

# Morphological Variation of the Baka Pygmies' Deciduous Second Molars

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## Research Article

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# Abstract

The Baka pygmies are known for their short stature resulting from a reduced growth rate during infancy. They are peculiar also for their teeth erupt earlier than in any other African population, and their posterior dentition is larger than in non-pygmies. However, the Baka's dental morphology, as several other aspects of their biology, is still understudied. In this study we explore the Baka's upper and lower second deciduous molars variation in comparison to a human sample including Africans, Asians, Europeans, and South Americans by means of 3D geometric morphometrics. We analyzed both the outer and inner aspect of the dental crowns, as well as their general size based on the natural logarithm of centroid sizes. Our results show largely overlapping morphologies between populations, especially for the lower molars. The distal region of the second molars is the most variable, with the Baka's lower second molars showing the most extreme range of variation for this aspect and in terms of crown height. Upper and lower second molars showed high morphological covariation ( $RV=0.82$ ). The Baka and South Americans' second molars were confirmed among the largest in our sample. Despite of the Baka's particular growth pattern, long-lasting isolation and extreme dental variation, it is not possible to distinguish them from other populations on the basis of their second molar morphology only.

# Introduction

The Baka people are a Central African population with an average male height under 155 cm, usually defined as pygmies<sup>1</sup>. Until recently, most African pygmies maintained semi-nomadic lifestyles based mainly on hunting and gathering<sup>1,2</sup>. Around 65-50.000 years ago the Baka diverged from the Bantu, their neighboring population, and until recently lived in almost complete isolation<sup>3</sup>. However, from the mid-20<sup>th</sup> century, the missionary and sedentarization programs influenced the lifestyle of the Baka populations<sup>4-9</sup> which moved closer to village sites inhabited by Bantu-speaking agriculturists. Some of the Baka started practicing horticulture in particular seasons of the year and trading products with their neighbors<sup>5,7,8</sup>. Nowadays, the Baka's hunting camps in the rain-forest last only for a few months per year during the major dry season<sup>5,8</sup>, but they remain an essential source of wild resources the Baka are highly depending on<sup>7</sup>.

Short average stature in pygmy populations depends on their particular growth patterns, but the actual underlying evolutionary mechanisms have been long debated<sup>3,10</sup>. Pygmies' small body size was mainly interpreted as an adaptation to environmental conditions, food shortage<sup>10-12</sup> and thermoregulation<sup>13</sup>. It is now established that the genetic basis of this specific phenotype is polygenic, including genes related to skeletal growth, allometric patterning, immunity and metabolism, with effects on the growth hormone axis, in particular the expression of the growth hormone-insulin-like growth factor I (GH – IGF1)<sup>14-16</sup>.

The life history variables (LHV) in the Baka pygmies seem to correspond with those of other non-pygmy populations, including puberty growth spurts and maturity reached at a very similar age<sup>3</sup>. Furthermore, their birth size and birth weight are within the standard limits of modern humans, differently from other

pygmy populations that are already born with smaller body size<sup>3,6</sup>. However, during the first two years of life, the Baka experience a significant deceleration of growth which causes a long-lasting growth delay throughout their whole development and results in a short adult stature (women's height average = 146.7 cm; men's height average = 153.5 cm)<sup>3</sup>. Although the tooth eruption timing is commonly strongly correlated with other LHV, in the Baka pygmies the permanent dentition erupts earlier than in any other African groups, including other pygmy populations (female UM1/LM1= 0.75y/0.71y earlier; male UM1/LM1= 0.63y/0.39y earlier)<sup>2</sup>. The Baka's permanent dentition has been studied with respect to other non-pygmy populations as well as in relation to their body size<sup>2,7,17-19</sup>. Their post-canine dentition was found to be larger than in their Bantu neighbors<sup>17</sup> as well as in other non-pygmy populations. Sexual dimorphism of the Baka's teeth has been identified where male molars are significantly larger than in females<sup>17</sup>. No consistent pattern of correlation was found between the Baka's teeth sizes and body height or weight<sup>18</sup>. Based on their results, Sardi and Ramirez-Rozzi<sup>20</sup> inferred that the genetic pathways regulating cranial growth and dental morphogenesis are most likely distinct. Several important aspects of the Baka's biology are still unknown, and the morphological variation of the Baka's teeth is yet unexplored. Given the peculiar set of phenotypical expression the Baka show, we want to contribute to the understanding of the Baka's variability by exploring their dental morphology. In particular, we perform here a morphological investigation of upper and lower deciduous second molars (dm2) of the Baka pygmies compared to a geographically diverse dm2 sample (Table 1) using 3D landmark- and semilandmarks-based methods and analysis of qualitative dental traits. Since the dm2 crown forms from the last prenatal trimester to about six month after birth, thus partly during the period of decreased growth rate in this population, a possible effect on the crown formation and its morphological variation cannot be excluded<sup>2</sup>. Working with  $\mu$ CT derived 3D surface models, we could safely capture the geometry of both inner and outer surfaces<sup>21</sup> of the crown, while the roots could not be investigated since they are completely resorbed in our sample. Similarly, the moderate degree of wear of the occlusal aspect of the crowns permitted the investigation of a limited number of discrete dental traits.

## Results

The general finding in all of our GM analyses for upper and lower dm2s was an overlapping distribution of all populations. The ldm2s of the Baka showed a wider range of variation in comparison to the udm2s that seemed to be less variable in terms of morphological variability. The opposite pattern was found for the European upper and lower dm2s. Depending on the analysis, 41 to 55% of the total variance can be explained by the first two principal components (PCs) as detailed in Table 2.

**Lower dm2 shape variation.** For the ldm2 dentinal crown (using landmarks resampling the EDJ marginal edge and the cervical outline; Figure 1a), shape variation along PC1 (explaining 32% of the total variance) concerned the relative bucco-lingual position of the hypoconulid corresponding with the relative bucco-lingual distal expansion of the crown, as well as the crown height. Variation along PC2 (16%) was driven by the mesio-distal elongation of the crown. Both along PC1 and PC2, the Baka exceeded the full range of shapes within this geographically diverse sample with particularly short and mesio-distally elongated

dentinal crowns, with relatively bucco-lingually narrow distal aspect. We observed 20% higher variance (see Supplementary Table 1 online) within the Baka sample (0.006) than within the European Idm2s (0.005). Supplementary Figure S1 shows the sample distribution along PC3. As expected, the analysis of the EDJ alone did not provide any additional information, therefore we find reporting on this analysis redundant.

