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TIES BETWEEN PORTUGAL AND BRAZIL: A CONTRIBUTION FROM DENTAL MORPHOLOGY.

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Introduction

In the 19th century, researchers such as G. Carabelli and C. S. Tomes described curiosities in dental anatomy, and consequently had dental non-metric traits named after them (SCOTT; TURNER, 1997). More systematic research into dental morphology was started in the early 20th century by workers such as Hrdlicka and Gregory. Other scientists, like A. Dahlberg, P. Pedersen and K. Hanihara kept the field alive until its blossoming, in the 1950's (SCOTT; TURNER, 1997, 2008). That decade saw the development of genetic, prehistoric, morphogenetic and forensic approaches to dental morphology (SCOTT; TURNER, 1997) and was marked particularly by Lasker's (1950) work that associated the modern synthesis and dental morphology, which introduced the field unto such matters as inheritance and genetics.

The main advantages of using dental morphology are its variation (occurring in several non-metric traits) and how it is mostly dependent on and correlated to genetic diversity. The dentition is formed independently of uterine influence. It evolves slowly (and probably is independent of natural selection). Little sexual dimorphism and the lack of correlation between traits are safe assumptions (which should, nonetheless, be confirmed). Finally, it presents discrete variables which depend on a small and stable portion of the genome (TYRRELL, 2000). Despite this, the interplay between genomic and environmental factors is relevant during development and can influence morphology (JERNVALL et al., 2000; JERNVALL;

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JUNG, 2000; SALAZAR-CIUDAD; JERNVALL, 2002, 2010; HUNTER et al., 2010; RIGA et al., 2013).

Dental morphological traits are most likely expressed through a quasi-continuous polygenic mode (SCOTT; TURNER, 1997; RIZK et al., 2008), but can also be transmitted through simple Mendelian or oligogenic inheritance (HILLSON, 2005). The genetic factor behind dental non-metric traits is the threshold effect, since the presence and quantity of particular alleles and chromosomal *loci* most likely affect the presence, expression and frequency of a trait in a population (SCOTT; TURNER, 1997, 2008; TYRRELL, 2000).

So, genomic factors are thought of as essential in the differences of dental non-metric trait frequencies between (polytypicism) and within (polymorphism) populations. Only gene flow (with minor exceptions) accounts for frequency variability (WILLERMET; EDGAR, 2009; SCOTT; TURNER, 1997). This biological variation is detectable in a world-wide scale, but also at regional, local and even familiar and individual levels (SCOTT; TURNER, 1997; STOJANOWSKI; SCHILLACI, 2006; RÍOS et al., 2010; EDGAR, 2013; STOJANOWSKI et al., 2013).

Archaeological data can attest to cultural change, which can be due to the cultural communication between populations. It cannot however provide the evaluation of biological continuities (or discontinuities) or direct evidence of human migration. In sum, cultural information does not distinguish cultural from biological contact, invasion or population replacement, while on the other hand, dental morphology can aid in those respects (IRISH, 2000; SILVA, 2002; RODRÍGUEZ, 2004; ULLINGER et al., 2005).

Dental morphology is able to inform on genetic changes that happen across time and space through the comparison of sample frequencies (JACKES et al., 2001; SCOTT; TURNER, 1997). These frequencies diverge when the samples are isolated from each other and converge when those groups contact and interbreed (SCOTT; TURNER, 1997). Data can be collected from the archaeological, anthropological and fossil records as well as from living individuals, making teeth unique resources in understanding population history (SCOTT; TURNER, 1997).

