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DENTAL MORPHOLOGY: A VALUABLE CONTRIBUTION TO OUR UNDERSTANDING OF PREHISTORY

by

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Abstract: Comparison among archaeological samples, using frequencies of dental morphological traits, allows us to develop hypotheses about the genetic history of an area. More accurate than the measurement of skulls or extrapolations from modern gene frequencies, often more feasible and simpler than studies of ancient DNA, the study of dental traits should be expanded.

We demonstrate the method using a limited amount of information from Portuguese samples dating ca. 8500-4500 calBP, discussing the approach needed for material from secondary burials. This provides a demonstration of the close genetic relationship between Mesolithic and later populations.

Capsian sites from North Africa (ca. 10000-7500 calBP) are included in the study to test recent speculation about the relationship of North African and Iberian Late Pleistocene-Early Holocene populations using modern genetic evidence.

Key-words: Dental morphology; Mesolithic/Neolithic; gene.

Resumo: A comparação da frequência dos caracteres morfológicos dentários de diferentes séries arqueológicas, permite avançar com hipóteses acerca da "história genética" de uma região. Mais precisa que as medidas cranianas ou a extrapolação da frequência moderna de genes, frequentemente mais viável que os estudos de DNA antigo, a análise dos caractéres dentários deveria expandir-se.

Com o presente trabalho pretende-se demonstrar a utilidade desta nova abordagem, utilizando a informação limitada de algumas amostras portuguesas datadas de aproximadamente 8500-4500 cal BP discutindo, inclusivamente, a estratégia necessária em sepulturas colectivas, onde os ossos humanos se encontram completamente misturados. Este estudo demonstrou um relação genética próxima entre as populações Mesolíticas e posteriores.

Algumas séries do Norte de África (10000-7500 cal BP) foram incluídas com o intuito de verificar a recente especulação, com base em evidências genéticas modernas, sobre a afinidade entre as populações do fim do Pleistoceno/início do Holoceno do Norte de África e da Península Ibérica.

Palavras-chave: Morfologia dentária; Mesolítico/Neolítico; gene.

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INTRODUCTION

A bioarchaeologist attempting to understand and interpret the similarities and differences among human skeletal samples from different sites must have some method of determining whether the controlling factors are genetic or environmental and, if the latter, whether primarily determined by diet, or the physical environment, or the pattern of daily activities, or some combination of all three. Unfortunately, this imperative is rarely satisfied, and there are few aspects of human biology which do not reflect the interplay of both structure and function, the interaction of the genetic substrate with exogenous factors intervening from conception to death.

Study of changes across transitions, such as at aboriginal/European contact in North America, or the Mesolithic/Neolithic shift in subsistence in Europe, may allow us to test whether osteological methods and assumptions are valid – whether, for example, palaeodemographical methods allow us to differentiate between Mesolithic and Neolithic fertility (Jackes et al., 2001). Many of the biological characteristics examined in this context are primarily dependent on behavioural and environmental factors: fertility, pathology, stress markers, the geometry of long bones and so on. But, in examining alteration in such characteristics across the Mesolithic/Neolithic transition (Lubell et al., 1994), we must consider the possibility that genetic change plays some part in the outcome (Jackes et al., 1997a).

Burmeister (2000: 559) has recently pointed out that physical anthropological data may be essential to a satisfactory resolution of the "methodological trilemma of distinguishing archaeologically among migration, trade, and diffusion": however, the bioarchaeologist has a methodological problem, a problem of distinguishing genetic from environmental factors, which requires a great deal more discussion.

THE QUESTION

Ammerman and Cavalli-Sforza (1984) proposed a model for the introduction of agriculture throughout Western Europe which concluded that "the neolithic transition forms the backbone of the geographic distribution of genes in Europe" (1984: 137). In the context, coupled with references to rapid change in the western Mediterranean possibly resulting from the use of boats (1984: 134), the implication seemed to be that Iberia would display high frequencies of eastern Mediterranean marker traits.

Support for the model of population replacement is now becoming hesitant (Richards et al., 2000) and Hewitt (2000) has recently stated that "the contribution [to our genome] from the Neolithic revolution may be less than we thought." Cavalli-Sforza and Minch (1997) have recently reduced the estimate for total contribution to Europe by implying a minority contribution from the Neolithic newcomers of 26%. At the same time, a recent paper can reply to the question "Where do the genes of the Europeans come from, and when did they come in? We think the best answer is still: Mostly from the Levant, mostly in Neolithic times..." (Barbujani and Bertolle, 2001: 24).

Immigration is certainly not ruled out, especially through Central Europe and in association with the rapid spread of the LBK (Linearbandkeramik) about 7500 years ago into areas of northern Europe with rich loess soils (Bogucki, 2000). In fact, a recent

suggestion links this with a sudden flooding of the Black Sea basin at 7600BP (for a comprehensive popular introduction, see Ryan and Pitman, 2000).

