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“Other” possibilities? Assessing regional and extra-regional dental affinities of populations in the Portuguese Estremadura to explore the roots of Iberia’s Late Neolithic-Copper Age

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Abstract: The relationship between the development of social complexity in the Iberian Peninsula during the 4th and 3rd millennia BCE (Late Neolithic and Copper Age) and population movement has been a longstanding question. Biological affinity analyses were used to explore Iberian demographic dynamics, and specifically, to discern whether there is evidence for migration and gene flow between northwest African, eastern Mediterranean, and Iberian populations. Affinities based on comparisons of nonmetric traits from the Arizona State University Dental Anthropology System were estimated among samples of burial populations from three key Late Neolithic-Copper Age sites in the Portuguese Estremadura: Cova da Moura (3700-2300 BCE), Bolores (2800-2600 BCE), and Pai Mogo I (2800-2600 BCE). Results indicate: 1) the possibility of genetic exchange with African and other Mediterranean peoples, 2) some measure of population continuity over time in the Estremadura, and 3) possible local isolation of populations, given distinctive patterning at the site of Pai Mogo, located 23 km north of Cova da Moura and Bolores.

1.1 Introduction

Understanding the relationship between social complexity and demographic dynamics is a central theme in several of the grand challenges recently identified for archaeology, especially those related to movement, mobility, and migration (Kintigh et al., 2014). In the Iberian Peninsula, the emergence of social complexity developed in the 4th and 3rd millennia BCE – in the periods known as the Late Neolithic and Copper Age. During this time a number of fortified or ditched enclosure sites emerged as important social, political, and ritual centers, particularly in the fertile Guadiana and Guadalquivir river valleys of southern Iberia. Some sites extended over large areas, such as Valencina de la Concepción (Sevilla) (450 ha) (Costa et al., 2010), Marroquíes Bajos (Jaén) (113 ha) (Zafra et al., 1999), and La Pijotilla (Badajoz) (80 ha) in Spain (Hurtado, 1997), and Porto Torrão (Beja) (70 ha) (Valera and Filipe, 2004), Alcalar (20 ha) (Morán and Parreira, 2003) and Perdigões (Reguengos de Monsaraz) (>16 ha) (Valera et al., 2014) in Portugal. A diversity of tomb architecture was utilized, including megaliths, rockshelters, natural caves, hypogea, pits, and tholos (Boaventura, 2009; Boaventura et al., 2014; Silva, 2002, 2003). The manufacture of technically complex objects and personal adornments, some made from exotic raw materials such as ivory, amber, copper, gold, variscite, and rock crystal (Morgado Rodríguez et al., 2015; Müller et al., 2007; Murillo-Barroso and Martinón-Torres, 2012; Murillo-Barroso et al., 2015; Odriozola et al., 2016; Schuhmacher et al., 2009; Sousa and Gonçalves, 2012; Thomas, 2011; Villalobos García and Odriozola, 2016; Valera et al., 2015), also attests to the formation of new identities and categories of social beings.

The relationship between the process of social differentiation during the 4th and 3rd millennia and population movement has been a longstanding question in Iberian archaeology. The Orientalist explanatory model was adopted by the main Iberian archeologists of the late 19th and early 20th centuries, especially in the Spanish Southeast and Portuguese Estremadura.

Since the pioneering studies of Siret (1913), and later work of Martin Almagro and A. Arribas at Los Millares, Afonso do Paço at Vila Nova de São Pedro, and E. Sangmeister and H. Schubart at Zambujal (Sangmeister and Schubart, 1981), the fortifications were associated with eastern Mediterranean colonists; the latter purportedly came to Iberia in search of metals and to establish outposts during the Iberian Copper Age (Siret, 1913). However, when archaeologists began applying radiocarbon dating in the 1970s, they increasingly recognized that material practices, such as megalith-building, predated their supposed exogenous models (Chapman, 1990). As a result, they turned to local social or economic factors to account for the changes between the 4th and 2nd millennia cal. BCE, and discredited “migrationism” and “diffusionism” as explanatory vehicles. Instead, they replaced their models with a “radical autochthonism” (Aranda Jimenez et al., 2015: 55). Demography took a back seat to economic and political dynamics (Gonçalves et al., 2013).

Through the development of analytical technologies to source raw materials and track the mobility of people, as well as new archaeological discoveries, the “Other” – both in the form of exotic materials and non-local individuals – is once again making its appearance in narratives of late prehistoric Iberian social history. For example, archaeologists had understood that ivory objects found in Copper and Bronze Age contexts pointed to long-distance exchange networks, presumably originating from sources (e.g., elephants, hippopotami) in North Africa and Egypt (Harrison and Gilman, 1977). However, recent studies by Schumacher et al. (2009) suggest the exchange was larger in scale than imagined; ivory from Asian elephants was sometimes used, as well as that from Pleistocene and African elephants. Furthermore, building on the work of Bosch Gimpera (1932) and Martínez Santa-Ollala (1941), Manen et al. (2007) submit that African exchange extended as far back as the Early Neolithic (i.e., 6th to 5th millennia BCE). Given their geographic proximity, could genetic exchange have also occurred between the human populations of Iberia and northwest

Africa, i.e., in the form of south-to-north gene flow and/or migration? And is there yet merit in the idea of eastern Mediterranean influence (Siret, 1913) that corresponds with the Iberian Late Neolithic-Copper Age?

To explore the viability of these possible scenarios based on archaeological evidence, we turned to the subfield of bioarchaeology. Specifically, we use biological affinity analyses to better understand the demographic dynamics of the time. Previous affinity studies of early Iberian populations focused on periods that, like across much of Europe, ushered in significant social and economic change, i.e., the Mesolithic-Neolithic (c. 5600 BCE) (e.g., Jackes et al., 2001) and Middle-Late Neolithic transitions (4th-3rd millennia BCE (Boaventura, 2009; Boaventura et al., 2014; Horwath et al., 2014). A primary goal of these studies was to assess whether the change was accompanied by population replacement or, minimally, discernable outside genetic input. Our research continues this diachronic emphasis.

Biological affinities based on comparisons of nonmetric traits from the Arizona State University Dental Anthropology System (Turner et al., 1991) were estimated among samples of burial populations from three key Late Neolithic-Copper Age sites in Portugal: Cova da Moura (3700-2300 BCE), Bolores (2800-2600 BCE), and Pai Mogo I (3000-2600 BCE). Dental trait data are ideal for this investigation because, like all local burial sites of this period, the remains are so fragmented and commingled that most skeletal elements can neither be measured (e.g., for craniometrics, geometric morphometric study, etc.) nor recombined into individuals. The three samples come from the Estremadura of west-central Portugal (Fig. 1), an important region for understanding biological diversity given its many mortuary sites and favorable conditions for skeletal preservation (Boaventura et al., 2014; Silva, 2002). They, in turn, were compared to four extra-regional samples affiliated with northwest Africa and three from the eastern Mediterranean to address the two questions posed above. If gene flow and/or immigration from either region did occur – in potential correspondence with the 4th-3rd millennia increase in social differentiation – it may be evident in the Portuguese samples.

[FIGURE 1 HERE]

At a basic level, the African scenario may be tested statistically by phrasing it in the form of a null hypothesis, viz.: there is no significant difference between one or more samples from the Portuguese Estremadura and northwest Africa. By substituting the latter region, a second null hypothesis can be created to test for any Mediterranean input. For both, the mean measure of divergence distance statistic (Irish, 2010; Sjøvold, 1977) was applied to compare the dental data among samples. If one or both of these hypotheses cannot be rejected, discernable extra-regional genetic input may have occurred. Of course, such complex problems are unlikely to be resolved through simply reaching or failing to reach an arbitrary alpha level; however, by considering the weight of evidence across all inter-sample comparisons, along with the aid of supplementary quantitative and illustrative methods (below), some pertinent insights may be achieved. As usual, all results are contingent upon two assumptions (Irish 2005, 2006, 2016; Irish et al., 2014) that: 1) all samples are representative of their corresponding populations, and 2) phenetic similarity provides some indication of genetic relatedness (Larsen, 1997; Martinón-Torres et al., 2007; Rightmire, 1999; Scott et al., 1983; Scott and Turner, 1997). In sum, our goal is to complement and build upon the findings of prior archaeological and bioarchaeological researchers to promote a better biocultural understanding of the ancient peoples of the Iberian Peninsula and, specifically, Portugal.

1.2 Materials

The three Portuguese samples are suitable for evaluating local biological/genetic variation during the Late Neolithic-Copper Age because: 1) Cova da Moura predates and temporally overlaps with Bolores, while the two sites are located just 2 km apart in the Rio Sizandro valley, 2) the Bolores and Pai Mogo I sites are largely contemporary, but the latter is located two river valleys to the north, 23 km distant near the Atlantic coast, and 3) Cova da Moura and Pai Mogo I also overlap in time and are spatially distinct. Dietary differences and differential, albeit low-level immigration based on stable isotopes have also been reported (Guiry et al., 2016; Waterman et al., 2014, 2015). All samples were studied as part of a broader analysis of social change in the Sizandro/ Alcabrichel river valleys between the 4th-2nd millennia BCE, codirected by the second author and Michael Kunst (Lillios 2015, Waterman et al., 2016).

Cova da Moura is a natural cave site in the Sizandro river valley. It was discovered in 1930, with preliminary excavations undertaken in 1932 (Belo et al., 1961). Subsequent fieldwork was conducted in 1961 by Belo and Trindade (Gallay and Spindler, 1970; Spindler, 1981). Seven radiocarbon dates were obtained on the human remains, which indicate that the site was used between 3700 and 2300 BCE. Based on duplicate skeletal elements the MNI is 90 individuals, including 15 sub-adults (Silva, 2002, 2003). However, as noted, all remains are fragmented and comingled, so multiple maxillae, mandibles, and loose teeth were combined to yield “composite” individuals for analyses following standard procedure (Irish, 1998a). Thus, the Cova da Moura dental sample consists of 41 such individuals. In terms of material culture, Cova da Moura is by far the richest burial site in the region. Grave goods include limestone and bone idols, green stone pendants, gold artifacts, engraved slate plaques, bone, ivory, and variscite rabbit figurines, beads, and pre-Beaker and Beaker ceramics (Belo et al., 1961; Gallay and Spindler, 1970; Spindler, 1981; Thomas, 2011).