Brazil presents one of the utmost human genetic diversities in the world (ALVES-SILVA et al., 2000; CARVALHO-SILVA et al., 2001; ABE-SANDES et al., 2004; MARRERO et al., 2005; SILVA et al., 2006). It was originally populated around 21.000 years BP by Amerindians, who were the sole inhabitants (around 2.5 million people) when Brazil was discovered in 1500 (ALVES-SILVA et al., 2000; CARVALHO-SILVA et al., 2001; ABE-SANDES et al., 2004; MARRERO et al., 2005; SILVA et al., 2006). The Portuguese colonization was accomplished through

0.5 million Europeans (between the late 15th and the early 19th century), mostly men, and around 3.5 to 4 million enslaved Africans, from the mid-16th to the late 19th centuries. The interbreeding of Portuguese (and other European) males, African and Amerindian females produced the basis of the contemporary Brazilian trihybrid population (ALVES-SILVA et al., 2000; CARVALHO-SILVA et al., 2001; ABE-SANDES et al., 2004; MARRERO et al., 2005; SILVA et al., 2006). The gene flow from Europe, Africa and, particularly in recent times, Asia was continued through migration into Brazil (ABE-SANDES et al., 2004). In Portugal, the political, social and economic contexts contemporary to the Industrial Revolution pressed many people into emigration, with Brazil as the main destination (REIS, 1987).

Admixture between Europeans and Amerindians was encouraged, since population growth was warranted (ALVES-SILVA et al., 2000). Amerindians suffered population decline from confrontation with the colonizers and diseases their immune-systems were not adapted to fight (ALVES-SILVA et al., 2000).

In spite of its usefulness, Brazilian and Portuguese populations were never compared through dental non-metric traits. Biological affinities between the contemporary Brazilian population from Rio de Janeiro and the Portuguese mid-19th to early 20th century population will be inferred from dental morphology. Secondarily, odontological discrete variables will be exemplified as valuable sources for the study of population history in archaeological contexts.

Materials and Methods

Rachel Tinoco (2010) studied the dental casts of 130 Brazilian individuals (59 males and 71 females) of diverse ancestries from the metropolitan area of Rio de Janeiro. All individuals had Brazilian parents and grandparents (and therefore were third generation Brazilians). Tinoco (2010) compared the sample's dental non-metric trait frequencies to other populations' without statistical tests, and suggested they were intermediately placed between African and European ancestry.

Marado (in preparation) scored the dental non-metric traits of 600 Portuguese individuals (300 of each sex; mainly from Coimbra) who lived between the 19th and early to mid-20th centuries and died between the ages of 7 and 97 years. These individuals are part of the "Trocas Internacionais" (International Trades) and "Escolas Médicas" (Medical Schools) collections housed at the Department of Life Sciences of the University of Coimbra (MARADO, in preparation).

The "Escolas Médicas" collection was amassed by Bernardino Machado between 1896 and 1903, through the recovery of cranial remains previously held at the Medical Schools of Oporto and Lisbon, and the Faculty of Medicine of

Coimbra (FERNANDES, 1985; ROCHA, 1995; SANTOS, 2000; WASTERLAIN, 2006; CUNHA; WASTERLAIN, 2007). "Trocas Internacionais", the most widely used collection, was put together by Eusébio Tamagnini between 1932 and 1942, with crania and mandibles coming from the Conchada cemetery in Coimbra (FERNANDES, 1985; ROCHA, 1995; SANTOS, 2000; WASTERLAIN, 2006; CUNHA; WASTERLAIN, 2007).

The world-wide samples used in comparison to the referred Brazilian and Portuguese samples are described in Scott and Turner's (1997) work and others cited therein. They hail from North Europe, Western Europe, South Siberia, Northeast Siberia, North Africa, West Africa, South Africa, China/Mongolia, Japan (recent sample), Northwest North America (Native Americans) and North and South America (Native Americans).

The ASUDAS (Arizona State University Dental Anthropology System; TURNER et al., 1991) was used in to score six dental non-metric traits: U1 shoveling, UM1 Carabelli's trait, UM1 metaconule (cusp 5/C5), UM2 hypocone (cusp 4/C4) absence, LM1 entoconulid (cusp 6/C6) and LM2 hypoconulid (cusp 5/C5). (The used breakpoints can be seen on Table 1.) The ASUDAS was developed from 1970 onwards by Turner and colleagues (SCOTT; TURNER, 1997, 2008; HILLSON, 2005), so as to standardize the scoring of crown and root variables which are expressed in a quasi-continuous form, and allow for the measure of different grades (SCHMIDT, 2008). Turner was inspired by the works of A. Dahlberg and K. Hanihara with ordinal scales and plaques in scoring methodology (SCOTT; TURNER, 2008). This method allows for standardized observations using plaster cast reference plaques that usually portray all different grade expressions, and allow the reduction of inter- and intra-observer error (TURNER et al., 1991; SCOTT; TURNER, 1997, 2008; HILLSON, 2005).

