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Variation of outer and inner crown morphology in upper premolars

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Abstract

Tooth morphology is often used for taxonomic classification purposes in Anthropology. However, some dental features can be obscured by wear while others might not be accessible on the real specimen. Virtual Anthropology approaches use non-destructive imaging techniques which allow to capture additional features, such as the enamel-dentine junction (EDJ). Based on Geometric Morphometric (GM) the shape and size of the EDJ can be analysed in a comprehensive way by means of landmarks and semilandmarks. In this study, we contribute to the understanding of the morphological variation of upper third and fourth premolars in diverse modern human populations using these techniques. Our hypothesis is that due to the absence of selective pressures, random shape variation should be the predominant pattern. Thus, all populations of *H. sapiens* should overlap in terms of their tooth morphology in upper premolars. However there could be some tooth regions showing higher variability than others.

Our sample covers seven modern human populations (n = 44): Khoesan, other Sub-Saharan African indigenous, middle Europeans, Indonesian indigenous, Papua New Guinean indigenous, Australian Aboriginals, and Avars, which lived in Europe from the 6th until the 9th century. As an out-group we used a sample of *Pongo pygmaeus* (n = 4).

All individuals were scanned at the Vienna μCT-Lab. The image data were segmented in order to produce 3D surface models of the crown and EDJ. Six non-metrical features were analysed on the OES and EDJ. Additionally four landmark configurations were collected on the EDJ. We identified landmarks at the buccal and lingual horn tips and at the mesial and distal fossae along with 20 curve semilandmarks on the marginal ridge. Furthermore 24 pseudolandmarks were gathered from the crown and cervical outlines. A new procedure of combining data from the EDJ with those of the cervical

outline was tested. All landmark configurations were normalized through General Procrustes Analysis and then a Principal Component Analysis was performed for each of the landmark configurations considered separately.
Our results show that the manifestations of two non-metric features (transverse crest and accessory ridge) are formed during tooth development on the *membrana praeformativa* and are then transferred onto the OES by the deposition of enamel. On the contrary, accessory marginal tubercles are not strongly connected to the EDJ. The analysed non-metrical traits showed some regional differences in their distribution. Therefore it is important to take great care which human populations are selected for comparative studies with archaic hominids.
The GM analyses revealed that both outline analyses have difficulties separating *Homo* from *Pongo* based on shape space. While both genera partially overlap for P^3s, they cannot be separated at all in P^4s. Conversely, both the EDJ and combined EDJ-cervical outline data set allowed to separate humans from orang-utans without problems. If size is included humans and orang-utans separate clearly in all four data sets.
Nevertheless, none of the four landmark configurations did show any differences between modern human populations. Therefore it is of minor importance which population is used in comparative studies with archaic hominids.
The main variation found in both upper premolars is the length-to-breath-ratio, which affects the whole morphology of the tooth. The general pattern is either a more ellipsoid or a more circular tooth. The ellipsoid form shows a high crown on the EDJ with relatively low horn tips, which are located far from each other. Circular teeth possess a low crown body, the horn tips, against it, are high, and they are closer together. There is a strong correlation between third and fourth premolars´ shape. Either both are ellipsoid or both are circular. Size has a very low impact on shape, however, taller teeth tend to have an ellipsoid shape while smaller ones tend towards a circular shape. In terms of size, middle European and Khoesan upper premolars are significantly smaller than those of Australian and Asian populations.
Our new approach of combining the EDJ and the cervical outline presents the advantage of considering the dentine crown surface as a whole from the cervical outline up to the horn tips. It shows all the features of both landmark configurations at the same time, how they vary with each other, and furthermore incorporates the crown height as well.

Zusammenfassung

Die Morphologie der Bezahnung wird oft verwendet um einzelne Individuen einer Population oder einem Taxon zuzuordnen. Jedoch können wichtige Merkmale der Zähne durch Abkauung verloren gehen oder gar nicht an der Zahnoberfläche (OES) präsent sein. Mithilfe von virtuellen Darstellungsmethoden ist es möglich, in das Innere von anatomischen Strukturen vorzudringen und so z.B. an der Grenze zwischen Dentin und Zahnschmelz (EDJ) morphologische Untersuchungen mit Hilfe von homologen Messpunkten durchzuführen. Diese Masterarbeit leistet einen Beitrag zum Verständnis der morphologischen Variation der oberen Prämolaren in rezenten *H. sapiens* mithilfe von Geometric Morphometrics (GM). Unsere Hypothese besagt, dass aufgrund des Fehlens eines selektiven Druckes zufällige Variation vorherrschend ist und daher keine Population sich in der Morphologie der oberen Prämolaren von den anderen unterscheidet. Allerdings kann es Zahnregionen geben, welche stärker variieren als andere.
Unsere Stichprobe besteht aus sieben Populationen (n = 44): Khoesan, andere Sub-Saharische afrikanische Ureinwohner, Mitteleuropäer, Indonesier, Ureinwohner aus Papua-Neuguinea, Aborigines und Awaren aus dem 6 bis 9. Jh. Als Vergleichsgruppe verwendeten wir *Pongo pygmaeus* (n = 4).
Alle Individuen wurden im Vienna μCT Lab der Universität Wien gescannt. Die Bilddaten wurden segmentiert um 3D Oberflächen der OES und EDJ zu erhalten. Auf diesen wurde die Präsenz von sechs nicht-metrischen Merkmalen dokumentiert. Zusätzlich wurden für jeden Zahn vier verschiedene Sets von Messpunkten gesammelt, welche die Morphologie widerspiegeln. Bestimmt wurden je 24 Punkte entlang des größten Umfanges der Zahnkrone und entlang des Zahnhalses. Weiters wurde die Form der EDJ erfasst indem am buccalen und lingualen Zahnhöcker und an den beiden tiefsten Stellen der mesio-distalen Vertiefung ein Messpunkt gesetzt wurde. Weitere

20 Messpunkte wurden entlang des Randkammes gesetzt. Das vierte Set besteht aus der Kombination der Zahnhals-Daten mit denjenigen der EDJ. Alle vier Sets wurden mithilfe der General Procrustes Methode normalisiert und mittels Hauptkomponentenanalyse und anderer Techniken ausgewertet. Unsere Ergebnisse zeigen, dass die Ausprägungsgrade zweier nicht-metrischer Merkmale (transversaler Kamm und akzessorische Kämme) schon während der Ontogenese in die *Membrana praeformativa* eingeprägt werden und durch die Ablagerung von Zahnschmelz auf die OES übertragen werden. Im Gegensatz hierzu stehen akzessorische Tuberkel, welche nicht auf beiden Oberflächen gleichermaßen ausgeprägt sind. Weiters ergaben unsere Analysen, dass es populationsspezifische Unterschiede in den nicht-metrischen Merkmalen gibt und man daher für komparative Untersuchungen mit Hominiden eine sorgfältige Auswahl der menschlichen Vergleichsprobe treffen sollte.
Die Auswertung der vier Messpunkte-Sets zeigte, dass die Umrisse von Zahnkrone und Zahnhals nur bedingt brauchbar sind um *Homo* und *Pongo* aufgrund ihrer Gestalt zu trennen. Während bei den P^3 beide Spezies nur teilweise überlappen, sind sie in den P^4 gar nicht zu unterscheiden. Die Daten der EDJ und des kombinierten Datensatzes für beide Zähne, können Menschen und Orang Utans klar trennen. Wird Größe mit in Betracht gezogen, können alle vier Sets beide Spezies voneinander differenzieren.
Die menschlichen Populationen lassen sich in keinem der vier Datensätze unterscheiden, wodurch man für Vergleiche mit Hominiden jede beliebige Population als Vergleichsmaterial verwenden kann. Generell variieren obere Prämolaren in *H. sapiens* zwischen ellipsoiden und kreisförmigen Zähnen. Auf der EDJ zeigt ellipsoide Form eine eher niedrige Zahnkrone mit hohen Höckern, welche weit auseinander stehen, während die kreisförmige Form eine hohe Zahnkrone mit niedrigen Höckern besitzt, welche nah beieinander positioniert sind. Die Gestalt von P^3 und P^4 korreliert stark. Entweder sind beide ellipsoid oder beide kreisförmig. Dafür hat Größe nur geringe Auswirkungen auf die Gestalt, wobei große Zähne ellipsoid und kleine kreisförmig sind. Werden Populationen aufgrund ihrer Größe verglichen zeigt sich, dass Mitteleuropäer und Khoesan kleinere Zähne als australische und asiatische Populationen besitzen.
Unser neuartiger Ansatz des kombinierten Datensatzes besitzt die Vorteile, dass die gesamte Gestalt der Zahnkrone vom Zahnhals aufwärts abgebildet wird und die zusätzliche Information der Höhe hinzukommt.

Contents

Chapter 1

Introduction

1.1 Background

In order to study human evolution based on morphological criteria it is necessary to focus on a part of skeletal remains that is highly endurable and therefore abundant throughout the human history. Teeth fit this criterion very well. They consist of the most resistant materials of the whole body, namely enamel and dentine. Therefore teeth are the most prevalent remains in human fossil record. Moreover morphological features on teeth are convenient to compare, because these features are less affected by sex or any ecological influences, like bones tend to be (Hillson, 1996; Scott and Turner, 1997). During evolution teeth mainly adapted in relation to dietary changes (Kay, 1975; Strait, 1997). The environment itself has a very weak impact on the total morphology of the dentition (Scott and Turner, 1997). All this characteristics contribute to the fact that teeth are taxonomically informative.

In the last centuries teeth were studied by means of measuring their external morphology with the help of multivariate statistical approaches, for instance by collecting distances and angles such as the bucco-lingual and mesio-distal diameter of human teeth, and the mesio-occlusal line angle or the disto-buccal point angle. Using these metric traits, individuals, populations or species were compared (e.g.: Garn et al., 1966; Wolpoff, 1971; Townsend and Brown, 1978).

A relatively new procedure for obtaining data with regard to dental morphology is geometric morphometrics (GM). Slice (2005) describes GM as:

"The suite of methods for the acquisition, processing, and analysis of shape variables that retain all of the geometric information contained within the data" (p. 5). This method avoids the ambiguities associated with distances measured with callipers or other traditional tools. Instead it relies on so called landmarks on 2-dimensional or 3-dimensional virtual representations of the individual. These landmarks can also be identified analogously to traditional measuring points (Knußmann, 1988) but they are able to provide more information. They allow capturing the morphology of interest as a whole, instead of atomizing the structure by numerous lengths or breadth indices. Moreover GM is able to preserve the morphological information throughout all analyses and visualize results in a way that can be intuitively understood. They can be located without getting in contact with the real object, solely based on a digital copy. The object itself can even be enclosed in a block of soil or matrix, as long as it is possible to obtain virtual data by means of a Computer Tomograph (CT). This also means that the chance of damaging precious findings is reduced.

Most of the studies concerning the morphology of teeth, either with classical approaches or geometric morphometrics, were applied on directly accessible features of the outer-enamel surface (OES) or on the roots. Various reasons urged researchers to go deeper into the material and test structures below the surface. Butler (1956) has combined previous investigations and concluded, that ontogeny of teeth starts with the *membrana praeformativa*. The dentine part is formed on the apical side of this membrane while on the occlusal side enamel is deposited. During the development of the tooth germ the *membrana praeformativa* has received a certain form which is preserved in the enamel-dentine junction (EDJ). This form is also more or less mapped onto the OES. However, due to the uneven thickness of the enamel, there can be slight differences in the appearance of the EDJ and OES. The first studies investigating the EDJ used destructive or semi-destructive methods to remove the enamel or cut the tooth in slices (Nager, 1960; Sakai and Hanamura, 1973; Korenhof, 1982; Corruccini, 1987; Olejniczak et al., 2004). Later computed tomography scanning systems were found to be very useful, since they provided high spatial resolution imagery. The straightforward choice was the medical CT, but the resolution is very coarse for small objects like teeth. Nowadays micro-CT's (μCT) are used, which are much better suited for small objects. For almost twenty years now radiographic methods

made bones and teeth available to scientific questions, without destroying them.

1.2 Research Goal

Based on this non-destructive technique this Master thesis focuses on the outer and inner variation of upper premolars. In the few published papers dealing with upper premolars, researchers found, at least partially, differences (Wood and Engleman, 1988) or did not find any specific differences between species when classical morphometric approaches were used (Bailey, 2002; Martinon-Torres, 2006), especially when they tried to distinguish between Neanderthals and *H. sapiens*. In contrast to this, Lavelle (1984) was able to show that there are differences between modern human populations in the OES of upper first premolars. Morris (1981) reached the same interpretation concerning the upper first premolars by comparing angular measurements. A recent GM analysis (Gómez-Robles et al., 2011) comparing the OES of different hominoid species stated that there are no distinct morphological differences among the most recent species, but the authors suggest an evolutionary gradient from the earlier to the later hominins.

Some researchers (Kraus et al., 1969; Brace et al., 1987; Wrangham et al., 1999; Lucas, 2004)may offer an answer why there are so varying results if scientists try to separate modern human populations based on morphological features of their dentition. It is suggested that the transition from a quadruped to a biped needed some profound changes in the function and structure of the whole human body. In quadrupeds teeth are used for fighting and defending, and of course for catching and preparing the food. In biped hominids the forelimbs took over a part of the activities of the teeth. The first reduction in hominid dentition took place in the canines. *Ardipithecus ramidus* (4.5 – 4.0 Ma) is the first hominid that shows no functional sex-related size dimorphism in canines and there is no evidence for a honing complex either (Lovejoy, 2009; White et al., 2009). The remaining function for the dentition was the breakdown of food items, which could be placed into the mouth with the help of the forelimbs. At 1.6 Million years BP there are the first hints for active use of fire, however acceptedubiquitous use of fire can be dated to 300 – 400 ky ago (Roebroeks and Villa, 2011;

Gowlett and Wrangham, 2013; Shahack-Gross et al., 2014). With the new method of extraoral food preparation, namely cooking, even the already decreased masticatory function was further reduced dramatically (Wrangham and Conklin-Brittain, 2003; Carmody and Wrangham, 2009; Wrangham and Carmody, 2010). Ultimately the invention of pottery and the new cooking method "boiling" softened food to an extent that teeth would not be needed any more for survival (Lucas, 2004). With extraoral food processing the active use of the dentition has declined drastically, and, like in all traits with decreased function, changes started to occur in the masticatory system without affecting the survival of the individual. Particularly the jaws and the teeth were reduced and they are still becoming smaller until today (Brace and Mahler, 1971; Brace et al., 1987). In all human populations some kind of food preparation prior to ingestion is taking place and therefore none of them should show any signs of specialisation towards their nutrition, even though *H. sapiens* has found very diverse ecological niches to sustain. But which features have to be maintained to preserve the masticatory function to the level still needed, and which traits are able to vary? This is one of the questions this Master thesis wants to answer.

In this Master thesis the main goal was to characterize the form of human upper premolars quantitatively and qualitatively using a Virtual Anthropology aproach. Based on the mentioned researches we do not expect any separation between human populations based on their metrical features. Therefore our first hypothesis is that all populations of *H. sapiens* overlap in terms of their tooth morphology in upper premolars. Our second hypothesis, however, states that not all regions of a tooth are equally stable, some might vary more than others. The third hypothesis is, that all non-metrical traits can be found on both, the OES and the EDJ.
Three different types of analyses were performed to detect variability in human upper premolars.

1.3 Non-Metric Features

Until now non-metrical traits were only examined on the OES. Therefore we analysed them on the OES and EDJ to test how these features are interrelated between the two surfaces. Non-metrical features should be found on

both, EDJ and OES if we follow Butler´s (1956) considerations regarding the *membrana praeformativa*.
Rarely present traits on upper premolars (found only in less than 5% of humans) are odontomes (Turner et al., 1991; Levitan and Himel, 2006), which are additional occlusal tubercles; Uto-Aztecan premolars, which are only found in Native American populations (Turner et al., 1991; Delgado-Burbano et al., 2010; Johnson et al., 2011); and tricuspid premolars (Turner et al., 1991; Scott and Turner, 1997). More often occurring are accessory marginal tubercles, which originate from a mesial or distal bifurcation of the central groove (Turner et al., 1991; Scott and Turner, 1997). In contrast to these rarely occurring features are maxillary premolar accessory ridges (Mx-PAR) (Burnett et al., 1996, 2010; Mihailidis et al., 2013), which are found frequently in all human populations. They are additional ridges running next to the paracone to the central groove on P^3 and P^4 and can be located mesial and/or distal of the tip. It seems that the distribution of this accessory ridge is heterogeneous between different populations (Burnett et al., 2010; Mihailidis et al., 2013). A rarely mentioned feature on premolars is the manifestation of the transverse crest (Bailey, 2002). This crest may or may not connect the paracone with the protocone. It can also occur as a doubled crest. Until now this feature has not been in the focus of research, and Bailey (2002) has only compared the expression of this crest between *H. sapiens* and *H. neanderthalensis*, which is much more accentuated in Neanderthals.

Our goal was to determine whether the present features on the OES of upper premolars find their correspondence on the underlying EDJ. Prior studies were able to show exactly this characteristic for other non-metric features on several teeth (Korenhof, 1982; Nager, 1960; Corruccini, 1987; Sasaki et al., 2002; Olejniczak et al., 2004; Skinner et al., 2008b, 2009b, 2010) or were not able to show a correspondence between EDJ and OES (Schwartz et al., 1998). Therefore we examined upper premolars for the occurrence of accessory marginal tubercles, accessory marginal ridges, transverse crests and additional odontomes or cusps.

1.4 Geometric Morphometrics

1.4.1 Outline Analyses

Most techniques for investigating teeth, especially those focused on the occlusal surface, can only be used for unworn or slightly worn teeth. On worn teeth crucial morphological features would be missing in the areas of interest. If abraded teeth have to be excluded, this reduces the sample size drastically, particularly for studies regarding hominids.
A technique that is not relying on present occlusal features is the investigation of crown and cervical outlines. Both traits are more likely well preserved even on worn teeth and they are only slightly affected by interproximal wear, which can easily be reconstructed. Both outlines are useful in distinguishing between modern humans and Neanderthals, at least in permanent upper and lower first molars (Benazzi et al., 2011a) and deciduous lower second molars (Benazzi et al., 2011b, 2012). Bailey et al. (2014) has claimed that the crown outline in deciduous upper second molars is able to separate between modern humans and Neanderthals, but there is an overlap between *Homo sapiens* and *H. erectus*. All together these studies state that the crown outline is more variable than the cervical one.

This thesis wants to capture the possible variability and main variation in crown and cervical outlines in permanent upper premolars of modern humans.

1.4.2 Morphological Analyses of the EDJ

The morphology of a tooth is not only represented in the non-metrical traits or in its outline. These mentioned features are poor in representing the overall shape of the tooth or the crown. Bernal (2007) showed with his approach of gathering linear measurements with the goal to compare them with landmark and semilandmark data from the same sample of teeth that size variablility is incorporated in both methods equally. However, the shape of an object is much better represented by landmarks than by linear measurements. Supplementary semilandmarks enhance the potential to observe real shape changes further. Further investigations to study the variation in morphology within and between hominin species with the help of GM have shown that the morphology of the EDJ is carrying taxonomical relevant in-

formation (Skinner et al., 2008a, 2009a; Gómez-Robles et al., 2013).
In this study, anatomical landmarks were chosen to capture the overall shape of the EDJ. Two landmarks where placed on the paracone and protocone horn tip (horn tips are the equivalent structure on the dentine in comparison to the cusps on the EDJ), and two further in the mesial and distal fossae. Also 20 curve semilandmarks were created along the marginal ridges (mesial and distal), connecting the two tips. This data set was collected to comprehensively capture the occlusal geometry of upper premolars. We expected variations in features like the crown height (measured from the central groove to the paracone horn tip), the relative height of the two horn tips (the buccal usually being higher, at least in third premolars), or the spacing between the two horn tips.
Additionally, a combined data set was computed by including the 24 pseudolandmarks gathered on the cervical outline to the set of four landmarks and 20 semilandmarks of the occlusal EDJ surface. This set helps to study the complete height of the crown and capture the changes in shape more precisely.

Chapter 2

Material

In this thesis we focus on permanent upper premolars. Human and all other primates have two premolars per dental arch. These can either be called first and second premolar or third and fourth. The naming convention depends on how close the work is associated with phylogenetic questions. The first mammalian had four premolars according to the eutherian tooth formula, but the two being the closest to the canine where lost during the evolution of modern primates. Therefore only the third and fourth premolars are left. However, in medicine they are referred to as first and second premolar because the phylogenetic view is not of such great importance in this field. In this contribution we are going to follow the palaeontologists nomenclature, thus using the terms third and fourth premolars, respectively P^3 and P^4.
Human premolars have an intermediate morphology between canines and molars, with two projecting cusps and an occlusal groove to provide for a masticatory function. The morphology is way more similar for both upper premolars than for lower ones. In general, upper premolars are buccolingually longer than they are mesio-distally broad. They are always bicuspids, with a buccal paracone and lingual protocone. Though the paracone is larger and taller, the two cusps usually tend to be rather similar in height and prominence. One main difference between the two cusps is their orientation. The paracone has its tip more or less on the transverse midline of the tooth whereas the protocone is usually placed slightly mesially. The cusps are connected through marked mesial and distal marginal ridges. Between the two cusps runs a mesio-distal groove, also called central groove, that touches the mesial and distal fossae, the two deepest constrictions. The

central groove is interrupted by the transverse crest if it is present (Kraus et al., 1969; Hillson, 1996).

