

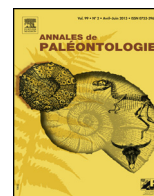


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Original article

Pleistocene herbivores and carnivores from France: An updated overview of the literature, sites and taxonomy



Herbivores et carnivores pléistocènes en France : bilan général récent bibliographique, des gisements et de la taxinomie

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ABSTRACT

This contribution presents a general account and summary of the research carried out over the past decades on the Quaternary faunas of France. This country is located in the center of Western Europe, and presents distinct topographical features and very varied climatic influences. This paper is the result of collaborative work between French teams and different researchers specialized in the paleontology of large mammals. Over a hundred paleontological or archaeological sites are mentioned in this review, which covers a broad chronological period, ranging from the Early (including the end of Pliocene/Gelasien) and Middle Pleistocene to the Late Pleistocene. One of the aims of this work is to present studies of the main families or subfamilies of herbivores (Equidae, Rhinocerotidae, Bovidae [Bovines, Caprines, Antilopines, and Rupicaprines], Cervidae, Proboscidae) and carnivores (Canidae, Ursidae, Mustelidae, Hyenidae, Felidae). It is not exhaustive at the generic and specific level, but details on the taxonomic status, evolutionary levels and biochronological importance of the most important taxa are given alongside an extensive and up-to-date bibliography of French works.

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RÉSUMÉ

Cette contribution expose un bilan général et synthétique des recherches menées ces dernières décennies en France sur les faunes Quaternaires de ce pays situé au centre de l'Europe de l'Ouest, avec une topographie et des influences climatiques très variées. Cet article est le résultat d'un travail collectif entre différents spécialistes et équipes françaises en Paléontologie des grands mammifères. Près d'une centaine de gisements, paléontologiques ou archéologiques sont concernés et couvrent une large période, depuis la fin du Pliocène, le Pléistocène inférieur et moyen jusqu'au Pléistocène supérieur. Un des buts du travail est de présenter les études réalisées sur les principales familles ou sous-familles d'herbivores (Equidés, Rhinocerotidés Bovidés [Bovins, Caprins, Antilopins, Rupicaprins] Cervidés, Proboscidiens) et de carnivores (Canidés, Ursidés, Mustélidés, Hyénidés, Félidés). Sans être exhaustif au niveau générique et spécifique, des précisions sur le statut taxonomique, les degrés évolutifs et l'importance biochronologique des taxons sont présentées, accompagnées d'une bibliographie abondante et à jour des travaux français.

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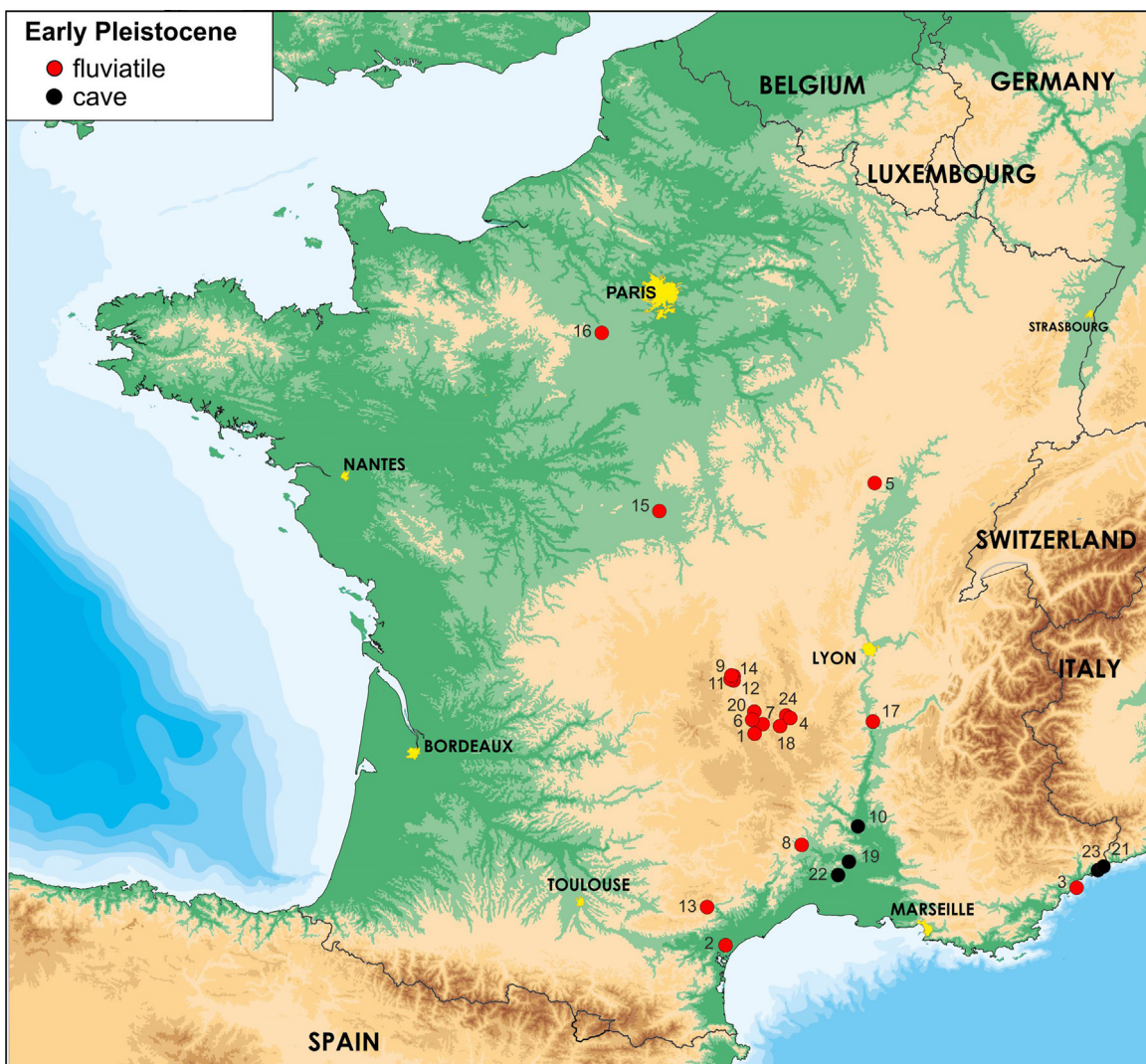
E-mail address: brugal@mmsch.univ-aix.fr (J.-P. Brugal).

1. Introduction

France is a distinct geographical area at the crossroads of several northern and southern European countries with diverse climatic influences (oceanic, semi-continental, mediterranean, mountainous) and a varied topography and river systems. At times, during the course of the Quaternary, these elements conditioned specific animal communities, as a result of the combination of these diverse influences in relation with the overall structure of mammal communities in the Western Eurasiatic region (Brugal and Croitor, 2007). In this contribution, we present an overview and an assessment of research on the main groups of herbivores and carnivores from French archaeological and paleontological sites, alongside a relatively exhaustive bibliography of the studies carried out to date in France.

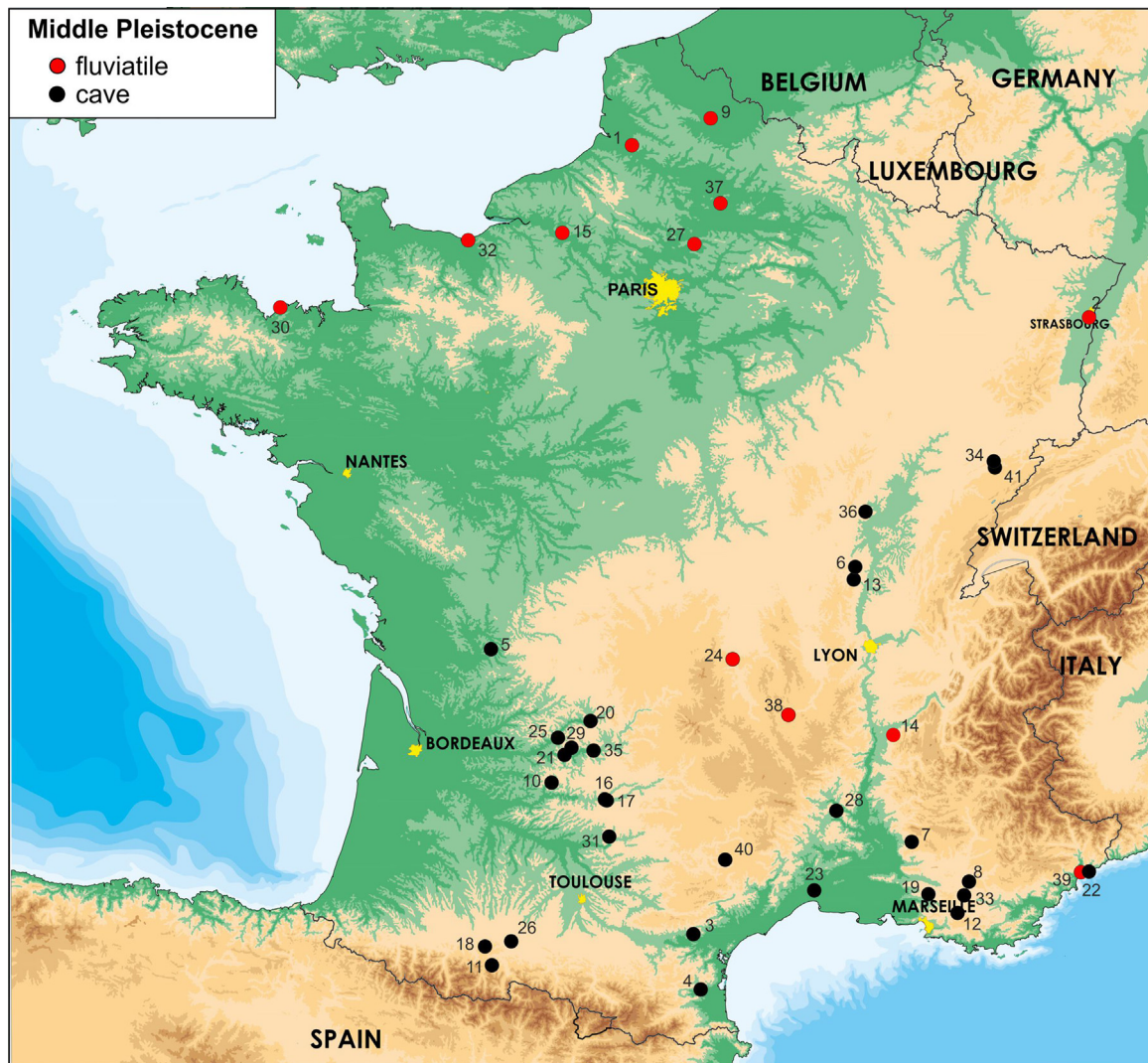
2. Material and presentation of sites

Over a hundred sites ($n = 106$, Figs. 1–3) are cited in this contribution, with the following chronological distribution: 22.6% of the sites are from the Early Pleistocene (including the end of Pliocene/Gelasien), 39.6% and 37.7% are from the Middle and Upper Pleistocene respectively. These are the most important sites, but this number could be multiplied by at least 20, in particular for the most recent periods, associated with Middle and Upper Palaeolithic human occupations. Generally speaking, archaeofaunas yield more fragmented and limited material, which are less suitable for paleontological analysis. The natural sites, such as sinkholes or dens, yield more complete fossil remains, often with higher numbers of individuals ('population' structure, herbivores and carnivores) and are usually more taxinomically diversified. Most of the Early



1 - Blassac la Girondie ; 2 - Bois de Riquet ; 3 - Cagnes sur Mer ; 4 - Ceyssaguet ; 5 - Chagny ; 6 - Chilhac ; 7 - Coupet, Le ; 8 - Durfort ; 9 - Etouaires, Les ; 10 - Grosse Marguerite ; 11 - Pardines ; 12 - Peyrolles ; 13 - Riège ; 14 - Roccaneyra ; 15 - Rozières ; 16 - Saint Prest ; 17 - Saint Vallier ; 18 - Sainzelles ; 19 - Sartanette, La ; 20 - Senèze ; 21 - Tour de Grimaldi ; 22 - Trois Pigeons, aven des ; ; 23 - Vallonnet, Le ; 24 - Viallette.

