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TOOTH MORPHOLOGY, MOLAR ENAMEL THICKNESS AND DENTAL MICROWEAR TEXTURAL ANALYSIS OF MODERN CERCOPITHECINES WITH APPLICATION ON EUROPEAN *Paradolichopithecus/Procynocephalus* AND COMPARISONS WITH PLEISTOCENE PAPIONINS FROM OMO VALLEY IN AFRICA.

MASTER THESIS

THESSALONIKI
2017

ΧΡΗΣΤΟΣ ΑΛΕΞΑΝΔΡΟΣ Α. ΠΛΑΣΤΗΡΑΣ
Γεωλόγος

ΜΟΡΦΟΛΟΓΙΑ ΟΔΟΝΤΟΣΤΟΙΧΙΑΣ, ΠΑΧΟΣ ΑΔΑΜΑΝΤΙΝΗΣ ΓΟΜΦΙΩΝ ΚΑΙ ΑΝΑΛΥΣΗ ΥΦΗΣ ΟΔΟΝΤΙΚΗΣ ΜΙΚΡΟΤΡΙΒΗΣ ΣΥΓΧΡΟΝΩΝ ΚΕΡΚΟΠΙΘΗΚΙΔΩΝ ΜΕ ΕΦΑΡΜΟΓΗ ΣΤΟΝ ΕΥΡΩΠΑΙΚΟ *Paradolichopithecus/Procynocephalus* ΚΑΙ ΣΥΓΚΡΙΣΕΙΣ ΜΕ ΠΛΕΙΣΤΟΚΑΙΝΙΚΑ PAPIONINS ΑΠΌ ΤΗΝ ΚΟΙΛΑΔΑ ΟΜΟ ΣΤΗΝ ΑΦΡΙΚΗ

Υποβλήθηκε στο Τμήμα Γεωλογίας στα πλαίσια του Μεταπτυχιακού Προγράμματος
Εφαρμοσμένη και Περιβαλλοντική Γεωλογία
Τομέας Γεωλογίας
Αριστοτελείου Πανεπιστημίου Θεσσαλονίκης
Ημερομηνία Προφορικής Εξέτασης:

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Αριθμός Παραρτήματος Επιστημονικής επετηρίδας Τμήματος Γεωλογίας Nº

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Preface and aknowledgements

The present study took place in the context of the master thesis program named "Applied and Environmental Geology" of the School of Geology of Aristotle University of Thessaloniki. This study is a result of the collaboration between the Laboratory of Geology and Paleontology of the University of Thessaloniki (**LGPUT**, Greece) and the Institut de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironnements (**iPHEP**, CNRS and Université de Poitiers, France). The study took place partly in the **iPHEP**, were all the training on the methods used here was conducted, during the time period of the Erasmus+ exchange program (3 months), and partly in the **LGPUT** were I did the analysis and I wrote the text. The study consists of five parts. The first part is an introduction for the taxa *Procynocephalus* and *Paradolichopithecus*, their history and general discussion about them, the Eurasian cercopithecid fossil record, the Greek cercopithecid fossil record and some questions regarding their evolutionary history and ecology. The second part gives briefly the geology and stratigraphy of the Dafnero fossiliferous sites. The third part concerns the materials and methods used in this study and basically explains the approach used to understand the ecology of *Procynocephalus* from Dafnero-3. The fourth part includes the results, and the fifth one is a general discussion concerning the methods used, some conclusions about the ecology of the genus based on the results and available literature and a parallel example in Omo valley, (Ethiopia, East Africa). The main aim of this study is to determine the dietary preferences of the cercopithecid cranium DFN3-150 found in Dafnero-3 and to explore the dietary capabilities of its dentition, to achieve a better understanding of its ecology and possibly extract some information about the paleoenvironmental conditions during the Plio-Pleistocene in Greece. To achieve that, i compared the microwear textural characteristics of the Dafnero cranium with a number of extant taxa with known dietary preferences, using the dental microwear textural analysis (**DMTA**). Additionally, i compared the microwear textural characteristics of a sample of fossil *Papio* from Omo Valley with the DFN3-150 cranium, focused on contemporaneous assemblages, to explore their feeding ecology and test the hypothesis of sympatry between them. To explore the dietary capabilities of the DFN3-150 dentition, i measured the enamel thickness of its molars and two indices that describe the flaring of the molars and compared it with a set of modern *Papio* sample and other fossil and extant forms found in the available literature.

This thesis would not have been possible without the help of a lot of people which I will briefly try to express my gratitude, hoping that I will not forget to mention anyone. All this work is dedicated to them, along with my deepest respect and appreciation. First of all, I would like to express my sincere thanks, gratitude and respect to my supervisor, Ass. Prof. Dimitris S. Kostopoulos for giving me this great research opportunity, being a major source of inspiration and providing me with his guidance and support all this time. Special thanks I would like to express to the members of the Supervising committee of the thesis: Prof. George D. Koufos which kindly supported and guided me during all my years of studies and shared his experience with me, his advice will always be priceless. Also, sincere thanks and gratitude to my supervisor in France, Gildas Merceron for his support and hospitality during my staying in Poitiers, for the meaningful discussions, and for trusting me with this valuable work. Also, my sincere thanks to Franck Guy who helped and supported me all the time I was in iPHEP, his contribution has been crucial and he played a significant part in the completion of this thesis. Special thanks I would like to express to Prof. Evangelia Tsoukala, for her support and advices all these years. Also, many thanks to all the technical and academic personnel of iPHEP for their hospitality and their help. I would like also to mention my friends and colleagues: Florian Martin for his useful comments concerning the study and several discussions during my staying in Poitiers and also Alexios Kotsakis and Zoi K. Kynigopoulou which helped and supported me all the time.

Finally, I would like to dedicate this thesis to my family and all of my friends for their patience and never ending support. They were always there and eager to help and I thank them for that. Last but not least I would like to thank Dimitrios Kavallieratos and Chrysanthos Makridis for their friendship and trust. Their support has always been most significant

CHAPTER 1. INTRODUCTION

1.1 Aims and Questions

The Eastern Mediterranean region was an important region for mammalian migrations between Asia, Europe and Africa during Neogene and Quaternary. This wide area of Eastern Mediterranean, consisting of the Balkan Peninsula, the Aegean Sea, Asia minor and the Middle East, served as a crossroad in mammalian exchanges and numerous fossil localities were discovered in this region (Koufos, 2005). These localities are very significant and provided with information that helps reconstructing the palaeogeographic background of the area during that time period. In Greece, the Pliocene localities are few in comparison to the Miocene ones which are well recorded. The Late Pliocene-Early Peistocene localities with large mammals are better recorded with more localities mainly from Northern Greece. The middle-late Villafranchian faunas (MN17) from Greece are used as standard for comparisons in Eastern Mediterranean (Koufos, 2006). One of these faunas is found in the locality of Dafnero (DFN) which was discovered in the early 90's in Northern Greece (Koufos *et al.*, 1991). The fossil remains of Dafnero were limited but include various significant taxa (Koufos, 2001 and unpublished data). In 2010, a Greek-French team started new field campaign that allowed locating two additional fossil sites Dafnero-2 (DFN2) and Dafnero-3 (DFN3), wich provided numerous fossils enriching remarkably the known fauna. Recently a fairly complete cranium of a large cercopithecid was unearthed from Dafnero-3 (Kostopoulos *et al.*, 2017) (**Fig.1**).

Modern cercopithecids are found mainly in Africa, Asia and rarely in Europe (i.e., Gibraltar) but that was not the picture in the past. Old World monkeys have a long fossil record in Europe traced from the Late Pleistocene back to the Late Miocene (Szalay and Delson, 1979; Jablonski, 2002). During the Turolian (8.7-5.3 Ma) the exclusive representative was the colobine *Mesopithecus* but during the Ruscinian (5.3-3.4 Ma) the colobine *Dolichopithecus* and the cercopithecines *Macaca* and *Paradolichopithecus* appeared (Eronen and Rook, 2004; Koufos, 2009; Elton and O'Regan, 2014). Until the Early Pleistocene only *Macaca* was present in Eurasia while all previous genera went extinct. At the same time the African genus *Theropithecus* briefly invaded southwestern Europe and also reached parts of Asia (Jablonski, 2002; Elton and O'Regan, 2014). The only Eurasian representative today for the Cercopithecines is *Macaca* represented by six species in mainland Southeast Asia. The presence of Cercopithecids in the Neogene of Greece is known since the beginning of the 19th century (Koufos, 2009). The main taxon of the family is *Mesopithecus* Wagner, 1839 found originally in the middle Turolian locality of Pikermi, Athens. During the last 45 years, new excavations have been carried out in various late Miocene localities of Greece, providing with several remains of *Mesopithecus* (Koufos, 2009). The genus was found in Axios Valley, Thessaly and Chalkidiki Peninsula and new species were described (i.e *Mesopithecus delsoni*, *Mesopithecus delsoni/pentelicus*, *Mesopithecus cf. monspessulanus*) (Koufos, 2009 and references there in). However, the taxonomic distinction between these species are still debated and new opinions suggest that only two different species existed (Alba *et al*., 2015). Nevertheless, these new findings provide important information considering the systematic and the biostratigraphy. Besides *Mesopithecus*, two other cercopithecids were found in the Pliocene of Greece. The genus *Dolichopithecus* Depéret, 1889, found in two early Pliocene localities of Northern Greece, Megalon Emvolon (late Ruscinian, MN15) and Ptolemais Basin, and the genus *Paradolichopithecus* Necrasov, Samson and Radulesco, 1961, discovered in the late Pliocene - early Pleistocene (middle Villafranchian, MN17) locality of Vatera, Lesvos Island (de Vos *et al.* 2002; Van der Geer and Sondaar 2002). Finally, there is also evidence for the presence of *Macaca sp*. in the early Pleistocene locality Tourkobounia 2 (fissure filling) near Athens (Koufos, 2009 and references therein).

The cercopithecid fossil record of Greece combined with other available data help us understanding better the ecology of the family Cercopithecidae and maybe to extract some information about the paleoenvironmental conditions in Eastern Mediterranean region during Neogene. The data available about the Ruscinian of Greece and Eastern Mediterranean region are very limited thus making it hard to reconstruct the paleoenvironment. However, the Ruscinian lignitic deposits of northern Greece indicate closed and wet conditions (Koukouzas *et al.*, 1979). Therefore, *Dolichopithecus ruscinensis* probably habited a relatively closed and wet environment (Koufos, 2009). So far, the genus *Paradolichopithecus* was found only in the early Pleistocene locality of Vatera, Lesvos Island but the Middle Villafranchian fauna composition suggests an open and dry environment (de Vos *et al.*, 2002; Van de Geer and Dermitzakis, 2008) during late Pliocene that prolonged through Pleistocene. The Middle Villafranchian is characterized by a decrease in global temperature and a trend to more arid and open habitats in Southern Europe (Koufos and Kostopoulos, 2016 and ref. therein). These environmental changes have affected also the mammalian diversity in Greece during that period. The paleoecological conditions during the Villafranchian in Greece, where initially studied by Kostopoulos and Koufos (1998, 2000 and ref. therein). The analysis of the authors of the large mammal faunas and the comparisons with faunas from known environments, combined with dental micro- and meso-wear analyses of the Sesklon (SES) locality herbivores (Koufos and Kostopoulos, 2016 and ref. therein), confirmed previous representations of open environment similar to modern woodland savannah (Kostopoulos and Koufos, 2000). The cercopithecid fossil record of Greece has provided important information regarding the Eurasian evolutionary history of Cercopithecidae, but still there are a lot of questions about the origin of the family, the dispersal pathways followed to the east or west and the possible reasons behind these expansions. Future findings like the Dafnero-3 cranium will enrich the poor early Pleistocene European cercopithecid fossil record and will provide additional and significant information about the complicated history of the family.

Procynocephalus was the first primate fossil formally described (Baker, 1836; Szalay and Delson, 1979) still the information about this taxon are limited. The type species *Procynocephalus wimani* Schlosser 1924 has been found in China. Specimens from India and Pakistan are usually assigned to other species such as *Procynocephalus subhimalayanus* von Meyer 1848 or *Procynocephalus pinjorii* Verma 1969, while the latter is often regarded as a junior synonym of the former (Nishimura *et al.*, 2014). Another large extinct Eurasian papionin is *Paradolichopithecus* Necrasov, Samson, and Radulesco 1961 (Delson, 1975; Delson and Nicolaescu-Pliopsor, 1975; Szalay and Delson, 1979; Jablonski, 2002; Takai *et al.*,2008). Most of the specimens were found in the early Pleistocene of Europe and assigned to the *Paradolichopithecus arvernensis* Depèret 1929 or *Paradolichopithecus geticus* Necrasov *et al.* 1961 (Delson, 1975; Delson and Nicolaescu-Pliopsor, 1975; Szalay and Delson, 1979; Jablonski, 2002; Takai *et al.*,2008). Besides the European occurences of the genus, there are two other species known: *Paradolichopithecus sushkini* Trofimov 1977 from Kuruksay, Tadjikistan (Trofimov, 1977) and *Paradolichopithecus gasuensis* Qiu, Deng and Wang 2004 from Longdan, Gansu, China (Qiu *et al.*, 2004). The specimens from China and India are usually assigned to the former genus and those from Europe and central Asia are to the latter, although some scholars argue that the latter was a junior synonym of the former (Nishimura *et al.*, 2010, Kostopoulos *et al.*, 2017). So far, the comparable fossil materials are very scarce for *Procynocephalus*, making the phyletic relationship between the two genera debateable.

Procynocephalus/Paradolichopithecus is an extinct papionin and one of the largest representatives of the Cercopithecidae family that inhabited Eurasia at Late Pliocene-Early Pleistocene. The oldest Eurasian occurences of *Procynocephalus/Paradolichopithecus* are coming from Hungary, Spain and France dated around 3.2 Ma thus suggesting Europe as the center of its origin. *Procynocephalus/Paradolichopithecus* probably appeared in the early Pliocene of Western Eurasia and then dispersed eastward (Takai *et al.*, 2010). While its taxonomic position is still not clear, there is also some controversy regarding the phyletic position of *Procynocephalus/Paradolichopithecus* in Cercopithecinae. Based on the cranial features *Procynocephalus/Paradolichopithecus* is thought to be more closely related to the macaques than to baboons (Delson and Frost 2004), despite the baboon-like terrestrial features (Jolly, 1967; Szalay and Delson, 1979; Takai *et al.*, 2008). This large cercopithecid, based on postcranial remains (Szalay and Delson, 1979) is thought to exhibit a primarily terrestrial way of life but probably used his arboreal nature in search for food resources or to avoid predators. Additional support for terrestriality in *Procynocephalus/Paradolichopithecus* derives from the paleoecological reconstructions which hypothesize a further spreading of grasslands and the shrinking of forest in the Pliocene. All Asian records of the genus are of early Pleistocene age (i.e., <2.6 Ma) corresponding to the age of the *Equus* event (Kostopoulos *et al.*, 2017). Since 2.5 Ma, grasses dominated the ground cover of Central Asia (Dennel, 2008) so it is possible that *Procynocephalus/Paradolichopithecus* may have increased its adaptability by including grass-land products such as seeds, bark and possibly underground storage organs (USOs) of C_4 and C_3 grasses in its usual diet (Williams *et al.*, 2011; 2012). Also, the exploitation of sedges (Cyperacea) and rushes (Juncacea) is possible, depending on the density of the wood cover and the humidity of the habitats. The faunal composition of the localities that this primate was found (Williams *et al.*, 2012; Sondaar *et al.*, 2005) suggest a representation of more open environments. Furthermore, based on the geographical distribution of this extinct and problematic genus, is presumed to be adapted to cooler, drier conditions in relatively high latitude areas (Takai *et al.*, 2014). If the herbaceous monocot hypothesis in cercopithecids monkeys in Eurasia, is correct, this would have implications on its dentition morphology and also its microwear textural characteristics. An increase in consumption of herbaceous monocots would produce a more anisotropic microwear texture and less complex, while the incorporation of USOs in diet would produce a less anisotropic and more complex microwear texture. Still there are a lot of questions regarding the ecology of this extinct genus and its swift expansion on such wide geographical range. While the evidence so far seems to correlate *Procynocephalus/Paradolichopithecus* fast eastward expansion to environmental shifts/pressures of the early Pleistocene (MN17) (Elton and O'Regan, 2014; Kostopoulos *et al.*, 2017), the rapid extinction of this genus seems to be far more enigmatic. Hopefully, future findings will help us reconstruct the ecology and history of this problematic genus.

To test the herbaceous monocots hypothesis, we compare the dietary proclivities of *Procynocephalus* thanks to a published comparative dataset of modern species with known diets and measured molar enamel thickness in addition with new data on modern *Papio* gathered in this study. Also, two indices that describe the molar flare are measured and compared with a sample of modern *Papio* and the available data found in literature (Singleton, 2003; Guy, 2013).

