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Herbivores dental wear analysis since the end of the Middle Pleistocene in different archaeological contexts of Morocco (Bizmoune, El Khenzira and Taforalt).

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Abstract

Currently, environments in Morocco can be divided into three broad zones. The North is characterized by a Mediterranean biome and the very strong influence of the Mediterranean Sea. The West coast is influenced by the Atlantic Ocean and the Sahara Desert has profound effects on the Southwest. To better document herbivore food habits and the plant cover in these biogeographical areas since the end of the Middle Pleistocene, we undertook dental wear analysis of herbivore teeth from recent excavations at Taforalt (Oujda region) and Bizmoune Cave (Essaouira), and from the mixed sample from El Khenzira (El Jadida) (Arambourg Collection / Bouzouggar Excavation). In this study we conducted the first mesowear and microwear analyses of archaeological ungulate teeth of North African herbivore teeth starting with a total sample of 129 teeth from 19 taxa. Our results highlighted dietary habits and ecological flexibility and revealed interspecific competitive relationships between some of the taxa as well as the paleoenvironmental contexts in which they evolved.

Résumé

Le Maroc actuel est caractérisé, au nord par la présence du biome méditerranéen et l'influence importante de la mer Méditerranée, sur sa côte occidentale par l'océan Atlantique, et enfin par l'influence du Sahara dans la partie sud-ouest du pays. Afin de mieux documenter les habitudes alimentaires des herbivores et le couvert végétal de ces zones biogéographiques depuis la fin du Pléistocène Moyen, nous avons mené des analyses d'usure dentaire sur du matériel provenant des fouilles récentes de Taforalt (Commune d'Oujda), de Bizmoune (Essaouira) et des collections anciennes et actuelles d'El Khenzira (El Jadida) (Collections Arambourg et Bouzouggar). Cette étude constitue la première analyse en méso- et microusure dentaire appliquée à l'Afrique du Nord. Elle se base sur un échantillonnage de 129 dents correspondant à 19 taxons herbivores. Nos résultats décrivent leurs préférences alimentaires, la flexibilité écologique et les relations de compétition interspécifiques pour certains d'entre eux ainsi que les contextes environnementaux dans lesquels ils ont évolué.

Keywords

Mesowear; Microwear; North African ungulates; Bovids; Cervids; Camelids; Equids; Rhinocerotids; Paleoenvironment; Paleoecology.

Mots-clefs

Méso-usure dentaire ; Micro-usure dentaire ; Ongulés nord-africains ; Bovidés ; Cervidés ; Camélidés ; Equidés ; Rhinocérotidés ; Paléoenvironnement ; Paléoécologie.

1. Introduction

The state of Morocco encompasses a fragmented geographical area located between the Atlantic Ocean, the Mediterranean Sea and the Sahara Desert. In addition to the coastal areas, the continentality is marked further inland with the influence of the Rif, the Middle, High and the Anti-Atlas Mountains. During the Pleistocene, it underwent many landscape transformations according to climatic oscillations (Hooghiemstra et al., 1992; 2006; deMenocal et al., 2000; Blome et al., 2012; Drake et al., 2013) which probably influenced human and animal distributions. Discoveries of the oldest remains attributed to *Homo sapiens* (Hublin et al., 2017), as well as the early Middle Stone Age ornaments (Sehassseh et al., 2021), highlighted the importance of the biogeographical context of Morocco and the emergence of cultural modernity. Therefore, analysis of paleoenvironmental proxies at a local scale is crucial to understand the context and environments experienced by past human populations.

Dental wear analysis is a powerful and widely used tool for reconstructing the ecology of herbivores (e.g. Rivals and Lister, 2016; Merceron et al., 2018; Hullot et al., 2019; Kelly et al., 2021; Uzunidis, 2021) and the environments they occupied (e.g. Rivals et al., 2017; Dumouchel and Bobe, 2020; Ramírez-Pedraza et al., 2020; Uzunidis, 2020). Two methods are implemented with different types of observations: dental mesowear and dental microwear. The former method describes the average diet of an individual over a long-time scale that can correspond to about the last year of life (Rivals et al., 2007; Louys et al., 2012; Ulbricht et al., 2015) or to an average of the lifetime diet (Ackermans et al., 2020). Dental microwear provides a more precise signal, corresponding to the diet of the last months to days of an individual's life (Teaford and Oyen, 1989; Hoffman et al., 2015; Merceron et al., 2016; Winkler et al., 2020). The combination of these two proxies allows for a discussion of diet over several phases of an individual's life, including seasonal variations (Sanchez-Hernandez et al., 2016).

This approach has never been applied to North African Pleistocene fossil herbivores, although paleoecological inferences have been made using other methods, for micromammals (e.g. Stoetzel, 2013) or for some large mammals in a few Moroccan deposits (e.g. Michel, 1990; Geraads and Amani, 1998; Aouraghe, 2000, 2001, 2004; Geraads, 2002; Bougariane et al., 2010; Fernandez et al., 2015; Croitor, 2016; Raynal and Mohib, 2016). However, in Europe, the ecological flexibility of several herbivore species during the Pleistocene has already been highlighted (e.g. Rivals and Lister, 2016; Rivals and Álvarez-Lao, 2018; Saarinen et al., 2016; Uzunidis, 2021), something which is also apparent for African taxa of this period (e.g. Kaiser and Franz-Odenaal, 2004; Schubert et al., 2006). Thus, palaeoecological inferences based on large mammals should take into account their flexibility.

Here we present a high-resolution dental wear analysis (micro- and mesowear) of fossil herbivores from three major Moroccan sites of Taforalt (Oujda region), El Khenzira (El Jadida) and Bizmoune (Essaouira). In considering their diet, we also focus on the faunal associations of each site to better understand the evolution of plant cover and dietary preference of Moroccan herbivores related to environmental fluctuations since the end of the Middle Pleistocene.

1.1 Description of the localities

Three Moroccan sites, Taforalt (TAF), El Khenzira (EKH) and Bizmoune (BZM) distributed along a north-south axis were studied (**Fig. 1**). TAF also known as Grotte des Pigeons (34°48'50"N - 2°24'14"W), is located in the north-east of Morocco, about 40 km from the present-day Mediterranean coast at about 720m amsl (above mean sea level) in the Beni Snassen mountains. The sequence covers the Upper Pleistocene and has been divided into different sectors (for details see Collcutt, 2019). Only dental specimens from Sector 10 (S10) and, from the very back of the cave, Sector 13 (S13), were

used for this study. Sector 10 yielded at least fourteen human skeletons (Humphrey et al., 2019; Barton et al., 2019) associated with numerous faunal and macrobotanical remains as well as lithic and bone tools (Barton et al., 2019; Humphrey et al., 2019; Humphrey et al., 2014; Desmond et al., 2018). Radiocarbon dates on human bone from S10 give ages of 15,077-13,892 cal BP (Humphrey et al., 2014). Herbivores teeth from a brown layer, directly underlying the burials were studied. Two layers of S13 are studied: the orange and dark brown layer. ¹⁴C dating is underway for S13 and the first unpublished date gives ages of 17,982-17,569 cal BP for the orange layer. The faunal evolutionary stage could indicate that the deposits of the dark brown layer in S13 is the same age or slightly earlier than the brown layer in S10. The remains of large carnivores such as *Ursus cf. arctos* and *Crocota crocuta* in S13-layer orange make it possible to hypothesize a use of the back of the cave as a den for large carnivores. Some burnt remains belonging to spotted hyena have been found, possibly involving periodic use in the back of the cave for different human activities (i.e. combustion waste, consumption) associated with the formation of the dark brown layer in S13.

The three caves of EKH (33°09'47"N - 08°37'12"W) are located in the municipality Moulay Abdallah (El Jadida), and lie at an elevation of ca. 20m amsl about 1 km from the current Atlantic coast. Here we focused on the two contiguous caves, I and II, and their contemporaneous layers A to C that were excavated in 1934 and published by A. Ruhlmann in 1936. Based on lithic artefacts, Ruhlmann established that the sedimentary infilling of the two caves was similar, with elements from the Middle Paleolithic (layer B) and Upper Paleolithic (layer C), layer A being sterile. Arambourg (1938) reached the same conclusion based on the abundant and extremely well-preserved faunal material from the two caves excavated by Ruhlmann and stored in the Museum National d'Histoire Naturelle of Paris (MNHN). In 2017, new fieldwork at the caves was undertaken under the direction of A. Bouzouggar (INSAP, Max Planck Institute, Leipzig) who clearly identified the layers A to C in Caves I and II with small sounding in Cave III.

