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Dental mesowear analysis of the late Miocene Bovidae from Toros-Menalla (Chad) and early hominid habitats in Central Africa

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ABSTRACT

This study aimed to reconstruct the environmental conditions that prevailed in the Chadian palaeo-lake basin ca. 7 Ma ago based on the feeding preferences of late Miocene Bovidae from Toros-Menalla (Chad). This is a key issue for understanding the circumstances (regional landscapes) under which the earliest known hominid *Sahelanthropus tchadensis* evolved. A dental mesowear analysis was applied to 117 specimens of bovids representing the four tribes present in the anthracotheriid unit localities: Hippotragini, Reduncini, Antilopini and Bovini. All these bovids fed on grasses, at least partially. Previous analyses and the present results indicate the presence of a mosaic-like environment containing various habitats from grasslands to woodlands in the surroundings of the Chadian lake basin. Indeed, our data support the availability of grass or grass-like plants and therefore open patches in the vicinity of the Chadian palaeo-lake shores.

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1. Introduction

Reconstructing late Miocene environments in Africa is a key issue for understanding the circumstances under which hominids evolved and especially the environmental conditions under which they acquired bipedal locomotion during the late Miocene. Recent studies suggest that bipedalism in early hominids may have arisen in wooded to forested environments (WoldeGabriel et al., 2001; Senut, 2006; White et al., 2009) in contrast to early opinions that favoured open savanna as the habitat in which bipedalism appeared. Reconstructing the environmental conditions that prevailed in Chad 7 Ma ago is therefore a key issue because *Sahelanthropus tchadensis*, the earliest known hominid, displays cranial features supporting a bipedal mode of locomotion (Brunet et al., 2002; Guy et al., 2005; Zollikofer et al., 2005).

Paleontologists often refer to the guild of herbivorous mammals to infer paleoenvironments, and particularly to bovids, which are the most common element among Neogene fauna (Plummer and Bishop, 1994; DeGusta and Vrba, 2003). Because bovids are vegetarian, their feeding preferences mirror the availability of vegetal resources. The dominance of species grazing mostly on monocotyledons that have a high concentration of silica phytoliths in the cell walls suggests the presence of either open areas or open patches in closed woody areas. Browsers, in contrast, prefer dicotyledons that have few silica phytoliths, and their abundance among fossil assemblages indicates the presence of forest or bushy/shrubby patches in open landscapes. Finally, intermediate feeders alternate between dicotyledons and monocotyledons and may exploit more varied habitats (Estes, 1991; Kingdon, 1997).

More than 400 vertebrate-bearing localities are known from the late Miocene of Toros-Menalla (TM) in the Djurab desert (Chad). Bovids represent 58% of the mammalian remains from the locality Toros-Menalla "TM 266", at which *Sahelanthropus tchadensis* was discovered (Brunet et al., 2002; Vignaud et al., 2002). They dominate the TM 266 mammal assemblage along with anthracotheriids (14%) and carnivores (11%), the remaining families and orders being less well represented (Le Fur et al., 2009). TM 266 and contemporaneous sites belong to the anthracotheriid unit of Toros-Menalla, which is dated at ca. 7.0 Ma (Vignaud et al., 2002; Brunet et al., 2005; Lebatard et al., 2008). Numerous bovids have been identified in the anthracotheriid unit: one species of Bovini, rare Boselaphini, two species of Hippotragini, Reduncini, Alcelaphini, Aepycerotini, and one species of Antilopini (Vignaud et al., 2002; Geraads et al., 2008, 2009). In this study, a sample of bovid dental remains from these localities was investigated to estimate their feeding preferences and obtain an environmental signal.

There are many complementary approaches used to reconstruct the ecology of extinct species of bovids. These approaches include ecomorphology (Kappelman, 1988; Plummer and Bishop, 1994; Scott

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et al., 1999; Kovarovic et al., 2002; DeGusta and Vrba, 2005a,b), stable isotope signals from dental tissue (Zazzo et al., 2000, 2002; Sponheimer et al., 2003; Merceron et al., 2006), dental microwear (Solounias and Moelleken, 1992; Merceron et al., 2004; Schubert et al., 2006; Merceron et al., 2007a), and dental mesowear analyses (Fortelius and Solounias, 2000; Kaiser and Rössner, 2007; Merceron et al., 2007b; Rivals et al., 2007). Here we consider this latter taxon-free approach for fossil bovids from this locality.

Dental facet development on the molar surfaces of living herbivorous ungulates appears to be strongly tied to their feeding styles (e.g. Fortelius and Solounias, 2000). In addition, dental mesowear patterns provide a long-term signal about the feeding habits of extinct ungulates (e.g. Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003; Rivals et al., 2007). Dental mesowear reflects the degree of attritive and abrasive wear on the occlusal molar surface. The former is due to tooth/tooth contact resulting in high relief between both cusp(id)s and sharp cusp (id) apices, whereas abrasive wear is due to the alteration of enamel tissue by food during mastication. It obliterates dental facets, reducing the depth between cusp(id)s and resulting in more rounded apices (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003). Therefore, individuals that browse on foliage from dicotyledons tend to have higher occlusal relief and sharper cusp(id)s than grazers (Fortelius and Solounias, 2000).