Though upper premolars seem very similar at first glance, there are distinctive features that distinguish them. P^3s have more prominent shoulders formed through the intersection of the buccal marginal ridge and the mesial and distal marginal ridges. The mesial and distal aspects of the tooth converge in a lingual direction which leads to a hexagonal appearance in occlusal view (figure 2.1). The buccal ridge is oriented slightly mesio-lingually in comparison to the lingual marginal ridge, and in the centre is a pronounced central groove. Basic variation in third upper premolars is found in the mesial and distal convergence, the intercuspal width, the inclination from the shoulders up to the paracone, and there is also a variation in the formation of one to three buccal lobes, shaped by shallow depressions beyond the buccal marginal ridge (Kraus et al., 1969).

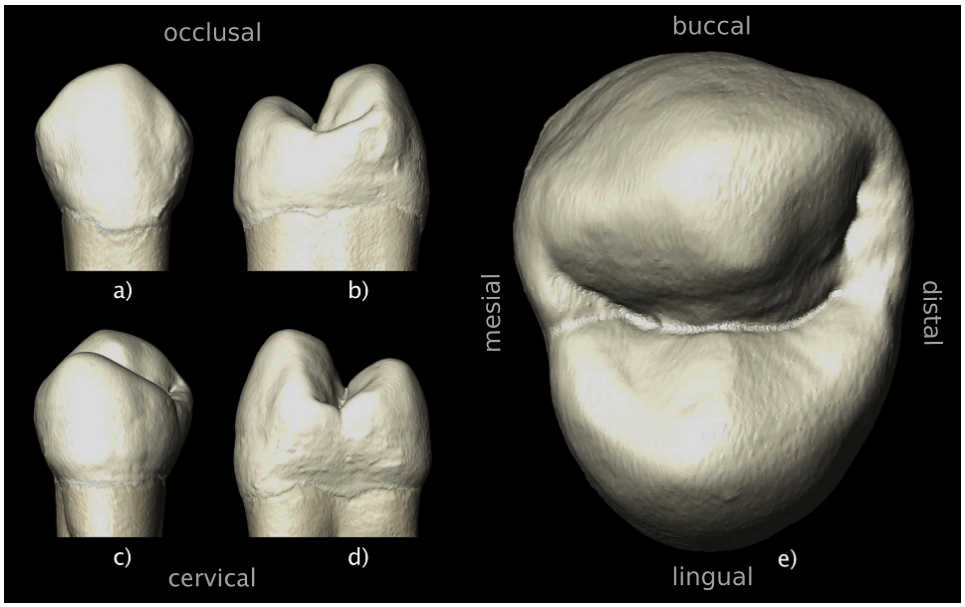

Figure 2.1: Left permanent upper third premolar of *H. sapiens* in a) lingual b) mesial c) buccal d) distal and e) occlusal view.

P^4s have an ovoid outline in occlusal view with the mesial and distal borders being parallel (figure 2.2). Also, the buccal and lingual marginal ridges are approximately parallel to each other, whereas the central groove is relatively short. All this promotes a rather symmetric appearance. Most

of the variation in fourth upper premolars occurs at the central groove. It can be a deep fissure, only a very shallow line, or just a single central pit. Often additional grooves can be present. Some variation is also found in the intercuspal width and the inclination from the shoulders up to the paracone (Kraus et al., 1969).

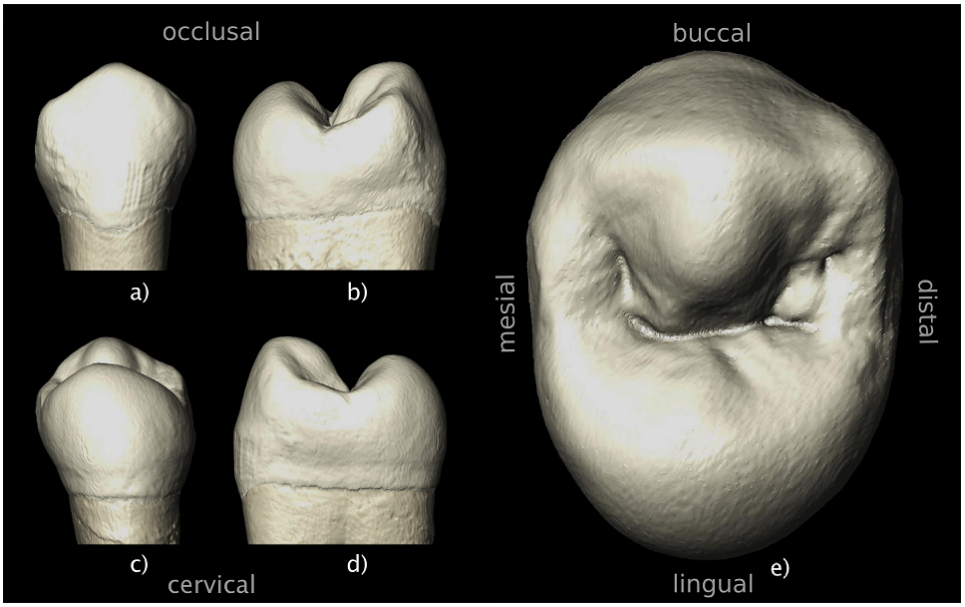

Figure 2.2: Left permanent upper fourth premolar of *H. sapiens* in a) lingual b) mesial c) buccal d) distal and e) occlusal view.

The sample in this study is based on permanent upper third and fourth premolars from seven different human populations (n=44) and four individuals of *Pongo pygmaeus* as an outgroup. These populations were chosen because they cover different human life styles and originate from quite diverse geographical backgrounds.

Included are the small sized Khoesan from South Africa. The Khoesan are hunter/gatherers and a genetically interesting group, because molecular evidence suggest that they diverged from the rest of the human DNA pool 90 000 – 150 000 years BP and are meant to be one of the oldest tribes of modern *Homo sapiens*. Therefore they show a unique pattern of diversity in their genome (Li et al., 2008). Based on mtDNA Behar et al. (2008) showed that early settlements already had matrilineary structures, while Knight

et al. (2003) studied the origin of click languages based on Y chromosomes. The Khoesan used in this study were collected together with an extraordinary diverse sample of Sub-Saharan African individuals by Rudolf Pöch during his expedition in 1907 to 1909 (Pacher, 1961) and are now a part of the skeletal collection at the University of Vienna. Some of these other Sub-Saharans were also included in this study as the second population.
The third population consists of middle Europeans and is based on skulls from the "anatomical collection" of the Natural History Museum of Vienna (NHM). The individuals were collected due to their interesting morphology or a visible pathology, like Cribrae orbitalia or a suture abnormality. These specimens lived around 1860 to 1880 mostly in the area of the old Austrian empire of the K&K monarchy.
The fourth population used are Avars, an ancient nomad tribe featuring a mixture of Asiatic and European traits that lived in middle Europe during 700 - 900 AD. The skeletal remains were excavated in Vienna in 1976 - 1977 and kept at the University of Vienna (Tangl, 1990).
From Asia we included Indonesians from the collection at the NHM and some indigenous specimens from Papua New Guinea, which were collected by Rudolf Pöch on his expedition from 1904 to 1906, now located in the skeletal collection of the University of Vienna (Bondy-Horowitz, 1930).
Our last group of *H. sapiens* are Australian Aboriginals. Rudolf Pöch bought these skulls in Australia. They have been part of the skeletal collection of the University of Vienna too, but have been restituted recently. For research purpose scans of these individuals were taken prior to re-burial (for more detailed information about all individuals see Appendix A).

To see how different other species would perform in our shape and form analyses, we used four specimens of a close relative of hominins i.e. *Pongo pygmaeus*. Two of them have been shot in their natural habitat, whereas the two others were bread and kept in the zoological garden Schönbrunn in Vienna. All skulls were a gift to the NHM Vienna. Upper permanent premolars in orang-utans have the same bicuspid form like in humans with a paracone and a protocone divided by a mesio-distal groove. In P^3 the paracone is higher and taller than the protocone, whereas in P^4 they tend to be of a more equal size (Swindler, 2002). However, in *Pongo* premolars are much more molariform and possess small ridges on the occlusal surface,

known as crenulations. This crenulations may cover the primary occlusal features, but should not affect the EDJ. In addition to the mesial and distal marginal ridges, upper premolars of orang-utans have two more crests. The mesial crest starts at the paracone, or may be displaced slightly mesially and runs down until it crosses the mesio-distal groove. The second one, called distal crest, connects the protocone with the distal aspect of the paracone (figure 2.3). This additional features divide the occlusal surface in three parts and are expected to be found on the EDJ as well.

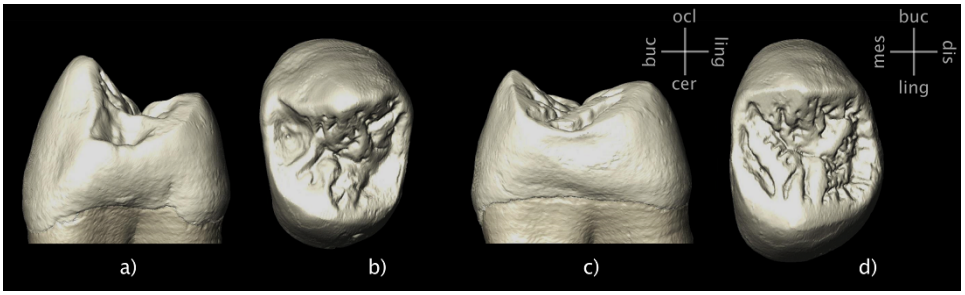

Figure 2.3: Left permanent upper third and fourth premolar of *P. pygmaeus*. P^3 in a) mesial and b) occlusal view and P^4 in c) mesial and d) occlusal view.

To be included in our sample, only individuals were selected that had upper premolars and molars and lower premolars still located in the jaw, to ensure all teeth belong to the same individual. All six teeth should be present on the same side for comparative studies. However, four individuals were included with just one upper premolar. One San and one Papuan miss one P^3, and two Europeans have lost their P^4s intra vitam. Additionally, the teeth should not be cariotic or have experienced any dental treatment such as inlays. Based on Molnar (1971) we only used teeth featuring one of the first three wear stages:

- 0 - unworn
- 1 - wear facets present, but no dentine exposed
- 2 - in fewer than three cusps there are small dentine patches exposed

Teeth with huge cracks were excluded because there is a danger that the overall proportions could have changed. Even though sex was known for some of the specimens, it was not used as a variable because 1) the sex determination of some specimens is questionable, and 2) it is general agreed

that sex has no consistent and significant influence on most dental features, except for canines (Scott and Turner, 1997). Furthermore we had a very limited sample size, in which case it is not possible to divide the sample further. For this study only left-sided premolars were included. If the left ones were missing, damaged or worn off, actual right premolars were mirror-imaged for further analysis.

The sample was combined to form three main continental groups (fig. 2.4):

1. Africans, including Khoesan and Sub-Saharan Africans (N=15; one P3 is missing),
2. Europeans, consisting of the Avars and middle Europeans (N=16; two P4 are missing),
3. Australasians, including Papua New-Guineans, Indonesians, and Australian Aboriginals (N=13; one P3 is missing).

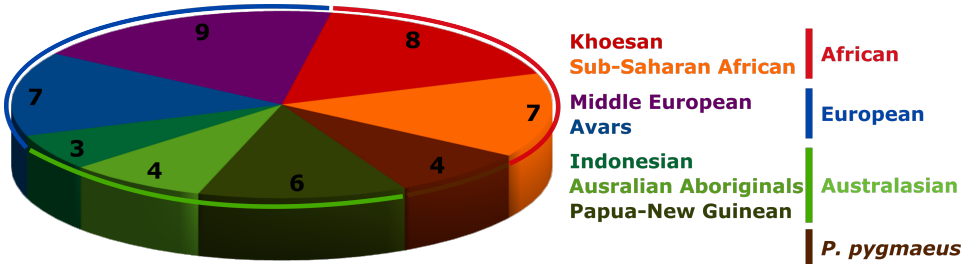

Figure 2.4: The distribution of the sample.

Chapter 3

Methods

3.1 Scanning & Virtual Reconstruction

All individuals were scanned at the Vienna μCT Lab, Department of Anthropology, University of Vienna with an industrial Viscom X8060 μCT scanner. This scanner rotates the object itself and not the tube/detector unit like in medical computer tomographs. This feature enables us to get the object closer to the tube, which results in higher resolution. The resolution is given in isometric voxels, a 3-dimensional equivalent of pixels in volume data sets, with all three dimensions having the exact same length for each voxel. For all individuals we used the following parameters: 110-140kV, 280-410mA, 1400-2000ms, 0.75mm cooper filter. In total 1440 scans were made per individual, which results in a shot from every 1/4 degree. For this research not the complete skull, but only the maxilla was scanned, in order to decrease the resulting voxel size. It ranged from 22μm to 60μm. To reconstruct consecutive slices of the volume, the raw images were subjected to a filtered back-projection algorithm and converted into TIFF image stacks using *XVR-CT*.
All individuals were segmented in *Amira 5.4.5* (Mercury Computer Systems, Chelmsford, MA) using the half-maximum height (HMH) protocol introduced in Spoor et al. (1993) to separate enamel and dentine (see also Skinner et al., 2008b) based on their distribution of grey values. The density of an object is represented through 256 grey shades, where air is black and the most dense material is white. The protocol takes the highest and lowest value along a projected line through two tissues with different densities and

calculates the value in the middle of both extremes as a threshold value. This threshold helps to select the voxels of one of the two tissues, because it is used as the lowest boundary for the grey value of the denser material. However, voxels with very similar grey values of both tissues cannot be separated due to the threshold. Therefore manual corrections had to be done. Based on Benazzi et al. (2011b) the interobserver error in the HMH protocol and segmentation is negligible. The visualization function of *Amira* shows segmented materials as triangle-based surface models (using unconstrained smoothing parameter).

Teeth were oriented based on a best fit plane created at the height of the cervical plane (Benazzi et al., 2014). This was gained by manually placing landmarks along the cervical outline. Afterwards a best-fit plane was computed with the help of these points (figure 3.1). The whole image stack was reoriented based on the cervical plane being parallel to the XY-plane of the Cartesian coordinate system. If necessary, actual right premolars were mirror-imaged to left ones. For further analyses in *EVAN-Toolbox 1.71* (EVAN Society) each surface model was reduced to 50,000 triangles and converted to an .obj file. Skinner et al. (2010) could not detect any interference on small features on teeth due to the reduction of triangles, therefore this should not have any influence on the following procedures.

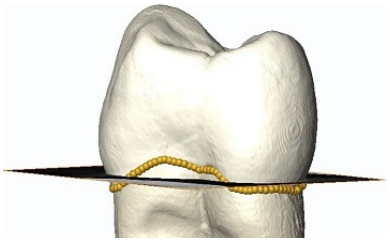

Figure 3.1: A tooth with manually placed landmarks along the cervical outline and the computed best-fit plane for reorientation.

3.2 Non-Metric Features

All teeth were visually inspected to capture the qualitative traits on OES and EDJ, and further compare the occurence of these traits between the two surfaces. The following features were recorded individually on the OES and EDJ: odontomes, Uto-Aztecan premolars, tricuspid teeth, accessory marginal tubercles, and accessory mesial/distal ridges. Additionally the transverse crest has been included into the analyses after a first inspection. All traits have been counted separately for P^3s and P^4s.
A cross-classified table has been done for every feature of the OES and EDJ

individually in the statistics program *IBM SPSS Statistics 22* (IBM).

Very rare are Odontomes, also called tuberculated premolars, occlusal tubercles or *dens evaginatus* (Turner et al., 1991; Levitan and Himel, 2006), which are additional occlusal tubercles in the central groove.
Another rarely occurring feature are Uto-Aztecan premolars, also called disto-sagittal ridges, which are exclusively found in first premolars of Native American populations (Turner et al., 1991; Delgado-Burbano et al., 2010; Johnson et al., 2011) and therefore we did not expect to find them in our sample. This feature is represented by a rotation of the main axis of the paracone in a bucco-sagittal direction, which produces an additional impression beyond the intersection of the paracone ridge and the mesial marginal ridge.
In upper premolars there is the possibility of a tricuspid tooth, signified by an additional lingual cusp. In this case on the OES the lingual cusp has to be divided through a small bucco-lingual groove into a protocone and an additional hypocone (Turner et al., 1991; Scott and Turner, 1997). On the EDJ, however, there are two separate horn tips (fig. 3.2). Uto-Aztecan premolars, odontomes and tricuspid teeth are classified as: (0) absent or (1) present.

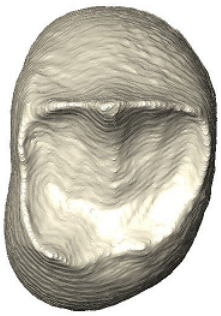

Figure 3.2: EDJ of a tricuspid P^3.

An expected feature in upper premolars are accessory marginal tubercles. On the OES they originate from a mesial or distal bifurcation of the central groove, which leads to a bulge or free standing accessory tubercle (Turner et al., 1991; Scott and Turner, 1997). It is possible to find four different types of accessory marginal tubercles (fig. 3.3):

- (0) no accessory tubercle present
- (1) mesial tubercle
- (2) distal tubercle
- (3) mesial and distal tubercle

On the EDJ however, these tubercles can not be determined through a certain feature (Turner et al., 1991). Below a tubercle on the OES might be an elevation on the marginal ridge of the EDJ, but this elevation does not

have to be there. To the contrary there can be an elevation on the EDJ, but without any tubercle on the OES.

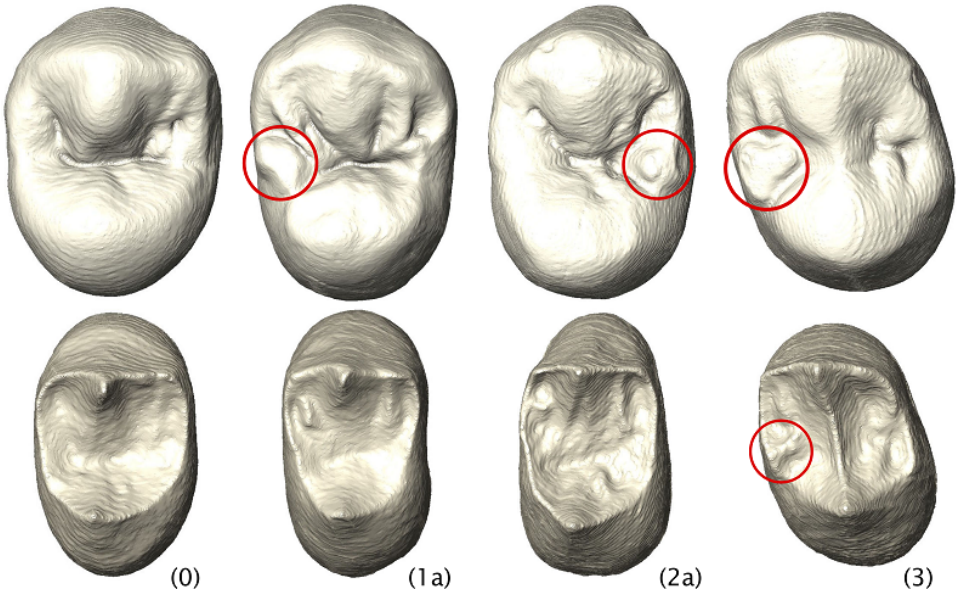

Figure 3.3: Variation of accessory marginal tubercles on the OES and EDJ: (0) no accessory tubercles present, (1a) mesial tubercle without elevation on the EDJ, (2a) distal tubercle without elevation on the EDJ, (3) mesial tubercle with elevation on the EDJ.