BZM is located near Essaouira (31°39'96"N - 9°34'09"W), about 12 km from the actual coast of the Atlantic Ocean. The cave lies at ~171m amsl on the flanks of Jebel Lahdid. It was found in 2004 by A. Bouzouggar and J. Collina-Girard (LAMPEA, 7269), with limited test excavations in 2007-2008 (Bouzouggar et al., 2010). The first regular field campaigns began in 2014, bringing to light artefact, faunal and archeobotanical remains from the Middle Stone Age (MSA), Late Stone Age (LSA) until Neolithic periods, within an excavation area of approximately 30m² (Bouzouggar et al., 2017). Recently, the U/Th dating results from the oldest layer (4c) from BZM extend the earliest date for the collecting, production and use of personal ornaments from marine gasteropods (*Tritia gibbosula*) to at least the later part of marine isotope stage 6 (Sehassseh et al., 2021).

2. Material

The three sites, TAF, EKH and BZM, vary according to taxonomy, dates, taphonomic contexts, and density of remains. For example, at BZM, the stratigraphy covers Marine Isotopic Stages (MIS) 6 to 1 with faunal units or individual layers dated by U-Series, OSL and ¹⁴C. Material is not very abundant in the sequence with bones and dental remains often entirely covered with calcite concretion. On the contrary, the very well-preserved sample of EKH, derived mostly from Arambourg's collection from Caves I and II, as well as from the recent Bouzouggar excavation, is considered here as a bulk sample covering the Upper Pleistocene (MIS 5 to 1) without further precision on layers A to C. The well-preserved material of TAF is much more constrained in time, with the two sectors, S10 and S13 covering MIS 2.

In each site, taxonomic determinations were based on the paleontological literature and the fossil/current mammal collections of the MNHN of Paris, the Musée des Confluences (Lyon, France), as well as the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP) (Rabat, Morocco). As often as possible, we tried to specify taxon to the level of species. For EKH, in a few

cases we modified the original determinations made by Arambourg on the collection of the MNHN. For all sites, the dental wear analysis was systematically conducted on adult specimens, preferentially on molars (M1 and M2) as well as premolars (excluding P2) following Xafis et al. (2017). Teeth with enamel that was poorly preserved or taphonomically altered were excluded from our analysis (King et al., 1999). Our observations were made on a sample of 44 teeth in TAF, representing 7 taxa, 63 teeth in EKH corresponding to 15 taxa, and finally 22 teeth in BZM related, representing 10 taxa (**Table 1**, **Table 2**, **Table 3**). In total, 19 taxa common to the 3 sites were studied.

3. Method

3.1 Dental mesowear

Mesowear analysis is a method based on the observation of wear patterns on ungulate cheek teeth cusps that indicate the diet of an individual animal (Rivals et al., 2007; Fortelius and Solounias, 2000). The sharpness and the morphology of cusps are correlated with relative attritive and abrasive dental wear. Thus, a diet with low abrasion (and high attrition) shows very sharp molar buccal cusps and, on the other hand, a diet with high abrasion will result in rounded and blunted cusps. There is no linear correlation between habitat parameters and mesowear scores (Kaiser et al. 2013; Schulz and Kaiser 2013) since both the vegetal composition of the diet and the presence of exogenous grit are involved in the mesowear signature (Kaiser et al., 2009). However, high level of abrasion is more likely due to the consumption of siliceous grass than the ingestion of soil or dust (Kaiser et al., 2013; Saarinen and Lister, 2016). It is unclear which time period of the animal's life is best represented by dental mesowear: authors have suggested it can correspond to a weekly or monthly (Danowitz et al., 2016), seasonal (Kaiser and Schulz, 2006; Schulz and Kaiser, 2013; Marom et al., 2018) or annual signal (Rivals et al., 2007; Louys et al., 2012; Ulbricht et al., 2015). Recent experiments have suggested that, at least in hand-fed small ruminants, the morphology of cusps reflect the general diet of the entire lifetime of the animal (Ackermans et al., 2020). Thus, in this study, mesowear is considered as a signal covering at least the last few years of life of an individual.

Unworn teeth, extremely worn teeth, and specimens with broken cusps were excluded from the analysis following Fortelius and Solounias (2000) or Rivals et al. (2007).

In this study, the standardized method proposed by Muhlbachler et al. (2011) and modified by Rivals et al. (2013) was employed. This method categorizes tooth wear into seven groups (numbered from 0 to 6), according to their shape (0 = high and sharp; 6 = blunt with no relief). The average value of mesowear data from a single sample corresponds to the “mesowear score” noted here as “MWS” (Muhlbachler et al., 2011; Rivals et al., 2017; Uzunidis et al., 2017; Uzunidis, 2020).

3.2 Dental microwear

The microwear analysis study follows the protocol established by Solounias and Semprebon (2002) and Semprebon et al. (2004). The occlusal surface of each tooth was cleaned using acetone, followed by 96% alcohol. The surface was then moulded with a high-resolution silicone (vinylpolysiloxane) and casts were made using clear epoxy resin. The transparent casts were then observed with a stereomicroscope at magnifications of x35. Observations were restricted to a standard surface of 0.16 mm² (using an ocular reticule). This approach is thought to record the signal corresponding to the type of diet over the last days to months of an individual's life (Teaford and Oyen, 1989; Hoffman et al., 2015; Merceron et al., 2016; Winkler et al., 2020). For equids, we focused on a portion of the enamel on the paracone or metacone fossettes to avoid the edges of the occlusal surface, as the edges are more prone to alteration by taphonomic processes (Uzunidis et al., 2021). Moreover, the morphology of the scratches and the pits were carefully inspected in order to detect and eliminate post-depositional alteration (Uzunidis et al., 2021).

We recorded various features following the classification of Solounias and Semprebon (2002) and Semprebon et al. (2004) such as: pits (small and large), scratches (fine, coarse and hypercoarse), and gouges. The scratch width score (SWS) is also calculated with a score of ‘0’ for teeth with

predominantly fine scratches per tooth surface, '1' for those with mixed fine and coarse scratches, and '2' for those with predominantly coarse scratches. The observed micro-traces, scratches and pits in particular are left on the occlusal surfaces during mastication due to the presence of phytoliths in the consumed plants (Walker et al., 1978) which are more abundant in monocot plants than dicot ones. Dust appears to have a lesser impact on the enamel surface (Merceron et al., 2016). Thus, the variability of the density of these traces is indicative of various diets: grazer, mixed-feeder and browser.

4. Results

4.1 El Khenzira

At EKH, the dietary variability within and between the taxa is very important and most probably related to the wide chronological interval of the sample associated with several different climatic stages.

The dental mesowear analysis shows fairly low MWS for the majority of the taxa (**Fig. 2; Tab. 1**). *Alcelaphus buselaphus* and *Bos primigenius* fall within the range for mixed-feeders (MWS = 3). All taxa known from a single tooth fit within the category of browsers: *Camelus dromedarius* (MWS = 2), *Redunca redunca* (MWS = 2), *Taurotragus derbianus* (MWS = 1) and *Connochaetes* sp. (MWS = 0). Usually *Connochaetes* is considered a grazer (Solounias and Semperebon, 2002) and its position may be surprising. Since this observation is based on a single tooth it should be considered preliminary and does not allow any conclusion to be drawn. Gazelles are either mixed-feeder with a browsing tendency (*Gazella* sp., MWS = 2.71; *Gazella atlantica*, MWS = 2.33) or total browsers (*Gazella dorcas*, MWS = 1.54). Unfortunately, the only two teeth of *Gazella cuvieri* show no strong signal for any specific diet, so the values for them are not interpretable. In general, the equids from EKZ have the highest values and fall within the range of variability of mixed-feeders, with grazing tendencies (MWS = 4.3). Some taxonomic identifications have been made to species level and these species display lower value compared to the general trend. *Equus* cf. *africanus/asinus* (MWS = 2.5) and *Equus* cf. *mauritanicus* (MWS = 2) fall within the range of variability of browsers and show no real differences between them, as is the case for the individuals of TAF (cf. infra).

