Inhaltsverzeichnis / Table of contents

A new method for estimating migration distances using landscape topography

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Abstract

Population genetics research of the last 50 years showed strong associations between geographic and genetic distances (isolation by distance). Moreover, it even revealed a negative relationship between within-population diversity of a founder population and its descendent populations that spread over previously uninhabited land masses. These findings were also shown to be valid for human populations. Consequently, identifying major human migration pathways in the context of the recent African origin theory has been a major topic in recent anthropological research, not only in order to describe and explain the ethnogenesis of different human populations, but also to study microevolutionary forces during these migrations. In this regard, different models for estimating human migration distances have been suggested. Unfortunately, these models have disadvantages, e.g. assuming that migrations occur along a straight line. In this study, a new model for estimating human migration pathways and migration distances is introduced. This model is solely based on global topographic landscape data and the assumption that migrations on lower altitudes are more likely than on high altitudes and over long sea distances. To test the quality of the model, migration distance estimates were used as predictors for within-population diversities in simple linear regressions. The within-population diversities were taken from previous studies that also provided distance estimates obtained from other models. In comparison to these models, the newly introduced topographic migration model explained as much variance as the common models in four cases, whereas three of the remaining four linear regression models were not valid due to the violation of assumptions (normal distribution and homoscedasticity of residuals). Migration pathways estimated via the topographic migration model matched the migration pathways estimated using molecular markers. Thus, the introduced topographic migration distance estimation model qualifies to be used in anthropological research. Moreover, this model requires less editing in comparison to former models, rendering it useful for future studies.

Key words: migration distance, within-population diversity, origin of modern humans

Introduction

The discussion on the geographic origin of first modern humans began with the publication of Charles Darwin's book "The Descent of Man" (Darwin 1871) in which he speculated that *Homo sapiens* had descended from African apes. The theory of a common African origin of modern humans became widely accepted and has more recently been supported by the hominin fossil record, genetic analyses, and genetic dating (e.g. Schlebusch *et al.* 2017, Stringer and Andrews 1988, Wallace *et al.* 1999). In order to understand the ethnogenesis of human populations and its microevolutionary processes, the reconstruction of migration pathways starting in Africa became a major topic in anthropological research.

One of the research findings was the negative correlation between geographic distances to founder populations and the within-population diversity of the descendant populations. Such associations between increasing geographic distance and a decrease of genetic similarity (measured as F_{ST}) or heterozygosity had already been proposed in the theory of "isolation by distance" (Malécot 1970) as well as the "stepping-stone model" (Kimura and Weiss 1964, Le Corre and Kremer 1998). Evidence for such associations in human populations was first shown for short distances, and, thus, on a regional basis (Morton 1973, Jorde 1980). However, studies on blood group polymorphisms (Cavalli-Sforza *et al.* 1994), and studies using microsatellite markers (Harpending and Rogers 2000), and even craniometric data (Relethford 2001) confirmed a strong relationship between geographic distances and within-population diversities.

For describing associations between geographic and genetic distances, Cavalli-Sforza *et al.* (1994) used the great circle distance (shortest distance between two points on the surface of a sphere) as a proxy for the true

geographic distance between two populations. However, this implies that migrations occur along a straight line, and without encountering potential migration barriers, such as high mountain ranges and large water bodies. For this reason, subsequent studies used methods adjusting for this simplification of migration distances and allowed a more accurate estimation of the relationship between within-population diversities and migration distances on a global scale (e.g. Ramachandran *et al.* 2005, Prugnolle *et al.* 2005a). In their model, Ramachandran *et al.* (2005) first defined five waypoints on the globe between which migration is allowed and that represented waypoints of the most likely migration routes out of Africa. They then calculated the shortest connection between a starting point (the potential origin of modern humankind in Africa) and any arbitrarily chosen population, using the distances between these waypoints, the chosen origin, and the geographic residence of the population of interest. Applying this model, Ramachandran *et al.* (2005) found a significant negative linear relationship between migration distances and autosomal microsatellite diversity in a sample of human populations. The authors' migration distances estimation model was adopted by other authors who were able to show the same association for autosomal SNP diversities (Li *et al.* 2008), cranial variations (Cramon-Taubadel and Lycett 2008), and even the phonemic diversity of languages (Atkinson (2011). Ramachandran *et al.* (2005) concluded that this pattern, the decrease of within-population diversities with increasing migration distances, is probably caused by serially occuring founder effects related to the migration distance. This global pattern can be used as null model in order to detect populations with higher or lower diversity than expected, caused by selection and other evolutionary forces (Handley *et al.* 2007).

A refined model of Ramachandran *et al.* (2005) was introduced by Prugnolle *et al.* (2005a). Instead of using only five waypoints, the authors used 30,000 equally spaced points distributed over the globe, between which migration seemed reasonably possible. The model allows editing of those waypoints and the exclusion of potential migration barriers. The authors then used an algorithm which allowed them to identify the shortest connection between the potential origin of modern humans (Ethiopia), all waypoints, and the location of the population of interest. With the estimated migration distances calculated using this refined model, Prugnolle *et al.* (2005a) and others (Prugnolle *et al.* 2005b, Liu *et al.* 2006, Manica *et al.* 2007, Betti *et al.* 2008, Balloux *et al.* 2009) were able to explain an even higher proportion of the worldwide human genetic variation in relation to migration distances than using the earlier model.

Although the migration models introduced by Ramachandran *et al.* (2005) and Prugnolle *et al.* (2005a) generate less biased migration distance estimates compared to the great circle approach (Cavalli-Sforza *et al.* 1994), both models do not incorporate topographic characteristics of the migration landscape (except the exclusion of migrations above an altitude of 2,000 m by Prugnolle *et al.* 2005a). However, the landscape topography has most likely played an important role during the human colonisation of the earth: Migration along rivers, in valleys, and at low altitudes in general may have been easier, and, thus, occurred with higher probability than migration over high mountain ranges and high altitudes (e.g. Krings *et al.* 1999, Oppenheimer 2009). Here, a topographic migration model for estimating migration pathways and migration distances is proposed, incorporating the topographic conditions of migration routes. In order to validate this topographic migration model, the obtained estimates for migration distances are compared to those published in Balloux *et al.* (2009) and Cramon-Taubadel and Lycett (2008).

Material and Methods

Within-population diversities and surveyed populations

For this study, genetic diversities of full mitochondrial DNA sequences (excluding the HVS-I and HVS-II regions, 628 sequences comprising 51 populations), sequences of the hyper-variable segment 1 (HVS-I, 5,000 from 109 populations), autosomal, X-, and Y-chromosomal microsatellites (783, 36, and 6 for 51 populations) as well as single nucleotide polymorphisms (SNPs, 51 populations) that are given by Balloux *et al.* (2009) were used. Balloux *et al.* (2009) estimated migration distances following the approach of Prugnolle *et al.* (2005). To compare the migration distance estimates obtained with the topographic migration model with those obtained with the model using great-circle distances and considering five waypoints (Ramachandran *et al.* 2005), within-population diversities (Relethford and Blangero 1990) calculated for 28 populations using craniometric variables (1,348 individuals, 57 craniometric variables) were taken from Cramon-Taubadel and Lycett (2008).

Beside the diversity estimates, both publications provided the geographic locations of the analyzed

populations. The given geographic coordinates of these locations were then used to estimate the migration distances with the topographic migration model.

Chosen origins of human within Africa

Even though different origins of modern humans in Africa have been suggested by various different authors (e.g. Stringer and Galway-Witham 2017, White *et al.* 2003), for this study Zambia (latitude: -12°, longitude: 25°) and Botswana (latitude: -20°, longitude: 25°) were selected as origins of *Homo sapiens* in Africa. The origins chosen were the same as the ones considered in Balloux *et al.* (2009) (Zambia) and Cramon-Taubadel and Lycett (2008) (Botswana).

