Another relatively similar case was found. A male individual, 550 ITC, born in Coimbra and dead in 1930, at the age of 47, presents a bone lesion on the

Figure 4.9.21. Palatal view of individual 550 ITC, with erosive destruction of the left palatal process of the maxilla.

Figure 4.9.22. Maxilla of individual 836 ITC, with an oval depression on the incisive canal.

left palate (Figure 4.9.21.), which characteristics are somewhat similar. However, there is irregular bone erosion on the cortical bone separating the palatal process from the maxillary sinus, which may indicate a different etiology, since a malignant neoplasm of the maxillary antrum can be identified by destruction of bone, when at an advanced stage (Kay, 1971). Other small bone lesions are found on the left frontal bone and, if etiologically related, could indicate a neoplastic nature for these alterations. Once again, radiography may enlighten this enigma.

Palatal cyst

The 66-year-old male carpenter born in Figueira da Foz (Coimbra), who died in 1932, 836 ITC, presents a regular ovoid depression at the palatal end of the incisive canal, or nasopalatal duct (see Figure 4.9.22.). This type of very regular alteration does not seem to correspond with a malignant neoplasia, and its very specific location pointed towards a probable diagnosis: nasopalatine duct cyst.

The nasopalatine duct cyst, the most frequent cyst of non-odontogenic etiology, appears in approximately 1% of the population and is developmental in origin. It is most common between the ages of 40 and 60 years, but can occur from childhood to senescence. Some authors report it as more prevalent in males. Symptoms can be swelling, drainage and pain, even though they can also be asymptomatic (Ely *et al.*,

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2001; Nelson and Linfesty, 2010). Nelson and Linfesty (2010) presented one such case: a 41 year old male with a nasopalatine duct cyst without history of pain or swelling.

In Brazil, 31 nasopalatine duct cysts were identified in 12591 biopsies. They were found in individuals with ages from 20 to 69 years, and mainly in male Caucasian individuals. The cysts were all walled by dense fibrous connective tissue, which presented relatively frequent inflammation and hemorrhage. Most cysts were enervated and some were vascularized. Lamelar bone tissue, mucous glands, cholesterol clefts, skeletal muscle and cystic fluid were occasionally present (Vasconcelos *et al.*, 1999).

Twenty seven cases were asymptomatic. The cysts were usually presented with a well circumscribed cortical bone border (Vasconcelos *et al.*, 1999). This seems to have been the case in this situation. There does not seem to be any inflammation of the cortical bone in the palatal process of the maxilla, and the well circumscribed cyst seems to correspond to a relatively common manifestation of the nasopalatal duct cyst.

Deformed mandibular condyle

Individual 636 ITC, a female who died in 1931 at 49 years, and was originally from Viseu, conserves an altered left mandibular condyle (Figure 4.9.23.). This condyle presents a deep anteroposterior depression across the articular facet, with corresponding alterations in the temporal articular facet of this joint.

The temporomandibular joint is a compound synovial articulation, since the articular disc is akin to a bone and produces two separate joints with each bone's fibrocartilage. The involved bones are the articular eminence of the temporal bone and the condyle of the mandible. This joint is highly adaptive in response to external stressors, and can present morphological changes that look unusual and are, in fact, part of the normal variability of this joint (Rando and Waldron, 2012). This, however, does not seem to be such a case.

Temporomandibular disorders are pathological events related to the masticatory muscles, the temporomandibular joints and surrounding structures. Osseous chances in the temporomandibular joints are more common with age, and can be associated with intrinsic and extrinsic factors. Age, genetics, sex, ancestry and excessive weight are possible intrinsic factors. Extrinsic factors can be chronic overload of the joint, through bruxism, reduced occlusal support, dental wear, and chewing hard foods (Levartovsky *et al.*, 2012).

Osteoarthritis is the destruction of the articular cartilage, which results in affected bone structures, with new bone formation, porosity, eburnation and morphological alterations to the joints (Rando and Waldron, 2012). Osteoarthritis of the temporomandibular joint is attributable to overload, and is a process of degradation and abrasion of the articular surface that results in its loss and in remodeling of the associated bone (Levartovsky *et al.*, 2012). It is a common temporomandibular disorder, and was therefore hypothesized as the type of lesion present in this mandibular condyle.

Despite the usual association with age, in a relatively young Roman-Byzantine Israeli sample, osteoarthritis in the temporomandibular joint was associated with the loss of molars. This may be justified by the low average age of the anthropological sample, but suggests the importance of molars in reducing the load on the temporomandibular joint during mastication (Levartovsky *et al.*, 2012).

The present individual is a female of 42 years at death, as noted, who only conserves the left LM2 in the mandible and has lost only the left UM2 *ante-mortem* in the maxilla. This pattern of tooth loss precludes the remaining molars of directly occluding opposite any tooth. So, that could be, like the Roman-Byzantine case mentioned above, the reason for this temporomandibular disorder. However, this alteration is unilateral, since the right temporomandibular joint is anatomically normal. Since this does not seem to be a malignant tumor, as there are no bone growths and the alteration does not seem to be osteolytic, this may be a congenital or developmental lesion.

Condylar hypoplasia is the unilateral or bilateral underdevelopment or improper morphology of the developed mandibular condyle. It can be congenital or acquired during growth. When acquired, its causes may be local factors, such as trauma, mandibular bone or middle ear infections, or irradiation; or systemic, like infections, toxic agents, rheumatoid arthritis or muccopolysaccharidosis. This condition is commonly found in association with ankylosis (Agrawal *et al.*, 2011).

Mandibular growth through bone deposition occurs in the posterior ramus in horizontal growth and in the upper area of the ramus (including the condyle), when vertical growth is concerned. In subadults, the deformation of mandibular condyles results in vertical adaptations (bone deposition in the lower part of the ramus) which cause a slight open bite due to the insufficient height of the alveolar processes. In adults, deformed condyles result in horizontal adaptations, which produce a retrognathic

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Figure 4.9.24. Maxilla of individual 323 MSC, with a leathery or parchment-like substance clinging to the palatal processes and anterior alveolar bone.

Figure 4.9.23. Mandible of individual 636 ITC, with deformed left condyle.

mandible (Dibbets *et al.*, 2013). Neither of these alterations are apparent in the present case, which can indicate this lesion is not of developmental etiology.

Further research and analysis of the specimen will allow for a more complete and conclusive differential diagnosis, which may allow for this lesion to be identified as a congenital or acquired condylar deformation.

4.9.8. Possible mummification of soft tissues

Figure 4.9.24. reveals a the palate and upper dental arcade of female individual 323 MSC, a 33 year-old house-maid who died in 1900, and was originally from Lisbon. Some yellowish, parchment-like substance clings to the palatal processes. The same material, albeit in a much diminish quantity, is also found on the female individual 349 MSC, a 35 year-old who also died in 1900 (not shown). This material likely is mummified skin (Laura Mateiro, personal communication, August 7th 2013).

After death, the soft tissue in the body tends to decompose, going through several stages of alterations due to the lack of circulation and autolysis (cellular self-destruction) as well as microbe action (Mateiro, 2010).

Tissue of no nutritional value, such as skin, can mummify. It survives the active decay of nutritionally rich tissues, and dehydrates or desiccates (Vass, 2001). Mummification results from rapid fluid leakage, which obstructs putrefaction and leads

to depletion of hydric tissue. Natural mummification is promoted by widespread hemorrhage and dehidration, and in older people or fetuses (Marella *et al.*, 2013). Mummification, which can be natural or artificial/intentional, is the dehydration of soft tissues that can occur in dry and hot, or ventilated and icy, environments. Dry or cold environments, with low oxygen supply, favor natural mummification (Vass, 2001; Mateiro, 2010; Marella *et al.*, 2013). Evisceration, the use of fire or certain substances in a cultural or traumatic context can result in an artificial, however unwilling, preservation of the body (Mateiro, 2010; Marella *et al.*, 2013). When there is intent on preserving the body, it is considered intentional mummification (Mateiro, 2010).

Saponification is also a natural occurrence which can result in the conservation of soft tissues, and consists in the hydrolysis and subsequent hydrogenation that derive from the dissolution of water and fatty tissues in the body, which accumulate as adipocere in the skin of the diseased. It is susceptible in hot or wet environments (Mateiro, 2010).

Mateiro (2010) was authorized to study six mummified individuals popularly viewed as "saints", since their bodies were conserved after death and found later. A macroscopic analysis of these individuals revealed diverse degrees of conservation, with reconstructed, skeletonized and mummified portions of their bodies. This study was not able to answer which phenomena interacted to promote the mummification of these individuals. The author was, however, able to confirm these mummifications presented no evidence of intentional preservation of the body, or of any intervention which unknowingly promoted an artificial conservation, and most likely were, therefore, natural mummifications.

The individuals from the present sample mentioned above belong to the Medical Schools Collections, as noted. This collection originated from material kept in medical schools and an anatomy museum (see 2.Sample). Presumably, some conservation technique or substance, or the air and temperature qualities of the place they were originally kept in promoted this mummification.

5.Conclusions

The dental crown and oral bone morphology of 600 individuals from Portugal was studied. Both sexes are equally represented within the sample. These individuals are kept in two identified collections of the Department of Life Sciences of the University of Coimbra. They were mostly born in Coimbra, and almost entirely born in Portugal, between the early 19th century and the early to mid-20th century. All died in Portugal between the mid to late 19th and the mid-20th century.