However, recent work on Y chromosome DNA (Semino et al., 2000) does not indicate colonisation into Central Europe at this time. Furthermore, study of cranial non-metrical characteristics in samples spanning the Mesolithic to the Neolithic from the Iron Gates Gorge of the Danube (Roksandi, 2001), does not provide evidence of an influx of people from a different gene pool, although the data of Bonsall et al. (1997) clearly suggest an alteration in diet around 8000 calBP. This alteration in diet, or the initiation of the trend towards a diet recognized as "Neolithic" at Lepinski Vir, accords with a wide-spread but short-lived period of very cold and dry climate (Alley et al., 1997; Barber et al., 1999). Research on dental morphology (Keleçevi, in progress) may elucidate the picture, but even here, where population influx is generally accepted as an accompaniment of cultural innovation, the early Neolithic may have preceded any considerable immigration.

If migration did occur, whether it accompanied the introduction of domesticates, or followed after the establishment of agriculture, there remains the question of being able to identify incoming genes. With regard to Iberia, at the western margin of Europe, we must ask whether a Neolithic diffusion of ideas and people along the Mediterranean coast would have led to an influx of genes sufficient to effect a perceptible alteration of allele frequencies (Jackes, quoted in Arnaiz-Villena and Lubell, 2000).

Semino et al. (2000) propose that four Y chromosome haplotypes can be regarded as Neolithic (Eu4, Eu9, Eu10 and Eu11 – the first phylogenetically distinct from the last three). Together, these haplotypes (inherited by males through their fathers) have a high incidence in the Middle East (74% in Lebanon). On the basis of these haplotypes, Semino et al. (2000) suggest that Neolithic immigration must have been greater along the central Mediterranean coast than anywhere else in Europe; the timing of this male influx may be suspect, since the high "Neolithic" component of Calabria (54%) is to be contrasted with the low "Neolithic" component in central and northern Italy (10%). Later colonization, together with mercantile enterprises along the coasts, seem a better explanation for this observed modern Italian gene distribution pattern than does population expansion with the introduction of agriculture. We will return to this question at the end of our discussion, in a test of whether osteological techniques can provide evidence of gene flow, and can help to provide greater chronological precision to population changes in prehistory.

Research on mtDNA suggests that a low frequency of modern Iberian genes (inherited through maternal descent) would be derived from immigration from the east: the proposed eastern origin Neolithic J haplotype is rare in Iberia (Richards et al., 1998). Richards et al. (2000: Table 5) show that the percentage input of Neolithic and Bronze Age maternal immigrant genes is as low for Iberia and Italy as for Scandinavia.

The periods from the Mesolithic and Neolithic to the Bronze Age will be the focus of this paper, so our questions are very clear:

Given that introduced genes from the eastern Mediterranean, dating to the late Pleistocene/early Holocene, are of low frequency in Iberia relative to most of the rest of Europe, can we expect a phenotypic change which could be discernible against the background of general European post-Pleistocene trends?

Given that "there is more plasticity in... osteological characters than in genes" (Kolman and Tuross, 2000: 19), can bioarchaeologists hope to identify gene flow?

Could we actually pinpoint immigrant marker characteristics? Jackes et al. (1997a) raised the question in the context of a discussion on the assumption that the Neolithic everywhere led to a reduction in health and nutritional status, and Zilhão (2000) has returned to the issue. An unequivocal statement of any immigration model will be required since the matter is a complex one, relating to demographics, the size and fertility levels of the groups, differential selective advantages, disease vectors, and the identification of immigrant characteristics. The question of relative numbers of immigrants needs to be discussed in detail (Jackes, in Arnaiz-Villena and Lubell, 2000), and heterogeneity in gene frequencies arising through genetic drift in small and scattered settlements must be taken into account. A recent study from the viewpoint of anthropological genetics concludes: "A model postulating changing selective conditions diffusing as a result of the borrowing of agriculture was shown to produce exactly the same clinal gradient as the population movement models" (Fix, 1999: 213). Bocquet-Appel and Paz de Miguel (2000) have begun to enquire into the demographic requirements of the competing models, and conclude that a model of cultural diffusion is more plausible than one of population influx at the Neolithic.

Knowledge of the heterogeneity of the Portuguese Mesolithic (Jackes and Lubell 1999a,b) is crucial, and the degree of heterogeneity or homogeneity in the Neolithic must also be assessed before we can reach firm conclusions. While understanding the heterogeneity within Iberian populations is essential to bioarchaeologists, it is very difficult to reach such an understanding unless the available samples are of adequate size and preservation and are well spaced in terms of both geography and chronology. Preliminary discussion of these basic concerns has been undertaken (Lubell et al., 1994; Jackes et al., 1997a: 647; Jackes and Lubell, 1999a,b).

