Ecological interpretations of early Pleistocene deer (Mammalia, Cervidae) from Ceyssaguet (Haute-Loire, France)

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ABSTRACT

The mesowear method is applied to reveal the type of forage eaten by the late Villafranchian deer of Ceyssaguet (Haute-Loire, France). Further, habitat properties of the paleoenvironment of Ceyssaguet are reconstructed. The most common deer species, *Eucladoceros ctenoides* Nesti, 1841 and *Metacervoceros rhenanus* Dubois, 1904, are interpreted as abrasion-dominated mixed feeders with close to 45% grass in their forage which was similar to that of the south east Asian hog deer and sambar. A third deer species, *Praemegaceros obscurus* Azzaroli, 1953, represented only by three fossil specimens, is interpreted as a more attrition dominated mixed feeder. Combined with mesowear analysis, taphonomical and morpho-functional data allow the reconstruction of the paleoenvironment of Ceyssaguet as an open grassland with wooded habitats near the lake, under cold climate.

KEY WORDS
Mammalia,
Cervidae,
early Pleistocene,
France,
mesowear analysis,
paleodiet reconstruction,
paleoenvironment.

RÉSUMÉ

Interprétations écologiques des cerfs (Mammalia, Cervidae) du Pléistocène inférieur de Ceyssaguet (Haute-Loire, France).

L'étude de l'usure de niveau intermédiaire (« mesowear ») est appliquée ici pour rechercher le type d'alimentation consommée par les cerfs villafranchiens de Ceyssaguet (Haute-Loire, France). Les espèces les plus communes, *Eucladoceros ctenoides* Nesti, 1841 et *Metacervoceros rhenanus* Dubois, 1904, sont interprétées comme brouteuses d'herbe, se nourrissant principalement d'herbes fraîches, comme les cerfs asiatiques tels que le cerf-cochon et le sambar. Une troisième espèce de cerf, *Praemegaceros obscurus* Azzaroli, 1953, qui n'est représentée que par trois spécimens, est interprétée comme brouteur mixte. Combinée à l'analyse de l'usure de niveau intermédiaire, les données taphonomiques et morphofonctionelles permettent de reconstruire le paléoenvironnement de Ceyssaguet comme une prairie ouverte, associée à des habitats forestiers au bord du lac, sous un climat froid.

MOTS CLÉS
Mammalia,
Cervidae,
Pléistocène inférieur,
France,
usure de niveau intermédiaire,
reconstruction du paléorégime,
paléoenvironnement.

INTRODUCTION

THE CEYSSAGUET SITE

The paleoecological reconstruction of the terminal Villafranchian period of Europe is of particular interest as it allows to reveal the dramatic climate shifts on the continent resulting in faunal changes in the Quaternary period. Herbivorous mammals are useful in paleoenvironmental reconstruction and can provide unique information on diet and thus allow reconstruction of elements of the paleoflora and the character of a fossil habitat (e.g., Vrba 1975; Cerling *et al.* 1997; MacFadden & Cerling 1998; Kaiser 2003).

In the present work, the mesowear method (Fortelius & Solounias 2000; Kaiser *et al.* 2000; Kaiser & Solounias 2003) is applied as a tool to reconstruct the paleodiet of herbivorous mammals in order to infer the type of forage available at the late Villafranchian site of Ceyssaguet (Haute-Loire, France) and to infer the paleoenvironment of this site.

The fossil site of Ceyssaguet formed in a lake within a volcano crater (Bonifay 1991, 1995), dated by K/Ar at 1.3 Ma (unpublished data from the Geochronology Laboratory of Clermont-Ferrand; M.-F. Bonifay pers. comm.). This is in agreement with the biochronological age (Bonifay 1991, 1995). The formation of the fossiliferous loess deposits underlied by basalt is estimated to cover 0.1 Ma (M.-F. Bonifay pers. comm.). This results in an age estimate of 1.2 Ma for the Ceyssaguet fauna (Bonifay 1991). The lower fossiliferous stratum yielded the majority of mammalian fossils, many of which are represented by articulated skeletons. This suggests that the fossil remains belong to carcasses that were initially buried in the lake deposits. The upper stratum has yielded isolated and often fragmented bones with traces of predation (Bonifay 1986).

MAMMALS ANALYSED

The Cervidae are the predominant mammal group in the Ceyssaguet mammalian fauna. Among the four recognized deer species (Croitor & Bonifay 2001), the largest number of specimens belongs to a large-sized species, *Eucladoceros ctenoides* Nesti, 1841 (Fig. 1A). A small-sized deer species, *Metacervoceros rhenanus* Dubois, 1904 (Fig. 1B), is represented by 10 specimens (one shed antler, seven dentition remains and two postcranial bones, a femur and a tibia) in the