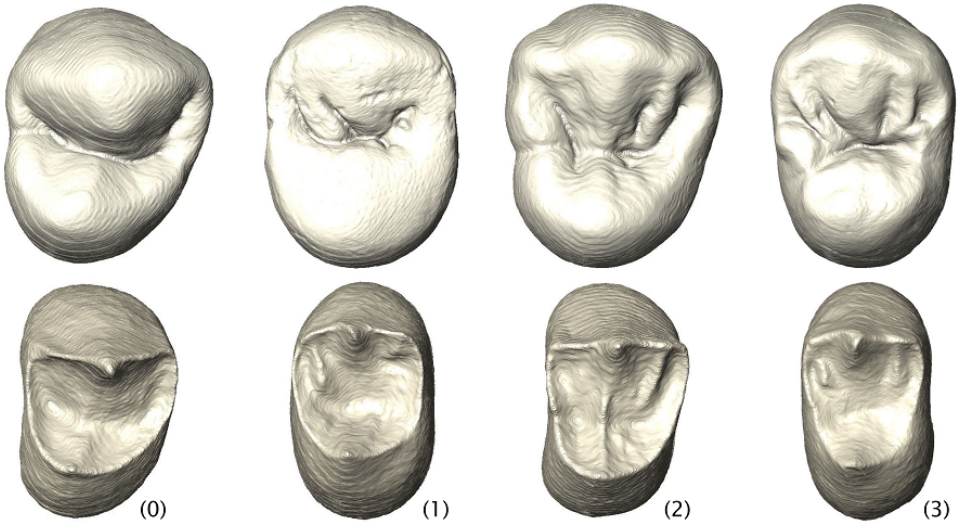

Figure 3.4: Variation of MaxPAR on the OES and EDJ: (0) no accessory ridge present, (1) mesial ridge, (2) distal ridge, (3) mesial and distal ridge.

In contrast to these rarely occurring features are maxillary premolar accessory ridges (MxPAR) (Burnett et al., 1996, 2010; Mihailidis et al., 2013), which are found frequently in all human populations on the OES and EDJ. They are additional ridges running next to the paracone to the central groove on P^3s and P^4s and can be located mesially and/or distally of the tip. The expression of the MxPAR is very variable, from very shallow to massive, and they are not limited to being straight or completely reach the central groove. Even though this trait presents no difference in the appearance between sexes, it has to be mentioned that the MxPAR tends to be more pronounced in males than in females. It seems that the distribution of this accessory ridge is heterogeneous between different populations. Burnett et al. (2010) claims that the MxPAR is more common in Asian populations and their descendants than in Africans or Europeans. In contrast to this Mihailidis et al. (2013) states that these ridges are more common in Europeans and Asians than in Australian Aboriginals and other pacific populations. However, both agree that the MxPAR is a widely spread feature.
The following variations can occur (fig. 3.4):

- (0) no accessory ridge present
- (1) mesial ridge
- (2) distal ridge
- (3) mesial and distal ridge

A rarely mentioned feature on premolars is the manifestation of the transverse crest (Bailey, 2002). This crest may or may not connect the paracone with the protocone. It can also occur as a doubled crest. Until now this feature has not been in the focus of research, and Bailey (2002) has only compared the expression of this crest between *H. sapiens* and *H. neanderthalensis*, which is much more accentuated in Neanderthals. It can be (fig. 3.5):

- (0) interrupted by the central groove
- (1) not interrupted through the central groove
- (2) divergent/doubled

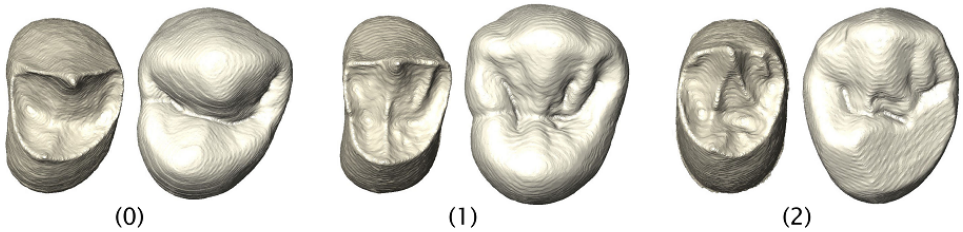

Figure 3.5: Variation of the transverse crest on the OES and EDJ: (0) interrupted by the central groove, (1) not interrupted by the central groove, (2) divergent/doubled.

3.3 Geometric Morphometrics

3.3.1 Outline analyses

The cervical and crown outlines were collected using *RapidForm XOR264 SP1* (INUS Technology). In the process of importing the teeth, both EDJ and OES surface models were automatically positioned based on the cervical plane being parallel to the XY-plane. First of all each tooth, more precisely the dentine and enamel surface together, had to be reoriented. This was done by a rotation constrained by the criterion that the buccal ridge should be aligned parallel to the X-axis. Afterwards outlines were collected. The crown outline is defined by the silhouette of the oriented crown seen from a occlusal view. For a reasonable comparison interproximal wear facets have been reconstructed if they were present. All crown outlines were projected onto the cervical plane. The cervical outline is defined as the perimeter of the dental crown at the intersection with the cervical plane (Benazzi et al., 2011a, 2012). First the silhouette for the crown outline was computed with the help of the polyline function. Afterwards both outlines were digitized using the spline function module.

After obtaining the outlines, the associated pseudolandmarks were extracted in *Rhinoceros 4.0* (Robert McNeel & Associates, Seattle, WA). The computed centroid of area of each outline was used to superimpose them all on the centre of a set of 24 equiangular spaced radial vectors. A first vector was oriented parallel to the Y-axis buccally, the other 23 proceed in a counterclockwise direction (Benazzi et al., 2012). Where these vectors intersect with the outline, they determine the position of the 24 pseudolandmarks

(figure 3.6). This procedure already anticipates the rotation and translation which are normally done in a General Procrustes Analysis.
Unlike a Procrustes Superimposition we rotated the teeth based on morphological features before placing the landmarks. That guaranties that the landmarks are all morphologically homologous and therefore were not slid but treated like real landmarks. However size still has to be excluded. As Benazzi et al. (2012) summarized, the process of determining the cervical plane and gaining the outlines and their 24 pseudolandmarks is a semiautomatic process with only a few subjective interventions, i. e. the rotation of the buccal ridge. Benazzi et al. (2012) claims, that there is no significant intra- or interobserver error associated with the manual process of reorientating.

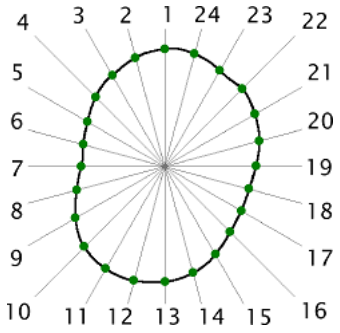

Figure 3.6: 24 equiangularly spaced radial vectors determine the counterclockwise pseudolandmarks on the outlines (green).

3.3.2 Morphological analyses

The EDJ surface models were loaded into *EVAN-Toolbox* to gather the following four landmarks and an additional curve semilandmarks:

1. Horn tip of the paracone
2. Horn tip of the protocone
3. Distal fossa of the central groove
4. Mesial fossa of the central groove

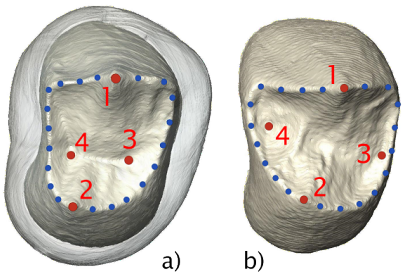

Figure 3.7: Position of the semilandmarks (blue) and landmarks (red): 1) paracone tip 2) protocone tip 3) distal fossa 4) mesial fossa in human and *P. pygmaeus*.

At first a curve was created following the marginal ridges of each tooth. Then the four landmarks were placed. In humans the third and fourth landmarks were placed at the deepest points of the central groove, according to the definition of the mesial and distal fossa (figure 3.7). Four P^4s only had a central pit instead of a mesio-distal groove delimited by the two fossae. In this case it was not possible to place the third and fourth landmark and therefore

these four specimens had to be excluded (two Africans and two Europeans). In orang-utans these landmarks were placed at the deepest points of the mesial and distal occlusal plane.
After finding the landmarks and defining the ridge curve, 20 equidistant semilandmarks were created along the curve on a template individual, ten semilandmarks on the mesial side of both tips, and ten on the distal side. Then the curve semilandmarks were projected onto the other specimens and slid along tangents based on the criterion to minimize the bending energy of the thin-plate spline function between the individual and the template (Gunz et al., 2005; Gunz and Mitteroecker, 2013). Semilandmarks were slid and projected back onto the curve until they reached the position with the least difference to the template. Afterwards all semilandmarks were treated like homologous landmarks for further analysis.

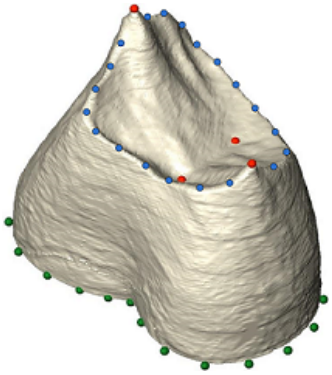

Figure 3.8: The combined data set: pseudolandmarks on the cervical outline (green), landmarks (red) and semilandmarks (blue).

In addition to the analysis for the landmarks on the EDJ and the pseudolandmarks of the outlines we constructed a combined data set consisting of landmarks and semilandmarks on the EDJ and pseudolandmarks of the cervical outline of each individual (figure 3.8). The EDJ landmarks and semilandmarks, respectively the pseudolandmarks on the outlines have different coordinate systems. Therefore one of the sets has to be projected into the coordinate system of the other. The pseudolandmarks were loaded into Amira and projected onto the surface of the respective tooth. The thereby adjusted coordinates of the pseudolandmarks were then combined with those from the EDJ. Through this method, we obtained a more comprehensive and more realistic data set per individual. This combination of information improves the possibility to discover shape changes of the whole tooth crown. In this case, the height of the tooth crown, from the cervical outline at the base of the crown up to the horn tips of the occlusal surface, is also captured by the data. Additionally the danger of possibly misleading visualizations is reduced through this method.*EVAN-Toolbox* is able to warp a template surface into the shape of

any other real or hypothetical specimen in morphospace. When only using landmarks on the EDJ (the occlusal surface), the warp can only be based on the information measured in this region, while other regions such as the side walls and the base of the crown have to be extrapolated by the algorithm which might lead to unwanted deviations, particularly in cases of flat occlusal reliefs. In addition, the combined data set allows to visualize how the EDJ shape interacts with the shape of the cervical outline.

3.3.3 Analyses

Analyses were done for the four different sets of landmarks separately:

- EDJ: landmarks and semilandmarks on the EDJ
- cervical: pseudolandmarks along the cervical outline
- crown: pseudolandmarks along the crown outline
- combined: EDJ combined with cervical outline

A Generalized Procrustes Analyses (GPA: Rohlf and Slice, 1990) was carried out in *EVAN-Toolbox* to standardize the values of each specimen to unit centroid size. Furthermore information about orientation, location and size were removed. This shape coordinates were analysed using a Principal Component Analysis (PCA) to observe the shape variation in the sample. Due to the fact that the outlines were already superimposed, they do not have to run through a GPA.
To detect if Principal Components (PC) can be interpreted separately we used the Sphericity Test for two consecutive Eigenvalues after Anderson (1963), adapted by Coquerelle et al. (2011):

$$2N * ln(a/g)$$

N = sample size

a = arithmetic mean

g = geometric mean (= n^{th} root of the product of n numbers)

This is an ordinary chi-square test with two degrees of freedom. The expected likelihood ratio is 2 at the 50% level and 3.5 at the 95% level. If the

Anderson value is lower than two, which means that the explained variance between two PCs is circular, than this PC should not be interpreted. It is likely that this PC is only reflecting noise. An Anderson value higher than 2 means that the explained variance by the pair of PCs is elliptical. Therefore only PC‘s with a value higher than two were analysed.
Furthermore we computed a Partial Least Square (PLS) Analysis for P^3s and P^4s for the combined data files. This should show how the shape of the third premolar correlates with the shape of the fourth premolar and vice verca, respectively what the common shapes are. PLS were also performed for the intra-tooth comparison of EDJ with crown outline, EDJ with cervical outline, and cervical outline with crown outline.
Finally we have performed a multiple linear regression for the combined data set, for P^3s and P^4s separately, to detect any allometric effects of size (measured as the natural logarithm of centroid size) on shape. Also the size factor (lnCS) was compared between *H. sapiens* and *P. pygmaeus*, between the continental groups, and between all seven human populations separately for all four data sets.

Chapter 4

Results

4.1 Non-Metric Features

First of all non-metric features were examined to see which traits could affect the geometric morphometric analyses. Table 4.1 presents all features and their grades (see chapter 3). For odontomes, Uto-Aztecan premolars and tricuspids the grades are as follow: (0) absent, (1) present. In the transverse crest the numbers stand for: (0) interrupted crest, (1) uninterrupted crest, (2) doubled crest. In marginal accessory tubercles and accessory ridges the grades signify: (0) absent, (1) mesial occurence, (2) distal occurence, (3) occurence on both sides.

This admittedly small sample did not include odontomes or Uto-Aztecan premolars. The latter were not expected, given that the sample does not include any Native American indigenous people. However we found a tricuspid third premolar (see fig. 3.2) within the San sample. In this case the trait is not visible on the OES, but it is clearly expressed on the EDJ with two lingual horn tips instead of a single protocone.

Table 4.1: Occurrence of non-metric features in the three continental groups on the EDJ/OES: AF - African; AA - Australasian; EU - European.

trait	grade	P3			P4		
		AF	AA	EU	AF	AA	EU
individuals		14	12	16	14	13	14
odontomes	0	14/14	12/12	16/16	14/14	13/13	14/14
	1	0/0	0/0	0/0	0/0	0/0	0/0
Uto-Aztecan	0	14/14	12/12	16/16	14/14	13/13	14/14
	1	0/0	0/0	0/0	0/0	0/0	0/0
tricuspid	0	13/14	12/12	16/16	14/14	13/13	14/14
	1	1/0	0/0	0/0	0/0	0/0	0/0
transverse crest	0	8/10	3/6	12/14	9/9	12/12	14/13
	1	2/0	5/2	4/2	4/4	0/0	0/0
	2	4/4	4/4	0/0	2/2	1/1	0/1
marginal accessory	0	14/14	12/12	16/16	14/14	11/8	14/14
tubercle	1	0/0	0/0	0/0	1/1	1/4	0/0
	2	0/0	0/0	0/0	0/0	1/1	0/0
	3	0/0	0/0	0/0	0/0	0/0	0/0
accessory ridge	0	9/7	7/8	5/7	4/4	4/2	3/3
	1	1/0	0/0	0/0	4/3	0/2	0/1
	2	2/5	4/3	5/3	3/3	2/2	3/3
	3	2/2	1/1	6/6	4/5	7/7	8/7

4.1.1 Transverse Crest

The three forms of the transverse crest (see fig. 3.5) tend to be distributed heterogeneously between the three continental groups (see fig. 4.1). In Europeans a doubled crest only occurs in one P^4 where it is only found on the EDJ. A transverse crest that is not interrupted only occurs in third premolars, with a frequency of 16.7% on the OES, and 41.7% on the EDJ. Australasians also present an uninterrupted transverse crest on their P^3s. While 12.5% have this feature on the OES, twice the number have this type expressed on their EDJ. Doubled crests occur in Australasians in both teeth. 33.3% in P^3 and 7.7% on P^4 show signs of a divergent crest on EDJ and OES. In the African group all three forms of the transverse crest can occur on both upper premolars. 14.5% of the third premolars present an uninterrupted transverse crest on the EDJ while no signs appear on the OES, and 28.6% exhibit a doubled crest on EDJ and OES. In fourth premolars 12.5% show a crest that is not interrupted on the EDJ, with twice the individuals

exhibiting it on the OES. A doubled crest occurs in 12.5% of the specimens EDJ and OES.

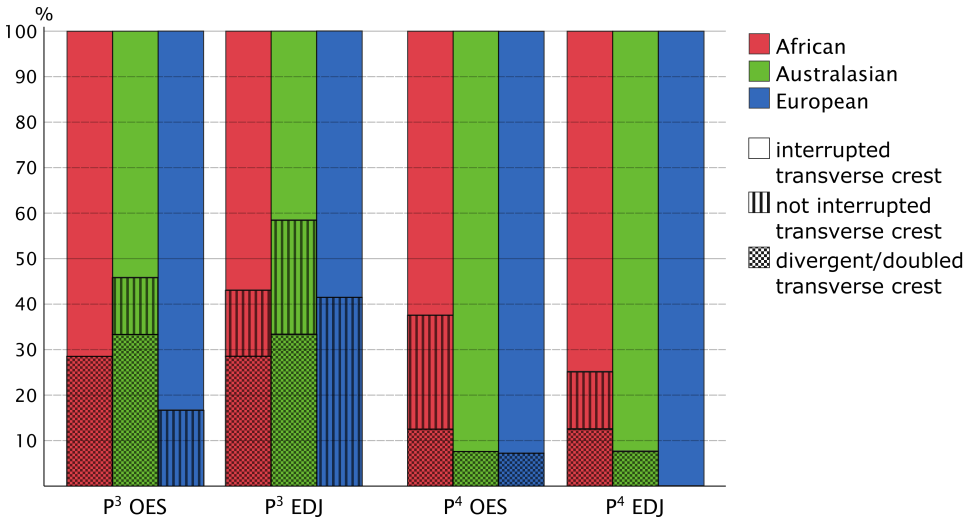

Figure 4.1: Occurrence of the three different types of the transverse crest.

4.1.2 Marginal Accessory Tubercles

Furthermore the occurrence of marginal accessory tubercles (fig. 3.3) was investigated. In this sample we have found them on fourth premolars only. This feature is present on the mesial locus in one African, three Australian Aboriginals and one Papuan, and on the distal locus in one Papuan. Only two specimens, an African and an Australian Aboriginal, have an elevation of the marginal ridge on the EDJ below the accessory tubercle. In total none of the Europeans is showing this accessory tubercle, in contrast to one African and five out of 13 Australasians. Furthermore we have found six P^3 and five P^4 in which an elevation of the marginal ridge occurs without any signs of an accessory tubercle on the OES.

4.1.3 Accessory Ridges

A wide spread feature in *H. sapiens* are maxillary premolar accessory ridges (see fig. 3.4). 47.6% of third premolars exhibit a MaxPAR on the enamel and on the dentine there are even more, with half the teeth presenting an accessory ridge (fig. 4.2a). In fourth premolars there are even more accessory ridges. 73.8% possess some on the enamel and 78.6% on the EDJ. A comparison of the mesial and distal locus reveals that there are nearly twice

as many distal than mesial MaxPARs in P^3s (fig. 4.2b). In P^4 the distribution is more homogenous, nevertheless there are more distal accessory ridges too. Most of the mesial ridges coincide with a distal one on the same tooth.

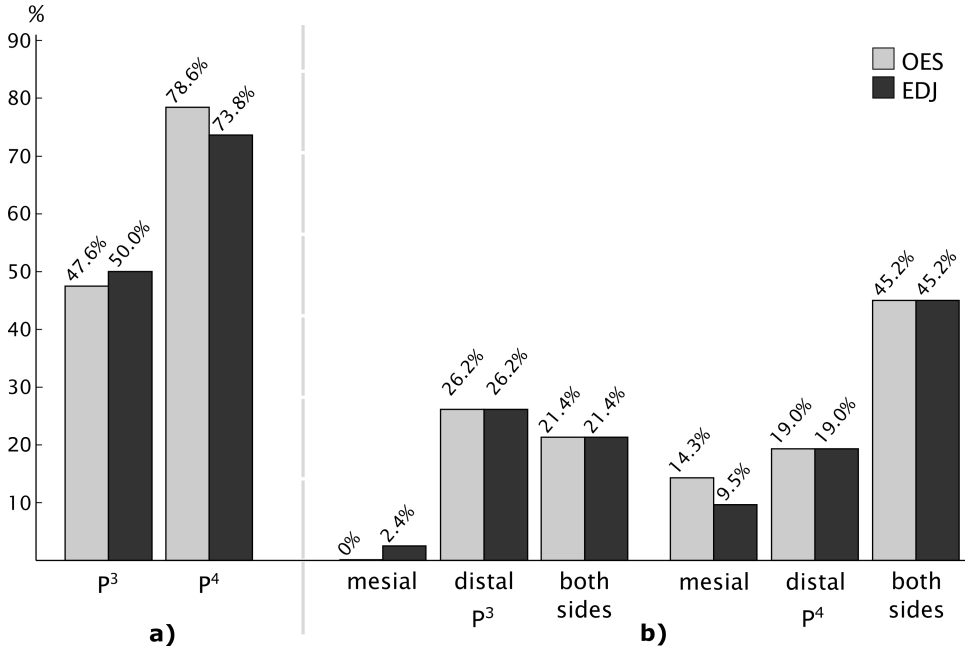

Figure 4.2: a) Total amount of maxillary premolar accessory ridges in P^3 and P^4. b) Comparison in occurrence of MaxPARs at the mesial and distal locus in P^3 and P^4.

All continental groups have in common that they show less accessory ridges on their P^3s than on the P^4s, and they also share that the ridges are more frequent on the distal locus (fig. 4.3). The highest frequency of accessory ridges in P^3s is found in Europeans. Africans exhibit a little bit less accessory ridges on their OES than Europeans with just 50%, in contrast to 56.3%. On the EDJ only 35.7% of the Africans exhibit this feature, whereas 68.8% of the Europeans have at least one accessory ridge. In contrast, only 33.3% of the Australasian group is showing MaxpARs on the OES and 41.7% on the EDJ. In P^4s the Australasian group leads, with 84.6% of the individuals presenting an accessory ridge on the distal and/or mesial locus on their OES, and 69.2% on the EDJ. In 78.6% of the Europeans an accessory ridge is expressed on the OES and EDJ. Africans have the lowest frequency with 73.3% of the individuals showing a MaxPAR on either EDJ or OES.