The Arizona State University Dental Anthropology System (ASUDAS) was the main methodology used to characterize the sample. Methods provided by Smith (1984), Hauser and De Stefano (1989), Galera and colleagues (1995), Irish (1998b) and Weets (2009), along with several statistical tests were also applied.

The time frame represented by the described sample was one of political and social turmoil in Portugal, as driven by the conservative qualities of those same political and social systems. A lack of sustainable growth or investment in the industrial or agricultural spheres threw the country into poverty. In spite of the large territory held by the Portuguese all around the world and the country's recent world power status, its people were mostly underemployed and underfed. During most of the time span of this sample, people emigrated in order to strive for a better life elsewhere, mainly in Brazil, a former Portuguese colony.

This work's main objective was to understand the biological results of the population movements that, like the emigration towards Brazil, marked the successive historical periods of the presently Portuguese continental territory. It also aimed (a) to understand the effect of the aforementioned poverty in the dental development of the Portuguese population, (b) to understand the morphological differences related to sex, asymmetry, health, birthplace and time of birth that can be found in the teeth and oral bones of the sample, and (c) finally, this research also intended to further test the reliability and reproducibility of the ASUDAS method and of dental nonmetric traits, through the analyses of the effects of intra-observer error, dental wear, intratrait correlation and count methods.

5.1. Intra-observer error

The intra-observer error (or precision) measure is an indication of a scorer's ability in reproducing his observations systematically. It also allows other workers to

understand the reliability of the shared data, and therefore infer the data's usefulness in further research. Besides this, the scoring error is a test to a method's quality, since it should be objective and easily learnt and applied.

The mean exact overall precision in scoring the coronal nonmetric traits was 89.4%, between the first and second full sample scoring sessions. These scoring sessions are valued the most, for their involvement of the whole sample and the use of the second observation on further analyses. For the same paired observations, precision within one grade was 96%, and precision on dichotomized (presence/absence) data was 94.5%. The only trait that posed a systematic problem in scoring reliability was UI2 *tuberculum dentale*, which was subsequently removed from further analyses. The complex morphological diversity of the trait was a confounding factor, and very often lead the scorer to question and hesitate on the precise grade to score each case. Besides this trait, only LC distal accessory ridge presented dichotomized data precision under 85%, which was likely caused by the trait's susceptibility to dental wear. The precision within one grade was 95.7%, which reinforces the difficulty was mainly on distinguishing weak expressions of the trait from its absence in the presence of wear.

The determination of the scorability of each trait's site was of high reliability, since it presented a mean precision of 97% between the main observations.

As for the dental wear evaluation of teeth, the mean overall precision was only 74.8%. However, precision within one grade of error was 99.6%, which illustrates how the overall precision was affected by threshold wear grades. This could easily cause teeth to be divergently scored on either of the main scoring sessions.

The oral nonmetric traits were also studied for intra-observer error. The mean exact overall precision between the first and second observations was low: 82.8%. When dichotomized data were compared, the precision only rose to 86.4%. This low result was mostly caused by the oral *tori*, palatine *torus* and mandibular *torus*, since the *foramina mentales* and the mylohyoid bridge were consistently scored. These traits were scored using the ASUDAS and Galera and colleagues' (1995) methodologies, so as to increase comparability. However, this probably resulted in greater confusion. These traits were not removed from the subsequent analyses. Nevertheless, they were scarcely used, and only when the battery of traits accompanying them was large.

The oral discrete traits were consistently considered as scorable between the main observations, with a 99.3% precision.

Intertrait correlation can affect some statistical tests, because it renders traits redundant when they are analyzed along with the traits they correlate to. Besides, they can have some relevance in the study of dental nonmetric trait development, since their dependence can help explain how that entails. The present sample did not yield any strongly correlated traits, besides some cusp number correlations to the presence of the cusps themselves, which was expected. Even traits that have been found to correlate in other samples, - like hypocone and Carabelli's trait (Scott, 1979a), - did not correlate in the Portuguese sample.

5.2. Fluctuating asymmetry

Asymmetry is usually only an issue of review in dental morphology when a small sample demands the use of the tooth count method. This is because a very asymmetric sample can cause excessive dispersal of frequencies when all teeth are considered.

In the present study, dental morphology fluctuating asymmetry (FA) was considered as a potential measure of developmental instability. The results for the sample are difficult to compare, since there are few published data on the subject. However, the overall asymmetry found was 9.2%. The asymmetry frequency of 63.5% was calculated when bilateral trait absence is removed (so as to render the sample comparable to biologically diverse populations, which can present very different trait frequencies). When traits with small samples are removed, the asymmetry frequency is 49.5%. These seem relatively high, and may indicate that poverty in Portugal affected development. However, further research is required before such conclusions can be arrived at.

5.3. Sexual dimorphism

There is statistically detected sexual dimorphism in 12 of the 61 dental and oral discrete traits evaluated for that parameter. Some sexual dimorphism was expected and its relatively low frequency is more than acceptable, since usually sexual dimorphism is not a hindrance in dental morphology studies when low differences appear. It was most likely found with statistical significance because of the large sample size, since

frequencies are mostly very similar. The separation of sexes would only confound any potential conclusions, and the even distribution of sexes in this large sample does not allow for either sex to condition the results.

These instances of sexual dimorphism may in part be caused by an interesting find: FA is consistently different between the sexes. This may be due to biological distinctions, or sociocultural differences in childrearing and early definitions of gender roles or statuses. A lack of statistical dissimilarities in FA between subadult and adult individuals questions the likelihood of early death of males affected by developmental instability, which can nevertheless be an explanation to the sexual dimorphism in FA.

The four "generations" (chronological divisions related to birth year) established for the present sample testified to some biological continuity across time within the sample, as expected. None of the "generations" was found to be an outlier, very different from the others. FA differences between the generations were also sought, and were not found. This indicates this population was submitted to a relatively constant developmental instability, which also testifies to the maintenance of the general state of the country between the 19th and the mid-20th centuries. There is a temporal trend in FA. However, it was found when the sexual differences between "generations" were compared. Apparently, the last three "generations", the ones with sizeable sample, present a decrease in the amplitude of FA difference between the sexes. This may be because of differences in sample numbers or because of an actual greater parity in the rearing of male and female children.

The sample was also found to be fairly biologically homogenous when separated by birthplace, in both the district and the regional scales, as long as smaller samples are not given disproportionate importance. The larger district samples of Coimbra, Viseu, Guarda and Leiria mostly clustered together. The Centre and North regions of Portugal, also better represented in the sample, were also close to one another. Despite of the existence of some variety in the average FA for each district, there is no statistical corroboration of that find, which may be due to random sampling. On the other hand, statistical results concerning this matter on different regions demonstrated mixed results, which demand further observations to understand clearly if average FA is indeed different in each of the three Portuguese regions. The sexual differences in FA among districts are not clear, because of most districts' small samples. Even so, they suggest this is a worthwhile avenue of research, since there could be a pattern of geographical differences in FA distribution between the sexes that would indicate

potential differences in historical childcare practices across the country. The broader scale presents smaller differences for the North and South regions, with the Centre displaying greater FA frequencies for females. The latter regions, however, should be further inquired into, since the samples are small (particularly the South region).

Individuals with low levels of FA present many traits with lower frequencies, when compared to individuals of high FA levels. Its cause is uncertain, but can be related to (a) the destruction of crowns, (b) increased FA in teeth with greater trait expression, (c) biological differences, and/or (d) developmental plasticity as a reaction to stress that prompted trait occurrence.

Since developmental instability may increase susceptibility to disease and mortality later in life, the mean percentages of FA for each death causing group of diseases were compared. Apparently, there is no connection between FA, as a measure of developmental instability, and cause of death. Nevertheless, more research on this subject will further enlighten the relation between development and life cycle.

5.4. Eurodonty

The thorough characterization of the Portuguese sample studied would not be complete before its general comparison with other European dental morphological variables' frequencies was accomplished. Eurodonty was recently defined by Scott and colleagues (2013). Some of the traits deemed important to that geographical characterization of trait frequencies distributions were also scored in the present sample. Those corresponded to the expected frequencies for a Eurodont population, with the exception of Carabelli's trait, which is present at a low frequency, considered unusual for Europeans and Caucasoids.

5.5. Biological affinity analyses

Coimbra's dental and oral nonmetric data were compared to that of many other populations, in a series of twenty-six analyses. These allowed for a clear understanding of Portugal as a European and Iberian population.

Other preliminary (since they were dependant on the diversity and quality of the bibliographically available data) conclusions were gathered. These include the

suggestion of a general biological resemblance among Iberian samples, particularly those of synchronic, or nearly so, provenance. Iberian samples tend to either cluster together (when compared to foreign samples) or establish equidistant positions (when only compared to each other. Portuguese samples, as a rule, are also nearer one another, which allowed the possible identification of a sample of unknown origin as Portuguese.

Also clearly hinted at is the influence of the North African presence in Iberia, noted in the compared populations that were older than the eight century, including the Coimbra sample. This is noticeable at several scales, from the comparison of world-wide samples, to the comparison of Coimbra with several (North and Sub-Saharan) African samples, and the analysis of many Portuguese and Spanish pre- and post--Islamic occupation samples.

The importance of the Roman Empire to World History cannot be denied, and Portugal in not an exception. Gene flow from this centuries' long phenomenon is calculated as feeble at the best, however. Although that may be the case, there is evidence that the presence of Roman envoys, armies and veterans in the Iberian Peninsula left a lasting biological effect in the Portuguese genetic landscape. This was demonstrated by the relative closeness of two Imperial Roman cities to Coimbra and other post-Romanization samples. Another possible interpretation might be shared ancestry or a greater previous biological proximity between the Lazio region and the Iberian Peninsula, particularly Portugal.