Bolores is a semi-artificial cave located in the Sizandro river valley, about 15 km from the Atlantic coast. Following testing in 1986, four seasons of excavation were conducted by the second author and a team from the University of Iowa (Lillios et al., 2015).

The site itself is about 3 x 5 m, subdivided by large stone blocks into three chambers. Approximately 75% of the site was excavated. The MNI is 36, which includes adults, adolescents, and children. Of these, 36 individual dentitions could be identified for analysis. Eleven AMS dates were obtained that put the use of the site between 2800-2600 BCE, with a short period of use near 1800 BCE. Material culture is relatively scarce, and consists of stone and shell beads, stone ‘idols’ of various forms, flint blades, and ceramic vessels.

Pai Mogo I (or Paimogo I) is a corbel-vaulted tomb on the Rio Grande, 1 km from the Atlantic coast. The site was first discovered in 1968, with excavations carried out in 1971. Four dates on human remains from the site indicate the site was in use from 3000 to 2600 BCE (Silva, 2002). Little information is available about the context of the human remains recovered from this burial (Gallay et al., 1973). The MNI is 413 (Silva 2002, 2003). Forty-nine composite dentitions were assembled for analysis. An extensive array of Late Neolithic and Copper Age artifacts was found, including decorated pre-Beaker and Beaker ceramics, groundstone and flaked stone tools, bone tools, limestone idols, other limestone objects, and copper implements (see Spindler and Gallay, 1973; Gallay et al., 1973).

Lastly, to assess potential outside genetic influence, the above were compared with seven extra-regional samples. Four are linked with northwestern Africa, i.e., Neolithic Capsian (n=24), precontact Canary Islanders (n=163), historic Kabyle (n=32) Berbers, and a fourth sample from an area once inhabited by Shawia Berbers (n=26). The remaining three samples derive from countries along the north shore of the Mediterranean: 1) Italy, which consists of 90 Roman and historic individuals, 2) Greece (n=77 individuals), dating from Classic and historic times, and 3) Turkey (n=40) that, along with individuals from nearby Cyprus, dates from Classic (Anatolian) to Ottoman times (Fig. 2). Although heterogeneous in composition, particularly the latter sample, they should at least yield some measure of characterization of eastern Mediterranean populations (re: Siret, 1913). All comparative samples, like the Portuguese, were recorded by the first author; thus, inter-observer error is not a concern and any intra-observer recording variation was found to be minimum and random. Background information has been presented elsewhere (Horwath 2012; Horwath et al., 2014; Irish, 1993, 1998b, 1998c, 2000). For quick reference, summary data for all 10 samples (n=578 total individuals) are listed in Table 1.

[FIGURE 2 HERE]

[TABLE 1 HERE]

1.3 Methods

1.3.1 Dental trait recording

Up to 125 nonmetric crown, root, and osseous oral traits were recorded in each dentition. For those with bilateral expression, both antimeres were recorded and, allowing for asymmetry, the side with the greatest expression was counted (Turner and Scott, 1977); the aim is to identify each trait's maximum genetic potential for each individual (Turner, 1985; Turner et al., 1991). Thirty-six of these traits (see list in Table 2) used by the first author in earlier dental studies (e.g., Irish, 1993, 1997, 2005, 2006, etc.) were recorded for the following analyses. Except for UI1 midline diastema (Irish, 1993), all are part of the Arizona State University Dental Anthropology System (ASUDAS); the traits are recorded with the aid of 23 rank-scale reference plaques that help standardize scoring by providing representations of minimum, maximum, and intermediate expressions (Scott and Turner, 1997; Turner et al., 1991). The ASUDAS traits have a range of advantages (Irish, 1993, 1998b, 1998c 2005, 2006), but in brief they: 1) can be recorded despite slight attrition (though see below) or are unaffected by it in the cases of root and osseous traits, 2) have nominal inter- and intra-observer error rates when recording (as above), 3) are easy to identify, and 4) represent all dental morphogenetic fields. Of greater importance, the traits have a high genetic component in expression (Larsen, 1997; Martinón-Torres et al., 2007; Rightmire, 1999; Scott, 1973;

Scott and Turner, 1997), and they are evolutionarily conservative, making them excellent markers for biodistance analyses (Larsen, 1997). Another advantage is an overall lack of sexual dimorphism (Bermúdez de Castro, 1989; Hanihara, 1992; Irish, 1993; Scott, 1973, 1980; Smith and Shegev, 1988), to permit the pooling of sexes for maximizing sample size. A complete description of the ASUDAS is presented in Turner et al. (1991) and Scott and Turner (1997).

1.3.2 Quantitative analyses

All rank-scale ASUDAS traits were first dichotomized into categories of present or absent, based on their appraised morphological thresholds (Nichol, 1990; Scott, 1973) according to standard procedure (Irish, 1993; Turner, 1985, 1987). Dichotomization simplifies the tabulation of trait frequencies for presentation, and is necessary before these data can be compared with most distance statistics, including the mean measure of divergence (MMD) as used here (Berry and Berry, 1967; Green and Suchey, 1976; Harris and Sjøvold, 2004; Irish, 2010; Sjøvold, 1973, 1977). However, relative to prior studies (Irish, 1993, 1997, 2005, 2006, etc.) breakpoints that define “presence” were shifted upward for two important traits: UM1 Carabelli’s (by 3 grades to describe cusp expression only) and LP2 lingual cusp (1 grade, to better discern cusp number). This strategy minimizes the potential for grade shift and sampling biases when scoring traits in the present samples, which exhibit marked attrition differences among geographic regions; it also helps to maintain all-important sample size (Burnett et al., 2013; Burnett, 2016).

Next, the MMD was used to estimate among-sample phenetic affinities by calculating a measure of dissimilarity between each sample pair, i.e., high values indicate divergence and vice versa. Beyond holding several advantages over other distance measures (Irish, 2010) the MMD works with pooled sample data, to better address missing data in archaeological remains and the use of composite individuals. However, it is important to thoroughly edit these data. Traits with little or no contributory information should be deleted (Harris and Sjøvold, 2004). Those which are invariant can be recognized qualitatively, whereas traits that are the least, or conversely most, likely to drive inter-sample variation may be quantitatively identified, e.g., with correspondence analysis (Irish, 2005, 2006) or, like in the present study, principal components analysis (PCA) (Irish, 2016; Irish and Guatelli-Steinberg, 2003). The MMD distances should also be based on as many traits as possible, although none should be highly inter-correlated – which could render the results inaccurate (Sjøvold, 1977). To identify such traits the rank-scale data were submitted to Kendall's tau-*b* correlation coefficient.

The MMD formula contains the Freeman and Tukey angular transformation to correct for low ($\leq .05$) or high ($\geq .95$) trait frequencies and small sample sizes ($n \geq 10$) (Green and Suchey, 1976; Sjøvold, 1973, 1977). To determine if two samples differ significantly, the MMD value is compared with its standard deviation (SD). If the MMD > 2 x SD, the null hypothesis of P1 = P2 (where P = sample population) is rejected at the 0.025 level. The MMD and standard deviation formulae, rationale for assessing significance, and other information can be accessed elsewhere (Irish, 2010; Sjøvold, 1977). Beyond presenting an MMD distance matrix, interval-level multi-dimensional scaling (MDS) (Kruskal and Wish, 1978) in SPSS 23.0 Procedure Alscal was used to create 3D spatial representations of the sample variation to aid interpretation.

Finally, the correlation between MMD and geographic distances in km was calculated with a two-tailed Mantel test (Smouse et al., 1986), and both distances were used as coordinates to plot pertinent sample pair relationships in 2D. These methods help explore if any Portuguese samples appear more similar to an extra-regional group than expected, under the assumption that genetic (and phenetic) relatedness among populations decreases exponentially as spatial distance increases (Relethford, 2004). Gene flow, the causative agent with isolation-by-distance (Wright, 1943), cannot pertain directly to the present diachronic samples; nevertheless, some indication of potential African or Mediterranean influence may be obtained to supplement the MMD results. The Geographic Distance Matrix Generator (vers. 1.2.3) (Ersts, 2014) was employed to calculate inter-sample straight line distances. The latter do not reflect reality on the landscape; however, because all comparative sample locations (especially eastern Mediterranean) are approximations, as would be potential migration routes toward Iberia, linear distances (though underestimates) should be less biased for analytical purposes.

1.4 Results

Percents of individuals that express each trait and the total number scored are listed in Table 2. The ASUDAS present/absent dichotomies are provided under each trait name. Samples with <10 trait observations adversely impact several traits, especially CAP (see table and figure captions for the key to three-letter abbreviations). The BOL and PAI samples are affected similarly for palatine torus, midline diastema, and rocker jaw. Such data are unlikely to be characteristic of the parent populations; results using them should be interpreted with caution and/or they should be addressed during the trait editing process.

[TABLE 2 HERE]

That said, the MMD is a very robust statistic, so to obtain a preliminary indication of affinities among samples all 36 traits were first compared. The distance matrix is presented in Table 3, and the MDS solution from it (Fig. 3) provides a good representation, where the r^2 value is 0.897 and Kruskal’s stress formula 1 is 0.113; for the latter value <0.10 is considered excellent and $\geq$0.15 unacceptable (Borgatti, 1997). Many significant MMD distances ($p \leq 0.025$) reflect the trait variation evident across samples (Table 2) including, among others, interruption groove UI1 [range of 0-46% (or 60% in the small CAP sample)], distal accessory ridge UC (8-74 %), rocker jaw (0-30%), and torsomolar angle LM3 (0-31%). However, the loose association of samples by geographic region in the figure (CDM/BOL/PAI, GRK/ITY/TRK, and CAN/CAP/KAB/SHA) is indicative of relative among-sample trait uniformity from those regions (again see Table 2).

[TABLE 3 and FIGURE 3 HERE]

Trait editing was then conducted as noted above. Non-contributory traits odontome P1-P2 (0-3% across samples), midline diastema (0-5%), mandibular torus (0-4%), and protostylid LM1 (0%) were removed. Percent data in the remaining 32 traits were submitted to PCA to identify less evident non-contributors in nine of the 10 total samples; CAP was not included after judging that many of its small and likely non-representative trait frequencies artificially increased several resulting loadings.