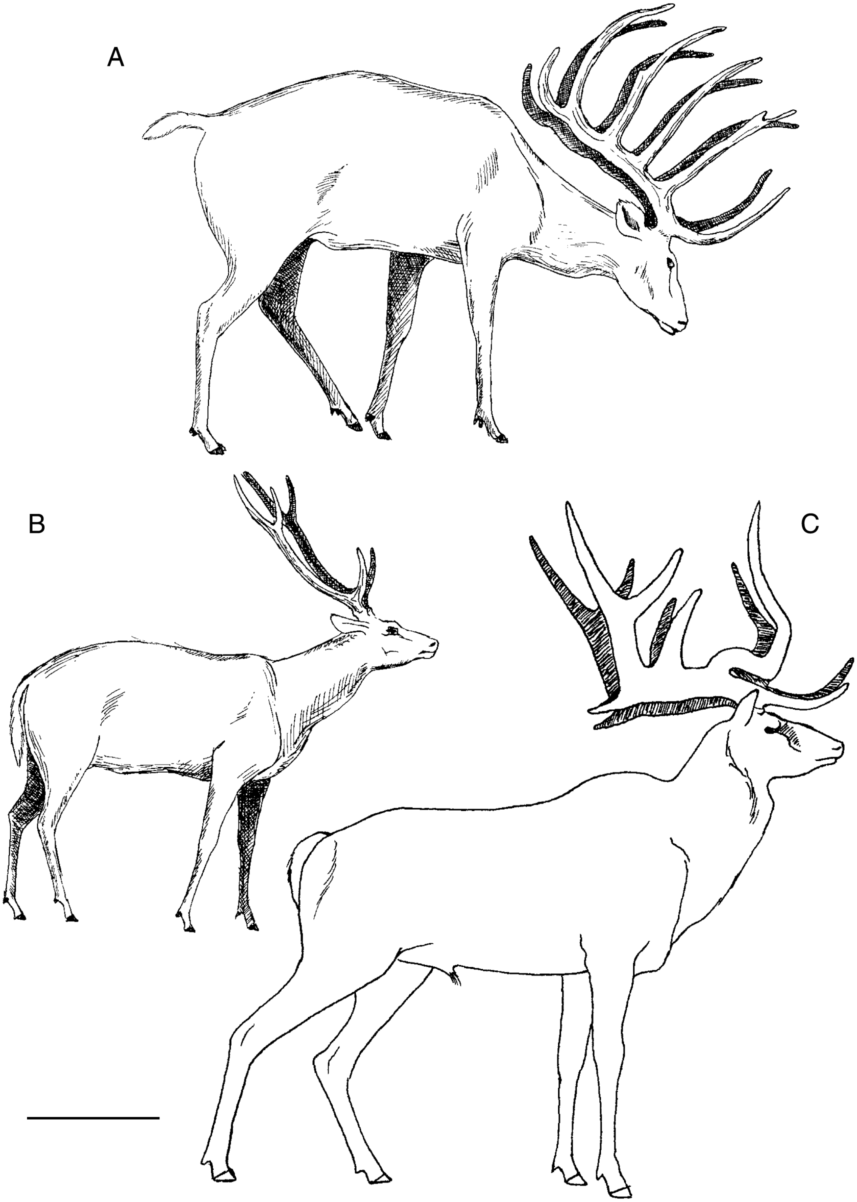


FIG. 1. — Habitus of *Eucladoceros ctenoides* Nesti, 1841 (**A**), *Metacervoceros rhenanus* Dubois, 1904 (**B**) and *Praemegaceros obscurus* Azzaroli, 1953 (**C**) from Ceyssaguet (Haute-Loire, France). The reconstruction of *P. obscurus* is based on material from the site of Pietrafitta (Italy). Scale bar: 50 cm.

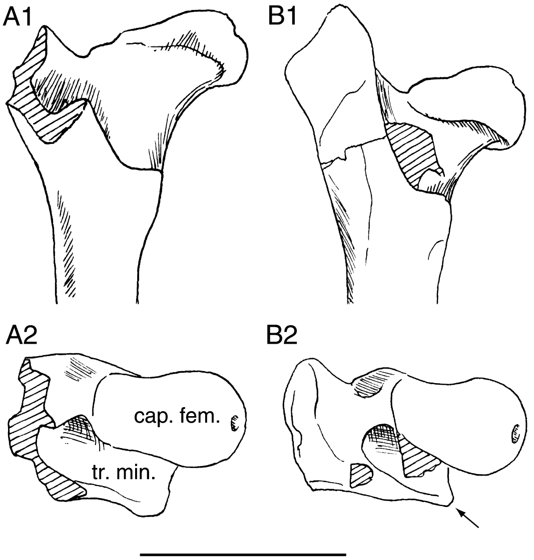


FIG. 2. — Proximal epiphysis of the femur (both found in articulation with tibiae and metatarsals of deer): *Eucladoceros ctenoides* Nesti, 1841 (**A**), *Praemegaceros obscurus* Azzaroli, 1953 (**B**); posterior aspect of the femur head (**1**), proximal aspect of the femur head (**2**). Note the long and medially prominent caput femoris (**cap. fem.**) in *E. ctenoides* and the more sharpened and prominent lesser trochanter (**tr. min.**) in *P. obscurus* (indicated by arrow). Scale bar: 10 cm.

fossil assemblage. *Praemegaceros obscurus* Azzaroli, 1953 (Fig. 1C) is another large-sized deer in the Ceyssaguet fauna, but is quite rare. Only two specimens, a radiocubitus (No. 2-11010) and a fragment of an upper mandible (No. 2-10332) were ascribed to an ancient fallow deer *Dama* sp. The paucity of the material does not allow a reliable species identification, however it has been supposed that the fallow deer from Ceyssaguet may be conspecific with *Dama vallonnetensis* De Lumley, Kahlke, Moigne & Moulle, 1988 from the latest Villafranchian-Postvillafranchian of Italy and southern France (Croitor & Bonifay 2001). Both late Villafranchian *Praemegaceros obscurus* and *Dama vallonnetensis* are represented by abundant fossil remains in the meridional areas of Europe as southern France and Italy (Abbazzi 1995; Croitor 2001a; Croitor & Bonifay 2001). The scanty remains of the above mentioned deer in the studied sample therefore indicate that it was a less common species at Ceyssaguet. All deer species included in this study went extinct on the European mainland before the first waves of glaciation. Due to the limited material of fallow deer from Ceyssaguet, this species is not considered here. A brief description of the species is in progress.

– *Eucladoceros ctenoides* (Ec) (Fig. 1A) is similar in size to a modern red deer. Based on the male skull from Ceyssaguet, the body mass is estimated 250 kg applying methodology by Janis (1990). It is characterised by comparatively simply build, light antlers and a narrow, long braincase. Compared to *E. dicranios* Nesti, 1841, the preorbital fossae are reduced and very small. The antlers are comb-like with up to six tines of variable shape inserted on the antler beam in the same plane. Upper molars have no additional enamel folds beside the hypocone spur. The internal enamel of the hypocone of upper premolars is well folded. The lingual wall of the P2 is cleft. As a primitive character the p4 shows a low degree of molarization. In some cases, however, an advanced morphology of the p4 has been reported (Azzaroli & Mazza 1992; De Vos *et al.* 1995; Croitor & Bonifay 2001).

Croitor & Bonifay (2001) pointed out some characters of *E. ctenoides* and *P. obscurus* that allow distinguishing the postcranial morphology of these two species, including the peculiar characters of the femur. In *E. ctenoides* (Fig. 2A1, A2), compared to *P. obscurus* (Fig. 2B1, B2), the caput femoris is comparatively long and more prominent medially, while the lesser trochanter is more prominent and extended posteriorly. Unlike *P. obscurus* and the closely related *E. dicranios* the distribution of *E. ctenoides* during the latest Villafranchian seems to be limited to northwest Europe (France, Holland) (Croitor & Bonifay 2001).