The samples' frequencies were compared by principal components analysis (PCA). PCA is a statistical tool that reduces data, by compounding variables and re-expressing them in composite axes. These axes display the interrelations within variables, underline the variation found among them, and eliminate variables of little use (IRISH; GUATELLI-STEINBERG, 2003; DELGADO-BURBANO, 2007a, 2007b; HARRIS, 2008). PCA also identifies the relative weight of each dental non-metric trait in the final inter-sample variation, by analyzing how the original variables and the resulting components correlate (IRISH; GUATELLI-STEINBERG, 2003; HARRIS, 2008). In sum, the PCA reduces the volume of data into more coherent and easier to interpret components. The PCA captures the pattern of diversity among the variables and the samples tested (IRISH; GUATELLI-STEINBERG, 2003; HARRIS, 2008).

Results

The PCA generated two components with an eigenvalue above 1, that represent 74.9% of the variation between all samples. Table 1 reports the weight of each dental discrete trait to the samples' distribution for each component. It also displays the eigenvalues and variances expressed by each principal component (PC). PC1 expressed 49.7% of the variance through strong positive loadings (>0.5) from UI1 shoveling, LM1 C6 and LM2 C5, and strong negative loadings (<-0.5) from UM1 Carabelli's trait. PC2 reflects 25.2% of the variance between samples and is characterized by strong positive loadings of UM1 Carabelli's trait and UM1 C5.

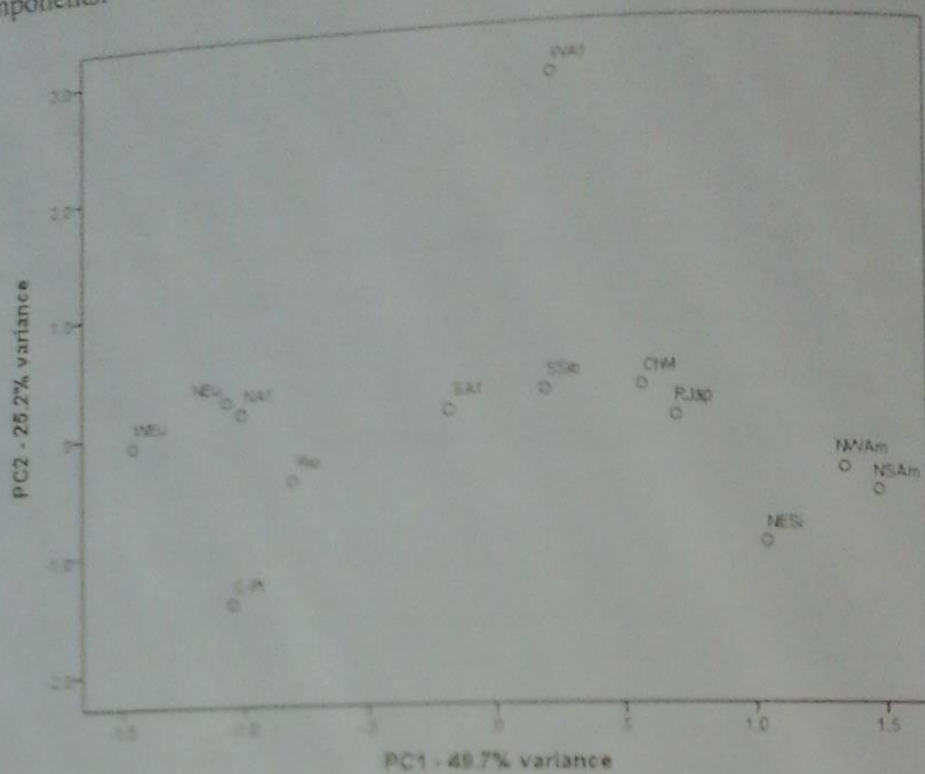
Table 1. Matrix of the component loadings, eigenvalues and variances of the PCA which analyzes Coimbra, Rio de Janeiro and world-wide samples.

