Scientific Annals, School of Geology Aristotle University of Thessaloniki (AUTH)	Special volume 98	109-122	Thessaloniki, 2006

ABOUT THE ABSENCE OF CAVE BEAR IN PROVENCE (SE FRANCE) AND THE VALLESCURE EXCEPTION

Jérôme QUILÈS[1] & Evelyne CRÉGUT-BONNOURE[2]

Abstract: The Provence region in the South-East of France, delimitated by the Alps to the East and the Rhône River to the North and the West, is characterized by a relative endemism of its Pleistocene fauna. Compared with Italy and the West Rhône River, relevant ungulate taxa of cold plains are very rare. The carnivore representation is also specific to this region with scarce evidences of *Crocuta crocuta spelaea, Cuon alpinus europaeus, Gulo spelaeus* and *Ursus spelaeus*, while *Ursus arctos* and *Ursus thibetanus* are well known. During Late Pleistocene, the Vallescure locality is the only site to have registered the presence of carnivore taxa absent from the rest of Provence. In this cave, carnivore remains are abundant and represented by twelve species: *Canis lupus*, *Cuon alpinus europaeus*, *Vulpes vulpes*, *Alopex lagopus*, *Ursus spelaeus*, *Ursus arctos*, *Gulo spelaeus*, *Crocuta spelaea*, *Panthera* (*Leo*) *spelaea*, *Panthera pardus*, *Lynx spelaea*, *Felis silvestris*. *Capra ibex* is the only herbivore present. The morphological study of cave bear teeth highlights the geographical isolation of Provence during the Late Pleistocene. Convergent arguments on ungulate and carnivore taxa, in particular cave bear, are relevant to demonstrate that the Rhône River acted as a major paleobiogeographical limit, seeming to be active since the OIS 4, at least for *U. spelaeus*.

Key words: *Ursus spelaeus,* Late Pleistocene, France, South-East, geographical isolation.

INTRODUCTION

The Provence region, in the South-East of France, is a karstic area abundantly provided with caves, in which archaeological and paleontological remains are known existing since more or less 1 Ma. The Pleistocene fauna is various (BRUGAL & CRÉGUT-BONNOURE, 1994; CRÉGUT-BONNOURE, 1995a; 2004a,b; CRÉGUT-BONNOURE & FERNANDEZ, 2004,) and Ursidae are represented by four species:

- *Ursus thibetanus* in three caves: "Les Cèdres" (OIS 6, Plan d' Aups, Var, CRÉGUT-BONNOURE, 1995b), Bérigoule (OIS 6, Murs, Vaucluse; CRÉGUT-BONNOURE, 1997), Cimay (OIS 7, Saint-Anne-d' Evenos, Var, CRÉGUT-BONNOURE, 1997);
- *U. arctos* in twenty six localities: Adaouste (OIS 5d, Jouques, Bouches-du-Rhône, DEFLEUR *et al*., 1994), «Bau de l' Aubesier» (OIS 4, Monieux, Vaucluse, CRÉGUT-BONNOURE *et al*., 1994), "Baume des Peyrards" (OIS 4, Buoux, Vaucluse; GAGNIÈRE, 1957), "La Masque" (OIS 4, Entrechaux, Vaucluse; Gagnière *in* LUMLEY-WOODYEAR, 1969), «Les Cèdres» (CRÉGUT-BONNOURE, 1995b), Vallescure (OIS 4, GAGNIÈRE & GERMAND, 1934), «Grotte aux Puces» (Cabasse, Var, GAGNIÈRE, 1954), Lazaret (OIS 6, Alpes-Maritimes, Patou, 1984), «Grotte Murée» (Holocene, Montpezat, Alpes-de-Haute-Provence, HELMER, 1979), "Aven de Vauclare" (Holocene, Esparron-de-Verdon, Alpes-de-Haute-Provence, COURTIN, 1974), La Fare (Holocene, Alpes-de-Haute-Provence, E. BLAISE, pers.com.), "Les Gras" (Escragnolles, Alpes-Maritimes, CRÉGUT-BONNOURE, 2002), Espiguières (Var, Aups, Courtin pers. com.), "Aven de Contadoux" (Holocene, Sault, Vaucluse, BUISSON-CATIL & CRÉGUT-BONNOURE, 1995), "La Clairière" (Holocene, la Roque-sur-Perne, Vaucluse, BLAISE *et al.,* 2004), "La Balance" (Holocene, Avignon; Vaucluse, HELMER, 1979), Mont Ventoux (Holocene, ten traps, Brantes and Savoillan, Vaucluse, CRÉGUT-BONNOURE *et al*., 2005);

---

[1] UMR 5608 (UTAH) 5, allées Antonio Machado 31058 Toulouse cedex 1 France.

[2] Muséum Requien 67, Rue Joseph Vernet 84000 Avignon France & UMR 5608 (UTAH) 5, allées Antonio Machado 31058 Toulouse cedex 1 France, evelyne.cregut@mairie-avignon.com

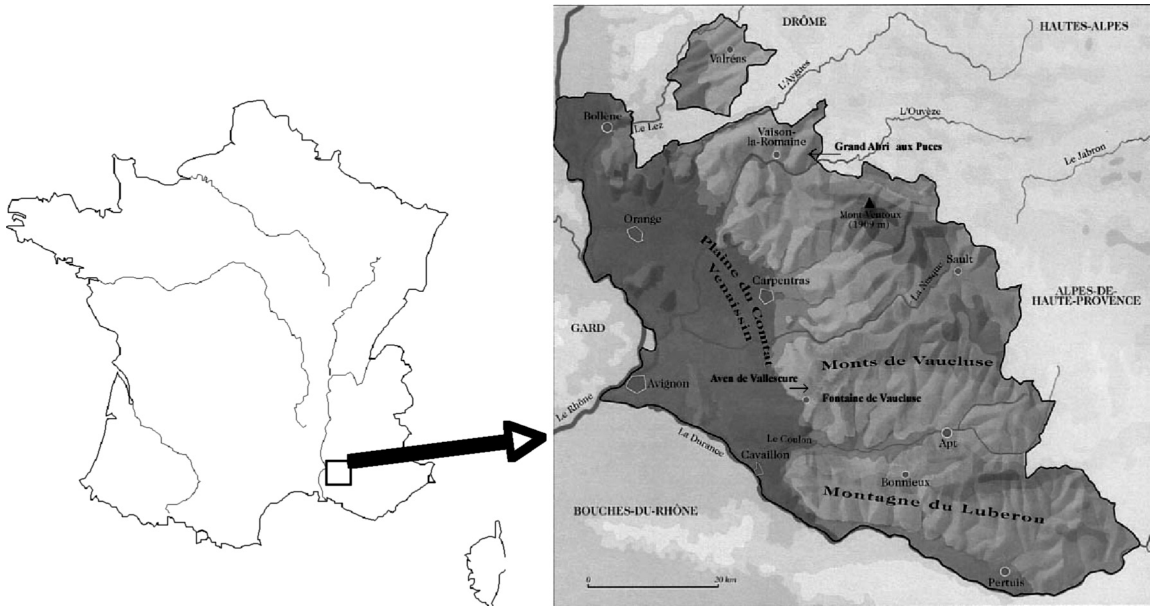


Figure 1. Geographical localization of "Grand Abri des Puces" and Vallescure. Modified from Olive (*in* Buisson-Catil *et al.,* 2004).