The material used in this analysis comes mainly from the second level of the Ceyssaguet stratigraphic column, which yielded the largest number of cervid remains in the fossil sample (Bonifay 1986). All individuals of *E. ctenoides* from Ceyssaguet including the two preserved skulls of male individuals, have their antlers shed.

This suggests that *E. ctenoides* inhabited the locality of Ceyssaguet mainly during the springtime and summer season when animals shed their antlers. Only three of 16 antlers show rodent gnawing marks. This suggests that most of the antlered individuals died during the winter season, when their carcasses were not subject to rodent activity.

– *Metacervoceros rhenanus* (Mr) (Fig. 1B) is a rather small deer, comparable in size to the modern fallow deer. Based on the male skull from Ceyssaguet, the body mass is estimated 70 kg applying methodology by Janis (1990). It has a long neurocranium and a short orbitofrontal region combined with long posteriorly sloping pedicles (Croitor & Bonifay 2001). The preorbital fossae are deep and large. The antlers are slender, and three-pointed. The basal tine springs off high above the burr. Upper molars have a hypocone spur, a protocone fold and a weak cingulum. The lower premolars, including p4, are comparatively simply built. The distribution of *M. rhenanus* during the latest Villafranchian period mainly coincides with the distribution area of *E. ctenoides* and these two species are often found together (Croitor & Bonifay 2001).

M. rhenanus is represented by individuals of various ontogenetic stages at Ceyssaguet. However, the fossil remains of this species are much less numerous compared to *E. ctenoides*. Among 26 antlers, nine are connected with pedicles (35%). Ten of 17 shed antlers are gnawed by rodents (about 60%), while only two of nine antlers which are inserted in pedicles are gnawed. It seems therefore that the majority of antlers still connected to the skull were unavailable to rodents after the death of their owners. This is possibly because these individuals drowned in the water during the winter season. It should be noted, that the taxon *Metacervoceros* is often cited as *Cervus* s.l. or *Pseudodama* Azzaroli, 1992 (Croitor & Bonifay 2001). Croitor (2001a) restricted the genus *Pseudodama* only to its type species *Dama nestii nestii* Azzaroli, 1947.

– *Praemegaceros obscurus* (Po) is the largest deer species discovered at the Ceyssaguet site (Fig. 1C). Based on the male skull from Pietrafitta (Italy), the body mass is estimated 400 kg. Its size thus more or less equals that of modern elk. Only nine remains were identified as belonging to *P. obscurus*. The species is characterized by large and robust antlers with a strong basal tine and a very long and flat second tine inserted on the medial side of the beam (Abbazzi 1995; Abbazzi *et al.* 1999). Compared to *E. ctenoides* the dentition is more advanced. The p4 is well molarized, and there are no additional enamel folds in the upper cheek teeth. The caput femoris is short and rounded compared to *E. ctenoides* (Croitor & Bonifay 2001). Abundant finds of *P. obscurus* were discovered in England and areas of continental Europe, like Italy, Romania and Moldavia (Abbazzi 1995; Abbazzi *et al.* 1999; Croitor & Bonifay 2001).

MATERIAL AND METHODS

MESOWEAR ANALYSIS

The mesowear method was developed by Fortelius & Solounias (2000). Mesowear is based on facet development on the occlusal surfaces of the ungulate upper molar teeth. The degree of facet development reflects the relative proportions of tooth to tooth contact (attrition) and food to tooth contact (abrasion), attrition creating facets and abrasion obliterating them. This methodology defines ungulate tooth mesowear by two variables: 1) occlusal relief and 2) cusp shape. Occlusal relief (OR) is classified as high (h) or low (l), depending on how high the cusps rise above the valley between them. Occlusal relief is used in the analyses as percentages % high and % low (Table 1). The second mesowear variable, cusp shape, includes three scored attributes: sharp (s), round (r) and blunt (b) according to the degree of facet development (see Fortelius & Solounias 2000: fig. 1). Cusp shape is also used as a percentage and is given in Table 1 as the three variables % sharp, % round and % blunt. When both (paracone and metacone) cusp apices were preserved, the sharpest of the two was selected for analysis as proposed by Fortelius & Solounias (2000).

TABLE 1. — Distribution of mesowear variables in the populations of *Eucladoceros ctenoides* Nesti, 1841 (**Ec**), *Metacervoceros rhenanus* Dubois, 1904 (**Mr**) and *Praemegaceros obscurus* Azzaroli, 1953 (**Po**) from Ceyssaguet (Haute-Loire, France). Abbreviations: **n**, number of available specimens; Mesowear variables: **l**, absolute scorings low; **h**, absolute scorings high; **s**, absolute scorings sharp; **r**, absolute scorings round; **b**, absolute scorings blunt; **% l**, percent low occlusal relief; **% h**, percent high occlusal relief; **% s**, percent sharp cusps; **% r**, percent rounded cusps; **% b**, percent blunt cusps.

Species	**n**	**l**	**h**	**s**	**r**	**b**	**% l**	**% h**	**% s**	**% r**	**% b**
Eucladoceros ctenoides	17	1	16	3	14	0	6	94	18	82	0
Metacervoceros rhenanus	12	0	12	2	9	0	0	100	18	82	0
Praemegaceros obscurus	3	0	3	1	1	0	0	100	50	50	0
Ec, Mr, Po; h,s,r	Chi-square = 1.2562, df = 4, *p*-value = 0.8688										
Ec, Mr; h,s,r	Chi-square = 0.0751, df = 2, *p*-value = 0.9632										
Ec, Po; h,s,r	Chi-square = 1.1592, df = 2, *p*-value = 0.5601										
Mr, Po; h,s,r	Chi-square = 0.9577, df = 2, *p*-value = 0.6195										
Ec, Mr, Po; l,h	Chi-square = 0.9108, df = 2, *p*-value = 0.6342										
Ec, Mr; l,h	Chi-square = 0.0317, df = 1, *p*-value = 0.8586										
Ec, Po; l,h	Chi-square = 1.0114, df = 1, *p*-value = 0.3146										

Fortelius & Solounias (2000) restricted their study of ungulate mesowear to the labial wall of the M2. This methodology was modified in selecting all M1-M3s of the species investigated following the "extended" mesowear method introduced by Kaiser & Solounias (2003). This methodology was chosen because it allows to include tooth samples with small numbers of individuals. It is recognized that applying the modified method by Kaiser & Solounias (2003), that was originally developed for use in hypsodont equids may not be immediately transferred to ruminant dentitions. Recent studies by Kaiser & Franz-Odendaal (2003) however indicate, that combined analysis of upper molars into mesowear investigation results in a valid mesowear signal in ruminants.