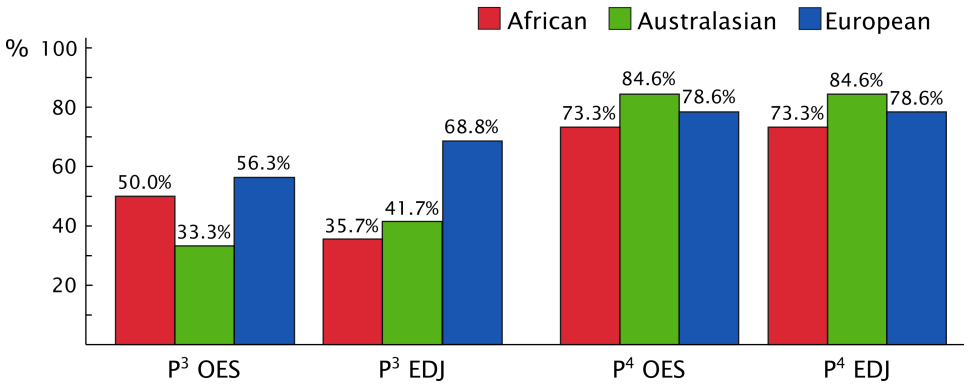

Figure 4.3: Occurrence of maxillary premolar accessory ridges in the human continental groups.

4.2 Geometric Morphometrics

After determining the qualitative traits and their frequencies in the continental groups, we now know which features could affect the results of our GM approaches. In table 4.2 the percentages of variation explained by the first five PCs for the four different data sets in both teeth are given. These were used to calculate the results of the Anderson test in shape space without *P. pygmaeus* as an outgroup (table 4.3). The values which exceeded 2 are highlighted. In those cases with a velue less than 2, the combination of two PCs reflects mainly noise, which means that we should not put much weight on the two-dimensional plot. However, if, for instance, PC1/PC2 is lower than 2 but PC2/PC3 lead to a value higher than 2, also PC1 can be used for evaluation. Only the first three principal components were taken into account for a detailed examination, because the higher-numbered ones explain to less variation and graphical display becomes difficult.

Table 4.2: The percentage of explained variation of the first five Principal Components in shape space.

	P^3				P^4			
PC	Crown	Cervical	EDJ	Combined	Crown	Cervical	EDJ	Combined
1	38,02	40,57	22,10	30,69	48,19	54,25	47,48	28,98
2	28,61	26,98	18,93	15,10	34,30	29,45	11,67	18,63
3	12,16	14,25	11,23	9,97	6,93	7,56	7,37	10,76
4	6,90	7,89	10,99	8,35	3,35	3,62	5,87	9,34
5	5,78	3,38	7,35	5,76	2,14	1,67	4,76	6,34

Table 4.3: Anderson Test for shape space.

	P^3				P^4			
PC	Crown	Cervical	EDJ	Combined	Crown	Cervical	EDJ	Combined
1 - 2	0,847	1,736	0,251	5,172	1,236	3,952	17,804	1,886
2 - 3	7,464	4,208	2,830	1,799	24,995	18,501	2,048	2,901
3 - 4	3,333	3,612	0,005	0,328	5,541	5,703	0,504	0,195
4 - 5	0,323	7,327	1,687	1,435	2,159	6,287	0,424	1,455

4.2.1 Principal Component Analyses

Crown outlines

The distribution of shape for crown outlines of upper third premolars is shown in figure 4.4 and for upper fourth premolars in fig. 4.6. The first three PCs explain 78.79% of the total variance for P^3s, 89.42% are explained in P^4s. Both teeth present widely overlapping distributions of the geographically diverse human populations. High positive scores along the PC1 in P^3s (38.02%) are associated with teeth which are broad in the mesiodistal aspect but short buccolingualy, whereas high negative scores stand for a longer but narrower tooth. In PC2 (28.61%) the buccal and lingual part of the outline can be of a more equal volume (high positive scores) or the buccal part is more pronounced while the lingual part is reduced (high negative scores).
When *P. pygmaeus* is included in the sample of upper third premolars, we can see a partial overlap of both species (4.5). Actually it is only one orang-utan specimen that comes close to humans. In orang-utans the buccal part projects further mesial than in humans, whereas the lingual part of the outline is mesially reduced but extends more distally. In humans both parts of the outline tend to be of a more equal size. Furthermore there is a counter

clockwise rotation of the buccolingual axis in orang-utans, in contrast to a slight clockwise rotation in humans.

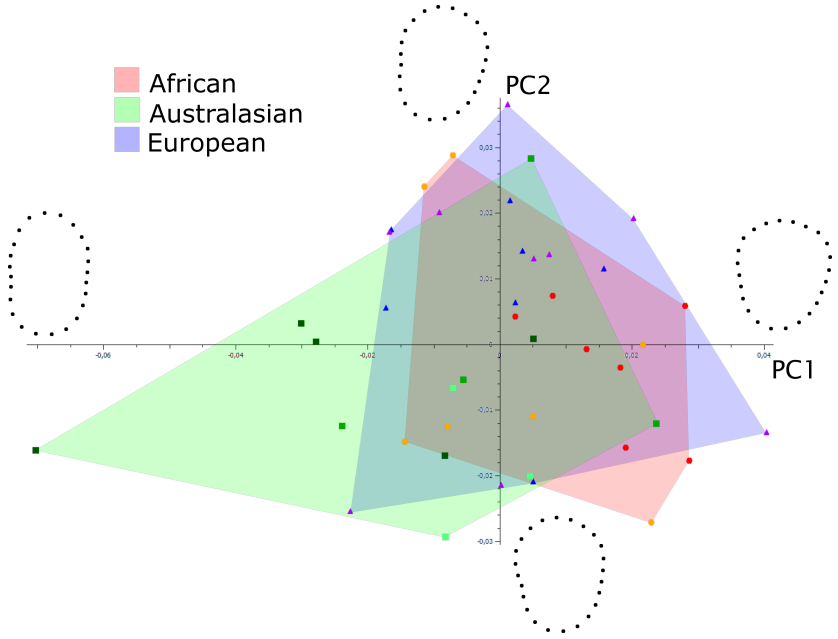

Figure 4.4: Variation of the crown outlines in UP^3 in shape space.

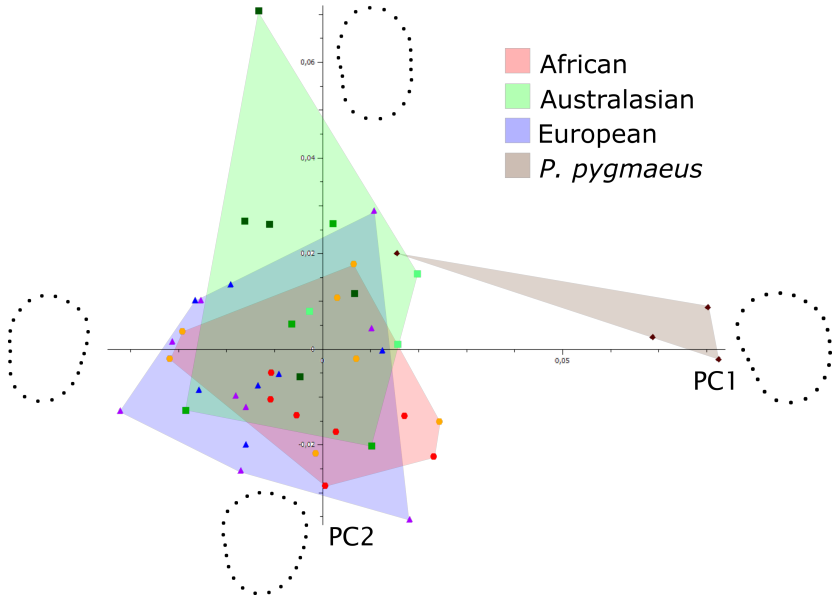

Figure 4.5: Variation of the crown outlines in UP^3 in shape space with *P. pygmaeus*.

In P^4s (see fig. 4.6) the same variable feature can be found on PC1 (48.19%), however the short but broad tooth is represented by high negative scores and a longer but narrower appearance is signified by high positive scores. PC2 (34.30%) however is associated by a clockwise (high positive scores) or counter clockwise (high negative scores) rotation of the buccolingual axis. This rotation is relative to the initial registration used in this approach, which fixes the tooth based on its buccal marginal ridge being horizontal. Based on the shape of the crown outline in upper fourth premolars, orang-utans cannot be separated from modern humans at all (fig. 4.6).

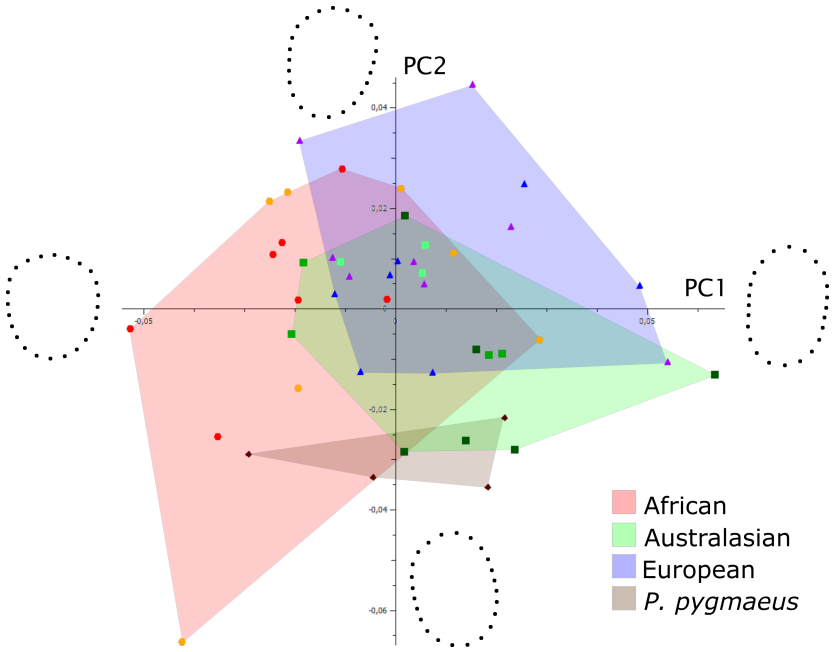

Figure 4.6: Variation of the crown outlines in UP^4 in shape space with *P. pygmaeus*.

Cervical outlines

All three continental groups overlap widely in the cervical outline in P^3s (fig. 4.7) with 81.79% of the total variance being explained through the first three PCs. Along PC1 (40.57%) there is a change in the relative size of the buccal part of the cervical outline compared to the lingual one. In high positive scores the lingual aspect is smaller than its counterpart. In high negative scores both parts are of a more equal size but the whole outline is

rotated in a clockwise direction. In PC2 (26.98%) there is a marked mesial constriction between the buccal and lingual part (high positive scores) versus no constriction (high negative scores).

In *Pongos* the cervical outline tends to possess a larger buccal aspect than in humans and the outline is rotated in between those species, but they partially overlap in shape space due to one individual of the orang-utans (fig. 4.8).

In P^4s the first three PCs account for 91.26% of total variance (4.9). A long and narrow cervical outline correlates with a high positive score in PC1 (54.29%). High negative scores indicate a shorter and broader outline which is rotated counter clockwise. While the European and Australasian continental groups overlap widely, the African group is shifted and expanding further in the direction of the low scores for PC1. In PC2 (29.45%) high positive scores are represented by an oval outline, whereas high negative scores represent a distal flattening.

P. pygmaeus cannot be distinguished from *H. sapiens* based on the shape of the cervical outline in fourth premolars (fig. 4.9).

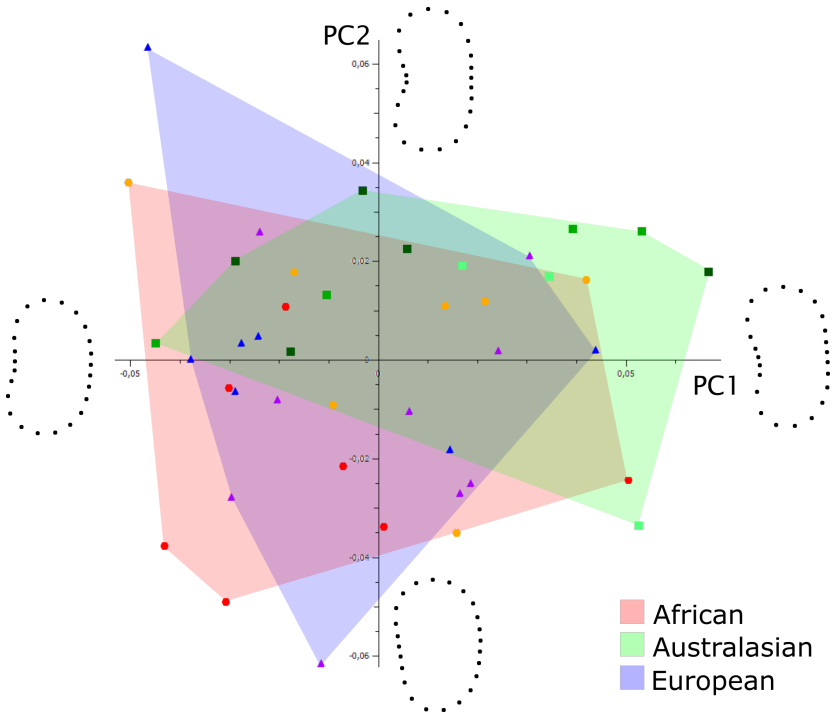

Figure 4.7: Variation of the cervical outlines in UP^3 in shape space.

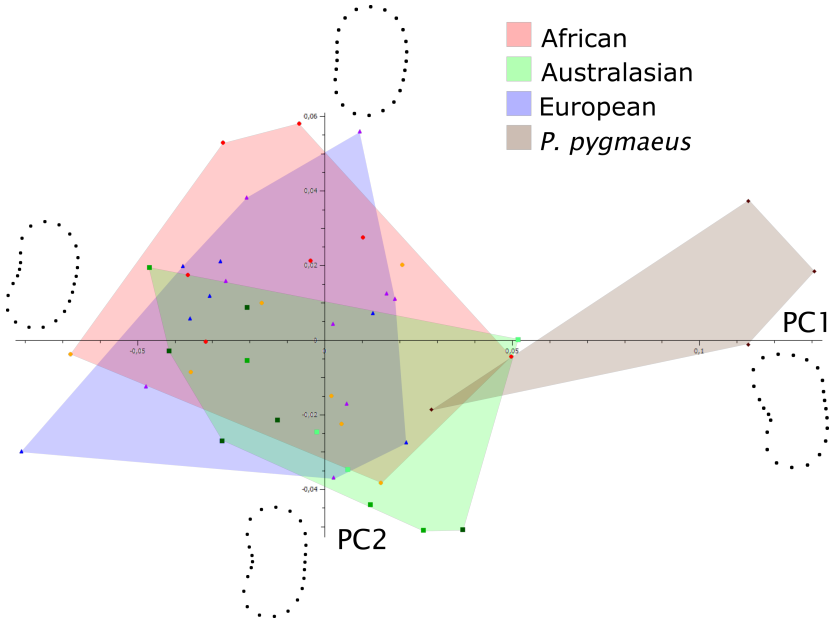

Figure 4.8: Variation of the cervical outlines in UP^3 in shape space with *P. pygmaeus*.

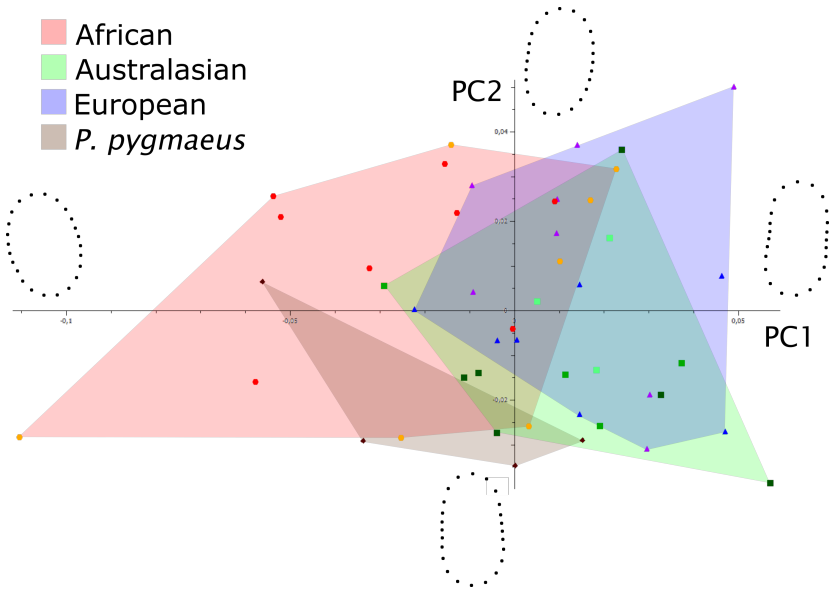

Figure 4.9: Variation of the cervical outlines in UP^4 in shape space with *P. pygmaeus*.

EDJ

The variability of the EDJ is represented in the figures 4.10 and 4.12. In third premolars 52.25% of the total variance is explained through the first three PCs. High positive scores in PC1 (22.10%) are attributed to a broad tooth with a long central groove. Especially the mesial and distal marginal ridges are far from each other and the tooth possesses relatively high horn tips, which are closer together. In high negative scores the central groove is short, which is reflected in the mesial and distal marginal ridges being close to each other and therefore the tooth gets a long but narrow appearance. The horn tips are low and far from each other. PC2 (18.93%) is assigned with high horn tips (high positive scores) versus low horn tips (high negative scores). Additionally the distal fossa moves from a more central position to a more distal position (high positive scores), respectively the distal part of the tooth is getting larger than the mesial one in high positive scores, whereas both parts are of a more equal size in high negative scores.

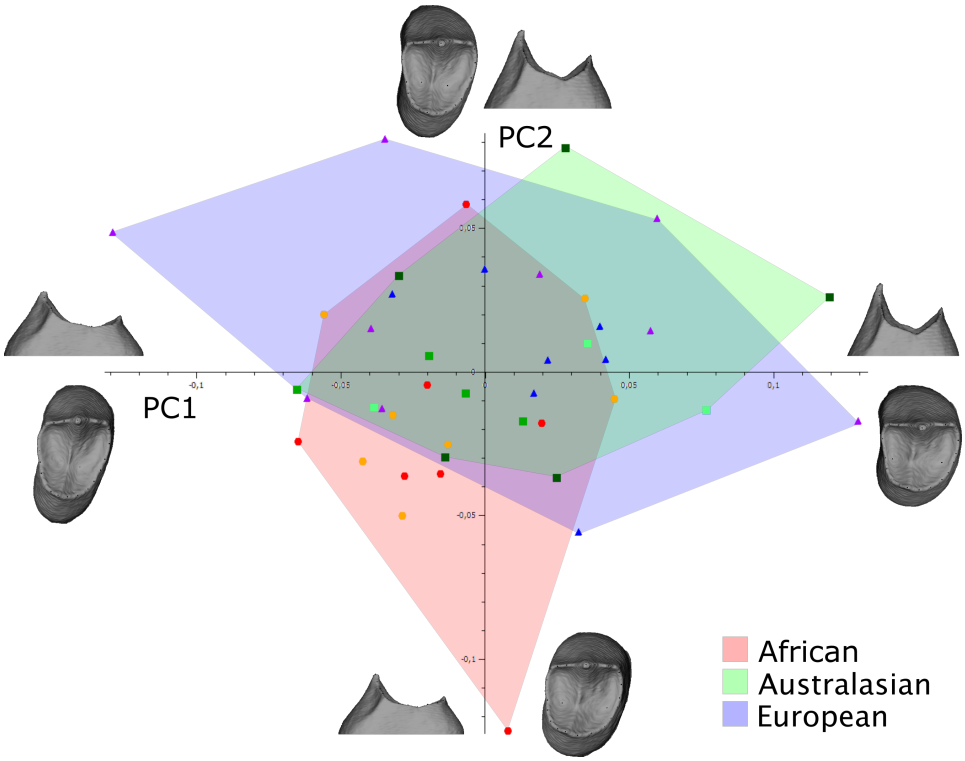

Figure 4.10: Variation of the EDJ in UP^3 in shape space.

Based on the EDJ orang-utans can be easily separated from humans in P^3s (4.11). They have much broader teeth, respectively the mesial and distal marginal ridges are much farther from each other than in humans, and *Pongos* have a longer central groove.