Fig. 1. Distribution map of Early Pleistocene (EU) French and Monaco sites mentioned in the text.
Carte de distribution des sites du Pléistocène inférieur mentionnés dans le texte, en France et à Monaco.



1 - Abbeville ; 2 - Achenheim ; 3 - Aldène ; 4 - Arago ; 5 - Artenac ; 6 - Azé ; 7 - Bau de l'Aubesier ; 8 - Baume Bonne ; 9 - Biache Saint Vaast ; 10 - Camp de Peyre ; 11 - Cap de la Bielle ; 12 - Cèdres, Les ; 13 - Château ; 14 - Châtillon Saint Jean ; 15 - Cléons ; 16 - Coudoulous I ; 17 - Coudoulous II ; 18 - Es-Taliens ; 19 - Escale, L' ; 20 - Fage I, La ; 21 - grotte XV (Vaufrey) ; 22 - Lazaret ; 23 - Lunel-Viel ; 24 - Malbattu ; 25 - Micoque, La ; 26 - Montmaurin La Niche ; 27 - Moru ; 28 - Orgnac 3 ; 29 - Pech de l'Aze II ; 30 - Piégu ; 31 - Rameaux, Les ; 32 - Ranville ; 33 - Rigabe ; 34 - Romain la Roche ; 35 - Saint Sol Belcastel ; 36 - Santenay ; 37 - Sempigny ; 38 - Soleilhac ; 39 - Terra Amata ; 40 - Vayssièrre, La ; 41 - Vergranne.

Fig. 2. Distribution map of Middle Pleistocene (MP) French and Monaco sites mentioned in the text.
Carte de distribution des sites du Pléistocène moyen mentionnés dans le texte, en France et à Monaco.

Pleistocene sites are open-air sites (from diverse sedimentary contexts: lacustrine, fluvial, aeolian. . . , 75%), but karstic cavities (caves, sinkholes, rock shelters) subsequently become predominant (71.4% and 92.5%, during the Middle and Upper Pleistocene respectively). There is a higher concentration of Early Pleistocene sites in the Massif Central, a higher altitude region in the center of France, whereas the Middle and Upper Pleistocene sites are more heavily concentrated in the southern half of the country with sites mostly located between plains (around the major hydrological basins, such as the Rhône and Garonne rivers) and highlands (Massif Central, Pyrenees, Alpes, Jura).

In this contribution we will first outline the mammal species identified in France, and then go into more detail on some recently studied taxa, complemented by a comprehensive review of the

literature of mainly French studies. Maps showing precise site location and some chronological dates are given, although the exact geochronological chart and duration/presence of taxa and evolutionary lineages still needs to be analyzed. The chronology of French sites, expressed by marine isotopic stage (MIS: [Table 1](#)), shows to some extent estimates, especially in the case of the Early Pleistocene sites. For this period, the time ranges are broad, covering several climatic stages but even if we cannot precise their exact dates (and climatic phases), they are relevant as a general order in the chronological succession of sites. The deposits of the second half of the Middle Pleistocene and of the Late Pleistocene are more often associated with radiometric dating's (OSL, U/Th, 14C. . .) and then present a better time frame resolution. It is notably reliable for the end of Late Pleistocene, allowing to finely correlate faunal

Table 1

French sites mentioned in the text (numbers as in Figs. 1–3) with location (French 'Département') by period (Early, Middle and Upper Pleistocene) with chronology expressed by marine isotopic stage (MIS).
Gisements français cités dans le texte (les numéros sont ceux de la Figs. 1–3) et leurs départements, établis par période (Pléistocène inférieur, moyen et supérieur) et chronologie suivant les stades isotopiques marins (SIM).

#	MIS	Sites	Département	#	MIS	Sites	Département	#	MIS	Sites	Département
Early Pleistocene				Middle Pleistocene				Upper Pleistocene			
1	24-21	Blassac-la-Girondie	Haute-Loire	1	15-13	Abbeville	Somme	1	2	Abeurador, Balma	Hérault
2	30-27	Bois-de-Riquet	Hérault	2	Middle-late	Achenheim	Bas Rhin	2	5 & 2	Adaouste	Bouches-du-Rhône
3	Late	Cagnes-sur-Mer	Alpes-Maritimes	3	10-9	Aldène	Hérault	3	3-2	Arquet, L'	Ardèche
4	36-34	Ceyssaguet	Haute-Loire	4	16-5	Arago	Pyrénées-Orientales	4	3-2	Balazuc II	Ardèche
5	Late	Chagny	Saône-et-Loire	5	Late	Artenac	Charente	5	2	Belvis	Aude
6	74-72	Chilhac	Haute-Loire	6	9-6	Azè	Saône-et-Loire	6	2	Bruniquel	Tarn-et-Garonne
7	70-68	Coupet, Le	Haute-Loire	7	7-6(5)	Bau de l'Aubesier	Vaucluse	7	3	Camiac	Gironde
8	26-24	Durfort	Gard	8	7-6	Baume Bonne	Alpes-de-Haute-Provence	8	2	Campefiel	Gard
9	92-86	Etouaires	Puy-de-Dôme	9	7-6	Biache-saint-Vaast	Pas-de-Calais	9	5	Caours	Somme
10	Late?	Grosse Marguerite	Gard	10	12	Camps-de-Peyre	Lot-et-Garonne	10	3-2	Chabot	Gard
11	36-35	Pardines	Puy-de-Dôme	11	6	Cap de la Bielle	Hautes-Pyrénées	11	2	Chinchon I	Vaucluse
12	32-30	Peyrolles	Puy-de-Dôme	12	6	Cèdres, Les	Var	12	2	Closeau, Le	Hauts-de-Seine
13	44-40	Riège	Hérault	13	15-14 et 6	Château	Saône-et-Loire	13	2	Colombier, Le	Ardèche
14	86-82	Roccaneyra	Puy-de-Dôme	14	9-7	Chatillon-Saint-Jean	Drôme	14	2	Cornille	Bouches-du-Rhône
15	28-26	Rosières	Cher	15	9	Cléon	Seine-Maritime	15	(6)-5	Coustaal, Le	Lot
16	28-26	Saint-Prest	Eure-et-Loir	16	7-6	Coudoulous I	Lot	16	3-2	Crouzade, La	Aude
17	85-84	Saint-Vallier	Drôme	17	6-4	Coudoulous II	Lot	17	3-2	Cuvée des Ours	Isère
18	44-39	Sainzelle	Haute-Loire	18	12-10	Es-Taliens	Hautes-Pyrénées	18	2	Dumas (Saut du Loup)	Gard
19	28-26	Sartanette	Gard	19	19-16	Escale, L'	Bouches-du-Rhône	19	5-3	Enfants, Les	Monaco
20	77-76	Senèze	Haute-Loire	20	9-7	Fage I, La	Corrèze	20	4	Fouvent	Haute-Saône
21	29-27	Tour-de-Grimaldi	Monaco	21	8-6	Grotte XV Vaufrey	Dordogne	21	2	Gazel	Aude
22	Late?	Trois Pigeons	Gard	22	8-6	Lazaret	Alpes-Maritimes	22	5e	Grand Abri aux Puces	Vaucluse
23	28-26	Vallonnet, Le	Alpes-Maritimes	23	9-8	Lunel-Viel	Hérault	23	3-2	Habarra	Pyrénées-Atlantiques
24	ca. 3 My	Vialette	Haute-Loire	24	Early	Malbattu	Puy-de-Dôme	24	3	Jaurens	Corrèze
				25	10-8	Micoque, La	Dordogne	25	3	Malarnaud	Ariège
				26	7-(5)	Montmaurin-La Niche	Haute-Garonne	26	3	Marie	Hérault
				27	Late	Moru	Oise	27	3-2	Marronnier, Le	Ardèche
				28	9-7	Orgnac III	Ardèche	28	(6)5-4	Moula Guercy	Ardèche
				29	6	Pech de l'Azé II	Dordogne	29	(7)5-3	Observatoire, L'	Monaco
				30	6-5	Piégu	Côtes d'Armor	30	3-2	Oullins	Ardèche
				31	9-7	Rameaux, Les	Tarn-et-Garonne	31	2	Peyrat	Dordogne
				32	6	Ranville	Calvados	32	5-4	Pont-du-Château	Puy-de-Dôme
				33	6	Rigabe	Var	33	5-3	Prince	Monaco
				34	6	Romain-la-Roche	Doubs	34	2	Quéroy, Le	Charente
				35	Late	Saint-Sol-Belcastel	Lot	35	2	Rigney	Ain
				36	6-5	Santenay	Côte-d'Or	36	4-3	Saint-Marcel d'Ardèche	Ardèche
				37	Late	Sempigny	Oise	37	3-2	Salpêtrière, La	Gard
				38	19-17	Soleilhac	Haute-Loire	38	2	Soulabé	Ariège
				39	11-10	Terra Amata	Alpes-Maritimes	39	4-2	Tournal	Aude
				40	16-18	Vayssiere, La	Aveyron				
				41	16-15	Vergranne	Doubs				



1 - Abeurador ; 2 - Adaouste ; 3 - Arquet, L' ; 4 - Balazuc ; 5 - Belvis ; 6 - Bruniquel ; 7 - Camiac ; 8 - Campefiel ; 9 - Caours ; 10 - Chabot ; 11 - Chinchon ; 12 - Closeau, Le ; 13 - Colombier, Le ; 14 - Cornille ; 15 - Coustal, Le ; 16 - Cruzade, La ; 17 - Cuvée des Ours ; 18 - Dumas ; 19 - Enfants, Les ; 20 - Fouvent ; 21 - Gazel ; 22 - Grand Abri aux Puces ; 23 - Habarra ; 24 - Jaurens ; 25 - Malarnaud ; 26 - Marie ; 27 - Marronnier, Le ; 28 - Moula Guercy ; 29 - Observatoire ; 30 - Oullins ; 31 - Peyrat, Le ; 32 - Pont du Château ; 33 - Prince ; 34 - Queroy, Le ; 35 - Rigney ; 36 - Saint Marcel d'Ardèche ; 37 - Salpêtrière, La ; 38 - Soulabé ; 39 - Tournal.