ANSWERING THE QUESTION

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Shifting the focus from post-cranial and cranial data, and from modern European gene frequencies to the study of ancient DNA, will provide some clarification. This has been started, and following several years work in perfecting techniques, results provide an initial, tentative suggestion of continuity in mtDNA between Portuguese Mesolithic and Neolithic individuals (Bamforth et al., 2001). Further research must encompass both mtDNA and Y chromosome alleles since there is the obvious possibility of an unbalanced sex ratio in immigrants. We will have to wait for results from several researchers of the analyses of the DNA of many individuals from many samples and regions. In view of the difficulties of extracting usable ancient DNA, the time and expense required, the enormous care in ensuring that there has been no contamination, the checking and cross-checking, preferably using several laboratories, no early answer can be expected.

Our best hope for getting some idea of genetic relationships may lie with studies of dental morphology. These can be done easily, quickly and cheaply on very large numbers of individuals. With the increasing standardization resulting from the acceptance of Turner's Arizona plaque set (ASU Dental Anthropology System), and an increase in the number of circum-Mediterranean samples studied by this method (Bailey et al., 1998; Coppa et al., 1998; Irish, 1998), we can expect that an extensive data base will become available. Only a few years ago there were "no detailed studies of European dental microdifferentiation" (Scott and Turner, 1988: 105); the situation is changing, and the change will surely be accelerated by the publication of a detailed introduction to the study of dental morphology (Scott and Turner, 1997).

There are, of course, problems. We cannot maintain that dental morphology is a simple matter, a simple phenotypic expression of some straight-forward genetic variation (Mayhall, 1999, provides a clear discussion of the problems of taking too simple-minded an approach to non-metrical dental traits). Observer and inter-observer errors will not be completely avoided, even when the Arizona plaques are used for reference. Differences in wear levels among different dietary regimes (especially important when discussing Mesolithic/Neolithic differences) will add possibilities of error, as will taphonomic differences introduced by varying mortuary practices. Finally, there is as yet no agreement as to the best methods of analysis to be used once the observations have been made.

However, all bioarchaeologists would agree that dental morphology is less environmentally sensitive than are cranial and post-cranial metric and non-metric characteristics, and thus provides valuable data. All bioarchaeologists will acknowledge that dental morphology is not sexually dimorphic and (at the population level) will not change from one generation to the next based on exogenous factors, unlike the size and shape of skulls (see the classic studies by Boas, 1912, 1916), and the morphology of long bones (Lieberman, 1996 discusses the implication of experimental work on activity-induced alteration to cortical bone and Pearson, 2000: 571 provides a neat diagrammatic summary of our understanding of the proximate causes of long bone morphology).

There is no doubt, however, that tooth size has altered over time, in Portugal as elsewhere (Jackes et al., 1997a: 648, 652-653: a proposal here relates to a reduction in birth interval, for which see Jackes et al., 2001). An important consideration is whether reduction in the size of the tooth crown may lead to a simplification or alteration of the occlusal details, since any microevolutionary study of European populations must assess whether trends through time may occur in the absence of population replacement. However, Scott and Turner (1997: 126) have stated that "Crown size and morphology interact weakly, if at all, so it appears that the factors involved in the development of morphologic traits are largely independent of tooth size" (see footnote below). Thus, at present, dental morphology provides our best instrument for reaching an understanding of genetic divergence.

METHODOLOGICAL APPROACH

We use here data from a variety of sources, some of them predating the appearance of the Arizona plaques, and for this reason we have had to restrict ourselves to a limited number of dental traits.

For the Portuguese data, we use only the Mesolithic in situ dentitions examined by Jackes and Meiklejohn, and some of the samples being studied by Silva using the ASU plaques (Silva, 2000 and in prep). Silva's samples are from collective burials of the late Neolithic and Chalcolithic, the bones having been recovered from several types of funerary monuments, natural and artificial caves and tholoi (vaulted chamber graves). Silva has also analyzed dentitions from the Coimbra collection of the Museum of Anthropology, stored at the Department of Anthropology (University of Coimbra, Portugal). The Coimbra collection consists of 505 identified Portuguese skeletons of individuals who were born between 1826 and 1922 and died between 1910 and 1936 (Silva, 1995: 109).

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Additional data comes from Ontario Iroquoian ossuaries. The reasons for the inclusion of these data include: outliers provide scale when studying genetic divergence among samples; the Ontario Iroquoian dentitions provide large samples (marred only by high rates of pathology which reduce sample sizes of observable teeth); the dentitions have been studied in detail. Extensive archaeological and osteological research, together with ethnohistorical sources, provide us with a clear understanding of the sites: because each site represents the dead of a limited period of time and of a specific area, the situation is unparalleled in bioarchaeology, and allows us to assess the meaning of the trait frequency divergence among samples. Here we look at sites dating from before the major disruptions caused by European infiltration. In order to be very sure of the data, we include only the two samples which have been the subject of the most detailed dental studies (we exclude Grimsby, used in Jackes et al., 1997a, since only castes were available for that dental morphological study, and the sample represents a time of disruption).