Eight components (eigenvalues >1.0) account for 100% of the total variance, though the PCA scree plot (not shown) indicates that the first three (58% variance) are most important; their un-rotated loadings are provided in Table 4. Those traits having very strong positive or negative loadings (i.e., >|0.5|) drive most of the variation as depicted in a graph of the group component scores in Figure 4. For Comp 1, loadings between 0.555 and 0.891 for tuberculum dentale UI2, distal accessory ridge UC, cusp 5 UM1, enamel extension UM1, root number UM2, anterior fovea LM1, deflecting wrinkle LM1, and cusp 7 LM1 push samples with high percents of these traits nearer the positive end of the x-axis (BOL, PAI, and to a lesser extent, CDM and ITY). Negative loadings of -0.589 to -0.855 for interruption groove UI2, congenital absence UM3, rocker jaw, cusp number LM2, and torsomolar angle LM3 typify samples toward the x-axis’ opposite end (e.g., TRK, GRK, SHA). Traits of greater importance are also evident on the y- (Comp 2) and z-axes (Comp 3). As such, palatine torus, shoveling UI1, double shoveling UI1, hypocone UM2, and lingual cusp LP2 (loadings <|0.5| on all axes) were dropped because they are mostly noncontributory. Varimax rotation, which maximizes differences between large and small loadings, provided similar results (not shown).

Kendall's tau-*b* correlations among the remaining traits revealed high values (>|0.5|) for molar cusp number LM1 with: molar cusp number LM2, deflecting wrinkle LM1, and cusp 7 LM1 (τ_b = 0.573, 0.670, and 0.818, respectively). Similarly high values were found between c1-c2 crest LM1 and anterior fovea LM1 and, again, deflecting wrinkle LM1 with cusp 7 LM1 (τ_b = 0.657, 0.787, and 0.706). Therefore, together with lower loadings than other non-correlated traits (Table 4), molar cusp number LM1 and mandibular torus were dropped. As a result 25 traits, as denoted by asterisks, in Table 4 were used in the final MMD comparison.

[TABLE 4 and FIGURE 4 HERE]

This MMD distance matrix is presented in Table 5. Heterogeneity is again evident by the number of significantly different MMD distances. However, with a focus on the three Portuguese samples, the greater emphasis on divergence after deleting invariant and other traits that are non-contributory served to make CDM, BOL, and PAI, more distinct – from the other samples and one another (i.e., note the increase in MMD distances). The MDS solution again provides a good representation of the matrix, with the r^2 and Kruskal's stress formula 1 values improving to 0.919 and 0.109, respectively. Greater separation among the Portuguese samples is evident, though the new configuration (Fig. 5) otherwise looks similar in patterning to the 36-trait MDS graph (Fig. 3) in the association of samples by geographic region. To quantify this apparent correspondence, the 25-trait MMD distances were compared to geographic distances among sites and/or regions (Table 6); the Mantel correlation between matrices, r=0.247 (p=0.102), is positive though weak (per Cohen, 1988).

[TABLES 5-6 and FIGURE 5 HERE]

Lastly, CDM, BOL, and PAI were plotted individually with the rest of the samples using pairwise geographic and MMD distances as coordinates on the x- and y-axes in Figures 6-8. In each plot, a linear equation reference line (solid black) with a slope (b) of 1 and y-intercept (a) of 0 is provided (i.e., $y = 0 + 1x$, where $y = a + bx$) to simply illustrate where the other Portuguese and extra-regional samples would be located if a 1:1 correspondence existed between spatial and phenetic distances. The real sample locations identify those which are phenetically closer to the respective Portuguese sample than expected (i.e., below reference line), and vice versa (above line), relative to geographic separation. By way of comparison, the actual regression coefficient is also provided as the line of best fit (dashed) through the data cloud in each figure. Assuming that phenetic affinity is a function of spatial separation (as above), coefficients of determination were calculated via the linear regression procedure in SPSS 23.0 for CDM (r^2=0.095, r=0.308, p=0.420), BOL (r^2=0.290, r=0.539, p=0.135), and PAI (r^2=0.764, r=0.874, p=0.002). Thus for CDM, 9.5% of the variability in MMD distances is associated with, or explained by, variability in the geographic distances. The corresponding values for BOL and PAI are 29.0% and 76.4%.

[FIGURES 6-8 HERE]

1.5 Discussion

Our overarching goal in this analysis was to ascertain if there is evidence of genetic input from northwestern African and/or eastern Mediterranean populations in late prehistoric peoples of the Portuguese Estremadura. Several high-frequency African traits (Irish, 1993, 1997, 1998a, 1998b, 1998c) are present in CDM, BOL, and/or PAI, including: UI1 labial curvature, Bushman canine UC, and LM1 cusp 7 (Table 2; also Table 4 loadings). In accordance, the 36- and, particularly, 25-trait MMD distances (Tables 3 and 5) and MDS scatterplots (Figs. 3 and 5; also see Fig. 4 PCA plot) indicate that the KAB and, to a lesser extent, SHA Berber samples, share very low and mostly insignificant phenetic distances with

CDM and BOL (25-trait MMD between 0.002 and 0.070), though not with PAI (0.125-0.128). As mentioned, archaeological evidence of African-sourced raw materials and artifacts is documented in southern Iberia (Harrison and Gilman, 1977; Manen et al., 2007), including ivory from North Africa at the site of Zambujal, a Copper Age settlement just 2 km south of Cova da Moura and Bolores (Sangmeister and Schubart, 1981). Perhaps an African contribution to the Estremadura gene pool did take place. However, ubiquitous traits in eastern Mediterranean populations, like UM2 hypocone reduction (grades <3) and two-rooted LC (Scott and Turner, 1997), also occur in the Portuguese. The same MMD matrices and inter-sample plots identify a west-east affinity, most notably BOL (25-trait MMD=0.031) and, to a lesser degree, CDM (0.043) with ITY. The PAI sample (0.108), from farther north in the Estremadura, is again an exception (discussed below). Imported artifacts and materials from the east are also known (Schumacher et al., 2009). So genetic exchange with eastern Mediterranean peoples may too have occurred.

Of course, these extra-regional dental similarities may simply be a function of Portugal's proximity to northwest Africa and Italy relative to more geographically divergent samples (per Relethford, 2004; Wright, 1943), as in describing a vast, circum-Mediterranean cline; a positive though weak correlation does exist between the MMD and geographic straight-line distances. On the other hand the resemblance of CDM and BOL to KAB, SHA, and ITY may be indicative of direct contact (à la Siret, 1913), as in actual migration and/or gene flow into southern Iberia and, specifically, the Estremadura. Based on isotopic evidence, Waterman et al. (2014) did find that four of 12 skeletons sampled at CDM were non-local. In support of external influence, only 9.5% of the variability in MMD distances for CDM and 29% for BOL, as noted, is associated with the variability in geographic distances with the remaining samples. These results imply that at least some of the latter are not plotted where they "should" be (Figs. 6-7), assuming phenetic affinity is directly related to spatial separation. Focusing only on extra-regional comparisons, CAP and, to a lesser extent, CAN are plotted above the solid black reference line, meaning they are more divergent phenetically from CDM than anticipated based on geographic location. Below this line the opposite is true for KAB and ITY, which share low MMD distances with CDM (Table 5), and SHA, GRK, and TRK, which differ significantly from this Portuguese sample. With some variation, inter-sample patterning for BOL is similar (Fig. 7). Therefore, based on the weight of the evidence, namely: 1) extra-regional traits in the Portuguese, 2) pertinent low and insignificant MMD distances, and 3) closer-than-expected plots of KAB and ITY, among others, neither of the hypotheses in the introduction can be rejected – though with qualification. Specifically, there is no significant difference between one or more samples from the south-central Portuguese Estremadura (CDM and BOL) and northwest Africa (KAB and SHA), nor between CDM and BOL and the eastern Mediterranean (ITY). The PAI sample does not exhibit overt extra-regional input based on these analyses. It differs significantly from all comparative samples (Table 5), and any similarities do indeed appear to be mostly a function of geographic distance (r^2=0.764, p= 0.002) (Fig. 8).

Within the Estremadura, dental heterogeneity is evident. The average intra-region 25-trait MMD among CDM, BOL, and PAI, is 0.058 (calculated from Table 5); despite issues affecting the composition of several comparative samples (above), the corresponding value for northwest Africa (CAN, CAP, KAB, and SHA) is 0.025, whereas that for the eastern Mediterranean (ITY, GRK, and TRK) is 0.015. The phenetic similarity between CDM and BOL is suggestive of short term continuity in the Rio Sizandro valley, but the MMD of 0.036 (p<0.025) is high considering a separation of 2 km between sites (Figs. 6-7). The uniqueness of PAI is clear (Fig. 8). Though most akin to CDM (MMD=0.058) and BOL (0.079), it is significantly different (p>0.025) from both; Pai Mogo 1 is situated 23 km north from Cova da Moura and Bolores yet, among other possible factors, this relatively small distance interspersed by two river valleys was seemingly a contributor to substantial biocultural isolation. As mentioned, differences in diet, artifacts, and architecture were also reported between areas (Gallay et al., 1973; Guiry et al., 2016; Spindler and Gallay, 1973; Waterman et al., 2014, 2015). This heterogeneity, the divergence of PAI in particular (at least compared to the samples in this study), reminds us that our understanding of the Iberian Late Neolithic/Copper Age must include recognition of variation – both regional and community-wide. Inhabitants of communities at this time may have been diverse in biological origin and, likely, the experiences of their worlds. Such diversity may help identify possible tensions within society that generated profound social changes by the Early Bronze Age, c. 2200 BCE, including the abandonment of settlements and emergence of new, individualized mortuary practices.