Fig. 3. Distribution map of Late Pleistocene (LP) French and Monaco sites mentioned in the text.
Carte de distribution des sites du Pléistocène supérieur mentionnés dans le texte, en France et à Monaco.

associations with certain climatic events, such as Heinrich or D-O events, within MIS 3 to 1, range of the 14C datings. Most of these sites are karstic cavities, which sometimes yield thick sedimentary multilayered sequences covering several isotopic stages and climatic phases. Due to these dating uncertainties, the local fauna dynamics in the context of global Quaternary climatic changes will not be discussed here, as it is beyond the scope of the present contribution. The French record corresponds to south-western European biomes and reveals the set-up of modern-type Pleistocene faunal associations from the Middle Pleistocene, coincident with the onset and subsequent amplification of high-latitude glacial cycles (onset of 100 kyr cycle from around 1 My) (Bonifay, 1996a, b; Bonifay and

Brugal, 1996; Croitor and Brugal, 2001; Brugal and Croitor, 2007). Nevertheless, a biochronological chart is presented based on the Pleistocene subseries/subepochs (Table 2). The systematic order is the following: Perissodactyles (Equids, Rhinocerotids), Artiodactyles (Bovids, Cervids), Proboscids, Caniforms (Canids, Ursids, Mustelids) and Feliforms (Hyanids, Felids). Other large mammal groups (Suids, Hippotamids) are not considered here as any recent works has been done on these groups, and we refer readers to Guérin and Patou-Mathis (1996) among them. Among the taxa, some are more likely to provide biochronological indications, based on evolutive stage, as in the Equids or large Bovids, but also in Caprines, Canids and some felines and bears.

3. Perissodactyles

3.1. Equidae

3.1.1. *Stenonians and Caballines*

Work on horses can be grouped into two sets: paleontological case studies and more general studies on morphology and adaptive traits, phylogeny, DNA, structure of populations, zooarchaeology and domestication, which are totally or partly based on fossils from French sites. Some case studies include that of *Equus stenonis* from Vallonnet (Moullé, 1992; Moullé et al., 2006a, b), but they mostly represent caballine Equids in the broad sense of the term (see [Supplementary Informations for latin terminology](#)). This is the case for *Equus mosbachensis* ssp., a more typical Middle Pleistocene form, and the different subspecies described; *E. m. campdepeyri* (Camp-de-Peyre, Fig. 4), *E. m. micoquii* (La Micoque), *E. m. palustris* (Lunel-Viel, Rigabe), *E. m. tautavelensis* (Caune de l'Arago) (Bonifay, 1980; Crégut, 1980a; Eisenmann et al., 1985; Guadelli and Prat, 1983, 1995; Guadelli and Prat, 1995; Bellai, 1998; Langlois, 2005; Uzunidis-Boutillier, 2017). Several studies have provided information on more problematic taxa, such as *Equus achenheimensis*, identified in particular at Achenheim and Romain-la-Roche (Eisenmann, 1991a; Boulbes, 2010), *Equus steinheimensis*, for example at Châtillon-Saint-Jean (Eisenmann, 1998) and *Equus taubachensis*, represented for example at Bau de l'Aubesier and Biache-Saint-Vaast (Auguste, 1995; Fernandez, 2006; Crégut-Bonnouire et al., 2010). For Caballines, in the strict sense of the term studies have focused on *Equus caballus piveteaui*, defined at Abri-Suard (Griggo, 1995; Guadelli, 2007; Uzunidis-Boutillier, 2017), and *E. c. germanicus*, *gallicus* and *arcelini*, which are almost always represented in Upper Pleistocene sites (Eisenmann, 1988; Guadelli, 1989a, 1991, 1995; Eisenmann and David, 1990, 2002; Bignon, 2003; Fabre, 2017).

More general work focus on morphology: identification keys for teeth and different skeletal elements, adaptive characters to the environment, and gives information on biochronology and the knowledge of paleoenvironments (Eisenmann, 1980, 1981, 1984, 1988, 1991a, b, 2006a; Eisenmann and Karchoud, 1982; Eisenmann and Guérin, 1984; Eisenmann and Beckouche, 1986; Dive and Eisenmann, 1991; Guérin et al., 2004; Bignon et al., 2005; Bignon and Eisenmann, 2006; Guadelli, 2013; Cucchi et al., 2017; Uzunidis-Boutillier, 2017). Furthermore, several paleogenetic studies have provided new indications on the origin and the phylogeny of Equidae or have confirmed former hypotheses, such as the date of the transition between Caballines in the broad (*E. mosbachensis*) and strict sense of the term (*E. caballus*) (Eisenmann,

2006b; Orlando et al., 2013), from MIS 6 onwards. Finally, from a more archeozoological viewpoint, several studies have focused on the structure of populations and domestication (Bogros, 1989; Bellai, 1995; Eisenmann and Arbogast, 1997; Eisenmann, 1998; Guadelli, 1998; Arbogast et al., 2002; Fernandez et al., 2006, 2017).

3.1.2. *Equus hydruntinus*

Along with “classical” studies, generally leading to biochronological results and the identification of biogeographic provinces (Eisenmann and Patou, 1980; Bonifay, 1991; Rousseau, 2008; Boulbes, 2009; Guadelli, 2011), paleogenetic research into the reconstruction of the phylogeny of *E. hydruntinus* (Burke et al., 2003; Orlando et al., 2006, 2009; Bennett et al., 2017) has developed over the past few years. These studies point to a proximity between *Equus hemionus* and *E. hydruntinus*, but we must admit that, for the moment, the situation is not as simple as it appears, as the paleontological and paleogenetic data do not seem to be compatible.

3.2. Rhinocerotidae

They are represented in France by three genera and six species (Guérin, 1980): *Stephanorhinus etruscus*, *S. hundsheimensis*, *S. hemitoechus*, *S. kirchbergensis*, *Coelodonta antiquitatis* and *Elasmotherium* sp. The incursions of the latter species into Western Europe seem to be very rare and are only recorded in France by a single dental fragment from the collections of Ault du Mesnil from the site of Abbeville, which were destroyed during the First World War (Agache et al., 1963).

The specific determination of *Stephanorhinus* is often problematic, and some series are ascribed to different species depending on the authors, which limits our knowledge of the succession of the taxa and their degree of evolution, and therefore their use in biochronology. Two taxa have been described for the Plio-Pleistocene in France: *S. megarhinus* (Guérin, 1980) and *S. jeanvireti* (Guérin, 1972), which disappear before the late Early Pleistocene. Then, *S. etruscus* appears at Perrier-Les Étouaires (Guérin, 1972) and Saint-Vallier (Guérin, 2004) and lasts until the end of the Early Pleistocene at Senèze (Guérin, 1980; Lacomat, 2003), Chilhac (Boivin et al., 2010), Cagnes-sur-Mer (Lacomat, 2003) (attributed to *Dicerorhinus etruscus brachycephalus* = *S. hundsheimensis* by Guérin, 1980), Sainzelles (Lacomat, 2003) (attributed to *Dicerorhinus etruscus brachycephalus* = *S. hundsheimensis* by Guérin, 1980) and Bois-de-Riquet (Bourguignon et al., 2016). *S. etruscus* seems to have persisted in the

Equus mosbachensis campdepeyri
Camp-de-Peyre



Guadelli J.-L. & Prat F., 1995

Fig. 4. Skull of *Equus mosbachensis* (#1955-04) from Camp-de-Peyre (MP, Lot-et-Garonne) (photo J.L. Guadelli).
Crâne d'*Equus mosbachensis* (#1955-04) de Camp-de-Peyre (MP, Lot-et-Garonne) (photo J.L. Guadelli).

South of France until more recently (1.3–1.1 Ma) than in the rest of Europe, apart from in the Iberian and Italian peninsulas (Pandolfi et al., 2017).

S. hundsheimensis, like *S. hemitoechus*, follows on from *S. etruscus*, and several assumptions have been made regarding its origin. Some authors suggest an Asian origin (Made, 2000), while others imply that it derives from *S. etruscus* (Guérin, 1980; Kahlke, 2001), or that it is completely distinct (e.g., Lacombat, 2003). In France, it is represented as early as 1.2 Ma at Ceyssaguet, la Tour-de-Grimaldi, le Vallonnet, Saint-Prest, Abbeville, Sempigny, Durfort, and Soleilhac and also at Vergranne (Guérin, 1980; Guérin et al., 2003; Lacombat, 2003; Schreve et al., 2007).

S. hemitoechus is regularly reported, in particular in the South of France, often in association with other rhinoceros taxa (*S. kirchbergensis* or *Coelodonta*). It is present from the beginning of the Middle Pleistocene at la Caune de l'Arago during MIS 12, then at la Baume Bonne, Terra Amata (Guérin, 1980; Lacombat, 2003), La Fage (Guérin, 1973), Orgnac III (Guérin, 1980; Lacombat, 2003), Lunel-Viel (Guérin, 1980; Lacombat, 2003; Uzunidis-Boutillier, 2017, attributed to *Dicerorhinus etruscus*=*S. etruscus* by Bonifay, 1973) and Rigabe (Bonifay, 1960; Uzunidis-Boutillier, 2017). It persists until the end of the Upper Pleistocene, where it is described namely at la grotte des Enfants at Grimaldi, Monaco, dated to MIS 3 (Lacombat, 2003) (attributed to *Rhinoceros mercki*=*S. kirchbergensis* by Guérin, 1980). It makes several incursions into the North of France during temperate climatic periods, in particular at Cléon (MIS 9, Auguste et al., 2003), Biache-saint-Vaast (MIS 7, Auguste, 1995), Piégu (MIS 7, Auguste et al., 2005) and Caours (MIS 5, Antoine et al., 2006).

Most authors agree that *S. kirchbergensis* derives from *S. megarhinus* (Guérin, 1980; Fortelius et al., 1993; Lacombat, 2003), although others are more cautious (Billia and Petronio, 2009). It appears in France at the beginning of the Middle Pleistocene at Solheillac (MIS 17, Guérin, 1980) and disappears towards MIS 3. Like *S. hemitoechus*, it is mainly identified in the South of France and is contingent on wetter climates (Guérin and Patou-Mathis, 1996). It is reported notably at Vergranne (Guérin, 1983), La Fage (Guérin, 1973), Lunel-Viel (Uzunidis-Boutillier, 2017), and in the sites of Aldène, la grotte du Prince and la grotte des Enfants (Lacombat, 2003). Like *S. hemitoechus*, it appears episodically in the North of France, namely at Biache-saint-Vaast (Auguste, 1995), Ranville (Auguste et al., 2005), Moru and Sempigny (Guérin, 1980). In France, this taxon is practically absent during glacial periods, with a single occurrence at Pech de l'Azé II (Lacombat, 2003; Uzunidis-Boutillier, 2017).

Coelodonta is a very regular component of the faunal spectra from the middle of the Middle Pleistocene until the end of the Upper Pleistocene in the North and the South of France. The taxonomy of this taxon is also a matter of debate: the first *Coelodonta* found in France appears to correspond to a western expansion of the territory of *C. tologojensis* (Kahlke and Lacombat, 2008). For some authors, the first French forms already appear to be much evolved and are related to *C. antiquitatis praecursor*, which reaches its final evolutionary stage during the Upper Pleistocene with *C. antiquitatis antiquitatis* (Guérin, 1980, 2010; Uzunidis-Boutillier, 2017). One of the earliest occurrences of *Coelodonta* in France comes from La Fage (MIS 8) and could be attributed to *C. tologojensis* (Kahlke and Lacombat, 2008) but is more likely to be *C. antiquitatis praecursor* (Made, 2000), as is the case at the site of Igue des Rameaux (MIS 9 or 7) (Rouzaud et al., 1990; Uzunidis-Boutillier, 2017). *Coelodonta* is present in France until MIS 2, namely at the site of Rigney (Ain), dated to around 14,940 years uncal. BP (Theobald and Szymanek, 1963; Evin et al., 1978).