Finally, Portugal was the center of its own Modern Age Empire, conquered mostly by sea and trade. The effect of the European conquest (which was not exclusive of Portugal) was particularly evident in South America, due to the replacement of Native Americans with individuals of European and African origin. The Portuguese gene flow into Brazil was analyzed, and revealed to be very extensive, since it was seemingly more important than any other found for the ethnically diverse sample of contemporary Rio de Janeiro. This testifies to the continuous gene flow from Portugal, which started in the late 16th century and has lasted until today, lately through migration to the long independent Brazilian Republic.

5.6. Dental wear

The quality of the ASUDAS as a method for evaluating dental morphological traits can be measured in several ways, such as the intra-observer error, mentioned above. Dental wear is probably the most relevant factor in the way of a scorer's accuracy and in evaluating the way ASUDAS is capable of characterizing the biological diversity within a sample. So, dental wear's relation with intra-observer error and trait frequencies was evaluated, so as to further inform on the reliability of the ASUDAS and its limitations.

Surprisingly, wear rate was almost constantly associated with better precision frequencies for each trait. This shows how ASUDAS is adequately adapted to be used to score teeth with moderate to high wear rates. Observer care in scoring worn teeth (as advised by the ASUDAS) most certainly contributed to this result. The lower precision associated to lower wear rates may be caused by a more relaxed approach of the scorer towards such teeth, or to a greater tendency to try and score them even when doubt arose. On the other hand, individuals that displayed higher mean wear rates were consistently associated to lower trait frequencies. This probably means that wear does affect the accuracy of the ASUDAS, and the mean wear level should always accompany reports on dental morphology, so it can be corrected for. Samples should only be confidently compared with samples with similar mean wear, so as to not have analyses affected by differences in the volume of dismissed data (because of high wear rates) or the volume of ill-scored crown traits. It should be noted that this, in general, is not a tragic conclusion. Wear rates are mostly similar, so samples are mostly comparable. Dental morphological analyses have successfully presented results that mimic those obtained from other sources, when analyzing migrations and population genetics. This means dental wear does not put the usefulness of coronal nonmetric traits into question.

5.7. Count methods

The count methods through which trait frequencies are determined are also very important to the analysis of dental and oral morphology traits and their comparison with other samples. In order to study the effect of the differences between count methods, they were compared and their distribution was analyzed statistically. They are not

randomly dispersed, and they should all be useable, even if the preference should always fall on the individual count method, which considers the most expressive phenotype as most closely representative of the genotype underlying it. The tooth count method is useful when sample size is too small to allow for any data to be wasted, and is the most reasonably expressive count method, next to the individual count method. This is because the side count method can express more divergent and disparate frequencies, and should never be used. Besides being wasteful (since it discards one side entirely), it is the less representative count method. The expression count method, which weighs the representation of trait grades, was used to analyze the biological differences within the sample, and its weighing considered the data from the individual count method. It is mostly useful to comparable biologically close samples (or subsamples) with little trait frequency differences.

5.8. Future research

Future research in the field of Dental Anthropology cannot ignore how some of the individuals involved in producing valuable data on some osteological series, namely of archaeological provenance, are not specialists in the area. In the case of the subfield of Dental Morphology, the establishment of a protocol would be extremely useful in the advance of the knowledge of population movements and interrelations. This should determine a minimum number of dental and oral nonmetric traits (and which teeth to observe) to analyze as a routine part of the paleoanthropological study of a sample. To complement such a protocol with clear indications to report all frequencies for each grade of each trait, or with a definition of which breakpoint to use when reporting data would be equally as important, to allow for a wide comparability of data by researchers.

The study of FA applied to dental and oral nonmetric traits requires further research. That should enlighten how FA frequencies are related to sex, population and environment, besides the self-evident role of genetics. A greater understanding of such (and other) variables will allow for stronger conclusions to be driven from the data, and a greater knowledge of the diversity in the expression of FA on dental and oral nonmetric traits should facilitate those same conclusions, through the provision of comparable data. The variation of FA frequencies across time in the Portuguese territory

and their relation with migratory and environmental history should provide an ample resource of pertinent scientific questions, resulting in plenty of work in the next years.

The particular traits that the present author suggests require further research are the mandibular molar pit-tubercle (MMPT), the midline diastema and *tuberculum dentale*. The first, MMPT, is still scarcely studied, and the distribution of frequencies of such variable is virtually unknown. Its usefulness will be further understood when such frequencies from other continents are published. As for the midline diastema, its relation with dental wear should be enquired. There is also need for data from more geographically and ethnically diverse origins, to better illustrate midline diastema's world-wide distribution. Finally, *tuberculum dentale* presented a clear and ultimately insurmountable challenge to the present investigation, since the error recorded among the observations was far too wide to be ignored (see above). This suggests that a new plaque, possibly complementary to the existing one should be devised, mainly because of the distinctions between shapes when the trait is present, which can severely condition the identification of the correct grade to attribute to each tooth.

The Portuguese Modern to Contemporary population can be considered thoroughly analyzed and characterized in terms of dental morphology, as a whole. However, the districts, the major administrative division of the Portuguese territory, are differentially represented, and have only been poorly compared to one another, when possible. Those comparisons could be of interest, and show the influence of different migratory patterns throughout Portugal. Besides this, the potential differences in FA frequencies could enlighten the causes underlying that phenomenon, as was suggested above.

The comparisons between Portuguese districts could be unfruitful if the migrations into Portugal were unknown, or largely so. That consideration gives way to what may be the most enthusiastic challenge of the study of dental morphology in Portugal: the assertion of the contribution of the presence of several waves of cultural and/or biological presences in our prehistory and history. The need for more data on Portuguese populations, from as early as prehistory, but also from protohistoric (with occupants or cultural providers such as the Celts) or historic contributors to the cultural, historical (and, potentially, biological) development of Portugal, such as the Romans, the Visigoths, the Suevi, the Muslims (and other contemporary immigrates), and the sub-Saharan African slaves, cannot be forgotten. The biological impact of the Portuguese presence on other continents, such as in Africa (Mozambique, Angola, Cape

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Verde, Guinea, São Tomé and Príncipe, etc.), South America (Brazil), Asia (India, Macao) and Oceania (East Timor) is another avenue of research which can benefit from dental morphology.

Historical migrations into and from Portugal, and particularly their biological impact in the subsequent populations, are of interest to biological archaeology and anthropology, since their study can enrich our knowledge on the cultural and biomedical intricacies of small scale evolutionary processes and on the History of Europe and the World.

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Appendix

Appendix 1. Identification of the individuals included in the studied sample.

