General palaeontology (Palaeoecology)

Feeding behavior and ecology of the Late Oligocene Moschidae (Mammalia, Ruminantia) from La Milloque (France): Evidence from dental microwear analysis

Comportement alimentaire et écologie des Moschidae de la Milloque (Oligocène supérieur, France) : apport de l'analyse des micro-usures dentaires

Alice Novello [a,b,*], Cécile Blondel [a], Michel Brunet [a,c]

[a] *IPHEP, CNRS UMR 6046, université de Poitiers, 40, avenue du Recteur-Pineau, 86022 Poitiers cedex, France*
[b] *CEREGE, CNRS UMR 6635, Europôle méditerranéen de l'Arbois, avenue Louis-Philibert, BP 80, 13545 Aix-en-Provence cedex 4, France*
[c] *Collège de France, Chaire de Paléontologie humaine, 11, place Marcelin-Berthelot, 75232 Paris cedex 05, France*

ABSTRACT

The site of La Milloque (Aquitaine Basin, south-western France), dated to the end of the Late Oligocene (MP29 reference level), has yielded an important fauna of mammals since its discovery in 1868. Notably, three different size species of Moschidae (Ruminantia) were identified at this locality: *Dremotherium quercyi*, *Dremotherium guthi* and *Bedenomeryx milloquensis*. Dental microwear analysis was used to determine their respective feeding preferences in comparison to various extant ungulates. The smallest one, *D. quercyi*, was close to leaf browsing extant species and to the mixed-feeding species *Tragelaphus scriptus*, and so fed mainly on leaves. The largest species *D. quercyi* and *B. milloquensis* showed affinities with grazing extant species, and so consumed grasses. Thus they constitute the oldest brachydont grazing ruminants analysed up until now. The results, in agreement with previous studies, imply the existence of a mixed environment at La Milloque, ranging from light forest to more open areas constituted of grasses.

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RÉSUMÉ

Le gisement de La Milloque (Bassin aquitain, Sud-Ouest de la France), daté de la fin de l'Oligocène supérieur (niveau repère MP29), est connu pour avoir livré une faune importante de mammifères depuis sa découverte en 1868. Notamment, trois espèces de Moschidae (Ruminantia) de tailles différentes y ont été identifiées: *Dremotherium quercyi*, *Dremotherium guthi* et *Bedenomeryx milloquensis*. L'analyse des micro-usures dentaires a été utilisée pour déterminer leurs préférences alimentaires respectives, par comparaison avec différentes espèces d'ongulés actuels. La plus petite espèce, *D. quercyi*, était proche des actuels brouteurs et du mangeur mixte *Tragelaphus scriptus*, et donc se nourrissait de feuilles. *D. guthi* et *B. milloquensis*, espèces de plus grande taille, montrent des affinités avec les paisseurs actuels, et donc consommaient des graminées. Par conséquent, ce sont les plus

anciennes espèces de ruminants brachyodontes consommatrices de graminées, analysées à ce jour. Ces résultats, en association avec de précédentes études, impliquent l'existence d'un environnement mixte à La Milloque, s'étendant de la forêt claire à des zones plus ouvertes constituées de graminées.

1. Introduction

The site of La Milloque (Aquitaine Basin, south-western France) is characterized by a set of molasses deposits called 'Molasses de l'Agenais', which underlie the Lower Miocene white limestone called 'Calcaire blanc de l'Agenais'. These deposits, since their discovery by Landesque in 1868, have yielded important fossil vertebrate fauna. The major part of this material was collected in the second half of the nineteenth century (Brunet, 1979; Richard, 1948). The site corresponds to the MP29 reference level of the mammal scale of western Europe and is dated close to 24 Ma (Aguilar et al., 1997). The largest part of the collected material has already been described in several publications (Brunet, 1979; Cirot and Wolsan, 1995; Jehenne, 1985). In particular, three different species of ruminants belonging to the family of Moschidae were discovered: *Dremotherium guthi*, *Dremotherium quercyi* and *Bedenomeryx milloquensis* (Gentry et al., 1999; Jehenne, 1985, 1988).