4. Artiodactyles

4.1. Bovinae

The Bovini tribe is represented by several genera or subgenera (Geraads, 1992, and see Bonifay and Brugal, 1996; Brugal and Croitor, 2007), with the presence of *Leptobos*, *Eobison*, *Bison* and *Bos* in France during the Pleistocene. Some genera, such as *Bubalus* or *Hemibos*, identified in Germany or in Italy, are absent in France. The earliest are the *Leptobos*, which are present in several forms in many French sites during the Villafranchian, corresponding to the Gelasian and the Early Pleistocene (see taxonomic description in Crégut-Bonnoure and Guérin, 1996, chronology after Cohen and Gibbard, 2019). They have been divided into two subgenera (Duvernois and Guérin, 1989; Duvernois, 1990, 1992): the sub-genus *Leptobos* (characterized by a double curve of the horns) with the *elatus* (Etouaires; Saint-Vallier, Crégut-Bonnoure and Valli, 2004) and *furtivus* species (Senèze; Coupet), and the sub-genus *Smertiobos* (horns with a simple curve); with the *etruscus* species (Upper and Final Villafranchian: Senèze, Blassac-la-Girondie, Peyrolle) and *bravardi* (Etouaires). The relationship between this polyphyletic group, with plesiomorphic diagnostic characters (Geraads, 1992), and other European forms (for example *vallisarni*, *stenometopon*), is still debatable.

From the end of the Early Pleistocene (Epivillafranchian, 1.2–0.9 Ma), archaic forms of bison are present in France, defined by the sub-genus *Eobison*, found for example in the sites of Riège, Sainzelle or la Sartanette (Ambert et al., 1996; Brugal and Lacombat, 2004–2005). They were rapidly supplanted by more 'modern' bison, with first of all a group comprising *Bison schoetensacki*, followed by the steppe bison *Bison priscus*. The first is present during the early and mid-Middle Pleistocene (Durfort, La Vayssière, Vallonnet) (Brugal, 1994–1995; Brugal and Fosse, 2005), but for some authors it persists until the end of the Pleistocene (Guérin and Valli, 2000; Palacio et al., 2017). It is important to recall that sexual dimorphism is very marked in bovines and that it must be taken into serious consideration in morphometric analyses, which is not always the case. The steppe bison is the dominant form from the mid-Middle Pleistocene to the Upper Pleistocene, and is regularly found in many archaeological and paleontological sites (e.g., Auguste et al., 2005; Brugal et al., 2013; Brugal, 2016). We can cite the fossil series from the sites of Romain-la-Roche, Habarra, Jaurens or Arquet (Guérin and Valli, 2000; Prat et al., 2003; Vercoûtère and Guérin, 2010; Gamberi Almendra de Carvalho et al., 2011), with abundant remains; for example, nearly 130 individuals, of both sexes, adults and juveniles (1- and 2-year-old), were found in the Arquet sinkhole dated to MIS 3 (Brugal, n.d.) The last bison in France date from the Tardiglacial and the question of a former coexistence with a form of *Bison bonasus* has recently been raised (Massilani et al., 2016; Grange et al., 2018). The presence of a chronological and ecological polymorphism in western European populations obstructs our perfect understanding of the taxonomy of the fossil assemblages, as well as of evolutionary mechanisms. We observe important variations in body size during the course of time (Magniez et al., 2017), and three chrono-subspecies have been identified (Brugal, 1999) at a European scale: *priscus*, *mediator* and *minor*, which will nonetheless require enhanced definition in the future.

The aurochs is regularly present during the Middle and Upper Pleistocene in France (and during the Holocene, Brugal, 1983), but is less frequent than the bison, and increases during temperate stages. Among the sites with abundant fossils, we can cite those from the second half of the Middle Pleistocene: Lunel-Viel in the South of France (Brugal, 1985) and Biache-Saint-Vaast in the

northwest (Auguste, 2009). Variations in body size among populations in Western Europe are observed in relation with climatic phases and seem to conform to Bergmann's rule. The Pleistocene form (*Bos primigenius trochoceros*) is larger than the Holocene aurochs (*B. p. primigenius*).

4.2. Caprinae, Antilopinae and Rupicaprinae

Three Bovidae subfamilies are part of the Pleistocene guild of herbivores in France. These are Caprinae, Antilopinae and Rupicaprinae. In addition to a first overview (Crégut-Bonnaire and Guérin, 1996), several studies and revisions over the past thirty years have focused on their anatomic characteristics and their chronological distribution (Delpech, 1983; Crégut-Bonnaire, 1984, 1987, 1992a, 1992b, 1992c, 1992d, 2002, 2006, 2007, 2009; Delpech, 1983; Crégut-Bonnaire, 1984, 1987, 1992a–d, 2002, 2006, 2007, 2009; Duvernois and Guérin, 1989). New species have been identified and some of the better represented taxa in natural and archaeological sites are important biochronological markers.

These three subfamilies are recorded during the Early Pleistocene, during the course of which nine genera and ten species have been identified. Caprinae are represented by *Pliotragus ardeus*, *Gallogoral meneghini*, *Megalovis latifrons*, *Praeovibos* sp., *Soergelia* sp., *Hemitragus orientalis*; Antilopinae by *Gazella borbonica*, *Gazella* sp., *Gazellospira torticornis*; Rupicaprinae by *Procamptoceras brivatense*. These taxa are currently present in 14 sites (Duvernois and Guérin, 1989; Crégut-Bonnaire, 2002, 2006; Crégut-Bonnaire and Valli, 2004; Lacombat, 2004–2005): Roccaneyra, Pardines, Chagny, Montoussé 5, La Rochelambert, Saint-Vidal, Cornillet, Vals-Le-Crozaz, Saint-Vallier, Le Coupet, Chilbac I and II, Senèze, Malbattu, Le Vallonnet. Although *Ovis* occurs at Senèze, this material could be more recent as it presents different fossilization (Crégut-Bonnaire, 1992b).

Among these taxa, three have been identified over the past few years in the Vallonnet site (Michel et al., 2017). These are *Praeovibos* sp., probably *P. mediterraneus*, which is identified at the same time in Greece, Italy and Spain (Crégut-Bonnaire, 2002, 2006). *Hemitragus* is also documented at the same site (*H. orientalis*, Crégut-Bonnaire and Spassov, 2002). The Caprine interpreted as *Ammotragus* (*A. europaeus*, Moullé et al., 2004) corresponds to mixed material from *H. orientalis* and *Soergelia* (Crégut-Bonnaire and Dimitijević, 2006). *Capra rozeti* from Malbattu (end of the Early Pleistocene) is also attributable to *Soergelia* (Crégut-Bonnaire, 2002, 2006).

The Middle Pleistocene is characterized by the appearance of an association of Bovidae, comprising several species from cold and open environments, depending on climatic fluctuations. Currently, seven genera and ten species have been identified. Caprinae dominate with seven species: *Praeovibos priscus*, *S. elisabethae*, *H. orientalis*, *H. bonali*, *H. cedrensis*, *Capra ibex*, *O. ammon antiqua*. Antilopinae are represented by a single species: *Saiga tatarica*, and Rupicaprinae by two species: *Rupicapra rupicapra* and *R. pyrenaica*.

P. priscus is well known in Western Europe (Germany, Poland, England etc., Crégut-Bonnaire, 1984, 2002, 2006), but has only been identified up until now in France at la Caune de l'Arago (Crégut and Guérin, 1979; Crégut, 1980b) where its morphometric characteristics have given rise to the sub-specific distinction *delumleyi* (Crégut-Bonnaire, 2002). At l'igüe de Saint-Sol-Belcastel, the material initially attributed to this musk ox is now ascribed to *S. elisabethae* (Philippe et al., 1980; Crégut-Bonnaire, 2002).

Among the Caprinae, *H. bonali* is widespread in Western Europe and in particular in France (Bonifay, 1974–1975; Crégut-Bonnaire, 1988, 2008; Crégut-Bonnaire, 1998, 2002, 2006, 2008). The hind cannon bone from Soleilhac-farm, dating from the beginning of the Middle Pleistocene, raises the question of the persistence of *H. orientalis* (Crégut-Bonnaire, 2006; Moullé et al., 2006b; Fernandez

and Crégut-Bonnaire, 2007). *H. cedrensis* is the descendant of *H. bonali*. It is present in the southeast of France at the end of the Middle Pleistocene (end of MIS 7, beginning of MIS 6): Cimay, Les Cèdres, Rigabe, Bau de l'Aubesier (Fernandez, 2006; Crégut-Bonnaire et al., 2010), but also during the same period at Coudoulous I in the southwest, where it is particularly abundant (Fernandez, in press). A P/3 attributed to *H. aff. cedrensis* was identified in Spain at Bolomor (Level IV), at the end of MIS 6 (Rivals and Blasco, 2008).

C. ibex appears in Western Europe during MIS 7, and in France the oldest sites with this species are Lazaret (Gagnière, 1955), Rigabe (Crégut-Bonnaire, 1989) and Le Coustal (Crégut-Bonnaire, 2002). The only *Ovis* present is *O. ammon antiqua*, identified at Pont-du-Château. It was also identified at Camp-de-Peyre (Delpech et al., 1978) and la Caune de l'Arago (Crégut, 1979). The latter site contains the highest concentration of remains of this species in Western Europe (Moigne et al., 2006). The migration of the Saiga antelope to Western Europe is well documented (Delpech, 1983, 1988; Crégut-Bonnaire, 1992a). It first colonized the southwest of France during MIS 6 (Combe-Grenal, Abri-Suard). The *Rupicapra* genus is present from the beginning of the Middle Pleistocene onwards in Eastern Europe (Fernandez and Crégut-Bonnaire, 2007; Sirakov et al., 2010), and perhaps as early as the Early Pleistocene (Crégut-Bonnaire, 2006); it appears in France during MIS 12 (Caune de l'Arago) (Crégut, 1979; Moigne et al., 2006; Rivals, 2006). The Pyrenean chamois *R. pyrenaica* is clearly differentiated during MIS 7 at La Niche (Crégut-Bonnaire et al., 2011) and Cap de Bielle (Clot and Marsan, 1986) (*R. pyrenaica occitania*), whereas (Masini and Lovari, 1988) attribute this latter taxon to *R. cf. pyrenaica*. In the southeast, from the end of the Middle Pleistocene, at Les Cèdres Cave (Crégut-Bonnaire, 1992a, b, 1995) and the large rockshelter of Bau de l'Aubesier (Fernandez, 2001, 2006), the Alpine group appears with *R. rupicapra* (Crégut-Bonnaire and Fernandez, 2004). The differentiation of this species could have occurred during an interglacial or an interstadial in Eastern Europe or in Asia Minor (Lovari and Scala, 1980; Pérez et al., 2002).

