

# EVOLUTION, ECOLOGY AND BIOCHRONOLOGY OF HERBIVORE ASSOCIATIONS IN EUROPE DURING THE LAST 3 MILLION YEARS



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## ABSTRACT

A study of the evolution of the herbivore community during the last three million years in Europe is proposed in this paper. The study includes the analysis of evolutionary changes of systematic and ecological structure (taxa diversity, body mass, diet specializations) related both with eco-physiological and environmental factors. Several biochronological phases can be envisioned. The most drastic change in the herbivore community structure coincides with the onset of the global glacial/interglacial cycle. It marks the emergence of the zoogeographical Palearctic region in Northern Eurasia that may be correlated with the base of Gelasian (2.6 Ma) and indicates the beginning of the Quaternary. This period (considered as an era/erathem) is specific in terms of the recurrent, relatively cyclic, faunal turnover. The two following stages of faunal evolution mark a beginning and the end of complex continuous changes in the taxonomic and structural composition of the herbivore associations that resulted in a dominance of large-sized ruminant herbivores of modern type. They are mostly opportunistic mixed-feeders and grazers that can endure a high content of cellulose in forage. Quaternary herbivore associations in Western Europe demonstrate a high ecological polyvalence and adaptive tolerance to a broad variation of environmental and climatic conditions.

**Key-words:** Ruminants, Cæcalids, Plio-Pleistocene, Evolution, Ecology.

## RÉSUMÉ

ÉVOLUTION, ÉCOLOGIE ET BIOCHRONOLOGIE DES ASSOCIATIONS D'HERBIVORES EN EUROPE SUR LES 3 DERNIERS MILLIONS D'ANNÉES

L'analyse de l'évolution des communautés d'herbivores européens est proposée pour les trois derniers millions d'années sur la base de la diversité, de la composition taxonomique et sur les structures écologiques (taille corporelle et stratégies alimentaires), mis en relation avec des facteurs éco-physiologiques et environnementaux. Plusieurs phases biochronologiques sont reconnues. Le plus important changement de structure des communautés d'herbivores coïncide avec l'installation au niveau global des cycles glaciaires/interglaciaires. Il est synchronique de l'émergence d'une nouvelle région paléarctique dans le Nord de l'Eurasie, corrélé à la base du Gélasién (2,6 Ma) qui indiquerait alors le début du Quaternaire. Cette période (considérée comme une ère) montre la spécificité de changement faunique régulier et relativement cyclique. Les étapes suivantes indiquent des renouvellements dans la structure et la composition des associations d'herbivores résultant dans la dominance d'espèces de grande taille de type moderne. Ce sont essentiellement des brouteurs et des 'mangeur-mixtes' qui tolèrent de grosses quantités de cellulose dans leur alimentation. Les associations d'herbivores du Quaternaire ouest-européen se caractérisent par une grande polyvalence écologique et une souplesse adaptative aux modifications importantes des environnements et des climats.

**Mots-clés:** Ruminants, Cæcalidés, Plio-Pléistocène, Évolution, Écologie.

## 1 - INTRODUCTION

The specific geographical heterogeneity and the regional climatic peculiarity make the European (sub)-continent an interesting object of paleozoogeographic study. During the last three million years, mammalian community dynamics in Europe have depended in great part in exchange and dispersal with other main regions. The Plio-Pleistocene European faunal evolution is a complex process marked by multiple faunal immigration from Asia and Africa related to quaternary climate changes (Spassov, 2003; Brugal & Croitor, 2004; Martinez-Navarro, 2004), and followed by competitive

adaptations of those 'external' immigrants (Koenigswald, 2006). The traditional analysis of a faunal evolution based on large-scale faunal dispersals correlated to crude-grained environmental and climate changes (*i.e.*, Kurten, 1963; Azzaroli, 1977, 1983; Torre *et al.*, 1992; Bonifay, 1996) gave way to more dynamic methods at a higher level of time resolution. All these reveal more complete systematical composition of associations (integrating all taxa), the ecological structure of faunas, like the body mass or diet specializations, the calculation of species richness and turnover rate (*e.g.*, Andrews, 1995; Gunnell *et al.*, 1995; Palombo *et al.*, 2002; Azanza *et al.*, 2004; Janis *et al.*, 2004).

The evolutionary interaction among guilds and species of different zoogeographic origin in Europe is less studied and mostly concerns special goals, as the interaction and dispersals for meat-eaters, especially between hominids and carnivores (Turner, 1992; Brugal & Fosse, 2004). Turner (1992) made an attempt to analyze the co-evolution of large-sized carnivore and ungulate paleoguilds from European Plio-Pleistocene based on their systematical composition and chronological frame in order to apply it in the study of early hominid dispersion in Europe (see also Stiner, 2002). Brugal & Fosse (2004) have analyzed the systematical and ecological structure of European Quaternary carnivore guild in the context of resource partitioning with hominids. The recent regional works on the paleoguilds structure and evolution give an accurate account of structure and dynamics of large-sized mammal communities in Spain (Rodríguez, 2004; Rodríguez *et al.*, 2004) and Italy (Azanza *et al.*, 2004; Palombo & Mussi, 2006).

The zoogeographical context of Plio-Pleistocene mammal dispersal events in Europe is interesting and rather complex. Asian and African species that entered Europe have evolved in different zoogeographical contexts and according to different evolutionary and ecological strategies. The modern communities of herbivores, especially the thoroughly studied African herbivore associations, have developed complicated and sophisticated patterns of ecological partitioning that ensure the high species diversity of herbivores and the effective use of ecosystem resources (Janis, 1990; Spencer, 1995). The structure patterns of modern herbivore communities depend on the history of faunal development, zoogeographical conditions, stage of ecosystem succession, climate conditions, productivity of ecosystem, and relationships with other faunal groups, among others in a prey-predator dynamic. Some of the enlisted factors have been considered in the previous paleofaunistic studies (Rodríguez, 2004; Rodríguez *et al.*, 2004; Turner, 1995).

However, one can expect that such a fine complementary co-evolution as found in mature modern African ecosystems was not evolved in the newly established Plio-Pleistocene faunas and mammal communities developed in quite specific conditions. The evolutionary heritage of each mammal group defines specific physiological and biological peculiarities that result in the group's pre-adaptations, ecological and ethological strategy that may be critical in the process of adaptation to a new environment. The dynamic and composition of European mammal communities through time were shaped by complex mechanisms of interaction among species of different geographical origin, which formed a new composite ecological guild. The evolutionary conditions of Plio-Pleistocene mammal associations represent a complicated newly emerged combination of factors (climate change, new mammal biome with poorly co-adapted immigrant species, cyclic mammal dispersals and extinctions), which must result in drastic ecological and evolutionary

competition. This context of Plio-Pleistocene fauna evolution is still little studied and may represent a promising direction of research of such evolutionary phenomena as co-adaptation of newly established mammal communities, advantages of different evolutionary strategies in the competition for the same ecological resources and ecological displacement within a guild (Brown & Wilson, 1956).

In the present work, we have attempted to analyze the main changes in the ecological structure (biodiversity, size, diet) of the main ungulate families during the last 3.2 million years (*i.e.*, since the onset of NH Glacial Cycles) in the territory of Western Mediterranean, and Central Europe. This approach is based on mega-communities, on a large geographical scale, smoothing the question of endemism or heterogeneous spatial distribution of taxa. One can expect that the global climate change must initiate deep modifications in faunal structure that implied complicated multiple-factor mechanisms of evolution (and possibly co-evolution), adaptation, going with dispersal and extinction. Fossil herbivore species, particularly the large-sized forms, are useful proxies of paleoecological conditions and a convenient tool for paleoclimate reconstruction (*e.g.*, Palmqvist *et al.*, 2003; Janis *et al.*, 2004). The dynamic of the structural change among eco-physiological groups could bring new insights in terms of timing and duration, and then provide a good ecochronological frame.

## 2 - MATERIAL AND RESEARCH METHODS

### 2.1 - TAXA STUDIED

The study involves 75 taxa of herbivores, as a minimal number, recorded from Late Pliocene to Holocene in Europe (tab. 1). The herbivores focus on the *Bovidae*, *Cervidae* (artiodactyls: ca. 77% of the total number of studied herbivore species) and *Equidae*, *Rhinocerotidae* (perissodactyls: ca. 23%). The list of cervid species included in the present work follows the recent systematic revisions (Croitor & Kostopoulos, 2004; Croitor, 2005; Croitor, 2006 a, b). The list of bovid species has been prepared according to recent systematical studies (Crégut-Bonnoure, 2002, 2007 for caprids; Crégut-Bonnoure & Valli, 2004; Brugal, 1995; Sher, 1997; Kostopoulos, 1997 for bovinds). The perissodactyl species are compiled from Guérin (1980, 1982), Lacombe (2003), Alberdi *et al.* (1995) and Aouadi (2001). The herbivore database is also based on more synthetic works developed from recent scientific meetings (*e.g.*, Aguilar *et al.*, 1997; Guérin & Patou-Mathis, 1996; Maul & Kahlke, 2004; Turner, 1995; Crégut-Bonnoure, 2005). Proboscideans, suids and giraffids are not included for the following reasons: the extremely large-bodied proboscideans represent specific adaptations that define their special ecological function in terms of dependence on landscape and ecological interaction with carnivores; moreover the

RUMINANTS			
CERVIDAE		BOVIDAE	
<i>Eostyloceros podoplitshkoi</i>	I	<i>Gazella borbonica</i>	I
<i>Muntiacus sp.</i>	I	<i>Saiga tatarica</i>	II
<i>Croizetoceros ramosus</i>	II	<i>Soergelia (minor+elisabethae)</i>	II
<i>Metacervoceros pardinensis</i>	II	<i>Megalovis latifrons</i>	II
<i>Metacervoceros rhenanus</i>	II	<i>Pliotragus ardeus</i>	II
<i>Cervus nestii</i>	II	<i>Gallogoral meneghini</i>	II
<i>Dama eurygonos</i>	II	<i>Ovis antiqua</i>	II
<i>Dama vallonnetensis</i>	II	<i>Capra ibex-caucasica</i>	II
<i>Dama dama</i>	II	<i>Procamptoceras brivatense</i>	II
<i>Capreolus suessenbornensis/cuzanoides</i>	II	<i>Rupicapra rupicapra</i>	II
<i>Capreolus capreolus</i>	II	<i>Hemitragus sp. (orientalis, cedrensis, bonali)</i>	II
<i>Procapreolus cusanus</i>	II	<i>Gazellospira torticornis</i>	II
<i>Procapreolus moldavicus</i>	II	<i>Leptobos stenometopon</i>	III
<i>Eucladoceros falconeri</i>	III	<i>Leptobos elatus (incl.merlai)</i>	III
“ <i>Cervus</i> ” <i>perrieri</i>	III	<i>Leptobos furtivus</i>	III
<i>Arvernoceros ardei</i>	III	<i>Leptobos etruscus</i>	III
<i>Eucladoceros ctenoides/senezensis</i>	III	<i>Leptobos vallisarni</i>	III
<i>Eucladoceros dicranios</i>	III	<i>Praeovibos sp.(P.priscus)</i>	III
<i>Praedama savini</i>	III	<i>Ovibos moschatus</i>	III
<i>Cervus elaphus (incl.acoronatus/rianensis)</i>	III	<i>Eobison sp. (incl.menneri)</i>	IV
<i>Dama clactoniana</i>	III	<i>Bison schoetensacki</i>	IV
<i>Rangifer tarandus tarandus</i>	III	<i>Bison priscus</i>	V
<i>Arvernoceros giulii</i>	IV	“ <i>Bos</i> ” <i>galerianus</i>	V
<i>Arvernoceros verestchagini/mirandus</i>	IV	<i>Bos primigenius</i>	V
<i>Praemegaceros obscurus</i>	IV	<i>Bubalus murrensis</i>	V
<i>Praemegaceros pliotarandoides</i>	IV		
<i>Praemegaceros verticornis</i>	IV		
<i>Praemegaceros solilhacus</i>	IV		
<i>Megaloceros giganteus</i>	IV		
<i>Alces gallicus</i>	IV		
<i>Alces carnutorum</i>	IV		
<i>Alces alces</i>	IV		
<i>Alces latifrons</i>	V		
CAECALIDS			
EQUIDAE		RHINOCEROTIDAE	
<i>Hipparion sp</i>	III	<i>S.etruscus</i>	IV
<i>Equus stenonis ssp. (incl.livenzovensis)</i>	III	<i>S.hundsheimensis</i>	IV+V
<i>Eq stehlini</i>	III	<i>S.jeanvireti</i>	V
<i>Eq hydruntinus</i>	III	<i>S.hemitoechus</i>	V
<i>Eq major+bressanus</i>	IV	<i>D.mercki/kirchbergensis</i>	V
<i>Eq mosbachensis</i>	IV	<i>C.antiquitatis</i>	V
<i>Eq taubachensis (incl. piveteaui)</i>	IV		
<i>Eq germanicus/gallicus/arcelini</i>	IV		
<i>Eq.chosaricus</i>	IV		
<i>Eq altidens</i>	IV		
<i>Eq sussenbornensis</i>	V		