Only 64.5% of the casts preserved dental microwear suitable for the diet study, reflecting better conservation than at BZM but worse than at TAF and can be considered as quite poor. The two aurochs specimens are placed almost opposite each other on the graph. One individual has many scratches (n = 35) and few pits (n = 6.5), typical of a grazing diet whereas the second shows fewer scratches (n=13.5) and more pits (n = 40), which would be typical of a browser (**Fig. 2; Tab. 1**). Among the equids, most into the grazer range or variability (mean scratches = 26.56; mean pits = 20.1) but several of them show a mixed-feeder pattern because of a large number of pits. On the other hand, there is no difference between the few teeth identified to species level (*E. africanus*, *E. asinus* or *E. mauritanicus*). This variability is also very high in gazelles, which fall among the ranges of variation for mixed-feeders (mean scratches = 17.13; mean pits = 33.86) as well as of browsers. Furthermore, we note that *G. atlantica* and *G. dorcas* are significantly¹ distinguished by the number of their pits (Mann-Whitney: Pits: W = 10.5; p-value = 0.01; Scratches: W = 26.5; p-value = 0.29). Pits are less frequent in *G. atlantica* (mean = 26.42) than in *G. dorcas* (mean = 37.11). Finally, some taxa are represented at EKZ by a single specimen, limiting our interpretations, but these teeth will contribute to future North African dental wear analyses. cf. *Connochaetes* falls within the range of variability of grazers. *R. redunca*, *C. dromedarius* would be grouped with the browsers. *T. derbianus* would also be a browser with a very large number of pits (**Fig. 2; Tab. 1**).

¹ In this study we choose significant level at $\alpha = 0.05$. Thus p-values < 0.05 are considered as significant.

4.2 Bizmoune

In contrast to EKH, dental wear analysis at BZM Cave was conducted on teeth from well-known archaeological contexts and a well-dated stratigraphic sequence covering the very end of the Middle Pleistocene and the Upper Pleistocene until the Neolithic. Unfortunately, few teeth per taxon are available limiting our interpretations. During MIS 6 and 5, the MWS recorded between the different herbivores from BZM are quite variable between taxa. *B. primigenius* (MWS = MIS 6/5: 2; MIS 5: 2.5) lies among the current browsers while the Bovini teeth *Syncerus/Pelorovis/Bos* (MWS = 3 and 4) as well as the *Gazella* sp. (MWS = 4) are associated to mixed-feeder. *Hippotragus equinus* definitively shows the pattern of a strict grazer (MWS = 6) (**Fig. 3; Tab. 2**). During MIS 5, *B. primigenius* is a mixed-feeder with a browsing tendency (MWS = 3 and 2) and *Gazella* sp. becomes a browser (MWS = 1). During MIS 4, 3 and 2, MWS values are quite similar to the previous period: *G. cf. atlantica* is a browser (MWS = 0). *E. cf. mauritanicus* is a mixed-feeder with a browser tendency (MWS = 2). *A. buselaphus* also appears to be a mixed-feeder, but with a grazing tendency (MWS = 4). During MIS 2/1, *Equus* sp. is very close to *E. cf. mauritanicus* from the previous period, which could argue for similar conditions in plant cover. During MIS 1, MWS values generally increase, especially for the equids as shown by *E. cf. mauritanicus* (MWS = 6) with a strict grazing diet. The Caprini *Ovis/Capra* are associated with mixed-feeder and browsing tendencies (MWS = 2). Finally, *Megaceroides algericus*, the last endemic representative of its species in the Maghreb (Fernandez et al., 2015) appears as is a mixed-feeder (MWS = 3).

At BZM Cave, only 57.9% of the selected teeth could be studied for the dental microwear analysis. This very poor state of preservation may be related to the significant calcite concretion covering the whole assemblage. During MIS 6/5, equids (*Equus* sp.) are clearly distributed with other grazers, very close to the large antelope *H. equinus* (**Fig. 3; Tab. 2**). *A. buselaphus* and *B. primigenius* are mixed-feeders, whereas *Gazella* sp., falls in the area associated with typical browsers. One of the two teeth of Bovini, *Syncerus/Pelorovis/Bos* falls among the mixed-feeders while the other groups with the grazers, which may indicate that they belong to two different species. During MIS 5, *B. primigenius* is still mixed-feeder as well as *Gazella* sp. representing a change from the previous period. In contrast, during MIS 4, 3 and 2, *A. buselaphus* becomes a grazer and the equids seem to be mixed-feeders, notably *E. cf. mauritanicus*. Apart from MIS 5, *G. cf. atlantica* typically shows evidence of a browser diet throughout this study. Finally, during MIS 1 or 2, *Equus* sp. is a mixed-feeder, as in the immediately preceding and following periods. During MIS 1, *E. cf. mauritanicus* and *M. algericus* are mixed-feeders, whereas *Gazella* sp. and *Ovis/Capra* are browsers.

4.3 Taforalt

According to mesowear analyses, *A. lervia* from TAF is always within the range of variability of the present-day browsers (MWS: sector 13, layers orange and dark brown = 2; sector 10, brown layer = 1.1) (**Fig. 4; Tab. 3**). This is not the case for equids, which fall into the range for grazers in S13 (MWS = 5.5) and mixed-feeders in S10 (MWS = 3). The teeth for which a species could be determined show similar values for each sector. Indeed, in S13, *E. africanus/asinus* and *E. mauritanicus* have the same values (MWS = 6 and 5), showing only a small difference between layers with individuals from the orange layer displaying slightly of a less grazing tendency. The other taxa available for observation are only represented in S13, where *A. buselaphus* is mixed-feeder (MWS = 3), *B. primigenius*, usually a mixed-feeder, demonstrates a grazing tendency (MWS = 4). The only teeth of *Gazella* sp. from the dark brown layer display characteristics of browsers while the two teeth of the orange layer plot with the current mixed-feeders.

For the microwear analysis, 76% and 89% of the casts, respectively in S10 and S13, were suitable for analysis showing good preservation in both sectors. Gazelles and Barbary sheep have a diet falling within the variability of current browsers. Furthermore, no difference is expressed between *A. lervia*

from S13 and S10 (Mann-Whitney: Pits: $W = 30$; p -value = 0.058; Scratches: $W = 13.5$; p -value = 0.53). The two hartebeests are mixed-feeders, whereas the equids and aurochs are typical grazers (**Fig. 4; Tab. 3**). As for *A. lervia*, no differences between sectors are discernible between equids (Mann-Whitney: Pits: $W = 74.5$; p -value = 0.86; Scratches: $W = 70$; p -value = 0.71). Finally, no difference appears between *E. africanus/asinus* and *E. mauritanicus*. Thus, according to dental microwear, a notable segregation between strictly grazing herbivores (*Equus* and *Bos*) and, strictly browsing herbivores (*Gazella* and *Ammotragus*) is apparent at TAF. Only *Alcelaphus* occupies an intermediate mixed-feeder position, which is unusual for this taxon (Schuette et al., 1998).

5. Discussion

5.1 Variability of the dietary behaviour of Moroccan Pleistocene herbivores

In order to analyse the variability of herbivore feeding behaviour over time and space, we focus on the mesowear evidence from the most abundant species, the ones more often present in all three Moroccan sites: *A. buselaphus*, *B. primigenius*, *G. atlantica*, *G. cf. atlantica*, *G. cuvieri*, *Gazella* sp., *E. africanus/asinus*, *E. cf. africanus/asinus*, *E. mauritanicus*, *E. cf. mauritanicus* and *Equus* sp. (**Fig. 5**). To go deeper and to synthesize our results, we regrouped all the equids and the gazelles, under the genus *Equus* and *Gazella* respectively as well as the species *B. primigenius* and *A. buselaphus* according to their respective MIS stage (**Fig. 6**).