The cervical outline (see Supplementary Fig. S2a online) varied mainly between round and hourglass-shaped. Shape variation along PC1 (30%) is associated with bucco-lingual constriction and mesio-distal elongation, which is characteristic of the Baka teeth. Along PC2 (26%), the cervical outlines varied from elongated and narrow, to short and broad.

Similar to the cervical outline, the crown outline (see Supplementary Fig. S2b online) varied from elongated and bucco-lingually constricted to rounded and bucco-lingually expanded along PC1 (32%) and from mesio-buccally expanded to bucco-distally expanded along PC2 (21%).

**Upper dm2 shape variation.** The results for the udm2s dentinal crowns (Figure 1b) showed again an overlapping distribution of Europeans and Southeast Asians with the Baka. Along PC1 (29%), udm2s dentinal varied between shorter with squared occlusal aspects, and taller with lingually displaced distal cusps (metacone and hypocone). Along PC2 (20%) variation was driven by the relative expansion of the trigon (consisting of the three main cusps and forming the central fovea) with respect to the talon (consisting of the disto-lingual cusp and fossa). In other words, the crowns possessed variably expanded central fovea with respect to the crown base. The Baka tend to have low, squared-shaped crowns, while Europeans are more variable and are characterized also by tall teeth with lingually shifted distal cusps, corresponding to a reduction of the metacone. There was a clear separation between the Baka and the Egyptians, Bedouins and South Americans (although these groups were represented by only two to four specimens). The analysis of variance (see Supplementary Table 1 online) revealed a 40% higher variance in the Europeans' udm2s (0.007) with respect to the Baka (0.005). Shape variation along PC3 are shown in Supplementary Figure S3 online. Similar to the analysis of the EDJ Idm2s, the EDJ analysis was not source of additional information with respect to the analysis of the dentinal crown.

For the cervical outline (see Supplementary Fig. S4a online), PC1 (34%) reflects the relative expansion of the disto-lingual and disto-buccal aspects with respect to each other, while PC2 (23%) represents the relative mesio-distal elongation of the cervical outline. The crown outlines (PC1, 37%) changed from oval to rounded along PC1 (37%; see Supplementary Fig. S4b online). This was associated with the relative mesio-buccal position of the paracone. Variation along PC2 (18%) consisted in the relative expansion of the talon with respect to the trigon.

**Covariation.** For the dentinal crown, the percentage of total squared covariance of udm2s and Idm2s for the Singular Warp (SW) scores 1 was 66% and the pairwise shape correlation between the antagonists was  $r_1 = 0.82$  (Table 3).

Udm2s and ldm2s clearly showed common trends of variation (Figure 2), being either short-crowned with reduced central and distal fossae, respectively, or taller with expanded opposing fossae. Moreover, lower crowns were associated with relatively higher horn tips than taller crowns. It was not possible to clearly separate the populations from each other based on the udm2 and ldm2 dyads, although the Baka tended to show extreme expression towards the low and elongated crown. Within the same tooth type the highest covariation coefficient was found between the ldm2s cervical and crown outlines ( $r_1 = 0.81$ ) (Table 3), while cervical and crown outlines in udm2s covaried the least ( $r_1 = 0.74$ ).

**Size.** The comparison of the Baka's natural logarithm of Centroid Size (lnCS) for the dentinal crown with respect to the rest of the sample, showed that the Baka's dm2s, following the South Americans, tend to be among the largest specimens within our sample. In a Mann-Whitney Test, we recognized that the cervical and crown outlines of the Baka's udm2s were significantly larger than the average of the rest of the sample (Table 4). With respect to the various populations (Table 4) (Figure 3a+b), Baka's dm2s differed significantly from Europeans (Table 4). South Americans and Baka showed the largest dm2 dentinal crowns within our sample, while Europeans and Egyptians feature the smallest. Similar results were obtained observing the crown outline. Interestingly, while the Baka possessed the largest cervical outline among the udm2s sample, in ldm2s the Egyptians showed the highest values. However, the findings for the groups with smallest sample size (i.e., Egyptians, South American and Southeast Asian individuals) require caution.

The multivariate regression of the dentinal crown on lnCS showed that only a low percentage of morphological variation in our sample can be explained by size (ldm2: ~3%; udm2: ~9%). In ldm2s, we observed size-related shape variation mainly connected to the expansion and reduction of the distal and occlusal aspects, and also in the height of the crown. Larger ldm2s showed low crowns with expanded distal aspects and rather elongated occlusal aspects. This underlines the fact that the largest teeth (the Baka) are short, narrow and elongated, while the smallest (Europeans) tend to be taller, mesio-distally shorter and distally broader. Shape changes in udm2s referred to the expansion and reduction of the metacone and the occlusal aspect, relative position of the hypocone and the height of the crown. Larger udm2s tended to show lower crowns with expanded metacone and buccally shifted hypocone, as in the Baka, resulting in a squared occlusal aspect.

**Non-metric traits.** The prevalence of hypocone and Carabelli cusp for the udm2s, and entoconulid and metaconulid for the ldm2s is presented in Table 5. The high degree of wear along with the resorption of the roots in the Baka specimens hampered further observations. The highest variability was scored for the hypocones in the udm2s than for any other trait. The prevalence of hypocone manifestation is 100%, most of it with high expression grade (4-6)<sup>22</sup>. The Baka showed a significantly higher frequency of a massive hypocone manifestation (96%) in comparison to the rest of the sample ( $\chi^2 = 11,7$ ;  $p = 0,001$ ). Most individuals of the sample, however, showed a medium grade of expression (3-4). In our sample, we found no or slight expression of the Carabelli cusp, of the entoconulid and of the metaconulid, with no significant differences between populations.

## Discussion

The Baka pygmies from south-eastern Cameroon, western Central African Republic and northern Congo<sup>3,5-8,17</sup> are characterized by their peculiar life history and growth pattern with respect to other pygmy and non-pygmy populations. They are also known for their rather large permanent molars and early eruption times of the permanent teeth. In terms of dental morphology, we found that deciduous second molars are indistinguishable from other non-pygmy populations. In fact, we observed a great overlap between populations in our lower deciduous second molars sample, which hampered the possibility to distinguish the diverse geographical groups based only on their tooth shape. Similar findings were made by Buchegger<sup>23</sup>, Teplanova<sup>24</sup>, Krenn et al.<sup>25</sup> and Halász<sup>26</sup> for permanent upper and lower premolars, and first and second molars.