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
9	TI	15	F	1911	1926	Criada de servir	Miranda do Corvo, Coimbra
15	TI	24	F	1889	1904	Costureira	Coimbra, Coimbra
21	TI	84	F	1843	1927	Doméstica	Coimbra, Coimbra
28	TI	49	F	1878	1927	Doméstica	Coimbra, Coimbra
31	TI	19	F	1908	1927	Doméstica	Coimbra, Coimbra
35	TI	19	F	1908	1927	Doméstica	Coimbra, Coimbra
37	TI	42	F	1885	1927	Doméstica	Miranda do Corvo, Coimbra
38	TI	12	F	1915	1927	Unknown	Figueira da Foz, Coimbra
40	TI	17	F	1907	1927	Enfermeira	Coimbra, Coimbra
43	TI	96	F	1831	1927	Doméstica	Coimbra, Coimbra
44	TI	33	F	1894	1927	Doméstica	Coimbra, Coimbra
48	TI	16	F	1911	1927	Doméstica	Coimbra, Coimbra
52	TI	45	F	1882	1927	Doméstica	Coimbra, Coimbra
58	TI	24	F	1903	1927	Doméstica	Coimbra, Coimbra
59	TI	34	F	1893	1927	Doméstica	Coimbra, Coimbra
71	TI	17	F	1910	1927	Doméstica	Coimbra, Coimbra
72	TI	23	F	1904	1927	Doméstica	Figueira da Foz, Coimbra
80	TI	27	F	1900	1927	Doméstica	Coimbra, Coimbra
93	TI	54	F	1873	1927	Doméstica	Coimbra, Coimbra
94	TI	18	F	1909	1927	Doméstica	Coimbra, Coimbra
95	TI	12	F	1915	1927	Encadernador	Coimbra, Coimbra
100	TI	63	F	1859	1923	Doméstica	Porto, Porto
107	TI	17	F	1910	1927	Doméstica	Coimbra, Coimbra
113	TI	10	F	1917	1927	Unknown	Coimbra, Coimbra
118	TI	28	F	1894	1922	Doméstica	Coimbra, Coimbra
126	TI	50	F	1878	1928	Doméstica	Arganil, Coimbra
128	TI	63	F	1865	1928	Doméstica	Coimbra, Coimbra
129	TI	13	F	1915	1928	Unknown	Santa Comba Dão, Viseu
131	TI	26	F	1902	1928	Doméstica	Coimbra, Coimbra
137	TI	18	F	1910	1928	Doméstica	Coimbra, Coimbra
138	TI	24	F	1904	1928	Doméstica	Coimbra, Coimbra
140	TI	19	F	1909	1928	Doméstica	Coimbra, Coimbra
142	TI	36	F	1892	1928	Doméstica	Penacova, Coimbra
163	TI	30	F	1892	1922	Vendedeira ambulante	Porto
164	TI	52	F	1876	1928	Doméstica	Coimbra, Coimbra
169	TI	57	F	1871	1928	Doméstica	Tábua, Coimbra
3	TI	27	M	1899	1926	Guarda cívico nº nº 68	Coimbra, Coimbra
4	TI	24	M	1899	1923	Trabalhador	Coimbra, Coimbra
8	TI	43	M	1883	1926	Trabalhador	Miranda do Corvo, Coimbra
10	TI	19	M	1904	1923	Sapateiro	Chaves, Vila Real
13	TI	57	M	1858	1915	Cortador	Coimbra, Coimbra
19	TI	24	M	1903	1927	Padeiro	Coimbra, Coimbra
20	TI	29	M	1898	1927	Proprietário	Pinhel, Guarda
22	TI	68	M	1859	1927	Empregado do comércio	Gouveia, Guarda
24	TI	21	M	1906	1927	Carregador dos caminhos de ferro	Montemor-o-Velho, Coimbra
27	TI	32	M	1895	1927	Soldado da GNR	Cantanhede, Coimbra
30	TI	33	M	1894	1927	Motorista	Coimbra, Coimbra
32	TI	43	M	1884	1927	Trabalhador	Celorico da Beira, Guarda
33	TI	47	M	1880	1927	Proprietário	Penamacor, Coimbra
34	TI	55	M	1872	1927	Pedreiro	Coimbra, Coimbra
36	TI	26	M	1901	1927	Marceneiro	Coimbra, Coimbra
39	TI	12	M	1915	1927	Unknown	Coimbra, Coimbra
41	TI	32	M	1895	1927	Moço de fretes	Coimbra, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
45	TI	23	M	1904	1927	Trabalhador	Figueiró dos Vinhos, Leiria
47	TI	28	M	1899	1927	Cocheiro	Coimbra, Coimbra
50	TI	47	M	1880	1927	Fogueteiro	Coimbra, Coimbra
51	TI	40	M	1887	1927	Pedreiro	Coimbra, Coimbra
55	TI	63	M	1858	1921	Fiscal do governo	Vila do Bispo, Faro
57	TI	16	M	1911	1927	Unknown	Coimbra, Coimbra
60	TI	11	M	1916	1927	Pastor	Coimbra, Coimbra
63	TI	28	M	1894	1922	Funcionário público	Cantanhede, Coimbra
65	TI	39	M	1888	1927	Empregado público	Coimbra, Coimbra
66	TI	43	M	1884	1927	2º cabo (Combatentes da Grande Guerra	Lousã, Coimbra
68	TI	32	M	1895	1927	Bolacheiro	Coimbra, Coimbra
77	TI	17	M	1905	1922	Estudante	Mealhada, Aveiro
83	TI	23	M	1904	1927	Empregado do comércio	Coimbra, Coimbra
84	TI	17	M	1910	1927	Fotógrafo	Coimbra, Coimbra
87	TI	65	M	1862	1927	Oleiro	Coimbra, Coimbra
89	TI	37	M	1888	1925	Jornaleiro	Boticas, Vila Real
91	TI	14	M	1908	1922	Empregado do comércio	Porto, Porto
92	TI	23	M	1904	1927	Guarda cívico	Coimbra, Coimbra
96	TI	23	M	1904	1927	Tipógrafo	Alijó, Vila Real
97	TI	29	M	1898	1927	Padeiro	Coimbra, Coimbra
98	TI	27	M	1900	1927	Empregado no comércio	Coimbra, Coimbra
99	TI	51	M	1871	1922	Sapateiro	Covilhã, Castelo Branco
104	TI	35	M	1892	1927	Marceneiro	Coimbra, Coimbra
105	TI	46	M	1881	1927	Distribuidor telégrafo-postal	Coimbra, Coimbra
108	TI	63	M	1864	1927	Oleiro	Coimbra, Coimbra
109	TI	28	M	1899	1927	Marceneiro	Coimbra, Coimbra
112	TI	30	M	1897	1927	Serralheiro	Coimbra, Coimbra
114	TI	21	M	1906	1927	Soldado do batalhão de metralhadoras 2	Coimbra, Coimbra
119	TI	25	M	1902	1927	Agricultor	Coimbra, Coimbra
124	TI	43	M	1885	1928	Moleiro	Condeixa, Coimbra
125	TI	67	M	1855	1922	Trabalhador	Gouveia, Guarda
127	TI	15	M	1913	1928	Trabalhador	Coimbra, Coimbra
133	TI	37	M	1891	1928	Carroceiro	Coimbra, Coimbra
136	TI	29	M	1899	1928	Padeiro	Coimbra, Coimbra
144	TI	26	M	1902	1928	Empregado do correio	Coimbra, Coimbra
146	TI	35	M	1893	1928	Alfaiate	Coimbra, Coimbra
147	TI	40	M	1888	1928	Guarda cívico	Penela, Coimbra
148	TI	32	M	1896	1928	Electricista	Évora, Évora
149	TI	59	M	1869	1928	Porteiro	Unknown
150	TI	28	M	1900	1928	Sapateiro	Coimbra, Coimbra
151	TI	83	M	1845	1928	Empregado público aposentado	Coimbra, Coimbra
154	TI	20	M	1908	1928	Cauteleiro	Coimbra, Coimbra
155	TI	13	M	1915	1928	Unknown	Coimbra, Coimbra
159	TI	34	M	1894	1928	Sapateiro	Figueira da Foz, Coimbra
165	TI	29	M	1899	1928	Pedreiro	Montemor-o-Velho, Coimbra
170	TI	47	M	1881	1928	Electricista	Covilhã, Castelo Branco
171	TI	17	M	1906	1923	Empregado no comércio	Coimbra, Coimbra
21	EM	34	F	1860	1896	Lavadeira	Miranda do Corvo, Coimbra
66	EM	65	F	1831	1896	Doméstica	Lisboa, Lisboa
92	EM	70	F	1826	1896	Doméstica	Condeixa, Coimbra
96	EM	23	F	1873	1896	Doméstica	Montemor-o-Velho, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
101	EM	40	F	1856	1896	Doméstica	Anadia, Aveiro
112	EM	22	F	1874	1896	Doméstica	Vila Real? [sic]
114	EM	29	F	1867	1896	Tecedeira	Coimbra, Coimbra
116	EM	34	F	1863	1897	Doméstica	Lousã, Coimbra
117	EM	38	F	1859	1897	Doméstica	Coimbra, Coimbra
118	EM	22	F	1875	1897	Doméstica	Sabugal, Guarda? [sic]
132	EM	78	F	1820	1898	Asylada	Gaia, Porto
148	EM	33	F	1865	1898	Doméstica	Gaia, Porto
159	EM	60	F	1838	1898	Doméstica	Braga, Braga
175	EM	22	F	1876	1898	Unknown	Porto, Porto
185	EM	56	F	1842	1898	Doméstica	Braga, Braga
209	EM	45	F	1853	1898	Asylada	Porto, Porto
227	EM	30	F	1868	1898	Unknown	Coimbra, Coimbra
229	EM	25	F	1873	1898	Doméstica	Coimbra, Coimbra
268	EM	33	F	1866	1899	Serviço de casa	Soure, Coimbra
306	EM	17	F	1883	1900	Meretriz nº 7091	Caldas da Rainha, Leiria
308	EM	27	F	1877	1900	Criada	Tábua, Coimbra
323	EM	33	F	1867	1900	Criada	Lisboa, Lisboa
341	EM	23	F	1877	1900	Lavadeira	Lisboa, Lisboa
348	EM	24	F	1876	1900	Doméstica	Certã, Castelo Branco
349	EM	35	F	1865	1900	Unknown	Unknown
353	EM	42	F	1858	1900	Doméstica	Lisboa, Lisboa
360	EM	31	F	1869	1900	Doméstica	Alcácer do Sal, Lisboa
378	EM	35	F	1865	1900	Todo o serviço	Coimbra, Coimbra
380	EM	40	F	1860	1900	Serviço de casa	Lisboa, Lisboa
417	EM	25	F	1875	1900	Criada	Proença-a-Nova, Castelo Branco
493	EM	23	F	1878	1901	Todo o serviço	Penela, Coimbra
175	TI	12	M	1916	1928	Unknown	Coimbra, Coimbra
177	TI	72	M	1856	1928	Guarda-fios	Montemor-o-Novo, Coimbra
178	TI	24	M	1904	1928	Empregado público	Barquinha, Barquinha
180	TI	19	M	1909	1928	Trabalhador	Coimbra, Coimbra
181	TI	36	M	1892	1928	Ourives	Figueira da Foz, Coimbra
185	TI	44	M	1884	1928	Moço de fretes	Coimbra, Coimbra
187	TI	38	M	1890	1928	Empregado do comércio	Coimbra, Coimbra
191	TI	20	M	1908	1928	Soldado do Batalhão de metralhadoras	Coimbra, Coimbra
192	TI	44	M	1884	1928	Trabalhador	Miranda do Corvo, Coimbra
197	TI	44	M	1884	1928	Comerciante	Coimbra, Coimbra
204	TI	47	M	1881	1928	Alfaiate	Tábua, Coimbra
205	TI	15	M	1913	1928	Unknown	Coimbra, Coimbra
207	TI	23	M	1905	1928	Sapateiro	Coimbra, Coimbra
212	TI	49	M	1879	1928	Trabalhador	Batalha, Leiria
215	TI	72	M	1854	1928	Industrial	Seia, Guarda
221	TI	20	M	1908	1928	Soldado	Coimbra, Coimbra
222	TI	50	M	1878	1928	Padeiro	Aveiro, Aveiro
224	TI	30	M	1898	1928	Trabalhador	Vouzela, Viseu
226	TI	61	M	1867	1928	Sapateiro	Coimbra, Coimbra
233	TI	42	M	1886	1928	Porteiro	Miranda do Corvo, Coimbra
240	TI	28	M	1900	1928	Revisor dos eléctricos	Coimbra, Coimbra
247	TI	71	M	1857	1928	Capitão reformado do exército	Cantanhede, Coimbra
248	TI	59	M	1869	1928	Funileiro	Unknown
251	TI	34	M	1894	1928	Latoeiro	Coimbra, Coimbra
253	TI	66	M	1862	1928	Agricultor	Coimbra, Coimbra
254	TI	48	M	1880	1928	Vigia municipal	Seia, Guarda