In general, the mesowear indicates that *A. buselaphus* is mixed-feeder or even mixed-feeder with a grazing tendency such as at BZM (MIS 4/3/2). This fits with the dental microwear analysis: hartebeest can be classified as a mixed-feeder at BZM (MIS 6/5) and TAF (S13, orange layer), or as a grazer at EKH and BZM (MIS 4/3/2) (**Fig. 6-A**). Thus, the feeding of *A. buselaphus* is always quite similar among the studied population and across time (during the last years and days of living of the individuals), indicating a low seasonal signal. Present-day *A. buselaphus* almost always belongs to the category of grazers according to dental mesowear studies (Fortelius and Solounias, 2000; Louys et al., 2011) as well as observations made on living populations (Gagnon and Chew, 2000). For example, in Burkina Faso (West Africa), the proportion of the grass in the diet of *A. b. major* is >95% with little seasonal variation in this percentage (Schuette et al., 1998). This would also be the case in East Africa where almost 100% grass consumption has been documented for two hartebeest subspecies *A. b. cokii* and *A. b. jacksoni* (Cerling et al., 2003). In contrast, in South Africa, hartebeests have been shown to incorporate more than 40% browse in their diet in arid grassland environments (van Zyl, 1965; Kok and Opperman, 1975). In the same country but in wetter grasslands, hartebeest consumption of grasses predominates again. Nevertheless, they occasionally browse and this behaviour increases significantly at the beginning of the wet season, which may be a reaction to limited food resources (Venter and Kalule-Sabiti, 2016). Even though the sample is limited in TAF, EKH and BZM, the generally low grazing behaviour of *A. buselaphus* since MIS 6 is therefore surprising and could be related to limited access to grasses. It is also possible that *A. buselaphus* had behaviours, preferences and habitats that were distinct from its sub-Saharan congeners. In the late 19th century, observers described this species as living in the mountains of the Maghreb and preferring rocky environments (Gruvel, 1937; Harper, 1945) which is very different from the open grassland they favour nowadays. The accuracy of these observations aside, the 19th century hartebeests were the last representatives of their species in the Maghreb and their behaviour probably did not reflect what it was during the Pleistocene. Further study to understand the ecological niche of *A. buselaphus* in North Africa is needed with more data.

According to dental mesowear, *B. primigenius* is always grouped with mixed-feeders at EKH but slightly more browser like at BZM (MIS6/5 and 5) or slightly more grazer like at TAF (S13) (**Fig. 5**). Seasonally, the diet of *B. primigenius* varies more than that of *A. buselaphus* because it is found among the mixed-feeders, at BZM (MIS 6/5 and 5) or among the browsers at EKH, or among the grazers at TAF (S13) and for the second individual from EKH (**Fig. 6-B**). In Europe, several studies of

the diet of *B. primigenius* have already highlighted the flexibility of this species. Generally, a mixed-feeder (Rivals and Lister, 2016; Uzunidis-Boutillier, 2017), it could adapt its diet seasonally. Although it most often focused on browsing (Rivals and Lister, 2016, Rivals et al., 2017; Uzunidis and Brugal, 2018), it could also consume a diet consisting of a majority of grasses (Rivals et al., 2009; Uzunidis-Boutillier, 2017). Finally, over a long period of time, it may also have become specialised either in browsing or grazing (Schultz and Kaiser, 2007). Several factors seem to lead these notable changes in the diet of *B. primigenius*, including climatic change (Schultz and Kaiser, 2007) and inter-specific competition (Rivals et al., 2017). According to our limited data, we hypothesize that in North Africa, *B. primigenius* could be seasonally more of a grazer than a browser, which might reflect a greater availability of grasses in comparison to Pleistocene Europe or different competitive relationships, especially with the diversified cohorts of African bovini.

Generally, the gazelles are classified as mixed-feeder (*G. atlantica*, *Gazella* sp.) or mixed-feeder with a browser tendency (*G. cuvieri*, *G. dorcas*) as recorded at in EKH, in S13- dark brown layer in TAF (*Gazella* sp.) or at BZM (MIS 5) (*Gazella* sp.). Nevertheless, some specimens are clearly typical browsers, such as *Gazella* sp. from TAF S13-orange layer and *G. cf. atlantica* (BZM, MIS 4/3/2) as opposed to *Gazella* sp. which is mixed-feeder with a clear grazer tendency in BZM (MIS 6/5) as is one of the two *G. cuvieri* from EKH (**Fig. 5**). With the exception of *G. atlantica* which probably became extinct from the Holocene, the eco-ethology of the present-days *G. dorcas* and *G. cuvieri* is relatively well-known. For example, *G. dorcas* usually considered as a mixed feeder is often found in desert areas (Loggers, 1992; Ward and Saltz, 1994). Its diet varies seasonally between strict browser and strict grazer (Loggers, 1991). *G. cuvieri* occupies varied biotopes corresponding to hilly terrain, including sparse oak forests, Aleppo pine forests, open terrain, and stony desert plateaus. In Morocco, this species can currently be found up to 2,600 m in altitude (Moreno and Espeso, 2008). This species is a mixed-feeder, with a dominant browsing tendency (Benamor et al., 2019). The diets of the gazelles at the three sites studied are therefore in line with the variability of the diets of present-day gazelles. The tendency of gazelles from BZM to have a slightly more abrasive diet during the MIS 5 and 1 (**Fig. 6-C**) may be related to the endemic argan tree (*Argania spinosa*) that was present in the area since the Miocene and perfectly adapted to the current climate conditions of the Souss region (southwestern of Morocco). Argan is a silica-rich dicot tree (Hullot et al., 2019) that can mimic the signature of monocots. A similar shift in dietary signals has already been shown in the diet of the Farasan gazelle living in *Acacia* (Wronski and Schulz-Kornas, 2015). At the beginning of the Quaternary period the argan tree probably covered a much larger territory (Baumer and Zeraïa, 1999) and charred macro botanical remains of this tree are present beginning in the late Middle Pleistocene levels of BZM (Sehasseh et al., 2021; I. Ziani pers. comm). In EKH, both dental mesowear and microwear indicate differences between *G. atlantica* and *G. dorcas* (**Fig. 2-A**, **Fig. 2-B**): in general *G. atlantica* shows a more abrasive diet than *G. dorcas*, which had more pits at the time of death. The diet of *G. dorcas* included more grit and can be associated with the category "dirty browsing" *sensu* Semperebon et al. (2011). These differences in the diet of the two gazelle species may reflect temporal or behavioural segregation. Either the two species were not present at the same time in the vicinity of EKH or they consumed different kinds of browse. Furthermore, the higher MWS of *G. atlantica* could indicate that this species was less specialized than *G. dorcas* (**Fig. 2-A**). The two teeth attributed to *G. cuvieri* display very different value, from browser (MWS = 1) to mixed-feeder with a grazing tendency (MWS = 4). With this size of sample, it is not possible to determine if this variability is related to the potential ecological flexibility of the species, if it reflects different time periods for the two specimens, or whether it simply illustrates individual behaviour.

According to the dental mesowear, the equids had a varied feeding behaviour. Observations that we have been made on two individuals from BZM, *E. cf. mauritanicus* and *Equus* sp., indicate that they were mixed-feeders with a browsing tendency respectively in MIS 4/3/2 and 2/1. On the contrary, in

MIS 1, a third individual determined as *E. cf. mauritanicus* is strictly a grazer (**Fig. 3-A**). In EKH, *Equus* sp. (n=3) was generally mixed-feeder with a more grazing tendency than *E. cf. mauritanicus* (n=1) and *E. cf. africanus/asinus* (n=2) also mixed-feeder with a browsing tendency (**Fig. 2-A**). Finally, in TAF, we pointed out that species from S13 (both layer) such as *E. africanus/asinus* (n=2) as well as *E. cf. mauritanicus* (n=2) had a much stronger grazing tendency than those in S10 with a single *E. africanus/asinus* and two *Equus* sp. (**Fig. 4-A**). The microwear analysis clearly indicates that equids were almost always grazers at the time of death at EKH, BZM MIS 6/5, and Taforalt in S10 and S13, but could also have been mixed-feeders (BZM MIS 4/3/2 and MIS 1) (**Fig. 2-B, Fig. 3-B, Fig. 4-B; Fig. 6-D**). This suggests that during the second part of the Upper Pleistocene of Morocco, the diet of equids was generally less abrasive than expected for this genus, which today is considered to be highly specialised in grass consumption (MacFadden 1988). This is in line with several studies that highlighted the flexibility of feeding behaviour in Pleistocene equids in Europe (Uzunidis, 2021) or in Africa (Kaiser and Franz-Odenaal, 2004). The Moroccan equids in this study *E. mauritanicus* and *E. africanus/asinus* are respectively often associated with zebrines and asinines forms (Sam, 2018). The feeding habits of asinines can vary from strict grazing (Kaiser et al., 2008) to strict browsing (Schulz and Kaiser, 2013) depending on their environment. In general, the diet of zebras relies on grass (Schulz and Kaiser, 2013) but it can also include browse seasonally as is the case for example for *E. zebra* at Bontebok National Park in South Africa (Strauss, 2015). Where specific determination was possible between zebrines and asinines forms, we found no evidence that might indicate that they may have occupied different ecological niches. This result is surprising and would indicate direct competition between the two forms of equids, whereas usually two close species avoid such competition (Saarinen et al., 2021). It could nevertheless explain the variability in some cases from mixed-feeder to strict grazing and their strategy of relying on a large number of different plant species.