**Tab. 1: List of taxa (with size classes) used in this study.**  
 Tab.1 : Liste des taxons (et classe de taille) utilisés dans cette étude.

inclusion of proboscidiens in the body mass structure analysis may obscure some important details among the evolution of herbivore guild. Pigs and giraffes are represented by very few rare species (with very limited distribution for giraffes), and thus do not significantly

influence the structure of herbivore associations. The taxa are mainly considered here at a specific level; nevertheless in some cases (e.g., specific evolutive lineage, case of caprids or antilopini) we have limited our database to generic level. Indeed, it seems more suitable for

our purpose to limit, and reduce, the number of taxa, especially when they represent similar ecological significance. The studied geographical area is defined, first of all, by synchrony of faunal dispersal events, so we have established a conventional paleozoogeographic border at the eastern foothills of the Carpathian Mountains, excluding from our database the paleontological records from South-Eastern Europe that differ chronologically in terms of bioevents (Spassov, 2003; Bajgusheva & Titov, 2004; Brugal & Croitor, 2004)

## 2.2 - BODY MASS STRUCTURE

The variables used in the body mass estimation in fossil mammals were restricted to the measurements that are more frequent in the fossil record and give the most adequate predictions (Janis, 1990). Thus, the body mass estimation in herbivores is based on dental measurements and condylo-basal length of skull. For some sexually dimorphic ungulates as Cervids and large-sized Bovids, the estimations are mostly based on male individuals (based on antler morphology for cervids). Data on body mass of modern mammal species are applied from Silva & Downing (1995) and other handbooks, recently re-analysed (Brugal, 2005), in order to evaluate the main shift in body size distributions, among European and African species respectively. As a result, the use of body size classing allows us to round up the taxa and facilitate the comparisons.

The evolution of body mass structure was considered separately according to family level and diet strategies. They must also have different evolutionary responses in front of the same environmental changes. In fact, approaches based on the amalgamation of all species from different guilds and different ecological forms gives a generalized, but rather useless, picture of body mass change dynamic through time. We have applied a more fractional division of body mass according to eco-physiological peculiarity. The smallest size class of herbivores (I, 1-20 kg) includes tropical forest dwelling ruminants (both cervids and bovids) known as stenobiotic browsers and concentrate feeders (Koehler, 1993). The small-medium size class (II, 20-100 kg) of herbivores includes ruminant species from various biotopes under moderate climates, like forest, woodland and savannah dwellers (cervids, antelopes), mountain forms (goat and sheep), and open plain inhabitants (*Saiga*). These herbivores normally evolve progressive narrow ecological specializations. The large-medium size class (III, >100-350 kg) includes ruminants with a broad and flexible ecological spectrum and in many cases they are opportunistic feeders (Koehler, 1993; Kaiser, 2003; Kaiser & Croitor, 2004). This body size group includes also non-ruminant herbivores (equids like *Hipparion* or stenonids), which occupy the niche of extensive grazers (Spencer, 1995). The large size group of herbivores (IV, 400-750 kg) in our study comprises a diversified group of Pleistocene cervids with opportunistic mixed or high-level feeding habits, but also large forms of Pleistocene equids. The

very large size group (V, 800-1000 kg) includes, mostly, large-sized grazing bovines, with only one cervid species (*Alces latifrons*). Finally, the giant size group (VI, more than 1000 kg) corresponds to a specific ecological niche occupied by non-ruminant rhinos.

## 2.3 - DIET CLASSIFICATION

The diet specialization of herbivores is based on the morpho-function of cranio-dental characteristics, as well as the eco-physiological strategy within systematical groups. The division of herbivores between ruminants (foregut fermenters) and non-ruminants (caecalids or monogastrics: hindgut fermenters) reflects two essential physiological and evolutionary strategies (Janis, 1976). This important difference defines not only their evolutionary reply to environmental changes but also the character of competition, ecological displacement and co-evolution within the guild. They correspond to two main digestive strategies characterizing ruminants, or artiodactyls (*Cervidae* and *Bovidae*), and non-ruminants, or perissodactyls (*Equidae* and *Rhinocerotidae*). The monogastric non-ruminant herbivores are slower growing and reproduce more conservatively; they are adapted to eat small amounts of low to modest nutriment at a frequent rhythm. The ruminants are adapted to eat large quantities of high-quality forage but less frequently (see Guthrie, 1990: 263 sq.; Janis, 1976).

Moreover, we used the classic simplified ecological classification recognizing browsers (herbivores specialized on forage with small content of cellulose, like leaves, fruits, dicotyledon herbs, etc.), grazers (herbivores adapted to rough grass forage with high content of cellulose), and mixed feeders, represented by ecological forms specialized to a mixed type of diet, or opportunistic feeders (Spencer, 1995; Kaiser, 2003). Indeed, the combination of both systematic and body size structure imply in themselves such relatively crude divisions.

## 2.4 - GEOCHRONOLOGICAL SCALE AND SPECIES TURNOVER

The Plio-Pleistocene is generally divided according to faunal units based on evolutive lineage, specific associations (*sensu* community) and degree of appearance and extinction of taxa (e.g., Guérin, 2007). These faunal units (biozone, standarzone, NMQ) are not always consistent between the European regions and beyond. Several biases obscure the use of such units, from taxonomical identification and evolutive processes to disjunction between micro- and macro-fauna into the fossil record, diachrony of appearance (related to biogeography) and taphonomic representation. The paucity of absolute date of local faunas, especially for older sites, is noticeable and limits correlations between sites and with marine records.

We have divided the 3.2 million year period of faunal evolution into 17 standard time units (STU), time slices of equal duration (0.2 Ma, that is to say  $\pm 0.1$  Ma) corresponding to the actual degree of chronological resolution. Such a length of STU is a result of compromise, since the longer time span of STU may obscure and distort some events of faunal evolution, while the application of STU with a higher resolution is limited by incomplete and not always precise absolute dating of European paleontological records.

The record of species turnover is based on the first (FAD) and the last (LAD) occurrence of taxa, at megacommunities scale analysis. We are well aware that this approach biases some repeated immigrations and retractions of species during the Pleistocene Glacial pulses (Koenigswald, 2006), however, in our case, the primary target is a guild structure, even if its evolution is not continuous in some parts of Western and Central Europe.

### 3 - DESCRIPTION

#### 3.1 - EVOLUTION OF RUMINANT HERBIVORE COMMUNITY

As a brief background we can indicate two points about the herbivores associations during the Early and Middle Pliocene (MN14, 4.9 - 4.2 Ma and MN15, 4.2 - 3.2Ma) (Costeur, 2005). The number of families decreases, starting at the end of the Miocene and continuing during the Pliocene, with less than 10 families, and modern herbivores appear and expand. This process becomes more intense during the Plio-Pleistocene with new evolutionary and ecological directions.

##### 3.1.1 - Taxonomic composition and diversity

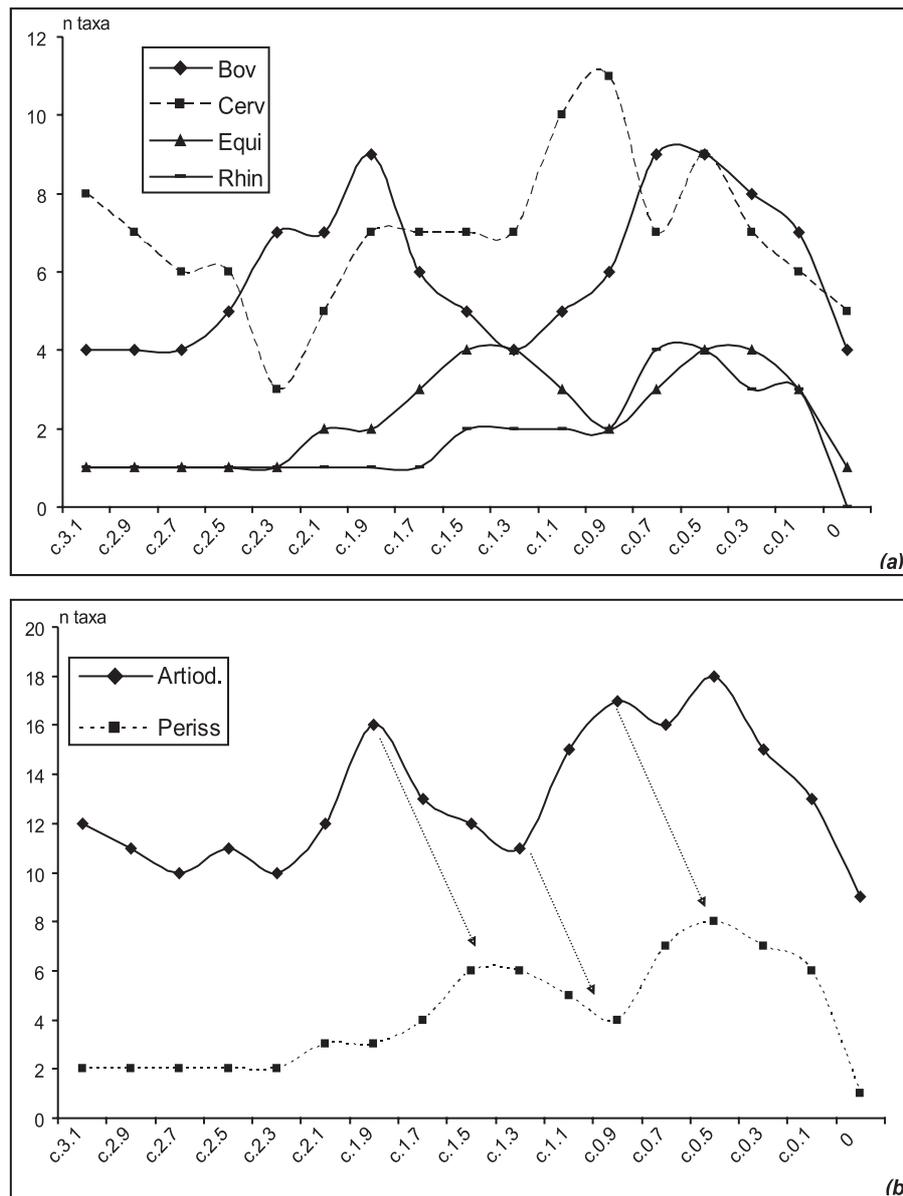
**Cervidae** (33 taxa) - The Late Pliocene guild of herbivores is characterized by a dominance of deer, which are represented by eight species, while bovids are represented by only four species (fig. 1a). The cervid group consists of small-sized Ruscinian holdovers of the genera *Muntiacus*, *Eostyloceros*, *Procapreolus*, *Croizetoceros*, and the first representatives of the true Cervinae group *Arvernoceros ardei*, "*Cervus*" *perrieri*, *Metacervoceros pardinensis*. The genus *Procapreolus* is represented by a small-sized form *P. cusanus* in France and Italy (Heintz, 1970; Abbazzi *et al.*, 1995) and a hog-deer sized *P. moldavicus* from Central Europe (Croitor, 1999). Muntiacinae deer are recorded in Slovakia (*Muntiacus sp.*, Hainäcka: Fejfar *et al.*, 1990), Romania (*Muntiacus cf. pliocaenicus*, Debren-2: Kovacs *et al.*, 1980), and Italy (*Eostyloceros cf. pidoplitschkoi*, Montopoli: Abbazzi & Croitor, 2003). Muntiacinae deer and *Procapreolus* disappear in Europe during the Early Villafranchian, while *Croizetoceros ramosus* survives until the beginning of Pleistocene, since its latest record is from Chilhac (France), dating back to 1.9 Ma (Boeuf & Mourer-

Chauvire, 1992). *Eostyloceros*, probably, became extinct somewhat earlier, during the mid-Late Pliocene climate shift. *Procapreolus* and *Muntiacus* are recorded in younger mammal faunas dated by MN16a. *Metacervoceros pardinensis* was substituted by its supposed descent *M. rhenanus* approximately 2.3 - 2.5 Ma, according to the absolute age proposed by Delson (1994) for Red Crag Nodule Bed (England) that yielded the youngest record of *M. pardinensis* (Lister, 1999).