Trait (tooth) and breakpoint	PC 1	PC 2
Shoveling (UI1) + = ASU 3-6	<u>0.911</u>	-0.237
Carabelli's trait (UM1) + = ASU 5-7	-0.642	<u>0.558</u>
C5 (UM1) + = ASU 1-5	0.087	<u>0.938</u>
Hypocone (UM2) + = ASU 0-1	-0.392	-0.448
C6 (LM1) + = ASU 1-5	<u>0.937</u>	0.180
C5 (LM2) + = 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.

Figure 1 illustrates the relative position of each of the compared samples along two axes, which represent the generated PC's. The sample nearest Coimbra is Rio de Janeiro (Brazil). The Brazilian sample is placed nearer North Africa and North Europe, although it is also near the Portuguese.

Figure 1. Bidimensional representation of the compared samples' distribution along the two PCA generated components.



Rio - Rio de Janeiro, Brazil; C-Pt - Coimbra, Portugal; NEu - North European; WEu - West European; NAF - North Africa; SAF - South Africa; WAF - West Africa; NESi - Northeast Siberia; SSib - South Siberia; RJap - Recent Japan; ChM - China/Mongolia; NWAm - Northwest North American Natives; NSAm - North and South American Natives.

The proximity among Portuguese, Brazilian, European samples and North Africa is obvious and mainly expressed via PC1. This component reflects almost half the dental morphological variance amongst all samples (when these six dental non-metric traits are considered). Rio de Janeiro is deviated from Coimbra on the direction of the African samples on PC1 (it should be noted that Scott and Turner's [1997] "South Africa" sample is composed of several Sub-Saharan African samples). This Brazilian sample is aligned with both Native American samples along PC2.

PC1 also sees West Africa, South Siberia, China/Mongolia, recent Japan, Northeast Siberia, Northwest North American Natives and North and South American Natives as furthest from the wide cluster which includes both Brazilian and Portuguese samples.

PC2 presents Coimbra as one the most divergent samples in the main cluster and West Africa as the main outlier, at a great distance from most other sampled populations.

Discussion

The proximity to Coimbra, North and West Europe places Rio de Janeiro as most likely mainly influenced by European genetic diversity. North Africa is the sample nearest Brazil. That could be explained by the admixture between European and Sub-Saharan African gene flow producing an artificial proximity to another sample which is likely related to some extent to both of them. The proximity to the Sub-Saharan African populations is evidenced by the position of South Africa, as near Rio de Janeiro as Western Europe. "South Africa" includes samples investigated by Joel D. Irish (e.g. IRISH, 1998) from West, East and Southern Africa, according to Scott and Turner (1997), and confirms slaves as the African component to the Brazilian genetic diversity.

Colombian slaves were Bantu speakers mainly from West and Central-West Africa, and can be genetically distant from the slaves forced into North America (DELGADO-BURBANO, 2007b). Slaves brought to Brazil were also Bantu speakers (SILVA et al., 2006), which can justify the relative proximity between Rio de Janeiro and the South Africa sample, which probably includes Bantu speakers. There seems to be a faint biological affinity between the Brazilian and Native Americans, by their mentioned alignment along the y axis (Figure 1).

Despite of the limited amount of information available (only six traits), dental morphology seems to suggest a network of biological relationships which might reproduce the result of the processes of gene flow into Brazil in the last five centuries.