The Moschidae, small hornless pecorans, consist of only one living genus today, *Moschus*, with five species (Novak, 1999). The preferred habitat of these of Asian musk deer is forests and brushlands in high altitudes. They are browsers with a diet consisting of a variety of vegetation, such as mosses, buds, young shoots, leaves, lichens and occasionally grasses. The moschids have an extensive fossil record with an Oligocene-Miocene radiation in Eurasia and a Miocene radiation in North America. The oldest documented representative of this family is *Dremotherium*. This genus appears at the beginning of the Late Oligocene (Blondel, 1997). *D. guthi* and *D. quercyi* appear at the MP28 reference level and survived until the MP30 level at the end of the Late Oligocene (Jehenne and Brunet, 1992). The genus *Bedenomeryx* appeared at La Milloque (MP 29) with the species *B. milloquensis* known to the MP 30 level. *Dremotherium* and *Bedenomeryx*, as for most of the European genera of moschids, did not reach the Middle Miocene.

The three moschids from La Milloque possess brachydont molars and so would be interpreted as browsers. According to this hypothesis, these species would have competed for the same general resources. The dental, cranial and postcranial skeletal anatomy indicates that *D. quercyi* was smaller than *D. guthi*, and *B. milloquensis* was the largest of the three species. This difference in body size suggests the existence of different feeding behaviours, which would then suggest that these species were able to coexist by occupying different ecological niches (Eisenberg, 1981; Pérez-Barberia and Gordon, 2001). Furthermore, the presence of these three ruminants at La Milloque at the end of the Late Oligocene in association with other herbivorous mammals such as cainotheriids, anthracotheriids and rhinocerotids (Brunet, 1979; Richard, 1948) could mean that rather favourable climatic conditions existed for developing new feeding strategies and ecological niches. Indeed, it is known that after a climatic cooling in the Lower Oligocene, a trend of warming appears to have begun in the Upper Oligocene and then continued until the climatic optimum of the mid-Miocene (Zachos et al., 2001). In particular, in southern France, several studies give evidence of warmer and wetter closed environments at the end of the Oligocene, in spite of the persistent, dry open areas (Blondel, 1998; Brunet, 1979; Comte, 2000; Costeur, 2005; Costeur and Legendre, 2008; Legendre, 1987; Vianey-Liaud, 1991).

The present work aimed to analyse the dental microwear patterns of the three ruminants of La Milloque in order to: (1) determine their dietary habits; and (2) estimate their ecological niches. Indeed, dental microwear analysis constitutes valuable method for the reconstruction of past environments. Moreover, this method is already well known through numerous studies on ungulates (Merceron et al., 2004a; Solounias et al., 2000). Microwears are directly linked to the ingested food, which, thanks to its physical properties, marks the enamel surface to differing degrees during the chewing cycle. Microwears result from the abrasion of teeth on items consumed during the last few meals. Their description and quantification allow very different dietary profiles to be determined: the browsers (exclusively consume leaves or fruits/leaves), the grazers (consumers of grasses), the mixed-feeders (graze or browse according to the environmental conditions) and the generalists.

2. Material

Dental specimens selected for this study had been inventoried by Jehenne (1985) and housed in the CVCU of Poitiers (Centre de Valorisation des Collections Universitaires). Eighteen specimens belonging to *D. guthi* and sixteen to *D. quercyi* were used for analyses. Only four specimens of *B. milloquensis* were included in this study due to the lack of available material. The material chosen included both lower molars (M2), directly selected on mandibles, and isolated upper molars (M1, M2 and M3) (Appendix A). The microwear signature is not significantly different between lower and upper molars, even if the positions of these last could not be determined (Teaford and Walker, 1984). The microwears were analysed on the lingual blade of the paracone and on the buccal blade of the protoconid (Merceron et al., 2005). In cases where these facets were not preserved, their analogous facets were chosen on the metacone or hypoconid.