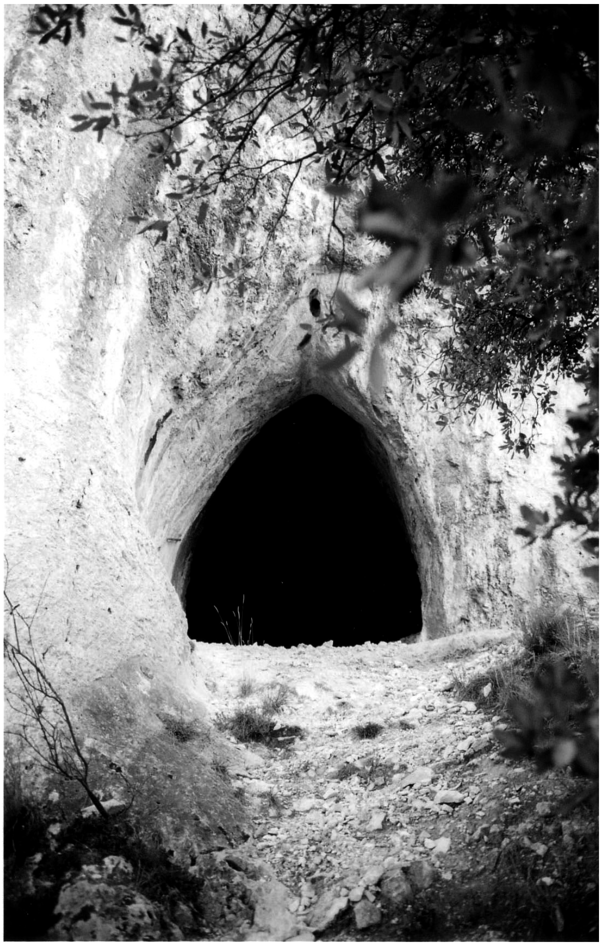


Figure 2. Entrance of Vallescure. Photograph E. Cregut-Bonnoure.

- *U. deningeri* in three caves: Vallonnet (Lower Pleistocene; Roquebrune-Cap-Martin, Alpes-Maritimes; Moullé, 1992), Escale (Lower Middle Pleistocene; Saint-Estève-Janson, Bouches-du-Rhône, Bonifay, 1971) and "Les Cèdres" (Crégut-Bonnoure, 1995b),
- *U. spelaeus* in three localities: Vallescure, perhaps «Grand Abri des Puces» (OIS 4, Entrechaux, Vaucluse; Crégut-Bonnoure, 2002), «L' Albarea» (Late Pleistocene, Sospel, Alpes-Maritimes, Moullé *et al.,* 2000).

Compared with other regions of France, *U. thibetanus* and *U. arctos* are relatively abundant while *U. deningeri* and *U. spelaeus* are poorly represented. The scarcity of cave bear, which is particularly numerous within the all Europe with more than a thousand of sites known, is under question.

VALLESCURE AND "GRAND ABRI DES PUCES" LOCALITIES

Vallescure (or Valescure) and "Grand Abri des Puces" (or Grotte Basse) are situated in the western border of Provence, called Vaucluse (fig. 1).

The Vallescure cave belongs to the Cretaceous karstic context of the famous Fontaine-de-Vaucluse. Two entrance porches give access to a 50 m² room, where a rich paleontological assemblage, dated from the OIS 4 (Gagnière & Germand, 1934) and associated with Mouste-

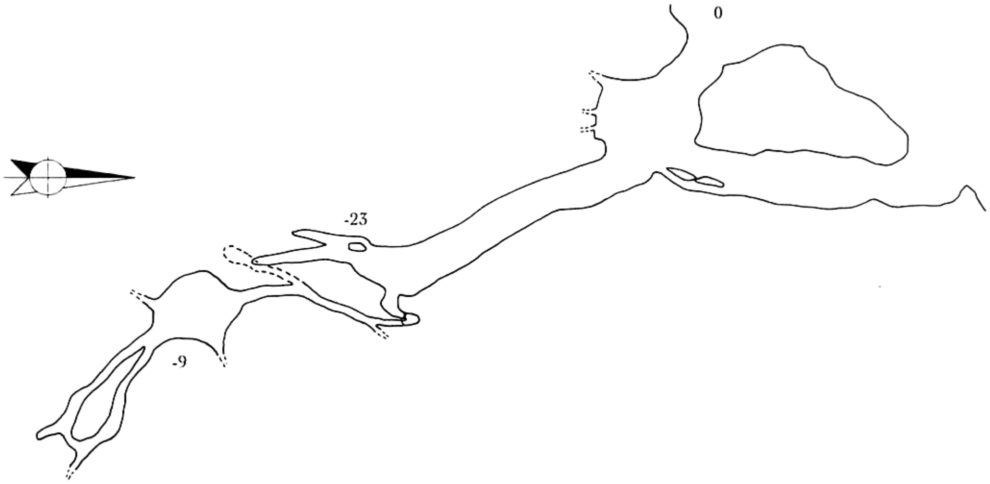


Figure 3. Plan of Vallescure after Groupe spéléologique de Fontaine-de-Vaucluse (Le Fahler & Fradin, 1995). Scale 16 mm for 10 m.

rian artefacts (Lumley-Woodyear, 1969) (fig. 2, 3) was discovered . The major part of the infilling and by consequence of the faunal material was destroyed during phosphates exploitation of the site. First scientific excavations were made by C. Chatelet, S. Gagnière, L. Germand, B. Girerd and D. Helmer, the collections of which are conserved in the Museum Requien of Avignon.

Carnivore remains are represented by twelve species: *Canis lupus*, *Cuon alpinus europaeus*, *Vulpes vulpes*, *Alopex lagopus*, *U. spelaeus*, *U. arctos*, *Gulo spelaeus*, *Crocuta crocuta spelaea*, *Panthera* (*Leo*) *spelaea*, *P. pardus*, *Lynx spelaea* and *Felix silvestris*. *Capra ibex* is the only Pleistocene herbivore present. All the material was found at the bottom of the entrance room, except wolverine bones found in a 15 m deep hole, corresponding to the beginning of a small horizontal gallery (fig. 4). This hole, used by local farmers, is also showing recent remains of *C. familiaris, Bos taurus* and *Ovis aries*. Bones of *Cervus elaphus* and *Sus scrofa*, less fossilized than the Pleistocene assemblage, are also present.

The "Grand Abri des Puces" is located just near the village of Entrechaux and the Ouvèze River, near the "La Masque" cave. This rock shelter was formed between two layers of Miocene limestone, and it is 10 m long and 5 m wide. Discovered by S. Gagnière, surface remains are composed by Mousterian artefacts and bones of ten mammal species: *C. lupus*, *U.* cf. *spelaeus*, *P.* (*L.*) *spelaea*, *Equus* sp. (*caballus sensu*), *Capreolus capreolus*, *Bos* or *Bison*, *C. ibex*, *Castor fiber*, an unidentified *Testudo* and *Emys orbicularis* (Crégut-Bonnoure, 2002; Cheylan, 1981; Hervet, 2000). This fauna is also conserved in the Museum Requien of Avignon.