As stated above, Brazil was inhabited by about 2.5 million Natives when it was discovered and invaded by half a million Europeans (mainly Portuguese) in the following four centuries. These populations kept the gene flow to Brazil through immigration, even after that initial wave. Besides Europeans, enslaved populations from Africa also were forced into Brazil, numbering at least 3.5 million (ALVES-SILVA et al., 2000; CARVALHO-SILVA et al., 2001; ABE-SANDES et al., 2004; MARRERO et al., 2005; SILVA et al., 2006).

The genetic contributions from those source populations to diverse Brazilian samples have been estimated in recent years. Brazilian Caucasians have inherited 90.0% of Y-chromosomes from Portuguese individuals and 60.0% either Native American or African mtDNA (PENA, 2002 apud TINOCO, 2010). Even in the Rio de Janeiro state (including, but not limited to the city), Y-chromosome markers of 127 unrelated individuals were analyzed by Silva and colleagues (2006), testing the expected great variability for this Brazilian state. Its homonymous city was

the main port of access to many travelers from the Eastern margins of the Atlantic Ocean (SILVA et al., 2006). These patrilineal markers are mostly of European origin (88.1%), and the Portuguese contribute with the main share (particularly haplogroup R1b3, identified by its M269 mutation, traced as of pre-Neolithic Iberian origin). African contributions rose to 8.7%, while the Amerindian male lines were limited to 1.6%. The authors also tested the differences between the Portuguese and the Rio de Janeiro state Y-chromosome gene pools. They found null distinctions between them and that only the Spanish could be regarded as another main source of gene flow, which removes Italians, Germans, Syrians, Lebanese and Japanese as potentially sizeable contributors. These results are paralleled by the ones reported here for dental morphological features.

Two-hundred Brazilian white males from four different regions were tested for their Y-chromosome variation. More than 90 North Portuguese individuals were analyzed as well (CARVALHO-SILVA et al., 2001). The found markers originated in Europe, mostly. The absence of statistical distinction between the Brazilian and the Portuguese Y-chromosome markers suggests all patrilineages could have come from Portugal. The authors propose other major contributions could have come from Italian, Dutch, Portuguese Jewish and Moroccan Jewish immigration. Amerindian patrilineages were not detected and Sub-Saharan African contribution was minimal. These proportions were not affected by class, since they were found for poor rural white individuals as well as for middle-class and upper middle-class samples. Variation was mainly found within the four regions, not between them (CARVALHO-SILVA et al., 2001).

As for mtDNA evidence, a study analyzed the genetic background of 247 (mainly white) middle class unrelated Brazilians from four regions found 33.0% Amerindian and 28.0% African matrilineal contribution (ALVES-SILVA et al., 2000). The authors hypothesized this could be a minimal value, should the middle-class status of the individuals involved have biased the results.

One hundred and nineteen white individuals from Rio Grande do Sul (88 from the city of Veranópolis and the others comprising the "general white sample") were genetically studied for both mtDNA and Y-chromosome markers (MARRERO et al., 2005). The Brazilian region now known as the Rio Grande do Sul state was only colonized from the 18th century onwards. The control of its territory successively changed hands between the Portuguese and the Spanish. Y-chromosome evidence showed an almost complete European ancestry for this sample (with rare Amerindian and African contribution in the "general white sample"). mtDNA variation revealed a similar pattern for Veranópolis (97.0% Europeans matrilineages), although a different distribution was verified on the "general white sample", despite the major contribution from Europe (48.0%). The

difference was caused by the comparatively high frequency of Amerindian (36.0%) and African (16.0%) haplogroups on mtDNA variability for the "general white sample" (MARRERO et al., 2005).

As mentioned above, colonists were encouraged to interbreed with the native population, in Brazil. That, when coupled with the probable free access European males had to African female slaves, is the most likely reason for the current admixture of African and Native American mtDNA into the Brazilian genetic variation, even when dealing with Caucasian individuals. Patrilineages, on the other hand, are mainly Portuguese, with some European, little African and almost no Amerindian contribution. This is a clear demonstration of the asymmetry in sexual access to different ethnical groups and its part on the design of the contemporary Brazilian gene pool. It also illustrates how the close biological affinity between Rio de Janeiro and Coimbra found through dental morphology analysis is supported by historical and genetic evidence.