Lastly, relationships among all 10 samples are instructive. The demonstrable distinction by geographic region (e.g., Figs. 3 and 5) and relative intra-region similarity (above), quantified by the Mantel correlation (r=0.247), support the viability of these dental nonmetric analyses. In fact, when northwest African-associated CAN is dropped from study, the r-value between the 25-trait MMD and geographic distances increases substantially to 0.05 (p=0.002), a strong positive correlation (Cohen, 1988). Canary Islanders are considered by researchers to be something of an outlier. Though descendants of early (potentially Neolithic) Berbers, the remote island location led to genetic isolation in these non-seagoing peoples, with only subsequent one-way gene flow – mostly from Europeans beginning in the 15th century CE (Bermúdez de Castro, 1989; Guatelli-Steinberg et al., 2001; Irish, 1993; Mercer, 1980; Schwidetsky, 1963). The low and insignificant MMD distances of CAN with both Berber samples and Neolithic CAP, plus comparable values with geographically distant but younger ITY, GRK, and TRK, though not older CDM, BOL, or PAI, are supportive of these known and suspected biological relationships. Other links between the northwest

African and eastern Mediterranean samples are obvious (Tables 3 and 5, Figs. 3 and 5). As well, high-frequency African traits are present to varying degrees in ITY, GRK, and TRK, and vice versa (Table 2). These findings are suggestive of more than just indirect contact among circum-Mediterranean populations, contra the strict anti-migrationism and diffusionism interpretations of some researchers.

In sum, our study has attempted to better understand the cultural and demographic dynamics of human communities within the Portuguese Estremadura, using three samples dated between 3700-2300 BCE. Results indicate intra-regional heterogeneity relative to samples from other Mediterranean regions, though with some measure of population continuity, particularly in the Sizandro River valley. That said, long-range genetic input from more distant, yet neighboring regions, such as northwestern Africa and the eastern Mediterranean, cannot be ruled out. These data parallel findings of human migration at Cova da Moura and elsewhere in the Late Neolithic and Copper Age, based upon isotopic analyses of human remains in collective burials (Waterman et al., 2014). This correspondence may imply that exotic materials recovered from settlement and burials of this time are indicative of down-the-line exchange but, again, actual immigration may be possible based on the present quantitative analyses. As usual, it was likely a combination of influences that led to the emergence of social complexity during the Late Neolithic/Copper Age in the 4th and 3rd millennia BCE, not mutually exclusive migrationism versus autochthonism. Whatever the case, all explanatory models should remain in play until fully discredited. Further dental nonmetric and (planned) genetic analyses of human remains in burials dating to earlier and contemporary periods in Portugal, and greater Iberia, should help to clarify these findings.

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Figure legends

Figure 1. Origin locations of the three Portuguese Late Neolithic-Copper Age samples.

Figure 2. Origin locations of the Portuguese and comparative samples. See Table 1 and text Section 1.2 for sample compositions.

Figure 3. Three-dimensional MDS of 36-trait MMD distances among the three Portuguese and seven comparative samples. The three-letter sample abbreviations are defined in Tables 1-3 and 5-6.

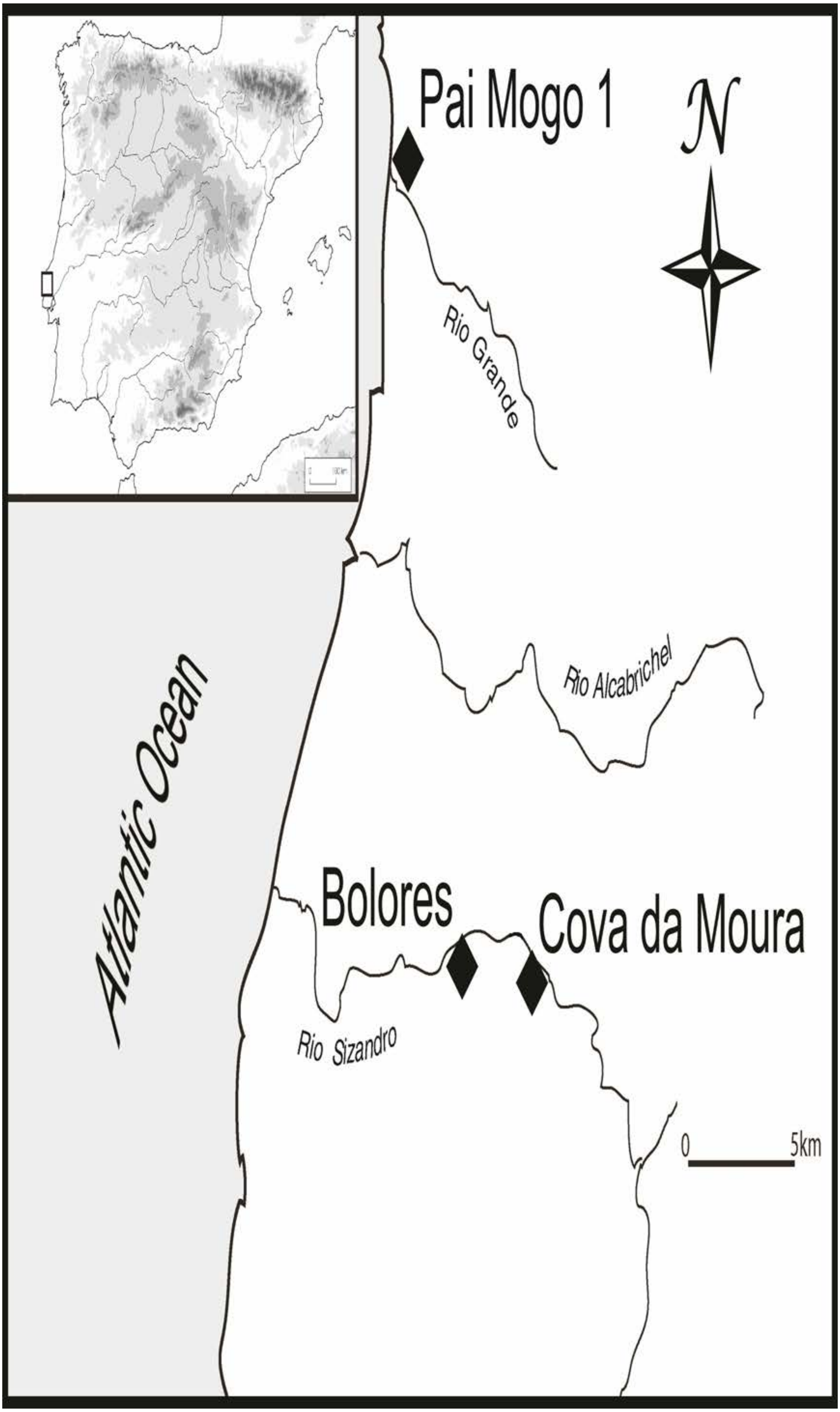
Figure 4. Three-dimensional scatterplot of the first three components among the three Portuguese and six comparative samples (without CAP; see text) for 32 dental traits from Table 4. Accounts for 58.14% of the total variance (23.32% on x-axis, 19.47% on y-axis, and 15.34% on z-axis). Sample abbreviations defined in Tables 1-3 and 5-6.

Figure 5. Three-dimensional MDS of 25-trait MMD distances among the three Portuguese and seven comparative samples. The three-letter sample abbreviations are defined in Tables 1-3 and 5-6.

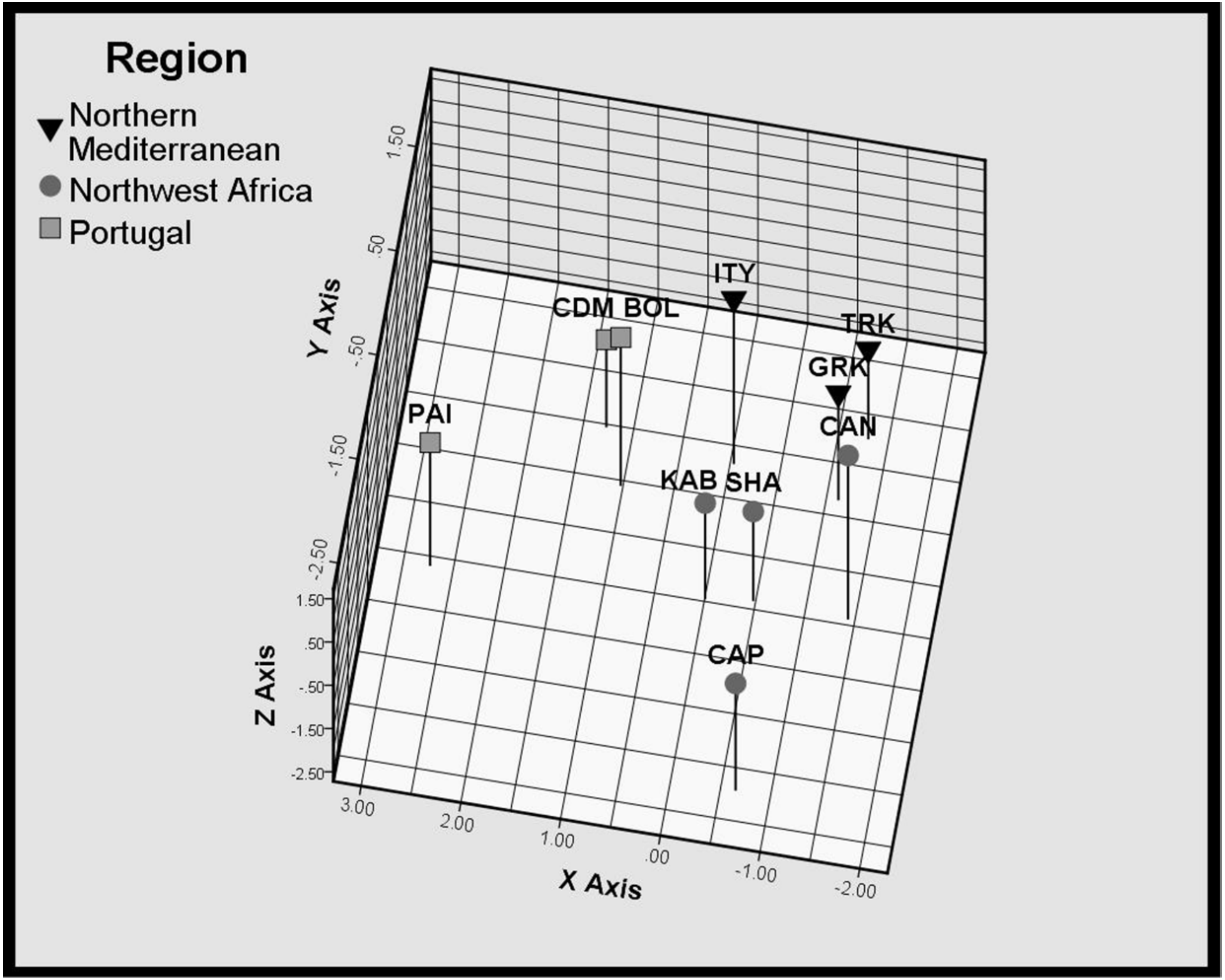
Figure 6. Two-dimensional scatterplot of the CDM sample relative to the other Portuguese and comparative samples based on geographic (x-axis) vs. phenetic (y-axis) distances. Solid black linear equation reference line with slope (b) of 1 and y-intercept (a) of 0 provided (i.e., $y = 0 + 1x$, where $y = a + bx$) to illustrate where the other samples would be if 1:1 correspondence existed between the distances. The actual regression coefficient is also provided as the line of best fit (dashed) through the data cloud in each figure (with equation provided). See text Section 1.4 for details.