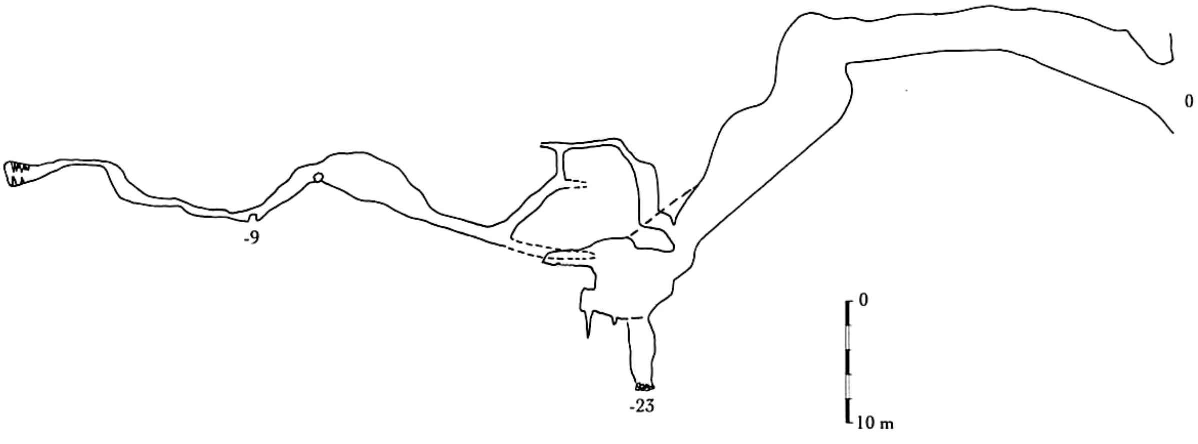


Figure 4. Section of Vallescure after Groupe spéléologique de Fontaine-de-Vaucluse (Le Fahler & Fradin, 1995).

Table 1
Skeletal representation of *U. spelaeus* remains from Vallescure.

	Adult	young		Adult	young adult	young		Adult	young adult	young		Adult	young adult
skull fragments	9	4	incomplete scapula	4			incomplete coxal	5			first phalanxes	54	
premaxillae	1		incomplete humerus	9	4		incomplete femur	5	11		second phalanxes	14	
fragmentary mandibles	3	2	incomplete radius	5	1	2	incomplete tibia	6	5	1	third phalanxes	55	
fragmentary canine	13	6	incomplete ulna	5	3	2	incomplete fibula	2	2	1	hyoid bones	2	
upper I1	1		pyramidal	3			patella	3			sternebrae	10	
upper I3	3		pisiform	3	2		talus	5	1		incomplete vertebrae	20	2
upper P4	5		scapholunar	7			calcaneus	4	5	1	sacrum	1	
upper M1	5		unciform	3			cuboid	4			incomplete rib	2	
upper M2	9		magnum	3	1		navicular	3	1				
lower I1	2		trapeze	2			cuneiform III	2					
lower I2	1		trapezoid	3			metatarsal I	3	1				
lower I3	8		metacarpal I	1			metatarsal II	1	1				
lower P4	2		metacarpal II	5	2		metatarsal III	4					
lower M1	6		metacarpal III	7			metatarsal IV	7	1				
lower M2	5		metacarpal IV	10	1		metatarsal V	5	3				
lower M3	4		metacarpal V	6	1		frag m. metapodials	10	4				
Total	77	12		76	15	4		69	35	3		158	2

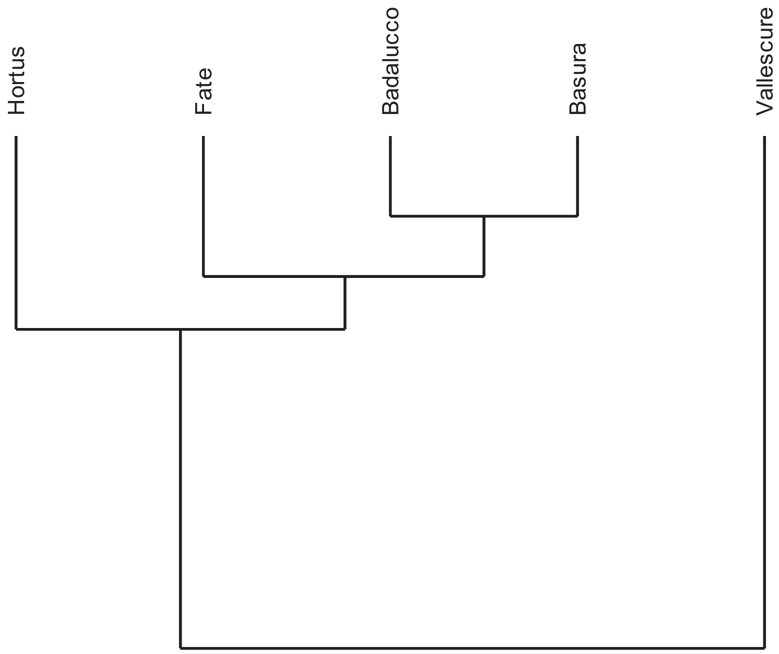


Figure 5. Cluster analysis on data from table 3 with Ward's algorithm (10000 bootstraps).

DESCRIPTION OF THE MATERIAL

"Grand Abri des Puces":

The cave bear material is scarce and composed of an isolated and incomplete mandible of an old adult (left; MR 4.01.681) (pl. 1a). The *ramus* is broken on the base of the canine and on the *fossa masseterica*. M/2 and M/3 are entire but their enamel has disappeared. Crown contours are showing characteristic constructions for spelaean bears, with a clear medial constriction of M/2 giving an "8" shape to the tooth, and the biconvexity of the labial part of the M3/. Even if Mousterian artefacts were found in the same level, diagnostic elements present on this bone are only sufficient enough to attribute it to *U.* cf. *spelaeus*.

Vallescure:

The material of Vallescure is known to be a sample of the original assemblage, due to uncontrolled lootings soon after discovery. The 451 remains of *U. spelaeus* belong to at least thirteen individuals (tab. 1). Unfortunately, important elements like skulls, mandibles and limb bones are incomplete and unusable for a paleontological characterisation. The biochronology based on P4 morphotypes (see RABEDER, 1999) is not reliable enough. Indeed, an amount of twenty teeth for each P4 is needed, and only four P4/ and two P/4 are available in this site (pl.1c to e and m, n). The strong sexual dimorphism and the high intraspecific variability, highlighted by many authors for cave bear (see QUILÈS, 2003 for details), invalidate the use of measurements comparisons.

A morphological grid of analysis on teeth has been preferred to define the Vallescure's sample (tab. 2). This grid summarizes 62 morphological criteria on upper and lower premolars and molars. Each criteria is divided using different coefficients (0, 1, 2…) in order to provide a quantified index (Number x Coefficient) in percentage of total occurrences of the criteria.

The Provence region is delimitated by the Alps in the East and the Rhône River in the West and the North. North Italian (Fate, Basura, Badalucco) and West of the Rhône River (Hortus) sites have been selected for comparisons with Vallescure. Given the high amount of cave bear individuals in each sites, cross comparisons over 62 criteria are reliable (tab. 3). Synthetic results are presented on a cluster tree made using Ward's algorithm during 10,000 bootstraps (fig. 5). Hortus cave (West of the Rhône) and North Italian populations are more closely related than with Vallescure lineage, even though distant from the Hortus locality by only 150 km. This isolation is effective given the OIS 4, represented by the cave bear assemblage from Fate.

Table 2
Morphodynamic study of cave bear teeth from Vallescure.