1.2. Geology and Stratigraphy

The fossil sites of Dafnero (DFN, DFN2 and DFN3) are situated in Grevena Basin (Western Macedonia). The locality is named after the nearby homonymous village close to the localities. The locality was discovered in the summer of 1990 in a ravine system that crosses perpendicular the Aliakmon river about 1 km SW of the Dafnero village (Koufos *et al.*, 1991). The localities DFN and DFN3 are part of the same fossiliferous layer of orange silty sands that were exposed by erosional processes. The fossiliferous horizon is placed below a1-2 m thick and dense conglomerate on the brink of a 20-m high section (Kostopoulos *et al.*, 2017, sub.). The fossiliferous deposits belong to the basal part of a thick (~60m) terrestrial lithostratigraphic unit of fluviatile origin that overlies unconformably molassic sediments thought to be part of the Tsotylion Formation of the Mesohellenic Trench (Fountoulis *et al.*, 2001). The fossils are tightly accommodated (**Fig.2F**) in eight successively exposed spots and they frequently suffer from pre- and mostly post-burial deformation that requires in situ conservation (**Fig.2D**). Data from micropaleontological datings from other geological section found along the Pramoritsas river, indicate that continental deposition in this area started ~3.4 Ma (Eltgen, 1986; Fountoulis *et al.*, 2001). The oldest known terrestrial fauna of the area comes from the Milia fossil site, dated around 3 Ma (Guérin and Tsoukala, 2013).

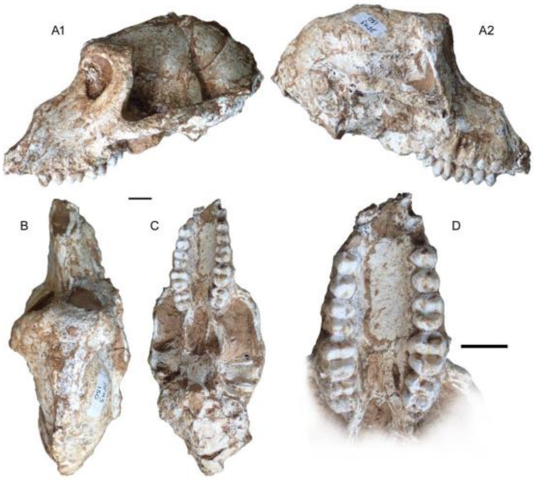

Figure 1 *Procynocephalus/Paradolichopithecus aff. arvernensis*, subadult female cranium DFN3-150, Dafnero 3, Western Macedonia, Greece (from Kostopoulos *et al.*, 2017 sub.)

Comparisons of the fauna unearthed from Dafnero locality with those from other European localities indicates similarities with Saint-Vallier, La Puebla, Olivola and Volax (Koufos *et al.*, 1991; Koufos and Kostopoulos, 1993). Considering all the above mentioned we can presume a middle Villafranchian age for the Dafnero fauna (Koufos *et al.*, 1991; Koufos and Kostopoulos, 2016) between 2.4 and 1.8 Ma (Koufos *et al.*, 1991; Koufos, 2001), but a magnetochronological study is also in progress for more precise dating.

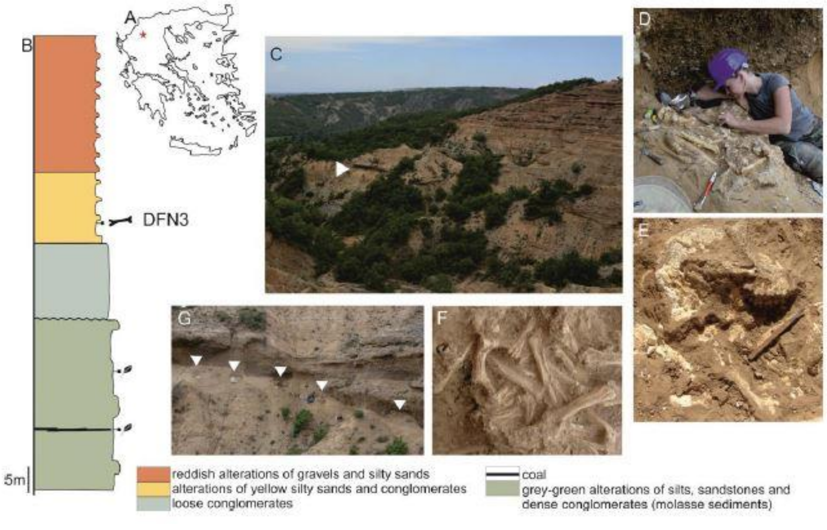

Figure 2 The Dafnero locality (**A**) and the stratigraphic section (**B**). White arrows indicate the position of the locality in the ravine (**C**) and the fossil spots (**G**). A fossil assemblage of Dafnero-3 (**F**) in situ conservation (**D**) and the DFN3-150 *Procynocephalus* cranium in situ (**E**) (from Kostopoulos *et al.*, 2017 sub.).

CHAPTER 2. MATERIALS AND METHODS

2.1 Reasoning and comparative material

To explore the dietary proclivities and the feeding ecology of *Procynocephalus* from Dafnero 3, we used two different approaches. The first approach concerns the enamel thickness and the dental morphology, the latter mostly focused on the molar flare. Dental enamel is the hardest biological tissue known and is the component of the tooth mainly responsible for overcoming the mechanical resistance of foods, resisting crushing stresses and reducing wear. The thickness and the distribution of enamel are thus likely to reflect aspects of dental adaptation to the diet (Shellis *et al.*, 1998). The enamel thickness is thought to be reliant on dietary behaviour (Kay 1981; Teaford, 2000; Guy *et al.*, 2015), but not solely dependent on it as, it is also strongly linked with phylogeny. As thick enamel works as a defence mechanism against the abrasion of the tooth from hard food objects, differences in enamel thickness among taxa have usually been regarded as an evolutionary adaptation to differing diets. The term molar flare characterizes the shape of the molar. As molar flare, we can define the virtual trapezoid structure that is created when we combine the basal area of the molar with the breadth between the cusps (**Fig. 18 Appendix**). In the previous studies about the molar flare (Benefit 1993, 1999, 2000; Singleton 2003) they calculated only in the mesial part of the molar. The molar flare is thought to be a good indicator of the mechanical properties of the food objects but variation in molar flare seems to be an outcome of a complex interaction of functional, phylogenetic and temporal effects (Singleton 2003). Benefit (1993, 1999, 2000) has found that pronounced molar flare to be functionally correlated with frugivory and hard-object feeding in cercopithecoid primates.

The molar sample used in enamel thickness and molar flare approach consists of three upper second molars of modern baboons (*Papio anubis* n=3, *Papio hamadryas* n=1) which belong to the osteological collections of iPHEP/University of Poitiers and the upper molar of DFN3-150 cranium of *Procynocephalus* housed in the Laboratory of Geology and Palaeontology University of Thessaloniki (LGPUT). Additional data were taken from the available bibliography (Beaudet *et al.* 2016; Olejniczak et al 2008) and the whole studied sample is given in Appendix (**Table 6**). The available sample maybe limited but it allows us to check the resemblance or the discrepancy between the fossil cercopithecid and the modern primates used.

The second approach concerns the microwear textural characteristics of *Procynocephalus* from Dafnero 3. Dental microwear, i.e, the study of the microscopic use-wear scars in enamel, reveals direct information about what an individual ate over a period of time before death (Rensberger, 1978; Walker *et al.*, 1978; Teaford and Oyen, 1989; Ungar and Teaford, 1996; Teaford *et al.*, 2008). Depending on whether a food item is hard, soft or tough, the tooth surface will wear differently. Therefore, the resulting texture will be different when the animal feeds on foods with different mechanical properties. Because of this, the texture parameters are considered to be good proxies for tracking what an individual ate (Calandra and Merceron, 2016). To explore the dietary habits of *Procynocephalus* from Dafnero 3 first we used a number of modern taxa from the available data from Scott *et al.* (2012). As *Procynocephalus* is regarded as principally terrestrial (Szalay and Delson 1979; Frost *et al.* 2005; Sondaar *et al.* 2005) we chose living taxa showing a similar way of life with well-known but distinct dietary profiles. Dedicated folivores, which consume mostly leaves also seeds and stems throughout the year represented in our sample by *Theropithecus gelada* (n=12) and *Semnopithecus entellus* (n=8); *Gorilla beringei* (n=16) represents generalized folivores-frugivores which eat terrestrial vegetation, ripe fruit if available, bark, leaves and occasionally invertebrates; omnivorous primates are represented by, *Papio cynocephalus* (n=27) and *Papio ursinus* (n=12), which are diet generalists and they are able to consume from grass and leaves to small mammals, and the crab-eating macaque, *Macaca fascicularis* (n=20) (Scott *et al.*, 2012 and citations therein). Williams (2012) tested the dietary proclivities of *Procynocephalus subhimalayanus* (GSI 18453) but did not considered *Papio*, *Macaca* and *Theropithecus gelada* in his study. This is because the omnivorous primates did not show to yield distinct microwear texture characteristics and their diet may be extremely variable across individuals within and between species. But *Procynocephalus* might have followed a similar feeding strategy so possible relationships in dietary terms should be tested. *Theropithecus gelada* is a predominantly grass-eating primate (Jolly, 1970; Teaford, 1993) with specialized dentition. These dental strategies have been considered in detail by various researchers (Jolly, 1972; Meikle, 1977; Jablonski, 1993, 1994). Although comparable dental specializations are absent in *Procynocephalus* (Jolly 1967) the similarity, or the discrepancy between *Procynocephalus* and *Theropithecus gelada* feeding habits can give us answers about the feeding strategies of the fossil genus. To test the hypothesis of vicariance between *Papio* in Africa and *Procynocephalus* in Eurasia, we explore the feeding ecology of these two taxa, focusing our efforts on contemporaneous assemblages of *Papio* specimens found in Early Pleistocene deposits along the Omo River, Ethiopia. The fossil specimens were unearthed by the International Omo Reasearch Expedition, between 1967 and 1976 (Heinzelin, 1983) and the new research in the Shungura formation by the Omo Group Reasearch Expedition (Boisserie *et al.*, 2008).

2.2 Technical implementation

2.2.1 Molar Flare and Enamel Thickness analysis

To capture the three-dimensional form of the molars, we used microtomography to retrieve all the detailed aspects of the dental morphology (e.g. occlusal enamel surface, enamel dentine-junction surface). The molars were scanned using Rx solutions at the Centre de Microtomographie at the University of Poitiers. In order to isolate the enamel from each molar, the virtual volumes from the microtomographic images are processed using segmentation tools and manual correction using © Avizo v7 commercial software. After the segmentation, the enamel crown is isolated from dentine and the pulp canals and the volume of the crown enamel is converted into a polygonal surface (3D triangular mesh) which corresponds to a set of three-dimensional points connected by edges. The resulting surfaces were processed using © Geomagic Studio 2013 software following the protocol of Guy et al. (2013). First, the crown enamel was decimated to reduce the number of triangles in half and then separated in two components, the occlusal enamel surface (**OES**) enamel-dentine junction surface (**EDJ**). Unnecessary artifacts from each component were removed using automatic tools and manual correction and re-meshed to achieve its constitution of 55,000 polygons. Next, in order to normalize our result, we oriented each molar in 3D virtual space using a common reference plane and axis. Each molar is aligned to a (*xy*) reference plane, which is the mesial plane that intersects the basin of the enamel-dentine junction surface. The z axis is positively oriented from the cervix to the occlusal relief of the molar. This plane was copied to the enamel crown in order to be parallel with the occlusal surface. The molar is oriented by having its mesial axis, the line joining the tip of the dentine horns at protocone and paracone, parallel to the x axis of the 3D space. Finally, the mesial plane and axis were aligned to the world axis and the points of the plane is set to (*x, y,0*), for convenience purpose.

Having all the molars oriented, first we proceeded with the morphological measurements of the basic dimensions of the molar, such as maximum length (ML, mm) and maximum breadth on the mesial and distal part (MMB and MDB respectively, mm) and also the mesial intercuspal breadth (MCB, mm). The molar flare (MFR) was calculated, following Benefit (1993), as the ratio of mesial intercuspal breadth to maximum mesial breadth (MCB/MMB) and then the index of molar flare (MF) from Singleton (2003), which is a linear transformation of the MFR (MF=1-MFR) whose value ranges between 0 (no flare) and 1 (maximum flare). Following the protocol of Guy (2013) the dentine flare index (DFI) was also calculated. Unlike the MF index that focus on the mesial part of the tooth, DFI includes the whole portion of the molar. The DFI index is the ratio between the surface of the two-dimensional projection of the dentine basin (DBS2D, mm^2) to the surface of the two-dimensional projection of the dentine surface (DS2D, mm^2). To calculate the DFI index we separated the dentine basin for each enamel-dentine junction surface, we removed any unnecessary artifacts and we projected them in two-dimensional space.

Linear measurements of the enamel thickness were taken from modern *Papio* (n=4) and *Procynocephalu*s from Dafnero 3 on the buccal and lingual part of the upper second molar (‘’Measurement’’ module available on Avizo v7.0) following the protocol of Suwa *et al.*, (2005). Three variables were measured in each specimen: volume of the enamel cap (EVOL, mm^3), volume of the coronal dentine that includes the coronal aspect of the pulp chamber (Vcdp, mm^3) and the enamel-dentine junction surface (EDJS, mm^2). The volume of the coronal dentine was obtained by virtually closing the EDJ component, that was previously separated from the OES component with © Geomagic Studio 2013.Then two indices of enamel thickness were calculated: 3D average enamel thickness (3D AET, mm) calculated as the ratio between EVOL and EDJS, and 3D relative enamel thickness (3D RET) given through the ratio 3DAET/ $(Vcdp)^{1/3}$*100, that allows direct and scale-free comparisons (Kono, 2004; Olejniczak *et al.*, 2008a). Finally, we visualized the 3D enamel distribution of the upper second molars (UM2) by computing the distances between the occlusal enamel surface and the enamel-dentine junction surface (‘’Surface distance’’ module on Avizo v7.0). The distances measured were visualized (**Fig.3**) ranging from dark blue, corresponding to thinner enamel, to red, that represents the thicker parts of the enamel (Macchiarelli *et al.*, 2008, 2013; Bayle *et al.*, 2011).

Table 1. Abbreviations and definitions of the measurements used in this study.

Molar Flare			
ML		Maximum Length	
MDB		Maximum Distal Breadth	
MMB		Maximum Mesial Breadth	
MCB		Mesial Intercuspal Breadth	
MF	1-(MCB/MMB)	Molar Flare Index	Singleton (2003)
DFI	2D-DBS/2D-DS	Dentine Flare Index	F. Guy (2013)
2D Enamel Thickness			Suwa et al., (2005)
BOCMAX		Buccal Occlusal Maximum Enamel thickness	
BLATMAX		Buccal Lateral Maximum Enamel thickness	
LOCMAX		Lingual Occlusal Maximum Enamel thickness	
LLATMAX		Lingual Lateral Maximum Enamel thickness	
3D Enamel Thickness			Kono (2004)
EVOL		Enamel Volume	
Vcdp		Volume of the coronal dentine	
EDJS		Enamel-Dentine junction surface	
AET3D	EVOL/EDJS	3D Average Enamel Thickness	
RET3D	AET3D/(Vcdp)1/3*100	(scale-free) 3D Relative Enamel Thickness	

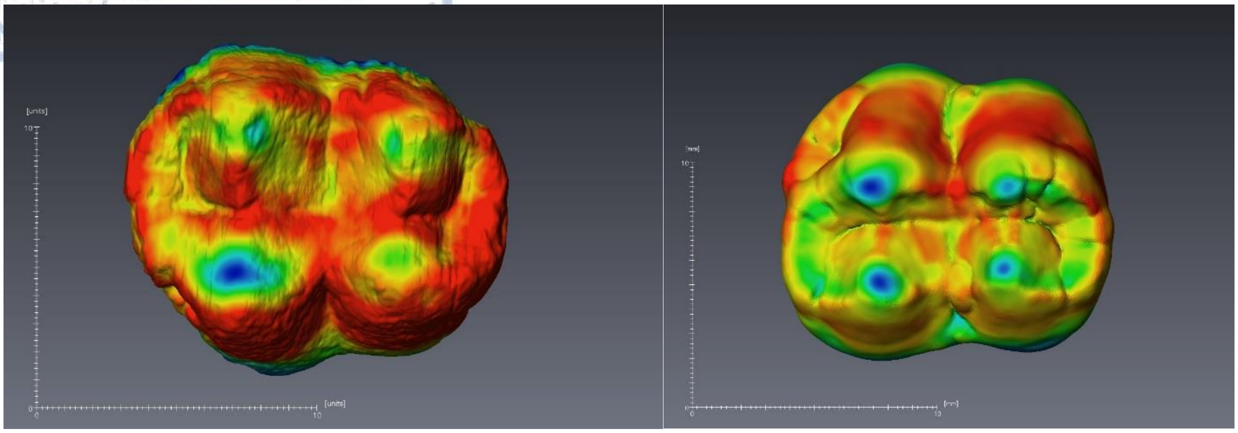

Figure 3 Enamel distribution on the UM2 of *Procynocephalus*, DFN3-150 (left) and *Papio anubis* iPHEP C2 dec (right). Red represents thicker enamel while blue represents thinner. It is noticeable that the surface quality of the fossil specimen is lower than that of the extant. This is due to postmortem alterations.