Figure 7. Two-dimensional scatterplot of the BOL sample relative to the other Portuguese and comparative samples based on geographic (x-axis) vs. phenetic (y-axis) distances. Solid black linear equation reference line with slope (b) of 1 and y-intercept (a) of 0 provided (i.e., $y = 0 + 1x$, where $y = a + bx$) to illustrate where the other samples would be if 1:1 correspondence existed between the distances. The actual regression coefficient is also provided as the line of best fit (dashed) through the data cloud in each figure (with equation provided). See text Section 1.4 for details.

Figure 8. Two-dimensional scatterplot of the PAI sample relative to the other Portuguese and comparative samples based on geographic (x-axis) vs. phenetic (y-axis) distances. Solid black linear equation reference line with slope (b) of 1 and y-intercept (a) of 0 provided (i.e., $y = 0 + 1x$, where $y = a + bx$) to illustrate where the other samples would be if 1:1 correspondence existed between the distances. The actual regression coefficient is also provided as the line of best fit (dashed) through the data cloud in each figure (with equation provided). See text Section 1.4 for details.


Pai Mogo 1
N
Rio Grande
Rio Alcabrichel
Atlantic Ocean
Bolores
Cova da Moura
Rio Sizandro
0
5km


Atlantic Ocean
N
Bolores
Cova da Moura
Pai Mogo 1
Italy
Greece
Kabyle
Capsian
Turkey
Shawia
Canary
Islanders