Coefficients	0	1	1.5	2	2.5	3	3.5	4	Total	Im
P4 sup.									4	
Morphotypes of the occlusal surface (Rabeder, 1999)				1		1		1	3	300
Angulation between para and metacone crests (0=strong, 2=flat)		1		2					3	166.7
Position of the deuterocone (0=very distal, 1=distal, 2=medial)		4							4	100
Development of the deuterocone (0=weak, 2=strong)				3					3	200
Individualisation of the deuterocone (0=valley, 1=cusp, 2=crest)	1			2					3	133.3
M1 sup.									5	
Development of para and metastyls (0=weak, 2=very strong)	3	1		1					5	60
Individualisation of para and metastyls (0=weak, 2=very strong)	3			2					5	80
Morphotypes of the lingual flanc of paracone (Rabeder, 1999)				1		2			3	266.7
Morphotypes of the lingual flanc of metacone (Rabeder, 1999)		3		1					4	125
Development and number of metaconule's cusps (0=weak+1,4= =very strong+3)			1	2			1		4	225
Link between protocone and metaconule (0=weak, 2=very strong)		5							5	100
Morphotypes of protocone (Rabeder, 1999)				1			2		3	300
Morphotypes of the basal cingulum (Rabeder, 1999)					2	2			4	275
Morphotypes of the talon's ornementation (Rabeder, 1999)		1		3					4	175
M2 sup.									9	
Shape of the distal margin of the talon (0=round, 1=sharp, 2=vestibular reduction)	2			4					6	133.3
Number of convexities on the lingual flanc				1		3			4	275
Morphotypes of the parastyle (Rabeder, 1999)	1	2		2					5	120
Morphotypes of the lingual flanc of paracone (Rabeder, 1999)		1	2	2					5	160
Morphotypes of the protocone (Rabeder, 1999)		2		3					5	160
Development of proto-meta-hypocones' crest (0=none,3=very strong)	1			1		2			4	200
Number of cusps on proto-meta-hypocones' crest						3			3	300
Morphotypes of the proto-meta-hypocones' crest (Rabeder, 1999)						1		2	3	366.7
Morphotypes of the link between para - and metacone (Rabeder, 1999)				4					4	200
Morphotypes of the link between metastyle and hypocone (Rabeder, 1999)		3							3	100
Morphotypes of the link between metastyle and hypostyle (Rabeder, 1999)		1		3					4	175
Morphotypes of the basal cingulum (Rabeder, 1999)					4				4	250
Morphotypes of the talon's crest (Rabeder, 1999)	1			4					5	160
Morphotypes of the talon's ornementation (Rabeder, 1999)				4					4	200

continued

Table 2 *(continued)*

P4 inf.									2	
Morphotypes of the occlusal surface (Rabeder, 1999)						2			2	300
Number of roots				2					2	200
Shape of the occlusal surface (0=ovoïd, 1=rectangular)		2							2	100
Position of the maximum height of protoconid (0=central, 2=mesial)				2					2	200
Number of antero-lingual cusps				1		1			2	250
Number of cusps on talonid		1		1					2	150
M1 inf.									5	
Morphotypes of metastylids (Rabeder, 1999)		2	1						3	116.7
Morphotypes of the entoconid (Rabeder, 1999)					1	2			3	283.3
Morphotypes of the entoconid (Argant, 1995)				1	2	1			4	250
Convexity of the vestibular flanc of the metaconid (0=weak, 2=very strong)	1	2							3	66.7
Orientation of mesial (mc) and distal (dc) crests of protoconid (0=equal, 1=mc>dc)		3							3	100
Individualisation of the paraconid (0=weak, 2=very strong)	1	1		1					3	100
Development of medio-lingual contraction (0=very weak, 3=very strong)						4			4	300
Morphotypes of the valley on talonid (Rabeder, 1999)						4			4	300
Morphotypes of the hypoconid (Rabeder, 1999)				3					3	200
Morphotypes of the lingual flanc of entoconid (Rabeder, 1999)								3	3	400
M2 inf.									5	
Development of the medial contraction (0=weak, 2=very strong)				4					4	200
Development of the basal cingulum (0=very weak, 3=very strong)		2		1					3	133.3
Number of cups on the medial crest				2					2	200
Morphotypes of the mesial crest (Rabeder, 1999)				2					2	200
Morphotypes of the trigonid (Rabeder, 1999)						1			1	300
Morphotypes of the distal crest of protoconid (Rabeder, 1999)		1	1						2	125
Number of cups on the inner flanc of the hypoconid				1		1			2	250
Morphotypes of the hypoconid (RABEDER, 1999)						2			2	300
Number of cusps on the mesial part of metaconid				1					1	200
Number of cusps on the distal part of metaconid		2							1	200
Number of cusps on the entoconid (0=1 cusp, 2= 3 cusps)		1		1					2	150
M3 inf.									4	
Morphotypes of crown's shape (Rabeder, 1999)		2		1					3	133.3
Number of lingual convexities		3							3	100
Number of vestibular convexities		1		2					3	166.7
Morphotypes of the lingual flanc of metaconid (Rabeder, 1999)	1			1					2	100
Morphotypes of the talonid (Rabeder, 1999)				1		1			2	250
Morphotypes of the entoconid (Rabeder, 1999)	1	1							2	50
Morphotypes of the hypoconid (Rabeder, 1999)			1						1	150

Table 3
Comparison of cave bear teeth morphotype indices between Vallescure, Fate, Badalucco, Hortus and Basura (after Quilès, 2003).

	Vallescure		Fate		Badalucco		Hortus		Basura	
	n	Im	n	Im	n	Im	n	Im	n	Im
P4 sup.										
Morphotypes of the occlusal surface (Rabeder, 1999)	3	300	127	102.8	14	171.4	10	215.0	64	269.5
Angulation between para and metacone crests (0=strong, 2=flat)	3	166.7	126	91.3	15	126.7	10	150.0	66	150.0
Position of the deuterocone (0=very distal, 1=distal, 2=medial)	4	100	94	147.9	14	150.0	10	100.0	65	167.7
Development of the deuterocone (0=weak, 2=strong)	3	200	98	128.6	14	114.3	10	140.0	64	156.2
Individualisation of the deuterocone (0=valley, 1=cusp, 2=crest)	3	133.3	104	101.9	14	135.7	10	130.0	64	187.5
M1 sup.										
Development of para and metastyles (0=weak, 2=very strong)	5	60	50	168.0	13	153.8	9	200.0	73	178.1
Individualisation of para and metastyles (0=weak, 2=very strong)	5	80	58	119.0	13	130.8	9	166.7	71	180.3
Morphotypes of the lingual flanc of paracone (Rabeder, 1999)	3	266.7	28	119.6	7	135.7	9	161.1	67	194.8
Morphotypes of the lingual flanc of metacone (Rabeder, 1999)	4	125	31	167.7	7	171.4	9	150.0	65	213.1
Development and number of metaconule's cusps (0=weak+1,4=very strong+3)	4	225	47	183.0	8	275.0	9	216.7	73	221.2
Link between protocone and metaconule (0=weak, 2=very strong)	5	100	41	131.7	8	162.5	9	77.8	71	160.6
Morphotypes of the protocone (Rabeder, 1999)	3	300	33	180.3	7	221.4	8	203.1	68	283.1
Morphotypes of the basal cingulum (Rabeder, 1999)	4	275	45	239.4	13	223.1	9	244.4	72	238.2
Morphotypes of the talon's ornementation (Rabeder, 1999)	4	175	37	200.0	8	175.0	9	200.0	72	194.4
M2 sup.										
Shape of the distal margin of the talon (0=round, 1=sharp, 2=vestibular reduction)	6	133.3	98	231.6	26	269.2	5	460.0	82	236.6
Number of convexities on the lingual flanc	4	275	58	200.0	25	224.0	4	275.0	83	225.3
Morphotypes of the parastyle (Rabeder, 1999)	5	120	46	171.7	13	238.5	5	220.0	95	208.9
Morphotypes of the lingual flanc of the paracone (Rabeder, 1999)	5	160	49	122.4	13	146.2	7	128.6	99	145.5
Morphotypes of the protocone (Rabeder, 1999)	5	160	45	128.9	14	150.0	7	121.4	90	152.2
Development of proto-meta-hypocones' crest (0=none,3=very strong)	4	200	60	225.0	19	205.3	6	183.3	88	234.1
Number of cusps on proto-meta-hypocones' crest	3	300	48	383.3	17	364.7	6	466.7	85	400.0
Morphotypes of the proto-meta-hypocones' crest (Rabeder, 1999)	3	366.7	47	380.9	18	452.8	6	366.7	94	435.6
Morphotypes of the link between para - and metacone (Rabeder, 1999)	4	200	44	92.1	21	209.5	6	208.3	90	172.8
Morphotypes of the link between metastyle and hypocone (Rabeder, 1999)	3	100	37	183.8	13	153.8	6	150.0	89	215.7
Morphotypes of the link between metastyle and hypostyle (Rabeder1999)	4	175	61	160.7	16	175.0	4	150.0	88	170.5
Morphotypes of the basal cingulum (Rabeder, 1999)	4	250	61	174.2	25	158.0	5	140.0	91	189.8
Morphotypes of the talon's crest (Rabeder, 1999)	5	160	52	116.3	16	106.2	4	150.0	84	132.1
Morphotypes of the talon's ornementation (Rabeder, 1999)	4	200	56	198.2	22	190.9	7	200.0	87	197.7