2. Material and methods

2.1. Material

2.1.1. Comparative database

The mesowear pattern of fossil species was investigated through comparisons with a database composed of living species whose feeding preferences and behaviours are well known (Table 1). All extant species and specimens used here for comparisons came from the database published by Fortelius and Solounias (2000). This database was originally composed of 64 species of herbivorous mammals representing 2200 adult individuals. However, the number of specimens and species was deliberately limited here compared to the original publication (Fortelius and Solounias, 2000). In fact, the latter authors claimed that the small sample sizes in extant species weaken the reliability of comparative datasets. Following their recommendations, all extant species with less than 20 individuals were excluded. Fortelius and Solounias (2000) also indicated that the different phylogenetic histories of mammals obviously constrained tooth development and morphology and consequently the way occlusal relief and cusp shape were worn. Therefore, the database is here restricted to the ruminant species that share common tooth morphology. Eventually, the original database was further restricted to the African Bovidae representing grazers, intermediate feeders, and traditional browsers, in order to cross-reference the mesowear scores with the dietary data of African bovids synthesized by Gagnon and Chew (2000). Nevertheless, the database was still composed of 798 wild-shot specimens representing 15 extant species. So, using only the African bovids for which we have dietary composition reinforces our results and interpretation on extinct bovids.

2.1.2. Fossil data

The molar mesowear pattern of 117 specimens of Bovidae, which belong to the four tribes that are well represented at TM 266 and contemporaneous localities from Toros-Menalla, was investigated. According to the analysis of faunal structure of the TM mammal assemblages (Le Fur, 2009; Le Fur et al., 2009), Hippotragini (two species: *Tchadotragus sudrei*, *Saheloryx solidus*) and Reduncini (two species) are both very common in the TM assemblages whereas Antilopini (one species *Gazella* sp.) and Bovini (one species) (Geraads et al., 2008, 2009) are common. Aepycerotini and Alcelaphini are rare and the Boselaphini tribe is represented by a unique horn-core fragment. The relative abundance of the different taxa is barely affected by biasing taphonomical processes. All skeletal elements are represented in similar proportions in the TM 266 mammal assemblage (Le Fur et al., 2009).

Following the protocol established by Fortelius and Solounias (2000), we first considered the upper second molars. However, the material sample can be increased by including the lower second molars. However, a preliminary study (Franz-Odendaal and Kaiser, 2003) stated that the mesowear score on lower dentition might favour a grazing signal. As a result, the mesowear score is displayed first for the upper

Table 1
Mesowear scoring for extant and extinct bovids. The variables are symbolized as follows: low relief with sharp (LS), round (LR) or blunt cusp(id)s (LB) and high relief with sharp (HS), round (HR) or blunt cusp(id)s (HB). The variable [1-%sharp] is computed following Mihlbachler and Solounias (2006).

		LS	LR	LB	HS	HR	HB	1-%sharp
Browsers	*Boocerus euryceros* (be; $N=27$)	0.00	0.00	0.00	40.74	59.26	0.00	59.26
	Litocranius walleri (lw; $N=69$)	0.00	4.35	0.00	33.33	62.32	0.00	66.67
Grazers	*Alcelaphus buselaphus* (AB; $N=76$)	5.26	15.79	22.37	11.84	42.11	2.63	82.89
	Connochaetes taurinus (CT; $N=52$)	5.77	13.46	23.08	15.38	36.54	5.77	78.85
	Hippotragus equinus (HE; $N=26$)	0.00	15.38	0.00	3.85	80.77	0.00	96.15
	Hippotragus niger (HN; $N=20$)	0.00	0.00	15.00	5.00	80.00	0.00	95.00
	Kobus ellipsiprymnus (KE; $N=22$)	0.00	4.55	0.00	0.00	95.45	0.00	100.00
	Ourebia ourebi (OO; $N=128$)	1.56	1.56	0.78	20.31	75.78	0.00	78.13
	Redunca redunca (RR; $N=77$)	1.30	5.19	2.60	5.19	85.71	0.00	93.51
	Syncerus caffer (SC; $N=31$)	0.00	0.00	0.00	0.00	93.55	6.45	100.00
Mixed feeders	*Antidorcas marsupialis* (Am; $N=26$)	3.85	0.00	0.00	69.23	26.92	0.00	26.92
	Gazella thomsonii (Gt; $N=146$)	5.48	4.79	1.37	52.74	35.62	0.00	41.78
	Tragelaphus angasi (Ta; $N=20$)	0.00	0.00	0.00	35.00	65.00	0.00	65.00
	Tragelaphus imberbis (Ti; $N=31$)	0.00	0.00	0.00	58.06	41.94	0.00	41.94
	Tragelaphus scriptus (Ts; $N=47$)	0.00	0.00	0.00	48.94	51.06	0.00	51.06
Fossil taxa	Antilopini ($N=19$)	5.26	10.53	15.79	15.79	52.63	0.00	78.95
	Lower molar sample ($N=18$)	5.56	11.11	16.67	16.67	50.00	0.00	77.78
	Upper molar sample ($N=1$)	0.00	0.00	0.00	0.00	100.00	0.00	100.00
	Bovini ($N=8$)	0.00	0.00	37.50	0.00	62.50	0.00	100.00
	Lower molar sample ($N=1$)	0.00	0.00	0.00	0.00	100.00	0.00	100.00
	Upper molar sample ($N=7$)	0.00	0.00	42.86	0.00	57.14	0.00	100.00
	Reduncini ($N=20$)	0.00	0.00	5.00	10.00	85.00	0.00	90.00
	Lower molar sample ($N=16$)	0.00	0.00	6.25	0.00	93.75	0.00	100.00
	Upper molar sample ($N=4$)	0.00	0.00	0.00	50.00	50.00	0.00	50.00
	Hippotragini ($N=70$)	1.43	4.29	10.00	5.71	78.57	0.00	92.86
	Lower molar sample ($N=50$)	2.00	2.00	12.00	4.00	80.00	0.00	94.00
	Upper molar sample ($N=20$)	0.00	10.00	5.00	10.00	75.00	0.00	90.00