Considering traditional dental diameters, most of the variation occurs within rather than between populations<sup>27,28</sup>. The high degree of shape variation observed in the Baka's lower deciduous molars is compatible with previous observations on Sub-Saharan populations, which have been proven highly variable in terms of both dental<sup>27</sup> and cranial dimensions<sup>29,30</sup>. Surprisingly, the extended shape distribution of the Baka's lower deciduous molars is not paralleled by the upper deciduous molar analysis. Interestingly, variation of the European deciduous second molars follows the opposite trend, with less variable lower molars and highly variable upper molars. This finding is consistent with our knowledge of the European upper deciduous second molars showing various degrees of hypocone and metacone reduction<sup>26</sup>.

Given the morphological resemblances of the deciduous second molars to permanent first molars<sup>31-35</sup>, we draw comparisons of our results with those from permanent first molars<sup>26,36,37</sup>. Distal and lingual aspects appear to be the most variable regions in both udm2s and ldm2s. This finding is in agreement with Halász's<sup>26</sup> research on M1s in various populations, and with Polychronis et al.<sup>37</sup>, who studied lower M1s in Greek populations. Likewise we found parallelisms between the deciduous molars' shape variations in this study and previously published results for first molars<sup>26,36</sup>. Yet, assigning an individual tooth to a certain population based on its shape alone remains impossible.

In terms of non-metric traits, our results for the hypocone contrasted the findings of Edgar and Lease<sup>31</sup> who observed a high percentage of reduced hypocone expression in deciduous molars in general. However, we compare our results showing expression of larger hypocones in the Baka than in Europeans to those in Lease<sup>38</sup> for African Americans and Europeans. Today it is known that the manifestation of the Carabelli cusp is equally common in all world populations<sup>39</sup>, which was confirmed by our findings for the deciduous upper second molars. However, the absence of the trait was the largest category in almost all of the populations, which is very similar to the results of Scott<sup>40</sup> but does not correspond to the outcomes of Halász<sup>26</sup> who observed the manifestation prevalence of 100% in African and Near Eastern M1s. According to Harris<sup>41</sup> the grade of expression of the Carabelli cusp in first molars and the tooth size are connected, with larger teeth showing this trait more often. We cannot support this result, since we did not

find any significant differences in Carabelli cusp manifestation between the populations in spite of the significant size differences. Likewise, the various populations used in our sample did not differ in terms of entoconulid and metaconulid frequency or expression.

Variation in dental size of the pygmies' permanent dentition in comparison to non-pygmy populations was assessed previously for various samples testing different hypotheses<sup>17-19,42</sup>. The general findings include the tendency of sub-Saharan African populations to show larger permanent teeth than Asians or Europeans<sup>28</sup>, which was confirmed by our results. According to Hanihara and Ishida<sup>28</sup>, the modern Australian aboriginals show the largest dental diameters, followed by a group of higher average-sized dentitions of sub-Saharan Africans, Native Americans and Southeast Asians. Europeans and populations of the Near East show the smallest tooth size. We observed the smallest dm2s sizes in Europeans and Bedouins, followed by Egyptians, Southeast Asians and sub-Saharan Baka pygmies. South Americans showed the largest tooth size. Our results matched these findings using a different measure of size, namely the lnCS, which depends also on the landmark configuration<sup>25</sup>. The dental size of the Baka and other pygmies was studied also in relation to their body size and developmental patterns<sup>18,19</sup>. Their permanent molars were considered larger than in any other non-pygmy population<sup>19</sup>, including the Bantu<sup>17</sup>. We can confirm that the Baka's deciduous second molars are larger than in most of the non-pygmy populations we have studied. Early dental eruption timing has not only been found in the Baka's dm2s<sup>2</sup> but also in other sub-Saharan populations' permanent<sup>43-46</sup> and deciduous teeth<sup>47</sup>. According to Lam et al. (2015)<sup>48</sup> the earlier onset of tooth eruption can be associated with postnatal factors such as increased rate of weight gain during the first three months of life. It is worth noting that, contrary to the Sua pygmies, the Baka's weight gain during the first years of infancy does not differ from that of the Bantu<sup>2</sup>. However, considering that the crown formation in deciduous second molars partially overlap with the time of growth decrease in the Baka, and the dm2s size is not affected, we can assume no or only very low correlation between dm2s and body growth of the Baka. Romero et al.<sup>17</sup> and Ramirez-Rozzi<sup>18</sup> underline this finding stating that short stature is likely an adaptation not related to dental shape and size variation, and is genetically inherited by the Baka's ancestors<sup>49</sup>. Furthermore, no clear genetic pathway affecting both the teeth and the somatic growth that could explain the phenomena we observed in the Baka has yet been found<sup>18</sup>. Earlier tooth eruption has been associated with lower degree of root growth<sup>50</sup>, although root development and morphology in the Baka have not been studied yet, therefore the mechanisms prompting early eruption of their teeth remain unknown.

Our sample comprising udm2s and ldm2s from the same individual is rather small and calls for cautious interpretation of the results. However, there seems to be a clear trend that points to an increased shape variation in the distal, bucco-distal and disto-lingual aspects of the crown. Moreover, we found mainly two general patterns for udm2s and ldm2s: tall and narrow-crowned with expanding central and distal fossae, and short and wide-crowned with reduced opposing fossae and relatively higher horn tips. This pattern of covariation was also observed in upper and lower M1s<sup>26</sup>. High pairwise correlation between opposing teeth developing in different jaws can be interpreted as a strong hint to a tight genetic control over the

dental development, and is explained by the fact that antagonists have to fit optimally to facilitate an effective mastication. These constraints are likely similar for any tooth type, as similar results were achieved for dyads of other dental types<sup>25,26</sup>.

Despite the Baka's long-lasting geographical isolation<sup>2,49</sup>, very low levels of genetic admixture with non-pygmy neighboring populations<sup>49,51</sup>, specific growth pattern and dental eruption timing, we did not find a morphological difference distinguishing the Baka from other world populations based only on their dental morphology. Yet, the Baka's Idm2s can be particularly narrow and elongated with respect to the rest of the sample analyzed, and udm2s also clearly exceed the range of low and squared-crown variation in the sample, despite the fact that they are less variable than the Idm2s. Outstandingly, differential patterns of variation of udm2s and Idm2s in Central Europeans and the Baka might reflect their different population history reaching back to the migration of the European ancestors out of Africa<sup>16</sup>.