continued

Table 3 *(continued)*

P4 inf.										
Morphotypes of the occlusal surface (Rabeder, 1999)	2	300	151	136.4	25	157.0	12	152.1	35	162.1
Number of roots	2	200	167	65.3	27	88.9	12	41.7	35	88.6
Shape of the occlusal surface (0=ovoïd, 1=rectangular)	2	100	137	60.6	26	57.7	7	42.9	34	58.8
Position of the maximum height of protoconid (0=central, 2=mesial)	2	200	138	132.6	26	161.5	10	150.0	34	150.0
Number of antero-lingual cusps	2	250	138	207.2	26	184.6	10	240.0	34	197.1
Number of cusps on talonid	2	150	136	83.8	25	104.0	7	157.1	34	97.1
M1 inf.										
Morphotypes of metastylids (Rabeder, 1999)	3	116.7	107	173.8	33	216.7	11	181.8	76	221.1
Morphotypes of the entoconid (Rabeder, 1999)	3	283.3	115	235.2	36	247.2	15	256.7	77	259.4
Morphotypes of the entoconid (ARGANT, 1995)	4	250	144	225.7	36	245.8	23	269.6	78	243.6
Convexity of the vestibular flanc of the metaconid (0=weak, 2=very strong)	3	66.7	71	126.8	34	105.9	10	80.0	65	129.2
Orientation of mesial (mc) and distal (dc) crests of protoconid (0=equal, 1=mc>dc)	3	100	52	84.6	27	74.1	10	70.0	72	86.1
Individualisation of the paraconid (0=weak, 2=very strong)	3	100	102	56.9	36	119.4	8	150.0	75	124.0
Development of medio-lingual contraction (0=very weak, 3=very strong)	4	300	78	248.7	40	215.0	7	214.3	78	223.1
Morphotypes of the valley on talonid (Rabeder, 1999)	4	300	113	300.0	37	294.6	15	300.0	75	298.7
Morphotypes of the hypoconid (Rabeder, 1999)	3	200	67	114.6	23	126.1	14	110.7	72	122.2
Morphotypes of the lingual flanc of entoconid (Rabeder, 1999)	3	400	29	150.0	21	226.2	13	153.8	56	225.9
M2 inf.										
Development of the medial contraction (0=weak, 2=very strong)	4	200	62	161.3	40	120.0	13	138.5	90	130.0
Development of the basal cingulum (0=very weak, 3=very strong)	3	133.3	49	202.0	38	178.9	12	158.3	91	131.9
Number of cups on the medial crest	2	200	91	157.1	31	161.3	16	193.8	95	172.6
Morphotypes of the mesial crest (Rabeder, 1999)	2	200	61	173.8	29	187.9	16	193.8	95	208.9
Morphotypes of the trigonid (Rabeder, 1999)	1	300	55	257.3	28	303.6	16	231.2	95	265.3
Morphotypes of the distal crest of protoconid (Rabeder, 1999)	2	125	55	115.5	33	139.4	16	118.8	92	161.4
Number of cusps on the inner flanc of the hypoconid	2	250	94	164.9	22	195.5	15	186.7	91	231.9
Morphotypes of the hypoconid (Rabeder, 1999)	2	300	58	148.3	22	161.4	15	156.7	90	207.8
Number of cusps on the mesial part of metaconid	1	200	69	184.1	40	200.0	17	188.2	93	210.8
Number of cusps on the distal part of metaconid	1	200	71	115.5	40	127.5	18	111.1	79	110.1
Number of cusps on the entoconid (0=1 cusp, 2= 3 cusps)	2	150	72	112.5	37	100.0	16	93.8	91	102.2
M3 inf.										
Morphotypes of crown's shape (Rabeder, 1999)	3	133.3	85	148.8	49	138.8	3	166.7	58	170.7
Number of lingual convexities	3	100	126	110.3	49	118.4	2	200.0	61	113.1
Number of vestibular convexities	3	166.7	126	167.5	50	200.0	3	166.7	61	200.0
Morphotypes of the lingual flanc of metaconid (Rabeder, 1999)	2	100	51	196.1	25	268.0	3	216.7	52	287.5
Morphotypes of the talonid (Rabeder, 1999)	2	250	61	199.2	29	262.1	2	250.0	49	250.5
Morphotypes of the entoconid (Rabeder, 1999)	2	50	74	135.1	25	178.0	3	200.0	50	172.0
Morphotypes of the hypoconid (Rabeder, 1999)	1	150	50	190.0	23	278.3	3	283.3	53	284.0

DISCUSSION

The morphological study of cave bear regional lineages is demonstrates the role of the Rhône River during the Late Pleistocene as a paleobiogeographical limit, isolating Provence from around regions. Convergent arguments on ungulate and carnivore taxa are relevant to demonstrate this role at different times. The geographical context and the climate of Provence have also to be considered in the repartitioning of Pleistocene species, because:

- the area is mountainous and plains are restricted to

the Mediterranean coastal margin and to the Rhône margin,
- the Rhodanian corridor (Rhône River valley) has favoured North winds and dryness.

During the Middle Pleistocene, some species well developed to the West of the Rhône River are scarce in Provence: *U. deningeri* restricted in two caves (cf. *supra*), the Reindeer *R. tarandus* ("Les Cèdres", CRÉGUT-BONNOURE, 1995b, Lazaret, PATOU, 1984) and the Woolly Rhinoceros *Coelodonta antiquitatis* only determined in the Lazaret cave (GUÉRIN, 1980). On the other side, the density of low to middle altitude mountains explains the largely represented species of rupicol ungulates like:

- *Hemitragus bonali*, identified in Escale cave (BONIFAY, 1974-75), Terra Amata (MOURER-CHAUVIRÉ & RENAULT-MISKOVSKY, 1980), "Baume Bonne" (OIS 8, Quinson, Alpes-de-Haute-Provence; PSATHI, 1996) and Bérigoule (CRÉGUT-BONNOURE, 1996).
- *H. cedrensis* recognized in "Les Cèdres", Cimay, Rigabe (Artigues, Var) (CRÉGUT-BONNOURE, 1989; 1995b) and "Bau de l'Aubesier" (FERNANDEZ, 2001; 2006).