3. Methods

The protocol established by Merceron et al. (2004b) was applied for the casting procedures and quantification of the microwear patterns on the enamel surfaces. The dental facets were digitized using a Leica DC 300 digital microscope camera and the image acquisition software Leica IM50 connected to a light stereomicroscope (Leica MZ125) at low magnification (×30). The dental microwear was quantified in a 0.09 mm^2 area using Optimas v. 6.2. image analysis software (Media Cybernetics®).

Microwear scars are defined as pits or scratches as follows: pits are circular to sub-circular scars in enamel whereas scratches correspond to lengthened straight scars with parallel edges. A scratch has a ratio between its minor and major axes lower than ¼, whereas a pit has a higher ratio (Grine, 1986).

Microwear quantification was made by a single observer (AN). The number of scratches (N_s) and the number of pits (N_p) were counted. The total number of microwear scars ($N_{tot} = N_s + N_p$) and the percentage of pits ($\%p = N_p/N_{tot \times 100}$) were calculated for each species.

The results obtained were compared with those acquired by Merceron et al. (2004a, 2004b, 2005) for 25 extant ungulate species with known varied diets extracted from the 'UNGULATES' database. These species are classified under five different feeding preferences, each reflected by a particular microwear pattern: leaf browsers, fruit/leaf browsers, grazers, mixed-feeders and generalists (Table 1).

Statistical analyses were undertaken to test whether the observed intergroup differences of microwear patterns were significant or not. All variables were rank transformed to ensure normality and homoscedasticity. Univariate analyses of variance (ANOVA) were applied to test the significance of the observed differences between samples

Table 1
Summary statistics (mean [M] and standard error [sem]) of dental microwear variables for extant species from the "UNGULATES" database and for extinct species.
Tableau 1
Résumé statistique (moyenne [M] et erreur standard [sem]) des variables de micro-usures pour les espèces actuelles de la base de données « UNGULATES » et les espèces fossiles.