In fact, the only exception divulged so far for mtDNA results, that of Veranópolis, is not towards a greater admixture of Native and African elements onto the genetic variation. It is exceptional, on the other hand, because of the almost exclusive presence of European diversity. In that city, as well as for the other samples tested, Y-chromosome evidence points to Amerindian or African males and European females having nearly no sexual access to each other. As Edgar (2009) suggested for a North American interpretation of dental morphological data, this seems to portray a continued habit of "racial" separation, reflected in the present genetic diversity found in Brazilian Caucasian individuals.

However, despite how strong this evidence may be, the Rio de Janeiro sample used to establish the biodistance between Brazil and Portugal through dental morphology was not composed of Caucasian individuals only (see TINOCO, 2010), and other ancestries were also the focus of genetic studies in Brazil.

Six Brazilian samples were studied for their Y-chromosome haplogroup diversity (ABE-SANDES et al., 2004). Four were of African descent (two urban and two isolated), one was of European ancestry and the other of Japanese origin. Genetic diversity was mostly found on the urban African and the European samples. Patrilinearity from European origin was more important in Afro-Brazilians than the Amerindian genetic contribution. The authors pointed out that genetic heterogeneity was hindered by preferential marriages within the same ethnicity.

The ancient genetic markers of ten rural quilombos (communities composed of Afro-Brazilians) were 30.7% African, 39.0% European and 21.3% Amerindian in origin (KIMURA et al., 2013).

mtDNA data from Africa (Cameroon and Congo) and Brazilians of African descent (mainly from rural quilombos, established by escaped slaves, though an urban sample was also included) showed European matrilineages to be non-existent in rural samples and scarce in the urban sample (ARAÚJO SILVA et al., 2006). The presence of Amerindian markers is probably due to the greater frequency of male slave escapees, which drove them to find Amerindian sexual mates. The urban sample had 5.0% European mtDNA haplogroups, despite only the report of exclusively African ascendancy. Afro-Brazilians also show possible ethnic-specific sex bias in the slave trade, as West-Central Bantu Africans are less represented than West Africans through mtDNA (ARAÚJO SILVA et al., 2006).

The genetic evidence in African descendant communities in Brazil also testifies that the European male sexual access to African females was much greater than the sexual access between European females and African male individuals. This was most likely a homogeneous phenomenon in the American continent. The presence of greater frequencies of Carabelli's cusp and *tuberculum dentale* in the younger generations of Barbados slaves could be a testimony to ethnic admixture in generations born in that island (CORRUCCINI et al., 1982). This suggests that, because of the generalized lack of sexual dimorphism in dental non-metric traits, differentiation in ethnic sexual interbreeding does not affect the results of genetic recombination on the dental morphology of subsequent generations. So, the low genetic contribution of African and even Amerindian populations to the Rio de Janeiro sample, apparent in the results of the PCA, may be mostly from female African and Native individuals.

The analysis of dental morphological variation of the Rio de Janeiro and Coimbra samples suggests close biological ties between Brazil and Portugal. It hints simultaneously at the historical (and perhaps contemporary social) differential sexual access between male and female individuals of different ethnicities. Despite the low number of dental non-metric traits available for comparison, the results allowed for a suggestion of Brazil's recent population history.

The potential for archaeological use of this dental anthropology approach is attested by how contemporary Brazilian genetic data support and help interpret the current results. Dental anthropology (and dental non-metric traits in particular) can help understand the pre- and post-conquest population dynamics that characterized Brazilian history and shaped the current diversity of the Brazilian population.

This work also underlines the interconnection of the histories of Brazil and Portugal and how that influenced the genetic landscape of Rio de Janeiro, Brazil and South America. The awareness that those genetic ties were molded by ethnic differences in sexual access also informs on the deeper role of racism in the formation of the New World populations.

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