Estimation of migration routes and migration distances

The topographic migration model introduced here is based on the generally accepted doctrine of a single replacement model of modern human origin in Africa (recent African origin, Stringer and Andrews 1988). Further assumptions of the topographic migration model are that lower altitudes facilitated migration, while migration on high altitudes (mountains) and over large water bodies inhibited migration. These assumptions are based on the idea of easier migration through landscapes with high carrying capacities (Currat *et al.* 2004).

Following these assumptions, the most parsimonious migration routes were estimated. These trajectory routes via which humans potentially spread across the earth are calculated in a graph as lines that connect all analyzed populations with the common location of origin (either Zambia or Botswana in Africa) by applying the topographic migration model. The model is based on geographic and topographic data with a 30′ resolution, forming a $2,400 \times 2,400$ raster of rectangles in the Mercator projection (https://www.ngdc.noaa.gov/mgg/topo/globe.html, Hastings *et al.* 1999). Each barycenter of these $2,400 \times 2,400$ cells (nodes) has an 8-neighborhood where all neighbors are connected with edges.

The topographic migration model comprises two calculation steps implemented in C++: The first step is the assignment of "costs" to all edges: If at least one of two neighboring nodes lies in the sea, a weight of $250 +$ (closest distance to node on a landmass in opposite direction of the migration direction $\times 100,000$) is assigned to the corresponding edge. Else, the edges connecting two nodes get the weight $1 +$ (average altitude of both raster cells $\times 0.01$). These weights were selected in order to represent a decreased probability for

migrations at high altitudes and across high mountain ranges or the sea in contrast to migration routes at lower altitudes, and to obtain migration routes similar to those derived by Cavalli-Sforza *et al.* (1994). In the second step, the Bellman-Ford algorithm (Bellman 1958, Ford 1956, Moore 1959) is applied in order to calculate the most parsimonious routes based on the assigned costs, originating at the previously assigned starting point and extending to the location of each of the analyzed populations. The Bellman-Ford algorithm identifies the shortest path between the starting point and the location of a population by finding the path which overall cost (sum of edge weights) is minimal. The length of the resulting paths were used as the assumed migration distances of the populations included in this study. One example for the graphical result generated via such a topographic migration model is shown in Fig. 1 for the locations of HVS-I populations analyzed by Balloux *et al.* (2009).

Statistical analyses

For the statistical comparison of the migration distance estimates obtained from the topographic migration model with the model estimates of Balloux *et al.* (2009) as well as Cramon-Taubadel and Lycett (2008), simple linear regression analyses of given within-population diversities and migration distances were performed. To further test the validity of the application of a simple linear regression model, the Breush-Pagan test for heteroscedasticity as well as a Shapiro-Wilk test for the normality of residuals were applied. Whether differences in the slope coefficients of the simple linear regression analyses of all models were significant, was tested with a t-test. To test if whether the coefficients of determination for the topographic migration models (R^2_t) and the corresponding reference models (R^2_r) differ significantly (H0: the true determination coefficients do not differ significantly), a randomization approach was used: Differences between the coefficients of determination, $R^2_r - R^2_t$, were calculated for resampled data sets of the same length as the original data sets in order to generate a null distribution. This null distribution was then used to calculate p values for observed differences between coefficients of determination. Since Cramon-Taubadel and Lycett (2008) did not provide their migration distance estimates, the null distribution was calculated using the given fixed R^2_r value and the R^2_t values obtained from randomized samples. All analyses have been conducted using the statistical programming language R (version 3.3.1).
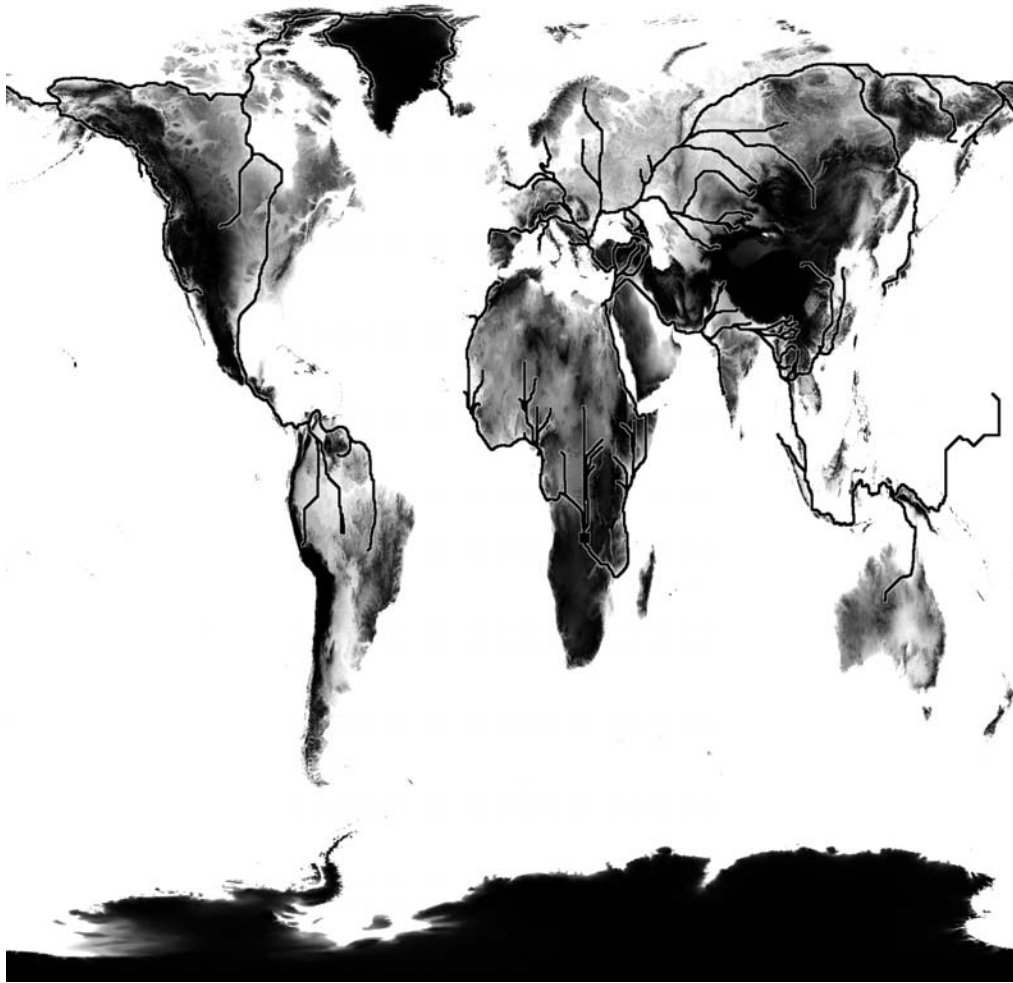
Figure 1. Estimated topographic migration model for the mtDNA populations. – The estimated migration pathways are shown as black lines which interconnect all populations that are indicated as terminal nodes with a common origin at -12° lat., 25° lon. (black square). Different grey scales of the map represent the above sea level (white) to the highest mountains (black).