## Methods

### Sample

Our sample consists of 60 upper and 59 lower modern humans deciduous second molars (Table 1). Of these, 55 teeth, including 23 udm2s and 32 Idm2s, are from 39 Baka individuals. The Baka deciduous second molars were collected by Ramirez-Rozzi after the Baka children naturally shed and donated them with the consent of their families. The rest of our sample was composed of individuals from different geographical regions. The comparative sample includes 22 upper and 11 lower teeth from Europe, six upper and seven lower teeth from Africa, five upper and three lower from Asia, two upper and four lower from the Near East, and two upper and two lower from South America, which is quite a large sample considering the paucity of infant and juvenile specimens in osteological collections. More so, the meta-data for the comparative sample is often incomplete since the individuals come from archaeological collections (Table 1). Another limitation of the sample size are the stage of wear and state of preservation. To successfully obtain a complete EDJ surface the wear cannot exceed stage 4<sup>52</sup>. Dental specimens showing a moderate abrasion of the horn tips (stages 3 and 4) were virtually reconstructed (see  $\mu$ CT acquisition and data segmentation below) before data collection. Specimens with wear stage greater than 4 or with decay in the occlusal area were either excluded from the sample or used only for the analyses of the crown and cervical outlines. The heavy wear, the poor state of preservation and occasional dental treatment made a large number of the Baka dental collection unusable for our study. The teeth were naturally shed and thus they were used approximately until the age of 11 which explain the advanced degree of wear. In some cases, the molars were kept by the Baka children or their families until the next visit of Ramirez-Rozzi, which likely led to the poor state of preservation of the teeth at the moment of image data acquisition (i.e. for the presence of numerous and deep cracks). Additionally, the Baka's traditional dental treatments are quite invasive, and entail the drilling of large cavities later filled with natural substrates<sup>9</sup>.

### $\mu$ CT acquisition and data segmentation

The dental datasets were imaged at three different facilities. The Baka teeth were scanned mainly at the Plateforme Imageries du vivant, Université de Paris, using a Micro CT-scanner PerkinElmer, Quantum FX (voxel size 20 - 40/30 - 59/10 - 20  $\mu\text{m}$ , 90 kV, 16 mA) and at the Hard Tissue Research Unit, College of Dentistry (NYU), with a SCANCO Scantron 40 Micro-CT scanner (voxel size 12  $\mu\text{m}$ , 70 kV, 275 mA, 200 ms). The comparative sample was scanned at the Vienna Micro-CT Lab, Austria, with a VISCOM X8060 NDT scanner (voxel size 21 – 60  $\mu\text{m}$ , 110 – 140 kV, 280 – 410 mA, 1400 – 2000 ms, 0.75 mm copper filter). X-ray images were taken from 1440 different angles. Using filtered back-projection in VISCOM XVR-CT 1.07 software, these data were reconstructed as 3D volumes with a color depth of 16,384 grey values.

The  $\mu\text{CT}$  data were then imported into Amira 2020 ([www.fei.com](http://www.fei.com)) and virtually segmented to separate the enamel from the dentine, pulp and from the surrounding material (i.e., air, alveolar bone). In case of a slight abrasion of the dentinal horn tips, the specimens were virtually reconstructed by using the “brush” tool and extending the contours of the dentine into the empty area.

In case both left and right dm2s of one individual were available, we preferred the left ones among our whole sample. However, if better preserved, we used the right tooth after virtual mirroring to the left side. Since there is no scientific evidence indicating the existence of directional asymmetry in human dentition, we assume that the choice of left teeth should not affect the results of this study<sup>53–55</sup>.

### **Reorientation and outline collection**

After segmentation, the surface models of the crowns were reoriented in Geomagic Design X 64 ([www.3dsystems.com](http://www.3dsystems.com)) following an established protocol<sup>56–58</sup>. The crown and cervical outlines were collected from the reoriented surface models and projected onto the cervical plane. Afterwards, the outlines were further processed using Rhinoceros 6 ([www.rhino3d.com](http://www.rhino3d.com)) and were split into 24 segments by 24 equiangular radial vectors originating from the centroid of the outline area. At the intersections of the outline and the radii, twenty-four pseudo-landmarks were placed.

### **Landmark collection on the EDJ**

To collection of the landmarks from the enamel-dentine junction (EDJ), followed established protocols<sup>56–58</sup>. For the ldm2s, we placed eight landmarks (LM) on the five main horn tips and three at the deepest points between Metaconid and Entoconid, Protoconid and Hypoconid, and between Hypoconid and Hypoconulid. Afterwards, 23 curve semilandmarks (sLM) were placed to represent the EDJ marginal edge. To ensure homology, we traced the EDJ occlusal edge by creating a spline curve, ignoring all the accessory cusps. For the udm2s, seven LMs were placed on the four horn tips, and on the deepest points of the central fovea and distal fossa, and the deepest point of the disto-lingual marginal ridge. The EDJ marginal edge was resampled by 47 sLMs. The LM collection was carried out in the EVAN Toolbox 1.75 ([www.evan-society.org](http://www.evan-society.org)), which uses the bending energy technique for the sliding of sLM<sup>59–61</sup>.

### **GM analysis**

The geometric morphometric analyses were performed separately for each set of landmarks, resulting in four different analyses per tooth type, namely: 1) cervical outlines; 2) crown outlines; 3) EDJ and 4) the combined dataset of EDJ and cervical outline. First, landmark configurations had to be normalized via General Procrustes Analysis (GPA)<sup>62,59,63</sup>. The translation and rotation of the landmark sets were not necessary for the outline configurations. We run the Principal component analysis (PCA) on the Procrustes shape coordinates and visualized the shape changes along the principal components by means of warpings, using the Thin-Plate Spline technique<sup>64,65</sup>. The analyses of the size were carried out using the natural logarithm of Centroid Size (lnCS). In the case of the combined EDJ and cervical outline, this is a measure of the 3D dentinal crown, including crown height, and therefore more representative than linear measurements. Furthermore, we performed a multivariate regression to analyze the influence of size on the shape of the dentinal crown. We explored shape covariation between udm2s and ldm2s as well as between different features of the same dental types by means of the 2-block partial least squares analysis (2B-PLS). Further statistical analyses, were carried out using R Studio ([www.r-project.org](http://www.r-project.org)), PAST 4.03 ([www.softpedia.com](http://www.softpedia.com)) and SPSS ([www.ibm.com](http://www.ibm.com)). We performed the analysis of variance on Procrustes shape coordinates of larger subsamples, i.e. the Baka and the Europeans, to assess their degree of variation in the morphological expression of udm2s and ldm2s. Mann-Whitney test was used to test significance in size differences between the Baka and the Europeans, and between the Baka and the rest of the sample. To assess the size differences on populational level across the whole sample, Kruskal-Wallis test was used. Prevalence of various non-metric traits in our sample was analyzed by  $\chi^2$  test.