The North African samples, all from sites which are usually considered Capsian, provide very limited data. We have added them because of continuing interest in the possibility: (1) of North Africa as a corridor for the spread of the Neolithic into Iberia, specifically the eastern Maghreb as a key area in the transmission of Neolithic elements in the western Mediterranean (Lewthwaite, 1989); and (2) that contacts across the Straits of Gibralter resulted in gene flow to the north (summary discussion in Arnaiz-Villena and Lubell, 2000 of a conference at which conflicting opinions were expressed; see also Bosch et al., 2000 and Bailey et al., 1998 regarding later time periods, again presenting opposing points of view).

We have chosen traits for which there has been a long history of study, for which there are very clear descriptions of what is to be observed, and for which we would expect little observer and inter-observer variation. Error should be minimal for these traits, even in the presence of some attrition, because, for example, we use positive Carabelli's features (tubercle and cusp), rather than negative features (grooves and pit) which are more difficult to observe.*

Burnett et al. (1998) have shown that there is a potential for error introduced by attrition when grades of expression (those involving increasing size in a feature) are considered. Traits may be recorded as smaller (at lower levels of expression) or absent. However, when attrition is severe, traits may be incorrectly scored as larger, indicating unconscious compensation by the observer. We acknowledge the possibility of error, especially the under-recording of lower levels of expression in samples with high levels of

wear. The Portuguese Mesolithic samples have higher levels of dental wear than the later Portuguese dentitions, but the focus of the research on the Mesolithic was dental attrition rather than dental morphology, making it less likely that worn teeth would have been included in observations of dental morphology, in that we were making no effort to maximize sample size for morphological observations.

Dental data are recorded by side rather than by individual. The use of side data was necessary, because a number of the sites are ossuaries, i.e. places for the secondary burial of disarticulated skeletons. In such sites dentitions are often broken and dispersed, and the rejoining of the left and right sides of mandibles and maxillae is not always possible. When dental traits are studied by individual, the side (antimere) with the highest level of expression is the one recorded, and this could be the method of analysis for a trait such as positive Carabelli's features, which may differ in expression along a continuum. However, by including together several levels of the trait, we avoid some of the problems associated with observation of a "quasicontinuous" (Grüneberg, 1952) character, while recognizing that such traits are not of the discrete "present-absent" type. Threshold effects of quasicontinuous traits are not relevant for several of the observations made here (the fissure patterns).

Since samples of observable teeth are often inadequate, we could pool sides, and it is, indeed, reasonable to pool sides in studies which seek to give an idea of the general population incidence of traits (Sjøvold, 1977: 107). Side differences are generally not found, although every study of dental morphology will include a check on whether there are significant differences between sides - Moskona et al. (1996) suggest that, under certain conditions of inbreeding and environmental stress, asymmetry may increase, though not markedly in basic characters such as cusp number. Because we use so few traits we have to be particularly conservative, and because some of our samples are inadequate, potentially comprising a very few individuals, we must avoid false inflation of sample sizes by pooling sides.

We use only one side for each trait, but we do not restrict ourselves to the left side (as is common in the European anthropological tradition). Intercorrelations among traits are complex, and may differ from sample to sample. In an effort to reduce intercorrelation of traits, we use different sides when considering different traits for the same tooth (e.g. left and right first lower molar), and we use opposing sides when considering the same trait on different teeth (e.g. right side for the first lower molar and left side for the second lower molar) when examining a particular cusp.

Finally, we do not use traits from anterior teeth, because of the high frequency of post mortem loss of these teeth, and of chipping and "signe du cordonnier" (indicating the use of anterior teeth as tools in leather working) in Portuguese dentitions. We do not use third molar traits because of their genetic instability (indicated by the high frequency of anomalous morphology common in third molars).

The traits:

- 1 mandibular right M2 with four cusps only;
- 2 mandibular left M1 with y cusp pattern (i.e. mesiolingual cusp meets distobuccal
- 3 mandibular left M2 with + cusp pattern (cusps meet centrally);
- 4 maxillary right M2 with three cusps only;

^{*} The question of the relationship between size and morphology is complicated by concerns regarding the identification of teeth in ossuary samples (see e.g. Jackes, 1992). For example, in Casa da Moura dentitions there is a significant positive correlation of .4 between the presence of a Carabelli's trait and upper molar length, especially the length of the molar lingual margin. There is a highly significant difference between the lengths of molars with and without Carabelli's traits of all types, and the significance is even greater for the difference between molars with and without a positive Carabelli's trait. The confounding factor is, of course, that the three upper molars are likely to have different mean lengths and different frequencies of Carabelli's traits: at a site like Casa da Moura, with thousands of loose teeth, the size and morphology guide the molar identification. Examining only in situ upper molars (i.e. molars with absolutely certain identification) confirms that teeth with and without Carabelli's grooves/pits/cusps do not differ in length or breadth.

- 5 maxillary right M1 with positive Carabelli's trait, i.e. slight/pronounced tubercle (not pit):
- 6 maxillary left M2 with positive Carabelli's trait, i.e. slight/pronounced tubercle (not pit);
- 7 mandibular left P4 with more than two lingual cusps.