2.2.2 Dental microwear textural analysis

Microwear analyses are used to correlate the pattern of the wear features (striations and pits) with the physical properties of the food items that the studied individual had ingested. On one of the earliest studies of dental microwear analysis (Walker *et al.* 1978), researchers used to qualitatively examine the number of features (scratches and pits) on photographs produced by 2D-scanning electron microscope. Many more studies followed in the next decades and eventually it became clear that a standardization was needed, as the microwear patterns seem to vary depending on teeth, facet, microscope settings and between different observers (Calandra and Merceron, 2016). Only after the development of 3D acquisition systems has allowed the automatic quantification of the microwear features. The use of confocal microscope, on microwear analysis was first suggested by Boyde and Fortelius (1991) as a solution to the need for a new instrument. More recently, Ungar *et al.* (2003) used confocal microscopy with scale-sensitive fractal analysis (SSFA). This analysis is based on the principle from fractal geometry that a surface can look different in different scales. Thus, surface textures that appear smooth at coarse scales can be rough at finer scales (Scott *et al.* 2006). SSFA can be applied to length profiles (length scale analysis) and to three-dimensional surfaces (area-scale and volume-filling analyses) (Merceron *et al.* 2009). This offered a more practical approach to characterizing microwear surface textures, now known as *dental microwear textural analysis* (DMTA) (Scott *et al.* 2005). Dental microwear textural analysis is capable of generating large samples of microwear surfaces and repeatable measurements (Scott *et al.*, 2005, 2006, 2009; Merceron *et al.*, 2006, 2009, 2010; Ungar and Scott, 2007, 2009; Ungar *et al.*, 2007, 2008a, b, 2010b, c; Krueger *et al.*, 2008; Prideaux *et al.*, 2009; El-Zaatari, 2010; Krueger and Ungar, 2010; Schubert *et al.*, 2010; Schulz *et al.*, 2010). Also, it is less time consuming and avoids intra-observer error unlike the previous methods used for obtaining textural characteristics. Dental microwear textural analysis uses five variables to characterize the microwear surface textures: *complexity* (*Asfc*), *anisotropy* (*epLsar*), *heterogeneity* (*HAsfc*), *scale of maximal complexity* (*Smc*) and *textural fill volume* (*Tfv*). Together they provide a far more complete and quantified characterization than any previous traditional measurement of microwear features such as pits and scratches. More ‘’complex’’ surfaces have microwear features such as pits and scratches of different sizes overlaying each other with no particular orientation (**Fig.4b**). On the other hand, more ‘’anisotropic’’ surfaces have relief that shares similar orientations (e.g many parallel striations; **Fig.4a**) and more ‘’heterogeneous’’ surfaces will have different textures from place to place across the surface (**Fig.4c)** (Scott *et al.* 2006). Here, we characterize the dental microwear quantitatively using this relatively new approach.

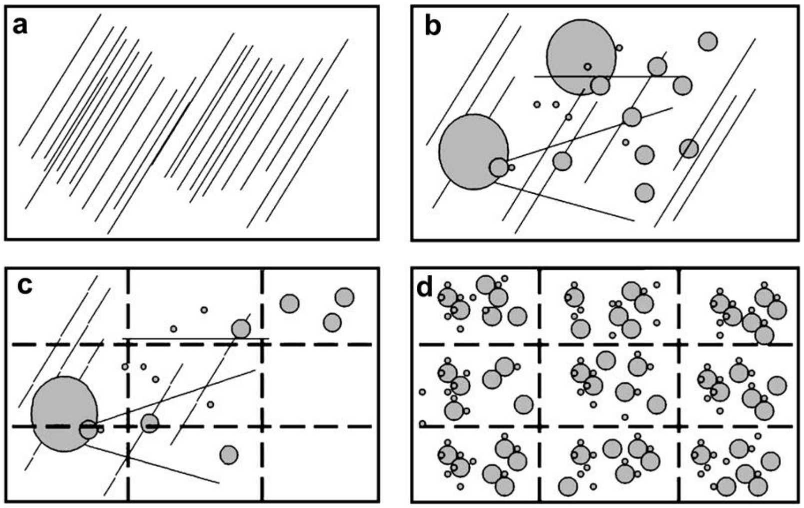

Figure 4 Example of schematic microwear surfaces showing anisotropic texture (a), complex texture (b) and heterogenous (c) and homogenous (d) textures (after Scott *et al.* 2006).

2.2.3 Surface data collection

The mastication process is divided in two intervals: ‘Phase I’ and ‘Phase II’ (Lucas, 2004). The former precedes centric occlusion and the latter follows it. During these intervals wear facets are produced due to the abrasion of the food objects. The wear facets in which wear features are product of the shearing action of the tooth are attributed to Phase I, while wear facets produced to the surface of the cusp were food is crushed are attributed to Phase II (Krueger *et al*. 2008). We examined microwear on wear facets of M^1s and M^2s of 67 fossil *Papio* individuals and one M^1 of *Procynocephalus* (DFN3-150) (**Fig.5**). We chose to explore the microwear characteristics of the M^1 of the Dafnero-3 primate because the M^2s were damaged by weathering. Fortunately, the M^1 was very well preserved, especially the central basin, in which signs of microwear were identified. The identification of the facets was done on negative replicas of the teeth created with silicone mold from the material. The replicas were first cleaned with cotton swabs soaked with acetone. Only those surfaces that clearly preserved antemortem microwear were included in the analysis, and artifacts, such as adherent dust particles, were excluded. The data collection for Phase I facets was focused on facet 3,4 for the upper molars and facet 6,5 for the lower molars, while for the Phase II we were focused on facet 9 (**Fig.5**), which is located on the lingual side of the protocone for the upper molars and the buccal side of the hypoconulid for lower molars (Kay and Hiimae, 1974, Maier, 1977). Given that sometimes facet 9 was not preserved due to factors such as postmortem alterations or it was fully worn, other facets (facets 12, 11 for the upper and facets 11, 10 for the lower molars; (Maier, 1977) were considered. Each specimen was scanned using Leica white-light confocal -microscope (Scott *et al.* 2006; Merceron *et al.*, 2016) using a x100 objective and the resulting data were analyzed in Toothfrax (Surfract, www.surfract.com) and SFrax using SSFA software packages (2006).

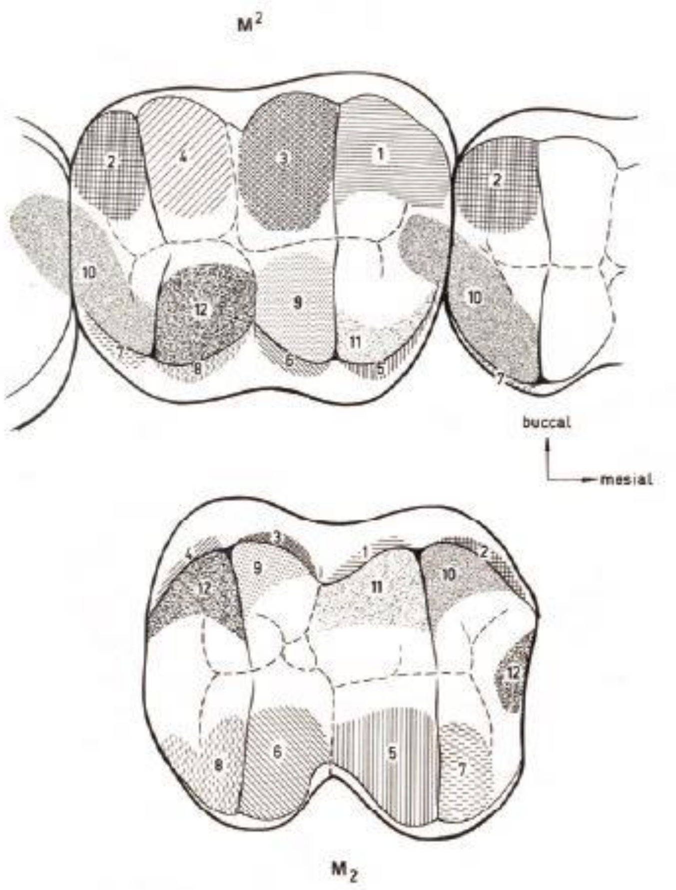

Figure 5 Right upper (top) and lower (bottom) molars of *Nasalis larvatus* showing Phase I (facets 1 until 8) and Phase II (facets 9 until 12) dental facets. (after Maier 1977).

2.2.4 Complexity and scale of maximal complexity

Complexity is a measure of changes in surface roughness at different scales. Changes in relative area with scale can then be used to characterize the complexity of the surface roughness. *Asfc* is the slope of the steepest part of the curve, fit to a log-log plot over the range of scales at which those measurements are made (**Fig.6**). The steeper the slope is, the more complex surface. Pits and scratches of different sizes overlaying one another would define a complex surface (Scott *et al.* 2006; Ungar *et al.* 2008). Complexity has been shown that is a good measure in distinguishing primates that eat more hard, brittle foods from those that consume more tough foods (Ungar *et al.*, 2003; Scott *et al.*, 2005). For each scan examined here, the relative areas were calculated for scales ranging from 7200 mm^2 to 0.02 mm^2 using Toothfrax software. The scale range over which *Asfc* is calculated (steepest part of the rel. area vs scale curve) may also be informative and is summarized here by the Scale of maximum complexity, *Smc* (Scott *et al.* 2006).

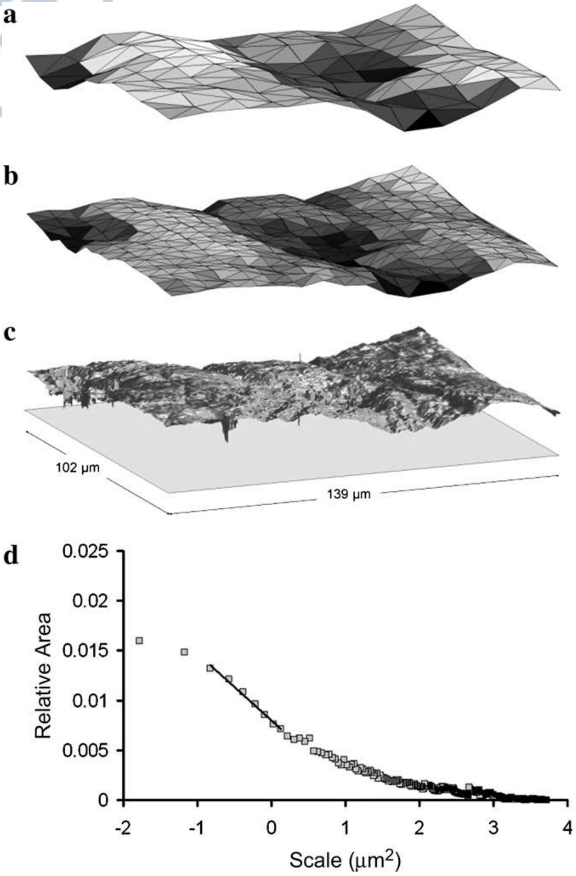

Figure 6 Area scale analysis. A virtual tiling algorithm using triangles of different sizes can be used to measure surface roughness (compare a, b and c). Complexity is represented by the steepest part of a curve fitted to the plot of relative area over scale (d) (from Scott *et al.*, 2006).

2.2.5 Anisotropy

Anisotropy is a measure of directionality, orientation of the surface relief. Relative lengths of depth profiles are different from orientation when the surface roughness is anisotropic (**Fig.7**). Relative lengths with specific orientation can be defined as vectors. The vectors calculated are at 5^o interval for a total of 36 measures, and normalized using the exact proportion method to determine a mean vector length. The length of the mean vector is a measure of anisotropy called *exact proportion Length-scale anisotropy of relief*, or *epLsar* (Merceron *et al.* 2009). It was calculated for each scan using Toothfrax (Surfract, www.surfract.com) at a 1.8 μm scale of observation (Scott *et al.* 2006). A surface which is dominated with scratches, linear striations following the same direction would present high value of *epLsar* (Ungar *et al.*, 2008).

2.2.6 Heterogeneity

While complexity and anisotropy provide us with useful characterization of the surface texture, their variation across the surface may also play an important role. For instance, two scans across a surface, focusing on different parts of the surface, can yield different values for *Asfc* or *epLsar*. Heterogeneity of Area-scale fractal complexity (*Hasfc*) can be calculated by splitting individual scanned areas into smaller subdivisions with equal number of rows and columns (4 cells, 9 cells, 16 cells, 25 cells … 121 cells) using Toothfrax software (Scott *et al.* 2006).

2.2.7 Textural fill volume

This measure examines the summed volumes of square cuboids that fill the surface at a given scale. The total volume filled is a function of two components: a) the shape of the surface, and b) the texture of the surface. A planar surface would have lesser total fill volume than a concave or convex surface even if the two textures are identical (Scott *et al.* 2006). Essentially, textural fill volume is computed as the difference in summed volumes of very fine cuboids and larger ones (2 μm and 10 μm on a side) (**Fig.8**). This procedure removes the structure of the overall surface and enables the characterization only of the microwear features. A surface dominated with more features in the mid-scale range would present high values of *Tfv* (Ungar *et al.* 2008).

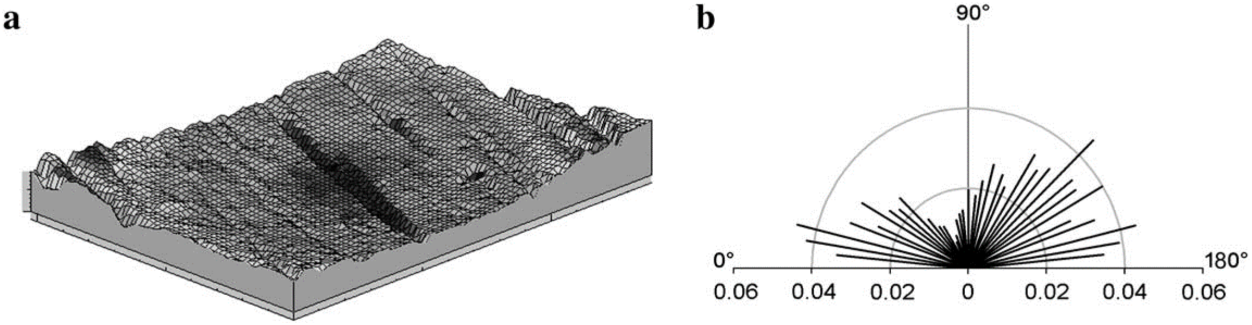

Figure 7 Three-dimensional rendering of striated surface (a) and the corresponding rosette plot of relative lengths taken at 36 different orientations (b) (from Scott *et al.* 2006).

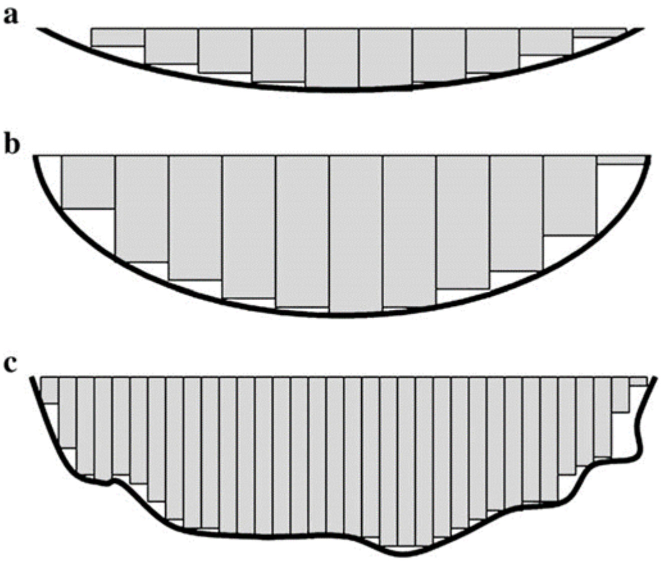

Figure 8 Drawing comparing surfaces with (a) lower and (b) higher structural fill volumes. Finer scale prisms (c) yield structural and textural fill volumes. Textural fill volumes by subtracting (b) from (c). (from Scott, *et al.* 2006).

2.2.8. Statistical analysis

Statistical analysis was performed using the SPSS 22.0.0 statistical software package. Comparisons of molar flare index (MF) between three dietary groups of hominoids, (i.e., frugivores, folivores, and hard-object feeders according to Singleton 2003 mostly based on their microwear patterns), the *Papio*-group (n=4) and *Procynocephalus* from Dafnero 3 were performed to explore the relationship between molar flare and diet. Relationships among the molar flare (MF) and dentine flare (DFI) indices were explored using correlation analysis only among the modern *Papio* and *Procynocephalus*. Comparisons between measurements of 2D linear enamel thickness were performed for the buccal and lingual functional parts of the molar crown among modern *Papio* and the Greek specimen. Considering the whole crown tissue proportions, the estimated 3D average enamel thickness and 3D relative scale-free enamel thickness is compared between modern *Papio*, *Colobus*, *Macaca* and *Procynocephalus* (**see Appendix**, **Table 6**).