### **Non-metric traits**

Non-metric traits were evaluated based on the Arizona State University Dental Anthropology System (ASUDAS)<sup>22,66</sup>. This system was originally developed to identify traits on the outer enamel surface, but many of the non-metric traits are visible on the EDJ as well. However, because of the high degree of wear of the Baka sample and root resorption, we focused on four among the most informative dental traits reflecting human neutral genetic variation<sup>21,67</sup>:

#### **1. Hypocone**

The fourth cusp of the upper molars that forms a separate region of the occlusal aspect, the trigon. Its manifestation varies from grade 0 to 6<sup>22</sup>. In this study we used dichotomous classes to represent the hypocone degree of expression: none/light (0-3) and moderate/heavy (4-6).

#### **2. Carabelli cusp**

The Carabelli cusp is an accessory cusp occurring on the protocone (mesio-lingual cusp) of the upper molars. This trait has been used as a diagnostic trait for European populations<sup>40</sup>, however according to more recent studies, there is no manifestation difference between populations<sup>22</sup>. According to ASUDAS, the Carabelli cusp's expression varies between grades 0 to 7, but for this study we used two categories: none/light (0-4) and moderate/heavy (5-7).

### 3. Entoconulid

The entoconulid, or cusp 6, can be found in the distal area of the occlusal aspect of lower molars between the hypoconulid and the entoconid. The manifestation of the entoconulid can be expressed between grades from 0 to 5 that are divided in our study into none/light (0-2) and heavy (3-5).

### 4. Metaconulid

The metaconulid, or cusp 7, can be found on the lingual aspect of the lower molars between the entoconid and metaconid. Its manifestation can be expressed with 6 grades of 0, 1, 1A, 2, 3 and 4. We dichotomized the scoring values to none/light (0 to 1A) and moderate/heavy (2 to 4).

## Declarations

Availability of materials and data:

All data generated or analyzed during this study are either included in this published article (and its Supplementary Information file) or available from the corresponding author on reasonable request.

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Author contributions:

C.F. and F.R.-R. initiated the project. C.F. designed the project and supervised it with G.W.W. P.G.Š. and C.F. performed the image data processing. P.G.Š. collected landmark data. P.G.Š. carried out the analyses supported by C.F. and G.W.W. P.G.Š. wrote the paper with contribution of C.F., G.W.W. and F.R.-R. P.G.Š. compiled figures and tables. L.S., J.S. acquired the  $\mu$ CT scans.

Ethics statement: We did not use any physical or destructive method in our study, and our sample includes only dental data obtained either from archaeological collections or from the Baka individuals with informed consent of their parents (as mentioned in the methods section). The Baka teeth were collected after they were naturally shed, and thus not extracted (Methods).

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## Tables

**Table 1 List of materials.** (U = udm2; L = ldm2; f =female; m =male; + = tip reconstruction/included; - = no tip reconstruction/excluded)

<i>Population</i>	<i>Nr.</i>	<i>Jaw</i>	<i>Sex</i>	<i>Wear (U/L)<sup>52</sup></i>	<i>EDJ reconstruction</i>	<i>Dental outline analyses</i>	<i>EDJ analysis</i>
<i>Baka</i>	baka_01 <sup>a</sup>	L	f	3	+	+	+
	baka_02 <sup>a</sup>	U+L	f	3/3	+/+	+/+	+/+
	baka_03 <sup>a</sup>	U	f	3-4	+	+	+
	baka_04 <sup>a</sup>	U+L	f	3/3-4	+/+	+/+	+/+
	baka_05 <sup>a</sup>	U	m	3	+	+	+
	baka_06 <sup>a</sup>	U+L	f	3-4/3	+/+	+/+	+/+
	baka_08 <sup>a</sup>	U+L	f	3/3	+/+	+/+	+/+
	baka_09 <sup>a</sup>	L	f	3	+	+	+
	baka_10 <sup>a</sup>	U+L	f	3/3	+/+	+/+	+/+
	baka_11 <sup>a</sup>	U	m	3	+	+	+
	baka_12 <sup>a</sup>	U	f	3	+	+	+
	baka_13 <sup>a</sup>	U+L	f	3/3	+/+	+/+	+/+
	baka_14 <sup>a</sup>	L	f	3	+	+	+
	baka_16 <sup>a</sup>	U	m	3-4	+	+	+
	baka_17 <sup>a</sup>	U+L	m	3-4/3-4	+/+	+/+	+/+
	baka_18 <sup>a</sup>	U+L	m	3 /4-5	+/-	+/+	+/-
	baka_19 <sup>a</sup>	L	f	3	+	+	+
	baka_20 <sup>a</sup>	U+L	f	3-4/3-4	+/+	+/+	+/+
	baka_22 <sup>a</sup>	L	f	3	+	+	+
	baka_23 <sup>a</sup>	U+L	m	3/3	+/+	+/+	+/+
	baka_24 <sup>a</sup>	L	f	3-4	+	+	+
	baka_25 <sup>a</sup>	U+L	m	3/3	+/+	+/+	+/+

	baka_28 <sup>a</sup>	U	m	3	+	+	+
	baka_29 <sup>a</sup>	L	f	3	+	+	+
	baka_30 <sup>a</sup>	L	m	3	+	+	+
	baka_31 <sup>a</sup>	L	f	3-4	+	+	+
	baka_32 <sup>a</sup>	L	f	3	+	+	+
	baka_33 <sup>a</sup>	L	f	3	+	+	+
	baka_34 <sup>a</sup>	U+L	m	3/3-4	+/+	+/+	+/+
	baka_35 <sup>a</sup>	U+L	m	5/3	-/+	+/+	-/+
	baka_36 <sup>a</sup>	L	m	3	+	+	+
	baka_37 <sup>a</sup>	L	m	3	+	+	+
	baka_38 <sup>a</sup>	U+L	m	3/3	+/+	+/+	+/+
	baka_39 <sup>a</sup>	U+L	m	3/3	+/+	+/+	+/+
	baka_40 <sup>a</sup>	U+L	m	3/2	+/-	+/+	+/-
	baka_41 <sup>a</sup>	L	f	3	+	+	+
	baka_43 <sup>a</sup>	U	m	2	+	+	+
	baka_44 <sup>a</sup>	L	m	5	-	+	-
	baka_45 <sup>a</sup>	L	m	5	-	+	-
<b>Europeans</b>	RHS_44 <sup>b</sup>	L	?	1	-	+	-
	RHS_52 <sup>b</sup>	L	?	1	-	+	-
	RHS_57 <sup>b</sup>	L	?	1	-	+	-
	RHS_75 <sup>b</sup>	L	?	1	-	+	-
	RHS_93 <sup>b</sup>	L	?	1	-	+	-
	RHS_96 <sup>b</sup>	L	?	1	-	+	-
	RHS_105 <sup>b</sup>	L	?	1	-	+	-
	RHS_113 <sup>b</sup>	L	?	1	-	+	-