Region
▼ Northern Mediterranean
● Northwest Africa
□ Portugal
Y Axis
1.50
.50
-.50
-1.50
-2.50
Z Axis
1.50
.50
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-2.50
X Axis
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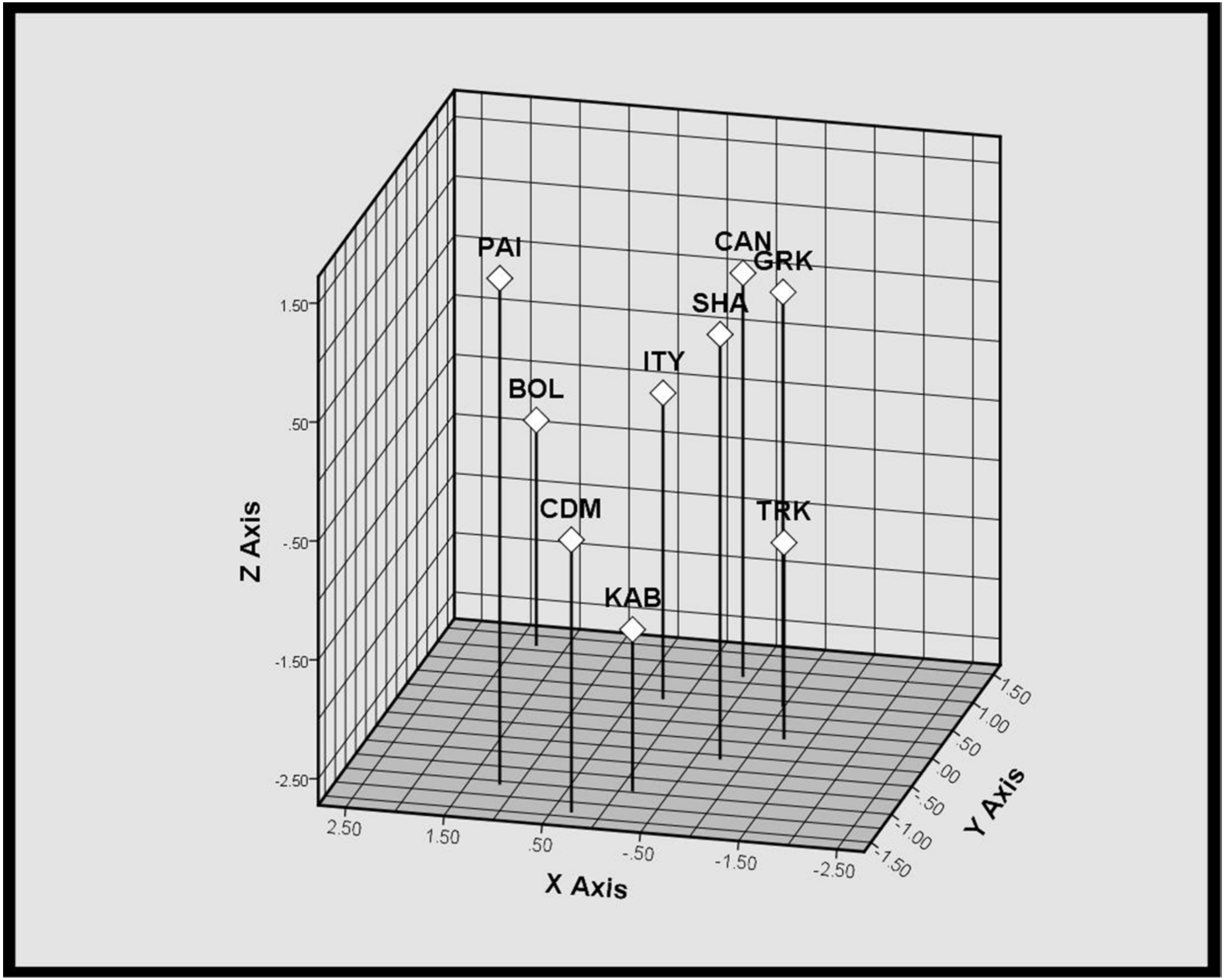
ITY
CDM BOL
TRK
GRK
PAI
CAN
KAB SHA
CAP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X Axis
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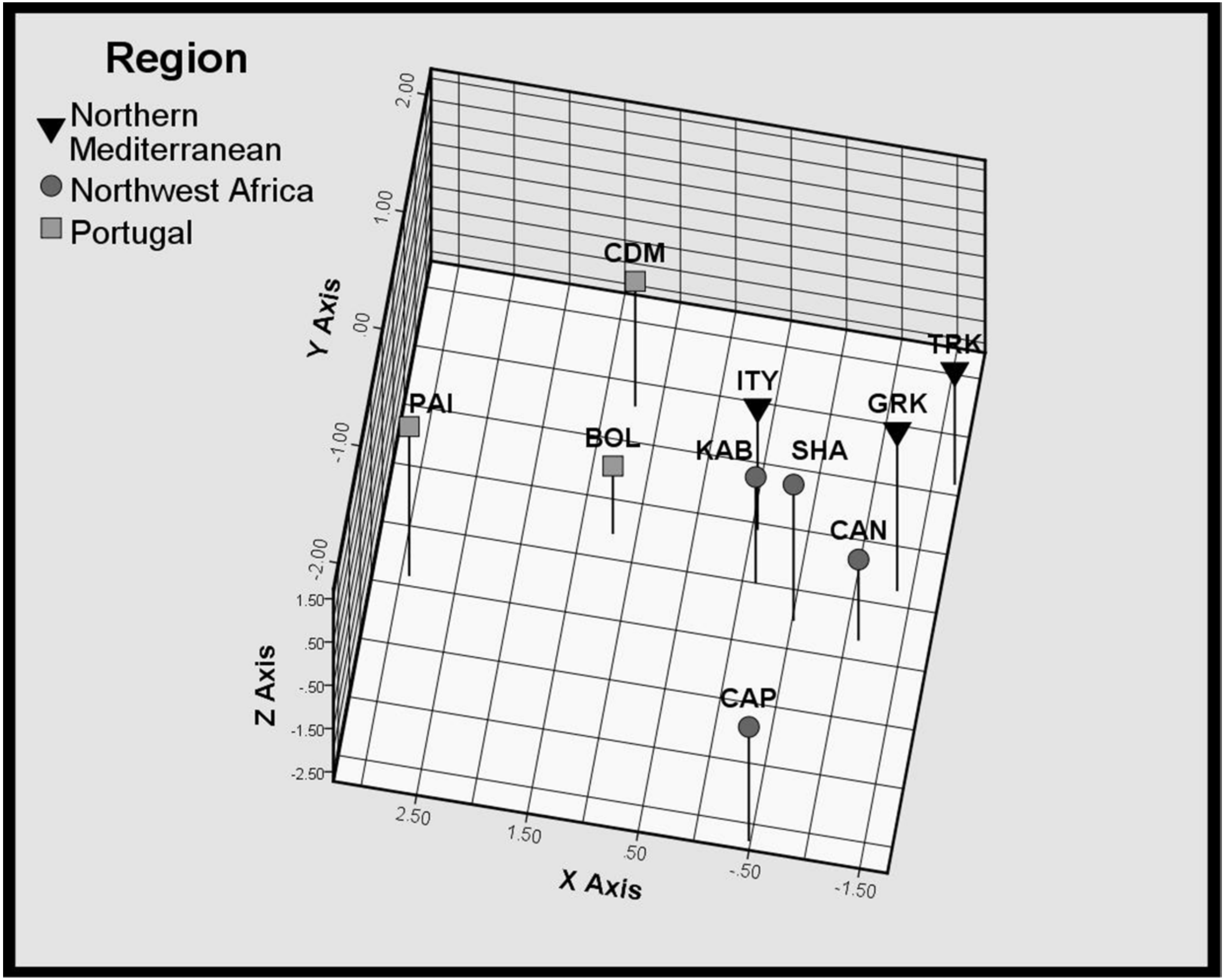
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● Northwest Africa
■ Portugal
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X Axis
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CDM
PAI
BOL
ITY
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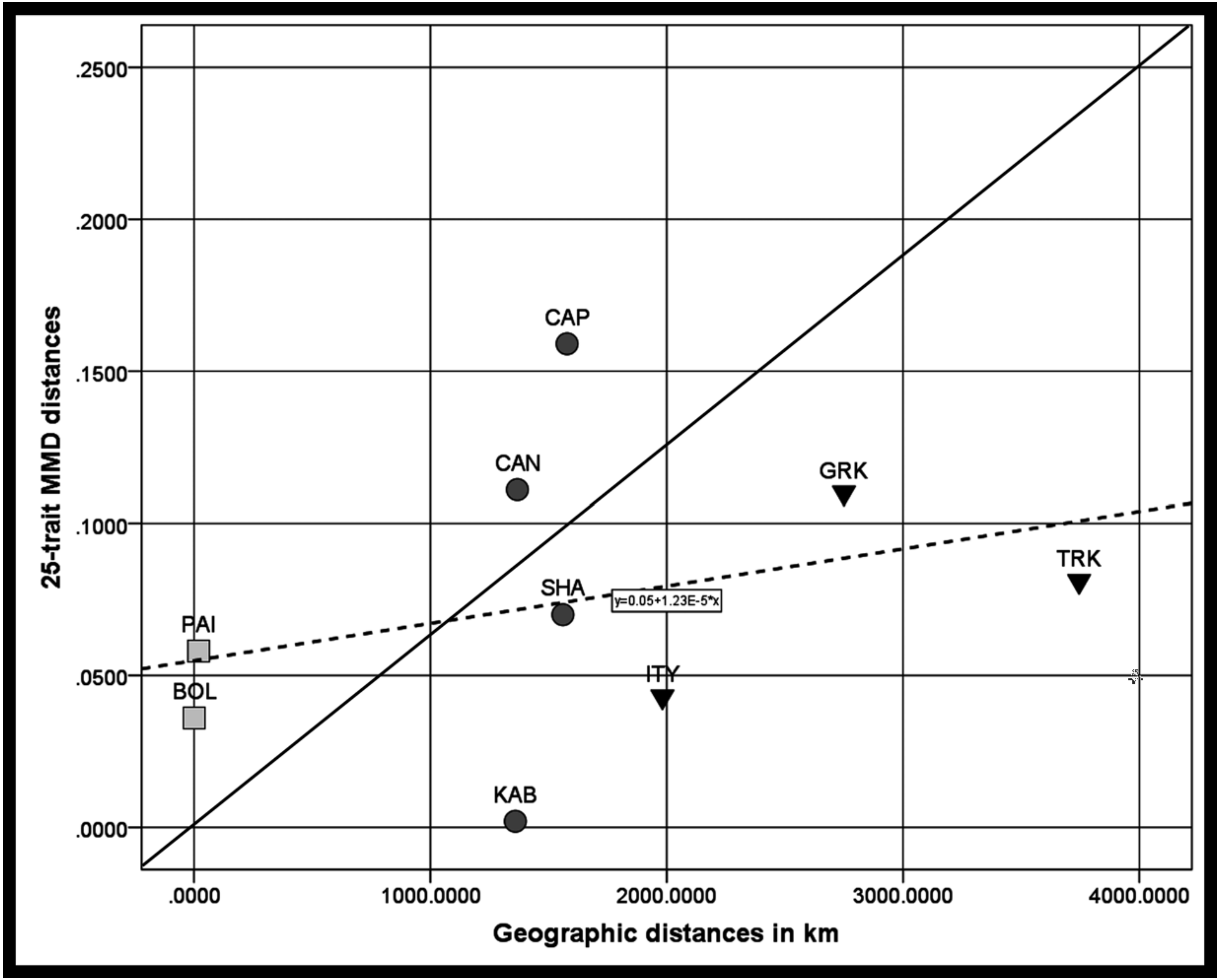
TRK
CAN
CAP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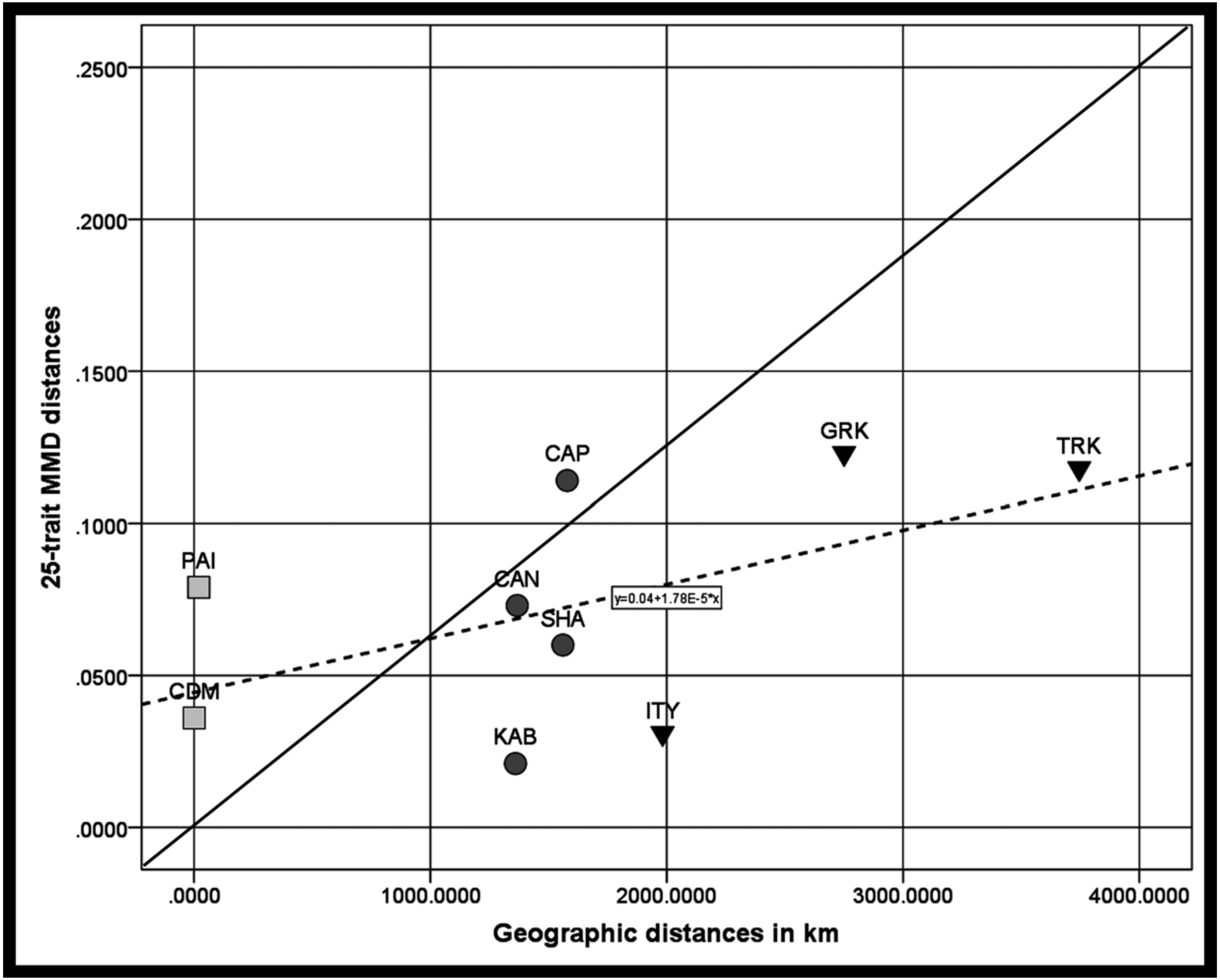
.2000
.1500
.1000
.0500
.0000
CAP
CAN
GRK
TRK
SHA
y=0.05+1.23E-5*x
PAI
BOL
ITY
KAB
.0000
1000.0000
2000.0000
3000.0000
4000.0000
Geographic distances in km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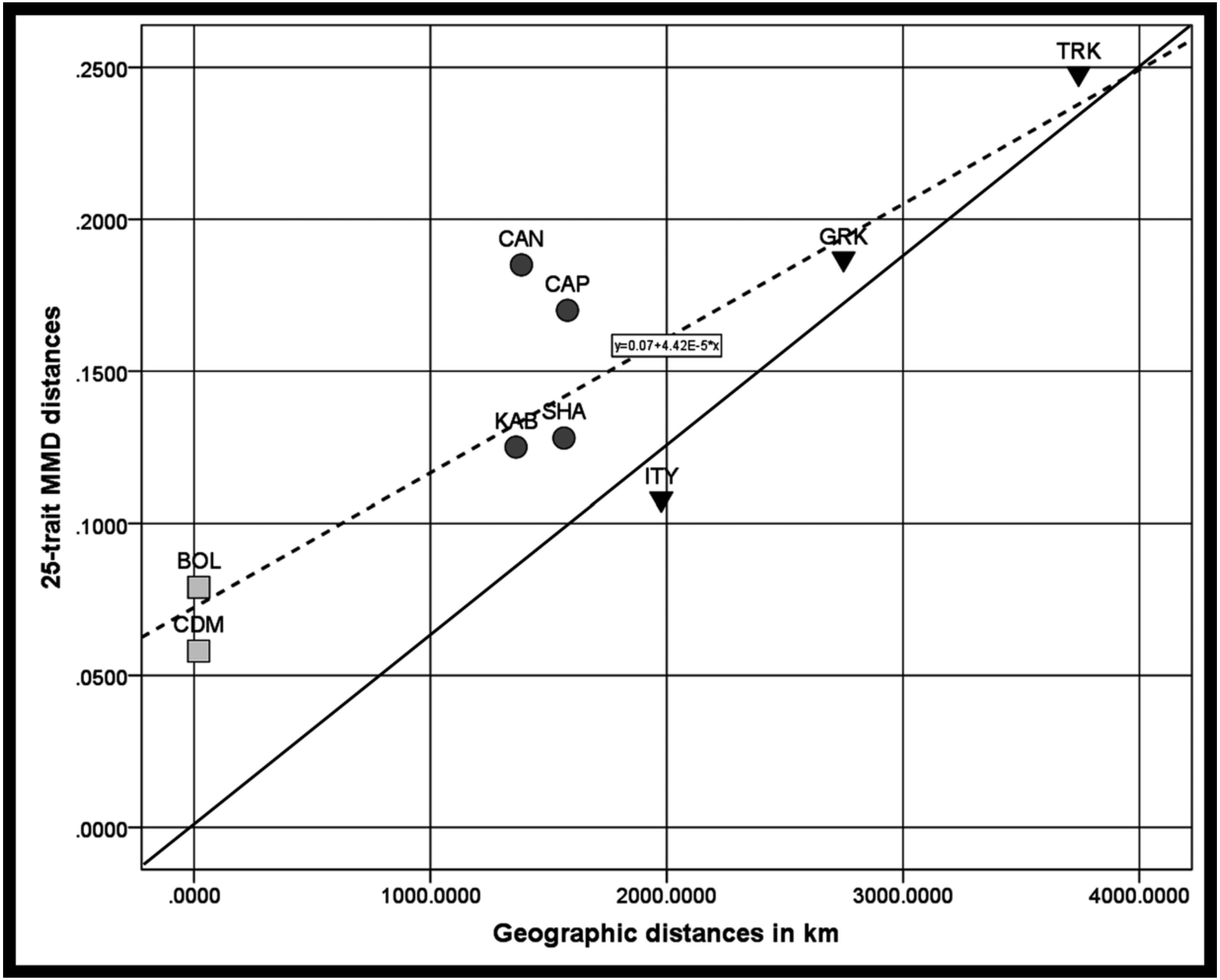
.2000
.1500
.1000
.0500
.0000
Geographic distances in km
.0000
1000.0000
2000.0000
3000.0000
4000.0000
PAI
CDM
CAP
CAN
SHA
KAB
ITY
GRK
TRK
y=0.04+1.78E-5*x


