



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

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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 brachyodont 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 pousseurs actuels, et donc consommaient des graminées. Par conséquent, ce sont les plus

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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.

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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 *Bedomeryx 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 *Bedomeryx* appeared at La Milloque (MP 29) with the species *B. milloquensis* known to the MP 30 level. *Dremotherium* and *Bedomeryx*, as for most of the European genera of moschids, did not reach the Middle Miocene.

The three moschids from La Milloque possess brachyodont 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.

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