To compare the microwear pattern characteristics of *Procynocephalus* with modern taxa, the analysis is focused on two variables, complexity (*Asfc*) and anisotropy (*epLsar*). We chose these two variables because it has been shown that they are promising in distinguishing primates with different diets (Scott *et al.*, 2012) and it would be the most conservative way to verge on the dietary habits of Dafnero 3 specimen. Descriptive statistics for each taxon are compared. Because in most cases the data of microwear analysis were not normally distributed, they were rank-transformed (Conover *et al.*, 1981) before differences among taxa were identified using Analysis of Variance (ANOVA). Tukey’s Honest Significant Differences (HSD) *post hoc* and Fisher’s Least Significant Differences (LSD) tests were run to balance risks of Type I and Type II errors (Cook and Farewell, 1996) and allowed us pairwise comparison. *Procynocephalus* was included in the analysis although is represented by two individuals (DFN3-150 and GSI 18453 from Williams *et al.*, 2012). Bubble-plots of the percent of specimens with complex microwear textures versus percent of specimens with anisotropic microwear textures were created in order to correlate the dietary habits of the fossil genus with modern taxa with known dietary preferences.

To explore the feeding ecology between the Dafnero specimen and *Papio* from Omo Valley, we compare the fluctuations of complexity (Asfc) and anisotropy (epLsar) in Phase I and Phase II facets of *Papio* specimens throughout geological members of the Shungura formation. The analysis is focused on the contemporaneous assemblages of the two taxa.

CHAPTER 3. Results

3.1. Molar flare and Enamel thickness

Estimations of the 2D linear enamel thickness in lingual and buccal part of the M^2 in modern *Papio* and *Procynocephalu*s from Dafnero 3 are shown in **Fig.9** and **Table 7** and **Fig. 17 (see Appendix).** All 2D linear measurements were taken on the mesial aspect of the molar, on the two cusps. The median values of buccal occlusal maximum enamel thickness (**BOCMAX**), do not present any significant differences as the single value from Dafnero 3 taxon is placed well within the range of extant baboons, being slightly lower than *Papio* median value (**Fig**.**9a**). On the other hand, in all *Papio* specimens (n=4) and *Procynocephalus* from Dafnero 3, the occlusal part of the molars was slightly worn., the former due to mastication, abrasion of the food objects and attrition and the latter due to postmortem alterations. So, the possibility of significant differences on occlusal maximum enamel thickness between the modern and fossil taxa, cannot be rejected with the present data and it might need further investigation with unworn and undamaged molars of both taxa. On the contrary, the median values of buccal lateral maximum enamel thickness (**BLATMAX**), taken on the lingual functional part of the molar, seem to differ among the modern and fossil taxa. *Procynocephalu*s from Dafnero 3, although represented by a single individual in this study, possess significantly thicker lateral enamel than *Papio*. The median values of the fossil primate for lingual occlusal (**LOCMAX**) and lingual lateral (**LLATMAX**) maximum enamel thickness are also higher than in the modern *Papio* (**Fig.9b**). Interestingly in this case there is difference on the thickness of the enamel on the occlusal region which is not consistent with the previous observation focused on the buccal functional part, in which the thickness of the enamel between fossil and modern taxa didn't show any significant discrepancy. In general, considering the buccal and lingual functional parts, enamel on the lateral region of the studied molars seem to be thicker than on the occlusal region.

Results of the 3D enamel thickness measurements for M^2s examined in this study are shown in **Fig**.**10**, (variable definitions and units are given in the materials and methods section **Table 1**). Summary enamel thickness measurements (average and relative) for each taxon are given in **Table 6** (**Appendix**). The enamel distribution of the studied molars is shown in **Fig.3** and additionally in **Fig. 15** of **Appendix** ranging from dark blue (thinner) to red (thicker) (Macchiarelli *et al.*, 2008, 2013; Bayle *et al.*, 2011). The 3D enamel thickness measurements seem to be consistent with the 2D linear enamel thickness measurements. *Procynocephalus* from Dafnero 3 shows higher median values of 3D average enamel thickness (**AET3D**) than all the other modern taxa used for comparison. The 3D average enamel thickness clearly distinguishes *Procynocephalus* from Dafnero 3 and *Papio* from *Macaca* and *Colobus,* the latter characterized as a small and folivorous primate considering its dietary habits. This result is however biased by the size of the taxa in comparison. After the removal of size effect with the 3D relative scale-free enamel thickness (**RET3D**) still *Procynocephalus* from Dafnero 3 shows the higher median values of all modern taxa. In this case, the folivore *Colobus* shows higher values of relative enamel thickness than the omnivorous *Papio* and *Macaca*, which is interesting if we consider that the primary diet of this primate consists of leaves. Thinner enamel is thought to be associated with folivorous diet. As the thin enamel rapidly perforates by dental wear, the raised edge of the worn enamel on the crest margins forms a sharp edge, which enhances the shredding and slicing functions of the crest during mastication (Covert and Kay, 1981). A leaf eating diet requires maximal food shredding, because leaves contain large quantities of structural carbohydrates, the digestion of which is greatly facilitated by reduced particle size (Sheine, 1979a, b). However, this is not observable in this sample of *Colobus* as it exhibits thick enamel, although the factor of sex and age of the sample studied here wasn't taken under consideration.

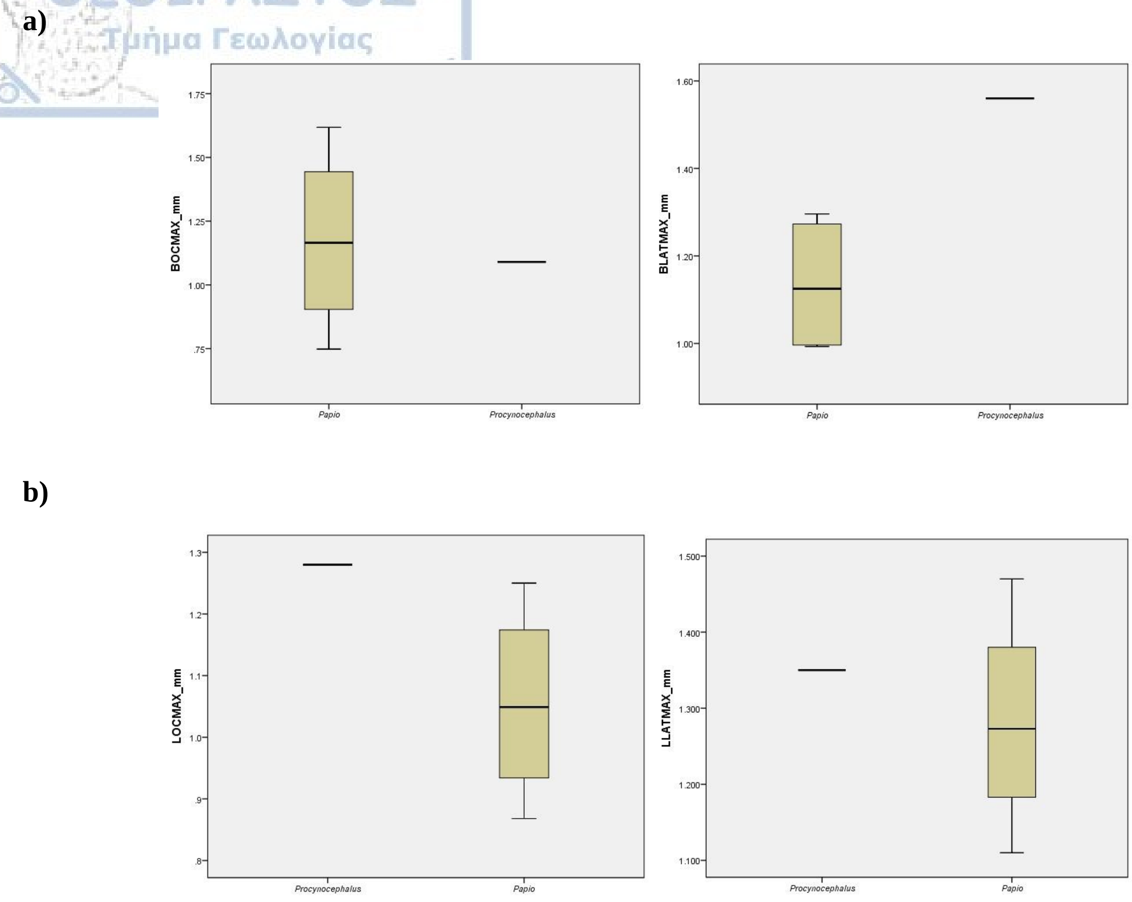

Figure 9 Boxplot of the 2D linear enamel thickness measurements in (a) buccal aspect and (b) lingual aspect of the upper second molar crown in modern *Papio* and *Procynocephalus* from Dafnero 3 samples. BOCMAX: buccal occlusal maximum enamel thickness; BLATMAX: buccal lateral maximum enamel thickness; LOCMAX: lingual occlusal maximum enamel thickness; LLATMAX: lingual lateral maximum enamel thickness. Each boxplot presents data minimum (i.e., lowest horizontal bar), the first quartile (i.e., lower edge of the box), median (i.e., bar inside the box), third quartile (i.e., upper edge of the box), and data maximum (i.e., highest bar).

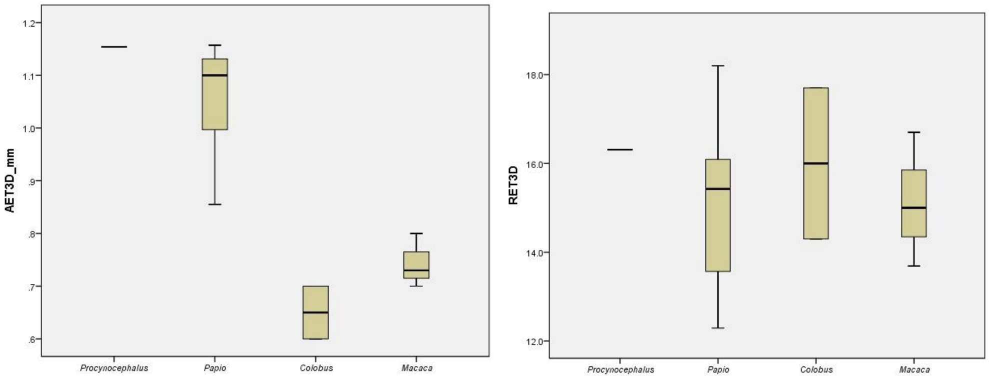

Figure 10 Boxplot of the 3D average enamel thickness (left) and 3D scale-free relative enamel thickness (right) in modern taxa and *Procynocephalus* from Dafnero 3. Each boxplot presents data minimum (i.e., lowest horizontal bar), the first quartile (i.e., lower edge of the box), median (i.e., bar inside the box), third quartile (i.e., upper edge of the box), and data maximum (i.e., highest bar).

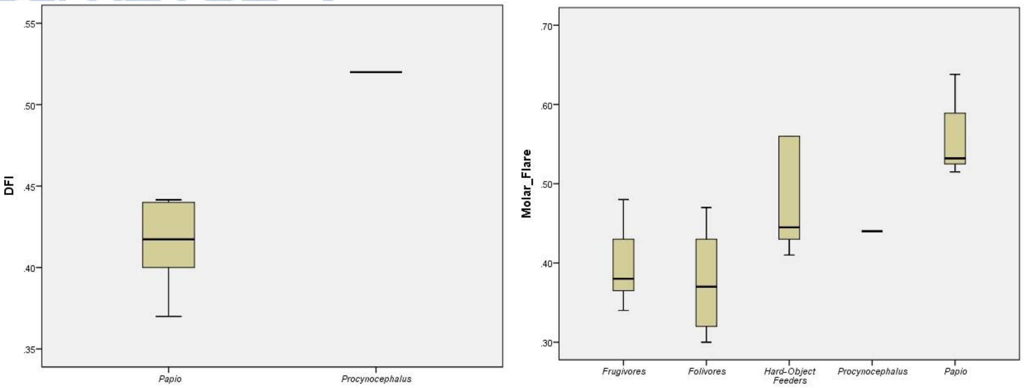

Figure 11 Boxplot of the dentine flare index (left)in *Procynocephalus* from Dafnero 3 and modern *Papio*, and molar flare index (right) in *Procynocephalu*s, modern *Papio* and three dietary groups of hominoids. Each boxplot presents data minimum (i.e., lowest horizontal bar), the first quartile (i.e., lower edge of the box), median (i.e., bar inside the box), third quartile (i.e., upper edge of the box), and data maximum (i.e., highest bar).

The comparisons of the molar flare index (**MF**) among *Procynocephalus*, modern *Papio* group and the three groups of hominoids with known dietary habits (Singleton 2003) are shown in **Fig.11.** These groups of hominoids consist mostly of fossil forms and three modern taxa with known dietary habits, each of the modern taxa representing a dietary group. (see Table 1 from Singleton 2003). The dietary assessment of the fossil taxa was based on dental microwear textural analysis (Teaford and Walker, 1984; Teaford *et al.*, 1996; Ungar, 1996; Palmer *et al.*, 1998, 2000; King, 2001), and shearing quotient analysis (Ungar and Kay, 1995; Teaford *et al.*, 1996; Kay and Ungar 1997; Palmer *et al.*, 2000), albeit the microwear analysis was given greater weight than the other factors. *Procynocephalus* is in the same relative position as the hard-object feeders group while modern *Papio* group show the higher values of the index. Based on this index *Procynocephalus* from Dafnero-3 and modern *Papio* have more pronounced molar flare compared to the hominoid groups. Singleton (2003) suggested that molar flare can be a useful diet indicator if used in the appropriate temporal and phylogenetic context. In this case the comparison is between two different phylogenetic groups, cercopithecoids and hominoids, with two different contrasted molar patterns. So, the correlation of *Procynocephalus* with a type of diet based on this comparison might not be accurate, but it shows that it possessed a strong flare. The comparison of *Procynocephalus* and *Papio* with dentine flare index (**DFI**) shows that the fossil primate had more pronounced molar flare than *Papio* (**Fig.11**). Benefit (1993, 1999, 2000) has found that pronounced molar flare to be functionally correlated with hard-object feeding among cercopithecoids. Hence, the use of this index seems to be more conservative because it represents the whole portion of the molar, does not include the influence of the enamel on the flare and the comparison is between taxa of the same phylogenetic group. The more pronounced flare of *Procynocephalus* from Dafnero 3 might indicate the better capability of this fossil primate to consume hard objects than *Papio*.

3.2. Dental microwear textural analysis

The analysis focused on the f9 (crushing/grinding) facet of the taxa, showed important differences between taxa (**Table 2**). Extant folivores, represented by *Theropithecus gelada* and *Semnopithecus entellus*, are characterized by very low values of complexity (Asfc) while the other taxa exhibit much higher values. *Procynocephalus* specimens, both DFN3-150 (**Fig.12**) and GSI 18453 (Williams *et al.*, 2012), shows the higher values of complexity followed by the omnivorous primates, *Papio cynocephalus*, *Papio ursinus*, *Macaca fascicularis* and the fossil *Papio* sample from Omo valley, while *Gorilla beringei* exhibit medium values. For anisotropy (epLsar) the higher values of are shown by *Theropithecus gelada* followed by *Semnopithecus entellus*, an expected result if we consider their high consuming of tough grass and leaves which are shown to correlate with high anisotropy values (Scott *et al.*, 2012). *Gorilla beringei* and *Macaca fascicularis* exhibit medium values of anisotropy while the modern baboons, *Papio cynocephalus*, *Papio ursinus*, the fossil *Papio* sample from Omo valley as well as *Procynocephalus* sample possess the lowest values of anisotropy.

The values of complexity (Asfc) seem to separate well the taxa into two distinct groups based on their dietary preference, the omnivorous primates *Papio cynocephalus*, *Papio ursinus*, *Macaca fascicularis* and the fossil *Papio* from Omo valley, i.e. the hard object feeders, and the folivorous primates, *Theropithecus gelada*, *Semnopithecus entellus* and *Gorilla beringei* i.e. the soft-tough object feeders. On the other hand, anisotropy (epLsar) clearly separates *Theropithecus gelada* and *Semnopithecus entellus* showing the highest values from all the other taxa while the rest of them seem to possess medium to low values.

Table 2. Descriptive statistics for complexity (Asfc) and anisotropy (epLsar).

Taxa	n	Statistic	Asfc	epLsar
Papio cynocephalus	27	Median	1.944E+00	3.000E-03
		std	3.234E+00	1.000E-03
Papio ursinus	12	Median	1.901E+00	2.000E-03
		std	1.343E+00	1.000E-03
Theropithecus gelada	12	Median	6.370E-01	5.000E-03
		std	2.090E-01	1.000E-03
Semnopithecus entellus	8	Median	5.290E-01	4.000E-03
		std	2.755E-01	1.000E-03
Gorilla beringei	16	Median	1.182E+00	3.000E-03
		std	1.454E+00	1.000E-03
Macaca fascicularis	20	Median	1.847E+00	3.000E-03
		std	1.393E+00	1.000E-03
Fossil Omo Papio	57	Median	1.502E+00	2.000E-03
		std	1.485E+00	1.000E-03
Procynocephalus	2	Median	2.390E+00	2.000E-03
		std	1.229E+00	2.000E-03

Table 3. Analysis of Variance results.