25-trait MMD distances
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.0500
.1000
.1500
.2000
.2500
.0000
1000.0000
2000.0000
3000.0000
4000.0000
Geographic distances in km
TRK
GRK
CAN
CAP
KAB
SHA
ITY
BOL
CDM
y=0.07+4.42E-5*x

TABLE 1. The three Portuguese and seven comparative dental samples.

Sample	**Geographic Origin**	**Affiliation**	**Dates**	**n**	**Institution***
Portugal					
Bolores (BOL)	Estremadura	Neolithic/Copper Age	2800-2600 BCE	36	MMLT
Cova da Moura (CDM)	Estremadura	Neolithic/Copper Age	3700-2300 BCE	41	MMLT
Pai Mogo I (PAI)	Estremadura	Neolithic/Copper Age	3000-2600 BCE	49	MMLT
NW Africa					
Canary Islanders (CAN)	Canary Islands	Precontact Guanche	400-900(?) CE	163	NMNH, MH
Capsian (CAP)	Algeria and Tunisia	Early to Middle Neolithic	6500–3000 BCE	24	UM
Kabyle (KAB)	Northern Algeria	Berber	1800–1900s CE	32	MH
Shawia (SHA)	Southern Algeria	Berber	1800–1900s CE	26	MH
S Europe					
Greece (GRK)	Greece	Classic to historic	475–300 BCE to historic	77	AMNH
Italy (ITY)	Italy	Roman and historic	30 BC–AD 395 to historic	90	NHM
Turkey (TRK)	Anatolia/Turkey and Cyprus	Classic to Ottoman	>300 BCE to ~14th Cent CE	40	AMNH

*Institutions in which the samples are curated: MMLT = Museu Municipal Leonel Trindade - Torres Vedras; NMNH = National Museum of Natural History, Washington, DC; MH = Museé de l’Homme, Paris; UM = University of Minnesota, Minneapolis; AMNH = American Museum of Natural History, New York; NHM = Natural History Museum, London.

TABLE 2. Dental trait percentages (%) and number of individuals scored (n) for the Portuguese and comparative samples

	Sample Trait		BOL	CDM	PAI	CAN	CAP	KAB	SHA	GRK	ITY	TRK
1)	Winging UI1	%	7.14	3.23	3.57	11.54	0.00	0.00	0.00	1.47	3.95	0.00
	(+=ASU 1)	n	14	31	28	130	5	29	26	68	76	36
2)	Labial Curvature UI1	%	19.35	23.08	10.42	18.18	25.00	50.00	28.57	20.00	24.14	40.00
	(+=ASU 2-4)	n	31	39	48	22	4	8	7	5	29	10
3)	Palatine Torus	%	0.00	0.00	3.70	23.85	0.00	3.45	0.00	4.29	10.39	0.00
	(+=ASU 2-3)	n	3	10	27	130	10	29	25	70	77	35
4)	Shoveling UI1	%	4.55	13.16	6.38	14.29	0.00	14.29	0.00	0.00	26.92	0.00
	(+=ASU 2-6)	n	22	38	47	14	5	7	7	5	26	10
5)	Double Shoveling UI1	%	3.45	5.13	8.89	0.00	0.00	12.50	25.00	0.00	0.00	0.00
	(+=ASU 2-6)	n	29	39	45	17	5	8	8	5	27	10
6)	Interruption Groove UI2	%	7.69	0.00	14.29	20.83	60.00	21.43	46.15	35.00	13.33	15.38
	(+=ASU +)	n	26	19	49	24	5	14	13	20	30	13
7)	Tuberculum Dentale UI2	%	47.83	38.89	29.17	33.33	60.00	50.00	25.00	5.26	36.67	15.38
	(+=ASU 2-6)	n	23	18	48	18	5	12	12	19	30	13
8)	Bushman Canine UC	%	4.00	0.00	0.00	2.70	22.22	0.00	0.00	8.70	2.56	0.00
	(+=ASU 1-3)	n	25	39	49	37	9	16	14	23	39	19
9)	Distal Acc. Ridge UC	%	30.00	51.52	73.91	21.74	42.86	27.27	22.22	8.33	19.23	6.25
	(+=ASU 2-5)	n	20	33	46	23	7	11	9	12	26	16

10)	Hypocone UM2	%	57.14	56.00	63.83	77.78	100.00	63.64	68.42	50.00	59.72	60.00
	(+=ASU 3-5)	n	14	25	47	99	10	22	19	54	72	25
11)	Cusp 5 UM1	%	29.41	8.70	17.02	12.99	30.00	11.76	10.00	5.66	17.46	4.55
	(+=ASU 2-5)	n	17	23	47	77	10	17	20	53	63	22
12)	Carabelli's Trait UM1	%	6.25	29.63	26.53	17.39	83.33	26.32	11.11	16.67	20.97	19.05
	(+=ASU 5-7)	n	16	27	49	69	6	19	18	48	62	21
13)	Parastyle UM3	%	0.00	0.00	4.76	1.32	0.00	0.00	7.69	0.00	0.00	0.00
	(+=ASU 2-5)	n	15	22	42	76	9	22	13	33	41	13
14)	Enamel Extension UM1	%	18.18	3.70	2.27	1.68	0.00	0.00	4.76	3.70	1.45	4.17
	(+=ASU 2-3)	n	11	27	44	119	13	23	21	54	69	24
15)	Root Number UP1	%	45.45	70.00	69.77	52.54	33.33	52.17	52.17	61.9	59.32	68.97
	(+=ASU 2+)	n	11	40	43	118	12	23	23	63	59	29
16)	Root Number UM2	%	92.31	57.14	89.80	84.81	85.71	68.42	72.22	58.33	76.92	62.07
	(+=ASU 3+)	n	13	21	49	79	7	19	18	36	39	29
17)	Peg-Reduced UI2	%	10.34	2.94	0.00	5.26	0.00	6.25	0.00	0.00	9.64	5.71
	(+=ASU P or R)	n	29	34	49	38	10	16	13	73	83	35
18)	Odontome P1-P2	%	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.70	0.00
	(+=ASU +)	n	35	40	44	85	12	22	23	44	74	30
19)	Congenital Absence UM3	%	0.00	6.90	8.33	16.54	16.67	3.45	23.08	17.65	23.46	21.88
	(+=ASU -)	n	18	29	48	133	12	29	26	68	81	32

20)	Midline Diastema UI1	%	0.00	0.00	0.00	6.87	0.00	5.00	0.00	3.03	4.88	0.00
	(+ 0.5 mm)	n	14	20	3	131	5	20	23	66	82	37
21)	Lingual Cusp LP2	%	30.77	63.33	31.71	64.00	53.85	53.85	61.54	50.00	23.26	29.41
	(+=ASU 3-9)	n	13	30	41	50	13	13	13	10	43	17
22)	Anterior Fovea LM1	%	55.56	58.82	80.56	23.53	45.45	60.00	29.41	36.36	51.43	40.00
	(+=ASU 2-4)	n	18	17	36	34	11	10	17	11	35	10
23)	Mandibular Torus	%	0.00	0.00	0.00	2.06	0.00	0.00	4.17	0.00	0.00	0.00
	(+=ASU 2-3)	n	9	34	39	97	19	19	24	34	73	30
24)	Groove Pattern LM2	%	30.43	32.50	52.08	47.56	41.18	27.78	36.84	43.48	26.23	5.88
	(+=ASU Y)	n	23	40	48	82	17	18	19	23	61	17
25)	Rocker Jaw	%	0.00	0.00	0.00	24.73	17.65	10.53	8.33	30.30	12.50	13.79
	(+=ASU 1-2)	n	6	10	28	93	17	19	24	33	72	29
26)	Cusp Number LM1	%	0.00	2.50	9.09	4.69	17.65	31.25	9.52	0.00	1.96	0.00
	(+=ASU 6+)	n	26	40	44	64	17	16	21	19	51	19
27)	Cusp Number LM2	%	20.00	23.68	40.43	48.57	38.89	33.33	31.58	47.62	35.56	41.18
	(+=ASU 5+)	n	20	38	47	70	18	18	19	21	45	17
28)	Deflecting Wrinkle LM1	%	21.74	20.83	43.90	2.17	20.00	6.67	5.00	17.65	12.50	6.67
	(+=ASU 2-3)	n	23	24	41	46	10	15	20	17	48	15
29)	C1-C2 Crest LM1	%	3.85	0.00	0.00	2.13	0.00	0.00	0.00	5.88	6.38	0.00
	(+=ASU +)	n	26	26	41	47	9	14	20	17	47	13
30)	Protostylid LM1	%	4.17	0.00	0.00	1.54	0.00	0.00	0.00	0.00	0.00	0.00
	(+=ASU 3-6)	n	24	30	42	65	15	16	21	19	51	17