Dental specimens included in this study are upper cheek teeth showing wear stages 2 and 3 of Kaiser *et al.* (2003). Unworn teeth, specimens in very early wear, and very worn teeth were excluded. The tips of labial cusp apices of upper molars are broken in some specimens. Those specimens were also excluded from the analysis. In the end, 17 specimens of *Eucladoceros ctenoides*, 12 specimens of *Metacervoceros rhenanus* and three specimens of *Praemegaceros obscurus* were available for this investigation (Table 2).

As comparative data for dietary classification, 54 extant species reported by Fortelius & Solounias (2000) were used. The set of fossil taxa was plotted within a nested set of extant ungulate species. Extant species were classified into the three broad dietary categories: browser, mixed feeder and grazer, following the "conservative" (CONS) classification of Fortelius & Solounias (2000). All statistics were computed using Systat 9.0 and Axum 6 software. Hierarchical cluster analysis with complete linkage (furthest neighbour) was applied following the standard hierarchical amalgamation method of Hartigan (1975). According to the default settings of Systat 9.0 the algorithm of Gruvaeus & Weiner (1972) was used to order the trees. The three mesowear variables % high, % sharp and % blunt were analysed in cluster statistics. We perform three cluster analysis using different sets of extant reference species. In Figure 4A we used all 54 extant species classified as "normal" and "typical" by Fortelius & Solounias (2000), in Figure 4B we use the reduced set of 27 "typical" species and in Figure 4C we only employ nine extant Cervidae as reference species.

Chi-square corresponding probabilities were computed for each dataset giving the probability that the null hypotheses of independence should be rejected (at an error probability of 0.05). The absolute frequencies of mesowear variables ("low", "high", "sharp", and "round") were tested for significance.

Table 2. — Maxillary cheek teeth attributed to *Eucladoceros ctenoides* Nesti, 1841 (**Ec**), to *Metacervoceros rhenanus* Dubois, 1904 (**Mr**) and to *Praemegaceros obscurus* Azzaroli, 1953 (**Po**) from Ceyssaguet (Haute-Loire, France). Abbreviations: **Spec-Id**, specimen number (**Cey**, Maison méditerrannéenne des Sciences de l'Homme, Aix-en-Provence, France); **Tooth**, tooth position; **Side**, side (**r**, right; **l**, left); **OR**, occlusal relief mesowear variables scoring (**h**, high; **l**, low); **CS**, cusp shape mesowear scores (**s**, sharp; **r**, round; **b**, blunt); (**P**), paracone cusp; (**M**), metacone cusp.

Spec-Id	Species	Tooth	Side	OR	CS (P)	CS (M)
Cey-8194	Ec	M1	r	h	r	r
Cey-4534	Ec	M1	r	h	r	r
Cey-7217	Ec	M1	l	h	–	r
Cey-10590	Ec	M1	r	h	r	r
Cey-2047	Ec	M1/2	l	h	–	r
Cey-12072	Ec	M1/2	r	l	r	r
Cey-6303 (12398)	Ec	M1/2	l	h	r	r
Cey-2292	Ec	M2	r	h	s	s
Cey-8194	Ec	M2	r	h	r	r
Cey-4534	Ec	M2	r	h	r	r
Cey-7217	Ec	M2	l	h	r	r
Cey-10590	Ec	M2	r	h	s	r
Cey-8194	Ec	M3	r	h	r	r
Cey-4534	Ec	M3	r	h	r	r
Cey-7217	Ec	M3	l	h	s	r
Cey-10590	Ec	M3	r	h	–	r
Cey-nn/a	Ec	M3	l	h	r	r
Cey-14393	Mr	M1	l	h	–	r
Cey-9412	Mr	M1	r	h	–	–
Cey-84-2176	Mr	M1	r	h	r	r
Cey-93-10755-a	Mr	M1/2	l	h	r	–
Cey-93-10755-b	Mr	M1/2	l	h	–	r
Cey-14393	Mr	M2	l	h	r	r
Cey-12303	Mr	M2	r	h	s	s
Cey-9412	Mr	M2	r	h	r	r
Cey-84-2176	Mr	M2	r	h	–	s
Cey-n/n-b	Mr	M2	r	h	r	r
Cey-14393	Mr	M3	l	h	r	r
Cey-n/n-b	Mr	M3	r	h	r	r
Cey-8949	Po	M1	l	h	–	–
Cey-8949	Po	M2	l	h	r	r
Cey-8949	Po	M3	l	h	–	s

RESULTS

In all three fossil cervid species compared in this analysis (Ec, Mr and Po), occlusal relief is at least 94% high. Cusp shape scorings ranged between 18% (Ec and Mr) and 50% (Po) sharp, 82% (Ec and Mr) and 50% (Po) round. There are no blunt cusps in either sample (Table 1; Fig. 3).

Chi-square analysis of all variables, however, indicates low significance of differences (p = 0.56-0.96). *Eucladoceros ctenoides* is most similar to *Metacervoceros rhenanus* as indicated by p = 0.96. Taken alone, also the occlusal relief variables do not permit separation of the populations (p-values range between 0.31 and 0.86).

The cluster diagrams (Fig. 4) depict the relations of datasets by joining them in the same clusters. The closer the data are, the smaller is the Euclidean distance (ED) at the branching point. Figure 4A shows three main clusters, cluster one containing only grazers, cluster two containing one part of the mixed feeders some of the grazers and very few browsers, and cluster three corresponding to the attrition-dominated end of the spectrum containing most of the browsers and the attrition-dominated mixed feeders, but no grazers.