ANOVA	Variables	F value	*p* value
Between group	Complexity (Asfc)	8.87	< 0.001
	Anisotropy (epLsar)	7.391	< 0.001

Table 4. Pairwise comparisons between taxa for complexity (Asfc).

Complexity (*Asfc*)		***P***	
		Tukey's HSD	**Fishers's LSD**
Fossil Omo Papio	*Papio cynocephalus*	0.177	**0.011**
Fossil Omo Papio	*Papio ursinus*	0.479	**0.046**
Fossil Omo Papio	*Theropithecus gelada*	**0.001**	**< 0.001**
Fossil Omo Papio	*Semnopithecus entellus*	**0.001**	**< 0.001**
Fossil Omo Papio	*Gorilla beringei*	0.997	0.486
Fossil Omo Papio	*Procynocephalus*	0.971	0.31
Fossil Omo Papio	*Macaca fascicularis*	0.962	0.286
Papio cynocephalus	*Papio ursinus*	1	0.911
Papio cynocephalus	*Theropithecus gelada*	**< 0.001**	**< 0.001**
Papio cynocephalus	*Semnopithecus entellus*	**< 0.001**	**< 0.001**
Papio cynocephalus	*Gorilla beringei*	0.193	0.013
Papio cynocephalus	*Procynocephalus*	1	0.857
Papio cynocephalus	*Macaca fascicularis*	0.958	0.278
Papio ursinus	*Theropithecus gelada*	**< 0.001**	**< 0.001**
Papio ursinus	*Semnopithecus entellus*	**< 0.001**	**< 0.001**
Papio ursinus	*Gorilla beringei*	0.364	**0.03**
Papio ursinus	*Procynocephalus*	1	0.903
Papio ursinus	*Macaca fascicularis*	0.976	0.326
Theropithecus gelada	*Semnopithecus entellus*	1	0.784
Theropithecus gelada	*Gorilla beringei*	0.41	**0.002**
Theropithecus gelada	*Procynocephalus*	0.099	0.006
Theropithecus gelada	*Macaca fascicularis*	**< 0.001**	**< 0.001**
Semnopithecus entellus	*Gorilla beringei*	**0.03**	**0.001**
Semnopithecus entellus	*Procynocephalus*	0.075	**0.004**
Semnopithecus entellus	*Macaca fascicularis*	**< 0.001**	**< 0.001**
Gorilla beringei	*Procynocephalus*	0.919	0.217
Gorilla beringei	*Macaca fascicularis*	0.847	0.158
Procynocephalus	*Macaca fascicularis*	0.999	0.542

(Values for *P* that are significant at α= 0.05 are shown in **bold** print.)

The ANOVA comparisons, for complexity (Asfc) and anisotropy (epLsar) yield statistically significant differences among taxa ($p<0.05$). For both anisotropy and complexity, the F values indicate that between taxa significant variation exists (**Table 3**). The results of Tukey's HSD and Fisher's LSD post hoc significance tests suggests that important distinctions occur among some of the pairwise comparisons of the taxa. For complexity (Asfc), *Theropithecus gelada* and *Semnopithecus entellus* are distinct from all taxa except each other, while the results of both post hoc tests for *Theropithecus gelada* and *Gorilla beringei* shows no clear distinction between them (**Table 4**). While complexity (Asfc) reveals clear distinction between taxa with distinct, except the not statistically clear relationship between *Theropithecus gelada* and

Gorilla beringei, the results of the post hoc tests for anisotropy (epLsar) seem to be more complex (**Table 5**). Important distinction exists between the fossil sample of *Papio* from Omo valley with all taxa except the modern baboons and *Procynocephalus*. *Theropithecus gelada* shows clear distinction from *Papio cynocephalus* and *Papio ursinus*, while its statistical relationship with *Gorilla beringei*, *Macaca fascicularis* and *Procynocephalus* is of "suggestive" significance (Cook and Farewell, 1996).

Table 5. Pairwise comparisons between taxa for anisotropy (epLsar).

Anisotropy (*epLsar*)		**P**	
		Tukey's HSD	**Fishers's LSD**
Fossil Omo Papio	*Papio cynocephalus*	0.109	**0.006**
Fossil Omo Papio	*Papio ursinus*	0.745	0.11
Fossil Omo Papio	*Theropithecus gelada*	**< 0.001**	**< 0.001**
Fossil Omo Papio	*Semnopithecus entellus*	**0.007**	**< 0.001**
Fossil Omo Papio	*Gorilla beringei*	**0.013**	**0.001**
Fossil Omo Papio	*Procynocephalus*	1	0.727
Fossil Omo Papio	*Macaca fascicularis*	**0.021**	**0.001**
Papio cynocephalus	*Papio ursinus*	1	0.691
Papio cynocephalus	*Theropithecus gelada*	**0.005**	< **0.001**
Papio cynocephalus	*Semnopithecus entellus*	0.641	0.079
Papio cynocephalus	*Gorilla beringei*	0.957	0.276
Papio cynocephalus	*Procynocephalus*	0.999	0.588
Papio cynocephalus	*Macaca fascicularis*	0.994	0.443
Papio ursinus	*Theropithecus gelada*	**0.01**	**< 0.001**
Papio ursinus	*Semnopithecus entellus*	0.581	0.065
Papio ursinus	*Gorilla beringei*	0.91	0.208
Papio ursinus	*Procynocephalus*	1	0.735
Papio ursinus	*Macaca fascicularis*	0.974	0.319
Theropithecus gelada	*Semnopithecus entellus*	0.794	0.13
Theropithecus gelada	*Gorilla beringei*	0.162	**0.01**
Theropithecus gelada	*Procynocephalus*	0.304	**0.023**
Theropithecus gelada	*Macaca fascicularis*	0.056	**0.003**
Semnopithecus entellus	*Gorilla beringei*	0.992	0.42
Semnopithecus entellus	*Procynocephalus*	0.865	0.17
Semnopithecus entellus	*Macaca fascicularis*	0.949	0.259
Gorilla beringei	*Procynocephalus*	0.975	0.324
Gorilla beringei	*Macaca fascicularis*	1	0.726
Procynocephalus	*Macaca fascicularis*	0.99	0.401

(Values for *P* that are significant at α= 0.05 are shown in **bold** print.)

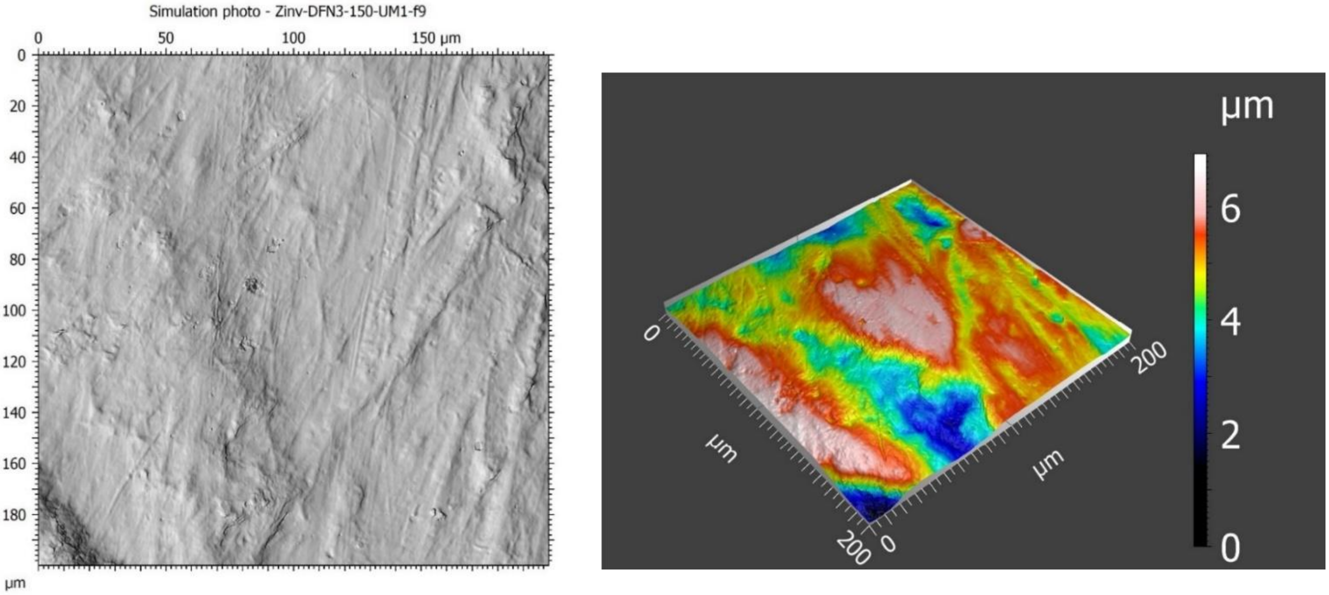

Figure 12 Photosimulation (left) and three-dimensional representation (right) of DFN3-150 microwear surface of the upper first molar.

The percent of the specimens of the modern and fossil taxa that surpassed the cutpoint values of complexity (Asfc) and anisotropy (epLsar) are given in **Table 9 (Appendix).** If the cutpoint value of the variables is exceeded (Asfc>1.5 and epLsar>0.003), the microwear texture of the individual is characterized "complex" and "anisotropic". Based on the percentage values of the "complex" and "anisotropic" microwear textures for each taxon, derives their position on the two dimensional plot, as illustrated in **Fig.13**. The bubble width is proportional to sample sizes of each taxon. This allows us to have a better view of the feeding strategies of the studied taxa and also explore the dietary relationships among them, if there are any. There is a clear separation on the plot between, the folivorous primates distributed along the perpendicular axis (*Theropithecus gelada* and *Semnopithecus entellus*) and the omnivorous (concetrated to the right part of the diagram). As expected *Theropithecus gelada* and *Semnopithecus entellus* are clearly separated from all the other taxa, possessing the lowest percentages of individuals with "complex" microwear textures, while having the highest percentage of individuals with "anisotropic" textures followed by *Gorilla beringei*. The position of *Gorilla beringei* in the plot is of much interest if we consider their usual diet, which is folivorous. There is substantial percentage of individuals with "complex" microwear textures (43.75%) , placing the taxon near the omnivorous primates on the plot. This percentage of individuals might represent a change in feeding strategy due possibly to temporal effects or the available food resources of their habitat (Vedder, 1984). All the omnivorous taxa show percentage of specimens with "complex" microwear textures higher than the half of the sample size, while the modern *Papio* also showing a substantial percentage of individuals with "anisotropic" textures. This reflects their highly flexible diet and supports the notion that baboons are essentially diet generalists (Van Doorn, 2010). *Procynocephalus* specimens, DFN3-150 and GSI 18453 (Williams *et al.*, 2012) is placed on the right side of the plot near the omnivorous primates. Although in this case the this analysis might not be the right way to explore the dietary habits of *Procynocephalus*, because the sample is constituted only by two individuals. However, the values of complexity for both *Procynocephalus* specimes used in the analysis (DFN3-150 and GSI 18453) are a lot higher than all the other folivorous taxa used for the comparisons. Additionally, only the Greek specimen possess anisotropy value within the range of values of the folivorous taxa (0.004 for epLsar for DFN3-150). These values of anisotropy suggest that the primate from Dafnero-3 might have followed a diet constituted on tougher food objects that was possibly dependent on the availability of food resources. When preferred foods were not present, this primate might have consumed herbaceous monocots as a fallback resource. But the values of complexity on the available material of *Procynocephalus* indicate that hard and brittle food objects were included in its diet. The consumption of herbaceous monocots for extended time periods has been observed in modern baboons but the portion of the grass eaten varied significantly throughout seasons (DeVore and Washburn, 1963). Based on the available material and all these observatios, similar dietary habits and strategies with modern and fossil *Papio* is suggested for *Procynocephalus*. Hence, this also suggests that it might have been possible for the fossil primate that hard objects such as seeds, bark, roots and underground storage organs (USO's), was a part of its usual diet.

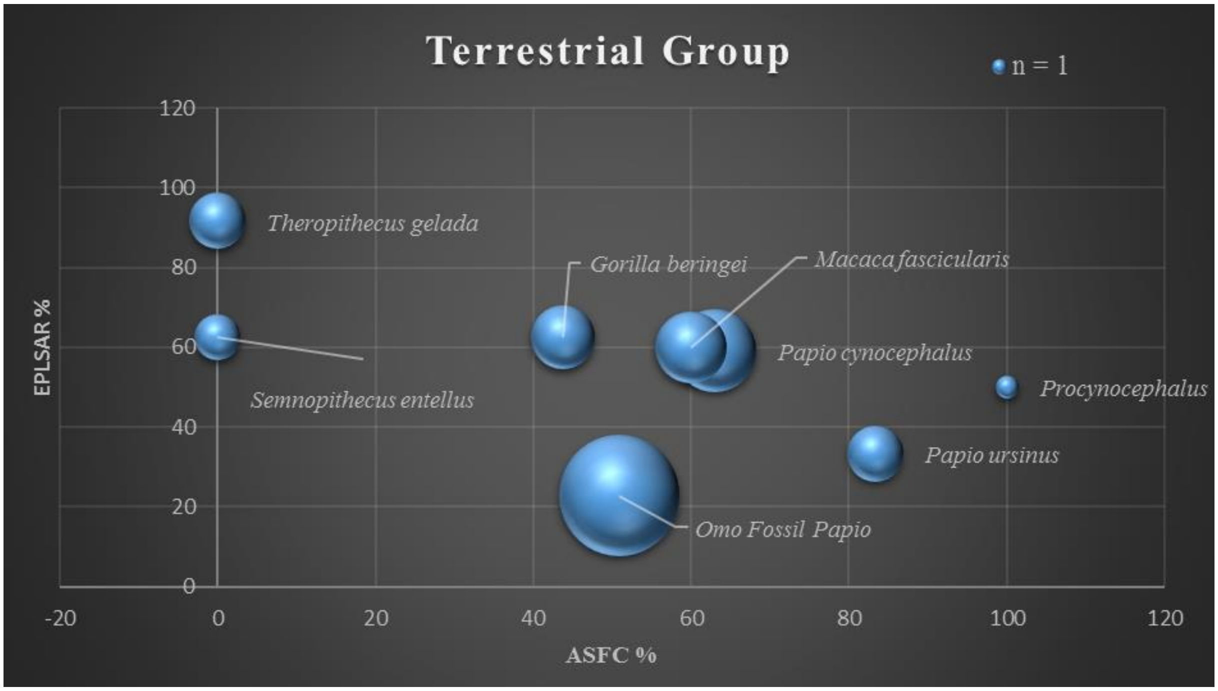

Figure 13 Bubble plot of percent of specimens with complex microwear textures versus percent of specimens with anisotropic microwear textures. Bubble widths are proportional to sample sizes.

3.3 Omo valley, Shungura formation

To explore the feeding ecology of the fossil *Papio* sample from Omo valley, we compare their microwear textural data among the geological members of the Shungura formation. Median values of complexity (Asfc) and anisotropy (epLsar) of the Omo *Papio*, were plotted to explore the fluctuations of the variables along the geological members. To test this hypothesis, we used both Phase I and II facets, the former correlated with the shearing action of the tooth while the latter is correlated with the grinding action of the tooth required to process hard food objects. Theoretically, the combination of both types of facets would allow us to track the fluctuation of toughness of the consumed plants that need to be sheared, through the microwear characteristics of Phase I facets (i.e shearing facets), while the microwear characteristics of Phase II facets (i.e crushing/grinding facets) should be able to track the hardness of the food consumed. If there is a common trend, we expect it to be observable in both type of facets.

A decrease in complexity values in both types of facets from geological member B to C is observed while at the same time anisotropy values increase in these geological members. This decrease of complexity and increase of anisotropy, may reflect a shift in diet from hard food objects, hard seeds/tubers and possibly USOs, to more tougher foods such as the herbaceous monocots. Furthermore, the dental microwear textural data of Omo *Papio* show that there is also a common trend of the variables between geological members E, F and G (lower and upper) (**Fig.14**). There is a decrease in the values of complexity from member E to F, and then again, they increase to member G (**Fig.14**), while at the same time the values of anisotropy increase from geological member E to F and then decrease in member G. A similar trend has been observed in microwear textural data of *Theropithecus* that was found in geological members B, C and D, F of the Shungura formation (Martin *et al.*, 2016 in press). This observation has been attributed to an increase of consumption of monocotyledonous herbs between member B and C and then D and F. Also, Martin *et al.*, (2016) linked these fluctuations of complexity (Asfc) with oxygen and carbon isotopic data from enamel of artiodactyls (Souron *et al.*, 2012; Bibi *et al.*, 2013; Negash *et al.*, 2015) and paleosoils (Levin *et al.*, 2011) collected from the Shungura formation and suggested that there is a trend to more open environments between 2.9 Ma and 2.4 to 2.3. Ma.