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molar, then for the lower molar, and finally as the combination of both the upper and the lower second molars.

Since the material is not always associated with cranial remains, specific taxonomic assignations are not possible for the vast majority of specimens (Appendix A). For this reason, the two species of Reduncini were clustered under the tribe name. The same procedure was applied for the two Hippotragini. Such a sampling procedure precludes extraction of a species-level dietary signal since the potential differences in dietary habits are muddled. However, the mesowear score obtained for these two tribes is still informative since it gives an environmental signal. Indeed, previous environmental reconstructions based on family-, tribe- or generic-level samples, such as faunal assemblage analyses (e.g., Vrba, 1980; Fara et al., 2005; de Bonis et al., 1992, 1999; Le Fur, 2009; Le Fur et al., 2009), carbon and oxygen isotopic analyses (e.g., Zazzo et al., 2000; Franz-Odendaal et al., 2002), micro and mesowear analyses (e.g., Bibi, 2007; White et al., 2009), and postcranial ecomorphological studies (e.g., DeGusta and Vrba, 2003, 2005a,b; Kovarovic and Andrews, 2007) provide useful proxies with which to estimate environmental and climatic parameters.

2.1.3. Selection of fossil specimens

In total, only 117 out of a total of 750 bovid dental remains could be investigated for the dental mesowear analysis. Such strict restriction in the sampling was due to the high frequency of taphonomic alteration of the dental remains. In fact, several hundreds of specimens had been strongly eroded by abrasive sand particles carried by the intense wind streams that naturally outcrop the fossil beds. In many cases, this taphonomic alteration goes much further by totally abrading the dental crown if the specimen is not gathered on time. Many mandibles and maxillae only have their roots remaining. These harsh taphonomic conditions strongly reduce the number of available specimens. However, many specimens were completely or partially preserved in cemented sandstone levels undestroyed by sand winds whereas others were preserved by coverage with iron–manganese–sandy concretions. The number of specimens per tribe (70 hippotragines, 20 reduncines, 19 antilopines and 8 bovines; Table 1) was in relative accordance with the original TM bovid community, with dominance by hippotragines and reduncines.

Using a lens, we excluded individuals when the dental surface was totally polished by the abrasive sand wind. In cases in which some microwear scars were still recognizable, we assumed that the lack of the enamel lamella was not significant enough to erase the mesowear signal, which was not investigated at the micrometric scale, but at the millimetric scale.

In addition, after examining all dental remains housed in the Département des Collections of the Centre National d'Appui à la Recherche at N'Djamena (Chad), several species were excluded from the present analysis. In fact, some are only represented by very few cranial specimens with molars that are too worn and/or too fresh (Fortelius and Solounias, 2000).

2.2. Methods

Mesowear analysis was assessed by using casts. Moulds of the teeth were taken with a polyvinylsiloxane silicone (Coltene President's Jet, regular body) impression material. Casts were then made with resin.

2.2.1. Mesowear analysis

Mesowear was scored as occlusal relief and cusp shape on the cutting edge of either the vestibular cusp on the second upper molar (M^2) or the lingual cuspid on the second lower molar (M_2). Both anterior and posterior cusp(id)s were examined. Because sharpness is never an artifact of wear stage whereas blunting may be so, only the sharpest cusp(id) was scored (Fortelius and Solounias, 2000).