During the same time interval, several new cervid genera appear that represent a new ecological type of large-sized forms (size classes III and IV): *Eucladoceros ctenoides* with several subspecies (*vireti*, *ctenoides*, *olivolanus*, *tegulensis*), and a lineage of specialized open-landscape odocoileini deer *Alces gallicus* - *Alces carnutorum* (Heintz & Poplin, 1981; Azzaroli & Mazza, 1992, 1993; Croitor & Bonifay, 2001; Breda & Marchetti, 2005). The oldest species of *Eucladoceros* from Western Europe is described under the species name *E. falconeri*, which is interpreted as an earlier rather small-sized forerunner of the genus (Azzaroli & Mazza, 1992). In fact, *E. falconeri* is based on a juvenile antler and most probably is a junior synonym of *E. ctenoides tegulensis*. *E. dicranios* is a sister species that evolved at the same time in South-Eastern Europe. The oldest remains of *C. gallicus* and *E. dicranios* are reported from Liventzovka, South Russia with an absolute age of 2.6 - 2.2 Ma (Bajgusheva, 1971; Bajgusheva & Titov, 2004). Apparently, these species entered Western Europe somewhat later (*ca.* 2.0 Ma).

Early Pleistocene deposits indicate the first record of modern genera *Cervus* and *Dama* in Europe. A primitive small-sized red deer, *Cervus abesalomi*, was described by H D Kahlke (2001:475) from fauna of Dmanisi (Georgia) dated back to 1.81 Ma (Lumley *et al.*, 2002). In Western Europe, the primitive archaic red deer is represented by a small-sized form *Cervus nestii* (= *Pseudodama nestii*) from Upper Valdarno (Croitor, 2006a) and may be by some remains from Olivola (Croitor, in prep.). The almost simultaneous appearance of the first *Cervus* in Western Europe and Georgia suggests its very rapid dispersal toward the west. The earliest known fallow deer *Dama eurygonos* is also recorded in Upper Valdarno (Croitor, 2006a) and probably its arrival in Western Europe was slightly later than the arrival of *C. nestii*, since there are no fossil remains from Olivola that can be ascribed to genus *Dama*. The exact time of arrival of these species cannot be precisely established; however it must fall into the period 1.8 - 1.7 Ma (Napoleone *vide* Azzaroli, 2001). Perhaps, some remains of small-sized deer from Olivola also belong to *Cervus* s.s. (Croitor, in prep.).

The entrance of several more advanced Asian megacervine deer of the genus *Praemegaceros* also marks the Early Pleistocene stage. *P. obscurus*, one of the most archaic representatives of this genus in Europe, substituted *Eucladoceros dicranios* around 1.4 Ma, while *E. ctenoides* coexist with *P. obscurus* in Western Europe until the end of the Villafranchian (Croitor & Bonifay, 2001). The last record of *P.*



**Fig. 1: Taxonomic diversity (n taxa) of herbivore families (a) and orders (b) during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**

*Fig. 1: Diversité taxonomique (nombre de taxa) des herbivores, niveau familial (a) et ordinal (b), du Plio-Pléistocène en Europe (abscisse: tranche d'âge de 0.2Ma + Holocène).*

*obscurus* is recorded in the Tamanian fauna from South Russia (Croitor, 2005), dated by *ca.* 1.0 Ma (Bosinski, 2006). *P. pliotarandoides*, an archaic forerunner of *P. verticornis*, is recorded in the fauna of Psekups from South-East Europe that, according to Tesakov (1995), dates back to *ca.* 2.2 Ma. The lineage *pliotarandoides-verticornis* of the genus *Praemegaceros*, is the oldest one in the European paleontological record; however, its distribution was limited to the South-East of Europe for a long time. The latest remains of *P. verticornis* are reported at Bilshausen, Germany (Pfeiffer, 2002), with an absolute age 0.4 Ma (Bittman & Mueller, 1996). The third lineage of the genus, represented by *P. solilhacus*, is recorded for the first time in Tamanian fauna (Croitor, 2006b). Its arrival in Western Europe also took place somewhat later and corresponds to the age

of fauna from Soleilhac (France). The latest well-dated remains of *P. solilhacus* are reported from Italian sites: Venosa (*ca.* 0.6 - 0.5 Ma according to Sardella *et al.*, 1998) and Isernia La Pineta (Abbazzi & Masini, 1997; *ca.* 0.6 Ma according to Coltorti *et al.*, 1998).

Another cervid genus from the Early Pleistocene, *Arvernoceros*, is still poorly known, although comparatively abundant fossil remains represent it. Croitor & Kostopoulos (2004) ascribed to this genus *Eucladoceros giulii* (Kahlke, 1997) from the latest Villafranchian site Untermassfeld (Germany). According to H.-D. Kahlke (1997), the remains of large-sized deer from Vallonnet (France), Selvella, Pirro Nord (Italy), Cueva Victoria (Spain) and some other sites may be ascribed to this new species. *Arvernoceros giulii* is represented in Europe by very abundant remains, but for an extremely

short time period, from *ca.* 1.0 Ma in Untermassfeld (Kahlke, 2000) to 0.8 Ma in Atapuerca TD6 (Van der Made, 1999). *Arvernoceros verestchagini* is another closely related but much larger sister species from South-East Europe. Remains of *A. verestchagini* are found in Moldova and Greece (Croitor & Kostopoulos, 2004). The youngest record of *A. verestchagini* is reported from the latest Villafranchian fauna of Apollonia, Greece (Croitor & Kostopoulos, 2004).

During the transitional phase between the Early to Middle Pleistocene, the new comparatively large cervid forms entered the European continent: *Cervus elaphus*, *Dama clactoniana* and *Praedama savini*. At this time, the Cervids reach their highest peak of diversity, with more than ten species (fig. 1a). The first remains attributable to modern *C. elaphus* are recorded in the composition of Taman' faunas (South Russia) and Saint-Prest (France) and may be dated to *ca.* 1.0 Ma (Vereschagin, 1957; Guérin *et al.*, 2003). The almost simultaneous appearance of red deer in Eastern and Western Europe suggests a very rapid dispersal westward. Perhaps, *D. clactoniana* appears almost simultaneously with red deer; at least the fossil remains that may be ascribed to this species are also recorded in Saint-Prest. The earliest record of *P. savini* is known from Tiraspol fauna (Moldova), while evidence of the latest presence of this deer in Europe comes from Süssenborn (Germany) dated by early Elster glaciation (Kahlke, 1971).

The largest Middle Pleistocene deer *Alces latifrons* is believed to be a direct descendant of the *gallicus-carnutorum* lineage (Heintz & Poplin, 1981). Its first occurrence is recorded in the fauna from Tiraspol (Kahlke, 1971) dated by *ca.* 0.8 Ma (Nikiforova *et al.*, 1971). The latest record of this species is reported at Bilshausen (Germany) and Fontana Ranuccio (Italy), both dated by 0.4 Ma (Bittman & Mueller, 1996; Ravazzi *et al.*, 2005). The extinction events of *A. latifrons* and the mainland large-sized species of *Praemegaceros* were almost simultaneous and were followed immediately by the arrival of the giant deer *Megaloceros giganteus* (Lister, 1994).

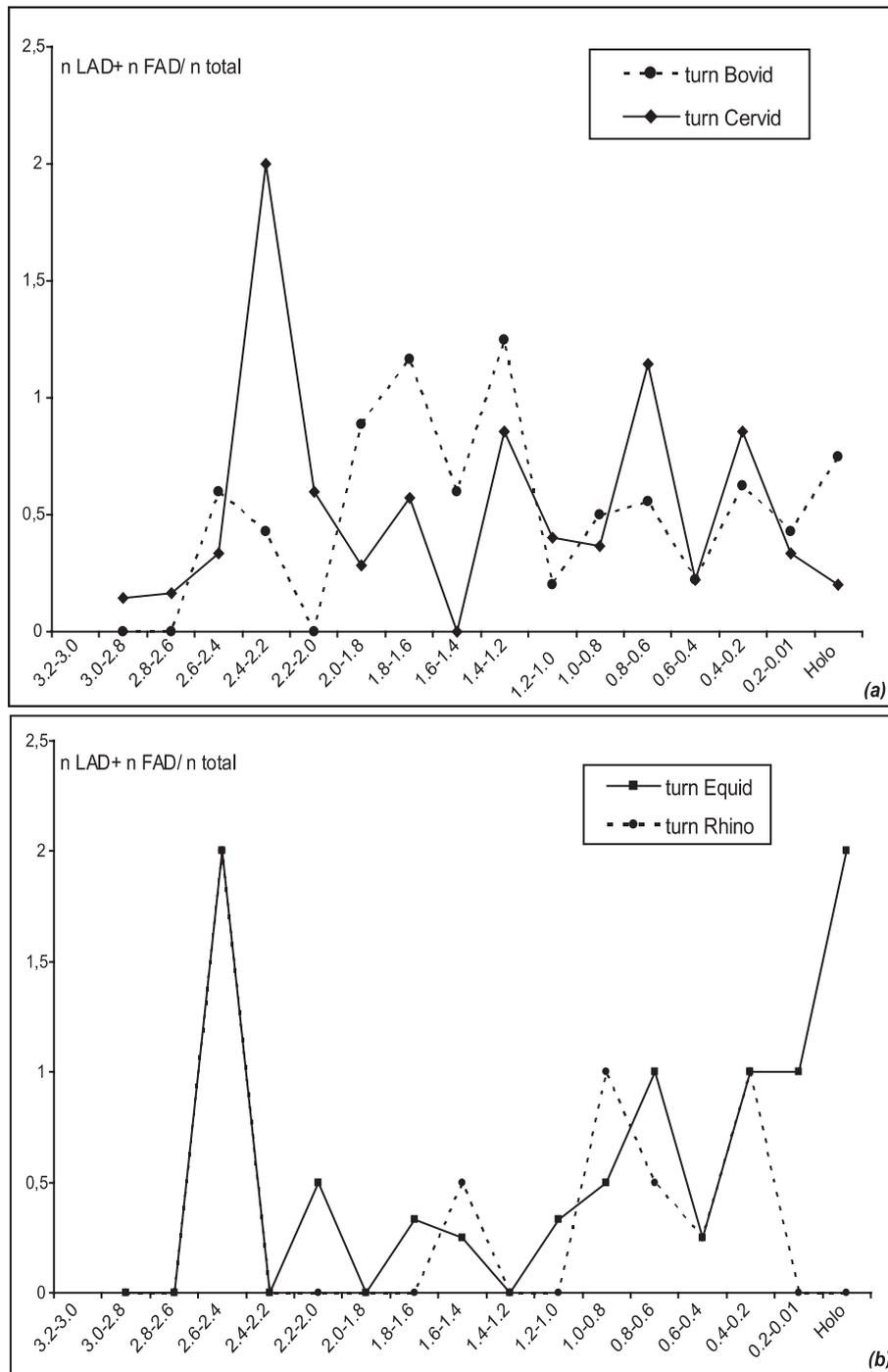
**Bovidae** (25 taxa) - The Late Pliocene bovids are represented by rather small-sized antelopes *Gazella borbonica*, *Pliotragus ardeus*, comparatively larger *Gazellospira torticornis*, and a new large-sized ecological type represented by *Leptobos stenometopon*. During the latest Pliocene (2.4 - 1.8 Ma), the number of bovid species increases significantly, while the cervid group becomes less varied (fig. 1a). The new bovid forms are the medium sized *Gallogoral meneghini*, *Procamptoceros brivatense*, and new large-sized species of *Leptobos* group (Crégut-Bonnoure & Valli, 2004; Gentili & Masini, 2005). The group of bovids reaches a peak of diversity around 2.0 - 1.9 Ma.

The next significant extinction event of bovids is observed just after, with a regular decrease of diversity until around 1.3 Ma. The small-sized bovids *G. borbonica* and *P. ardeus*, as well as the large-bodied

*Leptobos elatus* vanished. Shortly after these bovid disappearances, the numerous and morphologically variable new forms of cervids appear, with a peak of 10 species present during the time-slice 1.2 - 1.0 Ma (fig. 1a). The similar important increase of bovid species diversity starts somewhat later, at the beginning of the Middle Pleistocene. The period between *ca.* 0.8 - 0.4 Ma includes the highest diversity of ruminant species (9 species, both for cervids and bovids) recorded in Europe during the last three million years. However, it is necessary to stress that probably not all of those species were contemporaneous, especially in terms of biogeography and the present state of the faunal evolution sequence does not permit us to establish the exact chronological distribution of some Early Pleistocene ruminants.