RHS_115 <sup>b</sup>	L	?	1	-	+	-
RHS_116 <sup>b</sup>	L	?	1	-	+	-
RHS_319 <sup>b</sup>	U	?	1	-	+	-
RHS_322 <sup>b</sup>	U	?	1	-	+	-
RHS_429 <sup>b</sup>	L	?	1	-	+	-
RHS_513 <sup>b</sup>	U	?	1	-	+	-
RHS_549 <sup>b</sup>	U	?	1	-	+	-
RHS_Nr75 <sup>b</sup>	U	?	1	-	+	-
RHS_Nr115 <sup>b</sup>	U	?	1	-	+	-
RHS_Nr116 <sup>b</sup>	U	?	1	-	+	-
RHS_Nr396 <sup>b</sup>	U	?	1	-	+	-
RHS_Cs13 <sup>c</sup>	U	?	2	-	+	-
RHS_Cs305 <sup>c</sup>	U	?	2	-	+	-
RHS_Cs444 <sup>c</sup>	U	?	1	-	+	-
RHS_EH-U21 <sup>d</sup>	U	?	1	-	+	-
RHS_EH-U56 <sup>d</sup>	U	?	1	-	+	-
RHS_EH-U57 <sup>d</sup>	U	?	1	-	+	-
RHS_CA_T19 <sup>e</sup>	U	?	1	-	+	-
RHS_Med1_Batch1 <sup>e</sup>	U	?	1	-	+	-
RHS_Guid_T49 <sup>e</sup>	U	?	1	-	+	-
RHS_PM <sup>e</sup>	U	?	1	-	+	-
RHS_Tb36 <sup>e</sup>	U	?	1	-	+	-
RHS_Tb37 <sup>e</sup>	U	?	1	-	+	-
RHS_Tb44R <sup>e</sup>	U	?	1	-	+	-
RHS_Tb49 <sup>e</sup>	U	?	1	-	+	-
<b>Bedouins</b>	L	?	3	+	+	+

	BLZ_004 <sup>f</sup>						
	BLZ_273 <sup>f</sup>	L	?	3	+	+	+
	BLZ_279 <sup>f</sup>	L	?	1	-	+	-
	BLZ_294 <sup>f</sup>	L	?	1	-	+	-
	BLZ_441 <sup>f</sup>	U	?	1	-	+	-
	RHS_RCEH036 <sup>f</sup>	U	?	2	-	+	-
<b>South Americans</b>	A5380 <sup>g</sup>	U+L	?	3/2	+/-	+/+	+/-
	A5381 <sup>g</sup>	U+L	?	3/3	+/+	+/+	+/+
<b>Egyptians</b>	A113 <sup>g</sup>	U	?	3-4	-	+	-
	C120 <sup>g</sup>	U+L	?	3/3	+/+	+/+	+/+
	C392 <sup>g</sup>	U+L	m	4/2-3	+/+	+/+	+/+
	CN101 <sup>g</sup>	L	?	2	-	+	-
	CN141 <sup>g</sup>	L	?	3	+	+	+
	CN17 <sup>g</sup>	U	?	3	+	+	+
	CN233 <sup>g</sup>	L	?	2	-	+	-
	CN26 <sup>g</sup>	U+L	?	3/3	+/+	+/+	+/+
	CN61 <sup>g</sup>	U+L	?	3/3	+/+	+/+	+/+
<b>Southeast Asians</b>	SI3256 <sup>g</sup>	U	?	1	-	+	-
	FI3528 <sup>g</sup>	U+L	?	2/3	-/+	+/+	-/+
	I9664 <sup>g</sup>	U+L	?	1/1	-/-	+/+	-/-
	I9665 <sup>g</sup>	U	?	4	-	+	-
	NZ_3108 <sup>g</sup>	L	?	3	+	+	+
	NZ_3125-11 <sup>g</sup>	U	?	3	-	+	-

<sup>a</sup>University of Paris; <sup>b</sup>Austrian Children Collection; <sup>c</sup>University of Vienna; <sup>d</sup>University of Bordeaux; <sup>e</sup>University of Bologna; <sup>f</sup>Tel Aviv University; <sup>g</sup>Natural History Museum, Vienna

**Table 2 Percentage of variance explained by PC scores.** Analyses of the udm2s and ldm2s cervical outlines, crown outlines, combined EDJ and cervical outline (COMB).

PC	ldm2			udm2		
	COMB	Cervical outline	Crown outline	COMB	Cervical outline	Crown outline
PC1	32	30	32	29	34	37
PC2	16	26	21	20	23	18
PC3	10	15	12	9	12	12

**Table 3 Single warp score 1 results for pairwise correlation and percentage of total covariance in ldm2s and udm2s.** (COMB = combined EDJ and cervical outline)

Pairwise correlation		% of total covariance	
	udm2 COMB		udm2 COMB
ldm2 COMB	0.82	ldm2 COMB	66
	udm2 Cervical outline		udm2 Cervical outline
udm2 Crown outline	0.74	udm2 Crown outline	61
	ldm2 Cervical outline		ldm2 Cervical outline
ldm2 Crown outline	0.81	ldm2 Crown outline	51