Occlusal relief (OR) was classified as high (H) or low (L), depending on how the cusp(id)s rose above the valley between them (Fig. 1). The second mesowear variable, cusp(id) shape, included three scored attributes: sharp (S), round (R) and blunt (B), according to the degree of facet development (Fig. 1). Teeth were examined with the naked eye and using a low magnification (10×) hand lens. For all specimens, both cusp shape and occlusal relief were scored. Six conditions were thus identified: low relief with sharp [L–S], round [L–R] or blunt cusp(id)s [L–B] and high relief with sharp [H–S], round [H–R] or blunt cusp(id)s [H–B] (Table 1). This latter category was uncommon. Fortelius and Solounias (2000) scored such conditions for a few individuals amongst grazing ungulates. No fossil specimen investigated here displayed such a dental mesowear pattern.

The correlations between mesowear and dietary variables were also performed using the mesowear scoring system (1-%sharp) following Mihlbachler and Solounias (2006) and the dietary composition of each extant bovid (Gagnon and Chew, 2000). In this case,

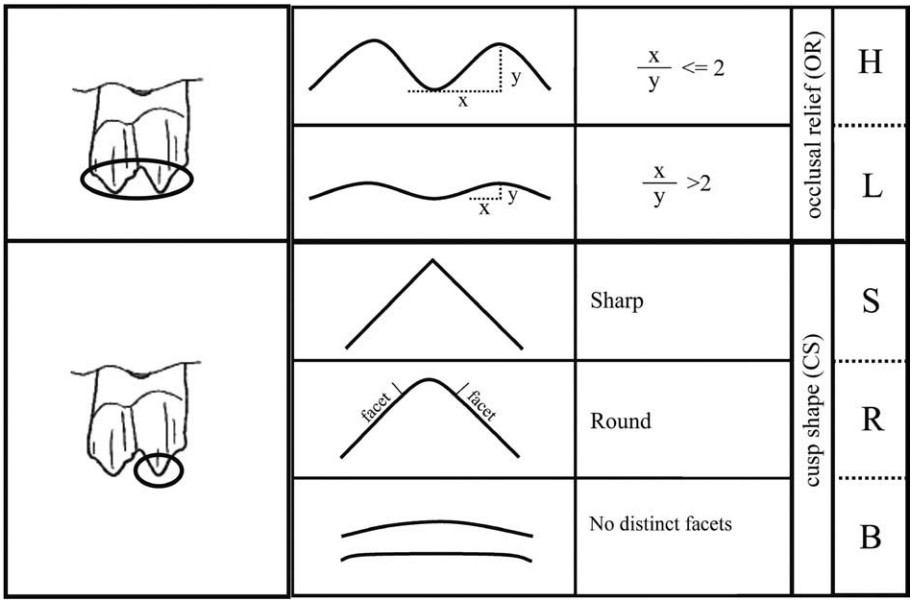

Fig. 1. The mesowear scoring convention for ungulate cheek teeth as defined by Fortelius and Solounias (2000) for upper second molars. Occlusal relief (OR) may be scored as "high" (H) or "low" (L); cusp shape (CS) is classified as "sharp" (S), "round" (R), or "blunt" (B).
Modified after Merceron et al. (2007b).

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only the cusp(id) shape (1-%sharp) score was considered for correlation (Tables 1 and 2).

2.2.2. Correspondence Factorial Analysis

Most of the previous dental mesowear analyses used a hierarchical classification (Kaiser and Fortelius, 2003 and citations therein) based on the calculation of Euclidian distances for separating and clustering species. Although this statistical approach provides interesting results, the insertion of extra fossil samples may bias the hierarchical classification structure based on the extant comparative species. In fact, different sets of fossil species may imply different states of clustering among living species themselves.

One of the main issues for an analysis based on comparisons between extinct and extant data is the ability to build a constant model set up with the latter data. Such a model allows objective discussions. In such a case, fossil species are not included in the analysis. If the fossil data have to be discussed through comparisons with extant datasets, these fossil species have to be inserted in an analysis without disturbing the model set up with the living species. In response to this issue, in this study a Correspondence Factorial Analysis (CFA, hereafter) was preferred to a Cluster Tree Analysis. The CFA allows extra data that do not interfere with the model to be inserted. Using this descriptive approach, the differences between species (rows) and mesowear variables (columns) were calculated using the Chi-square distance (Appendix B). The fossil samples were added as supplementary observations. The percentage of fruits [%F], dicots [%D] and monocots [%M] that constitute the diet of each living bovid used here were included as supplementary variables (Gagnon and Chew, 2000). This means that the CFA framework was only based on the set of living species and on dental mesowear scores. The fossil species and dietary data were superimposed into the analysis, but did not affect its framework.