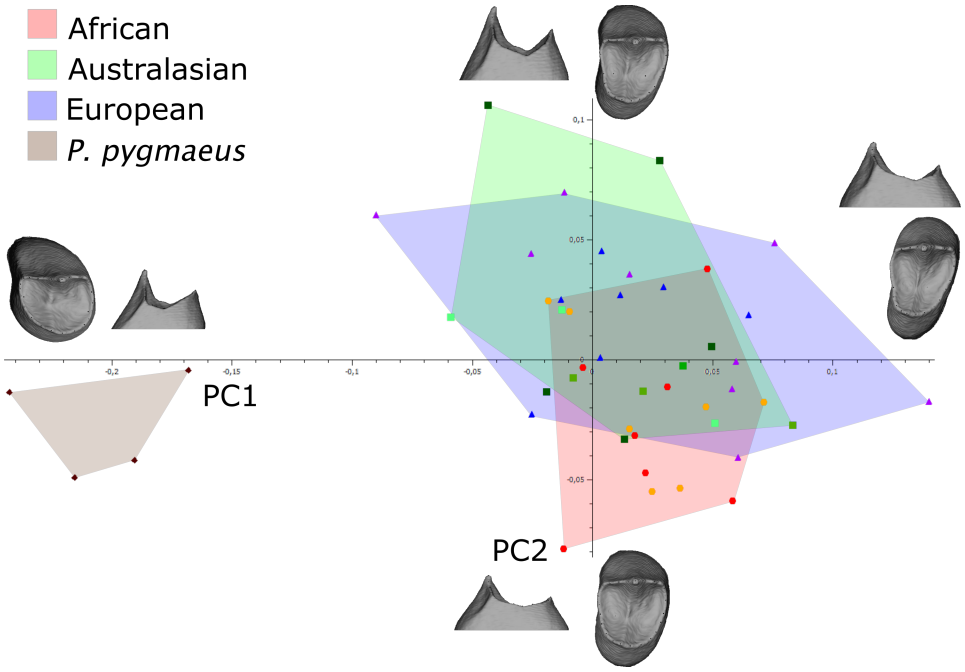

Figure 4.11: Variation of the EDJ in UP^3 in shape space with *P. pygmaeus*.

In fourth premolars EDJ (fig. 4.13) 66.52% of the total variance are attributed to the first three PCs. PC1 (47.49%) is associated with a broad tooth in which the central groove is long and therefore the mesial and distal marginal ridges are far from each other while the horn tips are close together (high positive scores). High negative scores are represented by a slim tooth with a short central groove in between narrow positioned mesial and distal marginal ridges, with the horn tips being far from each other. PC2 (11.67%) is signified by a more circular silhouette of the marginal ridges with low horn tips in high positive scores versus a more triangular position of the marginal ridges with high horn tips in high negative scores.
P. pygmaeus can be discriminated from *H. sapiens* through their longer central groove, and broader and more circular silhouette of the marginal ridges (4.13).

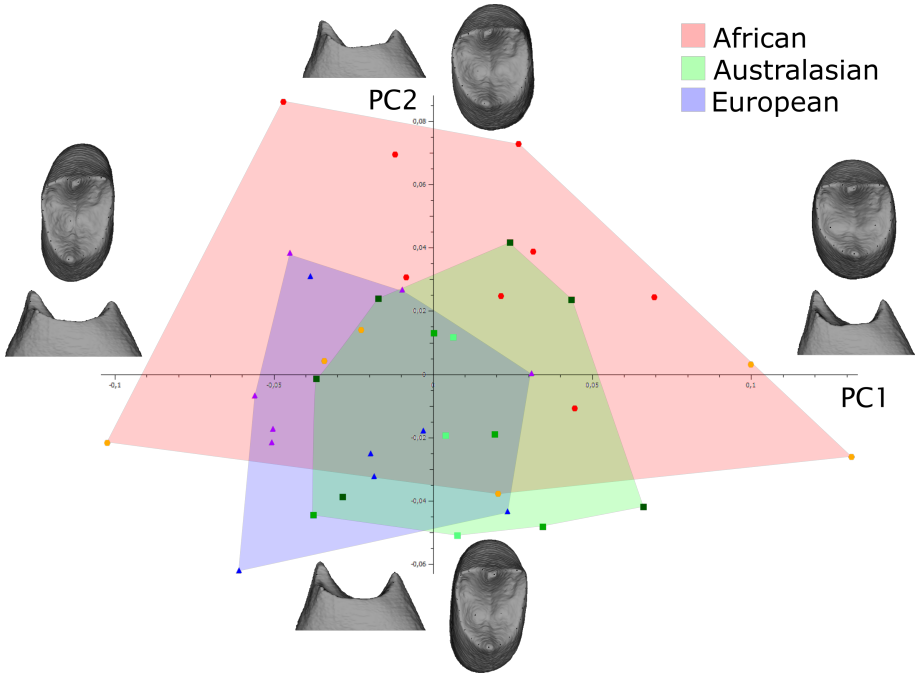

Figure 4.12: Variation of the EDJ in UP^4 in shape space.

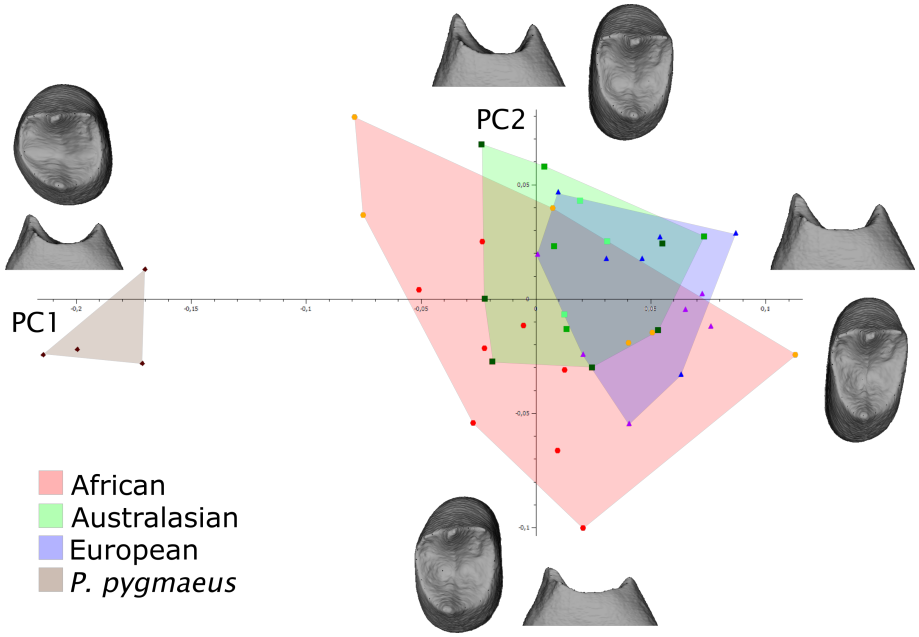

Figure 4.13: Variation of the EDJ in UP^4 in shape space with *P. pygmaeus*.

Combined data set

Finally the combined data set, the combination of landmarks and semilandmarks from the EDJ with the pseudolandmarks from the cervical outline, (see chapter 3.3.2) was examined. There is a complete overlap for all three human continental groups in both upper premolars for the combined data set. In P^3s (see fig. 4.14) the first three PCs explain 55.76% of the total variance, however only the first PC (30.69%) could be taken into account according to Anderson's sphericity test (see table 4.3). This applies to data with and without orang-utans included. High positive scores in PC1 indicate a long groove between the mesial and distal marginal ridges which are also far from each other, and therefore the whole tooth is broad. Additionally there is a medium crown height, measured from the cervical outline up to the base of the horn tips, and rather high horn tips themselves. In contrast, high negative scores indicate a short groove between mesial and distal marginal ridges, which are closer together, and thus representing a narrower tooth. We observed a mesial constriction at the height of the cervical outline. Additionally the body of the crown is quite high but the horn tips themselves are low. However, in both, positive and negative, scores for PC1 the horn tips of paracone and protocone tend to be of equal height.

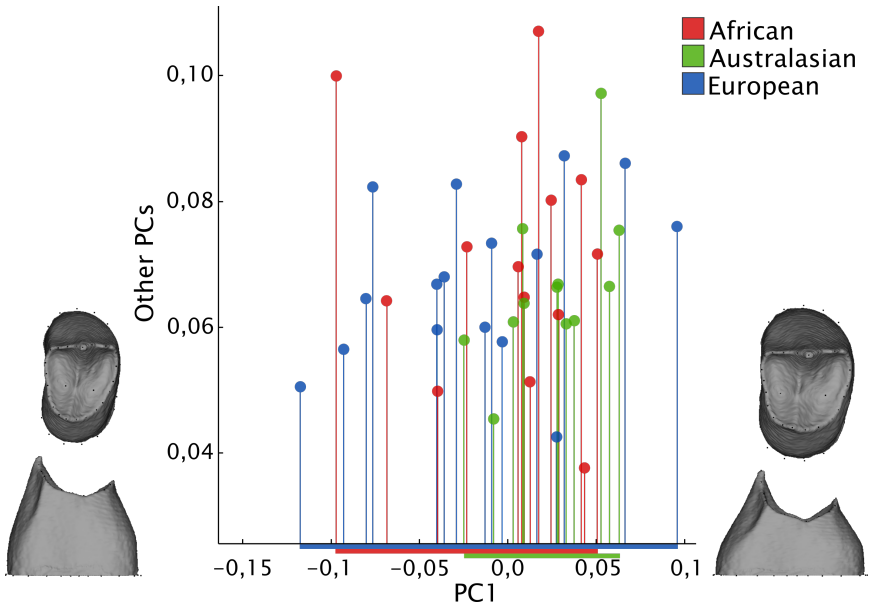

Figure 4.14: Variation of the combined data set in UP^3 in shape space.

Pongos differ from humans in their greater breadth of the tooth, naturally featuring a longer central groove. The crown itself is low, however the paracone is much higher than the protocone. Notably, there is no mesial constriction at the height of the cervical outline in orang-utans (see fig. 4.15).

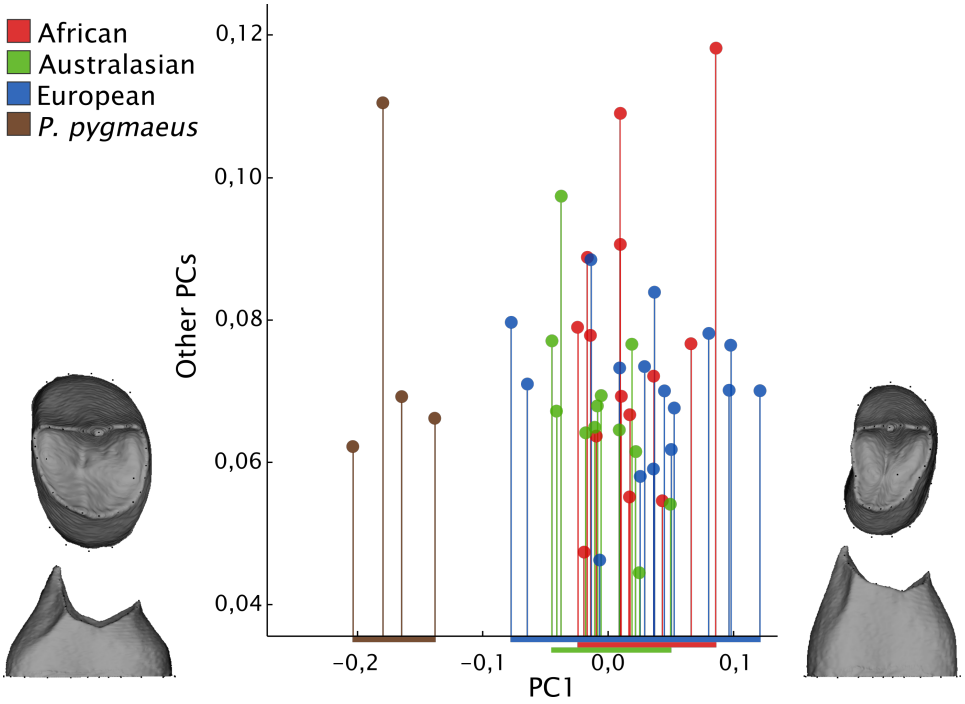

Figure 4.15: Variation of the combined data set in UP^3 in shape space with *P. pygmaeus*.

In fourth premolars (see fig. 4.16) the first three PCs account for 58.37% of the total variance. In PC1 (28.98%) high positive scores represent a low crown height with the distal fossa being positioned more lingually. Also the distal part of the buccal marginal ridge (distal from the paracone) tends to be in a straight line with its mesial counterpart (mesial from the paracone). In high negative scores the crown height is much larger, while the distal fossa is positioned buccally. The distal aspect of the buccal marginal ridge is curved and therefore the marginal ridges together have a more circular silhouette. High positive scores in PC2 (11.67%) stand for a narrow tooth with a short groove, surrounded by high marginal ridges, especially on the lingual side. The paracone is placed further mesially while the protocone is

further distal from the buccolingual axis. There is also a clockwise rotation at the cervical outline. In high negative scores the tooth is broad with a long groove surrounded by low marginal ridges. The paracone is positioned further distally while the protocone is further mesial of the buccolingual axis. The cervical outline rotates counter clockwise.
Pongos differ from humans in such a way that they have a broader tooth with a longer central groove and a lower crown height in contrast to the narrower tooth in humans with a shorter central groove, but a higher crown (see fig. 4.17).

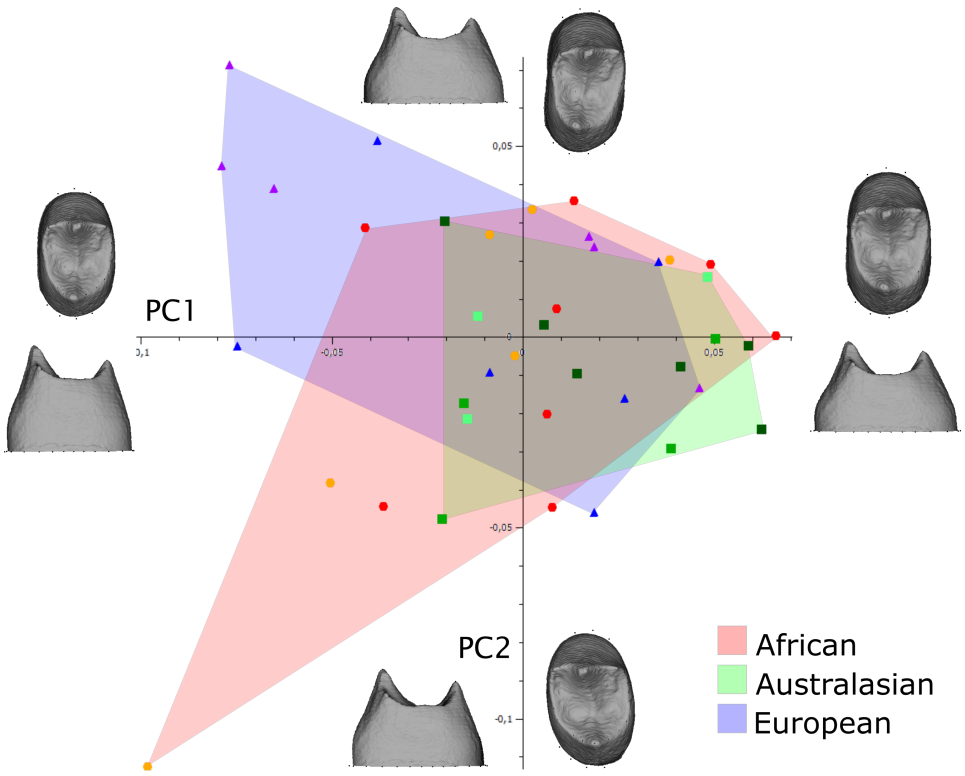

Figure 4.16: Variation of the combined data set in UP^4 in shape space.

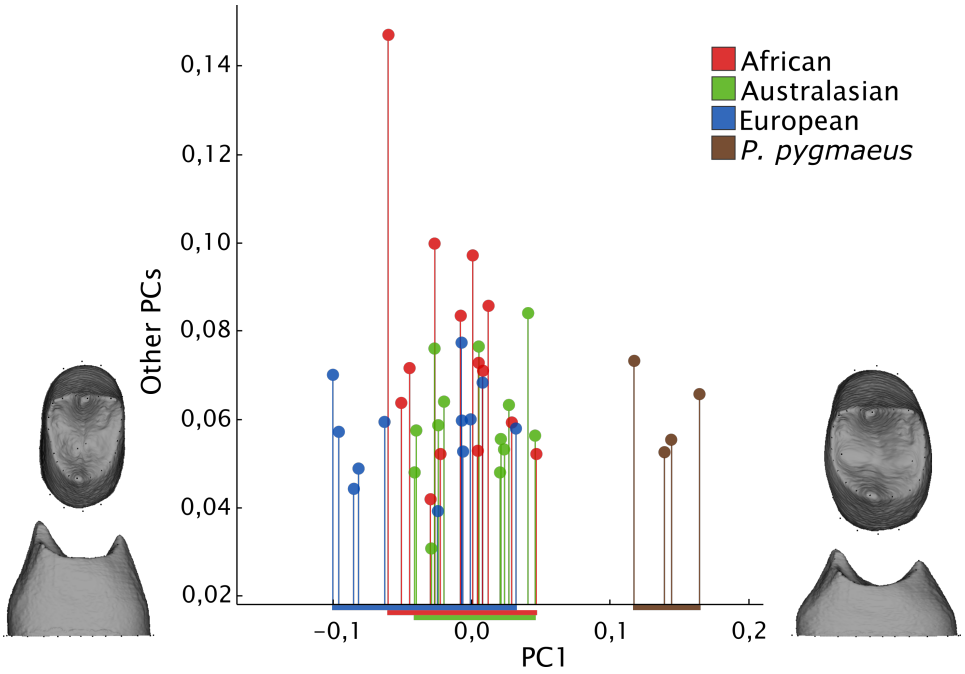

Figure 4.17: Variation of the combined data set in UP^4 in shape space with *P. pygmaeus*.

4.2.2 Partial Least Square Analysis

While it is interesting to analyse how single features vary in a particular tooth, it is also important to know how shape traits (cervical and crown outline, EDJ) covary together on the same tooth or how the two tooth types (PP^3, PP^4) covary. For each premolar type we compared the cervical and crown outline with each other and each outline with the EDJ. Additionally the combined data set was compared between P^3 and P^4. All our results of the Partial Least Square Analysis show a great overlap for all continental groups. None of these groups could be distinguished based on any of these covariations.

The plot for the left and right first singular warps (percentage of total squared covariance for pair 1 = 51.7%, pairwise correlation between singular warp 1 left and singular warp 1 right r1 = 0.648), and the actual shape changes correlated with each other are visualized in fig. 4.18 for EDJ and cervical outline in third premolars. They can be understood as shape changes in the EDJ that best explain shape variation in cervical outline,

and vice versa. The main changes affect the height of the horn tips and their relative distance to each other, the height of the marginal ridges and the orientation of the buccal marginal ridge on the EDJ, and the intensity of the mesial constriction on the outline. If the constriction is only slightly visible, than the tips arise high above their basement, and they are closer together. The marginal ridges are high too and the buccal marginal ridge proceeds from mesio-buccal to disto-central (in positive scores). In negative scores the constriction is more pronounced while the horn tips are low and far from each other. Additionally the marginal ridges are low themselves and the buccal marginal ridge proceeds from mesio-central to disto-buccal.

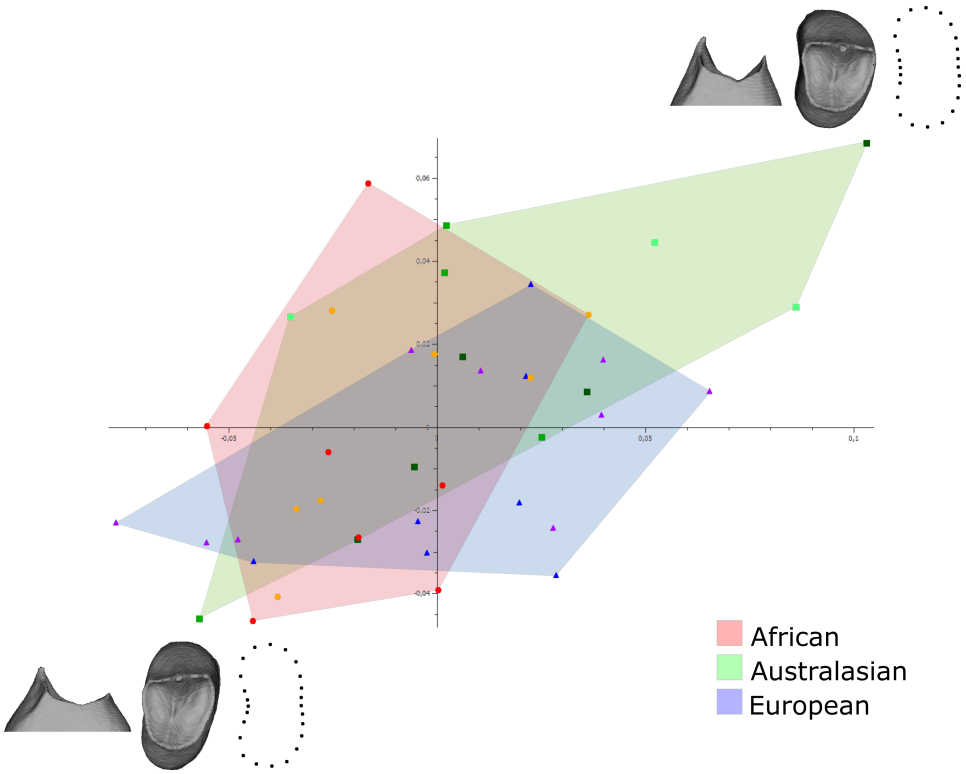

Figure 4.18: PLS in third premolars for EDJ against cervical outline.