The changes in Plio-Pleistocene bovid group generally follow the same trend observed in cervids, although it may be characterized by differential species turnover (fig. 2a). The richest Villafranchian bovid assemblage is discovered from the French site of Senèze (1.9 - 1.8 Ma). This community of bovid forms includes a variety of specialized ecological forms. A small-sized (less than 40 kg) Ruscinean holdover *Gazella borbonica* was apparently a woodland form. Another antelope *Gazellospira torticornis* of much larger size was perhaps also a semi-woodland form, deduced from its very large preorbital fossae. This specific organ of chemical communication in ruminants is used for territorial markings and social communication in forested species (Sokolov *et al.*, 1984). *Megalovis latifrons* was a large antelope with narrow pointed premaxillar bones (Schaub, 1943) indicating a stenophagous, specialized folivorous species. *Leptobos etruscus* is another large-sized bovid that contrasted from the previous species in its broader premaxillar bones; most probably it was an intermediate feeder (fig. 3). *Gallogoral meneghini* was a large specialized mountain form (Guérin, 1965), rather a mixed feeder according to its comparatively short face and slightly broadened premaxillar bones. Another mountain bovid species is *Procamptoceros brivatense* with much smaller body size.

A high level of diversity among Bovids characterizes very Late Pliocene and Early Pleistocene with new genus (*Sorgelia*, *Megalovis*, *Gallogoral*, *Procamptoceros*, first mention of *Hemitragus*, as well as *Praeovibos* at Casa Frata or *Ovis* at Senèze and Slivnista) (see Crégut-Bonnoure, 2007) accompanied by relative radiation of heavier bovini of the genus *Leptobos*. Two different lineages are recorded, as subgenus *Leptobos* and *Smertiobos* (Duvernois, 1990), and different species. This group shows a large chronological and spatial distribution, which has resulted in the description of different forms as subspecies. Last representatives (ex. *L. vallisarni*) are known from successive faunas of Val di Chiana, Italy, dated back to *ca.* 1.2 - 1.3 Ma (Gentili *et al.*, 1998), and they probably survived until 1.2 - 1.0 Ma in some refugee (south peninsular context: Spain, Italy) (e.g., Gentili & Masini, 2005). Successive important turnover took place during the Early Pleistocene



**Fig. 2: Rates of turnover of herbivore families (a) and orders (b) during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**

*Fig. 2: Taux de renouvellements fauniques des herbivores, niveau familial (a) et ordinal (b), du Plio-Pléistocène en Europe (abscisse: tranche d'âge de 0.2Ma + Holocène).*

leading to essential changes in bovid communities with modern structure.

The genus *Eobison* (*E. tamanensis* and associates) is apparently more or less closely related to *Leptobos* (*Smertiobos*), but belongs to a parallel lineage that appears in Europe at the end of the Villafranchian-early Galerian (Vereschagin, 1957; Kostopoulos, 1997; Bosinski, 2006). Sher (1997) described a new bovine species *Bison menneri* that may be closely related to *Eobison* and is believed to represent the first true species of the genus *Bison*; this species, identified at

Untermassfeld (Germany) could have a short time duration (Kahlke, 2000). Then the large-body bovids would have been replaced by more modern heavier forms such as *Bison* (*schoetensacki*, *priscus*) and *Bos* at the beginning of the Middle Pleistocene, around 1.0 - 0.8 Ma (Brugal & Croitor, 2004). This reflects the development of open landscapes; the smallest specialized mountain and forest bovids (*G. torticornis*, *G. meneghini*, *P. privatense*) became extinct, replaced by 'alpine' taxa like *Ovis*, *Hemitragus* and later on by *Capra* and *Rupicapra*. We can point out the peculiar

case of some taxa first recorded in earlier fossil records, on an ad hoc basis, when their development and full presence in Western Europe was not reported until later (ex. first mention of *Praeovibos* at Casa Frata, ca. 1.8 Ma and full presence from ca. 1.5 Ma; *Ovis* at Senèze and Slivinista with full presence around 1.0 - 0.8 Ma; *Rupicapra* reported at Kozarnika at ca. 1.5 Ma and full presence, with *Capra*, around 0.5 Ma) (see Crégut-Bonnoure, 2007). The Bovids diversity, as for Cervids, again becomes relatively high, with 8 to 9 taxa, during the Middle Pleistocene (fig. 1a).

### 3.1.2 - Ecological structure and species turnover

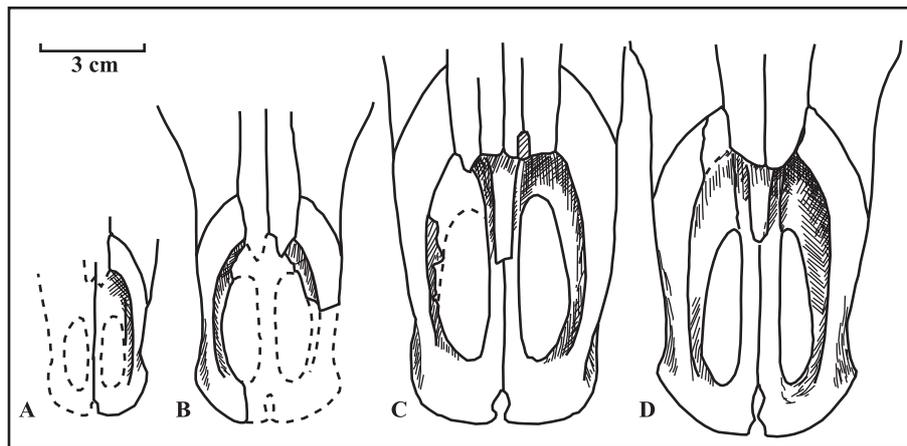
The increased ruminant diversity is followed by a very high rate of species turnover (fig. 2a), on a repetitive and cyclic base. Many taxa, especially cervids, have a comparatively short lifetime on the European continent often being replaced by newly emerged closely related or even sister species (for instance, *Eucladoceros* and *Praemegaceros* in cervids; *Leptobos*, *Eobison* and *Bison* in bovids). Interestingly enough, cervids and bovids during almost all of the Late Pliocene and Early Pleistocene period show a balancing relationship of their species diversity, when the increase of cervid species is followed by the simultaneous decrease of bovid species number, and vice versa (fig. 1a). They become more adjusted and trend in a more parallel way during the late Middle and Late Pleistocene.

The coexistence of cervids and bovids in Europe shows how the evolutionary strategy of each ruminant group shapes their response to the changing climate conditions. The main ecological and evolutionary strategy of deer is the feeding opportunism, the rather low degree of specialization to a certain type of food and the strong preference of highly nutritious food items (Geist, 1998). This kind of food habit supports the energetically costly male antlers that shed and grow again every year during the animal's life. The ecologically specialized forms are comparatively rare among cervids. The low feeding specialization of deer makes them rather weak competitors with bovids. The specialized cervid forms evolve only in the zoogeographic areas where bovids are absent or very poorly represented (for instance, such specialized new world deer, as fossil mountain deer *Navachoceros fricki* and modern tundra deer *Rangifer tarandus*). According to Geist (1998), deer are good colonizers flourishing in the young and new ecosystems, while bovids dominate in mature ecosystems. Cervids never achieve such a highly evolved ecological resource partitioning as in modern African bovid communities (Spencer, 1995). Apparently, cervids must be better adapted to the periods of climate changes and instability, than bovids. Probably, it explains the particular richness of cervid species in Europe during the Middle-Late Pliocene climate shift, and then during the period of climate instability of the transition between Early and Middle Pleistocene. The extinction of small-sized Middle Pliocene deer is caused mostly by the climate aridization

and retraction of forested areas. The latest remains of *Muntiacus* in Europe were discovered in the area of the Carpathian Mountains that may suggest the survival of this deer in the mountain forests of Central Europe. The opportunistic strategy enabled cervids to occupy the new ecological niche that appeared after the extension of open landscapes in the late Villafranchian. The Villafranchian large-sized *Alces gallicus* is the first Pliocene ruminant that represented the new large size class with clear specialization to open habitats (Geist, 1998).

Despite the differences in ecophysiological and evolutionary strategies, deer and bovids show a similar and relatively synchronous response to the major paleo-environmental changes in Europe (fig. 2a) that consist in the earlier arrival and development of large-sized forms (size IV and V). The most significant changes in the ecological structure of ruminant group are recorded around 1.4 Ma, but in fact, this change started at different times between Cervids (fig. 4) and Bovids (fig. 5). The latest Villafranchian large-sized bovids (1.4 - 1.2 Ma) belong to the sub-tribe Bisontina and represent the sister lineages (*Leptobos*, *Eobison*), that take over each other and represent different stages of specialization to arid and continental climate. Late Villafranchian large-sized deer (1.8 - 1.6 Ma) belong to several distant evolutionary stocks of Odocoileinae (the lineage of genus *Alces*), the Cervinae archaic lineage *Arvernoceros* and the lineage of genera *Eucladoceros* and *Praemegaceros* that gave a successful radiation of several species. The larger body size (size V) increases particularly during late Early Pleistocene-early Middle Pleistocene (1.0 - 0.8 Ma) where they constitute a dominating class of the herbivore guild in Europe (*A. latifrons*, *P. solihacus*, *Bison*, *Bos*) (cf. *infra*).

Ruminants were a flourishing and numerous, although very short-lasting, species. The recurrence of species turnover is explained by the gradual cooling and aridization of climate in Europe combined with the climate gradient from dry and continental conditions in the Asian heartland to mild and humid conditions in Western Europe (Brugal & Croitor, 2004). Thus, climate change caused consecutive migration waves of large-sized ruminants of the above-mentioned genera. Besides the very large size, the late Villafranchian species, apparently, also shared similar food habits that explains the high rate of extinctions following the arrival of new species. The large-sized *Eucladoceros* and *Praemegaceros* were opportunistic mixed feeders (Kaiser & Croitor, 2004; Valli & Palombo, 2005), while for *Arvernoceros verestchagini* high-level browsing is suggested. Perhaps, the large-sized bovids also shared with cervids the broad range of food habits and the foraging opportunism. The shape of premaxillar bones in Early Pleistocene deer and bovids defines them as mixed feeders and suggests a very insignificant food resource partitioning among those species (fig. 3). Palombo & Mussi (2001) point out the prevalence of herbivores with intermediate feeding habits in the early subsequent Galerian fauna of Italy.



**Fig. 3:** Shape of premaxillary bones in Villafranchian ruminants of Western Europe: A, *Cervus nestii* (Azzaroli), Upper Valdarno, Italy (IGF243, Museum of Geology and Paleontology, Florence); B, *Eucladoceros ctenoides* (Dubois), Senèze, France (National Museum of Natural History, Paris); C, *Praemegaceros obscurus* (Azzaroli), Val di Chiana, Italy (adapted from Abbazzi, 1995); D, *Leptobos etruscus* (Falconer), Upper Valdarno, Italy (IGF612, Museum of Geology and Paleontology, Florence).

*Fig. 3:* Forme du prémaxillaire chez quelques ruminants villafranchiens d'Europe de l'Ouest: A, *Cervus nestii* (Azzaroli), Upper Valdarno, Italie (IGF243, Musée de Géologie et Paléontologie, Florence); B, *Eucladoceros ctenoides* (Dubois), Senèze, France (Musée national d'Histoire naturelle, Paris); C, *Praemegaceros obscurus* (Azzaroli), Val di Chiana, Italie (d'après Abbazzi, 1995); D, *Leptobos etruscus* (Falconer), Upper Valdarno, Italie (IGF612, Musée de Géologie et Paléontologie, Florence).

Therefore, we conclude that the large-sized opportunistic herbivores had a certain advantage over the specialised feeders during the Early Pleistocene.

Another important extinction event of large-sized deer took place after 0.5 Ma. The almost simultaneous extinction of *Praemegaceros verticornis*, *P. solilhacus*, *Alces latifrons* and, probably, *Praedama savini*, resulted from unfavourable environmental changes of glacial epoch. We assume that the extinction was caused by the insufficient duration of the vegetation season that stopped the large-sized deer meeting the energy needs necessary to maintain their expensive biological cycle, including the growth of large antlers. For instance, the latest mainland survivor *Praemegaceros dawkinsi* already has small truncated and simplified antlers. Another instance is represented by comparatively smaller descendants of *Alces latifrons*, *Alces brevirostris* and *A. alces*, which also had relatively smaller antlers. The only surviving giant deer with enormous antlers, *Megaloceros giganteus*, had a specific adaptation for mineral element storage in the pachyostotic mandibles and cranial bones that, apparently, was used for the fast antler growth during a short summer season (Croitor, 2006b).