Morphometrical analysis indicate that *H. cedrensis* derives from the evolution of *H. bonali* in Provence during the Middle Pleistocene (OIS 7) (CRÉGUT-BONNOURE, 2002), demonstrating the role of the Rhône River as an ecological barrier at the end of the Middle Pleistocene (OIS 6). The same phenomena are perceptible with the Tibetan's bear *U. thibetanus,* present in three localities (cf. *supra*): morphology and proportions of the upper teeth being distinct in West of the Rhône River populations (CRÉGUT-BONNOURE, 1996; 1997). The geographic isolation is well known for Lagomorphs (Les Cèdres; CRÉGUT-BONNOURE, 1995c) and Rodents as the *Arvicola* from Lazaret (DESCLAUX *et al.* 2000) and *Pliomys* gr. *episcopalis* recognized until the OIS 6 in Provence (Les Cèdres and Lazaret; RADULESCU, 1995).

The cold period of the early Late Pleistocene is responsible for the presence in Vaucluse of *A. lagopus* and *G. spelaeus*, both identified in Vallescure (GAGNIÈRE & GERMAND, 1934; CRÉGUT-BONNOURE *in* BRUGAL & CRÉGUT-BONNOURE, 1994), and of polar fox in "Auzières II" near Méthamis (CRÉGUT-BONNOURE *et al.*, 1983). Therefore, these two taxa are totally absent from the rest of Provence, whereas they are identified in several localities at the West of the Rhône River. Cave hyena, *C. crocuta spelaea*, is also uncommon with three sites in Vaucluse: Vallescure (GAGNIÈRE & GERMAND, 1934), "Auzières II" (CRÉGUT-BONNOURE *et al.*, 1983), "Baume des Peyrards" (RAMBERT, 2000) and one site in Alpes-Maritimes at "Baume Périgaud" (Tourrette-Levens, CRÉGUT-BONNOURE, 2004c) and another in Bouches-du-Rhône at "Le Tonneau" (La Bouilladisse; CRÉGUT-BONNOURE, 2002). The painted dog's status, *C. alpinus europaeus*, is quite similar, recognized in Vallescure (CRÉGUT-BONNOURE *in* BRUGAL & CRÉGUT-BONNOURE, 1994), "Baume des Peyrards" (CRÉGUT-BONNOURE *in* RAMBERT, 2000) and Mars cave (Vence, Alpes-Maritimes; COPIN-VATHAIRE, 1966).

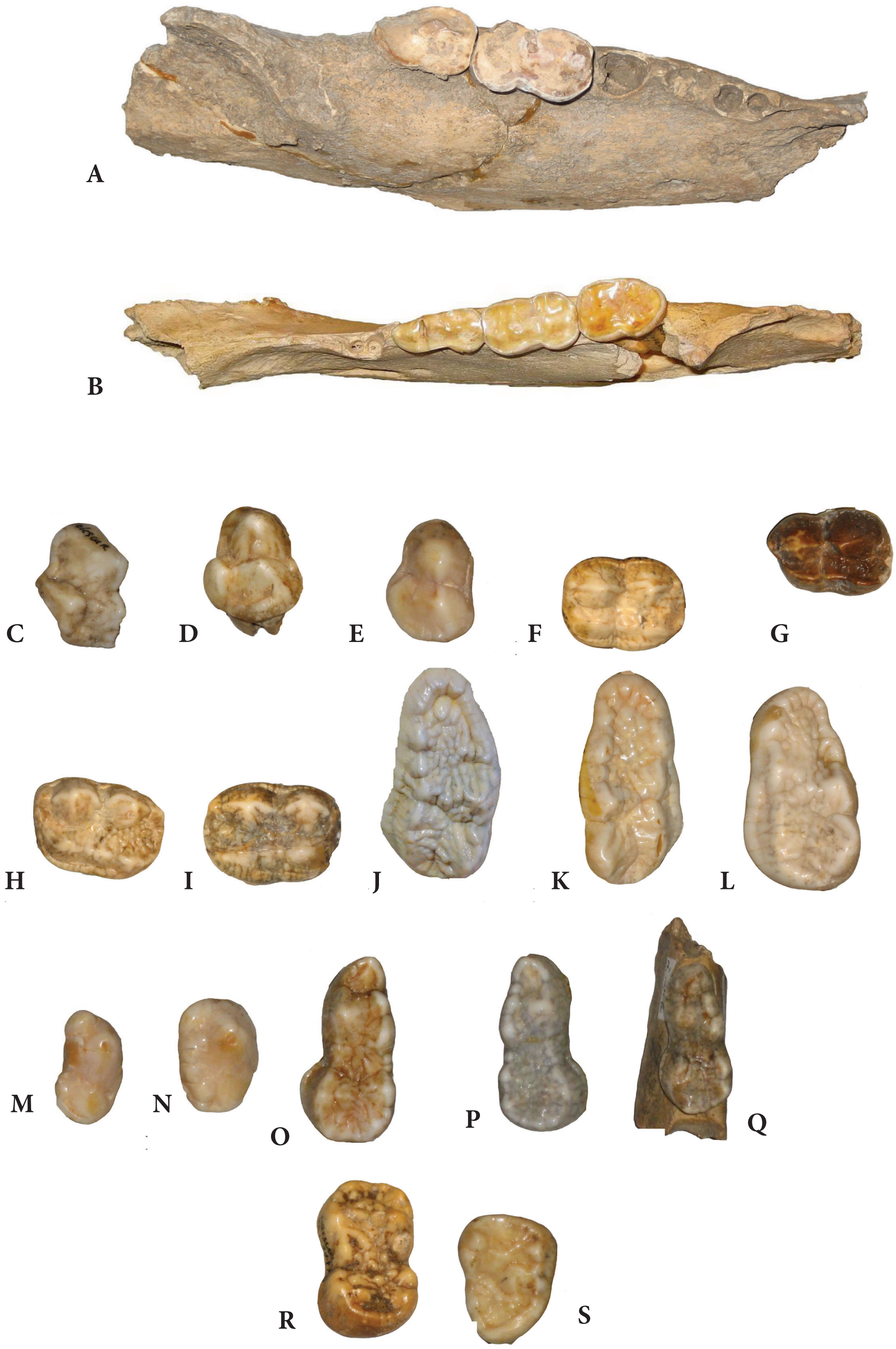
The Woolly Rhinoceros, which with Mammoth and Reindeer, is part of the classic cold faunal association of France Late Pleistocene, is again exceptional, determined only in "Auzières II" (CRÉGUT-BONNOURE *et al.*, 1983). The Mammoth *Mammuthus primigenius*, well developed to the West of the Rhône River and on the western side of the Rhodanian corridor (ROUSSELIÈRES 2006), is restricted to the Vauclusian area, in the locality of "Auzières II" (OIS 4, Monchot, pers. com.) and Chinchon I (OIS 2, CRÉGUT-BONNOURE & PACCARD, 1998). The Reindeer, highly common prey of Magdalenian hunters to the West of the Rhône River (CRÉGUT-BONNOURE, 1991), is only identified in six Provence sites. Two date from the beginning of this period: "Grotte aux Puces" (GAGNIÈRE, 1954) and Adaouste (DEFLEUR *et al.*, 1994). In Vaucluse, Reindeer is signalled in the archaeological sites of: "Bau de l' Aubesier" (FERNANDEZ, 2001; 2006), Chinchon I (CRÉGUT-BONNOURE & PACCARD, 1998) and Roquefure (OIS 2; Bonnieux; Gagnière *in* PACCARD 1963; CRÉGUT-BONNOURE & PACCARD, 1998). The Vauclusian aven of "Les Planes" at Monieux possesses a complete skeleton of a young male (AUJARD-CATOT *et al.* 1979), dated of 12660 ± 75 BP (Lyon 3138). At the exception of this skeleton, in all of the other sites mentioned, the species is represented by one or two rests only, rarely more.