5.2 Intra-site dietary analysis and paleoenvironmental reconstruction

5.2.1 El Khenzira

At EKH, the accumulation of herbivores in layers B to C covers the whole Upper Pleistocene. Thus, the variability of the diet that we pointed out for the different species should be interpreted mainly as an outcome of mixing material from different climatic and environmental contexts. Nevertheless, it can be noted that MWS are always quite low, whatever the taxon, and that the majority of individuals oscillate between browser and mixed-feeder variability, including taxa that are usually strict or variable grazers such as *A. buselaphus* (Schuette et al., 1998), *Connochaetes* (Gagnon and Chew, 2000) and *Redunca redunca* (Louys et al., 2011) (**Fig. 2-A**). Only equids have an MWS compatible with mixed-feeder with grazer tendencies. The results of dental microwear are somewhat more varied showing the presence of all three food categories (**Fig. 2-B**). Nevertheless, 61.5% of the individuals present fall within the variability of browsers, which would indicate that the environment must have been more favourable to this type of diet seasonally and in general, and therefore contained more dicots than monocots.

5.2.2 Bizmoune

The BZM stratigraphy covers the very end of the Middle Pleistocene and the Upper Pleistocene including Neolithic layers. Few teeth per taxon are available but the evolution of their dietary signal allows us to obtain preliminary observations on the evolution of the environment around BZM cave.

The mesowear analysis (**Fig. 3-A**) indicates that grazers and mixed-feeders with a grazer tendency are in the majority during MIS 6-5. Their presence decreases during the Upper Pleistocene, when most taxa are mixed-feeder or mixed-feeder with browsing tendency, and then seems to increase again during MIS 1. These observations could indicate an open environment at the time of formation of the older layer of BZM (4c, MIS 6). This is consistent with the analysis of charcoals that suggested open

plant formations dominated by *Juniperus/Tetraclinis* together with the presence of argan (*A. spinosa*) followed by taxa such as Angiosperms, *Pistacia* sp., or *Salix/Populus* (Sehassseh et al., 2021). Based on the distribution of present-day species, the climate would have been marked by sub-arid to semi-arid conditions (Fennane et al., 1999; Benabid, 1982, 1984, 2000). Starting with MIS 5, the environment became more closed and the dicots took precedence over the monocots. The mesowear signal of the gazelles could reflect a shift towards more abundant consumption of the argan tree (cf. supra). The two teeth corresponding to MIS 1 accumulated more precisely in Layer 1c during a period between -11,294 and -10,274 cal BP (LARATES Rabat, sample 290-S4/C4, $10,865 \pm 208$). This period was marked by a humid climate (Cheddadi et al., 2021; Ait Brahim, 2019) with maximum low-latitude summer insolation (Tjallingii et al., 2008) outside of a “Green Sahara” period (Larrasoana et al., 2013). It also corresponded to a reopening of the environment allowing *E. cf. mauritanicus* to have a strictly grazing diet (**Fig. 3-A**). On the scale of the dental microwear (**Fig. 3-B**), we observed a shift between the teeth dated to MIS 6/5 and the more recent Upper Pleistocene teeth: the latter have statistically more pits than the former. The presence of abundant pits on the enamel surface has been linked to the ingestion of vegetation with more grit (Semperebon et al., 2011). In North Africa, the late Middle Pleistocene is described as a dry period (Masojc et al., 2019) while the Upper Pleistocene has four 'Green Sahara' episodes across North and East Africa, as well as in the Arabian Peninsula and the Levant, coinciding with a humidification of the climate (Larrasoana et al., 2013). Vegetation, during wet periods, is likely to retain dust particles effectively (Ungar et al., 1995). The increase in the number of pits on the surface of the BZM ungulate teeth during the Upper Pleistocene would therefore be related to the development in woodland (noticeable through the dental mesowear) and increased climate humidity. Finally, the North African endemic cervid *M. algericus*, the diet of which had never been studied, was found in BZM between -6641 and -6009 cal BP (LARATES Rabat, sample 289-S1/C3, 7467 ± 172) which for now represents the last occurrence of the species (Fernandez et al., 2015). It has been hypothesized that the brachydonty of this species was adapted to a diet based on non-abrasive food, and that it may have been a browser (Abbazzi, 2004), which implied a limited competition with African grazers (Faith, 2014; Fernandez et al., 2015; Croitor, 2016). Both dental mesowear and dental microwear (**Fig. 2-A**, **Fig. 2-B**) place this species within the mixed-feeder variability reflecting an opportunistic feeding behaviour involving both dicots and monocots. These results are consistent with inferences obtained from the morphological description of the teeth (Fernandez et al., 2015). Furthermore, ecomorphological features (i.e weak mastication abilities, small low-crowned cheek teeth, reduced preorbital fossae, body size) suggest also semiaquatic or periaquatic habits of *M. algericus* and specialization to forage on soft water herbage (Croitor, 2016). The discovery of new individuals is needed to further describe the ecology of this particular species.

5.2.3 Taforalt

In TAF, S10 (brown layer) and S13 (orange and dark brown layers) represent the end of MIS 2. Analysis of the dental mesowear and dental microwear (**Fig. 4**) reveal that all diets are represented by the herbivore teeth from both sectors, reflecting the presence of monocots and dicots. In both sectors of the site, *A. lervia* is identified as a browser at both scales of observation but seems to have incorporate slightly more abrasive food in S13 since its MWS is a bit higher. Usually, this species is considered as a non-strict grazer (Gray and Simpson, 1980; Cassinello, 1998; Mimoun and Nouira, 2015) but in Taforalt it could have been out-competed by the more efficient equids, *B. primigenius* and *A. buselaphus*, in the acquisition of grasses.

We found differences in the diet of the two best represented taxa, *Equus* (including *E. africanus/asinus*, *E. mauritanicus* and *Equus* sp.) and *A. lervia*: the diet is more abrasive in S13 than in S10. This could reflect an open environment rich in monocots in S13, orange and dark brown layer and a reduction of this type of plant in S10. The differences between the dietary signals of S13 dark

brown layer and S10-brown layer could indicate different moment in the deposit of this accumulation with the S13-dark brown layer closer in time to the S13-orange accumulation.

6. Conclusion

The chronostratigraphic, taphonomic and taxonomic resolution are unequal in the three Moroccan sites of TAF, EKH and BZM. Nevertheless, the sample studied (129 teeth), corresponding to 19 taxa of herbivores, as well as the implementation of mesowear and microwear analyses, are unique for North Africa. Our results highlight varied feeding behaviours sometimes related to climate changes but also to competitive relationships and specific adaptive strategies for some taxa. These results, which are still preliminary, lay the foundations for a broader reflection that would aim to describe the evolution of Moroccan landscapes. But for this, more archaeological sequences and dates are needed. In this perspective, the existing continental and marine paleoenvironmental records indicate that the influence of the "Green" or "Yellow" Sahara associated with the major climatic pulses have played a leading role in altering the vegetation cover in North Africa. Also, the opening or closing of large terrestrial networks and corridors have probably been a driving force for the migration, competition and adaptation for some herbivores in Morocco. At the chronological and geographical scale represented by these three sites, a wide variety of diets have been described, reflecting the significant fragmentation of the territory of herbivores. Their exploitation of resources in the diverse environments surrounding each of the sites is likely to have influenced human use of landscape at different periods and conditioned the hunting strategies or the sites' occupants. Therefore, the careful reading of herbivore diets and paleoenvironmental reconstructions represent important tools for understanding past human societies.

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List of figures



Fig. 1: Geographical locations of Bizmoune, Taforalt and El Khenzira. Author of the base map: Eric Gaba – Wikimedia Commons.