### 3.2 - EVOLUTION OF NON-RUMINANT HERBIVORE COMMUNITY

**Equidae** (11 taxa) and **Rhinocerotidae** (6 taxa) - Unlike ruminants, Perissodactyl species were much less numerous, and they follow the same tendency of diversity during most of the Plio-Pleistocene. Equids are more diversified than rhinos; the former show two relative peaks of diversity with 4 species (respectively ca. 1.5 - 1.3 and 0.5 - 0.3 Ma) while the later reach this score only around 0.7 - 0.5 Ma (fig. 1a).

During Late Pliocene, *Equidae* and *Rhinocerotidae* are represented by a single genus/species respectively (*Hipparion* sp. and *Stephanorhinus jeanvireti*), which made up only 10-15% of the total number of large-sized herbivore communities. The arrival of the first true horse *Equus* in Western Europe is an important dispersal event dated by ca. 2.5 Ma (Azzaroli, 1983) (fig. 2b). Together with earlier form *E. stenorhinus* and some other closely related species, which constitutes the so-called "stenonid" group, they survived in Europe until the beginning of the Middle Pleistocene (Bennett & Hoffmann, 1999). The "stenonid" lineage coexisted during a long time period ca. 2.2 - 1.0 Ma with the more advanced "caballoid" lineage, represented by *Equus bressanus* and *E. altidens*. Another structural change occurred around 0.8 - 0.6 Ma (end of *E. sthelini* and development of larger caballine forms). Caballoid horses are relatively diversified during the Middle Pleistocene and seem to present very successful ecomorphological forms during that period.

*Rhinocerotidae* were presented in Late Pliocene faunas by only one species: large-sized Early Villafranchian *Stephanorhinus jeanvireti* was substituted by smaller *Stephanorhinus etruscus* that appears in European records simultaneously with the first stenonid. *S. etruscus* is a special case in the Plio-Pleistocene herbivores. This species has the longest time duration, existing for almost 2 million years, until the Middle Pleistocene. Its disappearance together with *S. hundsheimensis* and the arrival of woolly rhino *Coelodonta* constitute an important change (fig. 2b). *Rhinocerotidae* became comparatively more numerous in Europe during the Middle Pleistocene with several contemporaneous genera: *Stephanorhinus*, *Dicerorhinus* and *Coelodonta*. A special case, similar to anagenetical process, is observable in *S. hundsheimensis*, which evolved tremendously from a size IV to a size V around 1.0 Ma (Lacombat, 2003). The number of species of

perissodactyls increases and achieves 20-35% of the total number of herbivores during the Pleistocene (with about eight species during the Middle Pleistocene, fig. 1b), demonstrating a certain ecological and evolutionary advantage in the unstable climate conditions that favored large open landscapes. As for the ruminant species, an increase of body size is observed at the transition from Early-Middle Pleistocene (fig. 6).

Finally, we can see a time lag in terms of taxonomic diversity between artiodactyls and perissodactyls during all the Plio-Pleistocene (fig. 1b). A recurrent lag can be observed in peaks of diversity between these two main herbivore groups, with a delay for perissodactyls. A first turnover peak occurred around 2.6 - 2.4 Ma and a second one at the transition from Early to Middle Pleistocene. Lastly, the monogastrics are strongly affected at the end of the Pleistocene and most of them vanished (fig. 2b).

## 4 - DISCUSSION

### 4.1 - ECOLOGICAL CONSIDERATIONS OF HERBIVORE COMMUNITY

The most striking difference between ruminant and non-ruminant herbivores is the constant low species diversity of the two non-ruminant perissodactyl families (fig. 1b). The explanation for this difference must be sought in the general ecological and evolutionary strategy of foregut and hindgut digestive strategies. Ruminants and non-ruminants have evolved principally different physiological and anatomical adaptations to cope with cellulose. The cellulose contained by plants makes this type of forage difficult for digestion since multicellular animals are not able to produce the enzymes that can break down cellulose. Both ruminants and non-ruminants independently developed a physiologically different type of symbiosis with cellulose producing bacteria, providing a fermentation chamber within the digestive tract where those bacteria can break down the cellulose (Janis, 1976).

Ruminants have evolved complicated anatomical and physiological adaptations for an effective extraction of nutrients from forage, like multi-chambered stomach, the cud chewing, and the repeated fermentation of food in the rumen before it passes the digestive tract. The rumination (foregut fermentation) enables a higher degree of nutrient extraction from forage and thus a more effective use of food resources if compared to non-ruminant herbivores. However, the adaptation to rumination sets some evolutionary and ecological limitations. The size of orifice between the reticulum and omasum in the ruminant's stomach acts as a sieve and ensures the effective fermentation until the food particles are reduced to a certain size (Campling, 1969), so particularly fibrous food with low nutrient value needs a longer time of fermentation in the rumen to be reduced to a size necessary to pass through the omaso-reticular orifice. Consequently, the longer

fermentation time required for a low-quality food increases the time between the animal's food intakes. According to Janis (1976), the dependence of cellulose content in food sets a cut-off point in the percentage of fibre in the diet that a ruminant herbivore can tolerate, beyond which it would be unable to support itself. Such physiological and anatomical adaptation of ruminants made them highly competitive in the ecological niche of specialised herbivores with a preference for forage low in fibre. The rumination restricts the range of optimal body size from *ca.* 5 kg (ex. size of antelope Neotragini and Cephalophini) up to 1000 kg in grazers (ex. size of *Bison* and *Bos*) and *ca.* 1400 kg for browsers (the maximal size of a male of *Giraffa camelopardalis*) (Clauss *et al.*, 2003). Below the lower limit of the body mass the rumination cannot support the high rate of the animal's metabolism (Janis, 1976), while the upper size limit depends on the time food takes to pass through the gastrointestinal tract which becomes too long causing the destruction of nutrients by methanogene bacteria and the inadaptive increase of rumen capacity that requires the compensatory diminishing of size of other abdominal organs (Clauss *et al.*, 2003).

Non-ruminant herbivores (or caecalids/ monogastrics), have evolved a hindgut fermentation of food that does not depend on the time of fermentation and the size of food particles (Janis, 1976). The ingested food after the passage through the stomach is additionally processed by fermentation in the caecal part. The cellulose fermentation is less effective in this case, however the hindgut fermentation does not set the limitations on the food ingestion rate. Such a strategy is essential for the use of forage above the critical for a ruminant fibre content level and allows a caecalid to survive on low quality forage. Therefore, Equids developed a tolerance to high fibre content in forage, thus avoiding competition with ruminants. Such a specific ecological space occupied by Equids does not provide a variety of ecological niches and thus diminishes significantly the species radiation. Equids are known to be non-selective extensive grazers, which opportunistically may be mixed feeders if there is no direct competition with ruminants (Kaiser, 2003; Kaiser & Franz-Odentaaal, 2004).

*Rhinocerotidae* represent a different strategy in avoiding competition with ruminants. The animals of this group are very large graviportal herbivores. As hindgut fermentation herbivores, rhinoceroses have no physiological restrictions in body mass and normally attain a body size exceeding the physiological maximum for bovids. The extremely large size gives some advantages for rhinos in relatively smaller energetic requirements due to the lower rate of metabolism and a success in competition for food resources due to the simple ecological interference (Janis, 1976; Clauss *et al.*, 2003). However, from the other side, the extremely large body size diminishes the number of available ecological niches and, as in the case of Equids, causes poor species radiation. Beside the certain advantages of the ecotype evolved by Rhinocerotid, T.M.Kaiser and R.D.

Kahlke (2005) report the highly flexible foraging habits for Middle Pleistocene *Stephanorhinus etruscus*. The mesowear analysis of fossil samples of *S. etruscus* from Voigstedt characterized this species as a typical browser, while the paleodiet reconstruction based on the sample from Süssenborn characterized it as a moderate grazer (Kaiser & Kahlke, 2005). Perhaps, such an extreme ecological flexibility explains the unusual case among herbivores for the longevity of this species.

The increase of importance of non-ruminants in the herbivore communities during the Middle and Late Pleistocene can, probably, be explained by a combination of environmental factors, which were less favorable for ruminants, but did not significantly affect the ecological requirements of hindgut herbivores. The limiting factors for ruminants during this period could be the low nutritional quality of forage rich in cellulose, the dominance of open landscapes and severe climate conditions that affected mostly small and medium-sized ruminants. The explanation of the time lag in the non-ruminant taxonomic diversity dynamics (fig. 1b) must also be sought in the evolutionary strategy of this systematical group.

#### 4.2 - EVOLUTION OF BODY MASS STRUCTURE OF THE HERBIVORE COMMUNITY

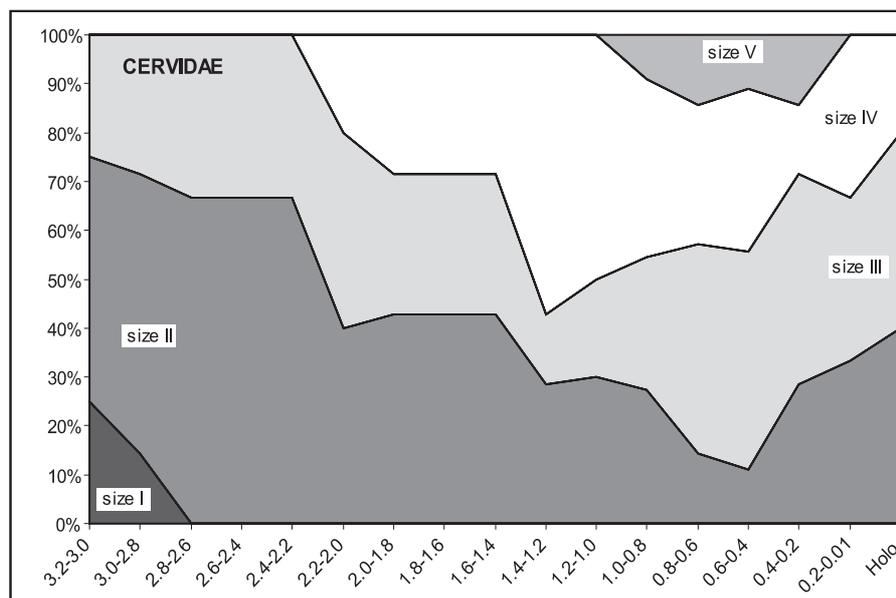
The body mass structure is depicted for Cervids, Bovids and Equids + Rhinocerotids respectively (fig. 4 to 6). Different body size compositions are present throughout time. The Late Pliocene artiodactyls are represented by very small-sized forms (size class I), small-medium size forms (class II), which represent almost half, and large-medium size forms (class III); the perissodactyls are size class III and V (this last is the giant rhinocerotid *S. jeanvireti*). A first important change in body mass structure in the herbivore commu-

nity took place around 2.5 Ma, when the size class IV emerged, especially in Cervids and Equids. This size class greatly expands to represent half of herbivores taxa. This process is concomitant with the diminution and extinction of size classes I and II; especially the forest-dwelling small cervids like *Muntiacus*, *Eostyloceros* and *Procapreolus*, and small Bovids, mostly caprines and antilopines.

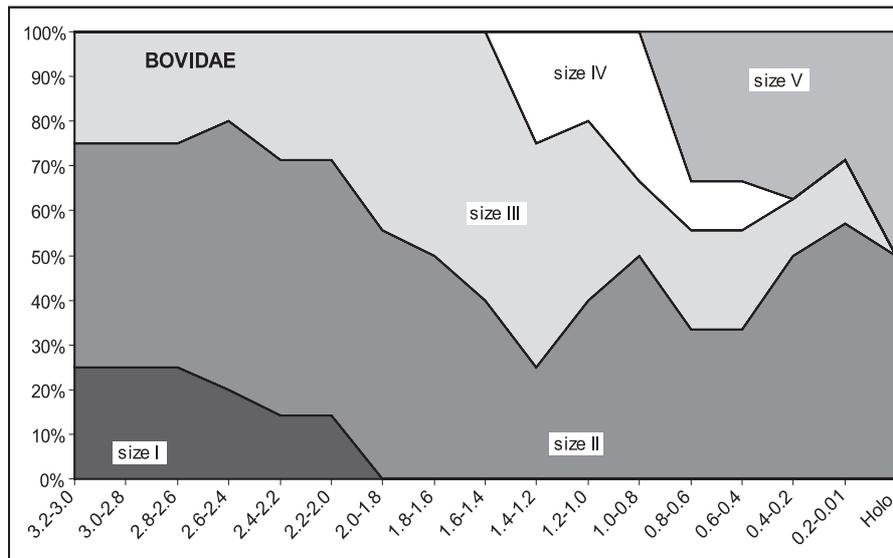
The evolution of body size structure within the groups of *Cervidae* and *Bovidae*, shows a similar trend with some delays between them (fig. 4, 5). This similarity suggests an evolutionary parallelism in those two families of ruminants. Nevertheless, a certain difference was observed in the time of extinction of smallest body size class I, which was more rapid in cervids, while the small-sized bovids survived until almost 2.0 Ma. Bovids also first occupied the new ecological niche of large-sized ruminant (class IV) in Late Pliocene. The similar ecological form in cervids (*Alces gallicus*) entered Western Europe later, ca. 2.0 Ma.