Results

The three linear regression models for autosomal, X-chromosomal, as well as Y-chromosomal microsatellite data presented in Balloux *et al.* (2009) did not meet the assumptions for a linear regression model: The Breush-Pagan tests indicated strong evidence for hetero-scedastic residuals ($p < 0.001$ for the autosomal microsatellite data, $p = 0.009$ for X-chromosomal SNPs), while the residuals of the linear regression for the autosomal and Y-chromosomal microsatellite data were not normally distributed ($p < 0.001$ and $p = 0.013$). Although this may already indicate that some of the regression models with the migration distance estimates calculated with the topographic migration model may

not meet the assumptions for a linear regression analyses, the regression analyses were performed in order to compare the topographic migration model with the models of Ramachandran *et al.* (2005) and Prugnolle *et al.* (2005a).

The p values obtained in the simple linear regression analyses using migration distance estimates calculated by the model of Balloux *et al.* (2009) are identical with the p values obtained in the simple linear regression analyses using migration distance estimates calculated by the topographic migration model considering identical geographical origins ($p < 0.001$ for both models) (Table 1), with one exception: when Y-chromosomal microsatellite data were used for the simple linear regression analyses, the p value obtained

for the topographic migration model was higher, though still significant (p = 0.020 for the topographic migration model, p = 0.002 for the model of Balloux *et al.* (2009) (Table 1). In contrast, the p value obtained for the topographic migration model was much smaller (p < 0.001) than the p value obtained for the model of Cramon-Taubadel and Lycett (2008) (p = 0.01) (Table 1).

The coefficient of determination obtained in the simple linear regression analysis for the model of Cramon-Taubadel and Lycett (2008) (R^2 = 0.260) was much smaller than the one obtained for the topographic migration model (R^2 = 0.442) (Table 1). However, when autosomal, X- and Y-chromosomal microsatellite data as well as SNP data were used for the simple linear regression analyses, the coefficients of determination obtained for the topographic migration model were smaller than the ones obtained for the model of Balloux *et al.* (2009) (R^2 see Table 1). The regression models using the topographic migration distance estimates explained a higher proportion of the variance of worldwide HVS-I and complete mitochondrial diversity and, thus, higher coefficients of determination were obtained (HVS-I: R^2 = 0.213 for the topographic migration model, R^2 = 0.191 for the model of Balloux *et al.* 2009; complete mitochondrial data: R^2 = 0.307 for the

topographic migration model, R^2 = 0.294 for the model of Balloux *et al.* 2009). Although the randomization approach revealed no significant difference between the coefficients of determination given above, the R^2 value for the topographic migration distance estimates tends to be higher than the R^2 value from the reference model for the full mtDNA data set (Table 1).

Discussion

In general, the migration distances calculated using the topographic migration model were always at least as long as or even longer than the migration distances calculated using the model of Ramachandran *et al.* (2005) and Prugnolle *et al.* (2005a). The shortest distance between two points on the surface of an ellipsoid (as proxy for the earth) is always a straight line (geodesic distance). Geodesic distances were the ones chosen by Ramachandran *et al.* (2005) and Prugnolle *et al.* (2005a) and implemented in their models, whenever there was no migration barrier (such as mountains, or the sea). The results of implementing geodesic distances can be seen in the migration map printed in Prugnolle *et al.* (2005a). In contrast, geodesic distances as most

Table 1. Statistical parameters for linear regression models of within-population diversity in relation to migration distance. – The table shows the p values (3rd column) and the coefficients of determination (R^2) (4th column) obtained by the linear regression analyses using the data sets (1st column) taken by Balloux *et al.* (2009) and Cramon-Taubadel and Lycett (2008) and the topographic migration estimates of the topographic migration model presented here. Additionally, the p values for the differences between the values of R^2 obtained for the topographic migration model and the models of Balloux *et al.* (2009) and Cramon-Taubadel and Lycett (2008) via a randomization approach are shown.

DATA SET	distance estimate used for regression	p value (regression model)	R^2 (regression model)	p value (difference of R^2 values)
mtDNA HVS-I	topographical	< 0.001	0.213	0.148
	Balloux *et al.* 2009	< 0.001	0.191	
full mtDNA	topographical	< 0.001	0.307	0.073
	Balloux *et al.* 2009	< 0.001	0.294	
autosomal STR	topographical	< 0.001	0.775	0.470
	Balloux *et al.* 2009	< 0.001	0.850	
X-STR	topographical	< 0.001	0.812	0.207
	Balloux *et al.* 2009	< 0.001	0.835	
Y-STR	topographical	0.020	0.105	0.293
	Balloux *et al.* 2009	0.002	0.181	
autosomal SNP	topographical	< 0.001	0.793	0.097
	Balloux *et al.* 2009	< 0.001	0.806	
craniometric	topographical	< 0.001	0.442	0.648
	Cramon-Taubadel, Lycett *et al.* 2008	0.010	0.260	

likely routes of migration were not implemented in the topographic migration model presented here. The model rather incorporated information on the topographic migration conditions of the potential migration routes. Thus, routes following a straight line are only calculated for migrations over large water bodies, such as the sea.

The p and R^2 values obtained by the simple linear regression analyses using craniometric data were much better for the topographic model than those obtained for the model of Cramon-Taubadel and Lycett (2008), maybe as a consequence of the fact that the topographic landscape conditions were taken into account when calculating migration distance estimates rather than geodesic distances. Higher albeit not significant different R^2 values were also obtained for the full mitochondrial and the HVS-I data regressed on the topographic migration distance than for the distance given by Balloux *et al.* (2009).

However, four data sets, the autosomal SNPs as well as autosomal, X-, and Y-chromosomal microsatellites, showed higher coefficients of determination in the regression model with the migration distances given by Balloux *et al.* (2009) than with the topographic migration distances. This worse performance of the regression models for these four data sets (autosomal SNPs and STRs as well as X- and Y-chromosomal STRs) may be associated with the violation of the assumptions of linear regressions (none of these linear regressions produced normally distributed residuals, $p < 0.001$ on a level of $\alpha = 0.05$) and the relatively low number of 51 populations incorporated in the analyses (compared to 109 populations in the HVS-I data set). This emphasizes the need of using a high number of populations incorporated in the analysis in order to reduce the risk of biased estimations by populations whose within-population diversities may have been influenced by non-neutral evolutionary forces.

Considering the violation of assumptions (homoscedasticity and normally distributed residuals) for the regressions of microsatellite diversities (Balloux *et al.* 2009), all regressions derived from the topographic migration model were highly significant and explained as much variance as the regressions with migration distances derived from common migration models. Although the randomization tests indicate no significant higher R^2 values for the topographic migration distance models, it tended to explain more variance in two cases ($p = 0.073$ for the full mtDNA as well as $p = 0.097$ for the autosomal SNP diversities) compared to the R^2 values of the migration model introduced by Prugnolle *et al.* (2005a).

The reconstructed migration pathways using the topographic migration model described here delivered similar routes (Fig. 1) than those reconstructed by Edwards and Cavalli-Sforza (1964) and Cavalli-Sforza *et al.* (1994) using classical genetic markers. It could be shown here that the reconstruction of migration pathways is possible when considering the more realistic topographic conditions humans may have encountered during their migration, and that the migration distance estimates obtained by implementing these conditions were at least as good as the ones obtained for the models used by other authors and implementing great circle or geodesic distances. The major prehistoric and historic migration routes were reconstructed well enough for the topographic migration model to be used in anthropological research, for instance to establish null models for particular genetic markers that can be used for the detection of selective forces affecting human populations (Handley *et al.* 2007).

Acknowledgments

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Dental nonmetrics: an asset to anthropology

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Dental nonmetric traits are a valuable tool for understanding relationships between populations. They can be observed on the entire dentition. These traits are anatomical variations observed on permanent and deciduous dentition. A series of equivalent terms is encountered in the literature – such as trait, character, variant, variable, anomaly, or shape – to which an adjective is added to qualify them as epigenetic, discrete, nonmetric, discontinuous, or threshold. In general, reference is made to traits that may be present or absent, or that reflect different stages of development. They may take the form of positive structures, such as the presence of tubercles or secondary crests, or negative, such as grooves. They may also be represented by variation in number, position or the size of cusps and roots (Fig. 1).