3. Results

3.1. Living species

In the CFA including all extant species of bovids, only the two first axes are considered. In fact, the drop from the second to the third eigenvalue is sufficiently important to exclude the subsequent factors (Appendix B). The first axis distinguishes the grazing species from both browsers and intermediate feeders (Fig. 2). In detail, *Alcelaphus buselaphus* and *Connochaetes taurinus* strongly differ from non-grazing species along the first axis while *Ourebia ourebi* plots very closely to browsers and mixed feeders. The two former species graze on short or medium height grasses while *O. ourebi* favours tall grass blades. Such differences in feeding behaviours might explain the differences in dental mesowear pattern. This distribution is due to three variables whose inertias and values of Cos^2 indicate their role along this first axis (Appendix B). Actually, [L–B] and [L–R] (44.7 and 13.6% of the inertia, respectively) places the grazing species, especially *C. taurinus* and *A. buselaphus*, at higher values along the first axis (Fig. 2). The role of the third variable [H–S] (32.5% of the inertia) explains why all intermediate feeders and browsers plot in a compact range of values along the first axis (Fig. 2, Appendix B). Along the second axis, [H–R] (39.8% of the inertia) has a positive coordinate whereas [H–S] (34.6% of the variance) has a negative one (Fig. 2, Appendix B). Along the second axis, intermediate feeders and browsers plot very closely, as along the first component (Fig. 2). Grazers tend to have higher values than both intermediate feeders and browsers. This is not true for *C. taurinus* and *A. buselaphus*, which plot within the intermediate feeders and the browsers along the second axis. This is due to the inertia of [L–B] that tends to shift these two species towards negative values (14.1% of the inertia; Fig. 2; Appendix B).

The supplementary variables, percentages of fruits [%F], of dicots [%D] and of monocots [%M], are distributed as follows: [%F] and [%D] have lower coordinates along the first axis than [%M]; the same trend is observed along the second axis (Fig. 2). This is congruent with the correlations investigated between mesowear variables and dietary data (Table 2). In fact, there are two significant correlations between the percentages of dicots [%D] and monocots [%M] on one hand and the frequencies of unsharp cusp(id)s (1-%sharp) on the other hand. The fruit composition is not significantly correlated with the dental mesowear scores, at least with that set of living species not highly involved in frugivory.

Table 2
Significance of the correlations between dental mesowear pattern and dicot, monocot and fruit components (expressed as percentage) in the annual diet of the living African bovids according to the Gagnon and Chew (2000) synthesis. Here the dental mesowear variable [1-%sharp] (Appendix B) is computed following Mihlbachler and Solounias (2006).

	m	s.d.	r	r^2	t	α
1-%sharp	71.77	23.73				
% Fruits	5.40	7.73	−0.226	0.051	−0.837	0.418
% Dicotyledonous	36.93	31.07	−0.892	0.796	−7.127	<0.005
% Monocotyledonous	57.33	34.67	0.853	0.728	5.903	<0.005

m: mean; s.d.: standard deviation; r and r^2: index of correlation and determination, respectively; t: test of Student.

3.2. Fossil species

The dental sample of fossil antilopines is over-dominated by lower second molars. Those mandible cheek teeth have a mesowear score that places them amongst grazing species along the first axis. The only upper molar plots close to *Kobus ellipsiprymnus*.

With both upper molars and mixed upper/lower molar samples, fossil bovines plot close to *Connochaetes taurinus* and *Alcelaphus buselaphus*, two present-day Alcelaphini that are highly involved in grazing (Gagnon and Chew, 2000). The only lower cheek tooth does not plot with those extant alcelaphines, but with other extant grazers.

Considering only the upper second molars, the Reduncini from TM plot with intermediate feeders and browsers. However, there are only four specimens. Including the lower dentition in the analysis, the mesowear scoring of the Reduncini shifts towards a grazing pattern.

The three samples of hippotragines from TM (including the upper second molars, the lowers, and the combination of the two) all plot between the two present-day hippotragines, *Hippotragus equinus* and *Hippotragus niger*. These species are both highly involved in grazing (Gagnon and Chew, 2000). The Hippotragini sample is large enough to estimate a possible shift towards more worn teeth due to the dominance of lower second molars, as suggested by Franz-Odendaal and Kaiser (2003). Sixteen percent of the lower molars have a low occlusal relief compared to 15% for the upper ones (Table 1). In addition, 90% of the upper molars and 94% of the lower ones do not have a sharp cusp. There is thus no evidence of such a shift due to the dominance of lower molars in that extinct Hippotragini sample.

4. Discussion

4.1. Diet and mesowear analyses

The correlation between dietary composition synthesized by Gagnon and Chew (2000) and the dental mesowear signal scored by Fortelius and Solounias (2000) (Table 2) is consistent with the hypotheses proposed by previous authors (Fortelius and Solounias, 2000; Schubert, 2006; Merceron et al., 2007a,b; Rivals et al., 2007). Indeed, the physical properties of food considerably affect the global wear of dentition. Browsing implies less intensive dental wear than grazing. Indeed, the consumption of grass and grass-like plants (*i.e.* sedges and rushes) implies intensive scratching and is therefore