	n	N_s		N_p		$\%p$		N_{tot}	
		M	sem	M	sem	M	sem	M	sem
Browsers	**242**	**20.5**	**0.4**	**34.7**	**0.9**	**61.3**	**0.8**	**52.2**	**1.1**
Leaf browsers	**50**	**15.6**	**0.6**	**33.4**	**2.4**	**65.7**	**1.7**	**49.0**	**2.5**
Litocranius walleri	16	15.1	0.6	34.5	4.9	66.5	2.3	49.6	5.0
Diceros bicornis	10	17.7	1.9	39.5	6.0	66.0	4.8	57.2	6.5
Giraffa camelopardalis	16	15.1	1.3	29.3	3.7	64.0	3.4	44.4	3.8
Tragelaphus strepsiceros	8	14.9	1.5	31.9	4.5	66.6	3.9	46.8	4.8
Fruit/leaf browsers	**192**	**21.8**	**0.5**	**35.0**	**1.0**	**60.6**	**0.8**	**56.8**	**1.1**
Muntiacus muntjak	8	28.0	2.7	51.1	3.9	64.4	3.5	79.1	3.7
Capreolus capreolus	128	21.8	0.6	32.6	1.1	58.8	0.9	54.4	1.3
Odocoileus virginianus	11	19.9	1.8	31.1	3.3	60.1	4.0	51.0	3.4
Tapirus sp.**	7	19.9	2.4	42.4	6.3	66.4	5.5	62.3	6.3
Sylvicapra grimmia	24	20.9	1.2	39.1	3.1	63.5	2.4	60.1	3.0
Cephalophus sp.*	14	25.4	1.5	42.7	5.0	63.5	3.1	62.9	5.7
Grazers	**153**	**24.9**	**0.4**	**15.1**	**0.7**	**35.6**	**1.0**	**40.0**	**0.9**
Alcelaphus bucelaphus	28	26.0	0.8	16.3	1.4	37.2	1.7	42.4	1.8
Damaliscus lunatus	14	22.6	1.4	12.7	1.9	33.7	2.6	35.4	3.1
Hippotragus niger	13	27.7	1.1	14.2	2.0	32.3	2.9	41.9	2.7
Kobus kob	26	26.3	0.9	16.9	1.5	37.4	2.3	43.2	1.9
Ourebia ourebi	18	22.7	1.1	20.8	3.1	44.2	4.1	43.6	3.0
Syncerus cafer	24	24.6	1.5	13.3	1.3	33.8	1.9	37.8	2.4
Equus burchelli	24	22.7	1.0	12.0	1.6	32.1	2.5	34.8	2.1
Equus przewalskii	6	29.8	1.5	11.7	2.1	27.2	2.7	41.5	3.3
Mixed-feeders	**37**	**21.6**	**1.2**	**23.2**	**1.9**	**50.5**	**2.1**	**44.8**	**2.5**
Aepyceros melampus	19	24.9	1.4	22.1	2.8	45.2	2.9	46.9	3.3
Tragelaphus scriptus	18	18.2	1.6	24.3	2.7	56.2	2.6	42.5	3.7
Generalists	**102**	**26.4**	**0.9**	**40.7**	**2.0**	**57.9**	**1.7**	**67.1**	**1.9**
Cervus elaphus	47	26.4	0.9	36.9	2.1	56.7	1.7	63.3	2.3
Ovibos moschatus	8	23.8	3.8	47.3	7.3	65.2	6.2	77.9	6.5
Ovis ammon	9	27.0	3.7	50.9	11.6	58.3	9.1	71.0	8.8
Rangifer tarandus	17	24.4	2.8	55.8	4.2	69.4	3.2	80.2	4.5
Rupicapra sp.***	21	28.9	1.9	30.2	3.9	47.9	4.1	59.1	3.6
Fossil species									
D. guthi	**18**	**22.8**	**1.2**	**17.2**	**1.3**	**42.3**	**1.5**	**40.0**	**2.3**
D. quercyi	**16**	**17.6**	**0.9**	**22.9**	**1.8**	**56.1**	**1.5**	**40.5**	**2.5**
B. milloquensis	**4**	**18.5**	**1.7**	**11.0**	**0.9**	**37.4**	**1.5**	**29.5**	**2.4**

N_s: number of scratches; N_p: number of pits; $\%p$: percentage of pits; N_{tot}: total number of microwear features ($N_s + N_p$).
* *C. callipygus* ($n = 2$), *C. dorsalis* ($n = 1$), *C. leucogaster* ($n = 3$), *C. sylvicultor* ($n = 8$); ** *T. bairdi* ($n = 2$), *T. terrestris* ($n = 5$); *** *R. pyrenaica* ($n = 16$), *R. rupicapra* ($n = 5$).

Table 2
ANOVAs with ranked data.
Tableau 2
ANOVA avec données ordonnées.

ANOVAs		df	SS	MS	F	p
N_s	Effect	6	2,233,690	372,282	15.7773	< 0.001
	Error	565	13,331,748	23,596		
N_p	Effect	6	6,542,740	1,090,457	68.1187	< 0.001
	Error	565	9,044,623	16,008		
%p	Effect	6	8,780,262	1,135,813	73.0883	< 0.001
	Error	565	15,595,142	15,540		

Variables are as follows: N_s: number of scratches; N_p: number of pits; %p: percentage of pits; df: degrees of freedom; SS: sum of squares; MS: mean squares; F: ratio of MS for the considered/MS of the Residual (Error).

Table 3
Results on pairwise comparisons of extinct and extant species according to their diet categories. Significance at $\alpha < 0.05$ indicated in normal font for Fisher's LSD tests in bold for both Tukey's HSD and Fisher's LSD tests.
Tableau 3
Résultats des comparaisons entre espèces fossiles et espèces actuelles, d'après leurs catégories alimentaires. Significativité à $\alpha < 0,05$ indiquée en caractères normaux pour le test LSD de Fisher, en caractères gras pour le test LSD de Fisher et le test HSD de Tukey.