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
260	TI	36	M	1892	1928	Decorador em madeira	Coimbra, Coimbra
265	TI	67	M	1861	1928	Alfaiate	Coimbra, Coimbra
271	TI	31	M	1897	1928	Ferrador	Coimbra, Coimbra
274	TI	34	M	1894	1928	Pintor	Coimbra, Coimbra
276	TI	31	M	1897	1928	Fogueteiro	Coimbra, Coimbra
278	TI	44	M	1879	1923	Agente comercial	Mangualde, Viseu
283	TI	60	M	1863	1923	Asfaltador	Alenquer, Lisboa
285	TI	48	M	1875	1923	Alfaiate	Santiago de Composela, Spain
288	TI	15	M	1914	1929	Estudante	Oliveira do Hospital, Coimbra
296	TI	18	M	1911	1929	Serralheiro	Coimbra, Coimbra
297	TI	36	M	1893	1929	Moço de fretes	Coimbra, Coimbra
300	TI	18	M	1916	1934	Serralheiro	Coimbra, Coimbra
306	TI	33	M	1896	1929	Unknown	Oliveira do Hospital, Coimbra
309	TI	23	M	1906	1929	Pedreiro	Coimbra, Coimbra
313	TI	27	M	1902	1929	Padeiro	Coimbra, Coimbra
318	TI	14	M	1915	1929	Pintor	Coimbra, Coimbra
323	TI	11	M	1918	1929	Unknown	Coimbra, Coimbra
326	TI	19	M	1910	1929	Tipógrafo	Coimbra, Coimbra
330	TI	21	M	1908	1929	Trabalhador	Figueira da Foz, Coimbra
332	TI	46	M	1893	1929	Funileiro	Coimbra, Coimbra
348	TI	55	M	1876	1929	Funileiro	Sabugal, Guarda
349	TI	25	M	1898	1923	Professor	Miranda do Corvo, Coimbra
351	TI	20	M	1909	1929	Unknown	Figueira da Foz, Coimbra
360	TI	15	M	1914	1929	Serralheiro	Coimbra, Coimbra
361	TI	44	M	1885	1929	Sapateiro	Coimbra, Coimbra
363	TI	27	M	1902	1929	Sapateiro	Coimbra, Coimbra
365	TI	30	M	1899	1929	Tamanqueiro	Ansião, Coimbra
368	TI	11	M	1918	1929	Unknown	Coimbra, Coimbra
369	TI	18	M	1911	1929	Soldado da companhia de saúde	Oliveira do Hospital, Coimbra
370	TI	41	M	1888	1929	Proprietário	Coimbra, Coimbra
371	TI	27	M	1902	1929	Ferreiro	Fornos de Algodres, Guarda
376	TI	38	M	1891	1929	Empregado da Câmara	Coimbra, Coimbra
381	TI	39	M	1890	1929	Alfaiate	Coimbra, Coimbra
385	TI	21	M	1908	1929	Empregado do comércio	Coimbra, Coimbra
387	TI	45	M	1884	1929	Trabalhador	Figueira da Foz, Coimbra
389	TI	27	M	1902	1929	Marceneiro	Coimbra, Coimbra
392	TI	24	M	1905	1929	Chauffeur	Pampilhosa da Serra, Coimbra
393	TI	17	M	1912	1929	Trabalhador	Coimbra, Coimbra
394	TI	37	M	1892	1929	Empregado no comércio	Braga, Braga
396	TI	57	M	1872	1929	Empregado de café	Spain
400	TI	25	M	1893	1918	Professor	Coimbra, Coimbra
402	TI	56	M	1868	1924	Pedreiro	Coimbra, Coimbra
420	TI	50	M	1880	1930	Empregado público	Trancoso, Guarda
425	TI	15	M	1915	1930	Unknown	Coimbra, Coimbra
428	TI	52	M	1878	1930	Barbeiro	Coimbra, Coimbra
430	TI	43	M	1887	1930	Cocheiro	Coimbra, Coimbra
433	TI	43	M	1887	1930	Comerciante	Pampilhosa da Serra, Coimbra
435	TI	65	M	1865	1930	Fundidor	Coimbra, Coimbra
437	TI	43	M	1887	1930	Proprietário	Coimbra, Coimbra
441	TI	30	M	1900	1930	Trabalhador	Sabugal, Guarda
445	TI	18	M	1912	1930	Barbeiro	Coimbra, Coimbra
448	TI	29	M	1901	1930	Pedreiro	Coimbra, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
452	TI	18	M	1912	1930	Trabalhador	Pinhel, Guarda
454	TI	15	M	1915	1930	Unknown	Coimbra, Coimbra
456	TI	24	M	1906	1930	Trabalhador	Figueira da Foz, Coimbra
459	TI	17	M	1913	1930	Alfaiate	Coimbra, Coimbra
462	TI	22	M	1908	1930	Tipógrafo	Coimbra, Coimbra
466	TI	35	M	1895	1930	Marceneiro	Coimbra, Coimbra
468	TI	32	M	1898	1930	Soldado	Oliveira de Azeméis, Aveiro
471	TI	19	M	1911	1930	Fotógrafo	Coimbra, Coimbra
472	TI	28	M	1902	1930	Trabalhador	Coimbra, Coimbra
477	TI	32	M	1898	1930	Serralheiro mecânico	Coimbra, Coimbra
481	TI	47	M	1883	1930	1º cabo da GNR	Coimbra, Coimbra
482	TI	28	M	1902	1930	Chauffeur	Coimbra, Coimbra
484	TI	24	M	1906	1930	Engraxador	Góis, Coimbra
488	TI	60	M	1870	1930	Correeiro	Coimbra, Coimbra
489	TI	16	M	1914	1930	Empregado do comércio	Coimbra, Coimbra
490	TI	18	M	1912	1930	Trabalhador	Cantanhede, Coimbra
491	TI	32	M	1898	1930	Comerciante	Pampilhosa da Serra, Coimbra
495	TI	50	M	1880	1930	Sapateiro	Coimbra, Coimbra
497	TI	13	M	1917	1930	Unknown	Figueira da Foz, Coimbra
500	TI	26	M	1904	1930	Ferroviário	Gaia, Porto
507	TI	64	M	1861	1925	Negociante	Seia, Guarda
514	TI	13	M	1917	1930	Unknown	Cantanhede, Coimbra
516	TI	26	M	1904	1930	Proprietário	Arganil, Coimbra
517	TI	23	M	1902	1925	Relojoeiro	Coimbra, Coimbra
518	TI	30	M	1900	1930	Trabalhador	Figueira da Foz, Coimbra
520	TI	23	M	1907	1930	Tipógrafo	Coimbra, Coimbra
526	TI	40	M	1890	1930	Trabalhador	Peso da Régua, Vila Real
529	TI	40	M	1890	1930	Trabalhador	Vila Nova de Ourém, Santarém
535	TI	30	M	1900	1930	Trabalhador	Castanheira de Pera, Leiria
538	TI	52	M	1878	1930	Chefe da estação de C.F.	Jeau, Spain
541	TI	24	M	1901	1925	Sapateiro	Coimbra, Coimbra
548	TI	20	M	1910	1930	Encadernador	Viseu, Viseu
549	TI	21	M	1909	1930	Sapateiro	Figueira da Foz, Coimbra
550	TI	47	M	1883	1930	Empregado público	Coimbra, Coimbra
551	TI	48	M	1877	1925	Guarda cívico aposentado	Coimbra, Coimbra
554	TI	69	M	1856	1925	Industrial	Coimbra, Coimbra
555	TI	45	M	1885	1930	Chauffeur	Carregal do Sal, Viseu
559	TI	12	M	1919	1931	Unknown	Ancião, Leiria
563	TI	26	M	1905	1931	Padeiro	Figueira da Foz, Coimbra
567	TI	23	M	1902	1925	Sapateiro	Fornos de Algodres, Guarda
569	TI	59	M	1872	1931	Agente da P.J.C. aposentado	Coimbra, Coimbra
576	TI	63	M	1868	1931	Funcionário público	Coimbra, Coimbra
579	TI	26	M	1905	1931	Trabalhador	Vila Nova de Ourém, Santarém
584	TI	48	M	1883	1931	Trabalhador	Pombal, Leiria
589	TI	40	M	1891	1931	Pintor	Coimbra, Coimbra
594	TI	62	M	1869	1931	Trabalhador	Vila Real, Vila Real
597	TI	46	M	1885	1931	1º Cabo do Batalhão de Metralhadoras nº2	Coimbra, Coimbra
601	TI	46	M	1885	1931	Trabalhador	Coimbra, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
607	TI	34	M	1897	1931	Cozinheiro	Lousã, Coimbra
608	TI	61	M	1870	1931	Guarda florestal	Leiria, Leiria
614	TI	38	M	1893	1931	Proprietário	Aveiro, Aveiro
617	TI	27	M	1904	1931	Trabalhador	Ancião, Leiria
620	TI	41	M	1890	1931	Industrial	Coimbra, Coimbra
629	TI	52	M	1879	1931	Ferroviário	Lisboa, Lisboa
630	TI	37	M	1894	1931	Polidor	Gaia, Porto
641	TI	40	M	1889	1929	Trabalhador	Montemor-o-Velho, Coimbra
642	TI	40	M	1889	1929	Picheleiro	Valongo, Coimbra
643	TI	78	M	1851	1929	Proprietário	Coimbra, Coimbra
646	TI	27	M	1904	1931	Comerciante	Pombal, Leiria
648	TI	40	M	1891	1931	Ferroviário	Pontevedra, Spain
653	TI	35	M	1896	1931	Moço de fretes	Coimbra, Coimbra
654	TI	70	M	1861	1931	Trabalhador	Alcobaça, Leiria
655	TI	24	M	1907	1931	Marítimo	Figueira da Foz, Coimbra
657	TI	17	M	1914	1931	Trabalhador	Vila Real, Vila Real
665	TI	21	M	1908	1929	Soldado do batalhão de metrelhadoras nº2	Mêda, Guarda
666	TI	16	M	1915	1931	Trabalhador	Caldas da Rainha, Leiria
668	TI	42	M	1889	1931	Agente técnico	Faro, Faro
669	TI	41	M	1890	1931	Empregado no caminho de ferro	Coimbra, Coimbra
673	TI	32	M	1899	1931	Empregado no comércio	Elvas, Portalegre
674	TI	50	M	1881	1931	Distribuidor postal	Coimbra, Coimbra
676	TI	23	M	1908	1931	Carpinteiro	Coimbra, Coimbra
677	TI	43	M	1888	1931	Trabalhador	Cantanhede, Coimbra
679	TI	22	M	1909	1931	Soldado aprendiz de seleiro correio do 2ºB. Reg. Art. Lig. 2	Almeida, Guarda
681	TI	39	M	1892	1931	Carpinteiro	Poiares, Coimbra
682	TI	29	M	1902	1931	Trabalhador	Gouveia, Guarda
692	TI	15	M	1916	1931	Unknown	Pombal, Leiria
693	TI	27	M	1904	1931	Trabalhador	Torres Novas, Santarém
694	TI	39	M	1892	1931	Empregado público	Arganil, Coimbra
697	TI	40	M	1891	1931	Trabalhador	Pombal, Leiria
700	TI	26	M	1905	1931	Tipógrafo	Coimbra, Coimbra
704	TI	58	M	1871	1929	Archeiro	Coimbra, Coimbra
707	TI	32	M	1899	1931	Assentador	Alter do Chão, Portalegre
708	TI	47	M	1884	1931	Trabalhador	Coimbra, Coimbra
712	TI	11	M	1920	1931	Unknown	Coimbra, Coimbra
718	TI	66	M	1865	1931	Agulheiro dos C. F.	Coimbra, Coimbra
721	TI	49	M	1880	1929	Ferroviário	Coruche, Santarém
723	TI	45	M	1886	1931	Proprietário	Porto de Mós
725	TI	29	M	1902	1931	Manipulador de massas	Coimbra, Coimbra
728	TI	16	M	1915	1931	Unknown	Oliveira do Hospital, Coimbra
733	TI	35	M	1897	1932	Soldado da G. N. R. Batalhão nº5	Sabugal, Guarda
736	TI	44	M	1888	1932	Trabalhador	Celorico da Beira, Guarda
738	TI	13	M	1919	1932	Unknown	Coimbra, Coimbra
739	TI	43	M	1889	1932	Comerciante	Anadia, Aveiro
744	TI	13	M	1919	1932	Unknown	Viseu, Viseu
749	TI	38	M	1896	1932	Professor	Lisboa, Lisboa
750	TI	25	M	1907	1932	Chauffeur	Coimbra, Coimbra
752	TI	15	M	1917	1932	Cordoeiro	Coimbra, Coimbra
758	TI	44	M	1888	1932	Magistrado	Chaves, Vila Real