An approximate two-fold increase in body mass is observed in various phylogenetic groups of large-sized deer and bulls during the Early Pleistocene: *Leptobos* (mean ca. 320 kg) - *Eobison* (ca. 500 kg) - *Bison* (ca. 700-750 kg); *Eucladoceros* (ca. 250-300 kg) - *Praemegaceros* (ca. 500 kg); *Arvernoceros sp.* from Liventzovka (ca. 345 kg) - *Arvernoceros cf. verestchagini* from Apollonia (ca. 700 kg); *Alces gallicus* (ca. 400 kg) - *Alces latifrons* (ca. 870 kg); *Dama vallonnetensis* (70 kg) - *D. clactoniana* (140 kg) (Brugal & Croitor, 2004). This phenomenon in body mass evolution is not observed in many ruminant groups specialized to mountain habitats (*Capridae*) or forests (*Capreolus*), where the body size is strongly controlled by specific ecological conditions.

The sharp increase in importance of larger size class IV+V starts from 1.6 - 1.4 Ma and achieves almost 60%



**Fig. 4: Dynamic of body mass change within family Cervidae during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**  
 Fig. 4: Dynamique des changements de taille (masse corporelle) chez les Cervidés du Plio-Pléistocène d'Europe (abscisse: tranche d'âge de 0.2Ma + Holocène).



**Fig. 5: Dynamic of body mass change within family Bovidae during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**  
 Fig. 5: Dynamique des changements de taille (masse corporelle) chez les Bovidés du Plio-Pléistocène d'Europe (abscisse: tranche d'âge de 0.2Ma + Holocène).

of the total herbivore community by ca. 0.8 Ma (fig. 8). Such a significant change in the community body size structure occurred mostly with the increased importance of large-sized deer of the genera *Alces*, *Arvernoceros* and *Praemegaceros*, and few large-sized bovids (*Eobison*, *Bison*) during the Early Pleistocene. This trend toward the increase of body mass in herbivores became stronger during the Middle Pleistocene, when the larger size class V becomes important (ca. 30%), composed by such very large herbivores as *Rhinocerotidae*, *Bovinae* (*Bison*, *Bos*) and one cervid species *Alces latifrons*. Bovids are more successful in this ecological niche than cervids. Early Middle Pleistocene representatives of the size class V *Bison schoetensacki* (ca. 900 kg) and *Alces latifrons* (ca. 800 kg) are the largest ruminant species from European paleontological records. However, the body size attained by *A. latifrons* is rather an exceptional case for cervids. It seems that the energy investment of large-sized deer in the yearly renewable antlers is very costly and sets the body size upper limit somewhat lower than in other ruminant families. The largest European fossil deer, *Arvernoceros verestchagini* (ca. 700 kg) and *Alces latifrons* (ca. 870 kg) have had relatively small and simple antlers that may be regarded as support for our conclusion. The majority of Pleistocene large-sized deer of genera *Praemegaceros* and *Megaloceros* did not surpass the estimated body size of 500 kg. Their relatively larger and more complicated antlers are a specific eco-morphological peculiarity. Apparently, the high energy costs of large antlers in cervids explains why the largest body size class was represented mainly by bovids, which attained the maximum possible body size for the ruminants according to the eco-physiological constraints suggested by Clauss *et al.* (2003).

The simultaneous body mass increase in several lineages of ruminants may be explained as a reply to the

environmental changes rather than the co-evolution with predators, since the body size of predators did not increase during that epoch. The selection forces toward the larger body size in Early Pleistocene ruminants may have a complicated and complex character. Apparently, the zoogeographic Bergman's Rule cannot fully explain the remarkable body mass increase in ruminants since there is no clear evidence of similar trends in body mass change in other mammal groups (carnivores, non-ruminants). Koehler (1993) claims the large body size as an advantageous adaptation for herbivores in the open-landscape conditions, since it enables them to successfully escape pursuing predators and to cover long distances while searching for new forage places and water. We assume that the climate dryness and the increase of cellulose fiber content in the plants may also be an important factor in the body mass increase, since the larger body size enables ruminants to tolerate the higher percentage of cellulose fiber in forage and maintain themselves on the low-quality forage, as Janis (1976) has shown for modern ruminants.

During the Late Pleistocene and Early Holocene, the size structure of European herbivores is composed of small-medium sized ruminants of size class II (almost 40% of the guild species), and in equal proportions the size classes III (*Cervus elaphus*, *Rangifer tarandus*), IV (*Equus caballus*, *Alces alces*) and V (*Bison bonasus*, *Bos primigenius*). Such a comparatively balanced size distribution of the large herbivore community established by the beginning of the Holocene, lacking very small herbivores and including several large-sized ruminants, has no analogues among the fossil faunas from the last three millions years. In the Early Holocene fauna, bovids dominate in the ecological group of small-sized specialized ruminants (*Rupicapra rupicapra*, *Saiga tatarica*, etc.) and giant mixed feeders (*Bos primigenius*, *Bison bonasus*), while deer occupied the niche of medium, medium-large

opportunistic mixed feeders (*Cervus elaphus*, *Dama dama*, *Rangifer tarandus*) and the large-sized browser (*Alces alces*), with partially overlapping areas of distribution. Only one deer species (*Capreolus capreolus*) belongs to the small-sized ecological group of ruminants, representing a very specific niche of boreal small-sized browser with such unusual biological adaptation to seasonality, as prolonged gestation (Geist, 1998).

### 4.3 - INTERACTION WITH THE COMMUNITY OF CARNIVORES

The Plio-Pleistocene development of carnivore community and its interrelationship with herbivores is an interesting and a promising subject of research (e.g., Brugal & Fosse, 2004). Here we quote some preliminary considerations regarding mammal predators as an ecological factor that, potentially, may influence the development of herbivore community. Unlike herbivores, carnivores are normally long-living ubiquitous species with a very large distribution range that, to a lesser extent, depends on minor climate shifts. The African carnivore guild had the modern structure and taxonomic composition since 1.5 Ma, while the archaic composition of mammal predator group including saber tooth felids lasted in Europe until ca. 1.2 - 1.0 Ma (Turner, 1992). The development of large-sized herbivores in Europe (1.0 - 0.5 Ma) was followed by the, more or less, simultaneous extinction of rather large felid predators like *Acinonyx pardinensis*, *Homotherium crenatidens*, *Megantereon cultridens* and *Puma pardoides* (e.g., Brugal & Croitor, in press). The dominance of large-sized herbivores in Early Pleistocene faunas gives an impression of unbalanced character of fauna with archaic Pliocene hypercarnivore predators that were mal-adapted to extremely large species of cervids and bovids that arrived in Europe from Asia. However, the causes of Pleistocene felid extinction may be more complicated. Most probably, the diminution of wooded habitats has also had a critical importance for the survival of specialized hypercarnivores. The highly advanced saber tooth felids appeared to be the most sensitive predators to environmental changes. Since most of the large felids were ambush-predators (Palmqvist, 2002), they were not able to successfully pursue large-sized prey in an open landscape. The expansion of open savannas in Africa caused the restriction of *Homotherium* and *Megantereon*'s area of distribution to the more wooded landscapes of Europe. The progressive dryness of the Early Pleistocene European climate and progressive reduction of woodlands could have had a dramatic impact on the survival of specialized hypercarnivore ambush-predators.

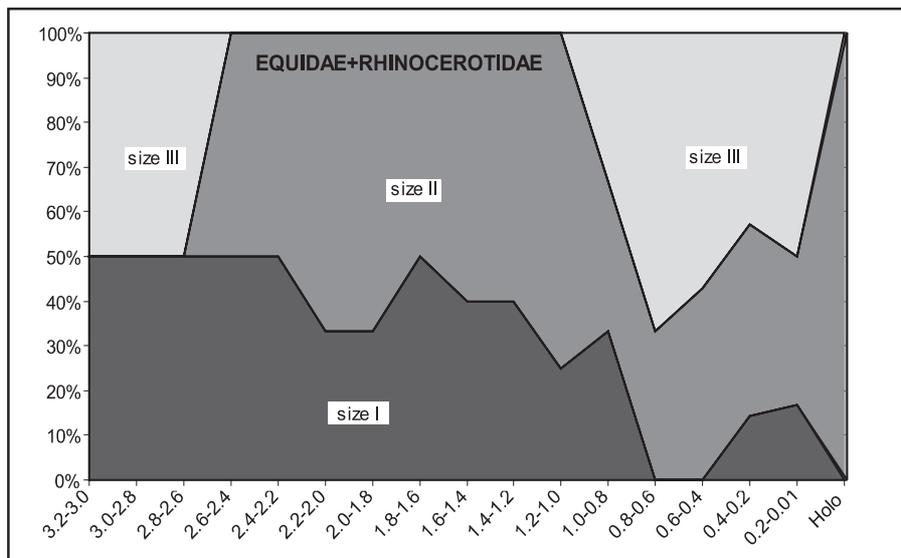
Anton *et al.* (2005) join the opinion of Balleisio (1963) and Marean (1989), who suggested that *Homotherium crenatidens* was poorly adapted for fast running and thus was not able to pursue prey in open habitats. This conclusion derived from the postcranial proportions with relatively long and strong forelimbs

and rather short hindlimbs. It suggests that this predator profited from the sudden attack of prey and fast killing by specialized canines. This kind of hunting must be less expensive energetically and efficient only if the prey is attacked suddenly from ambush, which required a wooded environment as a necessary condition. However, Anton *et al.* (2005) argued speculatively that it might be an open-landscape predator that compensated its low running capability by social hunting behavior. Apparently, the social behavior of a predator also depends on the character of the landscape. Pack hunting requires a more open environment that enables visual interaction between members of the predator group while pursuing the prey. Therefore, the social behavior of *H. crenatidens* seems to be improbable.

The genus *Megantereon*, probably depended even more strongly on wooded habitats than *Homotherium*. *Megantereon* was comparatively smaller, with relatively shorter and stronger limbs, reminiscent of a tree climbing type of predator (Savage, 1977). Marean (1989) assumed that the ecological partitioning between *Megantereon* and *Homotherium* could be vertical, since the latter felid is too large to be an effective climber. Such a strong ecological attachment to forested habitats may explain the earlier extinction of *Megantereon* than *Homotherium* in Europe.

The failure of the majority of Early Pleistocene mammal predators in the adaptation to new open environmental conditions and the dominance of large-sized herbivores are interesting. Andersson & Werdelin (2003) have noted that the adaptation to cursoriality and large body mass are two mutually exclusive directions of evolution in Tertiary carnivores. Savage (1977) has also noted that increase in body mass must greatly affect speed ability, which is an important condition in hunting success. Thus, body mass of a cursorial predator rarely reaches 100 kg, while larger mammal predators are not able to develop the adaptations to cursoriality. The majority of specialized cursorial carnivores, like extant canids, hyaenids and cheetah *Acinonyx jubatus* are far below the 100 kg limit (Andersson & Werdelin, 2003; Silva & Downing, 1995). So, the evolutionary direction toward the increase of body size combined with cursoriality was unsuitable for Pleistocene predators.

The lion *Panthera leo* that arrived in Europe ca. 1.0 Ma is a special case of the Pleistocene carnivore guild in Europe. Apparently, it was the most effective European predator in the open-landscape environment, with a maximal estimated body mass of ca. 200 kg. Nevertheless, lions maintain generalized felid postcranial proportions and are not able to pursue prey for long distances; but their cooperative hunting habits ensure their predation success. The rather unusual social behavior and group predation among felids reported for the modern African lions must be true also for the fossil European subspecies. A pack of Pleistocene lions were able to capture such large herbivores as bison. Therefore, lion was the top carnivore species that



**Fig. 6: Dynamic of body mass change within family *Equidae* and *Rhinocerotidae* during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**

*Fig. 6: Dynamique des changements de taille (masse corporelle) chez les Equidés et les Rhinocérotidés du Plio-Pléistocène d'Europe (abscisse: tranche d'âge de 0.2Ma + Holocène).*

successfully adapted to the open environments and domination of large-sized herbivores.