	Browsers	Grazers	Mixed-feeders	Generalists	*D. guthi*	*D. quercyi*
Grazers	**N_s N_p %p**					
Mixed-feeders	**N_p %p**	**N_s N_p %p**				
Generalists	**N_s** %p	**N_p %p**	**N_s N_p %p**			
D. guthi	N_p %p		%p	N_p %p		
D. quercyi	**N_p**	N_s N_p **%p**	N_s	**N_s N_p**	N_s **%p**	
B. milloquensis	N_p **%p**	N_s	N_p %p	N_s **N_p %p**		N_p **%p**

N_s: number of scratches; N_p: number of pits; %p: percentage of pits.
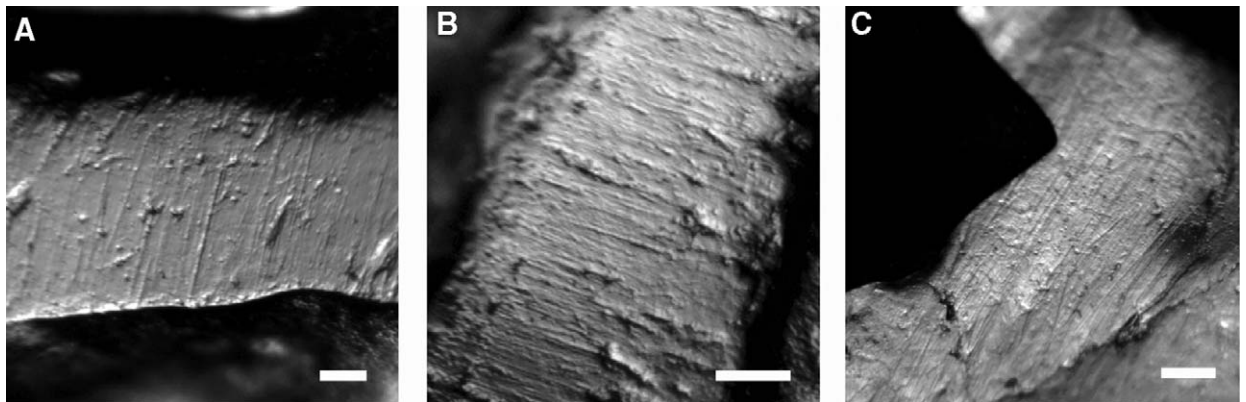
Fig. 1. Digitized photographs of the molar shearing facets from La Milloque ruminants. A. *Dremotherium quercyi*, LM1968-MA33. B. *Dremotherium guthi*, LM1968-MA64. C. *Bedenomeryx milloquensis*, LM1966-MA3. Scale bar = 100 μm.
Fig. 1. Photographies numériques des facettes coupantes des secondes molaires des ruminants de La Milloque. A. *Dremotherium quercyi*, LM1968-MA33. B. *Dremotherium guthi*, LM1968-MA64. C. *Bedenomeryx milloquensis*, LM1966-MA3. Barre d'échelle = 100 μm.

(Table 2). The combination of two pairwise tests (Fisher's least significant difference and Tukey's honestly significant difference) determined the sources of significant variation for each dental facet (Conover and Iman, 1981; Sokal and Rohlf, 1998) (Table 3).

4. Results

The majority of scratches observed on the enamel surface of fossil ruminants are very fine (Fig. 1). However, the microwear pattern observed on *D. quercyi* teeth tended to be qualitatively coarser than that observed for *D. guthi*, with the presence of wider scratches and more marked pits.

D. quercyi had a pit percentage (%p) of 56.1% whereas *D. guthi* possessed one of 42.3% (Table 1; Fig. 2). Furthermore, *D. quercyi* had a lower number of scratches (N_s) than that obtained for *D. guthi*. These observed differences were statistically significant (Tables 2 and 3) and decisive for the assignation of each *Dremotherium* species to a particular diet.