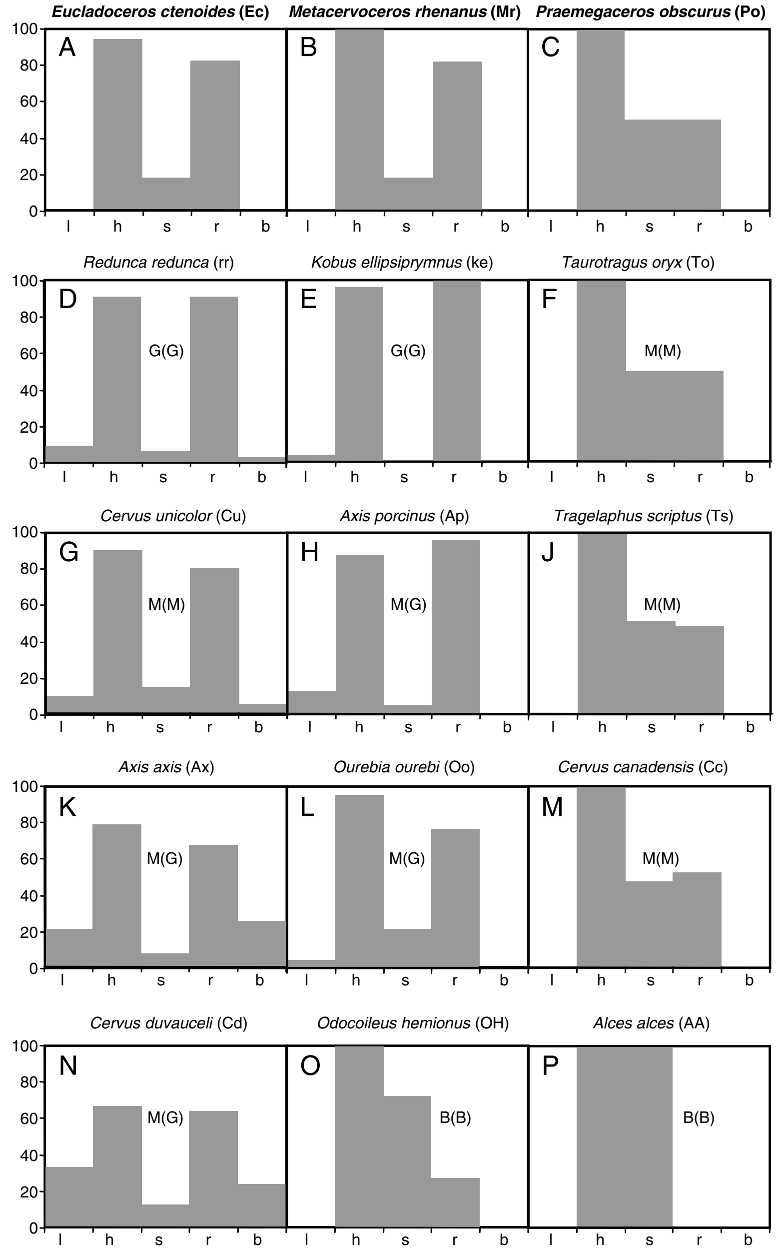


FIG. 3. — Histograms of mesowear variables % low (**l**), % high (**h**), % sharp (**s**), % round (**r**) and % blunt (**b**). Histograms of *Eucladoceros ctenoides* Nesti, 1841 (**A**), *Metacervoceros rhenanus* Dubois, 1904 (**B**) and *Praemegaceros obscurus* Azzaroli, 1953 (**C**) are based on the data given in Table 1. Comparative histograms are based on published data by Fortelius & Solounias (2000). *Redunca redunca* (bohor reedbuck) (**D**), *Kobus ellipsiprymnus* (common waterbuck) (**E**), *Taurotragus oryx* (eland) (**F**), *Cervus unicolor* (sambar) (**G**), *Axis porcinus* (hog deer) (**H**), *Tragelaphus scriptus* (bushbuck) (**J**), *Axis axis* (chital) (**K**), *Ourebia ourebi* (oribi) (**L**), *Cervus canadensis* (wapiti) (**M**), *Cervus duvauceli* (barashingha) (**N**), *Odocoileus hemionus* (mule deer) (**O**), *Alces alces* (elk, moose) (**P**). Letters in centre of graphs indicate dietary trait after Fortelius & Solounias (2000). Abbreviations: **G**, grazer; **M**, mixed feeder; **B**, browser. First character: **CONS** (conservative) classification; second character (in brackets): **RADI** (radical) classification after Fortelius & Solounias (2000).

The two species (Ec and Me) are in a sub-cluster of cluster two (ED = 24), containing mostly abrasion-dominated mixed feeders and grazers, but only two browsers (Fig. 4A). Within this cluster, the two deer species are closely linked to *Ourebia ourebi* Zimmermann, 1783 (Fig. 3L), an African bovid, whose diet consists of up to 80% grass (Van Wieren 1996). *Praemegaceros obscurus* is in the major cluster three (ED = 42). There it shares a sub-cluster of fourth order (ED = 14.4) with 12 mixed feeders and one browser. It is closest linked to the mixed feeding bovid *Taurotragus oryx* Pallas, 1766 (To) (Fig. 3F).

If cluster analysis is restricted to those extant comparison species, recognised to represent "typical" dietary categories by Fortelius & Solounias (2000), the pattern becomes even clearer (Fig. 4B). Clusters one and two contain only grazers. Ec and Mr are in cluster two. All mixed feeders share cluster three, which also contains Po. All browsers are within cluster four. Within a sub-cluster of ED = 16, the common waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833; Fig. 3E) (ke), bohor reedbuck (*Redunca redunca* Pallas, 1767; Fig. 3D) (rr), roan antelope (*Hippotragus equinus* Desmarest, 1804) (he) and sable antelope (*Hippotragus niger* Harris, 1838) (hn), all grazers, are the extant species classified next to Ec (Fig. 3A) and Mr (Fig. 3B). *P. obscurus* (Fig. 3C) remains closely linked to mixed feeders as eland (*Taurotragus oryx*; Fig. 3F) (To), and impala (*Aepyceros melampus* Lichtenstein, 1812) (Me).