The sites:

North African dental samples were studied by Irish. They come from heterogeneous sites in Algeria and are listed in Table 1. Table 2 gives information on the sites in Portugal studied by Silva. Figure 1 and Table 3 provide details on the Ontario Iroquoian samples used as outliers in this study. The Mesolithic sites in Portugal studied by Meiklejohn and Jackes are the two classic shell middens from the Muge river terraces, Moita do Sebastião and Cabeço da Arruda (see details in Jackes et al., 1997a).

Analysis

(for formulae see http://intarch.ac.uk/antiquity/jackes/non-metric.html)

The mean measure of distance is used in biology to assess the genetic relationships of mammal populations (e.g. Sikorski, 1982; Suchentrunk et al., 1994; Suchentrunk and Flux, 1996). Although Laughlin and Jørgensen had published on human discrete traits in 1956, the use of the mean measure of distance (C.A.B. Smith's MMD) was widely introduced to anthropologists by Berry (e.g. Berry, 1968), deriving from his work on "epigenetic" traits in mice and rats.

Berry (1968) discusses concerns regarding normalizing the variance of non-metrical characteristics, relating to the fact that many of them are not discontinuous traits (that is, traits which can be described as either present or absent). But nor are they continuous (variables which can be fully described by measurements). Several adjustments to the data have been proposed, Bartlett's, Freeman-Tukey's and Anscombe's, examined in most detail by Sjøvold in the context of a study of the red fox (1977). We will use the latter (Anscombe, 1948) here because it is considered to stabilize the variances most effectively (Sjøvold, 1977: 20-23, 103).

The MMD value alone is not necessarily informative when a limited number of traits is observed. Addition of the standard deviation, as in the value DI (= MMD-(sd*2)) (Jackes, 1988), will allow a rough assessment of the significance of the MMD value (at ca. .025; Sjøvold 1977: 30). However, groups compared may appear to be statistically identical when, in actual fact, the sample sizes may be too limited to allow us to identify divergence (or the particular traits are unable to differentiate the groups: Sjøvold, 1977: 30).

While we cannot overcome the problem of small sample sizes, we can alleviate it to some extent by employing one of several methods of standardisation: 1. the MMD divided by its standard deviation (Sofaer et al., 1986); 2. S (which is always = 0 in identical sites) is the sum of trait divergences; and 3. Z (see de Souza and Houghton, 1977). We report the standardised value known as "Z" because it takes into account the number of traits employed, and, when plotted, provides a clear idea of relative sample placement. In the data we report here, Z is most highly correlated with both MMD and with the variable (DI)

that tests for significance of the difference between samples: it thus provides for more meaningful results and increased differentiation of sites, despite inadequacies of sample sizes and the restricted number of traits. Examination of **Table 4** will, however, show that a sample size effect has not been completely avoided: it is important to note that the difference in sample size between the two Ontario sites has reduced the divergence between Glen Williams and the Portuguese and Capsian samples.

Ranking the Z scores allows us to avoid placing too much emphasis on the absolute values: we can see that the Ontario and Capsian samples are well removed from the Portuguese. Among the Portuguese samples, Monte Canelas I and then, equally, Moita do Sebastião and Dolmen junto à Estrada de Ansião hold central positions, with minimal differentiation from other sites.

For a detailed study, identification of traits demonstrating microdifferentiation within a particular area would be necessary. Furthermore, it is known that there are traits which are divergent on a global scale; for example, characteristics of the upper incisors would clearly differentiate between North Americans and Portuguese. However, the traits studied here were not chosen on the basis of their suitability for differentiating between, and among, North American and circum-Mediterranean samples. The traits are those available in the literature for all the sites, providing no missing data, and fair sample sizes (criticism of genetic studies in which the number of traits is increased at the expense of reasonable sample sizes, and missing data are provided by interpolation, is pertinent).

Nevertheless, Figure 2, a seven trait/eleven sample dendrogram using the average linkage (between groups) method of clustering, demonstrates large scale differentiation — despite the arbitrary choice of traits, and an analysis which could be considered weak, being based on only seven traits. We have here rescaled so that the tree can be easily understood as demonstrating a percentage degree of difference among samples. The degree of differentiation among all the Portuguese sites is roughly equivalent (coefficients = 1.6 and less) to the level of the divergence between the two Ontario sites (1.7), a situation which is also true of other methods of generating dendrograms, for example, the within groups, median and centroid methods of analyses. We may conclude that the relationships among the various Portuguese samples, Mesolithic and later, are close. The Portuguese samples are close relative to the Ontario Iroquoian samples which are close in space, time (see Figure 1 and Table 3) and culturally (Finlayson, 1998, in providing the results of multidisciplinary long-term research on an adjacent area, gives details of the archaeology of the Ontario Iroquois Tradition).

On this basis we can only postulate that the Portuguese Mesolithic population was more or less identical with its successor populations genetically: it should be emphasised that we are comparing the Mesolithic samples with others late enough in time to have allowed any incoming Neolithic population to have established itself within the gene pool, if we postulate an incoming population at selective advantage.