D. guthi possessed mean N_s, N_p and %p values which were not significantly different from those observed for the grazers. This result is clearly illustrated in Fig. 3, where *D. guthi* can be seen to fall within the range of grazing species (Table 1). In contrast, *D. quercyi* was statistically closer to both browsers and mixed-feeders (Table 3). This result is also well illustrated in Fig. 3, where *D. quercyi* is
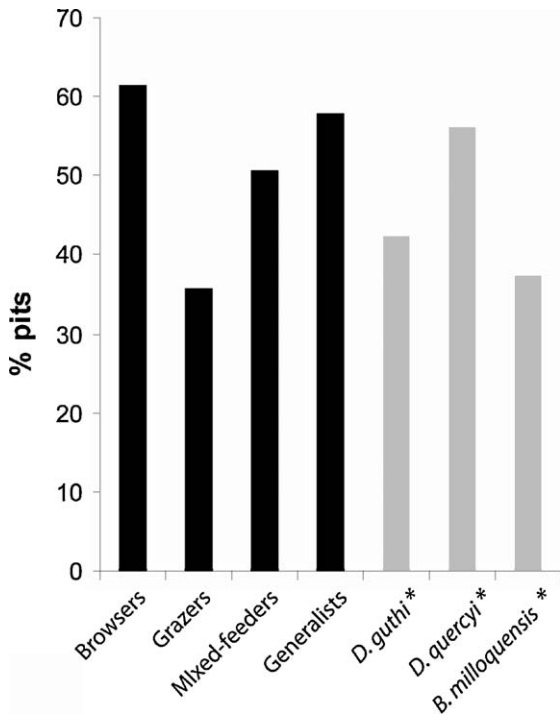
Fig. 2. Mean values of pit percentage (%*p*) for the extant ungulates (black) categorized following their feeding styles and extinct species from La Milloque (grey*).

Fig. 2. Valeurs moyennes du pourcentage de ponctuations (%*p*) chez les Ongulés actuels (noir), suivant leur préférence alimentaire et chez les espèces fossiles de La Milloque (gris*).

clearly comparable with the mixed-feeders in addition to possessing a mean N_s value which falls within the range of browsers.

Despite the small sample size, *B. milloquensis* presents a N_p (11.0) much lower than those obtained for the two

other fossil species and a %*p* sharply lower than 50% (37.4%) (Table 1). Even if this species was graphically outside of the distribution of dietary categories (Fig. 3), it was close to the grazers in having very low N_p and %*p* values which were not significantly different from those of the grazing extant species (Table 3).

5. Discussion

All of the analyses indicated that both *Dremotherium* species had different feeding preferences. From the variables tested, *D. quercyi* presented important similarities with the extant browsers and mixed-feeders. In particular, it is very close to the extant mixed-feeder *Tragelaphus scriptus* (Fig. 3). This species adopts different feeding strategies during the year. In the wet season, it preferentially feeds on young items of grasses and non-graminoid herbaceous plants, and throughout rest of the year it principally consumes dicotyledon leaves (about 80%). Thus, it is not surprising that its microwear profile is very close to the extant browsers and some studies classify *T. scriptus* in this category (Gagnon and Chew, 2000). Nevertheless, *D. quercyi* also possessed a high number of large pits probably reflecting its occasional consumption of fruits such as *Acacia* pods (Jacobsen, 1974). Considering these facts, we assumed that *D. quercyi* principally consumed leaves and also occasionally consumed some fruits such as pods, thus explaining its more marked pits and wide scratches.