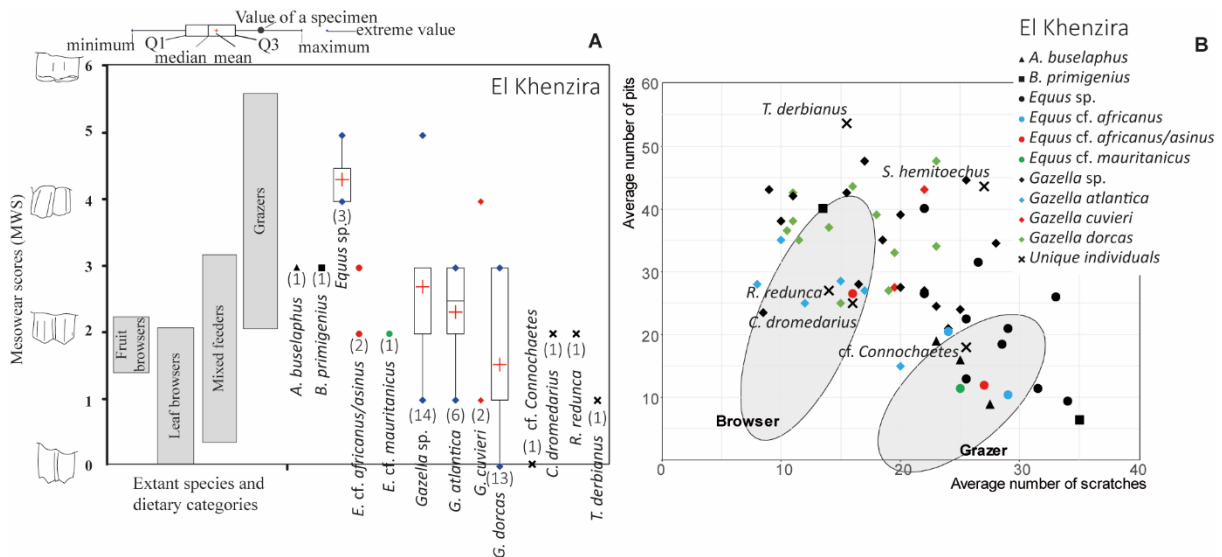


Fig. 2: Dietary variability of the herbivores from El Khenzira. A: Mesowear score of the herbivores compared to the values of recent ungulates published by Fortelius and Solounias (2000), Solounias and Semprebon (2002), Rivals et al. (2010, 2014). The numbers in brackets are the Number of Individual Specimens. B: Bivariate plot of the numbers of pits and scratches of herbivores. The ellipses correspond to the Gaussian confidence ellipse ($p = 0.95$) on the centroids of current grazers and browsers published by Solounias and Semprebon (2002). Original data from Table 1.

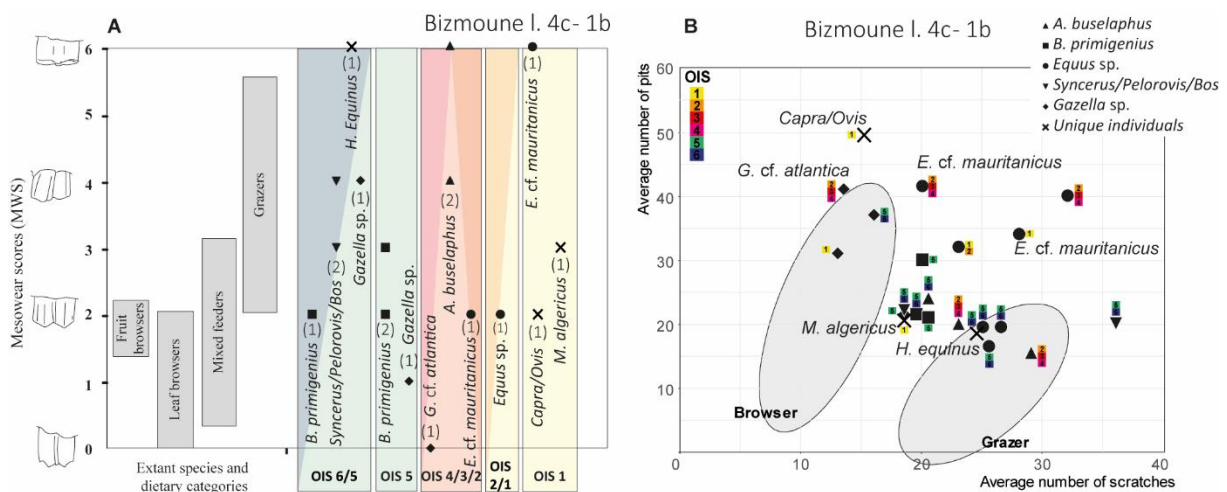


Fig. 3: Dietary variability of the herbivores from Bizmoune layers 4c to 1b. A: Mesowear score of the herbivores through time compared to the values of recent ungulates published by Fortelius and Solounias (2000), Solounias and Semprebon (2002), Rivals et al. (2010, 2014). The numbers in brackets are the Number of Individual Specimens. B: Bivariate plot of the number of pits and scratches of herbivores according to their MIS. Original data from Table 2. The ellipses correspond to the Gaussian confidence ellipse ($p = 0.95$) on the centroids of current grazers and browsers published by Solounias and Semprebon (2002).

Taforalt: Sector 13 - Orange layer, Sector 13 - Dark brown layer, Sector 10 - Brown layer

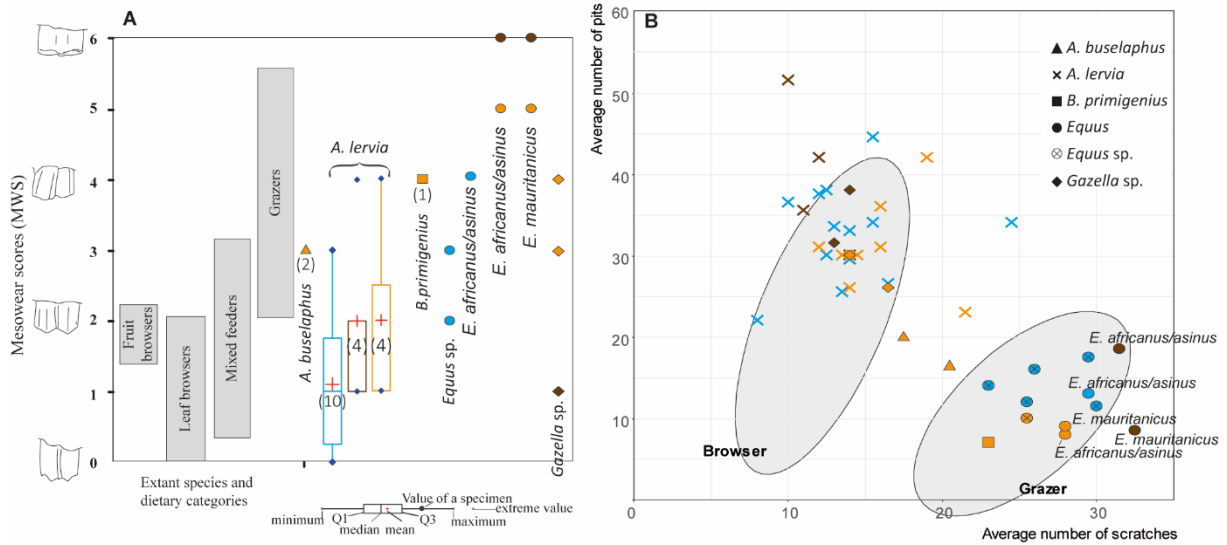


Fig. 4: Dietary variability of the herbivores from Taforalt sectors 13 and 10. A: Mesowear score of the herbivores through time compared to the values of recent ungulates published by Fortelius and Solounias (2000), Solounias and Semprebon (2002), Rivals et al. (2010, 2014). The numbers in brackets are the Number of Individual Specimens. B: Bivariate plot of the number of pits and scratches of herbivores according to their MIS. Original data from Table 3. The ellipses correspond to the Gaussian confidence ellipse ($p = 0.95$) on the centroids of current grazers and browsers published by Solounias and Semprebon (2002).