A less rigid way of viewing the same data is provided by multidimensional scaling (Figure 3), which avoids the connotation of a dendrogram, that some type of evolutionary relationship is necessarily implied. The Z matrix values here give a normalized raw stress value of. 024 (SPSS PROXSCAL v. 1). The stress is a measure of the goodness or, rather, the "badness" of the fit. Anything under.1 is acceptable, and thus the data here fit extremely well and 98% of the dispersion is explained after 17 iterations. This analysis was performed for a two dimension solution, the data treated as interval data, and the first dimension in

this type of scattering covers 67% of displayed variation. It appears that the method rescales the relative dispersion consistently to a two-thirds:one-third ratio on the dimensions.

The two Mesolithic Portuguese samples, Moita and Arruda, are not significantly different, as is to be expected from their geographical contiguity and overlap in time. No post-Mesolithic Portuguese sample is significantly different from Moita. Figure 3 makes the obvious point that, on the important dimension, dimension 1, the prehistoric Portuguese samples are very tightly clustered, while Coimbra, the modern sample, is slightly offset.

Further analysis of this type can be done, using a three dimensional solution, which reduces the stress to .016 after 19 iterations, and explains 98% of the dispersion. The first dimension encompasses 52% of the displayed variation, and the second and third dimensions display 27% and 21% of the dispersal respectively. Here we can rotate the solution; rotation through a third dimension gives another view of the relationship among the Portuguese samples (Figure 4), and displays clearly how they cluster on the first dimension. The rotation we provide in Figure 4 allows us to visualize the separation between the modern and prehistoric Portuguese samples very well. In Table 5 we provide the final coordinates for the three dimensions to allow readers to perform rotations.

A TEST CASE OF CHANGE

We return now to Y chromosome haplotype frequencies in southern Italy, to consider a question posed at the beginning of this paper, whether dental anthropology can help us understand the time-frame of genetic change. It will be recalled that Semino et al. (2000) propose that four Y chromosome haplotypes allow us to track Neolithic migration and suggest that a "Neolithic" component in southern Italy (of 54%) contrasts with the low "Neolithic" component in central and northern Italy (of 10%). An alternative theory might be that Hellenic colonization was the starting point for this divergence within Italy. Figure 5 uses data from Coppa et al. (1998) to demonstrate that, while the Latini population just south of Rome remained unchanged over 700 years, by contrast there was a very marked change in dental crown traits in Campania, south of Naples. This change can be pinpointed as already well underway in the 6th century BC, when there is a trend towards the Etruschi (significantly this was the period of Etruscan influence in Campania). Changes in morphology accumulated so that those Campanians still being buried in the necropolis at Pontecagnano (Salerno) at the end of its period of use had become significantly different in statistical terms from the Latini, and they had also become significantly different from those buried in their own ancestral Villanovan graves. Without data on the dental morphology of eastern Mediterranean populations we are unable to determine the source of the gene flow, but the accumulated effects of Greek settlement from the 8th century onwards at the neighbouring Greek colonies of Cumae, Pithekoussai, Neapolis, Poseidonia and Elea must be considered. The work of Coppa et al. (1998) clearly demonstrates, however, that systematic studies of dental morphology allow the detection of population change resulting from gene flow.

CONCLUSION

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Data from Italy suggest that the use of dental morphology in systematic analyses will allow anthropologists to test for genetic change over time, thus giving a clearer idea of whether or not there has been significant gene flow.

However, we see as little evidence for population discontinuity in the prehistoric western Iberian samples based on dental morphology, as we do for cranial size and shape (Jackes et al., 1997b), despite the fact that we can feel more confidence in the dental than in cranial metrical data. There may, of course, have been movement of people around Iberia, but this is not apparent from our bioarchaeological data. By contrast, we have firm evidence of change within the Mesolithic: in the subtle but incontrovertible changes in the details of dental attrition and pathology the change is along a trajectory which extends through into the Neolithic (Lubell et al., 1994). There may have been increasingly sedentary Mesolithic occupation (signalled by more common burial of infants) at a base camp. We do know that Arruda females differed from Moita females in their femoral cortical thickness and femoral cortical density (Jackes and Lubell, 1999b), so an interplay of increased sedentism and higher fertility is the likely scenario - potentially leading to increasing genetic heterogeneity. Thus the apparent picture of some dispersal, or slight heterogeneity, around the oldest site (Moita), makes sense. Gene flow from outside, specifically here gene flow from the Capsian Maghreb, is not shown to have been sufficient to alter autochthonous genotypes.