The cooperative cursorial hunters of the family *Canidae* represent the alternative direction of carnivore evolution. Sardella & Palombo (2007) regard the dispersal of several lineages of hypercarnivore pack hunting dogs at the beginning of the Pleistocene as an important bio-event that has changed the structure of carnivore community and the whole Pleistocene fauna. The collective hunting behavior is an ethological adaptation compensating the low cursorial abilities in lions and rather small body size in canids.

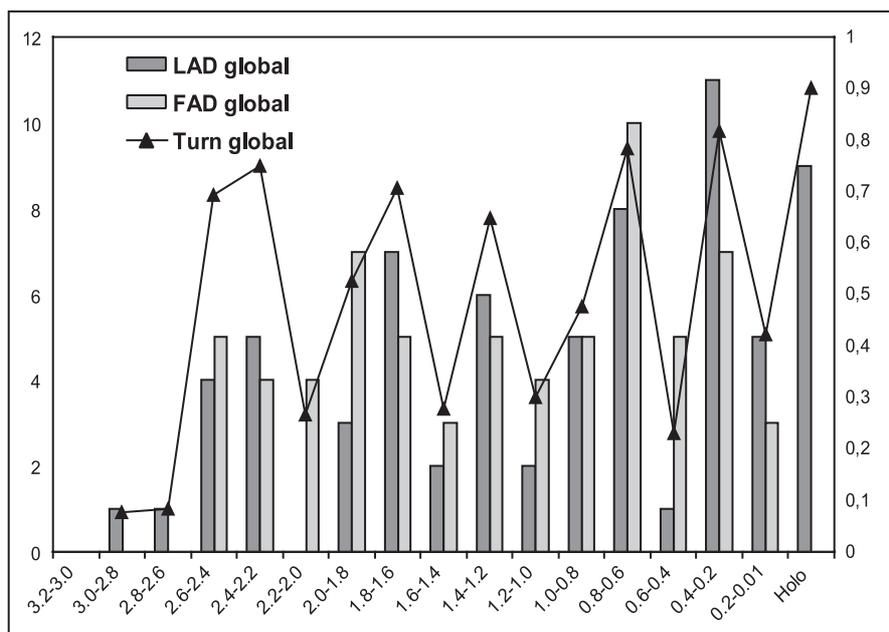
*Pachycrocuta brevirostris* is a very particular giant representative of the Hyaenidae family that attained a body size of modern lion. The area of origin of *P. brevirostris* is not yet clear, since the oldest remains of this species dated back to 3.0 Ma are reported from Africa and Eastern Eurasia (Turner & Anton, 1996). Arribas & Palmqvist (1999) assumed an African origin of this species and its dispersion to Europe in the context of hominid and *Megantereon* arrival in the European continent. However, in our opinion, this hypothesis is doubtful. The arrival of *P. brevirostris* in Europe is more or less synchronous with mass migration of large-sized ruminant herbivores from Asia to Europe (ca. 1.4 - 1.2 Ma). The giant hyena may be a result of evolutionary co-adaptation with large-sized and robust herbivores, and first of all cervids (*Alces*, *Arvernoceros*, *Eucladoceros*) and bovids (*Leptobos*), that appeared in the early Villafranchian in Asia. The postcranial proportions of *P. brevirostris* with short distal limbs suggest that it must be a less agile predator than modern spotted hyena (Turner & Anton, 1996). The extinction of *P. brevirostris* around 0.5 Ma, apparently, had a strong connection with the extinction of the last representatives of cervid genera *Praemegaceros*, *Praedama*, the disappearance of *Alces latifrons* and the

extinction of felids *Dinobastis latidens* and *Panthera onca gombaszoegensis*, which were ecologically associated with those large cervids. Turner & Anton (1996) have also assumed in general traits a complex mutually conditioned extinction event of giant hyena, large felids and some large-sized herbivores.

The question of a possible influence of carnivores over the evolution of Plio-Pleistocene large-sized ruminants is particularly interesting. But, according to the differential timing of turnover between preys and predators (Caloi *et al.*, 1997; Brugal & Croitor, in prep.), it seems not to be the case. First of all, the development of large-sized ruminants coincided with the extinction of several important solitary mammal predators. Lion, the large collective hunter of African origin, certainly could not be a factor of body size evolution in Asian cervids and bovids, while hypercarnivore dogs emerged much later than Asian large-sized ruminants. The only species that may be involved in co-evolution with large Asian herbivores is *Pachycrocuta brevirostris*, which, however, was a specialized scavenger; thus its selective importance in the body size evolution of herbivores could not be significant.

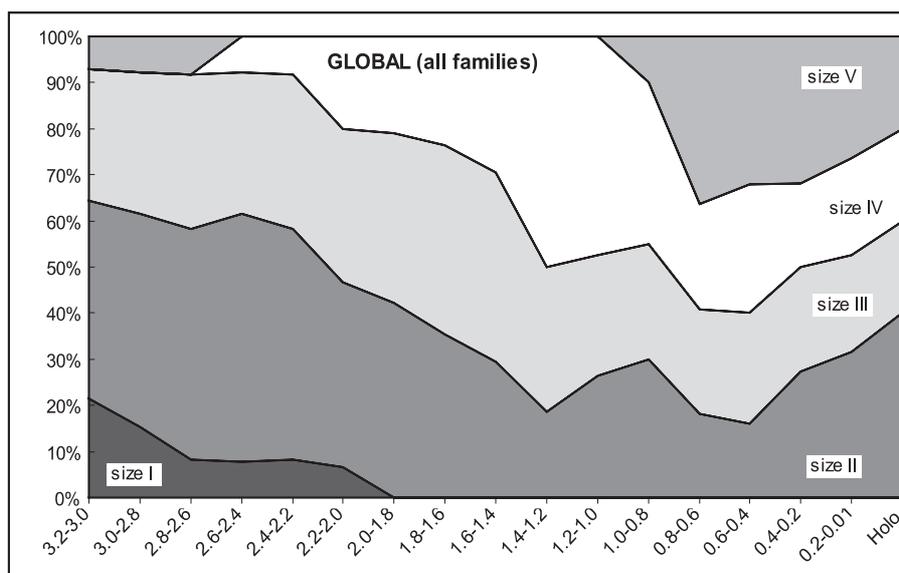
#### 4.4 - EVOLUTION OF HERBIVORE COMMUNITY AND BIOCHRONOLOGY OF QUATERNARY

Our analysis is based on different criteria: taxonomic diversity at specific and familial level, degree and relationships between apparition (FAD) and extinction (LAD) of species and/or lineage with main changes (turnover), and the ecological structure of herbivore associations expressed by body size classes according to familial, ordinal or global level. Global information, combining ruminants and monogastrics, are given in fig. 7 and fig. 8, and synthetic data are expressed in fig. 9.



**Fig. 7: Global (all families) turnover with Lad and Fad during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**

*Fig. 7: Changement faunique global (toutes familles confondues) avec dernière (LAD) et première (FAD) apparition des taxons du Plio-Pléistocène d'Europe (abscisse: tranche d'âge de 0.2Ma + Holocène).*

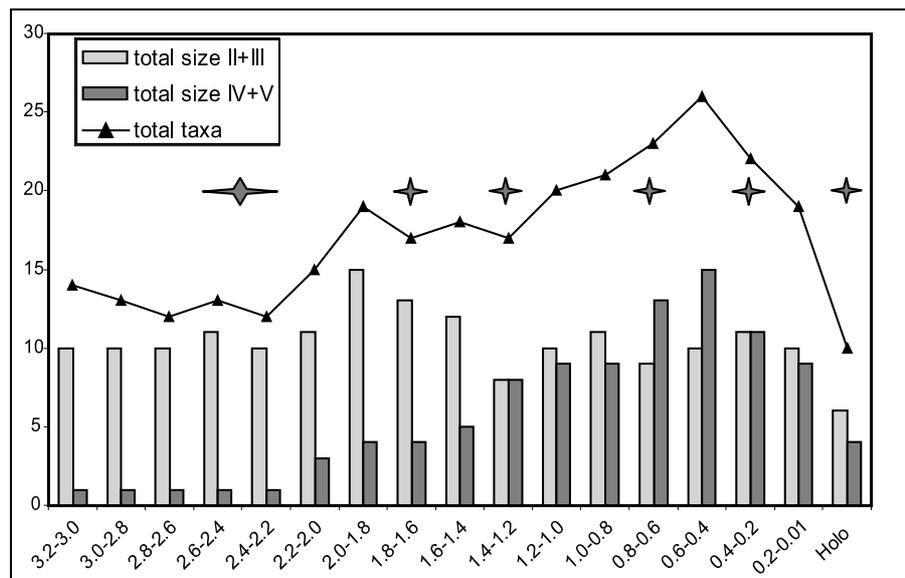


**Fig. 8: Global (all families) size change during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**

*Fig. 8: Changement de taille global (toutes familles confondues) des taxons du Plio-Pléistocène d'Europe (abscisse: tranche d'âge de 0.2Ma + Holocène).*

The ecological significance of digestive strategies and the dynamic of body mass changes constitute important factors which allow us to distinguish major bioevents. Several successive chronological phases can be recognized from European herbivore megacommunities. However, it is important to stress the question of differential responses among ruminants (Bovids vs Cervids) as well as between ruminants and monogastrics. The six main turnover peaks recorded for the last 3 million years are global (fig. 7) and are not accurate enough to express fixed and definitive chronological limits, and phases would be reported to the main and classical division of Plio-Pleistocene period.

**'Late Pliocene'** - A first main, and essential, turnover occurs for a relatively short period between 2.6 - 2.2 Ma, characterized by the end of small ruminant forms, of tropical (or 'tertiary') affinities and the appearance of herbivore body size IV, of modern design. This period is followed by FAD superior to LAD at the beginning and ending with more LAD at 1.8 - 1.6 Ma. The  $2.4 \pm 0.2$  Ma 'limit' is more or less synchronous with the establishing of the 41 kyr glacial cycles (De Menocal, 2004). The climate change in Europe was marked by the increased seasonality and significantly decreased precipitations (Mosbrugger *et al.*, 2005). The shift of climate to colder and drier conditions



**Fig. 9: Synthetic diagram about diversity, main size classes and turnover (stars) during Plio-Pleistocene in Europe (abscissa: 0.2 Ma time-slices + Holocene time).**

Fig. 9: Diagramme synthétique sur la diversité, les principales classes de taille et les changements fauniques (étoiles) au cours du Plio-Pléistocène en Europe (abscisse: tranche d'âge de 0.2 Ma + Holocène).

caused decisive changes in the structure of herbivore community. The number of deer species decreased due to the extinction of small-sized species, and soon after *Equus* and *Leptobos* appear in Europe. Bovids became a dominant group of the herbivore community (fig. 1a). This new ecological type of medium-large size herbivores indicates the significant decrease of forests and the extension of open wooded landscapes. Those faunal changes represent a part of Azzaroli's "Elephant-*Equus*" dispersal event marked by the arrival in Europe of primitive elephant *Mammuthus gromovi* and a true monodactyl equid *Equus livenzovensis* (Azzaroli, 1983).

The significance of this reorganization of Pliocene fauna needs a special comment in the context of the question of lower boundary of Quaternary proposed to be established at the base of the Gelasian stage (2.6 Ma). Actually, the faunal dispersals, as such, are of minor importance (especially in herbivores) since they have, in many cases, a local significance and cannot even be used as biostratigraphic markers between distantly located regions of Europe (Spassov, 2003; Brugal & Croitor, 2004). In our opinion, the zoogeographical processes that started at the base of the Gelasian are of greater importance. At this point, the climate shows an irreversible shift which produced important changes in herbivore fauna, including the extinction in Europe of the last tropical small-sized ruminants (*Muntiacus*, *Procapreolus*) and the development of larger forms, the appearance of a new adaptive ecological zone in Europe (open landscape with increased seasonality), the fragmentation of the area of distribution of some species with subsequent speciation (archaic *Eucladoceros*), the beginning of multiple cyclic migration events that caused a high rate of species turnover and continuous faunal migrations in Northern Eurasia for at least the next two million

years. The Ruscian paleozoogeographical regions vanished and the modern zoogeographical zonation started to evolve in Eurasia. Therefore, the setting up of a modern Palearctic zoogeographical region in northern Eurasia may be a potent indicator for the lower boundary of Quaternary.

**'Early Pleistocene'** - Two turnover peaks are marked by LAD superior to FAD, dated respectively at 1.8 - 1.6 and 1.4 - 1.2 Ma. Ruminant decreases, especially Bovids, whereas Equids increase relatively and the global diversity shows a plateau with a mean of 18 taxa. These events coincide with further climate cooling and higher amplitude 41 kyr cycles, inducing increase of seasonality and, for the first time in Europe, the drop of the mean temperature of cold month below freezing point, as it was shown for Central Europe (Mosbrugger *et al.*, 2005). The structural change concerns, first of all, the body mass structure of the herbivore community due to several migration events of large-sized forms.