The results indicated that *D. guthi* was very close to extant grazers such as the topi, ourebi and zebra, indicating that it had to have consumed grasses (Gagnon and Chew, 2000). Nevertheless, *D. guthi* possessed very fine scratches compared to these extant species which would indicate a consumption of C₃ grasses (Merceron et al., 2004a, 2005; Solounias and Semprebon, 2002). Indeed, such fine
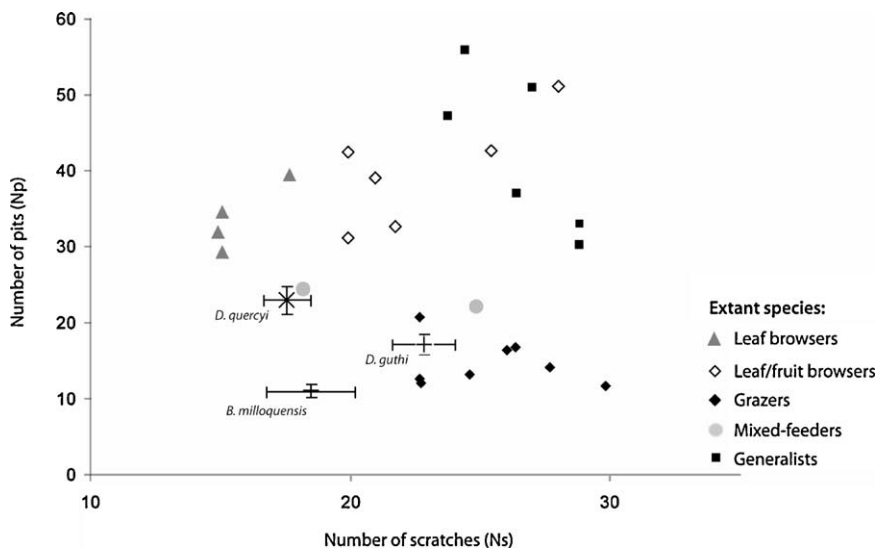
Fig. 3. Bivariate plot of the average number of pits versus average number of scratches for the extant ungulates categorized following their feeding styles and the ruminants from La Milloque. Standard deviations of mean Ns and Np are shown for each fossil species.

Fig. 3. Représentation graphique bivariée du nombre moyen de ponctuations par rapport au nombre moyen de stries chez les Ongulés actuels, suivant leur préférence alimentaire et les ruminants de La Milloque. Les erreurs standard des Ns et Np moyens sont présentés pour chacune des espèces fossiles.

scratches are clearly observable in an extant species of Equidae, *Equus przewalskii*, which exclusively consumes C_3 grasses. On the contrary, the microwear pattern was different from those observed in extant species which only feed on C_4 grasses, such as the zebra *Equus burchelli*.

To a lesser degree, *B. milloquensis* also displayed similarities with grazers. However, this extinct species possessed a very low number of scratches (mean N_s = 18.5) compared to *D. guthi* (mean N_s = 22.8) and all of the extant grazers studied (N_s ranging from 22.6 to 29.8). Consequently, it is possible that *B. milloquensis* had a diet principally composed of grasses, but maybe different to that of *D. guhi*. Nevertheless, this result was only supported by four specimens of *B. milloquensis* and has to be tested with supplementary material.

The existence of grasses at the end of the Oligocene is not surprising since their presence had been already attested in North American deposits dated back to the same period (Strömberg, 2002). Considering that the C_3/C_4 transition took place in the Late Miocene, Cerling et al. (1997) supposed that only C_3 grasses were widespread in Europe at the period studied. This assumption was notably supported by the presence of very fine scratches in the fossil species.

The consumption of grasses by two brachydont ruminants is unexpected. Indeed, the presence of low-crowned cheek teeth in an ungulate is often perceived as a browsing adaptation (Janis, 1990; Janis et al., 2000). Thus, Janis et al. (2002) linked the expansion of grasses to the appearance of hypsodonty in ungulates. High-crowned cheek teeth are considered to be an adaptation to an abrasive diet such as grasses, which are richer in phytoliths than other types of plants. Moreover, the evolution of hypsodonty seems to be closely connected to the diversification of C_4 grasses (richer in phytoliths than C_3 grasses) (Bouchenak-Khelladi et al., 2009; Hodson et al., 2005). To sum up, the hypsodonty/grasses co-evolution credibly became more marked during the Miocene, in spite of the previous establishment of C_3-grasslands during the Oligocene. Therefore, it is likely that brachydont *D. guthi* and *B. milloquensis* were forerunners in grass consumption at the end of the Oligocene. Additionally, it is necessary to keep in mind that the grass type supposedly consumed in our study was the C_3 type, which possessed a less important degree of abrasion than the C_4 type.