One of the advantages of these traits is the possibility of observing them on living individuals. This is not a minor advantage because it enables better understanding of their biological value, a relatively rare situation in bioanthropology. In addition, the tooth is one of the most resistant parts of the skeleton and often represents the best-preserved elements in archaeological contexts. These two points suggest that the analysis of dental nonmetric traits may be one of the more interesting approaches when applied to studies of past populations.

Of more than a hundred dental traits, only forty or so have been studied in detail, addressing the purely biological aspects of their development, mode of inheritance and heritability (Scott and Turner 1997):

- First, research has established that dental development, and in particular that of dental morphology, is highly subject to genetic control (Thesleff and Nieminen 1996; Cobourne and Sharpe 2003; Kimura *et al.* 2015). Several studies have demonstrated that the development of the dentition is controlled by a certain number of genes that act in different places and intervene at distinct moments of its formation (Thesleff 2003). While no trait follows a simple mode of inheritance, they are not as complex as those of models of polygenic inheritance in which many genes are involved. In addition, although we cannot deny a probable influence of environmental factors, we also cannot contest the fact that their effects are minor (Tyrell 2000; Scott and Irish 2013). Finally, studies based on genetic determinism have demonstrated that most of these traits seem to possess a large hereditary component (Scott and Potter 1984; Townsend and Martin 1992; Townsend *et al.* 2009; Scott and Irish 2013). Research also pointed out that dental nonmetric traits are usually low in inter-correlation; they are not correlated with age, and are lowly or not correlated with the sex of the individuals (Scott and Turner 1997; Irish and Scott 2016; Scott and Irish 2017).

- Second, the viability of the system of observation is an essential element in the validation of data. In effect, the lack of standardization of data can sometimes lead to entirely different results. The subjectivity of the observation has often been a determining element in the criticism of the study of dental traits. Nevertheless, it is possible to move past this obstacle, by using dental casts and precise definitions of the different variables. The Arizona State University, through C.G. Turner, C.R. Nichol and G.R. Scott (1991), conceived the most used dental trait system: the ASU-DAS system. The purpose was to assess crown and root morphological variation within and among population samples. They described a selection of traits observed on the permanent dentition. They described each trait, giving precise definitions of the traits and of the scaled expression. They also produced rank-scale casts for most scaled traits. It is also possible to move past this obstacle by eliminating traits that could pose possible problems of standardization by testing not only one's own accordance, but also that between different observers.

- Finally, studies on the value of dental nonmetrics when applied to modern populations are clearly reassuring. Comparison of results of dental morphology with different estimators, such as geographic proximity, linguistics and genetic data, have reinforced the idea that these variables are good indicators of biological distance between populations (Brewer-Carias *et al.* 1976; Kirverskari 1978; Scott and Dahlberg 1982; Higa *et al.* 2003; Ricaut *et al.* 2010; Scott *et al.* 2013).
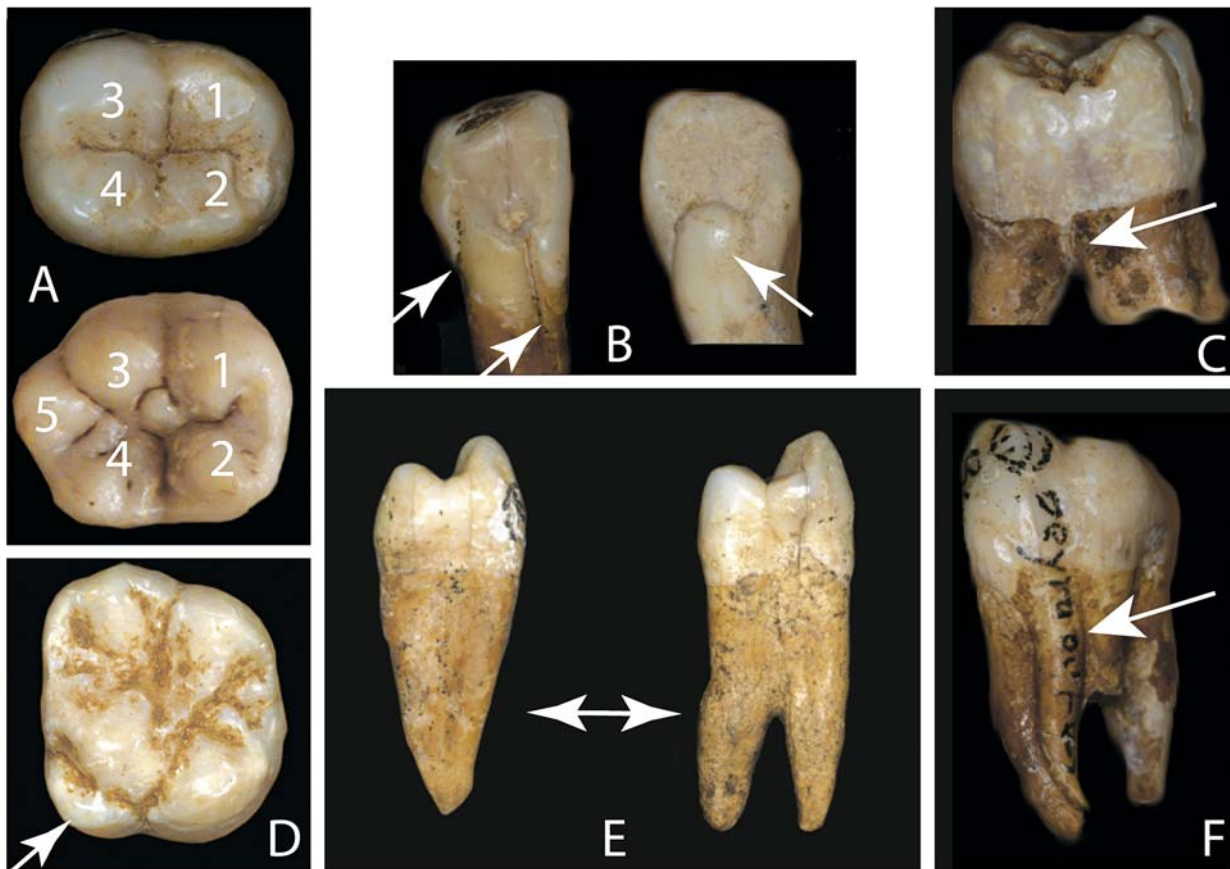
Figure 1. Some examples of dental nonmetric traits observed on permanent dentition: (**A**) number of cusps on lower molars, top, 4 cusps and bottom, 5 cusps; (**B**) left, lateral incisor with two grooves, one medial and one distal; right, lateral incisor with a dental tubercle on the lingual surface; (**C**) an extension of the enamel is present on the upper molar, (**D**) occlusal view of an upper molar showing the presence of Carabelli's tubercle, (**E**) number of roots of the first upper premolar, left, monoradicular; right, biradicular, (**F**) radix paramoralis present on a first upper molar.

Today, research on dental nonmetrics continues and leads to a better understanding of these variables. Even if some aspects should be better mastered, notably the genes responsible for the development of these variables, the genetic determinism underlying the expression of dental traits allows them to be used for comparative studies between populations.

Several studies concerning peopling dynamics during the third millennium BC, and mainly the Bell Beaker period are presented here to assess dental nonmetric potential for understanding relationships between populations. The first one concerns a study on mobility evidence during the Bell Beaker period in Western Switzerland: a dental nonmetric study, completed by a strontium isotopic study. The second example concerns a study on mobility evidence in the Alps, through the study of the Bell Beaker megalithic necropolis of Saint-Martin-de-Corléans (Aosta, Italy).