Our interpretation in this paper is sharpened by the inclusion of non-Iberian samples to provide scale. The Ontario data help us to interpret the meaning of the Iberian data. Several decades of work on Ontario sites by bioarchaeologists and dental anthropologists, more than a century of intensive archaeological investigation, coupled with the seventeenth century descriptions by Jesuit and Recollet priests which are of such detail that they allow us to test our osteological findings (Jackes, 1994, 2000), provide a unique gauge by which to judge the meaning of "genetic distance". In Figure 4 the relationship of Glen Williams and Kleinburg appears as relatively distant: however, investigating this by means of a study of 15 dental traits in seven Ontario samples provides a demonstration that Glen Williams and Kleinburg group on the first dimension. The conclusion of Molto (1980: 257-8) based on non-metrical cranial traits for 1022 skulls from 17 sites covering 1500 years was that "extensive gene flow was occurring among the Iroquois of south central Ontario" and that there was "a stable gene pool" even across the archaeological boundary between Middle and Late Woodland times. This conclusion would be supported by dental morphological studies.

Drawing upon Ontario Iroquoian data for comparative purposes in our analysis of Portuguese dental morphology has allowed us to conclude that Mesolithic to Chalcolithic samples provide evidence for the existence of a primary and enduring gene pool in Central Portugal. Similar data on an amplified series of 22 dental non-metrical traits from Portuguese Mesolithic and post-Mesolithic sites (as reported in Bamforth et al., 2001) supports this conclusion of a tight clustering of Portuguese samples based on genetically determined dental crown traits.

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Table 1 – North African dental samples studied by Irish from heterogeneous sites in Algeria

| Site name | n | Date or industry | Publication | Site type |
|---|---|---|--|----------------------------------|
| Mechta el Arbi | 2 | Capsian | | shell midden |
| Aïn Dokkara | 1 | Capsian: ca. 7500-8800 calBP | Balout 1955 | shell midden |
| Tebessa | 4 | | | several shell middens in area |
| Mechta-Chateaudun (Chateaudun du Rhumel) | 1 | | Balout 1955: 426-427 | shell midden |
| Abri des Aiguades | 2 | Capsian or Neolithic? | Vaufrey 1955: 339; Balout 1955 | rock shelter on NE coast |
| Grotte des Hyènes | 5 | Capsian; (Neolithic Vaufrey 1955) | Camps 1974 | |
| M'Chira | 1 | Capsian | Vaufrey 1935 | shell midden |
| Escargotière #12 | 4 | Capsian ca. 9000-8000 calBP | Sheppard 1987; Haverkort & Lubell 1999 | shell midden |
| Oum Et Tiour (Corneille) | 1 | Neolithic | Vaufrey 1955: 316 | |

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Table 2 - Sites in Portugal studied by Silva

| Site | maximum n | bp | 1 sigma calBP | lab reference number |
|---|--------------|-------------------------|-------------------------|---------------------------------------|
| Cova da Moura (natural cave) | 23 | 3950 ± 60 4715 ± 50 | 4520-4290 5580-54320 | UBAR - 536 UBAR - 593 |
| Dolmen junto à Estrada de Ansião | 20 | 4640 ± 90 | 5580-5080 | Sac - 1559 |
| Paimogo I (tholos) | 96 | 4250 ± 90 4130 ± 90 | 4960-4580 4830-4530 | Sac - 1556 UBAR - 539 |
| Monte Canelas I (artificial cave) | 16 | 4420 ± 60 4370 ± 60 | 5040-4850 5260-4870 | OXA - 5514 XA - 5515 |
| Hipogeu de São Paulo (artificial cave) | 22 | 3960 ± 190 3870 ± 70 | 4415-4153 4808-4099 | UBAR-629 UBAR-630 |
| Coimbra | 104 | 19-20 century | | modern collection Univ. of Coimbra |

Table 3 - Sites in Ontario providing Iroquoian samples used as analysis "outliers"

| Site | coordinates | maximum n. | date | references |
|---------------|------------------------|------------|----------------|------------------------------|
| Glen Williams | 43° 40' N 79° 55' W | 40 | A.D. 1400-1450 | Hartney, 1978 Grey, 1982 |
| Kleinburg | 43° 50' N 79° 38' W | 321 | A.D. 1585-1615 | Jackes, 1977 Wright, 1977 |

| | | 81 | 7 - 1 310 | | | 2000 | a a marginal | 441011 | | | |
|------------------|--------|--------|------------------|-----------|--------------|--------------------|---------------------|---------|------------------|-------------------|---------|
| | Moita | Arruda | Cova da Moura | Paimogo I | São Paulo | Monte Canelas I | Dolmen e. Ansião | Coimbra | Glen Williams | Kleinburg Capsian | Capsian |
| Moita | 0.000 | | | | | | | | · | | |
| Arruda | 0.342 | 0.000 | | | | | | | | | |
| Cova da Moura | 0.415 | 0.734 | 0.000 | | | - | | | | | |
| Paimogo | -1.373 | 1.819 | 2.227 | 0.000 | | | | | | | |
| São Paulo | -0.050 | 1.490 | 2.203 | 0.280 | 0.000 | | | | | | |
| Monte Canelas I | -2.138 | -1.045 | 1.113 | -1.290 | 0.051 | 0000 | | | | | |
| Dolmen e. Ansião | -1.442 | -0.461 | 1.965 | -0.451 | -0.269 | -1.633 | 0.000 | | | | |
| Coimbra | 0.759 | 2.839 | 2.581 | 0.547 | 2.190 | -0.613 | 0.176 | 0.000 | | | |
| Glen Williams | 7.483 | 8.203 | 8.478 | 8.559 | 7.656 | 5.733 | 7.723 | 9.972 | 0.000 | | |
| Kleinburg | 13.030 | 14.418 | 12.810 | 20.662 | 11.975 | 9.159 | 12.006 | 24.726 | 1.743 | 0.000 | |
| Capsian | 5.841 | 8.020 | 160.9 | 5.740 | 5.493 | 4.908 | 6.330 | 6.962 | 6.644 | 7.268 | 0.000 |
| | | | | | | | | | | | |