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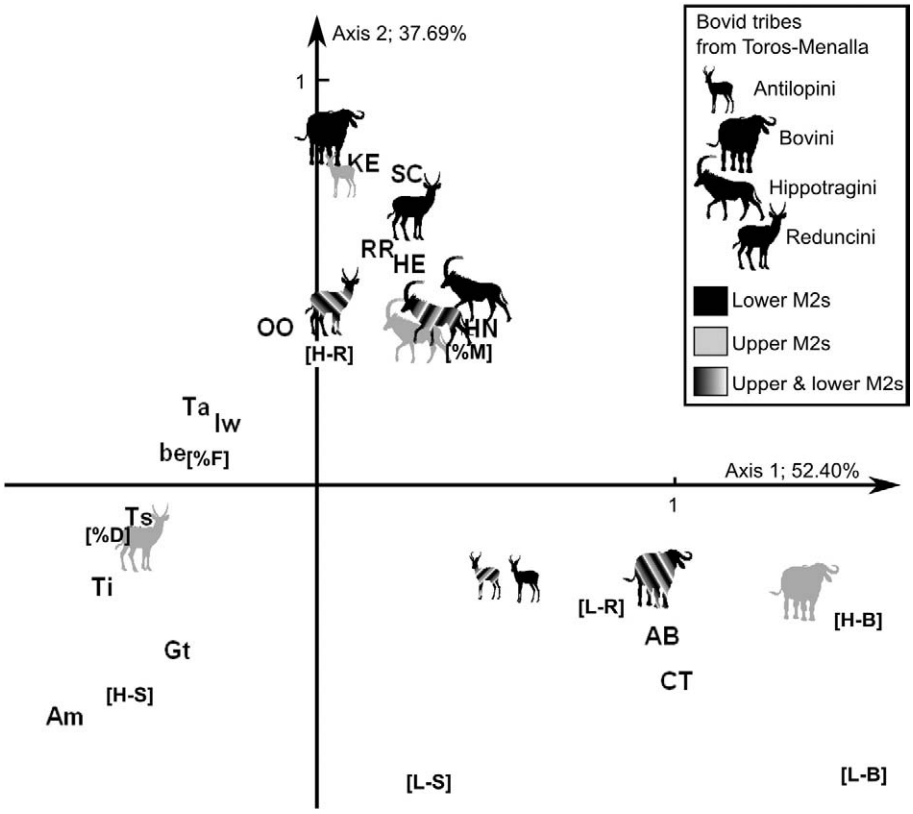

Fig. 2. Correspondence Factorial Analysis. The coordinates of extant grazers are symbolized by upper case letters, coordinates of extant browsers by lower case letters and coordinates of intermediate feeders by upper and lower case letters (see abbreviations in Table 1). The coordinates of fossil tribes from the second lower molars are represented by black silhouettes, the second upper molars by gray ones whereas the mixed gray and black silhouettes symbolize samples clustering upper and lower molars. The coordinates of variables are symbolized as follows: low relief with sharp [L–S], round [L–R] or blunt cusp(id)s [L–B] and high relief with sharp [H–S], round [H–R] or blunt cusp(id)s [H–B]. The supplementary variables are percentage of fruits [%F], dicots [%D] and monocots [%M]. Abbreviations: *Alcelaphus buselaphus* (AB), *Antidorcas marsupialis* (Am), *Boocerus eurycerus* (be), *Connochaetes taurinus* (CT), *Gazella thomsonii* (Gt), *Hippotragus equinus* (HE), *Hippotragus niger* (HN), *Kobus ellipsiprymnus* (KE), *Litocranius walleri* (lw), *Ourebia ourebi* (OO), *Redunca redunca* (RR), *Syncerus caffer* (SC), *Tragelaphus angasi* (Ta), *Tragelaphus imberbis* (Ti), *Tragelaphus scriptus* (Ts).

responsible for global dental wear. The differences in terms of silica concentration in cell walls (the monocotyledons having many more silica phytoliths) (e.g. Twiss et al., 1969; Mac Naughton et al., 1985; Carnelli et al., 2004) result in this dichotomy between the dental wear signatures of grazers *sensu lato* and browsers *sensu lato* (Solounias and Semprebon, 2002; Merceron et al., 2007a,b). A significant amount of dust deposits on leaves may also contribute to some degree to the global wear of the dentition (Ungar et al., 1995).