In contrast, Ibexes are abundant with two species:

- *C. caucasica praepyrenaica*, the Caucasian ibex discovered in Adaouste (DEFLEUR *et al.*, 1994) and "Bau de l' Aubesier" (FERNANDEZ, 2001; 2006);
- *C. ibex*, the Alpine ibex present in c.a. thirteen localities dated from the OIS 7 to Holocene (CRÉGUT-BONNOURE, 2002; 2006 a & b).

Morphometrical analysis indicates that early Late Pleistocene (OIS 4) populations of Alpine ibexes from each side of the Rhône River constitute distinct biometrical entities. The Eastern group (Vallescure, "Baume des Peyrards", "Le Tonneau" populations) has short lower M_1 and M_2 and extended M_3, while the Western group ("Les Pêcheurs", Mialet, "La Sartanette" population) shows the opposite and is characterized by a less triangular horn core section (CRÉGUT-BONNOURE, 2002; 2006 a & b).

Plate 1



A-Ursus cf. *spelaeus*, Grand Abri des Puces. Left mandible MR 4.01.681.
B to S: *Ursus spelaeus*, Vallescure. B: right mandible MR 4.00.401+4.00.729+4.00.768; C: left upper P4 MR 4.04.411; D: left upper P4 MR 4.00.782; E: left upper P4 MR 4.00.772; F: left upper M1 MR 4.00.786; G: left upper M1 MR 4.00.795; H: left upper M1 MR 4.00.781; I: right upper M1 MR 4.00.044 bis; J: right upper M2 MR 4.04.405; K: left upper M2 MR 4.00.789; L: right upper M2 MR 4.00.788; M: right lower P4 MR 4.00.773; N: right lower P4 MR 4.04.404; O: left lower M1 MR 4.04.399; P: left lower M1 MR 4.04.400; Q: left lower M1 MR 4.00.790; R: left lower M2 MR 4.00.778, S: left lower M3 MR 4.00.779.

From the OIS 3 to the beginning of the Holocene, the metaconid of the P/3 is dilating in the population of South Eastern France (Provence area) and the P/2 disappears (Crégut-Bonnoure, 1992) connected with a geographic isolation as in extant Spanish *C. pyrenaica* (Crégut-Bonnoure, 2002).

To summarize, ungulate and carnivore representations are clearly different between Provence and its surrounding regions since the Middle Pleistocene. For several taxa such as ibexes and cave bears, an evident lack of exchanges between populations across the Rhône River reflects a geographical isolation since the OIS 4 (Crégut-Bonnoure, 1992; 1997; 2002; 2006 a & b).

CONCLUSIONS

The Vaucluse is distinguishable from the eastern part of Provence by a greater biodiversity. The rich paleontological assemblage of Vallescure appears as an exception for its carnivore assemblage, registering the presence of taxa absent from the rest of Provence. The analysis of cave bear teeth morphology demonstrates a distinct lineage since the OIS 4, compared with around regions of the West of Rhône River and North Italy, documenting a geographical isolation. Other taxa like the Caprini *Hemitragus* and *Capra*, the Ursid *U. thibetanus* as well as Rodents and Lagomorphs indicate a recurrent endemism in Provence, which takes place from the end of the Middle Pleistocene to the Holocene. The probable scenario is that repeated periods of isolation occurred and alternated with periods of exchanges, in close correlation with glacial and interglacial oscillations and with the Rhône River fluctuations of the water level. During cold phases of Middle and Late Pleistocene, the Rhône acted as a major paleobiogeographical limit. The general mechanism of isolation of Provence lineages is now better understood, but there is no convenient issue to the presence of cave bear in Vallescure, that either reflect an ancestral eemian population or of a punctual passage across the Rhône River during the OIS 4.

REFERENCES

ARGANT, A., 1995. Un essai de biochronologie à partir de l'évolution dentaire de l' ours des cavernes. Datation du site de la Balme à Collomb (Entremont-le-Vieux, Savoie, France).- *Quaternaire*, Paris, **6(3-4)**: 139-150.

AUJARD-CATOT, R., CRÉGUT, E., GAGNIÈRE, S., GRUNEISEN, A. & MOURER-CHAUVIRÉ, C., 1979. Un squelette complet de renne, *Rangifer tarandus* (Mammalia, Artiodactyla), dans le Pléistocène supérieur du remplissage karstique de l'aven des Planes (Monieux, Vaucluse, France).- *Nouvelles Archives du Muséum d'histoire naturelle de Lyon*, **17**, suppl.: 15-20.

BLAISE, E., FURESTIER, R. & LEMERCIER, O., 2004. Economie, ressources et echanges.- *In* J. BUISSON-CATIL, A. GUILCHER, CH. HUSSY, M. OLIVE & M. PAGNI (Coord.), *Vaucluse préhistorique. Le territoire, les hommes, les cultures et les sites.* E. Barthélémy ed., Avignon, 229-234.

BONIFAY, M.-F., 1971. Carnivores quaternaires du Sud-Est de la France.- *Mémoire du Muséum national d'Histoire naturelle*, Paris, Série C, **21 (2)**: 377 pp.

BONIFAY, M.-F., 1974-1975. *Hemitragus bonali* HARLÉ & STEHLIN, Caprini de la grotte de l'Escale (Saint-Estève-Janson, Bouches-du-Rhône).- *Quaternaria*, Roma, **18**: 215-302.

BRUGAL, J.-Ph. & CRÉGUT-BONNOURE, E., 1994. La faune Quaternaire en Provence.- *In* J. BUISSON-CATIL (Ed.), Le Paléolithique moyen en Vaucluse. *Notices d'Archéologie vauclusienne, Avignon,* **3**: 55-69.

BUISSON-CATIL, J. & CRÉGUT-BONNOURE, E., 1995. Sault, aven du Contadoux.- *Bilan Scientifique D.R.A.C.*: 291-293.

BUISSON-CATIL, J., GUILCHER, A., HUSSY, Ch., OLIVE, M. & PAGNI, M. (coord.), 2004. *Vaucluse préhistorique. Le territoire, les hommes, les cultures et les sites.*- Barthélemy édit., Avignon: 320 p.

CHEYLAN, M., 1981. Biologie et écologie de la tortue d' Hermann *Testudo hermanni* Gmelin, 1789. Contribution de l'espèce à la connaissance des climats quaternaires de la France.- *Mémoires et Travaux de l'École Pratique des Hautes Études*, Montpellier, **13** : 404 p.

COPIN-VATHAIRE, D., 1966. *Les Canidés de la caverne Mars à Vence (Alpes-Maritimes).*- Mémoire de D.E.A., Université de Paris: 1 vol. 31 p. text & 12 pl. (unpublished).

COURTIN, J., 1974. *Le Néolithique de la Provence*. Klinsksieck édit., Paris.

CRÉGUT-BONNOURE, E., 1989. Un nouveau *Caprinae*, *Hemitragus cedrensis* nov. sp. (*Mammalia, Bovidae*), des niveaux pléistocènes moyens de la grotte des Cèdres (Le Plan d' Aups, Var). Intérêt biogéographique.- *Géobios*, Lyon, **22 (5)**: 653-663.

CRÉGUT-BONNOURE, E., 1991. L' environnement animal dans le midi de la France. *In*: *L'Homme de Cro-Magnon.- Les Dossiers d'Archéologie*, Paris, **156**: 43-63.