The idea of an environmental shift towards more open and dry habitats during the last period of Pliocene and at the beginning of Pleistocene has been discussed thoroughly by many researchers (Cerling, 1992; 2011, Reed, 1996; Bobe *et al.*, 2001; Demenocal, 2004; Fernández *et al.*, 2006; Bibi *et al.*, 2012; Martin *et al.*, 2016). and the evidence from the microwear textural data of the *Papio* of Omo valley seem to be consistent with this hypothesis. The decrease and increase in values of complexity and anisotropy respectively between the same geological members, can be interpreted as a decrease in consumption of hard food objects and a dietary shift towards tougher food objects at these time intervals.

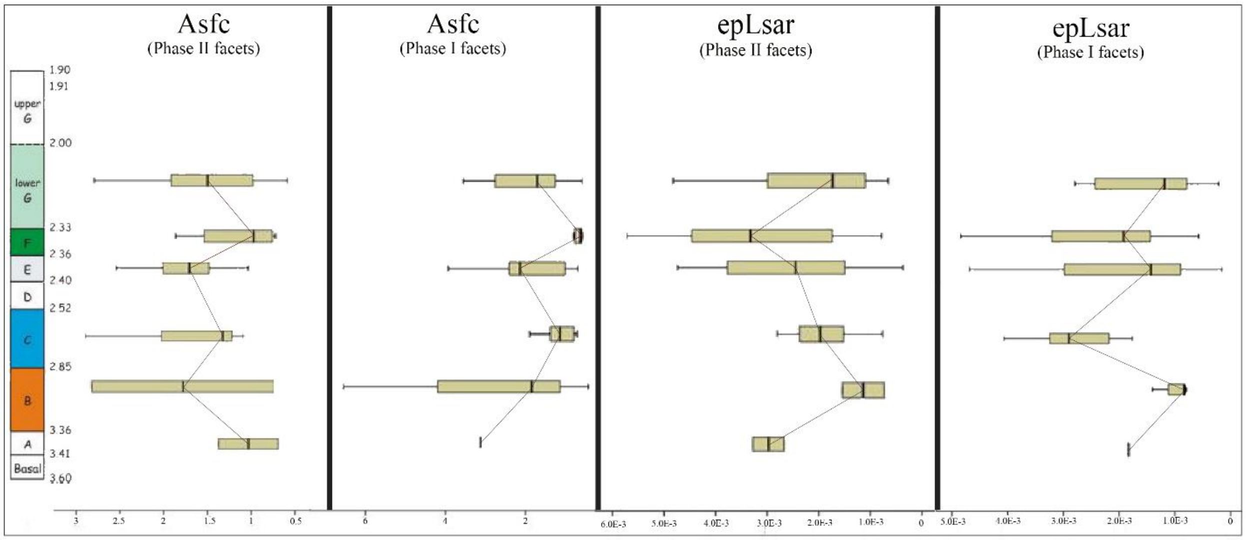

Figure 14 Fluctuations of complexity (Asfc) and anisotropy (epLsar) in Phase I and II facets, between geological members of the Shungura formation, Omo valley (stratigraphic column after Boisserie *et al.*, 2010).

CHAPTER 4. Discussion

The use of CT scan imaging combined with microwear textural analysis using confocal microscopy, presents fresh data to help understand the feeding ecology of *Procynocephalus* from Dafnero 3. Enamel thickness is known to vary among extant and fossil primates and it exhibits functional and/or phylogenetic information (e.g., Martin, 1983; Shellis *et al.*, 1998). The estimates of enamel thickness and the comparison with modern *Papio* brings information about the feeding capabilities of the fossil primate from Dafnero 3. The analysis of the molar flare and dentine flare (Guy, 2013) indices, enables us to characterize the mechanical properties of a portion of its diet and give us information about the morphology of the molars studied. The molar morphology is thought to be closely related to functional requirements imposed by the physical properties of the masticated food (e.g., Janis and Fortelius, 1988).

The dental microwear textural analysis and the comparison with modern taxa with known diets, gives additional data about the feeding habits of the fossil primate from Greece. While the available data for *Procynocephalus* are scarce and the comparative material here is limited (concerning the enamel thickness and molar-dentine flare data) still it allows us to come closer to understanding the dietary capabilities and preferences of this fossil genus. The combination of data of enamel thickness, molar-dentine flare indices and dental microwear textural analysis give us a better insight of the dietary strategy of this fossil genus and possibly helps us make a better representation of its ecology.

4.1. Enamel thickness

The results of the enamel thickness indicate that the dentition of *Procynocephalus* from Dafnero 3 was capable of processing and consuming hard food objects. All 2D measurements taken show higher values of enamel thickness for the fossil primate, with the exception of buccal occlusal maximum enamel thickness (**BOCMAX**) which has almost the same value with the modern *Papio* (**Fig.9**). In general, the measurements taken on the occlusal region have lower values than the ones taken on the lateral region of the molar. This is expected if we consider that the molars were slightly worn mostly due to abrasion during the mastication process, and the M^2 of the fossil primate was damaged by weathering (but not the M^1 as it was already mentioned). Nevertheless, the estimations of the 2D linear enamel thickness indicate that the fossil primate possessed relatively thicker enamel than the *Papio* sample studied here. On the other hand, Kono *et al.* (2008) investigated in detail the 2D-based linear measurements of enamel thickness, and found that occlusal and some definitions of lateral enamel thickness were methodologically unstable, and potentially misleading in characterizing both local and overall regional enamel thicknesses (Suwa and Kono 2005; Kono and Suwa, 2008). So, concluding remarks based on 2D linear measures of enamel thickness must be treated with caution.

While the two-dimensional approach to measure enamel thickness seem to have some problems, the three-dimensional approach of measuring enamel thickness does not present this kind of problems and also gives a better picture of enamel thickness distribution considering the overall tooth. The 3D average enamel thickness (**AET3D**) of *Procynocephalus* from Dafnero 3, is higher than all the other modern comparative taxa (**Fig.10**). However, the values of this measurement are being affected by the size of studied primates. So, the great difference between the average enamel thickness values between *Procynocephalus*, *Macaca* and *Colobus* is justified from the important difference in size, if we consider that the studied fossil primate is estimated to be one of the largest representatives of the Cercopithecidae family. On the other hand, the values of the 3D relative enamel thickness (**RET3D**), which are corrected for size effects, show again *Procynocephalus* possessed relatively thicker enamel than all the other comparative taxa. Therefore, based on the notion that the thickness of the dental enamel is functionally correlated with a type of diet as an adaptation to the abrasion from food objects and the data presented here, it is safe to presume that hard food objects was a part of the diet of the Dafnero 3 primate. The frequency of consumption of such objects was depended on factors such as temporal variation and availability of food resources in their natural habitat. Lambert *et al.*, (2004) suggested that it is not so much what is consumed most commonly (i.e soft, freshy fruit) that selects for enamel thickness, but the hardness of foods that are consumed infrequently when other, more preferred foods are not available. These fallback foods (FBFs) have been a topic of particular interest from many researchers that study the primate ecology and paleoanthropology (Constantino and Wright, 2009). The processing of preferred foods by primates, like fruits, would require little dental specializations, in contrast with the FBFs, such as leaves or seeds, which would require a more specialized dental morphology (Marshall and Wrangham, 2007 and references therein). The presence of forms with specialized dentition that exhibit generalist feeding behavior (Liem's paradox) seems to contradict this assumption of the correlation between the dental adaptation and the mechanical properties of food usually consumed by a primate (Robinson and Wilson 1998, Grine *et al*., 2006, Ungar *et al*., 2008). Hence, specialized dental morphology may reflect an adaptation to FBF processing, not an adaptation to preferred food items. If this is true, temporal variations and seasonal availability of the food resources on the natural habitat, might play a significant role in understanding the selection of thick or thin enamel among primates.

In a previous study, *Procynocephalus* was characterized as a baboon-like terrestrially adapted animal, based on limb bone features, and its dentition indicated omnivorous diet (Szalay and Delson, 1979). It is possible that this primate spent most of its time foraging on the ground and trying to exploit all the available food resources ranging from soft/tough to very hard objects. This kind of behavior is very common in all baboons which they also use their arboreal nature in search for food resources, for resting and avoiding the danger of predators. So, the speculation that *Procynocephalus* might have followed a similar strategy is of much interest. One feeding adaptation that thought to be shared in all baboons is the ability to subsist in relatively low quality diet for extended time periods (Nowak, 1999). This adaptation allows them to exploit any terrestrial habitat, like deserts, semi-deserts and dry grasslands. If *Procynocephalus* shared this adaptation, it would allow the fossil primate to successively exploit any habitat and it is possible that this might have helped its dispersal in the very wide geographic range of Eurasia where it is found (Delson, 1975; Delson and Nicolaescu-Pliopsor, 1975; Szalay and Delson, 1979; Pan and Jablonski, 1987; Jablonski *et al.*, 2002, Takai *et al.*, 2008, 2014, Nishimura *et al.*, 2014).

4.2. Molar flare

Molar flare is a shape trait whose polarity, phylogenetic distribution and functional significance have been sources of contention (Singleton, 2003). While variations of the molar flare appear to be a product of functional, phylogenetic and temporal effects, Singleton (2003) suggested that it does contain a dietary signal, but one which can be interpreted only in an appropriate temporal and phylogenetic context. A possible source of functional molar flare variation is thought to be enamel thickness. Enamel thickness is known to alter the crown geometry, reducing the shearing capacity and the crown relief while enhances the resistance to stress loads (Kay, 1984; Shellis *et al.*, 1998; Macho and Spears, 1999). However, the existence of thin enameled forms with very pronounced flare (Conroy *et al.*, 1995; Singleton, 2000) and thick-enameled forms with reduced flare (Bonis and Koufos, 1993) implies that enamel thickness cannot be the sole source of molar flare variation. Furthermore, previous studies (Benefit, 1993, 1999, 2000) have shown that pronounced molar flare is correlated with frugivory and hard object feeding in cercopithecoid primates. Results of the comparison of the molar flare index (**MF**) indicate that *Procynocephalus* from Dafnero 3 possessed a strong flare, while modern *Papio* exhibited the higher values of the index. The molar flare index clearly distinguishes the dietary groups of hominids, with the hard object feeders exhibiting the higher values. While the comparison between the groups of hominids seem to reveal the dietary signal of the molar flare, we refrain from referring to a specific type of diet comparing these groups and the fossil genus, because they belong in different phylogenetic groups. The results of the comparison of the newly advanced dentine flare index (Guy, 2013) (**DFI**) seem to contradict the previous observation, that the *Papio* exhibit more pronounced flare. This contrast might be due to various reasons. One possible explanation is that the molar flare index contains the effect of the enamel, while in the dentine flare index this effect is removed. Although as mentioned earlier enamel thickness can be a source of variation of the molar flare but not the sole. Another possible reason of this contrast is that the molar flare index is measured and refers only on the mesial part of the molar, while the dentine flare index refers to the whole portion of the molar. Additionally, following Singleton (2003) the comparison of both indices is not within the appropriate temporal context. Nevertheless, results of both indices combined indicate that *Procynocephalu*s from Dafnero 3 possessed pronounced molar flare. A pronounced molar flare, based on the presumption that a strong flare among cercopithecoids is correlated with hard-object feeding (Benefit, 1993, 1999, 2000), would indicate that the dentition of the Greek specimen was able to process hard food objects. Both indices, undependably, can give us intel about the "flaring" of the molars, but the use of both together seems to be the most conservative way. To conclude, *Procynocephalus* seem to possess strong molar flare based on the comparison of both indices, but still the comparisons is not among contemporaneous forms and the sample size is relatively small. In future studies, both indices should be explored among a substantial sample of modern or fossil taxa with known diets, belonging in the same phylogenetic group and in the same temporal context. This will allow us to have better view of the possible sources of variation of the molar flare.

4.3. Dental microwear textural analysis

The differences in microwear textures among the extant primates which exhibit a terrestrial way of living, indicate the dietary differences between the omnivorous and the folivorous primates. Terrestriality in primates has implications for the dietary items consumed (Williams *et al.*, 2011). Available food objects found on the ground sometimes carry a significant load of abrasive grit, especially if the living habitat is dry and dusty, that consequently can produce distinct microwear textural characteristics such as pits. On this context, microwear characteristics such as parallel striations found on the microwear textures are a product of the abrasive effect on the enamel surface of the mineral inclusions (phytoliths) found in the cells of many plants, especially grasses and sedges (Nystrom *et al.*, 2004). So far, there is no specific microwear signal that can help us identify a hard object feeder that exhibits terrestrial way of life from one that is arboreal. The same also applies for the folivorous primates, although differences in the values of complexity (Asfc) due to the adherent grit are possible. However according to Merceron *et al.*, (2016) which conducted controlled-food trials, they assessed the way and the extent to which dust contributes to dental microwear textures, and they found that dental microwear textures reflect a dietary signal not an environmental one. The adherent grit and dust, product of the environment did not significantly affect the dental microwear textural signal.

The consumption of hard and brittle foods reported for the omnivorous and the preference for soft and tough food objects, such as leaves and tough grasses, for the folivorous primates are clearly reflected by the significant differences in complexity (**Asfc**) and anisotropy (**epLsar**) between these extant forms. High values for complexity (**Asfc**) are found in the extant primates that regularly consume hard and brittle food objects, like *Papio cynocephalus*, *Papio ursinus* and *Macaca fascicularis*, while typically low values characterize folivores, such as *Theropithecus gelada* and *Semnopithecus entellus*. *Procynocephalus* exhibits very complex microwear textures compared to *Theropithecus*, *Semnopithecus* and also the mountain gorilla, *Gorilla beringei,* which interestingly exhibits intermediate values of complexity (**Asfc**) although its primarily folivorous diet. The values of complexity (**Asfc**) of *Gorilla beringei* indicate that this large primate which primarily forages ground vegetation, occasionally tends to consume hard and brittle food objects, such as seeds and bark, the latter one being a very hard fallback food for *Gorilla* (Williams *et al.*, 2012). Nevertheless, mountain gorilla has been reportedly observed consuming such food objects (Rothman *et al.*, 2007) and it is presumed that this dietary strategy depends on the altitude, climate and plant composition of their natural habitats. Similarities in dental microwear between *Gorilla* and *Procynocephalus* have been noted elsewhere (Williams *et al.*, 2011). In this study, *Procynocephalus* exhibits the higher values of complexity (**Table 2**) than all the omnivorous primates compared here, followed by *Papio ursinus* which is known to consume nutrient rich USOs, which have figured prominently in various hypotheses of hominin diets (Scott et al, 2012). The high values of complexity can derive either from the casual consumption of hard and brittle objects (i.e. fruits, seeds, bark, some insects, USOs), or from the accidental ingestion of adherent grit (grains of silicaceous sand, silt, or clay) (Teaford, 1988; Ungar, 1994). On the other hand, dust on the leaves of dicotyledonous herbs reduces the values of complexity (personal communication with Gildas Merceron). Still the accidental ingestion of adherent grit cannot be held solely responsible for the high values of complexity, hence it is presumed as a combined result of these two factors with more gravity attributed to the hard and brittle food object consumption.

While high values of complexity are observed in the hard-object feeders (omnivorous primates), high values of anisotropy (**epLsar**) are exhibited by the primarily folivorous primates, with the higher values exhibited by *Theropithecus gelada*, followed by *Semnopithecus entellus* and *Gorilla beringei*. All the omnivorous primates in this study exhibit low to intermediate values of anisotropy (**epLsar**), with the lower values exhibited by the fossil *Papio* sample from Omo valley. *Procynocephalus* exhibits relatively low values for anisotropy (epLsar) indicating that leaves and other potentially tough items were not regularly consumed by this fossil primate. High anisotropy (long and parallel striations) suggests that the items consumed do not require strength perpendicular to grinding dental facets but directional movements parallel to the dental facet surface (Merceron *et al.*, 2009). Hence, since anisotropy is relatively low and complexity is high, we can assume that *Procynocephalus* regularly consumed hard and brittle food objects.

The two variables used in this approach, complexity (**Asfc**) and anisotropy (**epLsar**), have proven to be the most useful to date for separating taxa by diet. Species that consume more hard-brittle foods tend to have higher complexity (**Asfc**) and lower anisotropy (**epLsar**) values than closely related taxa that consume softer, tougher items (Ungar *et al.*, 2012). This applies whether comparing primates, bovids, carnivorans or macropodid marsupials (Ungar *et al.*, 2007, 2010a; Prideaux *et al.*, 2009; Schubert *et al.*, 2010). All the extant taxa used seem to be well separated, in dietary terms, with the use of these variables and they are closely related to *Procynocephalus*, with only exception *Gorilla beringei*. Nevertheless, *Gorilla beringei* diet preferences and feeding strategies combined with their microwear textural characteristics present much interest thus providing a useful comparison to understand better the dietary proclivities of *Procynocephalus*. When preferred food is scarce, gorillas tend to consume fallback foods including leaves, second choice fruits herbs, pith and bark also insects. Vedder (1984) supported the idea that the selection of quality foods is important to *Gorilla beringei* and that the ranging patterns of a group of mountain gorillas are influenced by the distribution and abundance of high-quality foods. A nutrient rich fallback food, especially in adverse climatic conditions (such as cold, excessive heat and lack of light or drought) is thought to be the underground storage organs of geophytes. The consumption of these hard food objects would help ensure the survival of the animal in harsh climatic conditions but it will also lead to high complexity values, since it is a hard object and carries a significant load of mineral particles being underground. However, whether grit is associated with a specific type of diet, such as the consumption of USOs, is possible but it has been shown that dust particles and adherent grit do not significantly affect the dental microwear textures and the primary source of alteration of the dental microwear textures are the intrinsic properties of the ingested foods (Merceron *et al.*, 2016). Although up to now there are not specific microwear signals linked with the consumption of these underground organs, if *Procynocephalus* followed this feeding strategy like the mountain gorilla, it is possible that these storage organs played a part of its diet especially in times of climatic "crisis". Furthermore, the observed similarity in enamel surface texture properties between *Procynocephalus* and *Parapapio*, and the inferred USO consumption in *Parapapio* (Fourie *et al.*, 2008), suggests that *Procynocephalus* is likely to have also consumed underground organs of plants. In addition, the similarity of the microwear textural characteristics of *Procynocephalus* with *Papio ursinus* and *Papio cynocephalus*, which has been reportedly seen to consume USOs (the former more frequently than the latter) (Whiten *et al.*, 1987, 1991; Byrne *et al.*, 1993), is consistent with this assumption.