4.2. Feeding preferences of bovids from TM

4.2.1. Antilopini

The mesowear data indicate that the specimens of *Gazella* sp. from Toros-Menalla might have been more involved in grazing than in browsing. However, the possible shift towards a grazing pole due to the over-dominance of lower second molars in the sample should be considered. Present-day antilopines such as the nine species of African gazelles have a range of feeding preferences. For instance, *Gazella dorcas* is an intermediate feeder whereas *Gazella thomsonii* is described as a variable grazer (Gagnon and Chew, 2000). Such variable grazing habits for this latter gazelle are mirrored by its carbon isotopic signature ($\delta^{13}C = -3.7‰$, Cerling et al., 2003). Other modern antilopines from South and East Africa produce values of about −9.2‰ (±1.5‰) (Sponheimer et al., 2003). This undoubtedly reflects the mixed feeding habits with an emphasis on browsing for modern gazelles (Kingston and Harrison, 2007). Indeed, they have specialized dietary adaptations to drought by favouring browsing on dicot leaves that are rich in water rather than on dry grasses (Estes, 1991; Kingdon, 1997). Previous molar microwear and mesowear analyses (Merceron and Ungar, 2005; Schubert, 2006; Schubert et al., 2006; Ungar et al., 2007) and isotopic data (Lee-Thorp et al., 1989; Sponheimer and Lee-Thorp, 1999; Van der Merwe et al., 2003; Luyt and Lee-Thorp, 2003; Kingston and Harrison, 2007) also support the wide spectrum of feeding preferences ranging from browsing to grazing for Plio-Pleistocene African gazelles. Carbon isotope analyses on TM 266 *Gazella* gave a $\delta^{13}C$ mean value of −6.99‰ (±1.2, for $n = 7$) and therefore indicate a C3–C4 mixed diet, possibly including C3 and/or C4 grazing and C3 browsing (Jacques, 2007). The dental mesowear of the Chadian gazelles provides a relevant grazing signal for the Chadian late Miocene gazelles. However, as Franz-Odendaal and Kaiser (2003) suggested, this grazing signal might be over-evaluated due to the over-dominance of lower dentition; a bias which would be more frequent for mixed feeding ruminants than for browsing and grazing ungulates.

4.2.2. Bovini

The present mesowear analysis suggests that the single bovine species from Toros-Menalla was most likely a grazer. Today, living wild African bovines are limited to a single species, *Syncerus caffer*. This large bovine is water-dependent and is known as a grazer, even in forested areas (Sinclair, 1977; Blake, 2002). Although the proximity with *Alcelaphus buselaphus* and *Connochaetes taurinus* would imply definitive judgments about feeding habits for the fossil bovine, the small sample size for this fossil bovine prevents us from reaching such hasty conclusions. Based on a large range of $\delta^{13}C$ values (from −5.4 to 0.3‰), Pliocene bovini from Chad (Kossom Bougoudi and Koro Toro, Brunet and MPFT, 2000; Fara et al., 2005) are recognized either as being grazers from humid habitats or occasionally browsing grazers (Zazzo et al., 2000). The only analysed bovine specimen from TM 266 suggests a diet dominated by C4 metabolic

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pathway grasses ($\delta^{13}C = -3.36‰$). Indeed, this supports our results (Jacques, 2007). Based on dental microwear analyses, *Simatherium demissum* from Langebaanweg (Lower Pliocene of South Africa), a bovine related to the late Miocene Chadian form is depicted either as a grazer (Merceron and Ungar, 2005) or as a mixed feeder (Ungar et al., 2007). Although the mesowear analyses for Bovini from Aramis (Pliocene, Ethiopia) are unreliable due to the very low sample size, carbon isotope analyses ($\delta^{13}C = -0.66‰$) indicate that this Pliocene Ethiopian bovine was a grazer (White et al., 2009).

4.2.3. Hippotragini

The global mesowear signal for the extinct hippotragines (*Tchadotragus sudrei* and *Saheloryx solidus*) both clustered in a single sample, which might be represented by *Tchadotragus sudrei*. This species is very common in the TM mammal assemblages whereas the other species *S. solidus* is considered as common by Le Fur (2009). The dental sample including the two species indicates a feeding preference for grasses. This is consistent with the high crowned molar of these two species (Geraads et al., 2008). Their extant relatives (*Hippotragus niger* and *Hippotragus equinus*) are variable grazers and inhabit environments ranging from desert grasslands to open woodlands (Grobler, 1974; Estes, 1991; Gagnon and Chew, 2000). The $\delta^{13}C$ values for modern hippotragini from East and South Africa support a C4 grassy diet (Sponheimer et al., 2003). Such values were also mentioned for Pliocene hippotragines from Kossom Bougoudi (Chad) (Zazzo et al., 2000) and Aramis (Ethiopia) (White et al., 2009), whereas mixed feeding habits were found for TM 266 hippotragines ($\delta^{13}C = -5.04‰ \pm 2.06$) (Jacques, 2007) and for the Pliocene representatives from Laetoli (Tanzania) and Sterkfontein (South Africa) (Luyt and Lee-Thorp, 2003; Kingston and Harrison, 2007).