During the Upper Pleistocene, the number of small bovids decreases with five represented genera and eight species. Caprinae are represented by *Ovibos pallantis*, *H. cedrensis*, *C. ibex*, *C. caucasica* and *C. pyrenaica*, and Antilopinae and Rupicaprinae by the same genera and species as during the Middle Pleistocene. *Ovibos* is the only Upper Pleistocene Ovibovine. It is present in the northern and south-western plains (Crégut-Bonnaire, 1984, 2002). Its presence in the southeast, at Les Cèdres, has been invalidated (Crégut-Bonnaire, 1995). Among the Caprinae, *H. cedrensis* persists in some areas at the very beginning of the Upper Pleistocene (MIS 5e): Saint-Marcel d'Ardèche (Crégut-Bonnaire, 1989), Caune de l'Arago (Rivals, 2004, 2006), whereas it is absent from all the Upper Pleistocene levels of Coudoulous I (Fernandez, in press). A morphometric analysis based on 115 European sites and more than 5500 teeth brought to light an East-West and North-South gradient in the evolution of the size of the teeth of certain forms of the genus *Capra* (Crégut-Bonnaire and Fernandez, 2018). In France, *C. ibex* is observed in the southeast as early as MIS 5e: Grand Abri aux Puces (Slimak et al., 2010). From MIS 4 onwards, the species occupies practically all the mountainous zones of the South of France. The populations on either side of the Rhône River underwent different morphological developments. In the western part, the *cebennarum* subspecies emerges (Crégut-Bonnaire, 2002, 2006). The transformation of the dentition of the ibex east of the river is linked to a geographic isolate (Crégut-Bonnaire, 1992d, 2002, 2006). An MIS 5 morphotype is identified on either side of the Rhone, such as *C. caucasica praepyrenaica* (Baume Moulia Guercy, Moustierian levels of Adaouste, layer IV of Bau de l'Aubesier) (Defleur et al., 2001; Crégut-Bonnaire, 2002; Fernandez, 2006). This taxon is also present during MIS 4 in the Pyrenees (ex. Malarnaud, Soulabé,



Fig. 5. Skull of *Capra caucasica* from Soulabé (LP, Ariège) (photo P. Jugie).
Crâne de *Capra caucasica* from Soulabé (LP, Ariège) (photo P. Jugie).

Fig. 5) and the Massif Central. The transformation of the morphology of the horn cores towards a morphotype identifying the Pyrenean ibex is observable (speciation process). However, genetic analyses on current species do not validate this scenario as they highlight the proximity of the Alpine and Pyrenean ibex (Ureña et al., 2018). Genetic drift from the Alpine ibex is conceivable: morphological similarities with the Caucasian ibex would be simple analogies (Magniez, 2009). This scenario is not entirely satisfactory as certain anatomical characters are associated with other evolved characters (Crégut-Bonnoure, 2009). *C. pyrenaica*, which follows on from the preceding species, is considered to be confined to the Pyrenean massif, but its habitat range extended sporadically to the Massif Central and its fringes during MIS 2: le Marronnier, Baume d'Oullins, Abri (= rockshelter) Dumas, Abri du Colombier, La Salpêtrière, Grotte Chabot, La Crouzade, Grau de Padern, Gazel, Belvis, Bruniquel (Crégut-Bonnoure, 2002). The Saiga antelope is abundant throughout the southwest of France (Delpech, 1983; Dujardin and Tymula, 2005; Castel and Madelaine, 2006; Castel et al., 2010; Costamagno et al., 2016; Kuntz et al., 2016), with the presence of several whole skeletons at Quéroy (Tournepiche, 1982). It is also recorded in the Languedoc plain and on the edge of the Rhône River (Crégut-Bonnoure and Gagnière, 1981), as well as in the plains of the Lower Rhône Valley (Abri Cornille, Chinchon I) (Crégut-Bonnoure and Paccard, 1997). Finally, the chamois and the Pyrenean chamois rapidly colonized the whole southeast of France and the Pyrenean zone respectively. The specific status of *Rupicapra* is mostly uncertain for the Massif Central, but both taxa may have been present in this region, as shown by the existence of *R. pyrenaica* to the south of this massif, at Marie Cave (Crochet et al., 2007).

4.3. Cervidae

The French sites have yielded several rich fossil Cervidae collections, illustrating the diversity of this family. The typical Early Pleistocene forms clearly differ from the subsequent Middle Pleistocene forms populating Western Europe following faunal turnover.

After the seminal work of (Heintz, 1970), several studies of the representatives of this family during the Early Pleistocene note the

difficulties about the identification and phylogenetic reconstruction of fossil series. In short, large cervids are represented by the genera *Eucladoceros* (Croitor and Bonifay, 2001; Valli, 2004; Valli et al., 2006), *Praemegaceros* (Croitor and Bonifay, 2001; Guérin et al., 2003; Bourguignon et al., 2016), *Arvernoceros* (Croitor, 2009) and *Cervalces* (Heintz, 1970; Guérin et al., 2003). *Eucladoceros ctenoides*, with simple comb-shaped antlers, is the most abundant. Different forms, considered to be subspecies, have been described based on antler variability: *E. c. vireti* (Saint-Vallier), *E. c. senezensis* (e.g., Senèze; Fig. 6), Chilhac, a form probably synonymous with *E. c. falconeri* (Croitor, 2018), *E. c. tetraceros* (Peyrolles). *E. ctenoides* ssp. from Ceysseguet presents antler morphology characteristic of *E. c. ctenoides* from the Upper Valdarno in Italy. *E. dicranios* was reported in the diluvian sands of Riège under the name of *Cervus martialis* (Gervais, 1859). Rare *Praemegaceros obscurus* remains were discovered in the Final Villafranchian of Ceysseguet (Croitor and Bonifay, 2001). *Praemegaceros solilhacus* is described as being associated to the beginning of the Middle Pleistocene at Soleilhac and L'Escale (Bonifay, 1981). *Praemegaceros verticornis* is less frequent in France: the remains discovered at Bois-de-Riquet (*Praemegaceros* sp., Bourguignon et al., 2016), may be attributed to it and it is probable that the remains of a large deer from the Paris basin described by (Belgrand, 1883) as "*Cervus belgrandi*" may also be ascribed to this species (Croitor, 2018). *Arvernoceros giulii* is a large-sized form of deer from the end of the Early Pleistocene from Rosières. It is very likely that the large deer remains from Saint-Prest and le Vallonnet represent the same form (Croitor, 2018). The *Praemegaceros* genus persists throughout the first half of the Middle Pleistocene on the European continent (Croitor, 2006a). In Corsica, an isolated insular lineage of *Praemegaceros* is represented by two species: *P. rossii* during the Middle Pleistocene at Castiglione and *P. cazioti* from the site of La Coscia, a dwarf form existing until the Pleistocene/Holocene transition (Pereira, 2001; Croitor et al., 2006; Croitor, 2018).

The latest work on small and medium-sized cervids from this period in France seems to recognize three genera: *Croizetoceros* with a single species *C. ramosus* (Heintz, 1970; Valli, 2004), *Metacervoceros* and *Dama* (Croitor, 2006b). *M. rhenanus* remains are relatively abundant in Early Pleistocene sites [e.g., Saint-Vallier, Senèze, Chilhac, Ceysseguet (Heintz, 1970; Croitor and Bonifay,



Fig. 6. Skull (#16128) of *Eucladoceros ctenoides senezensis* from Sênèze (EU, Haute-Loire; side view of the antlered skull of the mounted skeleton, University of Lyon, France) (photo R. Croitor).

Crâne (#16128) d'*Eucladoceros ctenoides senezensis* de Sênèze (EU, Haute-Loire ; vue du crane avec bois du squelette monté, Université de Lyon, France) (photo R. Croitor).



Fig. 7. Maxillary of *Megaloceros giganteus* (#J25-c3-349; occlusal view) from Tournal (LP, Aude) (photo P. Magniez).

Maxillaire de *Megaloceros giganteus* (#J25-c3-349 ; vue occlusale) de Tournal (LP, Aude) (photo P. Magniez).



Fig. 8. Hemimandible of *Cuon alpinus europaeus* from Malarnaud (coll. Harlé H761, M.H.N. Bordeaux) (photo P. Fosse).
Hémimandibule de *Cuon alpinus europaeus* de Malarnaud (Coll. Harlé H761, N.H.N. Bordeaux) (photo P. Fosse).

2001]). *Dama* is rarer and is described at le Vallonnet (*D. vallonnetensis*, type locality), *Dama* sp. at Ceyssaguet (Croitor and Bonifay, 2001) and recently at Senèze on the basis of the analysis of the bony labyrinth of the inner ear (Mennecart et al., 2017).

The characteristic Middle and Upper Pleistocene genera are *Megaloceros*, *Cervus*, *Dama*, *Haploidoceros*, *Alces*, *Rangifer* and *Capreolus*. The giant deer *M. giganteus* (Fig. 7) is recognized in France from the end of the Middle Pleistocene to the end of the Upper Pleistocene (Magniez, 2010). The red deer *Cervus elaphus* arrives in Western Europe at the Early/Middle Pleistocene transition. In France, the sites of Soleilhac and la Caune de l'Arago (levels earlier than 500 ky) yield a form with no differentiated crown at the apex of the antlers: *Cervus e. acoronatus* (Magniez et al., 2013). From 500 ky onwards, crowns are more frequent (*Cervus e. elaphus*). Other forms are identified: for example, *C. simplicidens* (Guadelli, 1996) at Combe-Grenal; or, for exceptionally large red deer remains and antlers with basal beams on the same plane which could potentially be attributed to *C. canadensis*, as recently proposed in Moldova (Croitor and Obada, 2017). This taxon may have spread to Western Europe during a cold Upper Pleistocene phase (Croitor and Obada, 2017; Croitor, 2018). A larger fallow deer than the Early Pleistocene form, similar to *Dama clactoniana*, is reported at the Middle Pleistocene sites of Orgnac III (Aouraghe, 1990), Caune de l'Arago (Moigne et al., 2006) and La Fage (Bouchud, 1972). These determinations would invalidate the occurrence of *Cervus elaphoides* (Lister, 1990). The remains of "*Dama polignacus*" from Soleilhac belong to a juvenile *Dama clactoniana* specimen (Croitor, 2006a). According to another study (Magniez et al., 2013), the fallow deer remains from Soleilhac and la Caune de l'Arago correspond to *Dama roberti*. From the end of the Middle Pleistocene onwards, the fallow deer series can be attributed to *Dama dama*. The revision of the Cervidae from the sites of Lunel-Viel and Igue des Rameaux, from the second half of the Middle Pleistocene, led to the description of *Haploidoceros mediterraneus* (Croitor et al., 2008), recently found in Spain at the beginning of MIS 5 (Sanz et al., 2014). The genus *Alces* is very rare during the Middle Pleistocene. Remains belonging to *A. latifrons* were brought to light at Achenheim. The current form of the elk *Alces alces* was mainly identified in sites from the end of the Pleistocene and the Holocene (Chaix and Desse, 1981; Delpech, 1983). The reindeer, *Rangifer tarandus*, is represented in France from the Middle Pleistocene onwards [e.g., la Caune de l'Arago (Crégut, 1980; Magniez et al., 2013)]. It is relatively rare during the second half of the Middle Pleistocene and becomes very abundant during the Upper Pleistocene, when it is the main target

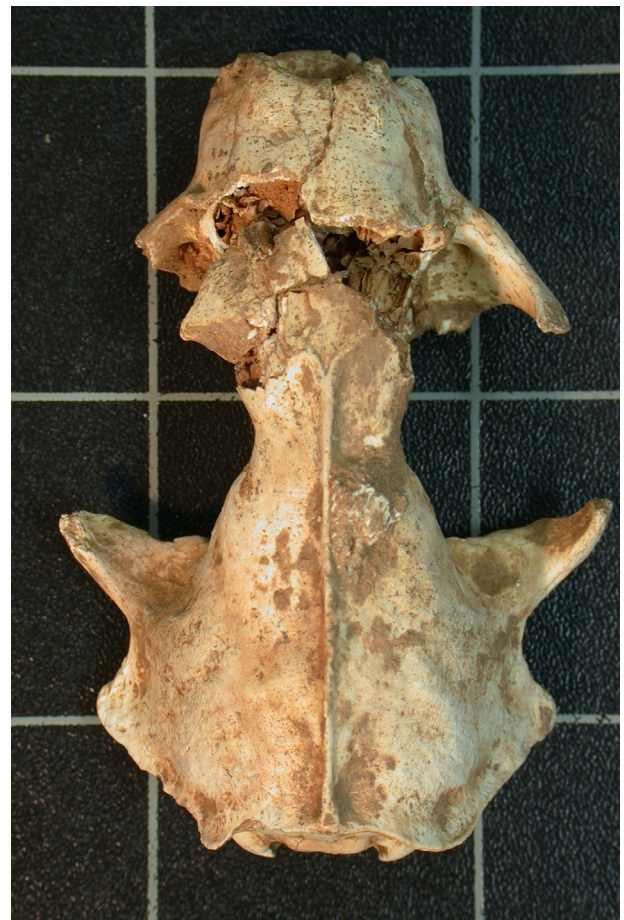


Fig. 9. Skull of *Mustela (Putorius) eversmanni* from Coudoulous II (level 9, MP, Lot) (scale square/white line: 3 cm) (photo J.-P. Brugal).
Crâne de *Mustela (Putorius) eversmanni* de Coudoulous II (niveau 9, MP, Lot) (échelle carré/ligne blanche = 3 cm) (photo J.-P. Brugal).

of Middle and Upper Palaeolithic hunters. The roe deer, *Capreolus capreolus*, is rare in French Middle Pleistocene sites and is better represented during the Upper Pleistocene, but often in small numbers.