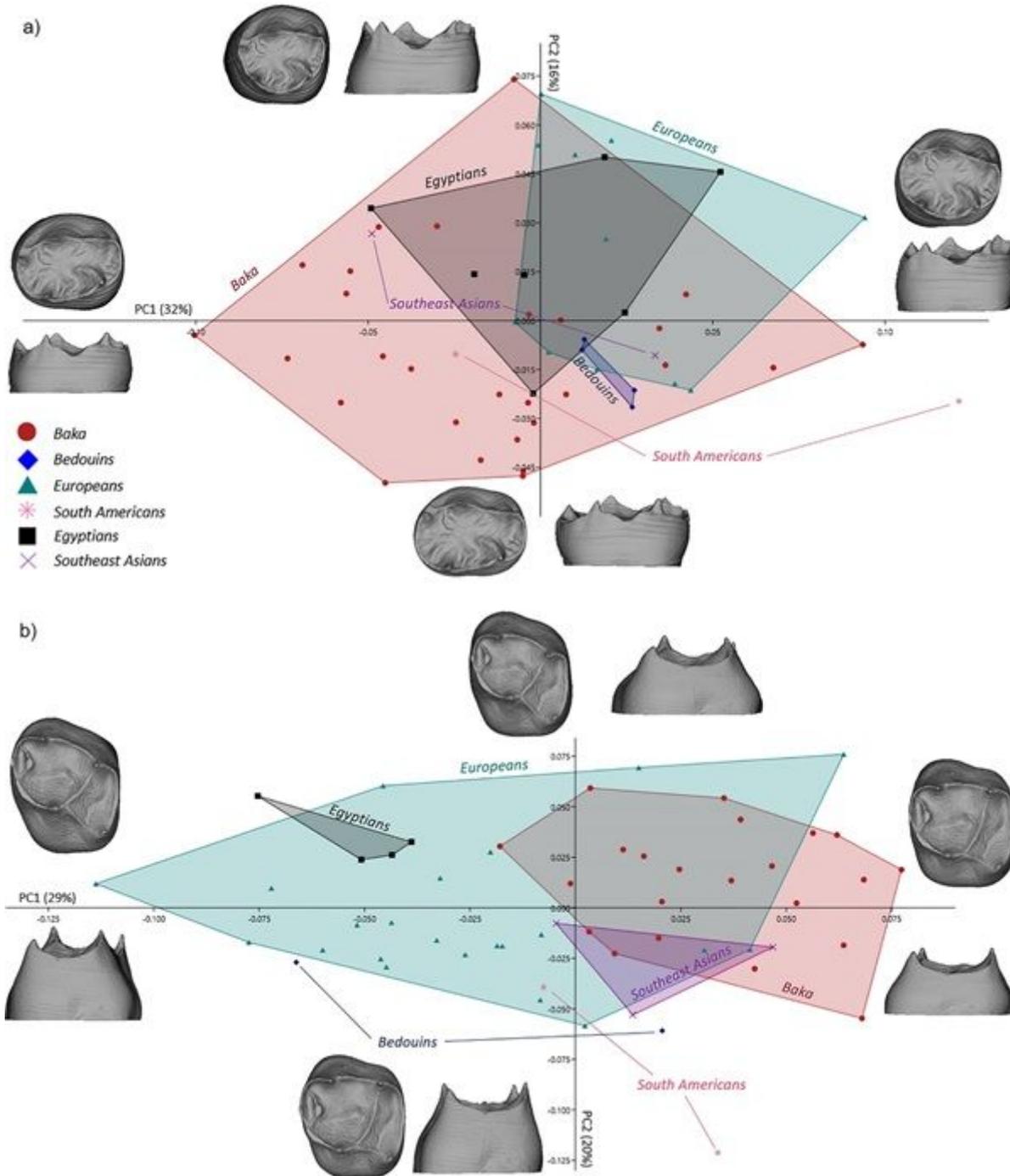
**Table 4 Mann-Whitney-U-test and Kruskal-Wallis-test.** Differences in dental sizes between the Baka and the comparative sample (B = Baka; W = world; N = number of individuals); Size differences between the Baka and the Europeans (B = Baka; E = Europeans; N = number of individuals); Differences in dental sizes on populational level.

	ldm2			udm2		
	Cervical outline	Crown outline	COMB	Cervical outline	Crown outline	COMB
<b>N (B/W)</b>	32/28	32/27	28/26	23/37	23/37	22/33
<b>Z</b>	1.044	1.072	1.462	3.740	2.934	1.898
<b>p-value</b>	0.296	0.283	0.143	<b>0.0002</b>	<b>0.003</b>	0.057
<b>N (B/E)</b>	32/12	32/11	28/11	23/22	23/22	22/22
<b>Z</b>	2.095	2.157	2.325	3.485	3.235	2.325
<b>p-value</b>	<b>0.036</b>	<b>0.030</b>	<b>0.020</b>	<b>0.0005</b>	<b>0.0012</b>	<b>0.020</b>
<b>Kruskal-Wallis-test</b>	10.1	6.783	7.834	18.45	16.58	10.97
<b>p-value</b>	0.074	0.237	0.1656	<b>0.002</b>	<b>0.005</b>	0.052

**Table 5 The list of analyzed non-metric traits, their expression grades and prevalence across the sample.**

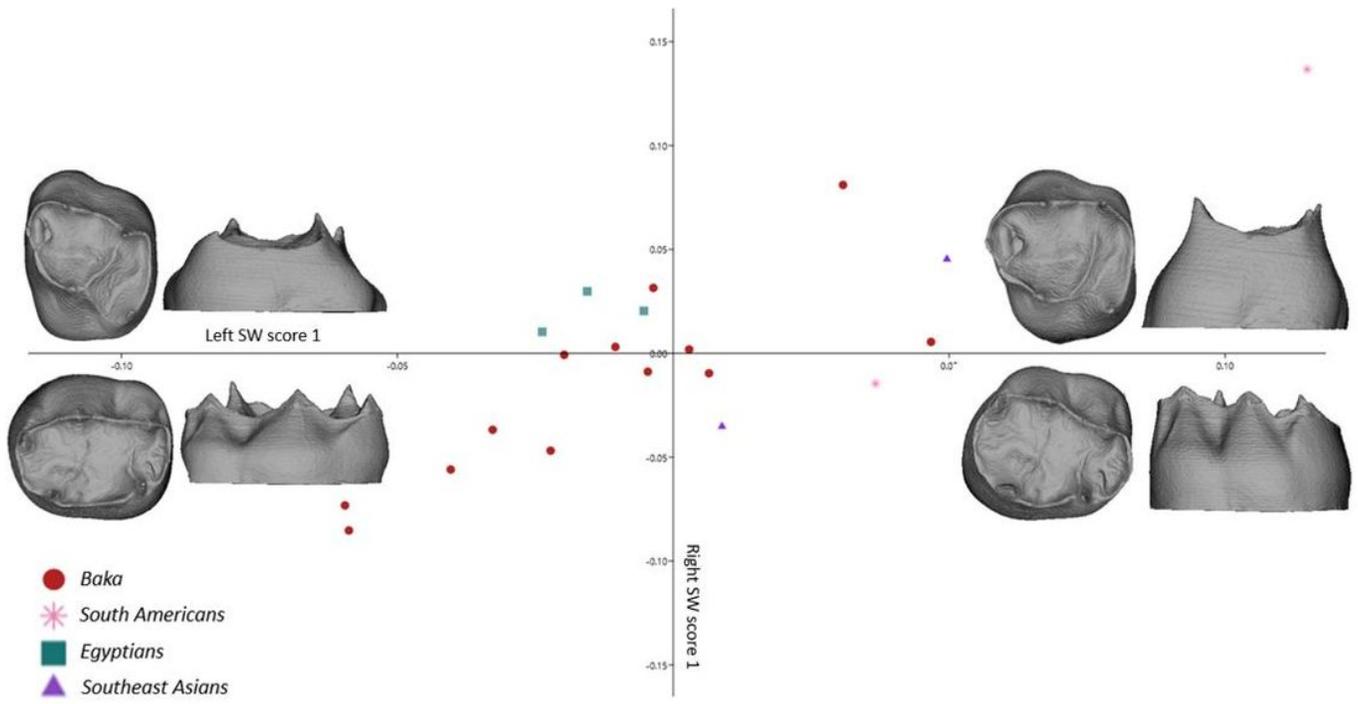
udm2	Hypocone		Carabelli cusp		ldm2	Entoconulid		Metaconulid	
	0-3	4-6	0-3	4-7		0-2	3-5	0,1,1A	2-4
Baka (n=23)	4%	96%	83%	17%	Baka (n=32)	88%	12%	75%	25%
Europe (n=22)	50%	50%	95%	5%	Europe (n=11)	100%	-	82%	18%
Southeast Asia (n=5)	40%	60%	100%	-	Southeast Asia (n=3)	100%	-	67%	33%
Egypt (n=6)	33%	67%	83%	17%	Egypt (n=7)	100%	-	72%	28%
South America (n=2)	100%	-	100%	-	South America (n=2)	100%	-	50%	50%
Bedouins (n=2)		100%	100%		Bedouins (n=4)	75%	25%	75%	25%
<b>Prevalence</b>	100%		60%			34%		54%	