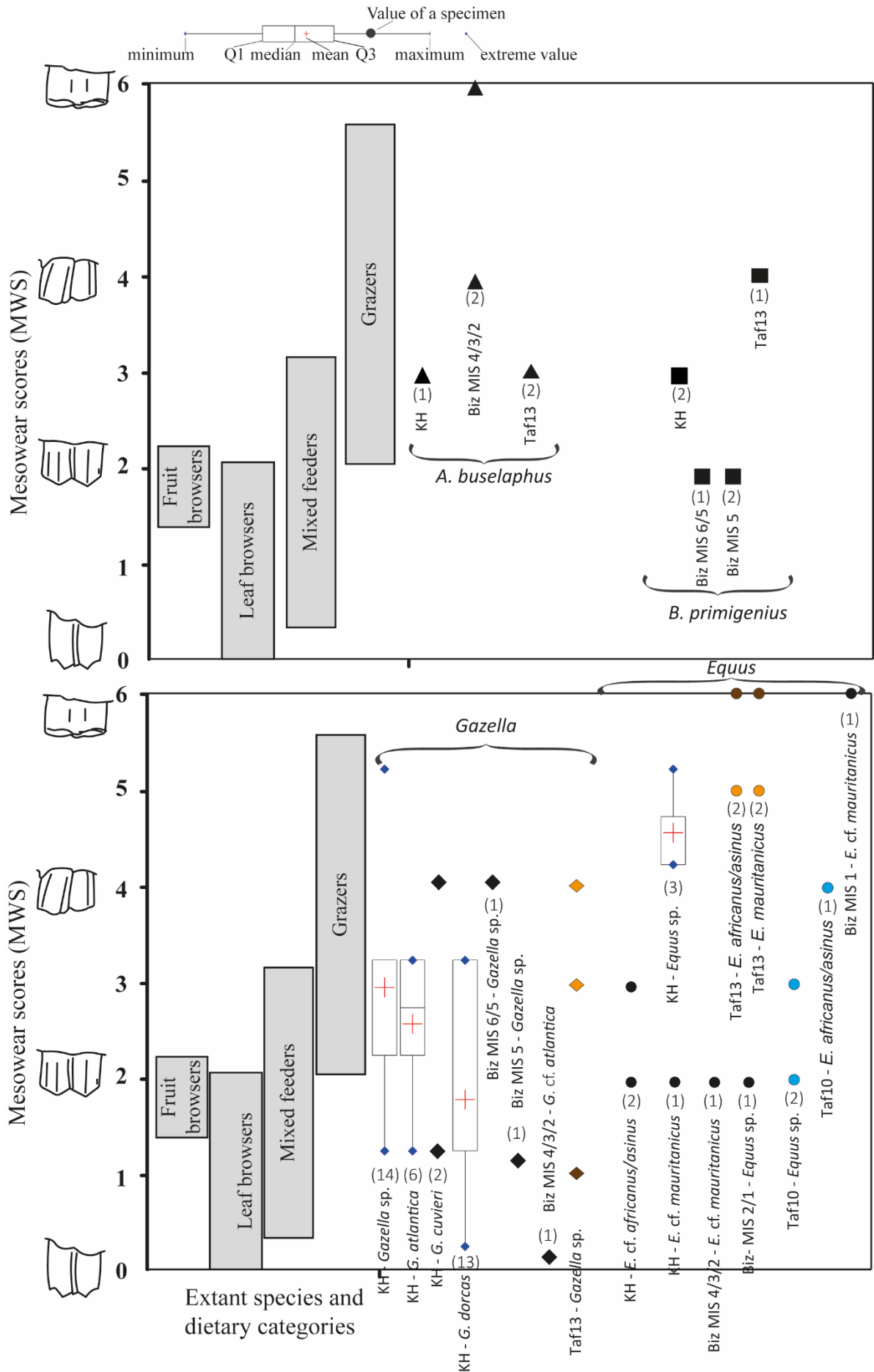


Fig. 5: Comparison of the MWS (Mesowear score) of the herbivores represented at El Khenzira, Bizmoune and Taforalt: *Alcelaphus buselaphus*, *Bos primigenius*, *Equus*, *Gazella*. The numbers in brackets are the Number of Individual Specimens. For the description of the grey area, see caption of figure 2. Original data from Table 1 to Table 3.

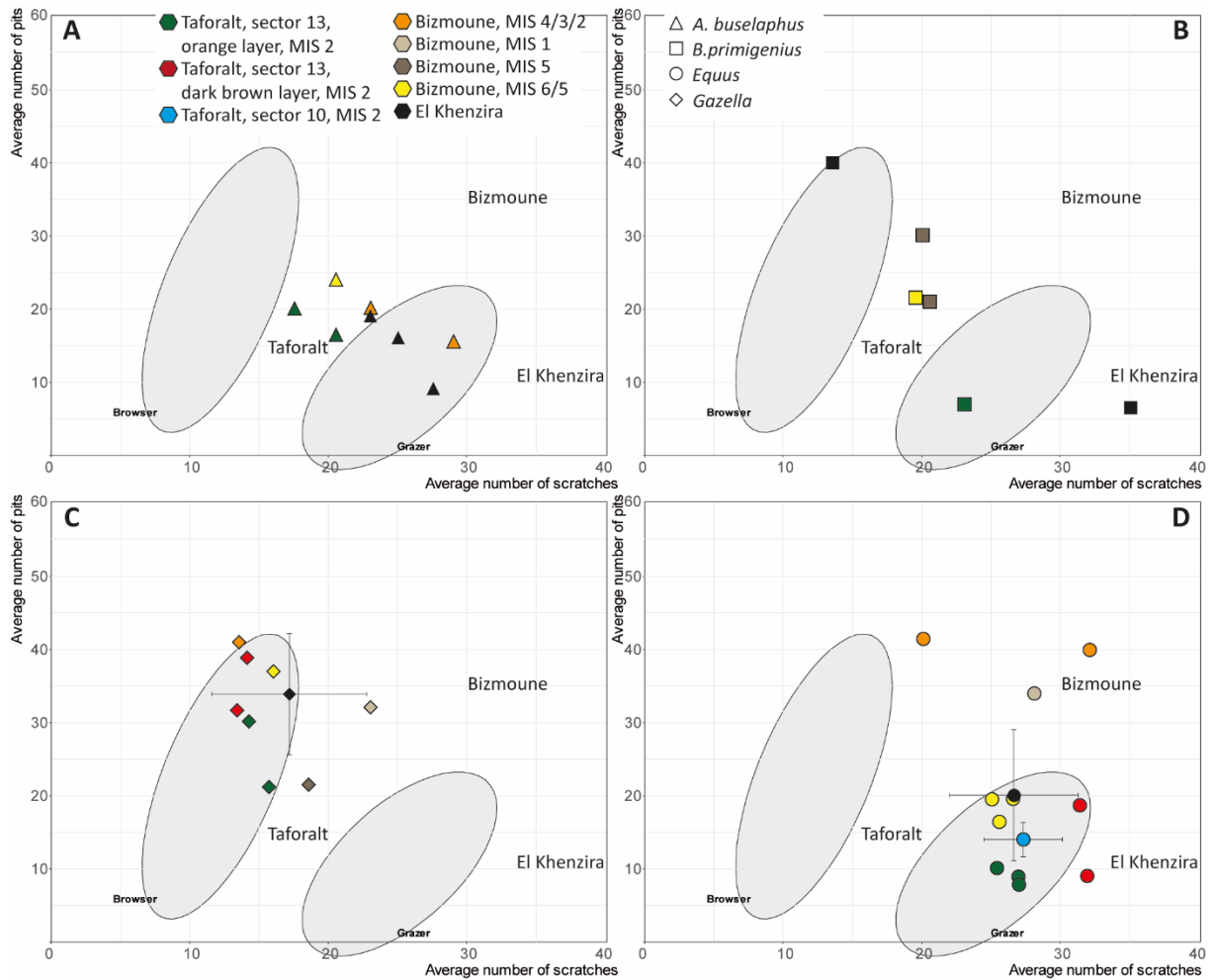


Fig. 6: Bivariate plots of the number of pits and scratches comparing the variability of the diet of A: *Alcelaphus buselaphus*; B: *Bos primigenius*; C: *Gazella*; D: *Equus* in El Khenzira, Bizmoune (l. 4c to 1a) and Taforalt (sectors 13 and 10). When the number of teeth is higher than 4, the cohort is represented by its mean with error bars corresponding to the standard deviation (± 1 SD). For the description of the grey ellipse, see caption of figure 2.