Reducing the set of extant species to the Cervidae, results in only two major clusters (Fig. 4C). Cluster one comprises all the browsers, one mixed feeder (wapiti) and Po from Ceyssaguet. Cluster two comprises four extant cervids and Ec and Mr from Ceyssaguet. Here Ec and Mr are closest to the sambar (*Cervus unicolor* Kerr, 1792; Fig. 3G) (Cu) and the hog deer (*Axis porcinus* Zimmermann, 1780; Fig. 3H) (Ap). Following the "conservative" (CONS) classification by Fortelius & Solounias (2000) all extant species in cluster two are mixed feeders. If the "radical" (RADI) classification scheme is applied, the sambar is the only mixed feeder, while the remaining three taxa are classified as grazers. The cluster models show a quite distant position of the deer from Ceyssaguet and the modern holarctic species like *Capreolus capreolus* (Linnaeus, 1758) (OL), *Alces alces* (Linnaeus, 1758) (AA) and *Odocoileus hemionus* (Rafinesque, 1817) (OH), which are linked with browsers. However, *E. ctenoides* and *M. rhenanus* share remarkable similarities with extant deer species from South-East Asia (Fig. 4C).

OBSERVATIONS ON TOOTH TIP DAMAGE

The tips of labial cusp apices of upper molars are broken in some specimens. This type of damage of cusp tips is often recorded in *M. rhenanus*, both in upper and lower cheek teeth. Damaged cusp tips are also found in some specimens of *E. ctenoides*. The broken tooth tips were freshly damaged or slightly polished by food, a fact that suggests that the tips were damaged during the animal's life shortly before its death. Since damaged cusp tips are not the result of stable mesowear equilibriums, those cusps were excluded from mesowear analysis.

DISCUSSION

The mesowear signal of *E. ctenoides* and *M. rhenanus* approaches the signals of the modern African bovids *Redunca redunca* and *Kobus ellipsiprymnus*, which live near rivers and feed on grass (Kingdon 1979). In both species grass makes up 80% of the diet (Van Wieren 1996). Gagnon & Chew (2000) classify these species as obligate or variable grazers respectively. It is interesting to note that among the extant Cervidae the mixed feeding (wapiti; Fig. 3M) and not the grazing species as the hog deer (*Axis porcinus* Zimmermann, 1780; Fig. 3H), the chital (*Axis axis* Erxleben, 1777; Fig. 3K) (70% grass) or the barashingha (*Cervus duvauceli* Cuvier, 1823) (80% grass) are the extant dietary analogues. However, it should be noted here, that all these species are classified as "normal" by Fortelius & Solounias (2000), which indicates that they found their mesowear signatures to not always correctly correspond to the known dietary

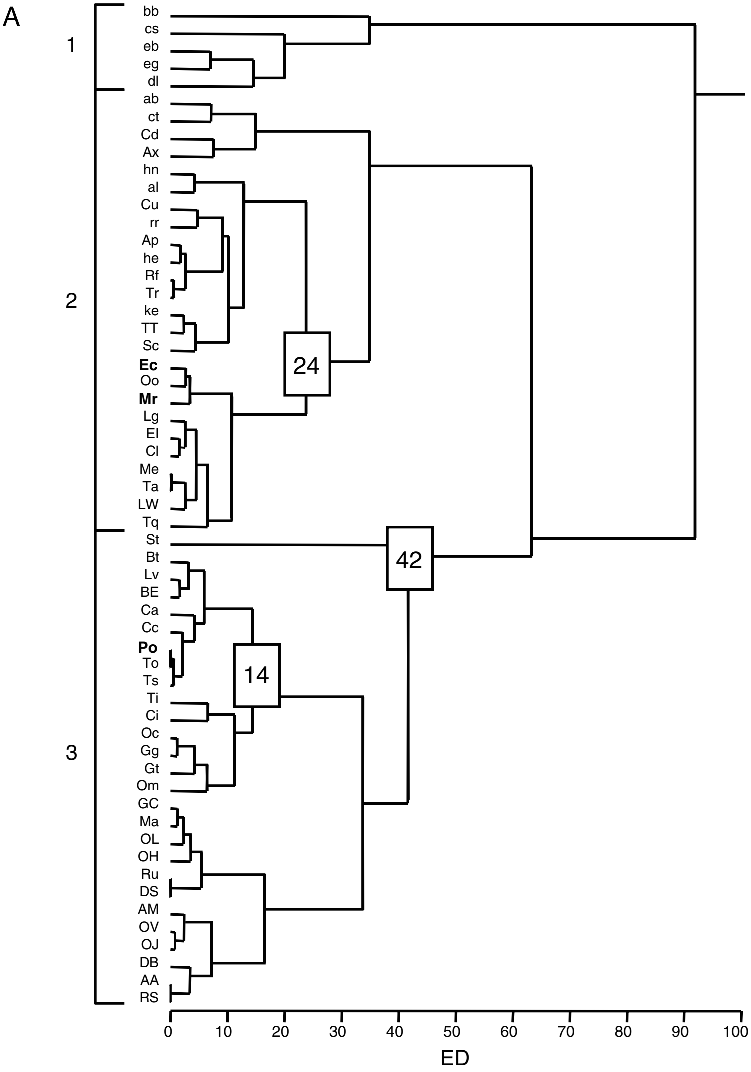
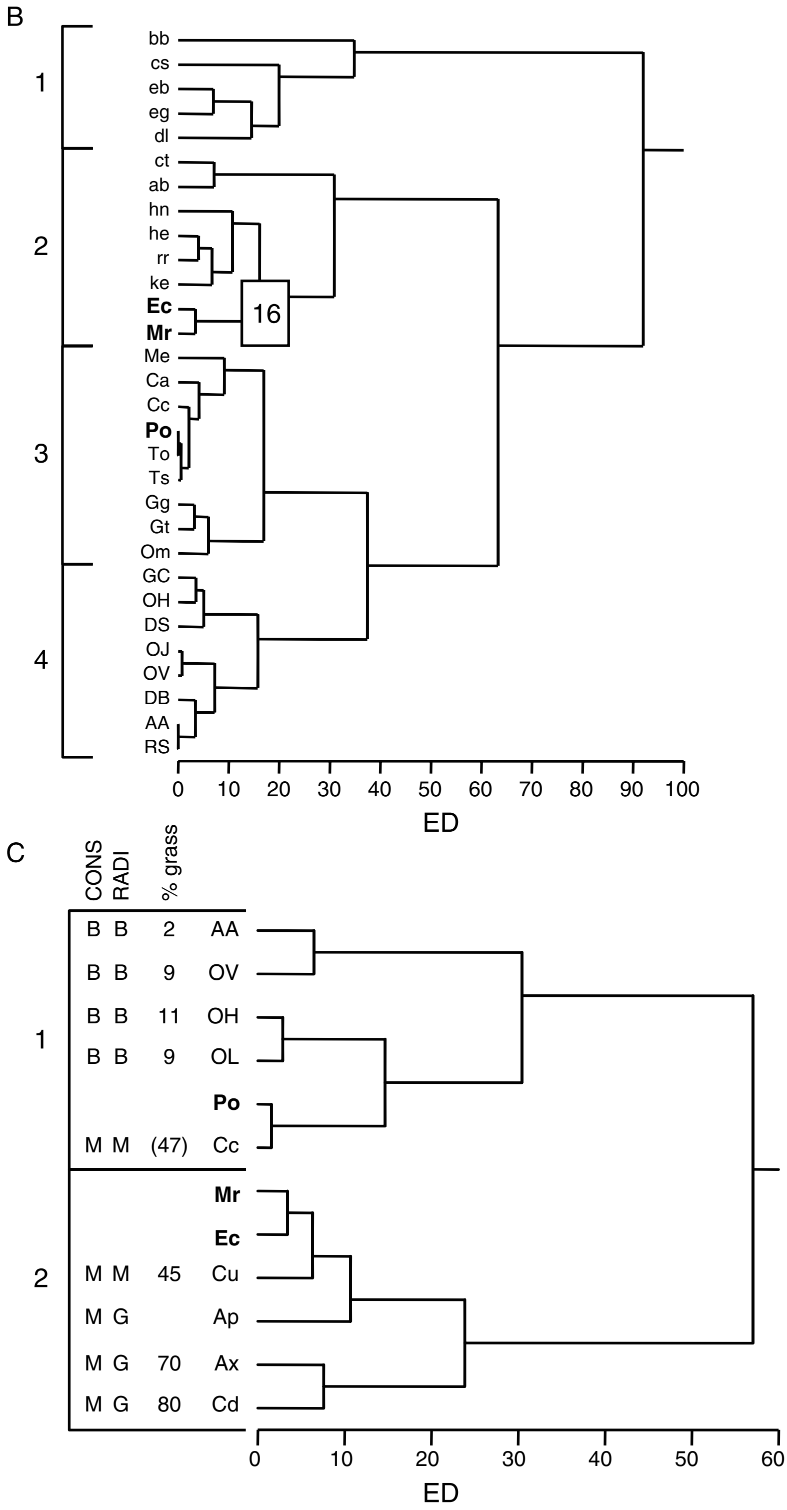