# Figures



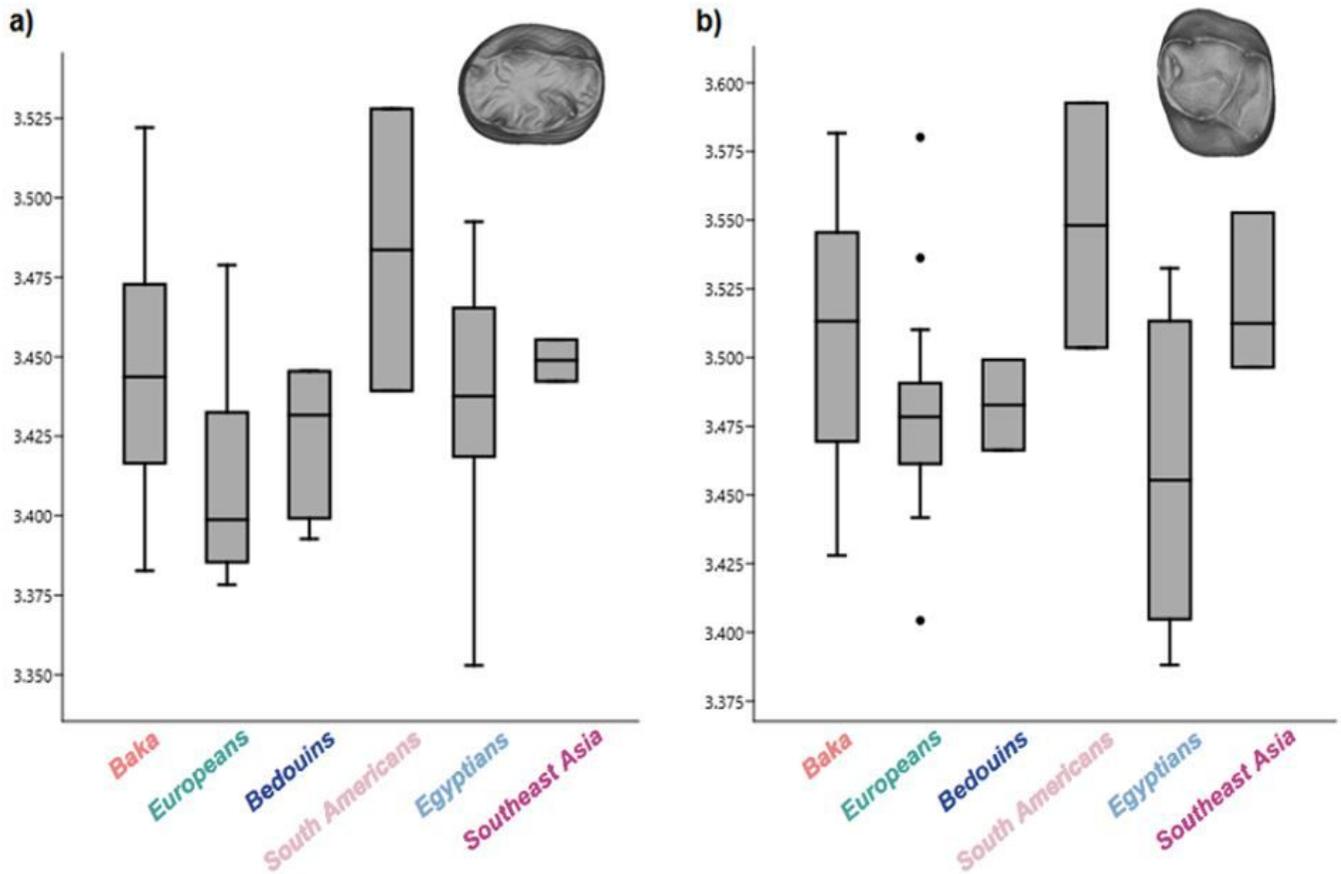
**Figure 1**

PCA plots for lower and upper deciduous second molars a) PC1 - PC2 plot for Idm2s in shape space for the combined EDJ and cervical outline (warpings at values  $\pm 0.15/\pm 0.07$ ). The Baka show an extreme range of morphological variation; b) PC1 - PC2 plot for udm2s in shape space for the combined EDJ and cervical outline (warping at value  $\pm 0.15$ ) The Baka show a less variable morphology, while the Europeans exceed the range of variation.



**Figure 2**

2B-PLS plot capturing the covariation between combined EDJ and cervical outlines of molar pairs (warpings at values  $\pm 0.15$ )



**Figure 3**

Boxplots of the natural logarithm of Centroid Sizes from the dentinal crown (combining EDJ and cervical outline) in a) Idm2s and b) udm2s. South Americans and the Baka possess the largest dm2s.

## Supplementary Files

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