31)	Cusp 7 LM1	%	11.54	0.00	6.25	6.41	16.67	5.88	4.76	5.56	5.36	0.00
	(+=ASU 2-4)	n	26	39	48	78	18	17	21	18	56	19
32)	Tome's Root LP1	%	5.26	16.13	18.37	6.90	0.00	5.26	10.53	7.14	10.53	0.00
	(+=ASU 3-5)	n	19	31	49	87	15	19	19	28	57	25
33)	Root Number LC	%	4.17	7.32	2.33	2.63	0.00	20.00	0.00	3.45	3.33	0.00
	(+=ASU 2+)	n	24	41	43	76	12	10	16	29	60	22
34)	Root Number LM1	%	5.88	0.00	0.00	2.99	5.88	0.00	0.00	0.00	0.00	5.26
	(+=ASU 3+)	n	17	36	30	67	17	17	22	22	43	19
35)	Root Number LM2	%	95.00	82.50	100.00	93.75	85.71	88.89	95.45	91.30	100.00	89.47
	(+=ASU 2+)	n	20	40	43	64	14	18	22	23	57	19
36)	Torsomolar Angle LM3	%	0.00	8.82	5.56	23.38	23.08	21.43	23.53	13.04	16.28	31.25
	(+=ASU +)	n	13	34	36	77	13	14	17	23	43	16

[1] BOL=Bolores, CDM=Cova da Moura, PAI=Pai Mogo, CAN=Canary Islanders, CAP=NW African Capsian, KAB=NW African Kabyle Berbers, SHA=NW African Shawia Berbers, GRK=Greece, ITY=Italy, TRK=Turkey (see text Section 1.2 for details).

[2] ASU rank-scale trait breakpoints from Irish (1993, 1997, 1998a, 1998b, 2005, 2006) and Scott and Turner (1997), with modifications (see text)

TABLE 3. Symmetrical MMD distance matrix for Portuguese and comparative samples based on 36 dental traits

	BOL	CDM	PAI	CAN	CAP	KAB	SHA	GRK	ITY	TRK
BOL	0	0.011	0.033	0.055	0.084	0.024	0.038	0.050	0.014	0.052
CDM	0.011	0	0.033	0.086	0.118	0.002	0.041	0.057	0.047	0.049
PAI	0.033	0.033	0	0.140	0.110	0.072	0.080	0.113	0.079	0.158
CAN	0.055	0.086	0.140	0	0.049	0.031	0.015	0.019	0.031	0.058
CAP	0.084	0.118	0.110	0.049	0	0.006	0.018	0.071	0.090	0.098
KAB	0.024	0.002	0.072	0.031	0.006	0	0.000	0.030	0.017	0.027
SHA	0.038	0.041	0.080	0.015	0.018	0.000	0	0.000	0.042	0.000
GRK	0.050	0.057	0.113	0.019	0.071	0.030	0.000	0	0.023	0.000
ITY	0.014	0.047	0.079	0.031	0.090	0.017	0.042	0.023	0	0.019
TRK	0.052	0.049	0.158	0.058	0.098	0.027	0.000	0.000	0.019	0

BOL=Bolores, CDM=Cova da Moura, PAI=Pai Mogo, CAN=Canary Islanders, CAP=NW African Capsian, KAB=NW African Kabyle Berbers, SHA=NW African Shawia Berbers, GRK=Greece, ITY=Italy, TRK=Turkey (see text Section 1.2 for details).

Underlined MMD distances indicate significant difference at the 0.025 level.

TABLE 4. Component loadings, eigenvalues, and variance explained for 32 traits in the three Portuguese and six of seven comparative samples

Trait	**Comp 1**	**Comp 2**	**Comp 3**
Winging UI1*	0.418	**0.555**	0.212
Labial Curvature UI1*	-0.465	-0.255	**-0.745**
Palatine Torus	-0.120	0.448	0.301
Shoveling UI1	0.245	-0.020	-0.183
Double Shoveling UI1	-0.034	-0.485	0.192
Interruption Groove UI2*	**-0.589**[1]	0.131	0.432
Tuberculum Dentale UI2*	**0.665**	-0.140	-0.459
Bushman Canine UC*	-0.081	**0.657**	0.204
Distal Acc. Ridge UC*	**0.678**	**-0.609**	0.350
Hypocone UM2	-0.092	0.069	0.260
Cusp 5 UM1*	**0.891**	0.376	-0.060
Carabelli’s Trait UM1*	-0.043	**-0.772**	-0.039
Parastyle UM3*	-0.031	-0.271	**0.660**
Enamel Extension UM1*	**0.555**	0.476	-0.226
Root Number UP1*	-0.202	**-0.550**	0.187
Root Number UM2*	**0.706**	0.374	0.283
Peg-Reduced UI2*	0.363	0.486	**-0.693**
Congenital Abs. UM3*	**-0.721**	0.235	0.317
Lingual Cusp LP2	-0.361	-0.271	0.167
Anterior Fovea LM1*	**0.699**	**-0.555**	-0.073
Groove Pattern LM2*	0.284	-0.029	**0.816**
Rocker Jaw*	**-0.711**	0.496	0.186
Cusp Number LM1	-0.018	**-0.511**	-0.234
Cusp Number LM2*	**-0.591**	0.222	0.471
Deflecting Wrinkle LM1*	**0.668**	-0.323	0.405
C1-C2 Crest LM1	0.077	**0.706**	0.085
Cusp 7 LM1*	**0.605**	**0.546**	0.141
Tomes’ Root LP1*	0.436	**-0.557**	**0.599**
Root Number LC*	0.122	-0.408	**-0.538**
Root Number LM1*	0.150	**0.587**	-0.427
Root Number LM2*	0.327	0.381	**0.519**
Torsomolar Angle LM3*	**-0.855**	0.004	-0.179
Eigenvalue	7.463	6.230	4.910
Variance (%)	23.323	19.468	15.344
Total Variance	23.323	42.791	58.135

[1] Values in bold-face indicate strong loadings (>|0.5|) as detailed in text.
*Denotes the 25 traits used in the final MMD comparison.

TABLE 5. Symmetrical MMD distance matrix for Portuguese and comparative samples based on 25 dental traits

	BOL	**CDM**	**PAI**	**CAN**	**CAP**	**KAB**	**SHA**	**GRK**	**ITY**	**TRK**
BOL	0	0.036	0.079	0.073	0.114	0.021	0.060	0.123	0.031	0.118
CDM	0.036	0	0.058	0.111	0.159	0.002	0.070	0.110	0.043	0.081
PAI	0.079	0.058	0	0.185	0.170	0.125	0.128	0.187	0.108	0.248
CAN	0.073	0.111	0.185	0	0.067	0.025	0.000	0.021	0.015	0.043
CAP	0.114	0.159	0.170	0.067	0	0.020	0.040	0.090	0.081	0.132
KAB	0.021	0.002	0.125	0.025	0.020	0	0.000	0.034	0.000	0.002
SHA	0.060	0.070	0.128	0.000	0.040	0.000	0	0.000	0.000	0.000
GRK	0.123	0.110	0.187	0.021	0.090	0.034	0.000	0	0.031	0.002
ITY	0.031	0.043	0.108	0.015	0.081	0.000	0.000	0.031	0	0.013
TRK	0.118	0.081	0.248	0.043	0.132	0.002	0.000	0.002	0.013	0

BOL=Bolores, CDM=Cova da Moura, PAI=Pai Mogo, CAN=Canary Islanders, CAP=NW African Capsian, KAB=NW African Kabyle Berbers, SHA=NW African Shawia Berbers, GRK=Greece, ITY=Italy, TRK=Turkey (see text Section 1.2 for details).

Underlined MMD distances indicate significant difference at the 0.025 level.

TABLE 6. Symmetrical geographic straight-line distance matrix (km) among the Portuguese and comparative samples (using actual or approximated center of each site or geographic region)

	BOL	**CDM**	**PAI**	**CAN**	**CAP**	**KAB**	**SHA**	**GRK**	**ITY**	**TRK**
BOL	0	2.0	19.9	1367.3	1578.6	1359.9	1560.8	2750.5	1982.3	3745.5
CDM	2.0	0	19.7	1367.8	1578.1	1359.4	1560.3	2749.9	1981.7	3744.9
PAI	22.9	22.7	0	1385.1	1580.1	1362.4	1565.3	2748.2	1976.9	3742.8
CAN	1367.3	1367.8	1385.1	0	2451.9	2226.8	2303.5	3674.6	3072.9	4647.8
CAP	1578.6	1578.1	1580.1	2451.9	0	232.1	241.9	1230.8	722.7	2222.2
KAB	1359.9	1359.4	1362.4	2226.8	232.1	0	249.1	1461.9	894.7	2454.2
SHA	1560.8	1560.3	1565.3	2303.5	241.9	249.1	0	1374.3	958.2	2345.5
GRK	2750.5	2749.9	2748.2	3674.6	1230.8	1461.9	1374.3	0	851.4	997.7
ITY	1982.3	1981.7	1976.9	3072.9	722.7	894.7	958.2	851.4	0	1799.9
TRK	3745.5	3744.9	3742.8	4647.8	2222.2	2454.2	2345.5	997.7	1799.9	0

BOL=Bolores, CDM=Cova da Moura, PAI=Pai Mogo, CAN=Canary Islanders, CAP=NW African Capsian, KAB=NW African Kabyle Berbers, SHA=NW African Shawia Berbers, GRK=Greece, ITY=Italy, TRK=Turkey (see text Section 1.2 for details).