Finally, the dental nonmetric study of the collective grave of Spreitenbach (Aargau, Switzerland) belonging to the end of the Neolithic is presented to precise its chronological attribution and populational affinities.

Mobility evidence during the Bell Beaker period in Western Switzerland

The Bell Beaker complex is defined, above all, by a ceramic style widespread across Europe during the third millennium BC. Its particularly large geographic distribution has provoked different interpretations: population displacements, long-distance exchange of prestige goods, and absence of a real Bell Beaker population with only diffusion of its cultural components. For Western Switzerland, the Bell Beaker period would have developed following influences

varying from both the Mediterranean region and Central Europe (Gallay 2006).

Bioanthropology makes it possible to test the first of these hypotheses, which proposes the diffusion of a culture by population displacement.

First, dental morphology was applied and more precisely dental nonmetrics. The objective was to identify whether the Bell Beaker phenomenon was characterized by a break or a continuity of the local population, by observing the dentition of pre-Bell Beaker populations, Bell Beaker populations and post-Bell Beaker populations. Two kinds of analysis were carried out: a Swiss regional analysis (from the middle Neolithic to the early Bronze Age) and an analysis of European Bell Beaker populations (Desideri 2011). Dental nonmetric results support the idea, for Western Switzerland, of a certain harmony in middle Neolithic populations and mobility or a moderate population contribution beginning in the final Neolithic and continuing during the Bell Beaker period (Desideri *et al.* 2010). Dental nonmetrics also demonstrate that the axis for external population influences at the end of the Western Swiss Neolithic is clearly from the West (Desideri and Besse 2010).

Then the necropolis of the Petit-Chasseur (Sion, Valais, Switzerland) has been selected in order to validate and quantify this external population contribution during the end of the Neolithic in this region (Desideri *et al.* 2010). Dental enamel of final Neolithic and Bell Beaker individuals from the Petit-Chasseur site has been analyzed for strontium isotope ratio (87Sr/86Sr). Geological Sr levels were measured for a previous analysis concerning both dentin and enamel in a post-mortem contamination assessment (Chiaradia *et al.* 2003). Complementary measures from human long bones and enamel fauna from the Petit-Chasseur site in order to measure Sr local variability were added. All these complementary values are within the range of the local levels. Results of strontium isotope ratio of the individuals analyzed are concordant with dental morphology results supporting mobility during the end of the Neolithic in Western Switzerland. Moreover, these results reveal some interesting points about the individuals who have changed their "geological" residence during their lifetimes:

- 32% of the final Neolithic population present outsider local values. It involves both adults and immature.
- 30% of the Bell Beaker population present outsider local values. It involves only adults.

These results are very interesting in terms of migration. The rates are similar but people involved in

displacements differ according to the period (all the population or only adults) (Desideri *et al.* 2010).

The results of all these bioanthropological studies used to approach the question of peopling dynamics at the end of the Neolithic in Western Switzerland go in a similar direction. An external population input is identified, for both the final Neolithic and the Bell Beaker period. Moreover, the study of dental morphology demonstrates that this input originates from Western Europe.

Mobility in the Alps: with integration of the site of Saint-Martin-de-Corléans (Aosta, Italy)

The megalithic necropolis of Saint-Martin-de-Corléans (Aosta, Italy) is not only contemporary of the Petit-Chasseur necropolis, but these two megalithic sites are similar in many ways. Often called the twins, they show great affinities on both sides of the Alps (dolmens with triangular bases, anthropomorphic stelae, reuse of collective graves...). For these reasons, the objective of its dental nonmetric study was to identify how much the populations buried in these two megalithic areas are biologically similar (Desideri *in press*).

The population of Saint-Martin-de-Corléans has been integrated in the previous studies presented for mobility evidence (European Bell Beaker populations and Swiss regional analysis). Dental nonmetrics demonstrate that the Italian population is clearly linked to the Western sphere of European Bell Beakers and presents a high affinity with the megalithic Petit-Chasseur site. More specifically, the population of Saint-Martin-de-Corléans reveals a close proximity to individuals belonging to the final Neolithic Petit-Chasseur megalithic area (Desideri *in press*).

Investigating the collective grave of Spreitenbach (Aargau)

A dental nonmetric study of the collective grave of Spreitenbach in Aargau, dating from the end of the Neolithic, was carried out to define the chronological attribution of this grave and their populational affinities (Desideri 2012). Two regions were selected: Western Switzerland with samples dating from the middle Neolithic to the early Bronze age and the Czech Republic with populations belonging to the Corded Ware, the Bell Beaker and the Unetice cultures.

Results were very interesting, and allowed us to precise the chronological attribution and the

populational affinities of this grave. The individuals of Spreitenbach show affinities with the Czech Bell Beaker populations, and especially with the populations from Western and Central Bohemia. By contrast, the Western Swiss populations are very different regardless of the periods studied (Desideri 2012).

To conclude…

Dental nonmetrics are a very interesting tool to understand relationships between populations. It is not the presence or absence of a trait, but the whole of the dental morphological variability that allows for the identification of affinities between populations and/or individuals. We have seen that dental nonmetric traits provide interesting information, allowing us to discuss the biological and chronological affinities of populations of the end of the European Neolithic. Moreover, combining dental morphology and other approaches, such as isotope studies, allows for new light to be shed, in more nuanced ways, onto the respective data brought by each of the approaches.

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Dental morphological variability as revealed by virtual techniques

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Teeth play a crucial role for the study of both living and extinct hominin forms. The reasons for this are several, including their relative abundance in archaeological and fossil assemblages. Owing to the central role of teeth in mastication, dental morphology can be used to reconstruct dietary adaptation (Lucas 2004). Tooth morphology tends to be rather conservative in primates, both for functional and genetic constraints. Dental morphogenesis is genetically regulated by a complex signalling pattern (Jernvall and Thesleff 2000; Kangas *et al.* 2004; Kavanagh *et al.* 2007), and once teeth are formed, they do not remodel under biomechanical stimulation as bones do. Therefore, the phylogenetic signal that teeth bear can be captured and interpreted for taxonomic purposes.

Nonetheless, the study of dental remains is challenging for a number of reasons. Hominin teeth are small and complex objects; thus, their whole geometry is difficult to capture and analyse. In addition, teeth are often found in isolation and might be incomplete or poorly preserved. Furthermore, wear is very commonly affecting teeth, and might obscure both the occlusal and the interproximal aspects.

The application of virtual imaging techniques in the field of dental anthropology has fundamentally enhanced the way teeth can be investigated, increasing the amount of information derivable from teeth. The use of virtual imaging techniques allows to create high-resolution three-dimensional replicas of the object investigated, and enables to access to dental inner structures in a non-destructive way (Fig. 1). As a result, teeth can be handled as virtual models. An advanced and comprehensive way to assess the morphology of a tooth is through the use of geometric morphometrics (Weber 2001), a landmark-based approach suitable for the quantification of biological shapes.

Various virtual techniques have found application in studies for the taxonomic characterization of hominins. In particular, those to which I contributed, span from the analysis of Early Pleistocene Southern African *Australopithecus* (Fornai *et al.* 2015) to that of Croatian XVI century modern human remains (Lauc *et al.* 2015). Some works have addressed Neanderthal dental variability with respect to that of anatomically modern humans (Benazzi *et al.* 2011a; Benazzi *et al.* 2012; Fornai *et al.* 2014). These studies were based on the analysis of the dental tissue proportions, and the geometric morphometric investigation of several aspects of the dental crown (Fig. 2). These approaches have proven suitable for distinguishing between these *Homo* forms, also in the case of worn dentition.