This feeding behavior probably enabled the avoidance of more intense interspecific competition during this period and may have been necessary for the survival of these moschids. Moreover, the appearance of a grazing adaptation early in the evolution of ruminants has already been demonstrated in the Early Miocene brachydont Procervidae and some Miocene Giraffidae (DeMiguel et al., 2008; Solounias et al., 1988, 2000).

The diversity of resources consumed by the ruminants of La Milloque justifies their body size differences and so implicates the presence of a relatively heterogeneous environment at the end of Oligocene. The smallest species, *D. quercyi*, had to live in rather closed environments by having a diet mainly composed of leaves. Notably, studies concerning the post-cranial skeleton of this species revealed that it must have been adapted to rather light forests (Blondel, 1998). The presence of rodents such as

Eomyidae, Gliridae, and anthracotheriids such as *Microbunodon minimum* at La Milloque also confirms the existence of close forested areas (Brunet, 1979; Comte, 2000; Lihoreau, 2003; Vianey-Liaud, 1991). *D. guthi* and *B. milloquensis*, whose diet consisted of grasses, probably fed in more open areas. Such environments were notably attested by the presence of the cursorial rhinoceros *Mesaceratherium* aff. *paulhiacense* and the Dipodidae (Brunet et al., 1981; Comte, 2000). Moreover, the La Milloque cenogram shows few large and medium mammals and a high number of small mammals, which characterizes an open and slightly arid environment in this locality (Legendre, 1987).

6. Conclusions

The dental microwear analysis revealed different feeding behavior for the moschids of La Milloque. The smallest species, *D. quercyi*, possessed a dental microwear pattern close to extant leaf browsers, and to the mixed-feeder *T. scriptus*. The largest species, *D. guthi* and *B. milloquensis*, were close to extant grazers. Thus, they constitute the oldest brachyodont ruminants to have included a significant proportion of grass in their diets. Notably, during this period, only C_3 grasses were likely to be widespread. Considering these results, we assert the existence of a mixed-environment at La Milloque, which probably ranged from light forest to more open areas composed of C_3 grasses. This conclusion is in agreement with previous studies. At last, DeMiguel et al. (2010) suggested that dietary specialization on leaves or grass occurred independently in several lineages of ruminants and that mixed feeding may have been the primitive dietary state of this group. In order to check this hypothesis, it would be interesting in future works to take into account the other Oligocene ruminant species and to combine dental microwear and mesowear analyses.

Appendix A. List of fossil material including specimen number, type of tooth and facet position

Fossil species	Tooth	Facet position	Number of specimens
Dremotherium guthi	M_2	Protoconid	LM1966-MA14; LM1966-MA18; LM1966-MA82 LM1966-MA89; LM1966-MA444; LM1968-MA15 LM1968-MA19; LM1968-MA64; LM1968-MA70

Appendix A (*Continued*)

Fossil species	Tooth	Facet position	Number of specimens
		Hypoconid	LM1966-MA10; LM1966-MA66; LM1967-MA1
	M^1 or M^2 or M^3	Paracone	LM1966-MA1041; LM1966-MA1044; LM1966-MA1061
		Metacone	LM1966-MA1215; LM1966-MA1232; LM1969-MA194
Dremotherium quercyi	M_2	Protoconid	LM1966-MA1; LM1966-MA36; LM1966-MA460 LM1968-MA3; LM1968-MA11; LM1968-MA24 LM1968-MA33; LM1969-MA3; LM1969-MA4
		Hypoconid	LM1966-MA80; LM1966-MA456; LM1966-MA458
	M^1 or M^2 or M^3	Paracone	LM1966-MA1176; LM1966-MA1260; LM1966-MA1289
		Metacone	LM1966-MA280
Bedenomeryx milloquensis	M_2	Protoconid	LM1966-MA1; LM1966-MA2; LM1966-MA3; LM1966-MA6

$M^{1,2,3}$ = upper molars; M_2 = lower molar.

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