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
759	TI	18	M	1914	1932	Estudante	Figueira da Foz, Coimbra
764	TI	61	M	1871	1932	Carpinteiro	Coimbra, Coimbra
768	TI	29	M	1903	1932	Soldado	Chaves, Vila Real
775	TI	53	M	1879	1932	Trabalhador	Montemor-o-Velho, Coimbra
776	TI	64	M	1868	1932	Barbeiro	Gouveia, Guarda
778	TI	24	M	1908	1932	Serralheiro	Coimbra, Coimbra
779	TI	54	M	1878	1932	Empregado público	Mealhada, Aveiro
787	TI	42	M	1890	1932	Trabalhador	Coimbra, Coimbra
793	TI	27	M	1904	1932	Sargento furriel da artilharia	Fornos de Algodres, Guarda
796	TI	11	M	1921	1932	Unknown	Nelas, Viseu
802	TI	73	M	1859	1932	Ferroviário	Elvas, Portalegre
803	TI	59	M	1873	1932	Sapateiro	Coimbra, Coimbra
804	TI	56	M	1876	1932	Trabalhador	Seia, Guarda
806	TI	26	M	1906	1932	Engraxador	Coimbra, Coimbra
808	TI	60	M	1872	1932	Proprietário	Figueiró dos Vinhos, Leiria
809	TI	40	M	1892	1932	Alfaiate	Castelo Branco, Castelo Branco
822	TI	26	M	1906	1932	Empregado de escritório	Coimbra, Coimbra
825	TI	39	M	1893	1932	Guarda de polícia	Guarda, Guarda
827	TI	17	M	1915	1932	Trabalhador	Arganil, Coimbra
830	TI	73	M	1859	1932	Trabalhador	Penalva do Castelo, Viseu
831	TI	43	M	1889	1932	Sapateiro	Coimbra, Coimbra
833	TI	26	M			Sapateiro	Coimbra, Coimbra
834	TI	52	M	1880	1932	Agricultor	Mealhada, Aveiro
836	TI	66	M	1856	1932	Carpinteiro	Figueira da Foz, Coimbra
838	TI	62	M	1876	1938	Proprietário	Oliveira do Hospital, Coimbra
839	TI	84	M	1848	1932	Sapateiro	Coimbra, Coimbra
841	TI	27	M	1905	1932	Empregado no comércio	Tarouca
844	TI	31	M			2º sargento	Coimbra, Coimbra
845	TI	33	M	1899	1932	Trabalhador	Belmonte, Castelo Branco
848	TI	11	M	1922	1933	Unknown	Cantanhede, Coimbra
850	TI	42	M	1891	1933	Sapateiro	Coimbra, Coimbra
851	TI	18	M	1915	1933	Trabalhador	Gavião, Portalegre
852	TI	24	M	1909	1933	Barbeiro	Coimbra, Coimbra
853	TI	39	M	1894	1933	Serrador	Leiria, Leiria
855	TI	45	M			Trabalhador	Coimbra, Coimbra
857	TI	15	M	1918	1933	Unknown	Coimbra, Coimbra
862	TI	59	M	1874	1933	Bengaleiro	Évora, Évora
865	TI	43	M	1890	1933	Trabalhador	Gavião, Portalegre
868	TI	25	M	1908	1933	Serralheiro	Coimbra, Coimbra
869	TI	75	M	1858	1933	Sapateiro	Coimbra, Coimbra
873	TI	30	M	1905	1933	Guarda livros	Coimbra, Coimbra
875	TI	29	M	1904	1933	Padeiro	Coimbra, Coimbra
876	TI	52	M	1881	1933	Proprietário	Coimbra, Coimbra
879	TI	33	M	1900	1933	Trabalhador	Miranda do Corvo, Coimbra
880	TI	60	M	1873	1933	Sarreiro	Penacova, Coimbra
884	TI	24	M	1907	1933	Trabalhador	Pinhel, Guarda
892	TI	36	M	1897	1933	Trabalhador	Seia, Guarda
895	TI	19	M	1914	1933	Tipógrafo	Coimbra, Coimbra
899	TI	20	M	1913	1933	Vendedor de jornais	Montemor-o-Velho, Coimbra
900	TI	47	M	1886	1933	Trabalhador	Figueira da Foz, Coimbra
902	TI	54	M	1879	1933	Trabalhador	Coimbra, Coimbra
906	TI	33	M	1900	1933	Trabalhador	Coimbra, Coimbra
907	TI	37	M	1896	1933	Trabalhador	Mortágua, Viseu
911	TI	23	M	1910	1933	Trabalhador	Coimbra, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
913	TI	27	M	1906	1933	Trabalhador	Cantanhede, Coimbra
919	TI	38	M	1896	1934	Moço de fretes	Montemor-o-Velho, Coimbra
924	TI	36	M	1898	1934	Tipógrafo	Coimbra, Coimbra
928	TI	31	M	1903	1934	Tipógrafo	Coimbra, Coimbra
933	TI	35	M	1899	1934	Sapateiro	Seia, Guarda
937	TI	29	M	1905	1934	Aluno do 5º ano da Faculdade de Medicina	Santa Ana, Madeira
174	TI	23	F	1899	1922	Doméstica	Aveiro, Aveiro
182	TI	38	F	1890	1928	Doméstica	Condeixa, Coimbra
194	TI	20	F	1909	1929	Doméstica	Coimbra, Coimbra
195	TI	15	F	1913	1928	Doméstica	Coimbra, Coimbra
198	TI	25	F	1903	1928	Doméstica	Coimbra, Coimbra
202	TI	51	F	1877	1928	Doméstica	Tábua, Coimbra
203	TI	34	F	1894	1928	Doméstica	Coimbra, Coimbra
208	TI	23	F	1905	1928	Doméstica	Seia, Guarda
213	TI	28	F	1900	1928	Doméstica	Coimbra, Coimbra
217	TI	15	F	1913	1928	Doméstica	Coimbra, Coimbra
219	TI	28	F	1895	1923	Doméstica	Coimbra, Coimbra
223	TI	56	F	1872	1928	Criada de servir	Montemor-o-Velho, Coimbra
225	TI	18	F	1905	1923	Doméstica	Coimbra, Coimbra
228	TI	15	F	1913	1928	Unknown	Coimbra, Coimbra
235	TI	88	F	1835	1923	Doméstica	Condeixa, Coimbra
236	TI	26	F	1897	1923	Doméstica	Coimbra, Coimbra
239	TI	29	F	1899	1928	Doméstica	Cantanhede, Coimbra
238	TI	43	F	1885	1928	Doméstica	Coimbra, Coimbra
244	TI	65	F	1873	1928	Doméstica	Coimbra, Coimbra
249	TI	24	F	1904	1928	Doméstica	Coimbra, Coimbra
256	TI	27	F	1901	1928	Doméstica	Penacova, Coimbra
263	TI	48	F	1880	1928	Doméstica	Coimbra, Coimbra
264	TI	29	F	1884	1923	Doméstica	Coimbra, Coimbra
267	TI	60	F	1868	1928	Doméstica	Coimbra, Coimbra
270	TI	22	F	1906	1928	Doméstica	Coimbra, Coimbra
273	TI	27	F	1891	1928	Doméstica	Carregal do Sal
275	TI	54	F	1869	1923	Doméstica	Tondela, Coimbra
277	TI	26	F	1902	1928	Doméstica	Coimbra, Coimbra
280	TI	38	F	1890	1928	Doméstica	Figueiró dos Vinhos, Leiria
284	TI	27	F	1891	1918	Doméstica	Coimbra, Coimbra
291	TI	30	F	1899	1929	Doméstica	Coimbra, Coimbra
294	TI	25	F	1893	1918	Doméstica	Coimbra, Coimbra
298	TI	52	F	1877	1929	Doméstica	Coimbra, Coimbra
299	TI	16	F	1913	1929	Doméstica	Coimbra, Coimbra
303	TI	44	F	1885	1929	Doméstica	Mealhada, Aveiro
304	TI	15	F	1914	1929	Unknown	Coimbra, Coimbra
307	TI	27	F	1902	1929	Doméstica	Soure, Coimbra
310	TI	18	F	1911	1929	Criada de servir	Coimbra, Coimbra
314	TI	52	F	1877	1929	Doméstica	Coimbra, Coimbra
315	TI	32	F	1897	1929	Doméstica	Montemor-o-Velho, Coimbra
316	TI	30	F	1899	1929	Doméstica	Soure, Coimbra
324	TI	45	F	1884	1929	Doméstica	Figueiró dos Vinhos, Leiria
328	TI	55	F	1874	1929	Doméstica	Figueira da Foz, Coimbra
329	TI	45	F	1884	1929	Doméstica	Coimbra, Coimbra
333	TI	72	F	1847	1929	Doméstica	Coimbra, Coimbra
340	TI	43	F	1886	1929	Doméstica	Coimbra, Coimbra
343	TI	18	F	1911	1929	Doméstica	Figueira da Foz, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
344	TI	54	F	1875	1929	Criada de servir	Coimbra, Coimbra
346	TI	19	F	1910	1929	Doméstica	Coimbra, Coimbra
350	TI	40	F	1884	1924	Criada de servir	Coimbra, Coimbra
353	TI	41	F	1888	1929	Doméstica	Coimbra, Coimbra
355	TI	23	F	1906	1929	Criada de servir	Oliveira do Hospital, Coimbra
358	TI	39	F	1890	1929	Doméstica	Arganil, Coimbra
359	TI	38	F	1891	1929	Doméstica	Penela, Coimbra
362	TI	40	F	1889	1929	Doméstica	Coimbra, Coimbra
372	TI	47	F	1882	1929	Doméstica	Caldas da Rainha, Leiria
373	TI	26	F	1903	1929	Doméstica	Coimbra, Coimbra
374	TI	69	F	1860	1929	Doméstica	Coimbra, Coimbra
375	TI	21	F	1908	1929	Doméstica	Coimbra, Coimbra
384	TI	26	F	1903	1929	Doméstica	Coimbra, Coimbra
388	TI	30	F	1899	1929	Doméstica	France
397	TI	42	F	1887	1929	Doméstica	Penacova, Coimbra
398	TI	14	F	1910	1924	Doméstica	Coimbra, Coimbra
399	TI	34	F	1885	1929	Doméstica	Coimbra, Coimbra
404	TI	22	F	1908	1930	Doméstica	Coimbra, Coimbra
409	TI	27	F	1903	1930	Doméstica	Seia, Guarda
410	TI	17	F	1913	1930	Doméstica	Mealhada, Aveiro
411	TI	60	F	1870	1930	Doméstica	Mortágua, Viseu
413	TI	29	F	1901	1930	Doméstica	Coimbra, Coimbra
417	TI	76	F	1848	1924	Doméstica	Coimbra, Coimbra
418	TI	21	F	1909	1930	Doméstica	Coimbra, Coimbra
419	TI	48	F	1882	1930	Doméstica	Amarante, Porto
424	TI	30	F	1900	1930	Doméstica	Tondela, Viseu
429	TI	59	F	1871	1930	Doméstica	Cantanhede, Coimbra
434	TI	46	F	1884	1930	Doméstica	Coimbra, Coimbra
438	TI	35	F	1895	1930	Doméstica	Viseu
439	TI	46	F	1884	1930	Doméstica	Cantanhede, Coimbra
440	TI	56	F	1874	1930	Doméstica	Poiares, Coimbra
443	TI	21	F	1909	1930	Doméstica	Coimbra, Coimbra
449	TI	59	F	1865	1924	Doméstica	Ancião, Leiria
451	TI	60	F	1870	1930	Criada de servir	Coimbra, Coimbra
453	TI	37	F	1897	1930	Professora de ensino primário	Coimbra, Coimbra
457	TI	15	F	1909	1924	Unknown	Vieira, Leiria
461	TI	25	F	1905	1930	Doméstica	Coimbra, Coimbra
465	TI	29	F	1901	1930	Doméstica	Coimbra, Coimbra
469	TI	48	F	1882	1930	Doméstica	Coimbra, Coimbra
473	TI	36	F	1889	1925	Doméstica	Santa Ana, Brazil
479	TI	46	F	1884	1930	Doméstica	Figueira da Foz, Coimbra
483	TI	45	F	1885	1930	Doméstica	Figueira da Foz, Coimbra
485	TI	12	F	1918	1930	Unknown	Figueira da Foz, Coimbra
494	TI	45	F	1885	1930	Doméstica	Coimbra, Coimbra
496	TI	24	F	1901	1925	Doméstica	Coimbra, Coimbra
498	TI	35	F	1917	1930	Unknown	Figueira da Foz, Coimbra
508	TI	22	F	1908	1930	Doméstica	Figueira da Foz, Coimbra
509	TI	28	F	1897	1925	Doméstica	Figueira da Foz, Coimbra
510	TI	40	F	1873	1913	Doméstica	Penacova, Coimbra
513	TI	14	F	1916	1930	Unknown	Santa Comba Dão, Viseu
522	TI	28	F	1902	1930	Doméstica	Seia, Guarda
524	TI	28	F	1902	1930	Doméstica	Lousã, Coimbra
527	TI	65	F	1865	1930	Doméstica	Viseu, Viseu
528	TI	48	F	1882	1930	Doméstica	Famalicão, Braga
531	TI	22	F	1908	1930	Doméstica	Coimbra, Coimbra
532	TI	20	F	1910	1930	Doméstica	Almeida, Guarda
544	TI	42	F	1888	1930	Doméstica	Coimbra, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
547	TI	24	F	1901	1925	Doméstica	Oliveira do Hospital, Coimbra
560	TI	22	F	1909	1931	Doméstica	Pombal, Leiria
562	TI	40	F	1891	1931	Doméstica	Coimbra, Coimbra
564	TI	33	F	1898	1931	Doméstica	Coimbra, Coimbra
566	TI	72	F	1859	1931	Doméstica	Penacova, Coimbra
568	TI	28	F	1903	1931	Doméstica	Coimbra, Coimbra
572	TI	16	F	1915	1931	Doméstica	Coimbra, Coimbra
578	TI	75	F	1856	1931	Doméstica	Coimbra, Coimbra
583	TI	48	F	1883	1931	Doméstica	Tondela, Viseu
586	TI	37	F	1894	1931	Doméstica	Montemor-o-Velho, Coimbra
591	TI	86	F	1845	1931	Doméstica	Gaia, Porto
595	TI	72	F	1859	1931	Criada de servir	Tábua, Coimbra
598	TI	51	F	1880	1931	Doméstica	Coimbra, Coimbra
603	TI	64	F	1867	1931	Doméstica	Coimbra, Coimbra
612	TI	46	F	1885	1931	Doméstica	Montemor-o-Velho, Coimbra
618	TI	16	F	1915	1931	Doméstica	Coimbra, Coimbra
623	TI	57	F	1874	1931	Doméstica	Coimbra, Coimbra
624	TI	34	F	1897	1931	Doméstica	Peso da Régua, Vila Real
625	TI	48	F	1883	1931	Doméstica	Coimbra, Coimbra
626	TI	27	F	1899	1926	Doméstica	Lisboa, Lisboa
628	TI	25	F	1906	1931	Doméstica	Montemor-o-Velho, Coimbra
631	TI	43	F	1888	1931	Doméstica	Coimbra, Coimbra
634	TI	22	F	1909	1931	Doméstica	Fundão, Castelo Branco
636	TI	42	F	1889	1931	Doméstica	S. Pedro do Sul, Viseu
638	TI	62	F	1869	1931	Doméstica	Coimbra, Coimbra
640	TI	48	F	1883	1931	Doméstica	Leiria, Leiria
645	TI	26	F	1905	1931	Doméstica	Anadia, Aveiro
649	TI	15	F	1916	1931	Doméstica	Coimbra, Coimbra
658	TI	27	F	1904	1931	Doméstica	Almeida, Guarda
659	TI	20	F	1911	1931	Criada de servir	Mortágua, Viseu
661	TI	36	F	1895	1931	Doméstica	Gouveia, Guarda
663	TI	7	F	1924	1931	Unknown	Anadia, Aveiro
671	TI	60	F	1871	1931	Doméstica	Paredes de Coura, Viana do Castelo
678	TI	18	F	1913	1931	Doméstica	Soure, Coimbra
680	TI	44	F	1887	1931	Doméstica	Alvaiázere, Leiria
687	TI	61	F	1868	1931	Doméstica	Coimbra, Coimbra
689	TI	18	F	1913	1931	Criada de servir	Coimbra, Coimbra
696	TI	37	F	1894	1931	Doméstica	Coimbra, Coimbra
698	TI	40	F	1891	1931	Doméstica	Castelo de Penalva, Viseu
716	TI	33	F	1898	1931	Doméstica	Soure, Coimbra
724	TI	20	F	1911	1931	Doméstica	Coimbra, Coimbra
735	TI	90	F	1842	1932	Doméstica	Coimbra, Coimbra
737	TI	34	F	1898	1932	Doméstica	Pombal, Leiria
741	TI	56	F	1876	1932	Doméstica	Soure, Coimbra
746	TI	17	F	1915	1932	Doméstica	Ilha do Príncipe, West Africa
748	TI	22	F	1910	1932	Doméstica	Coimbra, Coimbra
751	TI	22	F	1910	1932	Doméstica	Soure, Coimbra
756	TI	26	F	1906	1932	Doméstica	Figueiró dos Vinhos, Leiria
757	TI	27	F	1905	1932	Criada de servir	Alcácer do Sal, Setúbal
763	TI	41	F	1891	1932	Doméstica	Coimbra, Coimbra
772	TI	47	F	1885	1932	Doméstica	Viseu, Viseu
780	TI	47	F	1885	1932	Doméstica	Aveiro, Aveiro
781	TI	36	F	1896	1932	Doméstica	Figueiró dos Vinhos, Leiria
782	TI	24	F	1908	1932	Doméstica	Coimbra, Coimbra
783	TI	24	F	1908	1932	Doméstica	Coimbra, Coimbra