The exploration of the intra- and inter-specific variability of various dental features provides a reference for the morphological characterization of unclassified specimens, such as the Middle Pleistocene dental specimens from Qesem Cave, Israel (Fig. 2) (Fornai *et al.* 2016; Weber *et al.* 2016), and possibly the achievement of a taxonomic assessment, as in the case of the Uluzzian deciduous molars from Grotta del Cavallo, Italy (Benazzi *et al.* 2011b).

The research conducted with the aid of virtual imaging techniques has contributed to our knowledge on hominin dental variability, and has allowed the morphological and taxonomic assessment of dental specimens from different times and places of human evolution. The approaches used allow for accurate evaluation of the dental morphology and are highly reproducible. Moreover, they have proven to be suitable for addressing diverse biological questions, and are adaptable to different tooth types at various degrees of dental wear. At the same time, these contributions have shaded light on fundamental limitations inherent to the study of fossil teeth, that even state-of-the-art techniques cannot easily overcome. The main problem consists in the difficulty of classifying incomplete individuals, sometimes exclusively represented by teeth or by one tooth. The ranges of variation of the different hominin forms are not fully known and it is not unreasonable to think that they might overlap to various extent.

In summary, the exploration of the intra- and interspecific variation is a key factor for taxonomic assessment. Considering the rarity of fossils, and the paucity in paleontological settings of other biological evidence, it is crucial that as much information as possible is gathered from each (dental) remain. Therefore, designing new protocols for the evaluation of dental morphology is pivotal in the study of dental remains from extinct species.
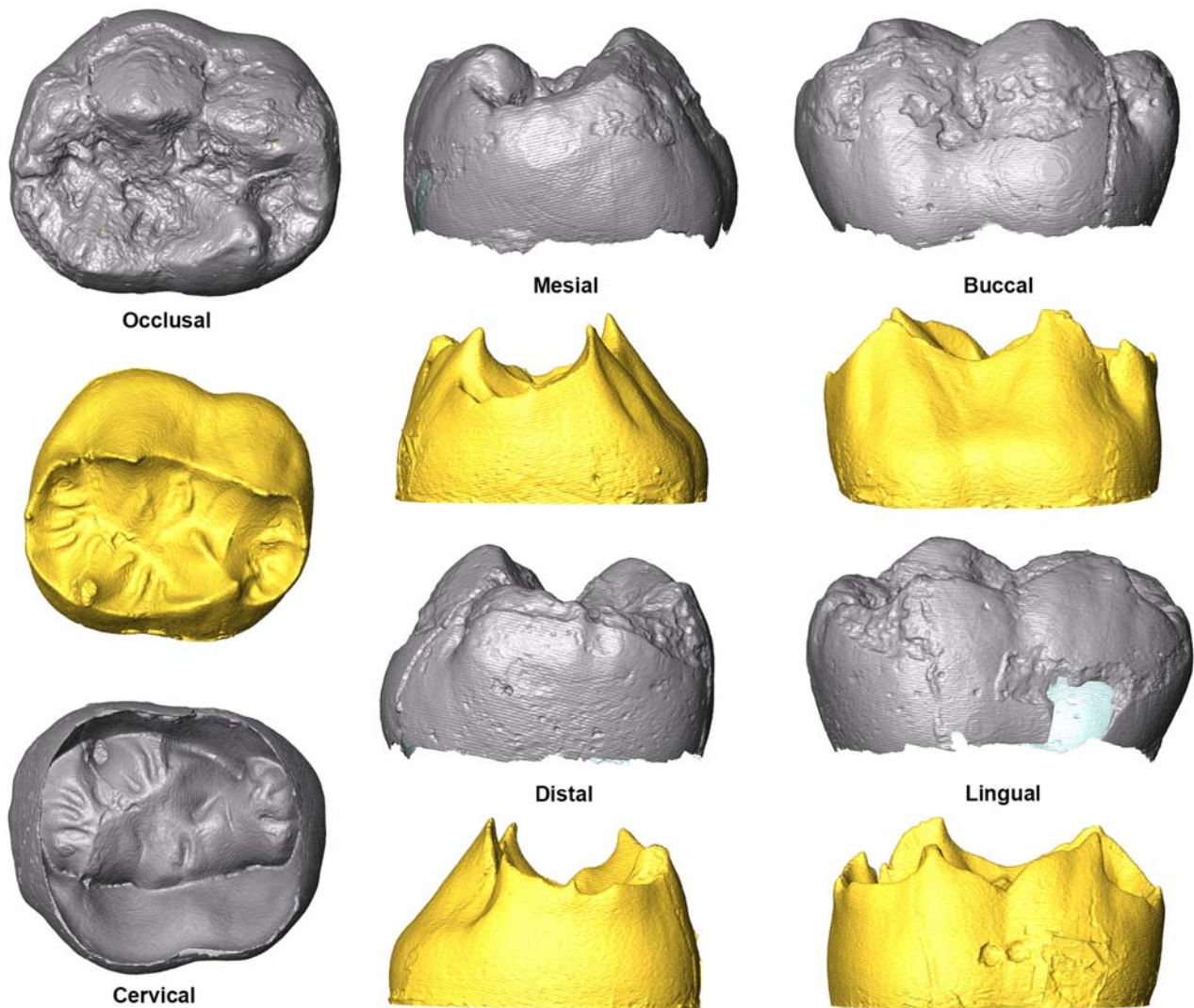
Figure 1. Different views of the 3D model of the dental crown of the lower second deciduous molar from Qesem Cave, Israel (dm$_2$-QC2). The enamel cap is virtually separated from the rest in order to expose the dentinal crown (from Fornai *et al.* 2016).

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Figure 2. Analysis of the dental tissues of dm$_2$-QC2 specimen from Qesem Cave, Israel through a topographic rendering of the enamel local variation with increasing thickness from blue to red (from Fornai *et al.* 2016).