In the PLS between EDJ and crown outline of third premolars (r1 = 0.6198 for pairwise correlation; 45.01% of total squared covariance; see fig. 4.19) the EDJ interacts in the same way with the crown like it has done with the cervical outline (see above). The main variation is found in the height and position of the horn tips, the height of the marginal ridges, and the orientation of the buccal marginal ridge. In high positive scores the crown outline has a big and broad buccal part while the lingual part is reduced which leads to a more triangular shape. In high negative scores both parts are of a more equal size and therefore the outline has a more oval shape.

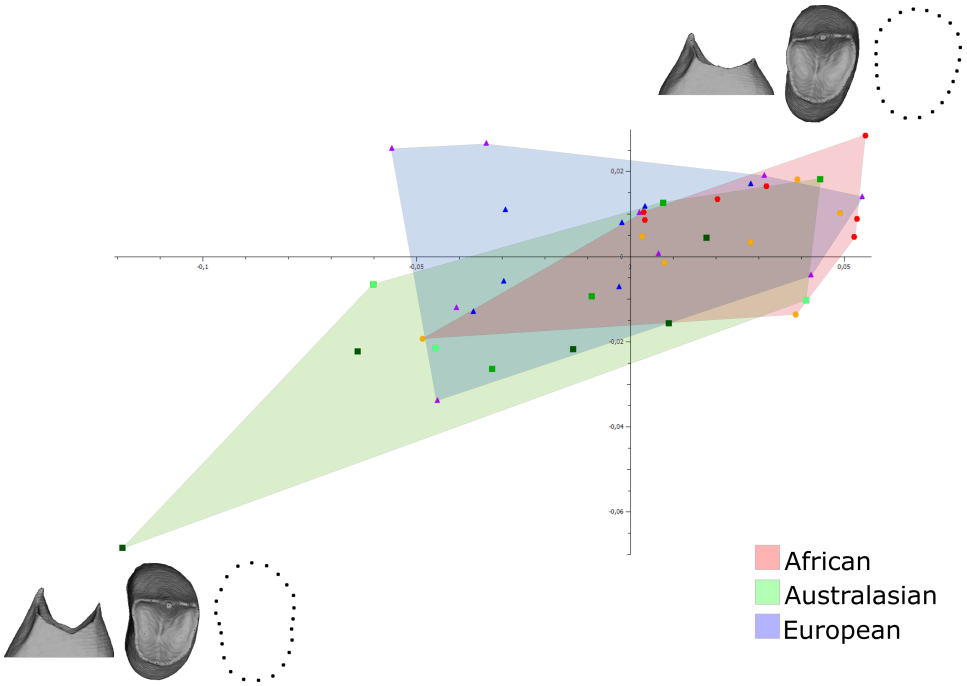

Figure 4.19: PLS in third premolars for EDJ against crown outline.

The crown outline and cervical outline were compared too in P^3s (r = 0.7016 for pairwise correlation; 49.62% of total squared covariance; see fig. 4.20). Both outlines keep very similar shapes from positive to negative scores. The main variation that can be found is a counter clockwise rotation for the cervical outline in negative scores accompanied by a slight clockwise rotation for the crown outline. In high scores the cervical outline does not show any signs of rotation whereas the bucco-lingual axis of crown outlines is rotated slightly counter clockwise.

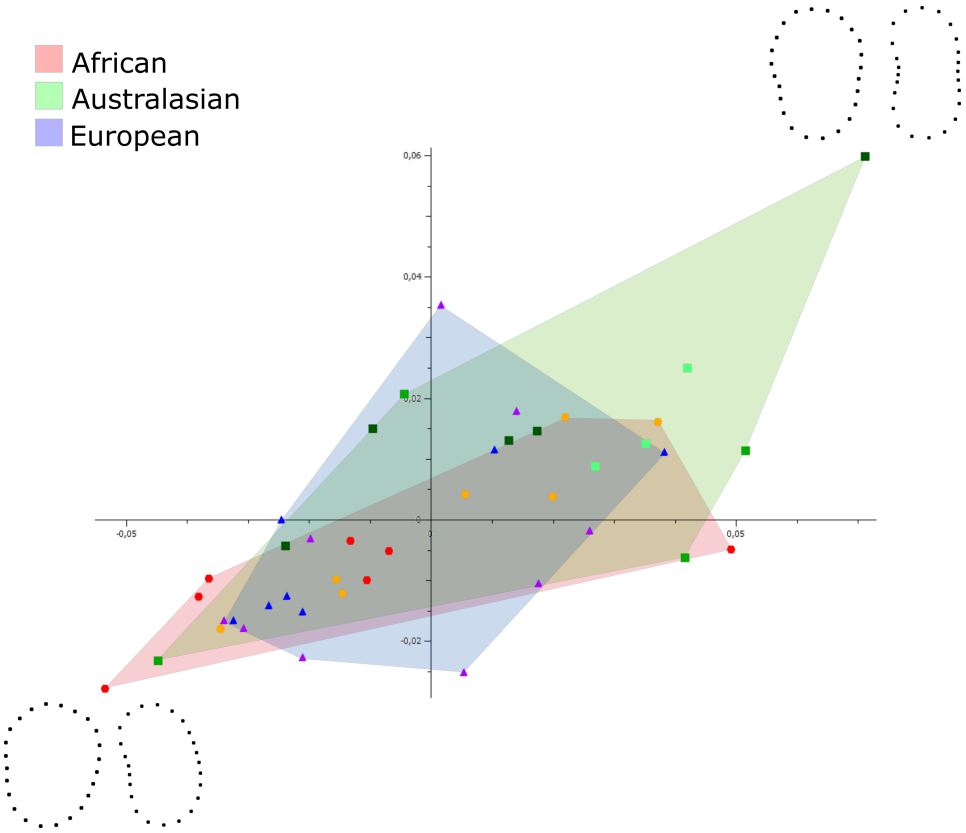

Figure 4.20: PLS in third premolars for cervical against crown outline.

In fourth premolars the PLS between EDJ and cervical outline (fig. 4.21) results in a pairwise correlation of r1 = 0.7564 (79.11% of the total squared covariance explained). In high positive scores the cervical outline is egg-shaped with a counter clockwise rotation, while the marginal ridges on the EDJ are far from each other, forming a circle and indicating a broad tooth. Therefore the two fossae are far from each other too. The horn tips however are positioned more centrally. In high negative scores the cervical outline is ellipsoid without any rotation. The EDJ shows that the mesial and distal marginal ridges are very close together, forming a triangular shape, and the tooth is much narrower. The central groove is very short and both horn tips are far from the centre.

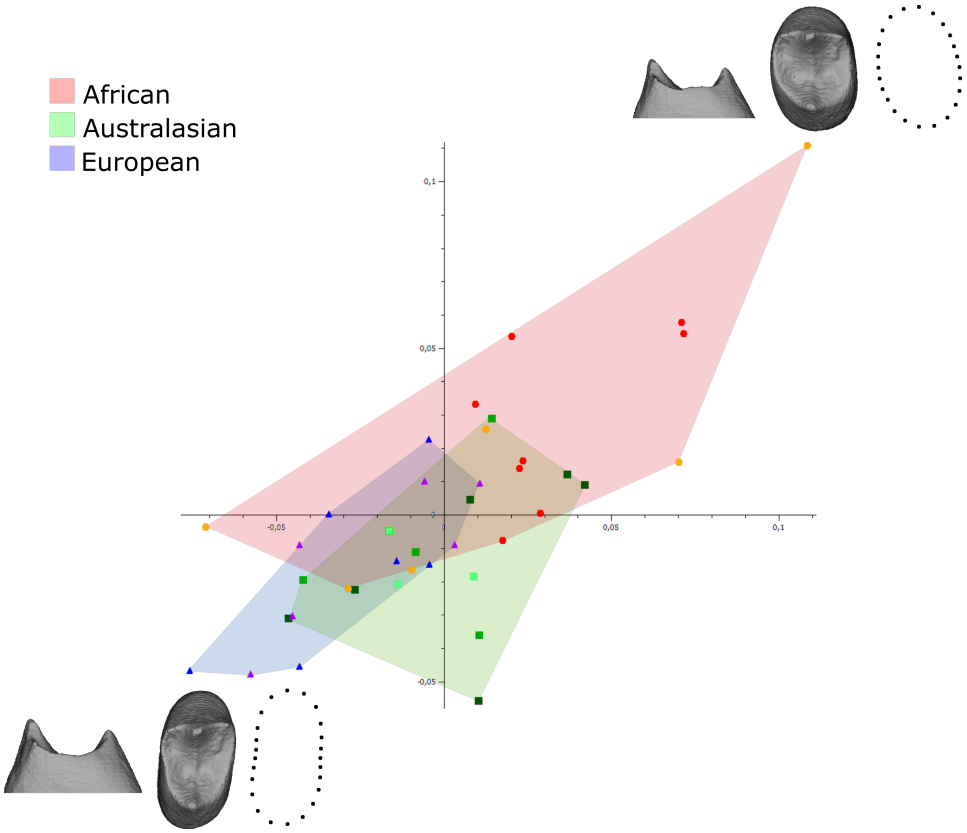

Figure 4.21: PLS in fourth premolars for EDJ against cervical outline.

In the PLS between EDJ and crown outline in P^4s (r1 = 0.7561 for pairwise correlation; 70.57% of total squared covariance; see fig. 4.22) high positive scores correlate with an ellipsoid crown outline and EDJ, both indicating a narrow and long tooth. The central groove is short, the marginal ridges form a triangle and the tips are far from each other. In high negative scores however the outline is broader and more circular. The EDJ features a circular silhouette of the marginal ridges with a long central groove and the horn tips being close together, which indicates a broad and short tooth.

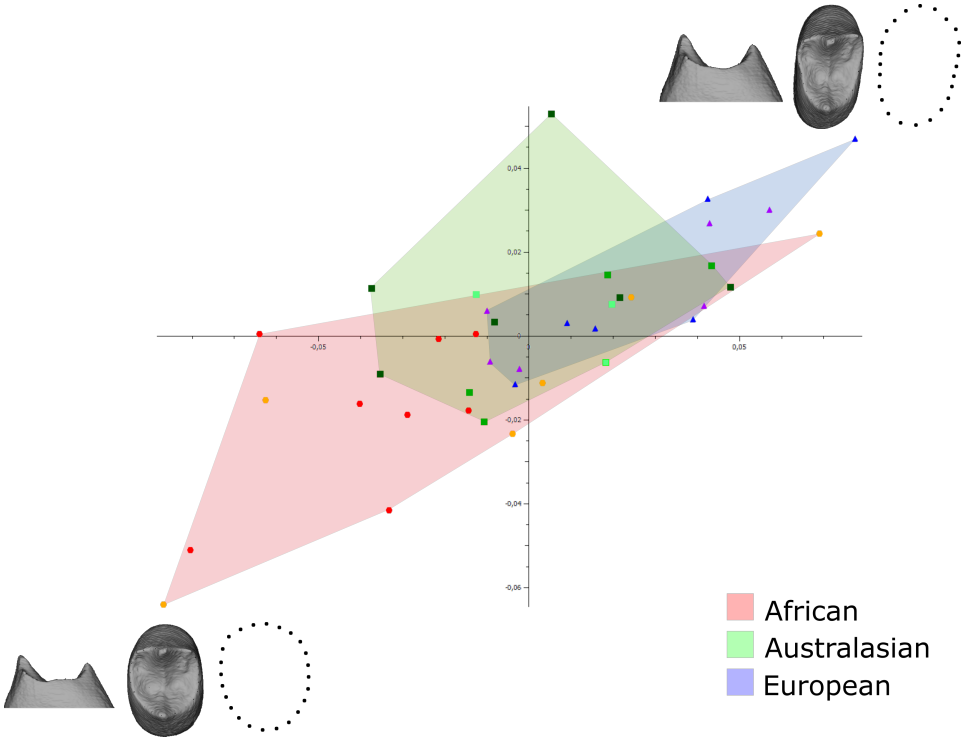

Figure 4.22: PLS in fourth premolars for EDJ against crown outline.

The pairwise correlation between cervical outline and crown outline for fourth premolars is r1 = 0.8524 with 75.68% total squared covariance (fig. 4.23). The main features that change is not only the rotation of both outlines in different directions, like in third premolars. In P^4s high positive scores of both outlines are ellipsoid. While the crown outline does not show any rotation, so does the cervical outline, with a slight counter clockwise rotation of the bucco-lingual axis. In high negative scores both outlines tend to be shorter and broader, especially the crown outline gets broader in the buccal half. The crown outline has a counter clockwise rotation whereas the cervical outline rotates in a clockwise direction.

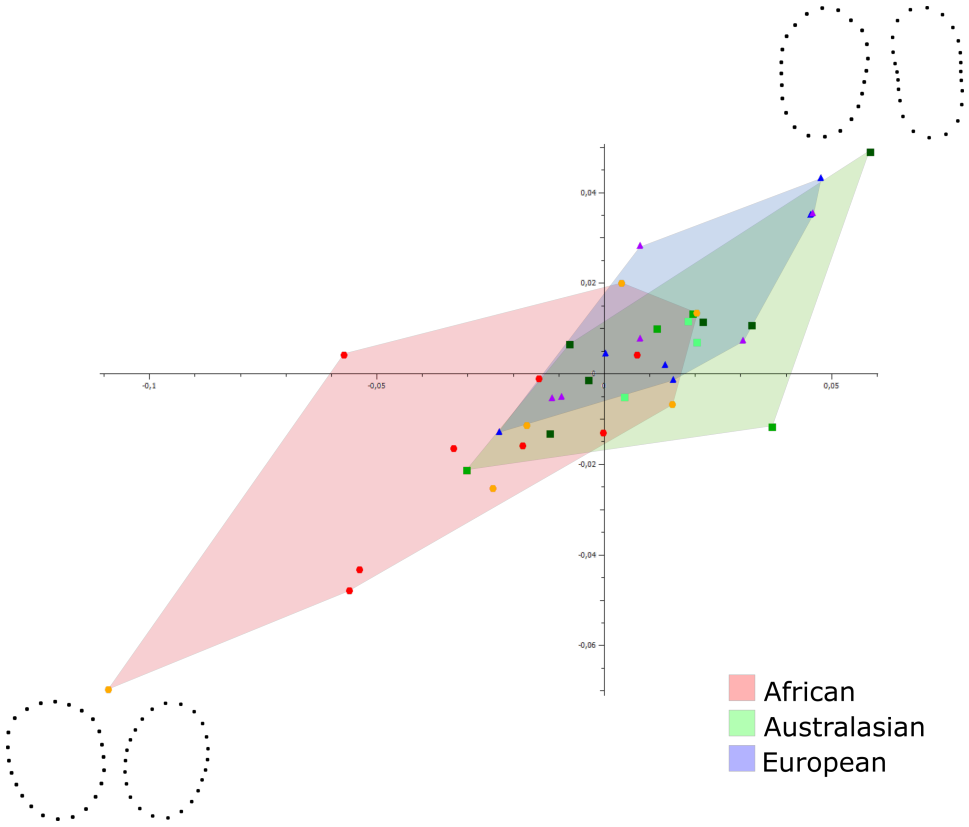

Figure 4.23: PLS in fourth premolars for cervical against crown outline.

To detect shape covariation between third and fourth premolars, a PLS was done for the combined data set (r1 = 0.8286; 71.50% of total squared covariation; see fig. 4.24). The most interesting observation is that the PLS confirms a speculation that seems obvious but was never proven before based on 3D data (or perhaps not even on 2D data), namely that both teeth would show coupled trends of shape variation. In high positive scores the relative height of the horn tips is low, but the whole crown is high. Both teeth are narrow and the marginal ridges possess a triangular shape. The P^3 has a mesial constriction at the cervical outline, which does not exist in P^4s. In high negative scores both teeth tend to be broader with circular marginal ridges. Their crowns are relatively lower, whereas the horn tips are a bit higher in positive scores.

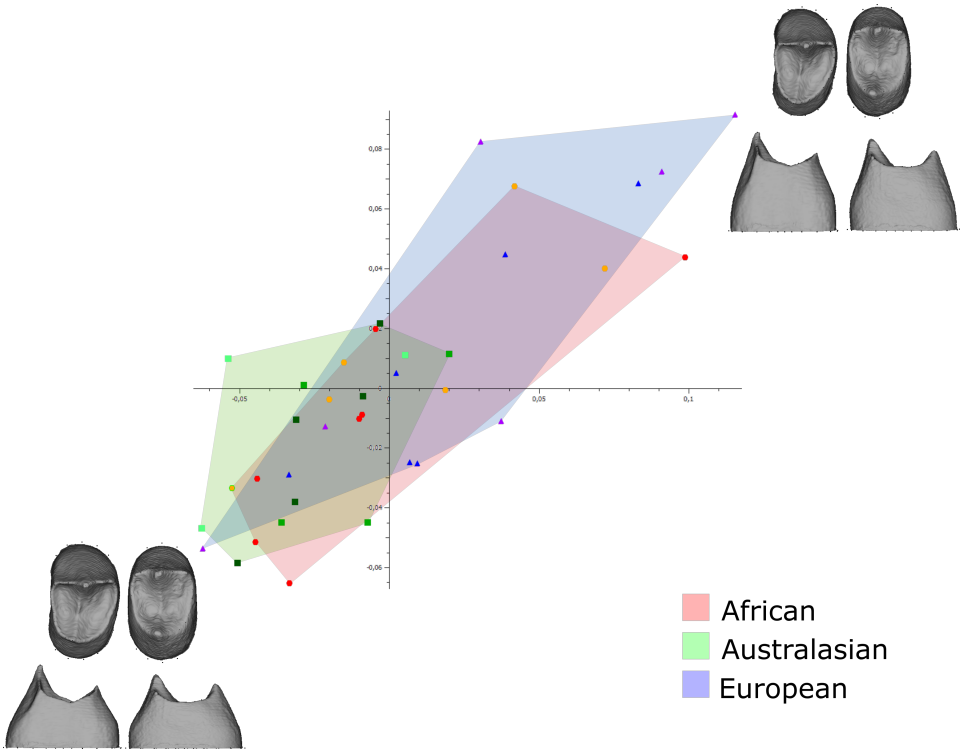

Figure 4.24: Variaton of the combined data set in UP4 in shape space.

4.2.3 The Influence of Size

A Principal Component Analyses in form space shows how big the teeth of *P. pygmaeus* are in comparison to *H. sapiens* (for example fig. 4.25 shows the PCA in form space of the combined data set in third premolars). Even though still all continental groups overlap widely, there is a slight tendency for larger and smaller teeth in some of the groups. For a clearer picture regarding size, we used the natural logarithm of centroid size (lnCS) to compare size information in all four data sets within human populations and between humans and orang-utans. Figure 4.26 presents the boxplots.

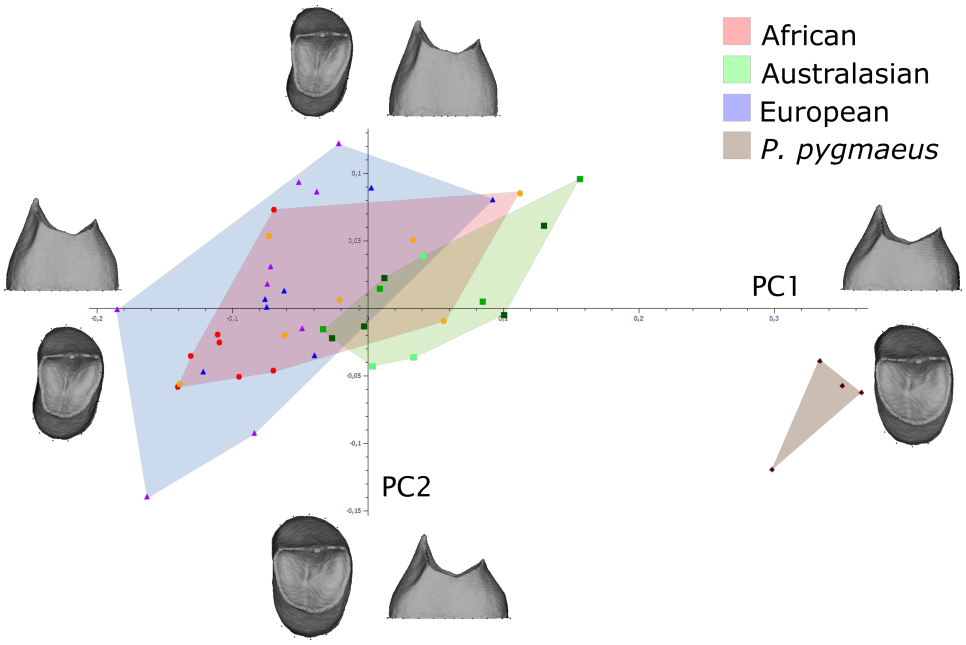

Figure 4.25: Variaton of the combined data set in UP^3 in form space.