Table 5 - Final Coordinates three dimensional solution from multidimensional scaling

| | Site number on diagrama | Dimension 1 | Dimension 1 | Dimension 1 |
|------------------|-------------------------|-------------|-------------|-------------|
| Moita | 7 | .282 | 023 | 046 |
| Arruda | 4 | .263 | .444 | .124 |
| Cova da Moura | 8 | .201 | .124 | .486 |
| Paimogo I | 9 | .464 | 234 | 208 |
| São Paulo | 10 | .184 | 249 | .220 |
| Monte Canelas I | 6 | .082 | .063 | 147 |
| Dolmen e. Ansião | 5 | .261 | .235 | 140 |
| Coimbra | 11 | .747 | 020 | 121 |
| Glen Williams | 2 | 751 | .155 | 339 |
| Kleinburg | 1 | -1.334 | .123 | .117 |
| Capsian | 3 | 399 | 619 | .053 |

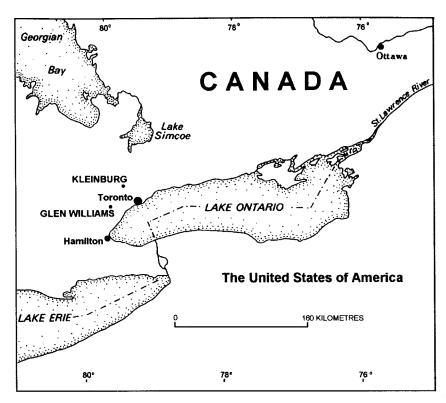


Fig. 1 – location of the two Ontario ossuary sites.

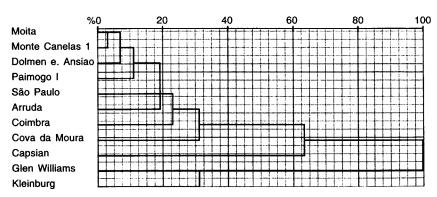


Fig. 2 – Dendrogram of average linkage (between groups) analysis of Z matrix generated by an Anscombe transformation mean measure of distance analysis of the frequencies of seven dental traits.

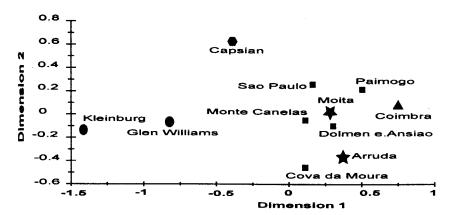


Fig. 3 - Two dimension solution from multidimensional scaling.

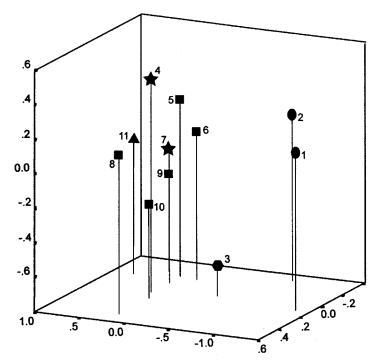


Fig. 4 – Three dimensional solution from multidimensional scaling with slight rotation. Key to samples: Kleinburg 1, Glen Williams 2, Capsian 3, Cabeço da Arruda 4, Dolmen Estrada de Ansião 5, Monte Canelas I 6, Moita do Sebastião 7, Cova da Moura 8, Paimogo I 9, São Paulo 10, Coimbra 11.

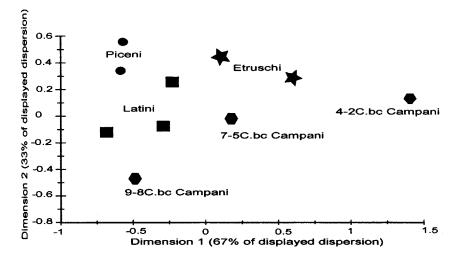


Fig. 5 – Two dimensional solution from multidimensional scaling of data from Coppa et al. 1998. Thirty six maxillary and mandibular traits, those with maximum sample sizes, were chosen for the analysis which covers changes in Italian coastal populations during the first millenium BC and draws attention to genetic changes in Campania over the period of establishment of Hellenic colonies like Cumae, while the Latini remained unchanged.