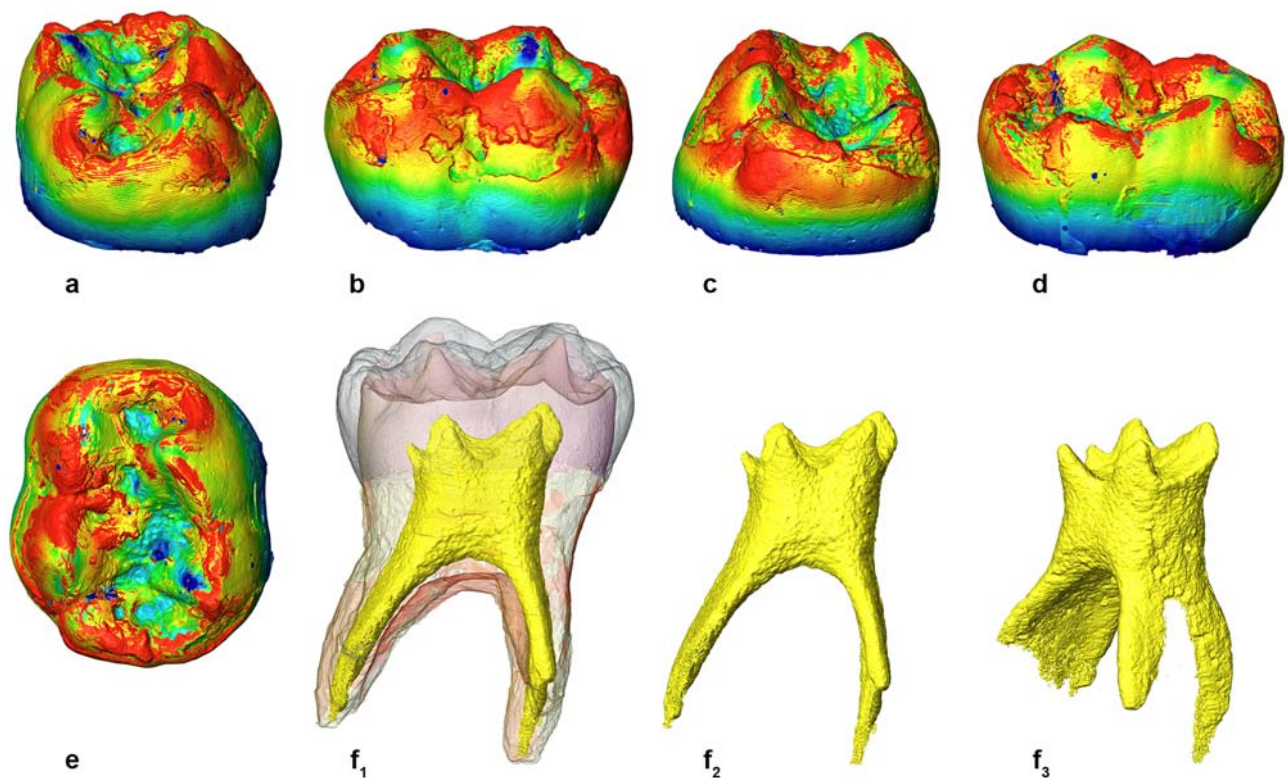Benazzi S, Fornai C, Buti L, Toussaint M, Mallegni F, Ricci S, Gruppioni G, Weber GW, Condemi S, Ronchitelli A 2012. *Cervical and crown outline analysis of worn Neanderthal and modern human lower second deciduous molars.* American Journal of Physical Anthropology 149: 537–546.

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The vertebral column of La Chapelle-aux-Saints – the evidence from spinal osteoarthritis for Neanderthal spinal curvature

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Boule's reconstruction of the La Chapelle-aux-Saints Neanderthal skeleton shaped the once popular notion of Neanderthals as primitive, brutish creatures. He described them as lacking a lumbar lordosis, but instead displaying a thoracic hyper-kyphosis and a straight neck with a primitive, forward inclined head position. Later, La Chapelle-aux-Saints' posture and distinct spinal curvature was attributed to pathology or to Boule's misinterpretation of the morphology, implying that the actual vertebral curvature of La Chapelle-aux-Saints did not differ from modern humans. Recent studies of the orientation of the inferior articular processes, however, again suggested a hypolordotic, flat lower back and spinal imbalance in Neanderthals including La Chapelle-aux-Saints. Here, we use the distribution and degree of the osteoarthritic changes as an alternative means to deduce spinal curvature in La Chapelle-aux-Saints. The extensive degenerative changes include Baastrup's disease of the spinous processes L4 to S1. Together with the nearthroses between the right laminae and superior articular processes of L4/L5 and L5/S1 due to disc space loss, the Baastrup's disease resulted in a fixed lordosis of the lower lumbar spine. In addition, severe facet joint osteoarthritis with eburnations and vertical subluxations suggest a relatively weak curvature of the upper lumbar and lower thoracic spine as well as a marked cervical lordosis in this old individual. A human-like degree of lordosis of the lower lumbar spine in the healthy condition as a young adult is also indicated by our reconstruction of the pelvis that shows a pelvic incidence of 56°, close to the mean of modern humans. Our findings suggest that the analysis of degenerative changes is a valuable tool to reconstruct posture and spinal mobility in Neanderthals.

Reconstructing occupational activity using manual muscle attachments from an extensively documented sample

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Multiple anthropological studies have widely utilized entheses (areas of muscle attachment on the bone) as markers of occupational stress. However, the reaction of entheseal form to mechanical loading is not yet understood. Furthermore, previous research relied on limited documentation, which only included the individuals' occupation-at-death. Past research identified two multivariate patterns among hand entheseal surfaces, which seemed to reflect fundamental manual muscle synergy groups (Karakostis and Lorenzo 2016). On this basis, this research project aimed at identifying the relationship between these multivariate patterns and habitual manual activity by applying a newly developed and highly precise method of quantification on a sample of 45 individuals which are extensively documented for their lifelong occupational activities. These specimens, which comprise part of the Spitalfriedhof Saint Johann collection (housed in the museum of Natural History in Basel), have lived in the mid-19th century. They were all male adults between 18 and 48 years old, who were not directly related, and showed no manual pathological conditions. The results of our quantitative method demonstrated that individuals with the same or comparable occupations present similar entheseal patterns (Karakostis *et al.* 2017). These patterns were not significantly associated with entheseal size, biological age, body mass, or bone length. Based on extensive historical sources, individuals involved in intense manual labor during their lifetime showed a distinctive pattern of hand entheses, consistent with the application of high grip force. By contrast, individuals with less strenuous and/or highly mechanized occupations presented an entheseal pattern related to the thumb and index finger intrinsic muscles. Currently, our research group has utilized the same sample for developing an original application of the geometric morphometric methods for analyzing the shape of hand entheseal surfaces and the factors regulating it. At the same time, the same methodology and comparative sample are being used for investigating entheseal variation in the hand bone remains of fossil hominins, with the objective of inferring habitual activity in the course of human evolution.

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Mandibular premolars' Enamel-Dentine-Junction: Morphology and discrete traits

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The Enamel-Dentine-Junction (EDJ) is a key aspect for the study of human dentition. It reflects the morphology of the outer enamel surface (OES), but it is more conservative, and it is affected by wear later in the lifetime of an individual. Therefore, it might be more convenient to study in archaeological or osteological settings. The EDJ has been variously investigated in different dental units, in order to explore hominin as well as primate dental variation. Traditionally, the EDJ was accessed through physical exposure (e.g., Kraus 1952; Kono *et al.* 2002), but more recent digital imaging techniques have made it possible to assess the inner structures of teeth none-destructively (e.g., Olejniczak *et al.* 2007; Skinner *et al.* 2008).