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
784	TI	47	F	1885	1932	Doméstica	Ancião, Leiria
786	TI	13	F	1919	1932	Unknown	Mira, Coimbra
791	TI	37	F	1895	1932	Doméstica	Aveiro, Aveiro
792	TI	43	F	1889	1932	Doméstica	Castelo Branco, Castelo Branco
795	TI	29	F	1903	1932	Doméstica	Soure, Coimbra
801	TI	39	F	1893	1932	Doméstica	Coimbra, Coimbra
810	TI	30	F	1902	1932	Doméstica	Alcobaça, Leiria
811	TI	56	F	1876	1932	Doméstica	Mangualde, Viseu
812	TI	40	F	1892	1932	Doméstica	Pombal, Leiria
816	TI	46	F	1886	1932	Doméstica	Vila Nova de Ourém, Santarém
817	TI	32	F	1900	1932	Doméstica	Poaires, Coimbra
818	TI	17	F	1915	1932	Criada de servir	Coimbra, Coimbra
823	TI	52	F	1880	1932	Doméstica	Viseu, Viseu
824	TI	31	F	1901	1932	Doméstica	Carregal do Sal, Viseu
828	TI	18	F	1914	1932	Costureira	Ramoin, Spain
840	TI	44	F	1888	1932	Doméstica	Vila Real, Vila Real
843	TI	27	F	1905	1932	Doméstica	Trancoso, Guarda
847	TI	65	F	1868	1933	Asilada	Coimbra, Coimbra
849	TI	25	F	1908	1933	Doméstica	Coimbra, Coimbra
859	TI	34	F	1899	1933	Doméstica	Soure, Coimbra
860	TI	42	F	1891	1933	Doméstica	Soure, Coimbra
866	TI	16	F	1917	1933	Doméstica	Trancoso, Guarda
871	TI	21	F	1912	1933	Doméstica	Torres Vedras, Santarém
872	TI	30	F	1903	1933	Doméstica	Condeixa, Coimbra
874	TI	21	F	1912	1933	Doméstica	Viseu, Viseu
877	TI	29	F	1904	1933	Doméstica	Figueira da Foz, Coimbra
881	TI	43	F	1891	1934	Doméstica	Ancião, Leiria
887	TI	31	F	1902	1933	Doméstica	Coimbra, Coimbra
888	TI	25	F	1908	1933	Doméstica	Penela, Coimbra
889	TI	21	F	1912	1933	Doméstica	Coimbra, Coimbra
897	TI	31	F	1902	1933	Doméstica	Porto de Mós, Leiria
904	TI	72	F	1861	1933	Doméstica	Oliveira do Hospital, Coimbra
905	TI	15	F	1918	1933	Doméstica	Coimbra, Coimbra
912	TI	55	F	1878	1933	Doméstica	Tábua, Coimbra
914	TI	24	F	1909	1933	Criada de servir	Aveiro, Aveiro
917	TI	17	F	1917	1934	Doméstica	Leiria, Leiria
920	TI	45	F	1889	1934	Doméstica	Montemor-o-Velho, Coimbra
921	TI	18	F	1916	1934	Doméstica	Coimbra, Coimbra
930	TI	33	F	1901	1934	Doméstica	Carregal do Sal, Viseu
931	TI	69	F	1865	1934	Doméstica	Coimbra, Coimbra
932	TI	42	F	1892	1934	Doméstica	Coimbra, Coimbra
934	TI	16	F	1918	1934	Doméstica	Poiares, Coimbra
939	TI	62	F	1872	1934	Doméstica	Tábua, Coimbra
950	TI	38	F	1896	1934	Doméstica	Cantanhede, Coimbra
953	TI	40	F	1894	1934	Doméstica	Coimbra, Coimbra
955	TI	41	F	1893	1934	Doméstica	Penacova, Coimbra
960	TI	47	F	1887	1934	Doméstica	Seia, Guarda
972	TI	50	F	1884	1934	Doméstica	Poiares, Coimbra
976	TI	26	F	1908	1934	Doméstica	Coimbra, Coimbra
980	TI	36	F	1898	1934	Doméstica	Rio de Janeiro, Brazil
989	TI	19	F	1915	1934	Criada de servir	Coimbra, Coimbra
991	TI	24	F	1910	1934	Doméstica	Pombal, Leiria
992	TI	97	F	1837	1934	Doméstica	Cantanhede, Coimbra
996	TI	45	F	1889	1934	Doméstica	Cantanhede, Coimbra
997	TI	36	F	1898	1934	Doméstica	Pombal, Leiria
1006	TI	56	F	1878	1934	Doméstica	Coimbra, Coimbra
1012	TI	77	F	1858	1935	Doméstica	Penacova, Coimbra
1019	TI	23	F	1912	1935	Doméstica	Lousã, Coimbra