Fig. 10. Skull of *Crocuta spelaea/crocota intermedia* from Lunel-Viel I (I.9#1133; MP, Hérault) (photo P. Fosse, Plate par J.B. Fourvel).
Crâne de *Crocuta spelaea/crocota intermedia* de Lunel-Viel I (MP ; Hérault ; c.9#1133) (photo P. Fosse, figure montée par J.B. Fourvel).

5. Proboscideans

Two families of proboscideans are present in France. Although regularly reported in palaeontological and archaeological sites, fossil remains of Mastodontidae are rarely abundant. There are no recent studies on this group, and just a brief summary will be briefly proposed (see Guérin and Patou-Mathis, 1996). *Anancus avernensis* is a Tertiary form (upper Miocene), which still survives until the middle Villafranchian (Saint-Vallier) and early in the upper Villafranchian, as in Chilhac with a subspecies described.

Two lineages of Elephantidae are known during the Pleistocene, well-represented in France. The first refers to *Elephas*, or *Paleoloxodon* (sub-genus) from Africa (Beden, 1979) and Europe. *P. antiquus* is present in several French sites, especially during the Middle Pleistocene and continues until the very beginning of the early Pleistocene. It is the ancestor of the island forms of the Mediterranean, Eastern particular (Crete, Cyprus, etc.). The second lineage, more emblematic of Prehistory, concerns the genus *Mammuthus*, which in Europe shows a continuous lineage with five successive taxa: *M. gromovi*, *M. meridionalis*, *M. trogontherii*, *M. intermedius* and



Fig. 11. Mandibles of *Lynx spelaea* from Observatoire (MP/LP, Monaco) (scale: 1 cm) (photo J.B. Fourvel & P. Fosse).
Mandibules de *Lynx spelaea* de l'Observatoire (MP/LP, Monaco) (photo J.B. Fourvel & P. Fosse).

M. primigenius. Only the last four species are present in France from almost a thousand sites listed (Labe, in progress).

If the first is not formally recognized in France, *M. meridionalis* is known in many deposits, since that of Saint-Vallier, but also Chilhac, Senèze, Saint-Prest and Durfort, and more sites from the valley of the Saône River. A complete skeleton from Durfort is exhibited in the paleontology gallery of MNHN (Paris), site attributed to the end of Early Pleistocene. *M. trogontherii* is the typical representative of the Middle Pleistocene (sites Abbeville, Saint-Acheul), and probably ancestor of *M. intermedius*. This taxon have been recently redefined from the material of La Fage I and Romain-la-Roche (Labe and Guèrin, 2005; Paupe et al., 2010) dated to the end of Middle Pleistocene. It is also recognized at Coudoulous II (level 9, Uzunidis and Brugal, 2018; Labe and Brugal, in press). This form is the direct ancestor of *Mammuthus primigenius*, common in the Upper Pleistocene site in all the French regions and regularly depicted in the rock and portable paleolithic art.

6. Caniformia

6.1. Canidae

Canidae are relatively omnipresent in fossiliferous sites and a lot of work has been carried out on them over the past four decades (e.g., review in Boudadi-Maligne, 2010). Several taxa occur regularly during the Pleistocene: *Canis etruscus*, *C. arvensis*, *Vulpes alopecoides* and *Xenocyon lycanoides* during the course of the Early Pleistocene, as shown by the sites of Saint-Vallier (Argant, 2004), le Vallonnet (Moullé et al., 2006a) or Ceysaguet (Argant, 2004; Tsoukala and Bonifay, 2004; Brugal and Boudadi-Maligne, 2011). *Canis mosbachensis*, *C. lupus*, *Vulpes praeglacialis*, *V. vulpes*, *V. lagopus* (= *Alopex lagopus*), *Cuon priscus* and *Cuon alpinus europaeus* occur throughout the country during the Middle Pleistocene. In Corsica, Canidae also occur during the Upper Pleistocene, mainly represented by *Cynotherium sardous* (Salotti et al., 2000) and more discreetly by a small fox *V. vulpes ichnusae* (Pereira et al., 2005). The canid species are of considerable biochronological interest and contribute in defining palaeoenvironments. The *Canis* genus has been continuously present in Western Europe since its appearance, more than three million years ago, until the present day. On account of this constancy, it is an excellent marker of the variation of palaeoenvironments, in spite of its ubiquitous character. However, the phylogeny of the *Canis* genus is still widely debated (Garrido and Arribas, 2008; Boudadi-Maligne, 2010; Brugal and Boudadi-Maligne, 2011). New fossil species continue to be described for the Early and Middle Pleistocene, complicating our knowledge of this genus and its evolution. This blurred vision can be explained by the absence of quantification of individual intra-specific variations, and

by the fact that spatially and temporally dispersal data are taken into consideration in phylogenies.

The wolf lineage is an excellent biochronological tool. From the end of the early Middle Pleistocene (MIS 10) and during the Upper Pleistocene (until MIS 3), the size of individuals increased continuously, leading to the description of three chrono-subspecies: *C. lupus lunellensis* [Lunel-Viel, (Bonifay, 1971), *C. lupus sante-naisiensis* (Santenay, Argant, 1991)] and *C. lupus maximus* (Jaurens, Boudadi-Maligne, 2012). This trend was brought to light at the end of the 1960s based on the antero-posterior diameter of the lower carnassial teeth (Bonifay, 1971; Brugal, 1981; Hadjouis, 1982; Patou, 1984; Argant, 1991; Valensi, 1994). The multivariate analysis of cranial, dental and post-cranial biometric data clarified and refined this intra-specific evolution, reinforcing the biochronological contribution of canids (Boudadi-Maligne, 2010, 2012). The *Cuon* genus is relatively well-represented in French sites and a comprehensive study (Brugal and Boudadi-Maligne, 2011) shows the possible distinction between the different chronological forms: *C. priscus* with two chrono-subspecies (*priscus* and *fossilis*) during the Middle Pleistocene, followed by *C. alpinus europaeus* (Fig. 8) during the Upper Pleistocene (and *C. a. alpinus* for present-day species).

6.2. Ursidae

Several taxa occur in French sites: *Ursus etruscus*, *U. deningeri*, *U. spelaeus*, *U. arctos*, *U. thibetanus*. The cave bear *Ursus spelaeus* is a remarkable case. It is abundant in closed cave environments where the remains of dead animals are well preserved over very long periods of time (hundreds of thousands of years, and hundreds or thousands of individuals), and it provides incomparable statistical series in the domain of paleontology. When it is well studied (e.g., Prat and Thibault, 1976; Argant, 1991, 1995), it becomes an important element for biochronology (sites with at least 20 individuals) or palaeoethology (Fosse et al., 2002). According to the widely accepted evolutionary lineage, the cave bear descends from *Ursus etruscus*, followed by the ancestral form *Ursus deningeri*, which is well-represented for example at Château and Azé, then the typical form, *Ursus spelaeus*. In reality, the situation is clearly more complex, as shown by the existence of the subspecies *U. spelaeus spelaeus*, *U. spelaeus ladinicus*, and the appearance of *Ursus eremus*, *Ursus ingressus* (Rabeder et al., 2004). These two latter species do not occur in France, where only *U. s. spelaeus* has been identified.

Ursus arctos also stemmed from the evolution of *Ursus etruscus* and developed successfully up until now. The oldest currently known *U. arctos* are the mid-Middle Pleistocene specimens from Vergranne and Château. This species is omnivorous, but more carnivorous than the cave bears (Bocherens, 2008) and probably better adapted to heat, and it resisted the Tardiglacial-Holocene



Fig. 12. *Panthera spelaea intermedia* from Igue des Rameaux (MP, Tarn-et-Garonne). Hemimandible and teeth: comparison with Jaurens (LP, Corrèze) and Château (MP, Saône-et-Loire) (photo A. Argant). 1 – *Panthera spelaea spelaea*, Jaurens (FSL 301 035). Right hemimandible, large form (Ballesio 1980): a – vestibular view; b – lingual view of the M/1 (FSL 300 821). 2 – *Panthera spelaea intermedia*, Igue des Rameaux, left hemimandible (IgRx-F4N-c.62-58), vestibular view. 3 – *Panthera spelaea fossilis*, Château Breccia: a – right hemimandible (CHA.1-D4-99), vestibular view; b–c – fragment of mandible with P/4 and M/1 (CHA.1-D5-20), occlusal and lingual view. *Panthera spelaea intermedia* de l'Igue des Rameaux (MP, Tarn-et-Garonne). Hémimandibules et dents : comparaisons avec Jaurens (LP, Corrèze) et Château (MP, Saône-et-Loire) (photo A. Argant). 1 – *Panthera spelaea spelaea*, Jaurens (FSL 301 035). Hémimandibule droite, grande forme (Ballesio 1980) : a – vue vestibulaire ; b – vue linguale de la M/1 (FSL 300 821). 2 – *Panthera spelaea intermedia*, Igue des Rameaux, Hémimandibule gauche (IgRx-F4N-c.62-58), vue vestibulaire. 3 – *Panthera spelaea fossilis*, Château Breccia : a – Hémimandibule droite (CHA.1-D4-99), vue vestibulaire ; b–c – fragment de mandibule avec P/4 et M/1 (CHA.1-D5-20), vues occlusale et linguale.

transition. *Ursus thibetanus* is also present in France, although it is not common. It occurs in France during the Middle Pleistocene, during MIS 7 for example at Coudoulous 1 (Argant, in press), and about a dozen other sites (Argant and Crégut-Bonnouire, 1996).

The OURSALP Programme brings together data on bears (fossil or subfossil *U. spelaeus* and *U. arctos*) from the Jura and the Alps. The multiplication of ^{14}C -AMS dates on bears now gives us an accurate chronological framework, which is indispensable for understanding population dynamics with isotopic and paleogenetic analyses. The reasons for their disappearance are undoubtedly multiple, but the disappearance of the cave bear can mainly be attributed to climate change at the end of the last Tardiglacial. The Chartreuse Mountains, which were not covered in ice during the last glacial maximum, yielded the last known *U. spelaeus*, dated to $13,990 \pm 50$ Ly-2545 (OxA). It comes from la Cuvée des Ours (1641 m asl) (Argant et al., 2012, 2018, 2019). This mountain range

probably corresponds to a refuge zone as the dates of extinction of the cave bear in Europe seem to be earlier. The disappearance of the brown bear is unquestionably due to direct human action owing to hunting and elimination, reinforced by the anthropogenic impact on the natural environment.