This study aims to facilitate investigation of the highly variable morphology of human mandibular premolars by focusing on the EDJ, and by creating a trait catalogue applicable to both lower P3s and P4s and based upon previous works on premolar OES (Kraus and Furr 1953; Ludwig 1957; Kraus *et al.* 1969; Turner *et al.* 1991; Hillson 1996; Scott and Turner 1997; Nelson and Ash 2010).
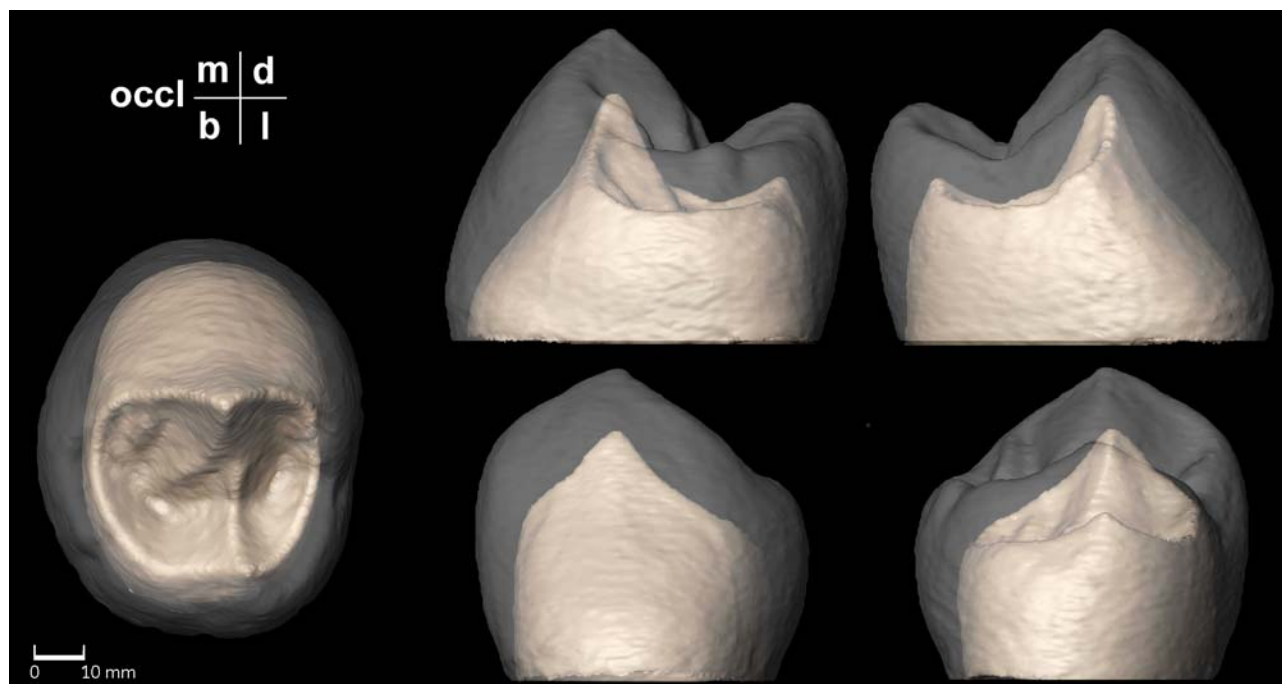

Figure 1. Mandibular P4 crown illustrating the underlying EDJ in different aspects.

We considered 144 teeth from 78 individuals from diverse human populations with broad geographical and ethnical background from all continents (except Antarctica). We found significant regional frequencies for several discrete traits. Additionally, we performed quantitative measurements using geometric morphometric techniques to capture the overall 3D shape morphology. All multivariate shape analyses show great morphological variability with considerable overlap of the various populations. Size, represented by the logarithm of centroid size, a 3D measurement captured from the overall geometry, varies between the continental groups. Furthermore, we observed sexual dimorphic trends in size variation.

The EDJ is a useful feature to assess premolar morphology qualitatively as well as quantitatively. In addition, its use is advantageous to increase sample size including moderately worn teeth.

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Die älteste Schweizerin aus Basel-Landschaft –
8 Jahrtausende und 5 AnthropologInnen später...

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Das Skelett aus der Birsmatten-Basisgrotte bei Nenzlingen BL hat eine (gender-)bewegte Geschichte. Nach seiner glücklichen Auffindung und Bergung durch Carl Lüdin im Jahre 1944 wurde es von Roland Bay erstmals anthropologisch untersucht. Seine Ergebnisse (Alter: matur, Geschlecht: sicher männlich) legte er in der Monographie zur Fundstelle vor (Bay 1964). Hansueli Etter (Nielsen *et al.* 1993) gab ebenfalls einem männlichen Geschlecht den Vorzug. Im Gegensatz dazu unterstützte eine Untersuchung durch Bruno Kaufmann (Sedlmeier und Kaufmann 1996) David Frayers Einschätzung (Frayer 1978), dass es sich bei der Bestattung um eine Frau handele. Das Skelett, in einer neuerlichen Analyse nun als mature Frau bestätigt, wird aktuell im Rahmen eines interdisziplinären Projektes untersucht (Sedlmeier und Pichler 2014).

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Babette Saxer – der erste dokumentierte Kaiserschnitt (1865) in Basel
Schicksal einer kleinwüchsigen Frau im frühindustriellen Basel

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Bei einer Ausgrabung im Jahre 1988/89 auf dem Basler Spitalfriedhof St. Johann wurde das Skelett einer kleinwüchsigen Frau geborgen (Abb. 1). Aufgrund der einzigartigen historischen Überlieferung konnte die Verstorbene als Babette Saxer identifiziert werden, bei der erstmals in Basel 1865 ein dokumentierter Kaiserschnitt an einer Lebenden durchgeführt worden ist.

Die damals 25-jährige Barbara, genannt Babette, Saxer lebte zusammen mit ihren Eltern und Geschwistern in Kleinbasel. Aus den archivierten Verhörprotokollen des Ehegerichts geht hervor, dass sie eines Tages, als sie sich allein in der elterlichen Wohnung aufhielt, von einem Fremden vergewaltigt worden war, der sich unter einem Vorwand Zutritt zur Wohnung verschaffte. Babette wurde schwanger. Sie wurde ob ihrer unehelichen Schwangerschaft vom Ehegericht zu einer Mindeststrafe von einer Nacht Freiheitsentzug verurteilt, obwohl sie Opfer einer Gewalttat geworden war.

Am 4. Dezember 1865 trat Babette Saxer laut Krankenakte in die Gebärabteilung des Bürgerspitals ein, nachdem sie bereits sechs Stunden Wehen durchgestanden hatte. Nach drei weiteren Stunden Wehen und Blasensprung schritten die Chirurgen zum Kaiserschnitt, in welchen „*die etwas idiot.[ische] Pat.[ientin]*" einwilligte, „*wenn es nicht zu weh thun würde*". Zuvor vermassen die Ärzte das Becken der ungefähr 1,22 m kleinen Frau und notierten die Masse in ihrer Akte. Es war das erste Mal, dass diese risikoreiche Operation am Bürgerspital durchgeführt wurde. Erst in der ersten Hälfte des 20. Jh. wurde solch ein Eingriff bei komplizierten Geburten regelhaft in Erwägung gezogen. Am Folgetag des Kaiserschnitts starb die junge Mutter.

Abb. 1. Skelett der kleinwüchsigen Babette Saxer. Deutlich fällt des fehlende Becken auf (Grab STJ-0534, Foto: Archäologische Bodenforschung Basel-Stadt).

Das Becken der jungen Frau wurde bald nach ihrem Tod zu medizinischen Lehrzwecken entnommen. Neben ihrer Körpergrösse konnte das Skelett aufgrund des fehlenden Beckens und der durchgesägten Femora zweifelsfrei als Babette Saxer identifiziert werden.

Das Skelett wurde im Sommer 2017 von uns anthropologisch untersucht. Der Epiphysenverschluss der kleinwüchsigen Frau war noch nicht abgeschlossen. Zudem fielen Verknöcherungsdefekte an Kniegelenken und Mittelfussknochen auf. Als Ursachen für ihre Kleinwüchsigkeit kommen vor allem eine Hypophysen- insuffizienz, eine Hypothyreose, Hyposomatotropismus, Embryopathien oder Deprivationen in Frage, auch eine Trisomie 21 konnte nicht ausgeschlossen werden.

Darüber hinaus beschäftigten wir uns mit dem Geburtsvorgang. Wahrscheinlich kam dieser zum Stillstand, da aufgrund der Beckenenge der Mutter der Kindskopf den Beckenausgang nicht passieren konnte. Da das Kind für eine Extraktion mit der Zange zu hoch gelegen haben wird und man Mutter sowie Kind für gesund befand, entschied man sich erstmals, eine Sectio Caesarea an der Lebenden durchzuführen. Laut Krankenakte verstarb die Patientin nach einer ruhigen Nacht am Folgetag. Möglicherweise starb sie an inneren Blutungen in Folge der Operation. Das Mädchen erhielt den Namen Cäsarea Elisabeth, gründete später eine eigene Familie und gebar sechs Kinder.

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