FIG. 4. — Hierarchical cluster diagram based on the reference tooth positions M1-M3 according to the “extended” mesowear method (Kaiser & Solounias 2003). **ED**, Euclidean distance (root-mean-squared difference). Clusters are based on a set of 54 “normal” and “typical” extant species (**A**), on 27 “typical” extant species (**B**) from Fortelius & Solounias (2000) and on nine “normal” and “typical” Cervidae (**C**) from Fortelius & Solounias (2000). **CONS**, conservative classification; **RADI**, radical classification (after Fortelius & Solounias 2000); **% grass**, percent grass in the diet of extant species (after a compilation by Van Wieren 1996).
Browsers (CONS): **AA**, *Alces alces*; **El**, *Ammodorcas clarkei*; **AM**, *Antilocapra americana*; **BE**, *Boocercus eurycerus*; **DB**, *Diceros bicornis*; **DS**, *Dicerorhinus sumatrensis*; **GC**, *Giraffa camelopardalis*; **LW**, *Litocranius walleri*; **OH**, *Odocoileus hemionus*; **OJ**, *Okapia johnstoni*; **OL**, *Capreolus capreolus*; **OV**, *Odocoileus virginianus*; **RS**, *Rhinoceros sondaicus*; **TT**, *Tragelaphus strepsiceros*.
Grazers (CONS): **ab**, *Alcelaphus buselaphus*; **al**, *Alcelaphus lichtensteinii*; **bb**, *Bison bison*; **cs**, *Ceratotherium simum*; **ct**, *Connochaetes taurinus*; **dl**, *Damaliscus lunatus*; **eb**, *Equus burchelli*; **eg**, *Equus grevyi*; **he**, *Hippotragus equinus*; **hn**, *Hippotragus niger*; **ke**, *Kobus ellipsiprymnus*; **rr**, *Redunca redunca*.
Mixed feeders (CONS): **Ap**, *Axis porcinus*; **Ax**, *Axis axis*; **Bt**, *Budorcas taxicolor*; **Ca**, *Capricornis sumatraensis*; **Cc**, *Cervus canadensis*; **Cd**, *Cervus duvauceli*; **Ci**, *Capra ibex*; **Cl**, *Camelus dromedarius*; **Cu**, *Cervus unicolor*; **Gg**, *Gazella granti*; **Gt**, *Gazella thomsoni*; **Lg**, *Lama guanicoe*; **Lv**, *Lama vicugna*; **Ma**, *Antidorcas marsupialis*; **Me**, *Aepyceros melampus*; **Oc**, *Ovis canadensis*; **Om**, *Ovibos moschatus*; **Oo**, *Ourebia ourebi*; **Rf**, *Redunca fulvorufula*; **Ru**, *Rhinoceros unicornis*; **Sc**, *Syncerus caffer*; **St**, *Saiga tatarica*; **Ta**, *Tragelaphus angasi*; **Ti**, *Tragelaphus imberbis*; **To**, *Taurotragus oryx*; **Tq**, *Tetracerus quadricornis*; **Tr**, *Boselaphus tragocamelus*; **Ts**, *Tragelaphus scriptus*. Fossil species: **Ec**, *Eucladoceros ctenoides*; **Mr**, *Metacervoceros rhenanus*; **Po**, *Praemegaceros obscurus*.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trait. Nevertheless, this observation may shed some light on the problem of inferring diet based on mesowear analogues belonging to different major taxa such as the Bovidae and the Cervidae. All extant grazers have at least a small percentage of low occlusal reliefs, and with only few exceptions (common waterbuck; Fig. 3E and sable antelope) some blunt cusps. In having only 4% low occlusal reliefs, the waterbuck is an exception among the species that are consistently classified as grazers. The three cervids classified as mixed feeders (CONS) or grazers (RADI), the hog deer (Fig. 3H), the chital (Fig. 3K) and the barashingha (Fig. 3N) more often have low reliefs, and the latter two species have more than 20% blunt cusps. Nevertheless, none of these species are consistently considered pure grazers. The oribi (Bovidae; Fig. 3L) and the barashingha (Cervidae; Fig. 3N) have almost exactly the same grass/browse ratio of 80/10% and 80/15% respectively (after compilation by Van Wieren 1996). When we compare mesowear signatures we find that both have more round cusps then sharp. The oribi, however, has almost no low reliefs and no blunt cusps while the barashingha dentitions are frequently low and blunt. This observation leads us to conclude, that deer dentitions are more sensitive to increased abrasion control in the mesowear equilibrium compared to bovids. This biomechanical sensitivity is probably the reason why the abrasive feeding deer species are all found in the "normal" group of Fortelius & Solounias (2000). And additionally this illustrates why in their bovid dominated model they found the mesowear of these cervids to not correctly correspond to the known dietary trait. We have not yet investigated the biomechanical background in detail, but adaptive strategies towards grazing are certainly less advanced in extant deer compared to the Bovidae.