6.3. Mustelidae

The Mustelidae family is much diversified and it is possible to identify (Crégut-Bonnouire, 1996a, b): *Gulo gulo* (ssp. *schlosseri* and *spelaeus*), *Mustela praeivalis*, *M. nivalis*, *M. palerminea*, *M. erminea*, *M. lutreola*, *M. putorius*, *M. eversmanni*, *Martes martes*, *Meles thoralis*, *Meles meles*, *Lutra lutra*. At the site of Saint-Vallier, *M. thoralis* is present as early as 2.2–2.5 Ma (Argant, 2004) and is subsequently replaced by *M. meles* during the Middle Pleistocene.

Table 2

Biochronological chart with species list and name of the French sites mentioned in the text (see Fig. 1 and Table 1).

Diagramme biochronologique avec la liste des espèces et le nom des gisements français cités dans le texte (voir Fig. 1 et Tableau 1).

Chronology	Equidae	Bovinae	Caprinae Antilopinae Rupicaprinae	Cervidae	Rhinocerotidae	Canidae	Proboscidea	Ursidae	Mustelidae	Hyenidae	Felidae	French sites (see text)
Late Pleistocene	<i>Equus caballus</i> (with different subspecies: <i>germanicus</i> ; <i>gallicus</i> and <i>arcelini</i>) <i>Equus taubachensis</i>	<i>Bison priscus</i> (<i>mediator</i> , <i>minor</i> ?) <i>Bison bonasus</i> <i>Bos primigenius</i>	<i>Ovibos pallantis</i> <i>Hemitragus cedrensis</i> <i>Capra ibex</i> <i>Capra caucasica</i> <i>praepyrenaica</i> <i>Capra pyrenaica</i>	<i>Cervus elaphus</i> <i>Rangifer tarandus</i> <i>Capreolus capreolus</i> <i>Alces alces</i>	<i>Stephanorhinus hemitoechus</i> <i>Stephanorhinus kirchbergensis</i> <i>Coelodonta antiquitatis</i>	<i>Canis lupus santenaisiensis</i> <i>Canis lupus maximus</i> <i>Vulpes vulpes</i> <i>Vulpes lagopus</i> <i>Cuon alpinus europaeus</i> <i>Cynotherium sardous</i> and <i>Vulpes vulpes ichnusae</i> (in Corsica)	<i>M. primigenius</i>	<i>Ursus spelaeus</i> <i>Ursus arctos</i>	<i>Meles meles</i> <i>Mustela nivalis</i> <i>Mustela erminea</i> <i>Mustela putorius</i> <i>Putorius eversmanni</i> <i>Gulo gulo</i>	<i>Crocuta crocuta/spelaea</i>	<i>Lynx pardinus</i> <i>Lynx lynx</i> <i>Panthera (Leo) spelaea</i>	Balma Abeurador; Adouste; L'Arquet; Balazuc II; Belvis; Bruniquel; Cabias; Camiac; Campefiel; Caours; Grotte Chabot; Chinchon I; Le Closeau; Abri du Colombier; Abri Cornille; Le Coustal; La Crouzade; Cuvée des Ours; Abri Dumas; Grotte des Enfants; Fouvent; Gazel; Grand Abri aux Puces; Grau de Padern; Habarra; Jaurens; Malarnaud; Marie; Le Marronnier; Mars; Moula Guercy; Grotte de l'Observatoire; Baume d'Oullins; Le Peyrat; Pont-du-Château; Grotte du Prince; Quéroy; Rigney; Saint-Marcel d'Ardèche; La Salpêtrière; Soulabé; Tournal
Middle Pleistocene	<i>Equus mosbachensis</i> (with different subspecies: <i>campdepeyri</i> ; <i>micoquii</i> ; <i>palustris</i> and <i>tautavelensis</i>) <i>E. piveteaui</i>	<i>Bison schoetensacki</i> <i>Bison priscus</i> (<i>priscus</i>) <i>Bos primigenius</i>	<i>Rupicapra rupicapra</i> <i>Rupicapra pyrenaica</i> <i>Saiga tatarica</i> <i>Praeovibos priscus</i> <i>Soergelia elisabethae</i> <i>Hemitragus orientalis</i> <i>Hemitr. bonali</i> <i>Hemitr. cedrensis</i> <i>Capra ibex</i> <i>Ovis ammon antiqua</i>	<i>Megaloceros giganteus</i> <i>Praemegaceros cazioti</i> (in Corsica) <i>Praemegaceros solilhacus</i> <i>Praemegaceros rossii</i> (in Corsica) <i>Megaloceros giganteus</i> <i>Cervus elaphus</i> <i>Cervus simplicidens</i> <i>Rangifer tarandus</i>	<i>Stephanorhinus hemitoechus</i> <i>Stephanorhinus kirchbergensis</i> <i>Coelodonta antiquitatis</i>	<i>Canis mosbachensis</i> <i>Canis lupus lunellensis</i> <i>Canis lupus santenaisiensis</i> <i>Vulpes praeglacialis</i> <i>Vulpes vulpes</i> <i>Vulpes lagopus</i> <i>Cuon priscus</i> (<i>ssp fossilis</i> and <i>priscus</i>) <i>Cuon alpinus europaeus</i>	<i>Mammuthus intermedius</i> <i>Palaeoloxodon antiquus</i>	<i>Ursus spelaeus</i> <i>Ursus arctos</i> <i>Ursus thibetanus</i>	<i>Meles meles</i> <i>Mustela nivalis</i> <i>Mustela palerminea</i> <i>Mustela erminea</i> <i>Mustela putorius</i> <i>Putorius eversmanni</i> <i>Gulo gulo schlosseri</i>	<i>Hyaena prisca</i> <i>Crocuta crocuta/spelaea</i>	<i>Lynx pardinus</i> <i>Lynx lynx</i> <i>Panthera gombazoenensis</i> <i>Panthera (Leo) spelaea</i>	Abbeville; Achenheim; Aldène; Caune de l'Arago; Artenac; Azé; Baume de l'Aubesier; Baume Bonne; Biache-saint-Vaast; Camps-de-Peyre; Cap de la Bielle; Grotte des Cèdres; Castiglione; Château; Cléons; Coudoulous I; Coudoulous II; Es-Taliens; L'Escaie; La Fage; Grotte XV (Vaufrey); Lazaret; Lunel-Viel; Malbattu; La Micoque; Montmaurin-La Niche; Moru; Orgnac III; Pech de l'Azé II; Piégu; Igue des Rameaux; Ranville; Rigabe; Romain-la-Roche; Igue de Saint-Sol-Belcastel; Santenay; Sempigny; Soleilhac; Terra Amata; Tourville-la-Rivière; Vayssière; Vergranne

Table 2 (Continued)

Chronology	Equidae	Bovinae	Caprinae Antilopinae Rupicaprinae	Cervidae	Rhinocerotidae	Canidae	Proboscidea	Ursidae	Mustelidae	Hyenidae	Felidae	French sites (see text)
	<i>Equus achenheimensis</i>		<i>Saiga tatarica</i>	<i>Dama clactoniana</i> <i>Dama roberti</i> <i>Dama dama</i> <i>Haploidoceros mediterraneus</i> <i>Alces latifrons</i>			<i>M. trogontherii</i> <i>Palaeoloxodon antiquus</i>	<i>Ursus deningeri</i>				
	<i>Equus steinheimensis</i>		<i>Rupicapra rupicapra</i> <i>Rupicapra pyrenaica occitania</i>				<i>M. trogontherii</i>					
Lower Pleistocene	<i>Equus stenonis</i>	<i>Leptobos elatus</i> ; <i>Leptobos furtivus</i> <i>Smertiobos etruscus</i> ; <i>Smertiobos bravardi</i> <i>Eobison</i> sp. <i>Bison schoetensacki</i>	<i>Pliotragus ardeus</i> <i>Gallogoral meneghinii</i> <i>Megalovis latifrons</i> <i>Praeovibos mediterraneus</i> <i>Soergelia elisabethae</i> <i>Gazella borbonica</i> <i>Gazellospira torticornis</i> <i>Procamptoceras brivatense</i> <i>Ovis ammon antiqua</i> <i>Hemitragus</i> cf. <i>orientalis</i>	<i>Eucladoceros ctenoides</i> [with different subspecies: <i>vireti</i> , <i>senezensis</i> = <i>falconeri</i> ?, <i>tetraceros</i> and ssp. (cf. <i>ctenoides</i> ?)] <i>Eucladoceros dicranios</i> <i>Praemegaceros obscurus</i> ; <i>Praemegaceros</i> sp. (cf. <i>verticornis</i> ?) <i>Arvernoceros giulii</i> <i>Croizetoceros ramosus</i> <i>Metacervocerus rhenanus</i> <i>Dama vallonnetensis</i> ; <i>Dama</i> sp.	<i>Stephanorhinus hundsheimensis</i> <i>Stephanorhinus etruscus</i>	<i>Canis etruscus</i> <i>Canis arnensis</i> <i>Vulpes alopecoides</i> <i>Xenocyon lycanoides</i>	<i>Mammuthus meridionalis</i> <i>Anancus arvernensis</i> <i>Zygodolophon borsoni</i>	<i>Ursus etruscus</i> <i>Ursus deningeri</i>	<i>Meles thorali</i>	<i>Pachycrocuta brevirostris</i> <i>Pachycrocuta (= Pliocrocuta) perrieri</i> <i>Megantereon cultridens</i> <i>Homotherium crenatidens</i> <i>Acinonyx pardinensis</i> <i>Puma pardoides</i> (= <i>Panthera schaubi</i>) <i>Dinofelis</i> sp. <i>Lynx issiodorensis</i> <i>Lynx lynx</i>	Les Etouaires; Violette; Saint-Vallier; Chilhac; Le Coupet; Senèze; Blassac-la-Girondie; Peyrolles; Sainzelles; Cagnes-sur-Mer; Roccaneyra; Ceyssaguet; La Sartanette; Riège; Bois-de-Riquet; Saint-Prest; Grosse Marguerite; Aven des Trois Pigeons; Tour-de-Grimaldi; Le Vallonnet; Durfort; Chagny; Pardines; Rozières	

Mustelidae are frequent in many French sites, but studies are still rare (Mallye and Guérin, 2002; Mallye, 2007). The site of Romain-la-Roche, related to MIS 6, contains *M. meles*, *M. nivalis*, *M. erminea*, *M. putorius* and probably *Putorius evermanni* (Fosse and Fourvel, 2010) (Fig. 9). This latter species occupies steppe-like environments and appears during the Middle Pleistocene at La Fage, dated to MIS 8-7 (Mourer-Chauviré et al., 2003). It is still present during the final stage of MIS 6 at Coudoulous II (Fig. 9) and becomes more abundant during the Upper Pleistocene (Tournepiche, 1996: fig. 18). The wolverine also occurs at La Fage (Bourgeois and Philippe, 2017) and in about fifteen other Upper Pleistocene sites (see figure 6 in Bourgeois and Philippe, 2017), and the subspecies *schlosseri* is reported in the early Middle Pleistocene of l'Escale (Bonifay, 1971). The otter is not frequent and little is known about its origin. It is sometimes controversially reported during the Middle Pleistocene, but generally occurs during the Upper Pleistocene, like at Balazuc II (Argant, 2018) and le Grand Abri aux Puces (Slimak et al., 2010).