4.2.4. Reduncini

The mesowear pattern for this tribe is unclear since the upper molars do not give a signal similar to that of the lower dentition, and in addition the sample size for the upper cheek teeth is reduced. When combined, the upper and lower dentitions indicate grazing habits whereas the upper molars only mirror either intermediate or browsing preferences. Several factors may explain such differences. First of all, the low number of upper molars may not reflect the total range of mesowear patterns. Second, the presence of two species with different feeding habits but clustered in a single sample may result in such a difference. Finally, the dominance of lower molars in the investigated sample may have shifted the signal towards the grazing pole. Such a difference between the upper and lower dentition was detected by Franz-Odendaal and Kaiser (2003) in a population of intermediate feeder bovids. However, such a pattern is not seen for the extinct hippotragines from TM. Assuming that the lower dentition might provide a mesowear signal that is shifted towards grazing, we may assume that the fossil Reduncini might not have been obligate grazers, but variable grazers or even intermediate feeders. Pure browsing habits for the Reduncini from TM are rejected here. In fact, Franz-Odendaal and Kaiser (2003) stated that such differences in mesowear signals between the upper and lower dentition are not apparent in extant browsers, but are visible in intermediate feeders. As a whole, the Reduncini from Toros-Menalla differed slightly from the living reduncine *Kobus ellipsiprymnus*, a fresh grass grazer, by having more sharp and blunt cusp(id)s (Estes, 1991; Gagnon and Chew, 2000). Such differences in comparison with the fresh grass grazer *K. ellipsiprymnus* were also mentioned for *Redunca darti* from Makapansgat (Pliocene of South Africa) by Schubert et al. (2006). However, most of the extinct Reduncini are believed to be grazers. Microwear data for *Kobus* (or *Redunca* according to Vrba and Haile-Selassie, 2006) *subdolus* from Langebaanweg suggest that this bovid was engaged in grazing (Merceron and Ungar, 2005). Such conclusions were also reached for a late Miocene reduncine *Dorcadoxa porrecticornis* from Central Asia (Merceron et al., 2004). Isotope analyses also indicate that Pliocene reduncines from Chad grazed and favoured open landscapes (Zazzo et al., 2000) whereas the specimens from the late Miocene hominid TM 266 locality have $\delta^{13}C$ values suggesting a mixed diet dominated by C4 plants (Jacques, 2007).

5. Conclusions

While wide-open environments have hitherto been considered to preclude the acquisition of a bipedal posture, the faunal and floristic assemblages associated with early hominids in East Africa indicate that bipedalism may have arisen in wooded environments (WoldeGabriel et al., 2001; Senut, 2006). Recently, the reconstruction of the Aramis (Pliocene, Ethiopia) biotope in which *Ardipithecus ramidus* lived suggested the presence of grassy woodlands and patches of true forest (White et al., 2009).

Faunal indicators such as proboscideans, giraffids and colobines in Toros-Menalla, the presence of many water-dependent vertebrates (Vignaud et al., 2002; Lihoreau, 2003; Boisserie et al., 2005; Louchart et al., 2005; Otero et al., 2006) and the analysis of the ecological and taxonomic structure of the TM large mammal assemblage (Le Fur et al., 2009; Le Fur, 2009) indicate a dominance of shrub/bushland and grassy woodlands in the surroundings of the Chadian lake basin. Indeed, our data support the availability of grass or grass-like plants and therefore open patches in the vicinity of the Chadian palaeo-lake shores.

The presence of hippotragines, reduncines, bovines, and antilopines at TM 266 and in other contemporaneous localities, all of them consuming grasses, indicates the presence of a wealthy herbaceous vegetal layer. Such an abundance of bovids grazing at least seasonally excludes dense forests as the habitat for these species. Body size, seasonal displacement and the exploitation of various habitats (wooded savannah, edge forests, drier grasslands, wet areas…) in a single region may have driven the niche partitioning between these extinct grazers. Bell (1971) pointed out such co-habitation among extant grazers in the Serengeti Park. Depending on precipitation and the length of the grasses, ungulates alternate their exploitation of grasslands, especially migrating species such as zebras (*Equus burchelli*), wildebeests (*Connochaetes taurinus*), and Thomson's gazelles (*Gazella thomsonii*). Other taxa such as African buffaloes *Syncerus caffer* keep foraging close to water whereas hartebeests *Alcelaphus buselaphus*, the least migratory and nomadic member of the Alcelaphini, are more flexible in terms of their feeding preferences (Estes, 1991). Such a co-habitation in recent ecosystems validates the co-occurrence of species belonging to four tribes of Bovidae at TM, all consuming grasses. Our results are confirmed by the analysis of the distribution of TM large mammal species, which indicate a high proportion of grazer species; this category represents 35% of all species in the TM 266 assemblage (Le Fur et al., 2009).

The ecological structure of TM bovids differs from that of the Aramis representatives. First, tragelaphines dominate at Aramis whereas they are lacking at TM, and in contrast rare hippotragines and reduncines at Aramis dominate the TM bovid assemblage. Secondly, the dental mesowear analyses and the enamel isotopic composition of Aramis bovids indicate that they were closer to browsers and mixed feeders than grazers. Finally, the bovid astragali functional morphology method predicts that these bovids inhabited a forest (White et al., 2009). Our data based on dental mesowear and the study of the TM 266 mammal assemblage associated with *Sahelanthropus tchadensis* (Le Fur et al., 2009) indicate a more open environment than that of the Early Pliocene of Ethiopia. It appears that the Late Miocene and Early Pliocene habitats associated with early hominids were much more diverse than previously thought. It is thus clear to us that an improvement in ecomorphological postcranial methods with a refined database of extant African and Asian bovids will improve our interpretation of the paleoenvironmental context of the earliest African hominid.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2010.03.042.

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