List of tables

Site	#	Mesowear		Microwear									
		N	MWS	N	NP	NS	%LP	%G	SWS	%HC	%XS		
El Khenzira													
<i>Camelus dromaderius</i>	63		2		25	16	0	100	2	100		100	
cf. <i>Connochaetes</i>	58		0		18	25.5	100	0	1	0		0	
<i>Redunca redunca</i>	13a/b		2		27	14	0	0	1	0		100	
<i>Stephanorhinus</i> sp.	77				43.5	27	100	0	1	0		0	
<i>Taurotragus derbianus</i>	26		1		53.5	15.5	0	0	1	0		100	
<i>Alcelaphus buselaphus</i>	31				9	27.5	0	0	0	0		100	
	32				16	25	0	0	0	0		100	
	33		3		19	23	0	0	0	0		100	
<i>Bos primigenius</i>	41				6.5	35	0	0	1	0		0	
	91		3		40	13.5	0	100	1	100		100	
<i>Equus</i> cf. <i>africanus</i>	82				20.5	24	0	0	1	0		0	
	84				10.5	29	0	0	1	0		0	
<i>Equus</i> cf. <i>africanus/asinus</i>	66		2		26.5	16	0	0	0	0		100	
	67		3		12	27	0	0	0	0		100	
<i>Equus</i> cf. <i>mauritanicus</i>	86		2		11.5	25	0	0	1	0		100	
<i>Equus</i> sp.		M	3	4.33	M	10	22	27.75	20	30	0.9	10	70
# 9,68,70,72-74,79,81,83,85		SD		0.58	SD		9.5	4.23					
<i>Gazella atlantica</i>		M	6	2.33	M	6	26.42	13.66	33.33	16.66	1	0	100
# 11,17,18,23,61,87		SD		0.81	SD		6.53	4.5					
<i>Gazella</i> cf. <i>cuvieri</i>	8			1		27.5	19.5	0	0	0	0	100	
	10			4		43	22	100	0	1	0	100	
<i>Gazella dorcas</i>		M	13	1.54	M	13	37.11	16.69	23.07	7.69	0.77	23.07	84.61
# 2,19,20,29,30,37,49,53,54bis,56bis,88-90		SD		1.13	SD		6.56	5.1					
<i>Gazella</i> sp.		M	14	2.71	M	16	33.84	18.34	75	18.75	0.75	0	93.75
# 1,3,5,6,12,21,22,34,36,39,46,52,55bis,60,76,92		SD		0.91	SD		8.74	6.23					

Tab. 1: Summary of dental meso- and microwear data of African herbivores from El Khenzira (layers A to C, from Arambourg Collection (MNHN, Paris) and Bouzouggar 2017 excavations, see details in text). Abbreviations: # = identifier of the teeth; N = Number of specimens; MWS = Mesowear score; NP = Mean number of pits; NS = Mean number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = scratch width index; %HC = Percentage of specimens with hyper coarse scratches; %XS = Percentage of specimens with crossed scratches; M = Mean; SD = Standard deviation.

Site					Microwear						
Taxa	Layer	MIS	#	MWS	NP	NS	%LP	%G	SWS	%HC	%XS
Bizmoune l. 1b to 4c											
	4c	6/5									
<i>Hippotragus equinus</i>			6803	6	18.5	24.5	0	0	1	0	100
<i>Syncerus/Pelorovis/Bos</i>			9356	3	20	36	0	100	0	0	0
<i>Alcelaphus buselaphus</i>			5767		24	21.5	0	100	1	0	100
<i>Equus</i> sp.			7022		19.5	25	0	100	0	0	0
<i>Gazella</i> sp.			9113	1	37	16	0	0	0	0	0
	4a-4b	6/5									
<i>Syncerus/Pelorovis/Bos</i>			1101	4	22	18.5	0	100	1	0	0
<i>Bos primigenius</i>			1398	2	21.5	19.5	0	100	1	0	100
<i>Equus</i> sp.			6327		16.5	25.5	0	100	0	0	0
			1394		19.5	26.5	0	100	0	0	0
	3c	5									
<i>Bos primigenius</i>			8783	2	30	20	0	0	1	0	100
			5772	3	21	20.5	0	100	1	0	0
<i>Gazella</i> sp.			6199	4	21.5	18.5	0	100	0	0	0
	2b	4/3/2									
<i>Alcelaphus buselaphus</i>			10405	4	20	23	0	0	0	0	100
			9880	6	15.5	29	0	0	1	0	0
<i>Equus</i> sp.			11039		41.5	20	0	0	0	0	100
<i>Equus</i> cf. <i>mauritanicus</i>			2971	2	40	32	0	100	0	0	0
<i>Gazella</i> cf. <i>atlantica</i>			10405	0	41	13.5	0	0	1	100	0
	2a	2/1									
<i>Equus</i> sp.			11754	2	32	23	0	100	1	100	100
	1c	1									
<i>Equus</i> cf. <i>mauritanicus</i>			10446	6	34	28	0	100	0	0	100
<i>Gazella</i> sp.			10243		31	13	0	0	0	0	0
	1b	1									
<i>Megacerooides algericus</i>			58	3	20.5	18.5	0	100	100	0	0
<i>Ovis/Capra</i>			43		49	16	0	0	1	0	100

Tab. 2: Summary of dental meso- and microwear data of African herbivores from Bizmoune (layer 1a to 4c). Abbreviations: # = identifier of the teeth; MWS = Mesowear score; NP = Mean number of pits; NS = Mean number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = scratch width index; %HC = Percentage of specimens with hyper coarse scratches; %XS = Percentage of specimens with crossed scratches; M = Mean; SD = Standard deviation.

Site Taxa	Sectors and layers	#	Mesowear		Microwear									
			N	MWS	N	NP	NS	%LP	%G	SWS	%HC	%XS		
Taforalt sectors 13 and 10														
	13													
<i>Alcelaphus buselaphus</i>	Orange	17864		3			20	17.5	0	0	1	0	100	
	Orange	16864		3			16.5	20.5	0	0	1	0	100	
<i>Bos primigenius</i>	Orange	18127		4			7	23	0	0	1	0	100	
<i>Ammotragus lervia</i>	Orange		M	4	2	M	7	38.28	14	0	0	1	0	14.28
# 33, 35, 41, 42, 43, 45, 46, 48, 51, 61, 62, 64	Dark brown		SD		1.41	SD		7.49	3.21	20	0	1	0	80
	Dark brown		M	4	2	M	5	28	15.1					
	Dark brown		SD		1.41	SD		3.39	3.7					
<i>Equus africanus/asinus</i>	Orange	16964		5			8	28	0	0	1	0	100	
	Dark brown	16477		6			18.5	31.5	0	0	1	0	0	
<i>Equus cf. mauritanicus</i>	Orange	18424		5			9	28	0	0	1	0	100	
	Dark brown	16437		6			8.5	32.5	0	0	1	0	100	
<i>Equus sp.</i>	Orange	17531					10	25.5	0	0	1	0	100	
	Orange	18097					9	28	0	0	1	0	100	
<i>Gazella sp.</i>	Dark brown	18309					38	14	0	0	1	0	100	
	Orange	18207		3			31.5	13	0	0	0	0	100	
	Dark brown	18121		1			26	16.5	0	0	1	0	100	
	Orange	16721		4			30	14	0	0	0	0	100	
	10													
<i>Ammotragus lervia</i>	Brown		M	10	1.1	M	13	32.65	13.96	7.69	0	0.54	0	84.61
# 2,6,7,9,10,12,13,15, 17-19,63,66			SD		0.99	SD		5.99	3.9					
<i>Equus africanus/asinus</i>	Brown	14343		4			13	29.5	0	0	1	0	100	
<i>Equus sp.</i>	Brown		M	2	2.5	M	5	14.2	26.8	0	0	0.8	0	80
	Brown		SD		0.7	SD		2.56	2.92					

Tab. 3: Summary of dental meso- and microwear data of African herbivores from Taforalt (sectors 13 and 10). Abbreviations: # = identifier of the teeth; N = Number of specimens; MWS = Mesowear score; NP = Mean number of pits; NS = Mean number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = scratch width index; %HC = Percentage of specimens with hyper coarse scratches; %XS = Percentage of specimens with crossed scratches; M = Mean; SD = Standard deviation.