In a previous study, Williams *et al.*, (2012) used dental microwear textural analysis to explore the dietary preferences of *Procynocephalus subhimalayanus* (GSI 18453) of the Upper Siwaliks, India but did not included the close related extant papionins, *Papio*, *Macaca* and *Theropithecus*, in the comparisons. The diets of *Macaca* and *Papio* may be extremely variable considering its dental microwear properties across individuals within and between species and *Procynocephalus* lacks the extreme dental specialization that characterizes *Theropithecus*. Even so, comparisons between these species can yield significant information about the feeding habits of the fossil genus. The microwear textural properties of *Theropithecus gelada* are very different from *Procynocephalus* (both DFN3-150 and GSI 18453 specimens) indicating that the fossil genus had different diet than its extant relative. The microwear textural characteristics of *Procynocephalus* resembles a lot the omnivorous *Papio cynocephalus*, *Papio ursinus* and *Macaca fascicularis* so it is possible that this fossil primate had and opportunistic and catholic type of diet as its extant omnivorous relatives.

Although only two individuals of the genus *Procynocephalus* could be included in this study (DFN3-150 and GSI 18453), still they allow us to extract useful information of the feeding habits of this genus. Even though *Procynocephalus* from Dafnero 3 showed signs of postmortem alteration on many teeth including the two M^2s, the evidence of microwear were clear and unaltered on facet 9 of the first upper molar as shown in **Fig.10**. Future discoveries will provide additional information, which is very few, of this fossil genus that dwelled Eurasia at early Pleistocene and may also help us understand its rapid expansion and cause of extinction.

4.4 Ecology

Ecological changes towards more arid conditions in the eastern Mediterranean and South Asia began to occur in Late Miocene (~7 Ma), while these climatic conditions deteriorated between ~2.6 Ma (Middle Villafranchian, MN16) and 1.8 Ma (Koufos *et al.*, 2005). These climatic fluctuations greatly affected the mammalian migrations and dispersion. This time period is characterized by the development and expansion of more steppic floras in the Mediterranean, characterized by *Artemisia* and *Ephedra* (Suc, 1986; Suc *et al.*, 1995), and also the presence of faunas more adapted to drier and colder conditions, especially in Southeastern Europe. These paleoecological conditions changed gradually towards western Mediterranean delaying their presence (Koufos *et al.*, 2005). Hence, during Early Pleistocene the climatic conditions appeared to be more arid in the eastern than the western Mediterranean. As a result, the middle-late Villafranchian faunas from Greece, Turkey and neighboring areas already had a more open and dry character than the isochronous faunas from Southwestern Europe (Kostopoulos and Sen, 1999; Kostopoulos and Koufos, 2000). The fauna of the Greek locality of Dafnero (Middle Villafranchian, MN17) is an example of this type of faunas that were present in the eastern Mediterranean. The presence of giraffid forms (*Palaeotragus inaxpectatus*) and stenonoid horses (*Equus stenonis*) supports the hypothesis of the spreading grasslands during Plio-Pleistocene. Furthermore, the fauna composition of the Upper Siwaliks, India, where the first *Procynocephalus* specimen was found (GSI 18453), suggests an open grassland habitat (Dennell, 2008).

In the Early Pleistocene locality of Vatera, Lesvos, Greece *Procynocephalus/Paradolichopithecus*, was unearthed (referred to as *Paradolichopithecus arvernensis* in de Vos *et al.*, 2002), along with other various mammalian remains. The fauna composition of Vatera suggests a picture of a forest clearing and forest edge environment (Sondaar *et al.*, 2005). The microwear textural characteristics of *Procynocephalus/Paradolichopithecus* from Northern India, are associated with the ingestion of grit and with the exploitation of C_4 plants (Williams *et al.*, 2011). According to Eronen and Rook (2004), *Procynocephalus/Paradolichopithecus* of Europe, was found with a community of herbivorous mammals having a molar hypsodont index suggesting a certain type of dietary adaptations that corresponds with relatively more humid and closed habitats during the Pliocene, while in the Latest Pliocene-Early Pleistocene the suggested habitats were more open and arid. This reflects the ability of this extinct papionin to adapt in climatic trends. In this regard, *Procynocephalus*/*Paradolichopithecus* seem to be a very adaptive large cercopithecid form, like its extant baboon relatives. The ability to adapt in various climatic conditions also reflects its variable diet. The available data so far suggest that this primate was an omnivorous primate, following dietary strategies similar to modern baboons, which they tend to consume any food object available, especially in times of food scarcity.

The results of this study help us understand the dietary capabilities of *Procynocephalus* from Dafnero 3 and also reveal parts of its usual diet. The thick enameled dentition combined with its molar morphology suggests that this extinct papionin was capable of processing very hard food objects. Though, its usual dietary habits/preferences might have been different from what it was capable of consuming. The microwear textural characteristics of *Procynocephalus* available material indicate that hard and brittle food objects (seeds, bark, pith and possibly USO's) were a part of its diet but is possible that its dietary strategy was dependent on the seasonal availability of food resources. This strategy is common among large cercopithecids like the modern baboons and also to the *Gorilla*. In conclusion, it is possible to represent the locality of Dafnero as an open grassland with scarce wood cover with possible riparian woodland at the edge of riverine systems, which is consistent with the idea of the expansion of more open habitats due to colder and drier climatic conditions in the Late Pliocene-Early Pleistocene.

4.5 Omo valley

The Shungura formation is one of the most complete and well dated continental sequence found (Heinzelin, 1983). The paleontological and archaeological record of this formation is extensive and it has provided important information regarding the human evolution. Being so complete and containing abundant fossils from various taxa and with well dated horizons, it becomes also a good record of the environmental shifts that took place in late Pliocene to early Pleistocene. Faunal, floral and paleoclimate proxy records have identified 2.8-2.5 Ma as a period of drying in Africa (de Menocal, 1991; Bonnefille, 2010). In the Shungura mammalian fossil record, 2.8 Ma coincides with a period of ecological and taxonomic turnover that reflected more arid conditions and reduction of humid-forested environments (Bibi *et al.*, 2012). Although, mammalian, pollen and palaesol isotope records indicate that the habitats of lower Omo Valley remained relatively mesic with no significant grassland expansion until 2.6 or later (Levin *et al.*, 2011, Bonnefille *et al.*, 1983, Bobe *et al.*, 2004). The microwear textural properties of the fossil *Papio* sample of the Shungura formation present additional information about the climatic shifts that took place in Africa during that time span. The fluctuations of complexity (**Asfc**) and anisotropy (**epLsar**) recorded in fossil *Papio* (**Fig.14**) may be linked with a change of dietary preferences between geological members B to C and E to G. This change might also reflect an environmental shift. The increase of values of anisotropy may signify an increase in consumption of more tough food objects such as herbaceous monocots, while the decrease of complexity will signify a decrease in consumption of more hard and brittle objects such as seeds, nuts, bark and fruits. According to Martin *et al.*, (2016), the microwear textural properties of *Theropithecus* found in the Shungura formation highlight a similar trend that suggests a possible common environmental driver. Furthermore, the earliest appearance of zebra-like horses (Hooijer and Churcher, 1985) on the African continent is recorded in the lower Member G of the Shungura formation, at about 2.3 Ma (Lindsay *et al.*, 1980; Eisenmann, 1985) which supports the idea of expanded grasslands at that time period.

A climatic change would eventually have implications on the diets of the animals that inhabited Omo Valley in that time span. Not being able to follow their usual dietary strategy, they would have to adapt in the new conditions, thus adapting also their diet. This would probably be visible in the microwear textural properties of their dentition. Our evidence identifies such a change in diets of *Papio* between members E to G, which correspond to the age of *Procynocephalus* specimen from Dafnero. Although to attribute this change to a common environmental trend, it must be identified also in other mammalian taxa. As previous mentioned this signal is also observed in *Theropithecus* from Omo Valley, thus suggesting a common environmental trend. Concluding, our findings do support previous indications of a gradual change towards increasingly arid habitats in the Early Pleistocene of Eastern Africa.

4.6 Conclusions

Procynocephalus/Paradolichopithecus was a large terrestrial representative of Cercopithecidae in Eurasia in the Late Pliocene to Early Pleistocene, this coincides with the available postcranial materials found for this problematic genus so far.

The comparisons of the enamel thickness show in general that the primate from Dafnero-3 (DFN3-150) possessed thick enamel. Although concluding remarks based on the 2D linear measurements of enamel thickness must be treated with cautions because it has been show that some definitions are methodologically unstable and potentially misleading. In addition, some measurements seem to be affected also by intra observer errors. The 3D measurements of enamel thickness avoid all these above-mentioned problems and produce more trustworthy results. The 3D measurements of enamel thickness indicate that *Procynocephalus* from Dafnero possessed thicker enamel than its more closely related extant *Macaca* and *Papio*.

The molar flare functional significance and phylogenetic distribution has been source of contention, but it seems to be correlated with a type of diet. The variation of the molar flare among forms of primates still needs to be further analyzed if its correlated with temporal effects, the enamel signal or phylogeny, but the analysis should be focused on the same phylogenetic and temporal context. Both indices used in this study, MF and DFI, give us intel about the molar flare. But the use of the dentine flare index in this case seems to be more appropriate. In future studies the use of DFI possibly will help us understand better the functional significance of molar flare concerning the whole molar, not only a part of, and the effect of the enamel on it. Nevertheless, the use of both indices in a substantial sample size which fulfils the requirement of relatively same age and phylogeny, should be the most conservative way of exploring the molar flare.

The microwear textural characteristics of *Procynocephalus* seem to be similar to primates that tend to consume hard and brittle food objects (omnivorous). Although the analysis uses only two individuals, it is safe to presume that hard and brittle food objects were part of the Dafnero-3 primates diet. In this regard, we suggest that the foraging and dietary strategy of *Procynocephalu*s resemble modern and fossil baboons and possibly was dependent on the season and spatial availability of food resources.

All the available data for *Procynocephalus/Paradolichopithecus*, such as the fauna composition of Dafnero, Upper Siwaliks and Vatera, and the presence of flora adapted in drier and colder conditions in eastern Mediterranean region, suggest drier and colder conditions at Late Pliocene to Early Pleistocene. This coincides with the previous interpretations of open and dry grasslands with scarce wood cover for Dafnero locality.

Finally, the microwear textural characteristics of fossil *Papio* from Omo Valley, Ehiopia, support the previous hypothesis of a climatic shift towards more open and arid conditions in East Africa at Late Pliocene to Early Pleiostocene. The test of vicariance between *Procynocephalus* from Dafnero and fossil *Papio* from Omo valley, shows that despite the geographical difference between them, they might have shared a similar feeding strategy, possible dependent on climatic trends. So even though *Procynocephalus* tended to consume hard and brittle food objects, it might have occasionally shifted towards a diet based on fallback foods in case of preferred food scarcity. This would allow him to successfully inhabits all kinds of habitats. Future research on the Eurasian fossil Cercopithecidae archive and the available material for *Procynocephalus/Paradolichopithecus* will provide important information for the paleoecology and the evolution of Old World monkeys.

Abstract

In this study, we explore the feeding ecology of the recently unearthed cranium of the fossil primate genus *Procynocephalus* from the Early Pleistocene site of Dafnero-3, Northern Greece. To succeed that we compare dental microwear textural analysis data from the Greek specimen, using confocal microscopy, in comparison with a set of fossils *Papio* specimens and also extant primates with known dietary differences (*Papio cynocephalus* n=27, *Papio ursinus* n=12, *Theropithecus gelada* n=12, *Semnopithecus entellus* n=8, *Gorilla beringei* n=16, *Macaca fascicularis* n=20). To explore the dietary capabilities of *Procynocephalus* from Dafnero 3 we measure 2D and 3D enamel thickness (using CT scan imaging) and two indices: molar flare index (MF) and dentine flare index (DFI), in comparison with modern *Papio* and three dietary groups of hominoids. Additionally, to explore the feeding ecology of a set of fossil *Papio* from Omo Valley, Africa and the vicariance between them and *Procynocephalus* from Dafnero-3, we compare the variation of complexity (Asfc) and anisotropy (epLsar) variables, focusing our efforts on contemporaneous assemblages with the fossil from Greece. Results indicate that the microwear texture from Dafnero 3 specimen differs from the extant folivorous primates compared and instead resemble more closely the hard object feeders/omnivorous primates. Results of the enamel thickness combined with data from the two indices that describe the morphology of the molars (MF and DFI), indicate that *Procynocephalus* from Dafnero 3 was capable of consuming hard food objects and may have played an important part of its diet depending on spatial and seasonal availability. The dental microwear texture characteristics of *Procynocephalus* from Dafnero 3 and the fossil *Papio* from Omo Valley, supports the hypothesis of the expansion of grasslands at Early Pleistocene and highlight a trend towards more open environments between 2.36 and 1.9 Ma.

Περίληψη

Στην παρούσα εργασία, διερευνάται η διατροφική οικολογία του απολιθωμένου πρωτεύοντος *Procynocephalus* από την απολιθωματοφόρο θέση Δαφνερό-3 που χρονολογείται στο Κάτω Πλειστόκαινο (Μέσο Βιλλαφράγκιο). Για την επίτευξη του σκοπού αυτού, συγκρίνονται δεδομένα οδοντικής μικροτριβής του πρωτεύοντος από το Δαφνερό-3, (με χρήση ομοεστιακού μικροσκοπίου) με δεδομένα από ένα σύνολο απολιθωμάτων του γένους *Papio* και μορφές σύγχρονων πρωτευόντων με διαφορετικές διατροφικές συνήθειες (*Papio cynocephalus* n=27, *Papio ursinus* n=12, *Theropithecus gelada* n=12, *Semnopithecus entellus* n=8, *Gorilla beringei* n=16, *Macaca fascicularis* n=20). Για την εκτίμηση των διατροφικών δυνατοτήτων της οδοντοστοιχίας του πρωτεύοντος από το Δαφνερό-3, τελούνται μετρήσεις πάχους αδαμαντίνης, δισδιάστατες και τρισδιάστατες (με τη βοήθεια εικόνων αξονικής τομογραφίας), υπολογίζονται δύο δείκτες που περιγράφουν την γομφική διέυρυνση (**MF** και **DFI**) και συγκρίνονται με σύγχρονα *Papio* και τρείς ομάδες ανθρωποειδών με διαφορετικές διατροφικές συνήθειες. Επιπλέον, για να διερευνηθεί η διατροφική οικολογία του συνόλου απολιθωμένων *Papio* από την κοιλάδα Όμο (Αιθιοπία, Αφρική) και η αντιπαράθεση τους με τον *Procynocephalus* από το Δαφνερό-3, συγκρίνονται οι διακυμάνσεις δύο μεταβλητών, πολυπλοκότητα (**Complexity**, **Asfc**) και ανισοτροπία (**Anisotropy**, **epLsar**), στα γεωλογικά μέλη του σχηματισμού Σουνγκούρα που αντιστοιχούν στην ηλικία του πρωτεύοντος από το Δαφνερο-3. Τα αποτελέσματα δείχνουν ότι η υφή οδοντικής μικροτριβής του δείγματος από το Δαφνερό-3 διαφέρει από τα σύγχρονα πρωτεύοντα του τρέφονται κυρίως με φύλλα και μοιάζει περισσότερο με την υφή των πρωτευόντων που εμφανίζουν διατροφή βασισμένη σε πιό σκληρά διατροφικά αντικείμενα. Τα αποτελέσματα του πάχους της αδαμαντίνης των γομφίων σε συνδυασμό με τα δεδομένα των δύο δεικτών που περιγράφουν την μορφολογία των γομφίων (**MF** και **DFI**), δείχνουν ότι το πρωτεύον από το Δαφνερό-3 ήταν ικανό να καταναλώσει σκληρά διατροφικά στοιχεία. Τα τελευταία φαίνεται ότι αποτελούσαν σημαντικό τμήμα της διατροφής του ανάλογα με την χωρική και εποχική τους διαθεσιμότητα. Τα χαρακτηριστικά της υφής της οδοντικής μικροτριβής του *Procynocephalus* από το Δαφνερό-3 και των απολιθωμένων *Papio* από τη κοιλάδα Όμο (Αιθιοπία, Αφρική), υποστηρίζουν την υπόθεση της επέκτασης των ανοιχτών εκτάσεων με φυτοκάλυψη στο Κάτω Πλειστόκαινο και επισημάνεται μία τάση για πιό ανοιχτά περιβάλλοντα ανάμεσα στα 2.36 και 1.9 εκ. χρόνια.