Appendix 1. (Continued.)

Number	Collection	Age at death	Sex	Birth year	Death year	Ocupation	Origin
1024	TI	18	F	1917	1935	Estudante da Universidade	Coimbra, Coimbra
1026	TI	31	F	1904	1935	Doméstica	Tábua, Coimbra
1030	TI	17	F	1919	1936	Costureira	Coimbra, Coimbra
1033	TI	45	F	1891	1936	Doméstica	Góis, Coimbra
1037	TI	12	F	1924	1936	Unknown	Cantanhede, Coimbra
1038	TI	24	F	1912	1936	Doméstica	Coimbra, Coimbra
1042	TI	28	F	1908	1936	Doméstica	Mangualde, Viseu
1045	TI	31	F	1905	1936	Doméstica	Seia, Guarda
1048	TI	15	F	1921	1936	Unknown	Coimbra, Coimbra
1053	TI	63	F	1873	1936	Doméstica	Gouveia, Guarda
1060	TI	26	F	1910	1936	Doméstica	Nelas, Viseu
1062	TI	28	F	1908	1936	Doméstica	Vila Nova de Ourém, Santarém
1067	TI	14	F	1922	1936	Unknown	Coimbra, Coimbra
1068	TI	23	F	1913	1936	Doméstica	Pombal, Leiria
1070	TI	40	F	1896	1936	Doméstica	Vila Nova de Ourém, Santarém
1075	TI	52	F	1884	1936	Doméstica	Figueira da Foz, Coimbra

EM: Escolas Médicas (Medical Schools Identified Collection); TI: Trocas Internacionais (International Trades Identified Collection); F: Female individual; M: Male individual.