That grazing bovids on the one hand and mixed feeding and grazing cervids on the other hand both classified as "typical" are closest to *E. ctenoides* and *M. rhenanus* indicates, that quite abrasive food components were a readily available forage for the Ceyssaguet deer. Grass is mostly rich in abrasive phytoliths. C3 grasses as, e.g., *Agrostis* and *Phalaris* species are frequent in extant central European forests and near lake shores, where they constitute large parts of the herb layer. This applies also for relatively cold climate conditions that Bonifay (pers. comm.) deduces for the Ceyssaguet site. The loess deposits, where the fossils were buried, are good evidence for these dry habitat conditions.

Based on the bovid and cervid species that we identify as extant analogues, we estimate the ratio of grass eaten by *E. ctenoides* and *M. rhenanus* to range between 45% and 80%. The observation of difference in mesowear signatures between bovids and cervids, however, should have an impact on our interpretation. We therefore infer that the grass ration was probably closer to 45% (the sambar ratio) than to 80% (the waterbuck ratio).

The fact that there are no significant differences observed in the mesowear signature between *E. ctenoides* and *M. rhenanus* supports the hypothesis that these two species were dependent upon the same source of forage. Therefore it is concluded that the ecological resource partitioning between these two species was achieved by differential habitat preferences rather than by different foraging strategies as found, for instance, in the modern African bovids (Kingdon 1979; Spencer 1995).

This hypothesis is supported by the postcranial anatomy and some other eco-morphological observations. The postcranial morphology of *E. ctenoides* shows peculiar characteristics indicative for a quite particular habitat preference. The long and medially prominent caput femoris found in *E. ctenoides* from Ceyssaguet (Fig. 2A) seems to control the movements of the hind-limb in the parasagittal plane, as it was shown for open-landscape bovids (Sokolov *et al.* 1964; Kappelman 1991; Kostopoulos 2000). Some differences in the femoral morphology are also evident in the shape of the lesser trochanter, which is less rounded and prominent in *P. obscurus* (Fig. 2B2) than in *E. ctenoides* (Fig. 2A2) (Croitor & Bonifay 2001). It is evident that the difference in lesser trochanter shape transmits the functional load of the muscles (m. quadriceps femoris and m. iliopsoas) inserted in this area

(Kappelman 1991). According to Kappelman (1991) the more pronounced posterior projection of the lesser trochanter observed in closed-habitat bovids provides a larger moment arm for the external rotator muscles. These peculiarities of the femoral morphology indicate *E. ctenoides* to be a cursorial runner inhabiting more open habitat settings. The reduced preorbital fossae and the extremely high number of fossil remains also give evidence that *E. ctenoides* from Ceyssaguet was rather a gregarious open-landscape species. Among deer, the reduced preorbital fossae are observed only in the open-landscape species like *Praemegaceros cazioti* (Deperet, 1897) from the late Pleistocene of Sardinia and *Megaloceros giganteus* (Blumenbach, 1803) from the late Pleistocene of Eurasia (Croitor 2001b).

M. rhenanus presents a different ecological type, which, according to Köhler's classification (Köhler 1993), may be assigned to an inhabitant of wooded habitats. This type of adaptation is indicated by the small body size, the simple three-pointed antlers, the simple morphology of teeth and the well developed preorbital fossae. The antlers preserved still attached to the pedicles suggest that *M. rhenanus* inhabited the area near the lake during the winter season. During this season the diet of *M. rhenanus* would have included higher proportions of rough and abrasive food components like dry grass, tree shoots and bark. This seasonal change in diet could have caused the observed damage of tooth tips with subsequent polishing by abrasive material.

Compared to *E. ctenoides* and *M. rhenanus*, *P. obscurus* is consistently classified as a mixed feeder, closer to the browse dominated part of the spectrum. However, the difference in the mesowear signature is not statistically significant because of the small sample available. *P. obscurus* is represented in Ceyssaguet by only nine remains that probably belong to very few individuals.

CONCLUSIONS

The Villafranchian of the area near the ancient lake from Ceyssaguet was an important source of grass forage in a rather dry and cold open-country setting which had wooded areas nearby. The ecological resource partitioning among the two best represented deer species was based on different habitat choice rather then on differential forage selection. *M. rhenanus* probably preferred the dense and tall grass and woods near the water and seems to have lived in small groups. *E. ctenoides* was a larger gregarious species that inhabited more open habitats in the Ceyssaguet lake area.

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