7. Feliformia

7.1. Hyenidae

This family is well-represented in France by the following species: *Pachycrocuta brevirostris*, *Pachycrocuta* (= *Pliocrocuta*) *perrieri*, *Chasmaporthetes lunensis*, *Crocota spelaea*, *Hyaena prisca*. The two species of giant hyenas (*P. brevirostris* and *P. perrieri*) of the *Pachycrocuta* genus develop during the Early Pleistocene, and then became extinct around 600 ky with the last representative of this genus (Turner and Anton, 1996). In France, these early forms have only yielded a few remains. *P. perrieri* has been identified in several Plio-Pleistocene sites in the Massif Central: e.g., Saint-Vallier (Argant, 2004), Chagny (Argant, 1991), Senèze (Bœuf, 1997) or Vialette (Lacombe et al., 2008). The giant hyena *P. brevirostris* (defined at Sainzelles) has only been described in six sites, including la Sartanette (Bonnet, 1980), Ceyssaguet (Tsoukala and Bonifay, 2004), la Grosse Marguerite and the Trois Pigeons sinkhole (Fourvel and Lateur, 2015) and Bois-de-Riquet (Bourguignon et al., 2016). It only seems to have occurred during a relatively short lapse of time, between 1.2 Ma and 0.9 Ma (Fourvel and Lateur, 2015).

The fossil striped hyena *Hyaena prisca* is sometimes described as a subspecies of the striped hyena: *H. hyaena prisca*. This species evolves during the Middle Pleistocene and disappears from our regions at the end of the same period. It has been reported in several Middle Pleistocene assemblages in France, including Lunel-Viel (Bonifay, 1971; Fosse, 1994), L'Escale (Bonifay, 1971; Crégut-Bonnoure, 1996b), Igue des Rameaux (Rouzaud et al., 1990) or Es-Taliens (Clot and Duranthon, 1990). The question of the phylogenetic links between *H. prisca* and *P. perrieri* is still widely debated.

The spotted fossil hyena belongs to the *Crocota* genus. The specific phylogeny of this genus is also controversial: are there distinct species, i.e., do modern African and fossil European forms, correspond to *C. crocuta* or *C. spelaea*? Moreover, at least two chrono-subspecies are recognized in the fossil record: *intermedia* (Fig. 10, ex. Lunel-Viel) and *spelaea*, with an increase in size throughout time. The genus appeared in Europe during the Middle Pleistocene (around 800 ky at Calsa Selce in Italy in Sardella and Petrucci, 2012) and was the most frequent form of hyena until it disappeared, seemingly around 25,000 years BP (Fosse, 1994; Discamps, 2011; Fourvel, 2012). The cave hyena is found in many paleontological sites, among which we can cite the dens of Camiac (Guadelli, 1989b), Lunel-Viel (Fosse, 1994), Orgnac 3 (Testu, 2006) or Fouvent (Fourvel, 2012) (and see the taphonomic aspect of dens in Brugal et al., 1997).

7.2. Felidae

Felines are much diversified during the Pleistocene in France, with a wide taxonomic distribution (in terms of genus and species) and high variations in body size. The following species have been identified: *Megantereon cultridens*, *Homotherium crenatidens*, *Dinobastis latidens*, *Dinofelis piveteaui*, *Felis lunensis*, *F. minuta*, *F. silvestris*, *Lynx issiodorensis*, *L. spelaea*, *L. pardinus*, *L. lynx*, *Acinonyx pardinensis*, *Puma pardoides*, *Panthera gombaszoegensis*, *P. pardus*, *P. (Leo) spelaea*. Only some taxa are presented in detail below.

Recent excavations at the site of Saint-Vallier (1993–99, by M. Faure and C. Guérin), and other excavations at Senèze (2001–2006, M. Faure, C. Guérin, E. Delson), led to the identification of the carnivore species reported in earlier studies and clarified their taphonomic and paleoenvironmental conditions (Faure and Guérin, 2004). Large classical Villafranchian carnivores are present at both of these sites: *Megantereon cultridens*, *Homotherium crenatidens*, *Acinonyx pardinensis*. The site of Saint-Vallier contained the rare *Puma pardoides* (= *Panthera schaubi*) (Argant, 2004), which was not identified at Senèze but is still potentially present. The re-examination of the early material from Senèze indicates the probable presence of the Machairodontinae *Dinofelis* sp. (Argant, submitted). These two sites are chronologically close; Saint-Vallier is about 2.2 Ma and Senèze is more recent, about 2 Ma. In the past, the site of Senèze yielded two famous whole reference skeletons, the *Megantereon cultridens* skeleton, curated at the Museum of Basel (NMB-Se#311) and the *Homotherium crenatidens* from the Claude-Bernard University – Lyon 1 (FSL 210991) (Ballesio, 1963).

The earliest mention of the lynx is related to the terminal Pliocene (around 3.0–3.5 Ma, Perrier) and the beginning of the Early Pleistocene (around 2.0–2.5 Ma, Saint-Vallier, in Argant, 2004) by the early large-sized *L. issiodorensis*. The last known representatives of these species come from Untermaßfeld in Germany around 0.9–1.2 Ma. Following on from the Issoire lynx, the cave lynx *Lynx pardinus* var. *spelaea* and the Boreal Pleistocene lynx *L. lynx* coevolves. However, the most recent study suggests an earlier appearance of the Boreal lynx with a mention at Ceyssaguet around 0.9–1.2 Ma (Tsoukala and Bonifay, 2004). The cave lynx is abundantly represented in the French sites, at L'Escale and Lunel-Viel (Bonifay, 1971), la Caune de l'Arago (Crégut, 1979), Malarnaud (Dufour, 1989), as well as in Vaufrey Cave (Delpech, 1988). We note in particular 89 remains in the Observatoire Cave in Monaco (Brugal et al., 2017) (Fig. 11), abundant remains at Campefiel (Bonifay, 1971) or 183 remains identified at Lazaret Cave (Valensi, 1994). The Iberian lynx *L. pardinus* is mainly attested in France during the most recent phases of the Pleistocene. We can cite, for example a skeleton estimated to date from the Dryas III from la Balma Abeurador (Clot and Duranthon, 1990), or another from Cabias Cave, dated to 4000 cal. BP (Rodríguez-Varela et al., 2015).

Panthera gombaszoegensis, the European jaguar, occurs in about ten French sites, including L'Escale (Bonifay, 1971) and Artenac (Tournepiche, 1984). The large-sized well-represented jaguar from la Brèche de Château (NMI=7 including one “whole” skeleton), is one of the median Middle Pleistocene forms (Argant A. and Argant J., 2011, 2018). *P. (Leo) spelaea fossilis* from the Middle Pleistocene is close to an early cave lion form, characterized by its large size and powerful, well-marked muscles on the bones: Château (Argant et al., 2007) (Fig. 12), Artenac, Arago. The site of Igue des Rameaux yielded a very rich fossil series (nearly 30 individuals of all ages), resulting in the characterization of a new subspecies, *P. (Leo) spelaea intermedia* (Argant and Brugal, 2017). The Upper Pleistocene forms of *P. (Leo) s. spelaea* decrease in size until they reach the size of the present-day lion. The lion from Closeau is dated to 12,248 ± 66 years BP (Bodu and Bemilli, 2000), and the lion from Peyrat to 10,590 ± 70 years BP (Fosse et al., 2017 with geochronological occurrences for the southwest of France), which marks the

end of the presence of the species in Western Europe. Between the two, the situation varies considerably, with small lions during MIS 6, and larger animals during MIS 5, undoubtedly as a result of climatic, geographic and genetic variations and specific morphotype population dynamics. It is still difficult to clarify the biochronology of *P. spelaea* during this interval.

8. Conclusions

France is a crossroads of differentiated climatic and biological influences during the Quaternary in Western Europe due to its geographic position and topography (mountains, rivers). It regularly underwent cycles of relative isolation and connection (e.g., with Great Britain, Italy, Northern Europe...), as a result of glacial maxima (extensions of glaciers and snow-covered zones, drops in sea level) and interglacial optima. These cycles encouraged adaptive factors, sometimes with a hint of endemism, but were also conducive to the regular introduction of new migrants or new genetic forms. These mechanisms occur in all western European regions characterized by marked geotopographic division with peninsular conditions (Iberia, Balkans, Italy, Great Britain, Scandinavia), major mountain chains (in particular the Alpine Arc), major rivers and a Germano-Polish plain linking the subcontinent to the immense Russian and Asian plains, a somewhat less heterogeneous region. This conditioned partitioning and resulted in mammalian populations (micro- to macro-faunas) with differentiated eco-evolution processes, which make biostratigraphic correlations sometimes difficult to establish. In this respect, the example of Mediterranean regions is particularly significant (e.g., Bonifay, 1996a, b; Croitor and Brugal, 2001; Brugal et al., 2004; Valensi, 2009). Most of the French Pleistocene sites are located in the southern half of the country, with possibilities of exchanges with northern European regions, and also with the south (Iberia and Italia), and do not present any particular endemism and/or particular survival of taxa, as seen in these peninsular regions. Overall, the herbivore and carnivore palaeocommunities in France are similar through time to those from the rest of Western Europe, at least in terms of ecological structure and trophic levels. However, their taxonomic composition may vary, and is more or less diversified, and some taxa are different or absent in some regions depending on geo-topography and the climatic phases of Pleistocene. Table 2 presents a summarized overall view of species distribution and sites in France during the Pleistocene subseries/subepochs.

The aim of this collective contribution was to propose a general review of the large mammal faunas in France during the Pleistocene, without claiming to be exhaustive, based in particular on recent studies and a bibliography search focusing on French studies. This overview of herbivores and carnivores from the French Pleistocene highlights the dynamism of recent research, enhanced by the revision of formerly studied sites, newly published sites or university works (Quillès, 2003; Olive, 2005; Testu, 2006; Boudadi-Maligne, 2010; Goubel, 2011; Bon, 2011; Discamps, 2011; Fourvel, 2012; Uzunidis-Boutillier, 2017; Pelletier, 2018... to quote but a few). The contribution of paleogenomic data is also increasingly vital for our taxonomic understanding of fossil populations and their phylogeographic structures. The ¹⁴C-AMS, U/Th-ESR dating corpus and isotopic or micro- and meso-dental wear studies has also considerably expanded. They now provide a reference framework which enables us to approach the history of species, their evolution and population dynamics more rigorously than in the past. The development of a database based on these works and complementary research approaches (such as taphonomy, Brugal, 2017), should allow us to establish an integrative view of climatic palaeoenvironments in the near future, faunal successions and

palaeoecological (in particular body size) and evolutionary data of species in France.

Author contributions

J.-P. Brugal coordinated and planned the paper. The sections on Equids, Large Bovids, Caprids et al., Cervids, Rhinocerotids, Proboscids, Canids, Ursids, Mustelids, Hyenids, Felids were respectively written by J.L. Guadelli, J.-P. Brugal, E. Crégut and P. Fernandez, P. Magniez and R. Croitor, A. Uzunidis, J.-P. Brugal, M. Boudadi-Maligne, A. Argant, A. Argant and B. Labe, J.B. Fourvel and P. Fosse, A. Argant and J.B. Fourvel. P. Fosse designed Figs. 1–3 with help from J.-P. Brugal for the site list. Suppl. Information was written by J.L. Guadelli.

Disclosure of interest

The authors declare that they have no competing interest.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.annpal.2019.102384>.

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