The considerable size of the *P. pygmaeus* teeth is striking, but expected. They deviate high significantly from humans in terms of size in all traits and for both teeth (Mann-Whitney-Test with a Monte Carlo permutation: $p < 0.001$). To test for size differences among the three continental groups, a Kruskal-Wallis-Test with a Monte Carlo permutation was performed. In third premolars it showed that there are disproportionally more differences than could be expected by chance (EDJ: $p < 0.001$; cervical: $p < 0.001$; crown: $p < 0.001$; combined: $p = 0.003$). In fourth premolars both outlines

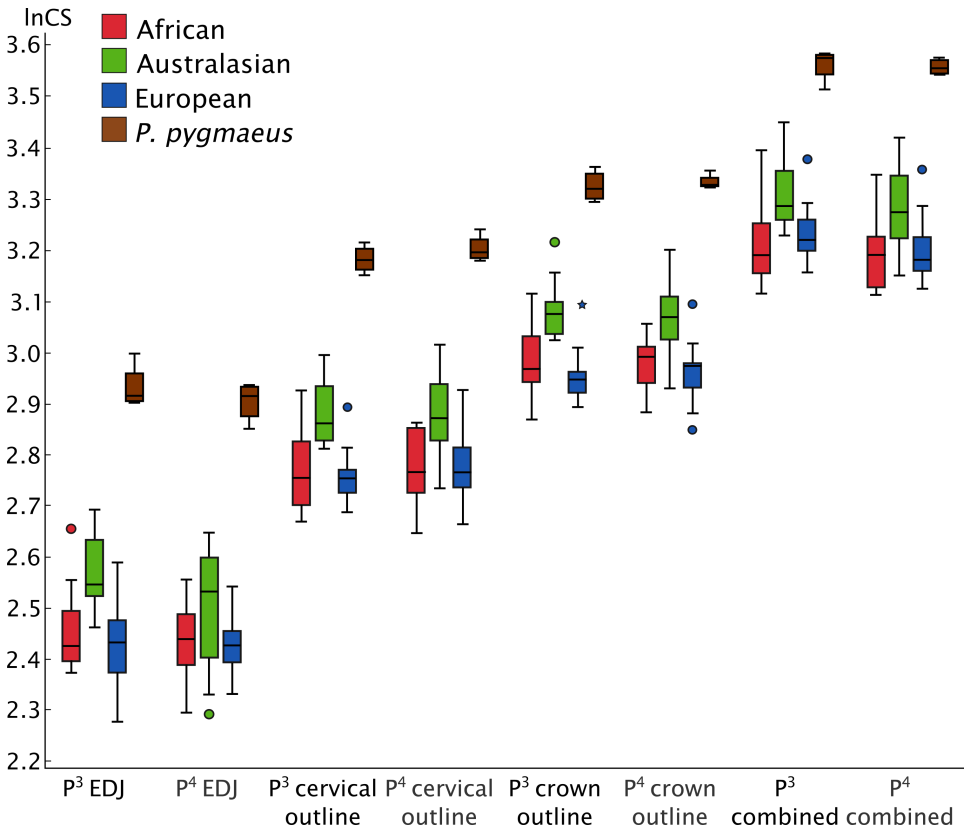

Figure 4.26: Size differences between *P. pygmaeus* and the human continental groups in both upper premolars.

show a highly significant difference (cervical: p = 0.004; crown: p = 0.006), whereas the combined data set (taking the EDJ combined with the cervical outline into account) exhibits only significant size differences (p = 0.03). Based on a 5% level of significance, there are no differences in size in the EDJ (p = 0.061) To determine deviations between pairs of continental groups, a Mann-Whitney-Test with a Monte Carlo permutation was performed for each possible pair. These tests suggest that European and African upper premolars do not differ significantly in size, based on the four compared traits (table 4.4). Nevertheless there is a significant or even highly significant size difference between Australasians and the other two continental groups. Their teeth tend to be bigger for the compared traits.

Also the particular populations were tested for deviations in size (fig. 4.27). A Kruskal-Wallis-Test with a Monte Carlo permutation showed that there are disproportionally more differences than could be expected by chance in the combined data set for P^3s (p = 0.013), but not in P^4s (p = 0.203).

Table 4.4: Level of significance for size differences between the continental groups: AF - African; AA - Australasian; EU - European (Mann-Whitney-Test with a Monte Carlo permutation).

tooth type		trait							
		Cervical		Crown		EDJ		Combined	
		EU	AF	EU	AF	EU	AF	EU	AF
P^3	EU		0.922		0.179		0.579		0.724
	AA	< 0.001	0.003	< 0.001	0.003	< 0.001	0.002	0.001	0.003
P^4	EU		0.769		0.221		0.587		0.511
	AA	0.003	0.004	0.004	0.011	0.047	0.043	0.053	0.012

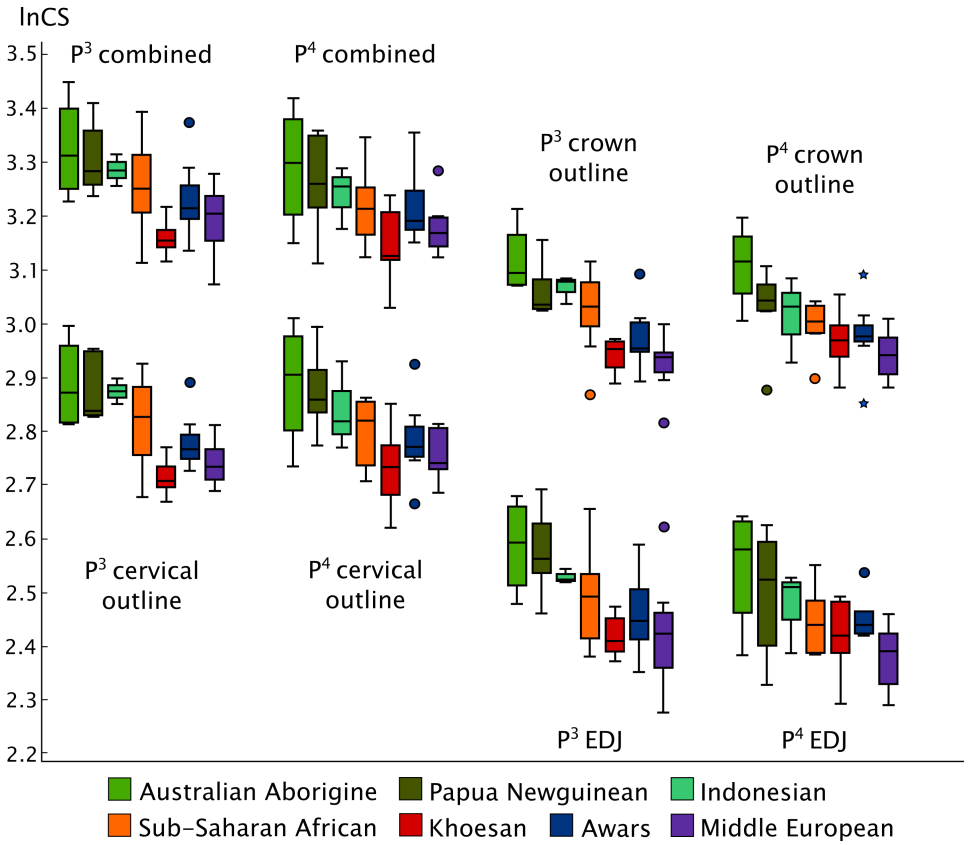

Figure 4.27: Size differences between human populations in both upper premolars.

In third premolars, the Khoesan have significantly smaller teeth than Australian Aboriginals or Papua New-Guinean indigenous people, and middle Europeans have smaller teeth than Australian Aboriginals, Papua New-Guinean or Indonesians (table 4.5).

Table 4.5: Level of significance for size differences between third premolars in human populations for the combined data set (Mann-Whitney-Test with a Monte Carlo permutation).

	Papuan	Indonesian	African	Khoesan	Avars	European
Aborigine	1.00	0.859	0.172	0.027	0.105	0.034
Papuan		1.00	0.171	0.019	0.109	0.013
Indonesian			0.384	0.085	0.261	0.035
African				0.285	0.827	0.332
Khoesan					0.157	0.541
Avars						0.611

To summarize, the Australasian continental group tends to have bigger teeth than Africans or Europeans. Especially third premolars of middle Europeans and Khoesan are small compared to the Australasian continental group. The question arises, whether there is an effect of size on the shape of upper premolars. To answer this question, a multivariate regression was performed for the combined sample in third and fourth premolars. The shape variables were treated as dependent variable, lnCS as the predictor. The percentage of total shape variance explained by size is called allometry (fig. 4.28).

Altogether, allometry is very small in human upper premolars. In P^3s, only 4.3% of the shape variance can be explained by size. Small teeth are relatively broader with the paracone horn tip being slightly more distal and the protocone horn tip more mesial from the buccolingual centre line. Also the paracone is much higher than the protocone. The buccal marginal ridge is very long and features, together with the other marginal ridges, a broad appearance of the EDJ, with the protocone being closer to the centre of the tooth. In large teeth, both horn tips are of a more equal height and positioned along the buccolingual centre line with the protocone being far from the centre. In total, the appearance of large teeth is slender with higher mesial and distal marginal ridges, and a mesial constriction at the level of

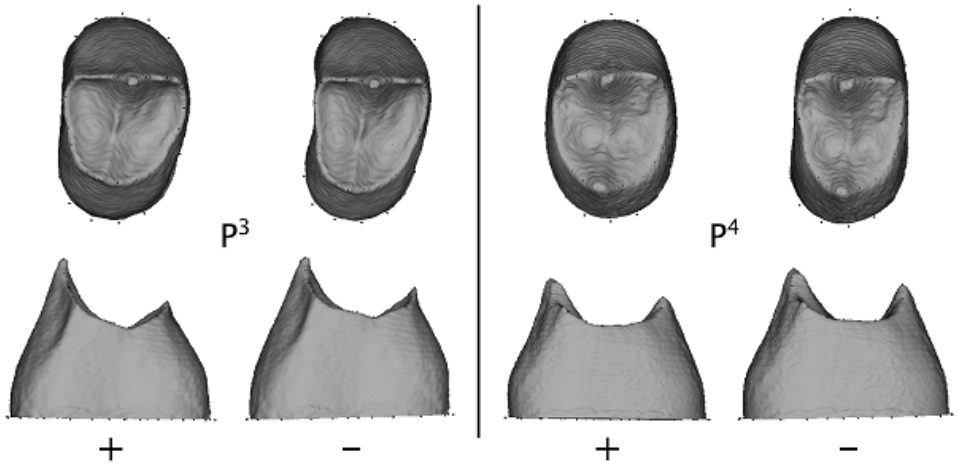

Figure 4.28: Allometry in third and fourth upper premolars. The morphs show a 25% positive and negative difference in size from the mean.

the cervical outline for the roots of the canine.

The allometry for P^4s is 4.6%. Small P^4s are short but broad, in total fairly oval, with both horn tips being very low above their origin. The marginal ridges together form an oval. In contrast large teeth are long but slender, both horn tips arise high above their origin, and the marginal ridges form a triangle.

Even though our female sample is very small (combined data set: $P^3 = 8$ females, 21 males; $P^4 = 5$ females, 22 males) we tested if size is different for the two sexes in the combined data set. A Mann-Whitney-Test with a Monte Carlo permutation was performed for lnCS in the two groups. In P^3s we found a significant size difference between male and female individuals ($p = 0.019$), whereas in P^4 the size difference remained at the border of being significant ($p = 0.050$).

Chapter 5

Discussion

The aim of this Master thesis was to determine the shape and size variability of the 3-dimensional crown morphology in modern human upper premolars, as well as to include the variability of some qualitative traits.

5.1 Non-Metric Features

In the case of the non-metrical traits the results are mainly consistent with previous studies which are solely based on the outer morphology (OES) of teeth. According to Scott and Turner (1997) odontomes, Uto-Aztecan teeth, and tricuspid premolars are very rare, with a frequency of roughly 5% in human populations. More precisely, Uto-Aztecan premolars have been found in Native American populations only (Delgado-Burbano et al., 2010; Johnson et al., 2011); accordingly, their appearance in this sample, which does not contain any Native Americans, cannot be expected. Due to the declaredly small sample we were not able to find any of the former mentioned features, neither on the OES nor on the enamel-dentine junction (EDJ), except for one tricuspid third premolar out of 42 individuals. In this specific case the second lingual cusp can only be found on the EDJ, but not on the OES. While there is a distinctive additional horn tip on the EDJ, on the OES a tricuspid tooth would be formed by a buccolingual groove dividing the lingual cusp into a protocone and an additional hypocone (Turner et al., 1991).
Accessory marginal tubercles are more common than the before mentioned

non-metrical traits, even though they occur only on fourth premolars in our sample. They are more frequently found on the distal locus than on the mesial one. One seventh of the sample is showing an accessory tubercle on the OES, but only one third of those individuals featuring a tubercle on the OES shows also an elevation on the marginal ridge on the EDJ beneath. However this elevation does sometimes occur without any signs of an accessory tubercle on the OES. Turner et al. (1991) state that apparently there is no involvement of the dentine in the formation of the accessory marginal tubercle (or premolar mesial and distal accessory cusps, as they are calling it). Skinner et al. (2010), but also Corruccini (1987) or Butler (1956), state that ameloblasts can be responsible for certain features on the enamel which might not occur on the EDJ. It is possible that accessory marginal tubercles are among those features which are mainly formed due to uneven deposition of the enamel during the tooth development. Furthermore it is worth noting that accessory tubercles appear in quite different frequencies in our continental groups, i.e. in 6.7% of the Africans, 38.5% of the Australasians, and none in Europeans. In upper first molars Kanazawa et al. (1990) was able to find a similar pattern, where Europeans tend to have low abundances of anomalous cusps or tubercles, while they are much more common in Asian populations, Australian aboriginals and African populations. A bigger sample would be needed to ascertain the frequencies of accessory marginal tubercles in upper third and fourth premolars, particularly, how often they occur on the EDJ in contrast to the OES, and to determine if there is a statistically significant difference between human populations.

The transverse crest on premolars has not found much attention yet in literature. Even though Bailey (2002) found this crest to be much more robust in *H. neanderthalensis* than in *H. sapiens* on the OES, there was no focus yet to compare the transverse crest and its manifestations on upper and lower premolars between different human populations. The comparison of EDJ and OES showed that all manifestations of the crest tend to be equally represented on both surfaces. The generalized version of the transverse crest starts at the paracone and is following a bucco-lingual direction until it is interrupted by the mesio-distal groove (see chapter 3.2). An uninterrupted form, where the crest proceeds to the protocone, is occurring more often on third than on fourth premolars. It is most frequently found in Europeans, followed by Australasians, and least often in Africans. The doubled crest is

more often present in P^3s than in P^4s and does not occur in our European sample at all, while it is most frequently found in Australasians, followed by Africans.

The most common qualitative trait in upper premolars are accessory ridges. Half of the third premolars in our sample, and nearly three quarters of fourth premolars, have an accessory ridge expressed on the EDJ, which is consistent with the results of Burnett et al. (2010) and Mihailidis et al. (2013), who both focused on the OES for the evaluation of this trait. Concordant with these two studies accessory ridges are found more often on the distal aspect of the tooth than on the mesial aspect. Additionally we suppose that the occurrence of a mesial accessory ridge is connected with the occurrence of a distal ridge on the same tooth. The general pattern of frequency of accessory ridges in third and fourth premolars, and the frequency of appearance at the distal and/or lingual locus were found to be similar in all continental groups. When comparing the accessory ridges between populations it shows that most accessory ridges on P^3s are found in Europeans, followed by Australasians and Africans. In P^4s we find more equal distributions in the continental groups. In contrast to our work, Burnett et al. (2010) arrive at somewhat different results in their study. They have found the highest frequency of accessory ridges on P^3s in North-East Asian/Asian derived populations, and lower frequencies in Africans and Europeans. Even though the North-East Asian and Asian derived populations are leading in P^4s too, the rate of accessory ridges is much more similar between the populations. The difference in the prevalence of accessory ridges in Burnett et al. (2010) and this current study can probably be explained by the difference in sample size, which is much larger in Burnett et al.'s study. However, results of the two studies are consistent in the fact that maxillary accessory ridges in fourth premolars are much more uniformly distributed across human populations than in third premolars.

5.2 Geometric Morphometrics

The geometric morphometric analyses of cervical and crown outline, EDJ, and the combined data set (combination of EDJ and cervical outline) produce the results expected under our null hypothesis. There are no differences

between the three continental groups, even though the individuals were sampled from quite diverse populations with extremely varying lifestyles and nutritional habits. These outcomes corroborate the cooking hypothesis (Kraus et al., 1969; Brace et al., 1987; Wrangham et al., 1999; Lucas, 2004).This hypothesis is based on the assumption that the human dentition has lost a great deal of its functional demands due to the invention of cooking. Now there is only a minimal need to chew and break down the food into small particles remaining, an activity that would be energetically expensive (Carmody and Wrangham, 2009; Wobber et al., 2008). This function of the masticatory apparatus is now partly replaced by cooking the food which leads to an improved digestibility because the heat breaks up starch, denatures proteins, and as a side effect also kills pathogens in the nourishment (Wrangham and Conklin-Brittain, 2003; Wrangham and Carmody, 2010). Humans can even satisfy their nutritional needs without having any teeth in their jaw, because they can eat cooked papescent food. For all other species losing all permanent teeth would be a warranty to die, given that the individual is no longer able to subsist. Due to this partial loss of function, teeth had more opportunities to vary in form randomly without affecting the fitness of their carrier too much (of course within limits because, for instance, malocclusions might cause many other problems, including breakage of teeth or problems with the temporo-mandibular joint). Additionally they were reduced in size, like most of the organs, that reduced their function (Brace and Mahler, 1971; Brace et al., 1987).

To evaluate the variability in upper premolars it is important to contemplate which factors might affect them. The morphology of teeth is strongly influenced by the form and function of adjacent teeth and their antagonists. According to Kraus et al. (1969) the gradual transition from an anterior to a posterior tooth form is best represented in the premolars. All posterior teeth, starting with the third premolar, are divided through the central groove into a buccal and a lingual part. While the third premolar still has a canine-like buccal aspect with a very tall and pointed paracone, the fourth premolar is more similar to the adjacent first molar, with both, buccal and lingual part, being much closer in size and morphology (Hillson, 1996, see also). The cusp height decreases from the canine to the molars in general.

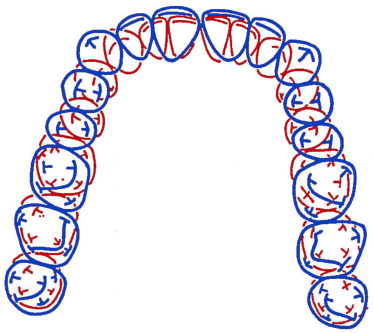

Figure 5.1: Outlines of upper teeth (in blue) supperimposed over lower teeth (in red) during occlusion (reproduced from Hillson, 1996).

The tooth antagonists in maxilla and mandible ought to be complementary counterparts of each other. During occlusion the protocone of upper premolars makes contact with the lingual and distal marginal ridge areas of the lower premolars and the lingual marginal ridge area of the first lower molar, in case of the P^4 (fig. 5.1). Therefore the protocone is called supporting cusp and the paracone is called guiding cusp. The supporting cusp usually is positioned more centrally in the tooth than the guiding cusp to provide a more stable occlusion (Kraus et al., 1969; Hillson, 1996).For the same reason the supporting cusp is usually more roundish then the guiding cusp and has contact on all sides to the antagonistic teeth, while guiding cusps only have contact on one side. In the case of upper premolars this is the lingual side of the paracone. This guides the movement of the mandible relative to the maxilla during phase I of the power stroke, which is essential for masticatory function. The supporting cusp should be less variable to maintain a proper occlusion during the central phase of the power stroke (maximum intercuspation), whereas the guiding cusp can vary more because it is mainly involved in the first and third phase of occlusion (Kraus et al., 1969). This assumption is supported by the non-metric traits, which are occuring more often on the guiding cusp in upper premolars or the corresponding structures like the central groove or the mesial and distal ridges. In contrast to this we cannot find a uniform pattern for a differentiated variability of certain cusps in our metrical analyses. Both tips always vary together in their height, either both are tall or both are low. However, the breadth of the paracone (seen in the crown outlines) is much more variable, than the one of the protocone. Our hypothesis is at least in some points confirmed. The paracone is more variable than the protocone in terms of non-metrical features, however, in metrical terms there is no consistent result. At least the breadth of the paracone supports our hypothesis, whereas the height of the horn tips does not. In contrast to lower premolars Krenn (2015) it seems that both cusps in the upper premolars are subject to tightly associated shape constraints that generate limits

for diverging metrical variation.