The first faunal turnover is traditionally called "the wolf event", based on carnivore dispersal (Azzaroli, 1983); like the arrival of a rather small-sized wolf *Canis etruscus* and a giant hyena *Pachycrocuta brevirostris*. The appearance of cursorial pack hunters and powerful scavengers seem to be perfectly adapted to large-sized herbivores. Azzaroli's term "wolf event" itself is rather arbitrary since the occurrence of wolf similar to *Canis etruscus* in Europe is recorded much earlier, in Podere del Tesoro (Torre, 1967) dated by *ca.* 2.5 - 2.6 Ma (Azzaroli, 2001). According to Sardella & Palombo (2007), the simultaneous dispersal of several lineages of canids and the advantage of a new ecological type of pack hunters is a much more important bio-event characterizing the "wolf event". This stage is marked by the extinction of archaic ruminants

*Croizetoceros*, *Gazellospira*, *Gallogoral*, *Procamptoceras* (Torre *et al.*, 2001) and is followed by *Megalovis* and the first archaic representatives of *Cervus* and *Dama*; the second turnover is correlated with the extinction of *Eucladoceros* as well as some species of *Leptobos*.

These bioevents are particularly important and led to a phase, until 1.0-0.8 Ma called the 'end-villafranchian' event, where the fauna show a lower degree of diversity with strong biogeographical factors, reinforced by the particular topographic feature of Western Europe with peninsular conditions. The period bracketed between 1.8 - 1.6 to 1.0 - 0.8 Ma, which are usually regarded as separate events of faunal turnover in Europe, represents the beginning and one of the latest phases respectively of a complicated and continuous process of faunal changes resulting from multiple immigrations of herbivore species from the Asian continent. These newly formed faunas were rather unbalanced. The changing unstable cold Pleistocene climate gave the advantage to large-sized opportunistic herbivores with flexible ecological habits and a broad range of food specialization (Lister, 2004).

The case of large-sized deer (ex. *Praemegaceros*) may demonstrate the zoogeographical mechanism of such multiple and asynchronous immigrations. It seems to be a sister lineage that evolved from an archaic Late Pliocene *Eucladoceros* form with a very large area of distribution ranging from China to Western Europe located along the northern side of the Alpine mountain chain. The climate shift toward aridity and seasonality caused the fragmentation of this originally large distribution area. It induces the evolution of several *Eucladoceros* species in Europe and China as well as several *Praemegaceros* lineages in the area of Central Asia (Croitor, 2006b). The subsequent climate deterioration during the Early Pleistocene caused the migration of Asian cervid species toward Western Europe. These new migrants co-existed and overlapped with European species counterparts. Open treeless landscapes became predominant in Europe, with the possible exception of North-Western Europe where, under the influence of the Gulf Stream, the relict forests allowed the survival of some archaic Villafranchian herbivores (like cervids); it can also be the case for mountainous area (ex. French Massif Central) (Brugal & Croitor, 2004).

The "end-Villafranchian event" is marked by the extinction of the majority of Villafranchian ruminant species, like *Eucladoceros ctenoides*, *Metacervoceros rhenanus*, *Praemegaceros obscurus*, small-sized Villafranchian *Cervus* and *Dama*, *Eobison tamanensis*. *Leptobos* and *Eucladoceros dicranios* became extinct somewhat earlier. Descendants of some Villafranchian deer lineages survived into the Middle Pleistocene in limited areas of Western Europe, such as *Praemegaceros dawkinsi*, a possible descendant of *P. obscurus* (Croitor, 2006b) and "*Eucladoceros*" *mediterraneus* (a possible descendant of *Metacervoceros rhenanus*, Croitor, Bonifay and Brugal, submitted).

**'Middle-Late Pleistocene'** - A very high turnover peak with prevailing extinction events occurred around 0.8 - 0.6 Ma. This was a complex event that started at *ca.* 1.0 Ma and included several faunal events of different origin; FAD is superior to the LAD during all the period 0.8 to 0.4 Ma with high herbivore diversity. It is correlated with a significant climatic change occurring after the Jaramillo magnetic reversal event of 0.95 - 0.9 Ma and establishing Pleistocene glacial/interglacial cycles with very broad temperature oscillations of 100 kyr cycles (Palombo *et al.*, 2002; Azanza *et al.*, 2004; De Menocal, 2004; Sardella *et al.*, 2006). We assist in Europe at a maximal predominance of large-bodied herbivores (size V) due to regular and multiple migrations waves of ruminant species of genera *Praemegaceros*, *Arvernoceros*, *Cervus*, *Dama*, *Ovibos*, *Bos* and *Bison* from Asia. They constitute herbivore associations of modern type and of larger body size. The migration ways follow the East-West climate gradient from strong continental and seasonal conditions in the Asian heartland to a mild humid climate that maintained in Western Europe for a longer time (Brugal & Croitor, 2004).

Finally, a higher peak of turnover marked by numerous extinctions (LAD > FAD) started from 0.4 Ma to Holocene. The faunal change during the Late Pleistocene is mostly restricted to the extinction of large-sized herbivores, especially Cervids. We can point out the extinction of species such as *Praemegaceros verticornis*, *P. solilhacus*, *Praedama savini*, *Alces latifrons*, *Soergelia elisabethae*, *Praeovibos*, *Bison schoetensacki*. The steppe bison lineage shows a clear size reduction. The larger equid forms of Equids (*mosbachensis*, *sussenbornensis*) disappear, and smaller taxa appear (*hydruntinus*, *germanicus/gallicus*). The reduction of taxa diversity is noticeable in Western Europe until the Holocene, and constitutes a final turnover leading to the recent herbivore community.

## 5 - CONCLUSIONS

The analysis of evolution, species turnover, dynamics of ecological structure and paleozoogeography considerations of the herbivore community (with the exception of proboscids and suids) during the last 3 million years, has revealed a relative correlation of herbivores to climate changes, although the evolutionary response has varied in different taxonomical groups. These responses are largely due to their evolutionary and ecological strategies. The herbivore community shows a relatively continuous and cyclic species turnover, a rather variable lifetime of species depending on climate stability and a deep reorganization of ecological structure (taxonomic composition, body mass structure) as a feedback to climate changes. The first important peak of turnover within the herbivore paleocommunity is recorded at STU 2.4 - 2.6 Ma, synchronous with the establishing of the 41 kyr glacial cycles (De Menocal, 2004) and climate shift toward

drier conditions. The most vulnerable herbivores like Ruscinean tropical and subtropical *Muntiacinae* and *Odocoileinae* deer became extinct and the modern type of ruminants, with large body size appeared. At this point, and connected to induction of global glacial/interglacial cycle, regular and cyclic faunal changes occurred in Western Europe for the last 3 Ma. This phase ( $2.5 \pm 0.1$  Ma) corresponds to the setting up of a new zoogeographical Palearctic region in Northern Eurasia and we consider that it indicates the beginning of the Quaternary period starting at the base of Gelasian (2.6 Ma).

After a period of relative stability (2.2 - 1.6 Ma), the guild of herbivores renewed with repetitive species turnover at 1.8 - 1.6 Ma, 1.4 - 1.2 Ma and 0.8 - 0.6 Ma, accompanied with large variation of taxa diversity according to the different taxonomic and feeding groups. This period of faunal evolution coincided with higher amplitude 41 kyr cycles and a shift toward cooler conditions with more contrasting seasonality. The increase of glacial cycle amplitude after *ca.* 1.8 - 1.6 Ma gave advantage to opportunistic mixed feeders like *Leptobos*, *Eucladoceros*, *Praemegaceros*, *Cervus*, *Dama*, and seems concomitant with an increase of perissodactyls. This process became more pronounced with the onset of high amplitude 100 kyr cycles around 1.0 Ma, implying radical turning in the evolution of the herbivore community (known as the “end-Villafranchian” event). The structural changes of the herbivore community during the Early Pleistocene occurred, mostly, due to the intensive evolutionary processes and migrations of ruminants, namely bovids and cervids. The complicated morpho-physiological specialization to foregut fermentation made ruminants particularly sensitive to floral and climate changes. Lastly, starting from the late Middle Pleistocene, extinction events dominated in the herbivore guild.

Multiple immigrations of large-sized cervids and bovids took place from the Asian continent. The driving factors in immigration were the increase of global climate aridity and continentality, as well as the gradient of climate across the continent from relatively more arid continental conditions in Eastern Europe to the mild, humid climate in the west of the continent. Hygrometric factors, such a change in timing, duration and importance of rainy season, could be as important as change in paleotemperatures (Bonifay & Brugal, 1996). As a result of faunal migrations, a two-fold body size increase is observed simultaneously in several lineages of bovids and cervids. Since such a parallel evolutionary response is recorded only in ruminants, and is not observed in non-ruminant herbivores and in carnivores, the most plausible explanation is that the adjustment of body size to the cellulose content in the available forage is the leading factor defining body size in this case.

Interestingly enough, the number of small-medium and medium-large herbivore species (size II and III) is rather constant during all the Plio-Pleistocene and varies around 10 species (fig. 9). The stable number of this

body-size group, which includes various specialized forest, woodland, and mountain species, suggests a permanent existence of woodland and mountain ecological niches in Europe, favored by local rain distribution. This point also stresses the importance of biogeographical factors in the faunal spreading into the sub-continent (Bonifay & Brugal, 1996); as for example, the case of peri-Mediterranean regions or at a south-European scale. The group of large and very large herbivores (size VI and V) does not show such stability. The apparition of this group, called giants for size V, started at the beginning of the Late Pliocene and increased regularly toward a peak recorded during the Middle Pleistocene, coinciding with the highest richness of the herbivore community. Such development indicates the emergence of a new adaptive zone, which provided a variety of ecological niches for large and very large herbivores. Another important point can also be raised concerning the differential adaptive response between the two main herbivore groups, between ruminants and non-ruminants, and even the variation observed in faunal renewal between Bovids and Cervids. Then, the calculation and global based analysis of turnover can induce misinterpretations of complex ecological phenomenon.

The specific evolutionary response causes a transitional phase of “unbalanced continental fauna” and a remarkable contrast between herbivore and carnivore communities. The Early Pleistocene carnivore guild of Europe is dominated by solitary ambush-predator felids and rather small-sized cursorial species contrasting with the late Villafranchian large-sized herbivores. The critical climate changes recorded around 1.0 Ma caused the extinction of specialized solitary ambush-predating hypercarnivores, which were mal-adapted for open landscapes inhabited by a new type of prey. Since the large body size and cursorial adaptations are mutually exclusive evolutive trends in carnivores, the most successful evolutionary directions in Pleistocene predators were the rather small-sized cursorial pack hunters (*Canidae*) (Sardella & Palombo, 2007) and the large-sized collective hunter *Panthera leo*. Both species successfully survived until Holocene. Generally, the influence of mammal predators over the evolution of the herbivore community was insignificant.

The Early Pleistocene herbivore community is marked by the dominance of large-sized opportunistic mixed-feeder and grazer forms. The similar foraging strategy and adaptations in many Early and Middle Pleistocene herbivores (ruminants and non-ruminants) brings out an interesting problem on resource partitioning among the Pleistocene herbivores. The modern guild of herbivores of African savannahs, for instance, represents a finely co-adapted community with sophisticated specializations in feeding apparatus ensuring the partitioning of food resources (Spencer, 1995). The Pleistocene herbivore assemblages of Europe are different. They represent newly established communities of species with quite similar ecological requirements and strategy, so their broad range of feeding habits and

opportunism must provoke severe competition. The stabilizing co-evolution within the herbivore guild and evolving of resource partitioning were also impeded by the climate change. The absence of ecological partitioning between Pleistocene ruminant herbivores, severe ecological competition and the changing climate caused the extremely high rate of herbivore species turnover during the Early and Middle Pleistocene and their comparatively brief presence in the palaeontological records.

Generally, a universal evolutionary trend is observed in the herbivore paleocommunity starting from the beginning of Middle Pleistocene. The ecologically opportunistic species with a broad range of food habits had a certain advantage over the specialized stenophagous species and became dominant in the Late Pleistocene fauna of Europe. Of course, the outlined model of faunal change does not suppose unidirectional shifts to permanently drier environmental conditions. The ecological polyvalence and tolerance to a broad variation of environmental and climatic conditions are the main evolutionary acquisitions of Plio-Pleistocene herbivores.

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