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Appendix

Table 6 Summary of sample and measurements used for comparisons of 3D Enamel Thickness used in this study.

	3D Enamel Thickness							
	Code	**Species**		**EVOL(mm3)**	**Vcdp(mm^3)**	**EDJS(mm^2)**	**AET3D(mm)**	**RET3D(mm)**
Present study	DFN3-150-UM2	*Procynocephalus*		304.625	353.707	263.77	1.154	16.31
	97-020-M-0004	*Papio hamadryas*		308.75	371.401	266.703	1.157	16.09
	Z3770	*Papio anubis*		203.264	336.694	237.6353	0.855	12.291
	C2 dec	*Papio anubis*		279.955	396.818	280.5917	0.997	13.567
	80-44-M-101	*Papio anubis*		312.46	394.094	276.0436	1.131	15.426
Olejniczak *et al.* 2008	Macaca	*Macaca nemestrina*		70.41	150.27	96.74	0.73	13.69
Beaudet *et al.* 2016	*Papio (n=4)*		mean	232.4	237.2	205.9	1.1	18.2
			range	163.6-285.4	159-281	167.4-231.5	1-1.2	17.3-18.8
	Macaca (n=2)		mean	90.4	100.5	123.8	0.7	15.8
			range	75-105.8	74.7-126.3	106.8-140.7	0.7-0.8	15-16.7
	Colobus (n=2)		mean	49.8	58	81.1	0.6	16
			range	49.5-50.1	52.5-63.5	74.7-87.6	0.6-0.7	14.3-17.7

Table 7 Summary of sample and measurements used for comparisons of 2D Enamel Thickness used in this study.

		2D-Linear Enamel Thickness			
Code	**Species**	**BOCMAX(mm)**	**BLATMAX(mm)**	**LOCMAX(mm)**	**LLATMAX(mm)**
DFN3-150-UM2	*Procynocephalus*	1.09	1.56	1.28	1.35
97-020-M-0004	*Papio hamadryas*	1.27	1.25	1.25	1.47
Z3770	*Papio anubis*	0.749	0.993	0.868	1.29
C2 dec	*Papio anubis*	1.06	1	1	1.11
80-44-M-101	*Papio anubis*	1.618	1.296	1.098	1.256

Table 8 Summary of sample and measurements used for comparisons of the Molar Flare index and Dentine Flare index.

	Species	**ML(mm)**	**MDB(mm)**	**MCB(mm)**	**MMB(mm)**	**2D-DBS(mm^2)**	**2D-DS(mm^2)**	**MFR**	**MF**	**DFI**
DFN3-150-UM2 (Sin.)	*Procynocephalus*	13.8442	10.75418	6.4748	11.5728	55.4080	105.9711	0.56	0.44	0.5528
97-020-M-0004	*Papio hamadryas*	13.5302	10.8972	5.6344	11.8622	44.4574	119.167	0.475	0.525	0.373
Z3770	*Papio anubis*	13.029	10.5378	5.5122	11.3642	44.3053	100.3164	0.485	0.515	0.4416
C2 dec	*Papio anubis*	8.08068	6.437836	3.52428	6.95984	44.7455	110.7225	0.468	0.532	0.4039
80-44-M-101	*Papio anubis*	9.696816	7.7254032	4.229136	8.351808	54.9594	122.7514	0.411	0.589	0.4477

Table 9 Percentage of specimens that surpass the cutpoint values of Asfc and epLsar.

Taxa	**Complex % (Asfc>1.5)**	**Anisotropic % (epLsar>0.003)**	***n***
Omo Fossil *Papio*	50.87	22.8	57
Papio cynocephalus	62.96	59.25	27
Papio ursinus	83.33	33.33	12
Theropithecus gelada	0	91.66	12
Procynocephalus	100	50	2
Semnopithecus entellus	0	62.5	8
Gorilla beringei	43.75	62.5	16
Macaca fascicularis	60	60	20

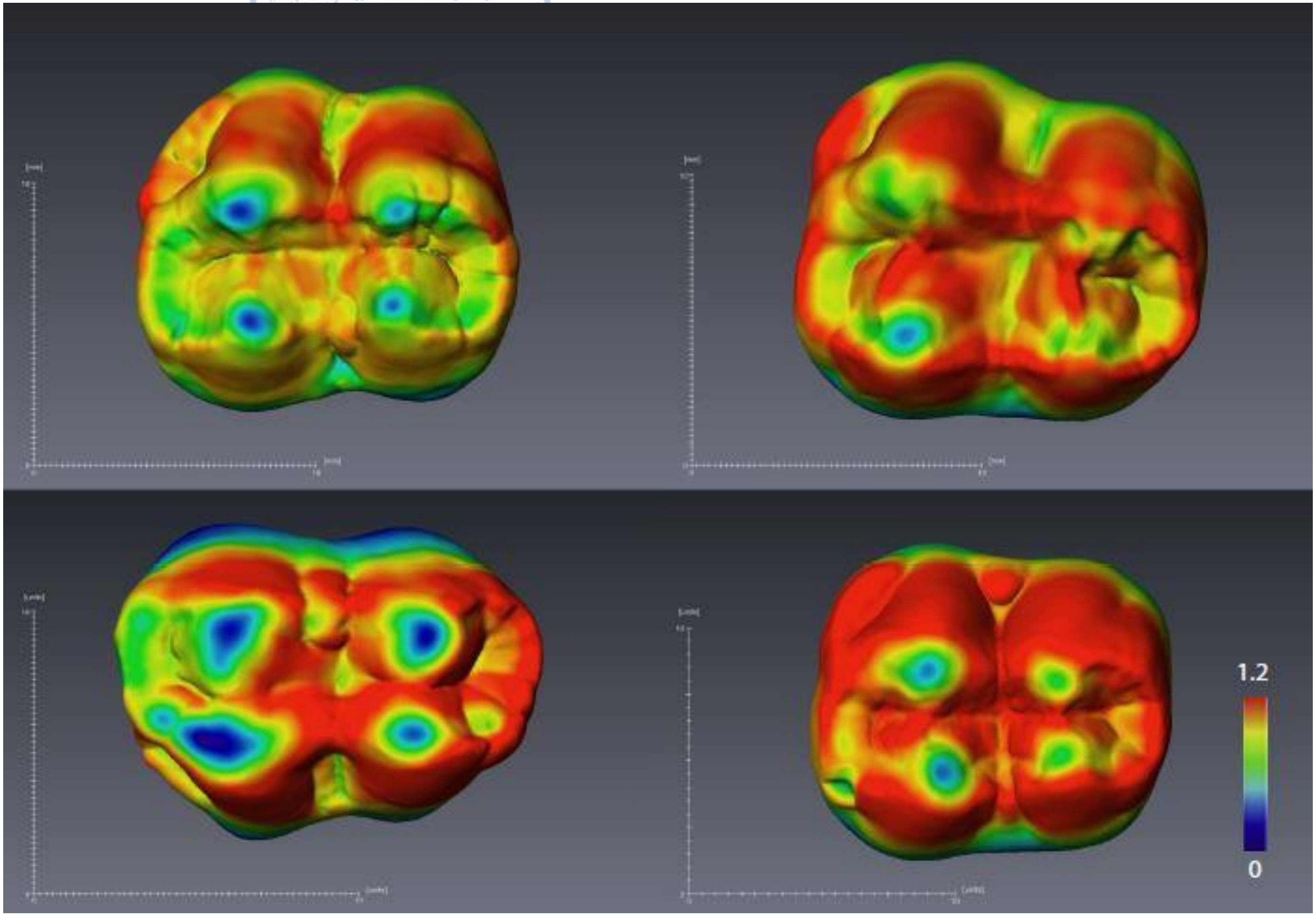

Fig. 15 Enamel distribution of modern *Papio* molar sample. *Papio anubis* iPHEP C2 dec (top left), *Papio anubis* 80-44-M-101 (top right), *Papio anubis* Z3770 (bottom left), *Papio hamadryas* 97-020-M-0004 (bottom right). Red represents thicker enamel while blue represents thinner.

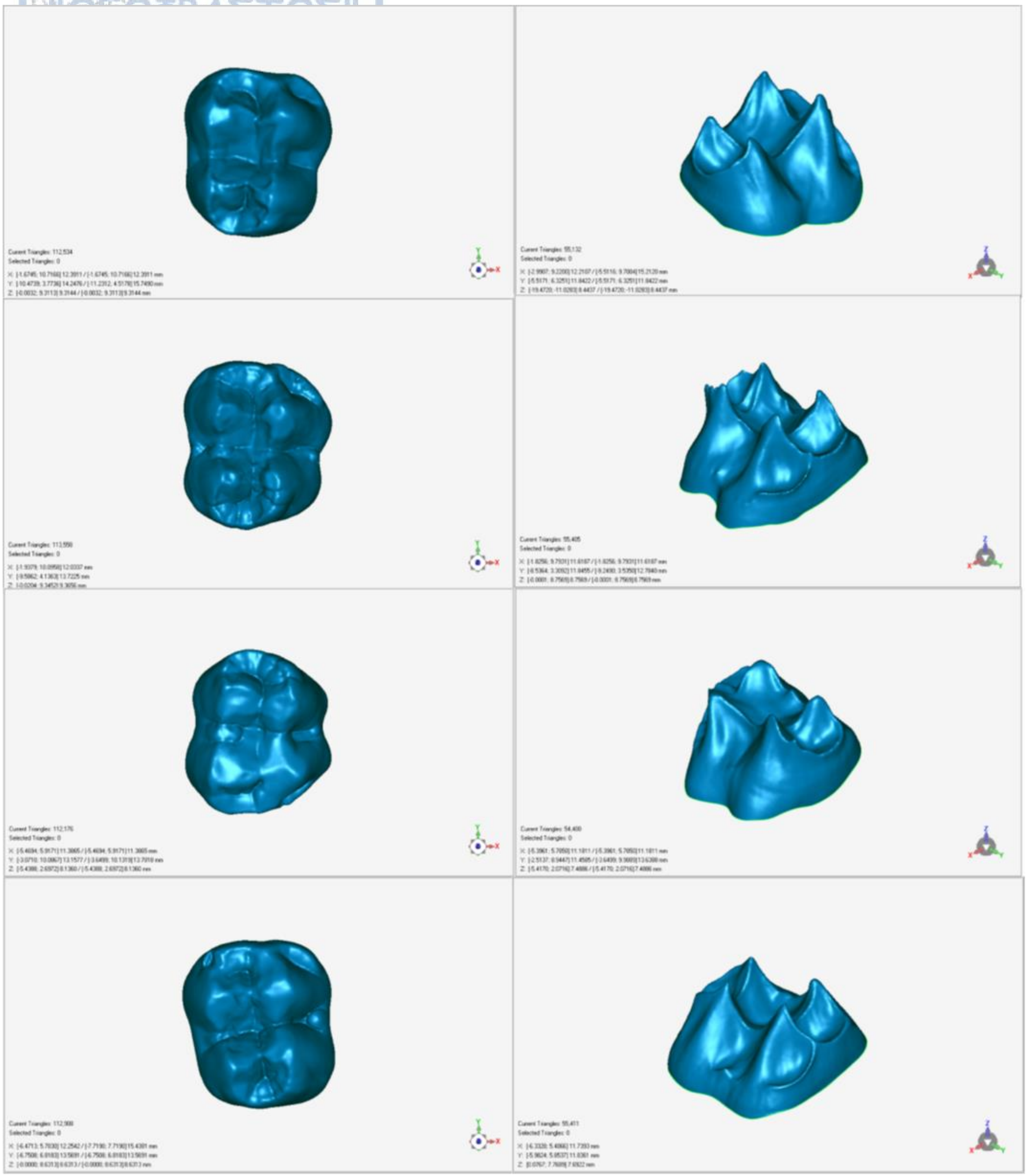

Fig. 16 Occlusal enamel surfaces (left) and enamel-dentine junction surfaces (right) of modern *Papio* sample used in this study. *Papio anubis* 80-44-M-101, *Papio anubis* iPHEP C2 dec, *Papio anubis* Z3770, *Papio hamadryas* 97-020-M-0004 (from top to bottom).

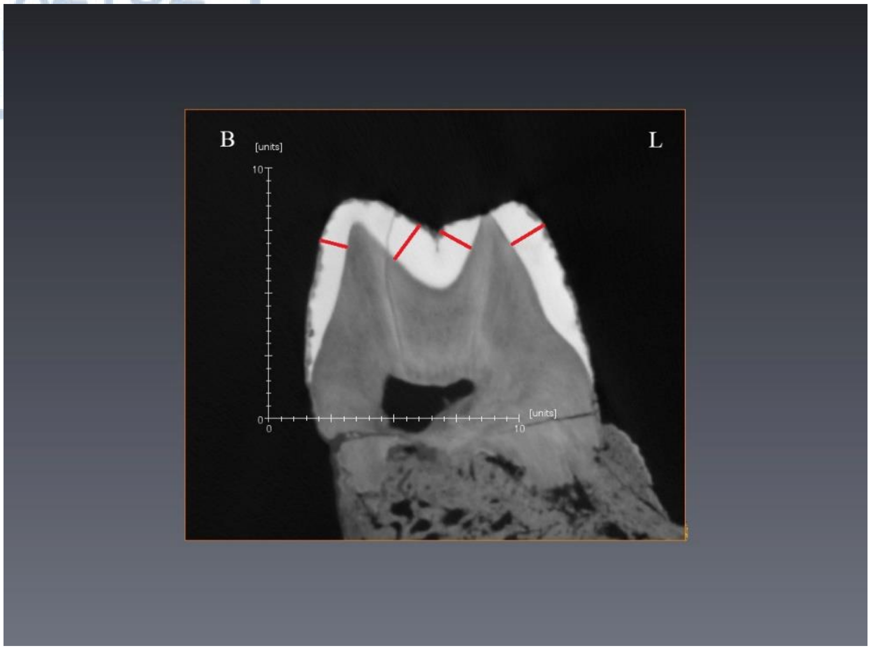

Fig. 17 2D linear measurements (red lines) performed in this study. From left to right: Buccal lateral maximum enamel thickness (**BLATMAX**), Buccal occlusal maximum enamel thickness (**BOCMAX**), Lingual occlusal maximum enamel thickness (**LOCMAX**) and Lingual lateral maximum enamel thickness (**LLATMAX**), on *Procynocephalus/Paradolichopithecus aff. arvernensis* (DFN3-150), following the protocol of Suwa *et al*., (2005).

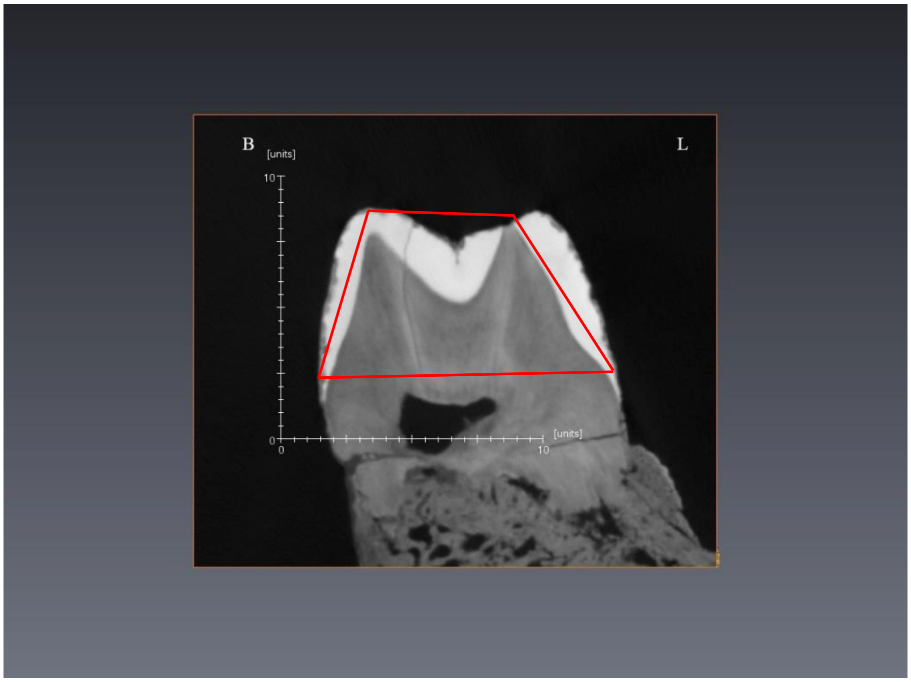

Fig. 18 Schematic representation of molar flare. Acccording to Singleton (2003) MF= 1- MFR, where MFR is the ratio of mesial intercuspal breadth (MCB) to maximum mesial breadth (MMB) (Benefit, 1993).