One feature that we observed to vary extensively on the EDJ and on both outlines of both upper premolars is the length-to-breadth ratio. There are rather ellipsoid teeth, which are bucco-lingually elongated, in contrast to more circular teeth, which are mesio-distally broader. The crown outline exhibits an oval shape in the elongated form or a more triangular shape in circular teeth. Another markedly varying feature on the EDJ is the shape of the horn tips. In third premolars the paracone is always taller than the protocone whereas in fourth premolars the horn tips are much more similar in height, which is consistent with Kraus et al. (1969) and Hillson (1996) for the OES. In addition to the relative height of horn tips to each other, both horn tips together can show a higher relief or a lower one instead. They can also vary in their relative position to each other, i.e. being closer together towards the centre of the tooth or being far apart near the margins (see fig. 4.10 - 4.17). When examining the combined data set, it shows that a higher relief with horn tips positioned closer together is correlated with a circular shape and a lower body of the crown, while a lower relief correlates with more separated horn tips, an ellipsoid tooth, and a quite high crown body. To sum it up, upper premolars tend to vary more in the over all morphology than in any single specific trait. While in P^3s the guiding cusp shows more variation than the supporting cusp, in P^4s we were not able to verify the before mentioned assumption that the supporting cusp is more stable, at least when metrical data is used.
There is a strong correlation between third and fourth premolars for their shape. Either both are ellipsoid or both are circular, which was expected due to the fact that both teeth are influenced by the same genes during the development of the dentition (Jernvall and Thesleff, 2000). According to Townsend (1985) there is a significant sexual dimorphism for both upper premolars in the mesio-distal and bucco-lingual crown dimensions, at least in Australian Aboriginals, where females tend to have ellipsoid tooth crowns while males have more circular crowns. However, intercuspal measurements, the distance between paracone and protocone, did not show any sexual dimorphism but rather higher variability and fluctuating asymmetry than in the crown diameters. It is not possible to reproduce these results in our study, because we do not have reliable information about the sex of the

individuals for most of our sample. Nevertheless, Townsend's explanation could apply to the variation found in our sample.

A conspicuous trait appeared in the cervical outline data, and accordingly also in the combined data set: a constriction that is found exclusively on the mesial side of the third premolar which results in a kidney shape of the outline (fig. 4.7). It was never found on the cervical outline of fourth premolars or on any of the crown outlines. This mesial constriction of the third premolar has been mentioned by Kraus et al. (1969), and Hillson (1996). In both cases they talk about a mesial concavity at the height of the cemento-enamel junction which extends to the mesial interradicular groove. Additionally Hillson (1996) noted that this concavity is not only present in third premolars with two or three roots, but it can also be found in specimens with only one root. Neither Martinon-Torres (2006) nor Gómez-Robles et al. (2011) have mentioned any signs of the mesial constriction in their research, where they were focusing on landmarks on the OES and semilandmarks along the crown outline. This supports our assumption that the mesial concavity can only be found at the height of the cemento-enamel junction. We propose this constriction could be related to spatial needs of the canine´s root, given that there is no diastema in humans. Therefore the roots of the canines could affect the adjacent premolars. According to Kraus et al. (1969, p. 245) *"... teeth are almost never aligned in the dental arch with their center axes parallel to a vertical line. Generally there is a slight mesial and a buccal or lingual inclination of the crown to varying degrees, ..."* This implies that the roots of the dentition are always orientated into a distal direction to varying degrees (fig. 5.2). The highest degree of mean angulation (measured from a vertical projection onto the occlusal plane) in the maxillary dentition is found in the incisors (29°in both). Canines possess the second highest angulation in the maxilla with 20.6°. In comparison to this, upper premolars are

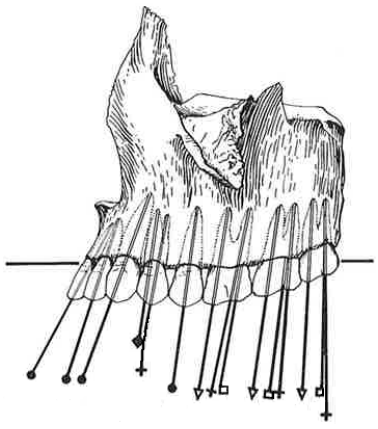

Figure 5.2: Lateral view of the upper dentition. Longitudinal axes of the roots are shown in orthographic view (repoduced from Kraus et al., 1969).

more perpendicularly aligned to the occlusal plane with their axial centres (P^3 buccal root: 9.6°; P^3 lingual root: 10.4°; P^4 root: 8.6°). This more pronounced angulation in maxillary canines than in premolars could be the reason for this constriction, to create space for the more distally projecting root of the canine. To validate this hypothesis a morphological comparison between canines and premolars of the same jaw would be needed to see whether or not the canine roots relate to the cervical outlines of third premolars.

If *Pongo pygmaeus* is included in our sample, some limitations of the outline analyses in shape space emerge. The two genera *Pongo* and *Homo* partially overlap in third premolars, and cannot be distinguished at all in fourth premolars. With size included (=form space), however, *H. sapiens* and *P. pygmaeus* are neatly separated. In contrast, the EDJ and combined data set do not show this problem. These analyses are able to separate clearly humans and orang-utans, both in shape and form space.

When comparing all four trait complexes, we suggest that the new technique of combining the EDJ surface with the cervical outline is much better suited to reflect the real three-dimensional morphology of the studied teeth, for instance, because the crown height from the base to the top is now part of the data. Moreover it is possible to see how the shape of the EDJ and the shape of the cervical outline affect each other. Skinner et al. (2008a, 2009a) was using a similar approach in his analyses, in which he was using landmarks and semilandmarks on the EDJ as well. However, the morphology of the cervix was gathered slightly differently. While this Master thesis is using pseudolandmarks on the projection of the cervical plane, Skinner and colleagues used semilandmarks along the cemento-enamel junction. The absence of real landmarks along the cervix, which would determine the starting point for the sequence of semilandmarks, is the major drawback of the method Skinner and colleagues used. The position of the first cervical semilandmark is depending on the configuration of true landmarks on the EDJ which leads to individual rotations of the whole set of semilandmarks that cannot be controlled. In contrast to this we constructed pseudolandmarks on the cervical plane by orientating the tooth based on the buccal marginal ridge of the premolars. This process also has a disadvantage, namely that

it is dependent on manually orientation. Still, it is more precise in premolars than the same process in molars, because the buccal marginal ridge in premolars is always very distinctive imprinted onto the EDJ, whereas molars are generally orientated with the help of the mesio-distal groove, the lingual groove, and the lingual side (Benazzi et al., 2012) or according to some points, which should result in a line that can be used for orientation (Benazzi et al., 2011a). Due to this reorientation all pseudolandmarks start their sequence (1 to 24) at roughly the same location and thus better comply to the argument of being homologous than if they were rotated depending on the relative position of a few true landmarks on the EDJ horn tips. We therefore think that this approach gives us a clearer picture of the morphological changes on the outlines.

With the factor size excluded, we were able to detect even subtle changes in morphology in shape space. However, in nature there is substantial size variation too. Thus size could be a parameter which effects the morphology of upper premolars among the investigated populations. Based on shape, our sample of *H. sapiens* does not differ markedly among the different populations. However in size at least some populations are different. As mentioned before Brace (1971; 1987) argued that he has found some evidence supporting the cooking hypothesis. In his papers he does not only mention morphological features as evidence, but more importantly he has concluded, that size reduction of teeth is the main event that had happened since humans started to cook. Brace states that there is a size gradient from the north, with smaller teeth, to the south, with bigger ones. Our results confirm that upper premolars of modern Europeans are significantly smaller than those of Australian Aboriginals, Papua New Guinea indigenous, and Indonesians. However, samples from Khoesan living in South Africa are not consistent with this hypothesis. In the research of Haeussler et al. (1989) they claim that Khoesans have microdontic teeth in comparison to nearby living Bantu populations. Our sample of Khoesan does not differ significantly from the sample of Sub-Saharan Africans,but is smaller than Australian Aboriginals and Papua New Guinea indigenous. Nevertheless, the effect of size on shape is quite small in upper premolars. Less than 5% of the shape variability in both teeth can be explained by size. In general taller teeth tend to be more circular, while smaller teeth are more ellipsoid. This could also imply that

taller circular teeth belong to males and smaller ellipsoid teeth belong to females (Townsend, 1985), especially when we consider that dental allometry is positively correlated with body weight (Corruccini and Henderson, 1978; Gingerich et al., 1982). Even though our sample only included a few females (and the morphological sex diagnosis is questionable in some cases), our combined data set showed a significant size difference between the two sexes for P^3s, but not in P^4s, confirming smaller P^3s in females. This could support the research of Townsend (1985), but our sample size is ways too small for truly supporting or declining this claim. A bigger sample size would be needed to reliably verify Townsend´s results.

Chapter 6

Conclusion

The main goal of this study was to investigate the intra- and intergroup variation in different modern human populations based on the morphology of both P^3s and P^4s.

Neither odontomes nor Uto-Aztecan premolars (also called disto-sagittal ridge) were detected on the OES or EDJ. However an additional lingual horn tip was found on the EDJ of one third premolar, but there was no indication for a tricuspid tooth on the OES. The rarely described transverse crest between paracone and protocone shows three different manifestations, an interrupted crest, an uninterrupted crest or a bifurcated one. All these versions of the transverse crest are represented in similar frequencies on the OES and EDJ, though on P^4s the uninterrupted crest and the bifurcated crest are rarely found. The three types are heterogeneously distributed in the three main continental groups of Africans, Europeans, and Australasians. The bifurcated form is mainly found in Africans and Australasians, while the uninterrupted crest is much more common in Europeans. The very common accessory mesial and/or distal ridges are equally represented on the inner and outer morphology of upper premolars too. In general accessory ridges are much more common on the distal locus than on the mesial ones and more often found in P^4s than in P^3s. In P^3s the frequency of occurrence is Europeans ¿ Australasians ¿ Africans, while in P^4s all continental groups show similar frequencies. Due to the fact that both features are equally represented on EDJ and OES we can assume that the manifestations of the transverse crest and accessory ridges are formed during tooth ontogeny on

the *membrana praeformativa* and are then transmitted onto the OES. The only non-metrical trait that is not equally expressed on OES and EDJ is the accessory marginal tubercle. An elevation of the marginal ridge on the EDJ underneath an accessory tubercle is only found in one third of the individuals presenting this feature on the OES. However, this elevation can also be found in individuals without any sign of a tubercle on the outer surface. Therefore we argue that this feature is not interrelated with any structure on the EDJ. Accessory marginal tubercles are mainly found in Australasians. In contrast to this there were only a few in the African continental group, and none in the European group. To sum it up, non-metrical traits are not equally distributed between modern human populations and therefore great care should be taken when performing a research that is based on a comparison between modern human populations and archaic hominids. In this case it would be much better to choose a wide sample from all over the world to represent the mean of modern humans.

Our geometric morphometric exploration of several morphological traits showed that both crown and cervical outlines are not suitable features to distinguish between *Homo* and *Pongo* based on shape space. Conversely, both the EDJ and combined EDJ-cervical outline landmark configurations allowed to separate these two genera on the basis of both P^3s and P^4s. If size is included both species separate clearly in all four data sets. If only human populations are considered, all four data sets show a complete overlap of all populations in shape space for both upper premolars, although we used a very diverse sample in terms of provenience, lifestyle, and diet. This outcome has been predicted by our hypothesis, because teeth have lost a great deal of their main function due to the cooking abilities of mankind (Wrangham et al., 1999; Lucas, 2004; Wobber et al., 2008; Wrangham and Carmody, 2010). In the absence of strong selective pressures, we cannot expect to find significant signs of adaptations to any lifestyle or diet in different modern human populations, but rather random variation. Our results exactly confirm this hypothesis. For dental anthropology based on metrics this implies also that it is only of minor importance which modern human population is chosen for comparisons with other groups such as archaic hominids because shape variation in modern human upper premolars is very similar.

Our results suggest that the main variation found in both upper premolars is the length-to-breath-ratio, which affects the whole morphology of the tooth. At the one hand there are ellipsoid teeth, which are bucco-lingually elongated on the cervical outline, crown outline, and also on the EDJ. They possess an oval crown outline, while the crown is higher with lower dentine horns. Additionally the horn tips are far apart from each other. On the other hand there are circular teeth, which are mesio-distally broader in all aspects. However, the crown outline is triangular, while the combined data set shows that the crown body is low. The relief of the horn tips is high and the horn tips themselves are closer together. There is a strong correlation between third and fourth premolars for their shape. Either both are ellipsoid or both are circular, which was expected due to the fact that both teeth are influenced by the same genes during the development of the dentition (Jernvall and Thesleff, 2000).
Nonetheless, the P^3s present a peculiar constriction on the mesial side of the cervical outline, also called mesial concavity, which is not seen in P^4s. We suppose that this constriction is caused by the upper canine root, which is on average deviating 20.6° (Kraus et al., 1969) from a vertical orientation in the jaw and projects strongly distally, whereas premolars are much more vertically orientated.
Our new approach of combining the EDJ and the cervical outline presents the advantage of considering the dentine surface from the cervical outline up to the horn tips. It shows all the features of both landmark configurations at the same time, how they are vary with each other, and furthermore incorporates the crown height as well.

In form space we can find a tendency between human populations. A test for size differences showed that middle Europeans possess significantly smaller upper third premolars than Australian Aboriginals, Papua New Guinean and Indonesian indigenous, while the third premolars of Khoesan are significantly smaller than those of Australian Aboriginals and Papua New Guinean. However the effect of size on the morphology is faint. In general, taller teeth tend to be more circular, while smaller teeth are ellipsoid.

Acknowledgement

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Finally I want to thank my family for the support through my whole study.

Appendix A

Table A.1: Further information regarding the sample.

Population	Individual	Age	Sex	Location	P3	P4
Khoesan	S16	9 – 13	?	South-Africa, Noitgedagt	+	+
Khoesan	S46	14 – 18	female	Valse Pan near Kuris	+	+
Khoesan	S68	25 – 30	male	Gordonia-district	+	+
Khoesan	S121	25 – 30	male	Kuruman-district	+	+
Khoesan	S103	12 – 15	male	Kalahari	/	+
Khoesan	S111	20 – 30	male	Kuruman-district	+	+
Khoesan	S61	25 – 30	male	Gordonia-district	+	+
Khoesan	S97	12 – 15	female	Kuruman-district	+	+
Sub-Saharan African	C333	?	?	Uganda	+	+
Sub-Saharan African	122.421/1464	adult	male	Congo	+	+
Sub-Saharan African	S29	30 – 40	male	South-Africa, Noitgedagt	+	+
Sub-Saharan African	S128	?	?	Middledrift	+	+
Sub-Saharan African	S87	?	?	Guinee-Francaise	+	+
Sub-Saharan African	S85	?	?	Kamerun	+	+
Sub-Saharan African	S138	?	?	Ramah	+	+
Middle European	ID-120-123/1043	10	male	?	+	+
Middle European	ID-300-510/578	11	female	?	+	/
Middle European	ID-125-028/1089	10	female	?	+	/
Middle European	ID-120-074/711	6	male	Czech Republic	+	+
Middle European	122.510/1554	22	male	Italy, Venice	+	+
Middle European	122.511/1555	adult	female	Italy, Padua	+	+
Middle European	19710	20	?	?	+	+
Middle European	126.804/1171	29	male	Czech Republic	+	+
Middle European	122.199/961	20	male	Austria	+	+

Population	Individual	Age	Sex	Location	P3	P4
Avar	654	3 – 5	?	Csokorgasse, Vienna	+	+
Avar	495	7 – 8	?	Csokorgasse, Vienna	+	+
Avar	502	13 – 15	?	Csokorgasse, Vienna	+	+
Avar	428	16 – 18	male	Csokorgasse, Vienna	+	+
Avar	498	25 – 30	female	Csokorgasse, Vienna	+	+
Avar	582	19 – 25	female	Csokorgasse, Vienna	+	+
Avar	541	19 – 30	female	Csokorgasse, Vienna	+	+
Indonesian	122.342/13	28	male	Java	+	+
Indonesian	122.335/13	36	male	Java	+	+
Indonesian	122.369/14	?	?	Sulawesi, Makssar	+	+
Papuan	CN5	adult	male	Zepa	/	+
Papuan	CN220	matur	male	Kai	+	+
Papuan	Cn230	adult	male	French-islands/ Siar	+	+
Papuan	CN232	adult	male	French-islands/ Siar	+	+
Papuan	CN236	matur	male	French-islands/ Siar	+	+
Papuan	CN264	ca. 30	male	Baining	+	+
Australian Aboriginal	C54	?	male	Balmoral Beach, New South Wales	+	+
Australian Aboriginal	C55	?	male	Dine-Dine Nymagee	+	+
Australian Aboriginal	C104	juvenil	?	Northern Territory	+	+
Australian Aboriginal	S89	?	?	Queensland	+	+
P. pygmaeus	657	infantil	?	?	+	+
P. pygmaeus	658	adult	female	Indonesia	+	+
P. pygmaeus	B5414 / 800	adult	female	?	+	+
P. pygmaeus	28801	adult	female	?	+	+

Appendix B

Curriculum Vitae

Ausbildung:

Okt. 2012 – April 2015	Universität Wien Masterstudium Physische Anthropologie *Masterarbeit: "Variation of outer and inner crown morphology in upper premolars in modern human populations" unter a.o. Univ.-Prof. Dr. Gerhard Weber.*
16. Jän. – 29. Mai 2014	Universidad Autonoma de Madrid und Univerdsidad Complutense Madrid, Spanien *Erasmus-Semester im interuniversitärem Masterstudium „Antropología Física: Evolución y Biodiversidad Humanas".*
Okt. 2009 – Sept. 2012	Universität Wien Bachelorstudium Biologie: Schwerpunkt Humanbiologie
Sept. 2001 - Juni 2009	BRG Fadingerstraße in Linz, Schwerpunkt Naturwissenschaften

Professionelle Erfahrungen:

02.02. – 22.2.2015	Johannes Kepler Universität Linz, Institut für Biophysik, *Praktikum PCR, EMSA, ELISA, Zellkultur, Patch-Clamp Technik***.**
Wintersemester 2014/15	Universität Wien *Tutorin in den Kursen „Osteologie: Epigenetische Merkmalsvariationen und pathologische Veränderungen am Skelett ", „Traditionelle Messmethoden".*
17.09 – 21.09.2014	„Meeting of the European Society for the Study of Human Evolution" in Florenz, Italien *Posterpräsentation: "Variation of the enamel-dentin junction morphology of upper premolars in modern human populations".* *Mitarbeit in der Organisation und bei der Betreuung der Teilnehmer während des Meetings.*
Sommersemester 2014	Universität Wien *Tutorin im Kurs „Virtuelle Anthropologie – 3D Anwendungen und Software".*

19.09 – 21.09.2013	„Meeting of the European Society for the Study of Human Evolution“ in Wien *Mitarbeit in der Organisation und bei der Betreuung der Teilnehmer während des Meetings.*
15.10 – 10.11.2012	Naturhistorischen Museum Wien *Mitarbeit an der neuen Dauerausstellung „Evolution des Menschen“: Erstellung von Abgussformen und deren Abgüssen; Montage der Objekte.*
Jänner 2012 – Jänner 2014	Naturhistorischen Museum Wien, Abteilung für Anthropologie unter Doz. Ao. Univ.-Prof. Dr. Maria Teschler-Nicola *Bearbeitung des Skelettmaterials aus der bronzezeitlichen Fundstelle Franzhausen 2: Bestimmung von Geschlecht, Alter und Pathologien.*
05.09 – 02.10.2011 12.07 – 06.08. 2010	Biologiezentrum Linz *Datenverarbeitung für die Online Bibliothek.*
07.07 – 25.07.2008	Johannes Kepler Universität Linz, Institut für Biophysik, *Praktikum PCR, Gelelektrophorese und wie man diese interpretiert, Klonieren von DNA in Bakterien und wie man sie für weitere Analysen wieder frei setzt, Zellkultur***.**

Stipendien:	Februar 2015	Leistungsstipendium der Universität Wien
	Februar 2014	Leistungsstipendium der Universität Wien
	Februar 2012	Leistungsstipendium der Universität Wien

Sprachen:	Deutsch	Muttersprache
	Englisch	fließend
	Spanisch	Grundkenntnisse

EDV-Kenntnisse:	MS-Office	ausgezeichnete Anwenderkenntnisse
	Latex	ausgezeichnete Anwenderkenntnisse
	Lightroom	gute Anwenderkenntnisse
	Amira	gute Anwenderkenntnisse
	EVAN-Toolbox	gute Anwenderkenntnisse
	SPSS	gute Anwenderkenntnisse

Linz, am 24.03.15

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