CRÉGUT-BONNOURE, E., 1992. Dynamics of Bovid migration in Western Europe during the Middle and the Late Pleistocene.- *Courier Forschungsinstitut Senckenberg*, Francfurt, **153**: 177-185.

CRÉGUT-BONNOURE, E., 1995a. La faune de grands mammifères en Provence de la fin du Pléistocène à l'Holocène.- *Forêt Méditerranéenne*, Marseille, **16 (3)**: 234-238.

CRÉGUT-BONNOURE, E., 1995b. Les grands mammifères.- *In* A. DEFLEUR & E. CRÉGUT-BONNOURE (Dir.), *Le gisement Paléolithique moyen de la grotte des Cèdres (Var). Documents d'Archéologie française*, Paris, **49**: 54-142.

CRÉGUT-BONNOURE, E., 1995c. Les Lagomorphes.- *In* A. DEFLEUR & E. CRÉGUT-BONNOURE (Dir.), *Le gisement Paléolithique moyen de la grotte des Cèdres (Var). Documents d' Archéologie française*, Paris, **49**: 143-147.

CRÉGUT-BONNOURE, E., 1996. A review of small Middle Pleistocene bears from France.- *Acta Zoologica Cracoviensia*, **39(21):** 89-101.

CRÉGUT-BONNOURE, E., 1997. The saalian *Ursus thibetanus* from France and Italy.- *Géobios*, Lyon, **30(2):** 285-294.

CRÉGUT-BONNOURE, E., 2002. *Les Ovibovini, Ovini et Caprini (Mammalia, Artiodactyla, Bovidae, Caprinae) du Plio-Pléistocène d'Europe: systématique, évolution et biochronologie*.- Thèse de Doctorat d' Etat ès Sciences, Université de Lyon I, n° 1-2002: 1 vol. 429 pp. text, 1 vol., 686 fig. & XXXIII pl., 1 vol., 212 tabl.

CRÉGUT-BONNOURE, E., 2004a. Au Paléolithique moyen, une faune vauclusienne particulière.- *In* J. BUISSON-CATIL, A. GUILCHER, Ch. HUSSY, M. OLIVE & M. PAGNI (Coord.), *Vaucluse préhistorique. Le territoire, les hommes, les cultures et les sites*. E. Barthélémy ed., Avignon: 62.

CRÉGUT-BONNOURE, E., 2004b. La succession de faune au Paléolithique supérieur et au Mésolithique.- *In* J. BUISSON-CATIL, A. GUILCHER, Ch. HUSSY, M. OLIVE & M. PAGNI (Coord.), *Vaucluse préhistorique. Le territoire, les hommes, les cultures et les sites*. E. Barthélémy ed., Avignon: 110.

CRÉGUT-BONNOURE, E., 2004c. La faune de la Baume Périgaud (Tourrette-Levens, Alpes-Maritimes).- *In* G. ONORATINI, *Aux origines de l'outil. Les premiers chasseurs préhistoriques de Tourrette-Levens*. Artcom' édit., Paris: 84-85.

CRÉGUT-BONNOURE, E., 2006a. Nouvelles données paléogéographiques et chronologiques sur les *Caprinae* (*Mammalia, Bovidae*) du Pléistocène moyen et supérieur d'Europe. *In Homenaje a Jesús Altuna. Munibe*, San Sebastian, **57 (1)**: 205-219.

CRÉGUT-BONNOURE, E., 2006b. European *Caprinae* (*Ovibovini, Ovini, Caprini*) from the Plio-Pleistocene: new interpretations. *In* L.C. MAUL, R.D., KAHLKE & P. MAZZA ed., *Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations*. 18th International Senckenberg Conference, VI International Paleontological Colloquium in Weimar.-*Courier Forschungsinstitut Senckenberg*, Francfurt, **256**: 139-158.

CRÉGUT-BONNOURE, E. & FERNANDEZ, Ph., 2004. Tahrs, chamois et bouquetins, des espèces importantes pour la biochronologie des sites vauclusiens.- *In* J. BUISSON-CATIL, A. GUILCHER, Ch. HUSSY, M. OLIVE & M. PAGNI (Coord.), *Vaucluse préhistorique. Le territoire, les hommes, les cultures et les sites*. E. Barthélémy éd., Avignon: 69.

CRÉGUT-BONNOURE, E. & PACCARD, M., 1998. La faune à *Saiga tatarica* de Chinchon I à Saumanes (Vaucluse). *Quaternaire*, Paris, **8(4)**: 391-407.

CRÉGUT-BONNOURE, E., FAURE, M. & GUÉRIN, C., 1994. Diversité et complémentarité des principaux gisements vauclusiens: Bau de l' Aubesier.- *In* J. BUISSON-CATIL (Ed.), *Le Paléolithique moyen en Vaucluse. Notices d'Archéologie vauclusienne*, Avignon, **3**: 116-118.

CRÉGUT-BONNOURE, E., GUÉRIN, C. & MOURER-CHAUVIRÉ, C., 1983. La faune des Auzières II à Méthamis (Vaucluse).- *Nouvelles Archives du Muséum d'histoire naturelle de Lyon*, **21**, suppl.: 53-58.

CRÉGUT-BONNOURE, E., ARGANT, A., ARGANT, J., AYACHE-DONAT, B., BILLIOU, D., BOCHERENS, H., BOUCHER, Ch., BUISSON-CATIL, J., DEBARD, E., HÄNNI ,C., LAUDET, F., MOURER-CHAUVIRE, C., MEIN, P., OBERLIN, Ch., ORLANDO, L., PHILIPPE, M., QUILES, J. & THINON, M., 2005. Les cavités karstiques du Mont Ventoux (Vaucluse, France): des ours brun (*Ursus arctos* L.) et des milieux d'altitude à l'Holocène.- *Bulletin du Musée d'Histoire naturelle de Toulouse*, **141(1)**: 5-18.

DEFLEUR, A., BEZ, J.-F., CRÉGUT-BONNOURE, E., DESCLAUX, E., ONORATINI, G., RADULESCU, C., THINON, M. & VILETTE, Ph., 1994. Le niveau moustérien de la grotte de l' Adaouste (Jouques, Bouches-du-Rhône). Approche culturelle et paléoenvironnements.- *Bulletin du Musée d'Anthropologie Préhistorique de Monaco*, **37**: 11-48.

DESCLAUX, E., ABASSI, M., MARQUET, J.C., CHALINE, J. & KOLFSCHOTEN, T. VAN, 2000. Distribution and evolution of *Arvicola* Lacépède, 1799 (Mammalia, Rodentia) in France and Liguria (Italy) during the middle and the Late Pleistocene.- *Acta Zoologica Cracoviensa*, **43 (1-2)**: 107-125.

FERNANDEZ, PH., 2001. *Étude paléontologique et archéozoologique des niveaux d'occupations moustériens au Bau de l'Aubesier (Monieux, Vaucluse): implications biochronologiques et palethnologiques*.- Thèse de Doctorat, Université Claude-Bernard, Lyon I, 1 vol. text : 306 p., 1 vol. fig. & pl., 1 vol. tabl. (unpublished).

FERNANDEZ, PH., 2006. Etude paléontologique des ongulés du gisement moustérien du Bau de l'Aubesier (Vaucluse, France): morphométrie et contexte biochronologique.- *Documents des laboratoires de Géologie de Lyon*, **161**: 1-231.

GAGNIÈRE, S. 1954. Chronique d'informations de la XII° circonscription préhistorique.- *Gallia,* Paris, **XII**: 127-142.

GAGNIÈRE, S., 1957. Remarques sur la faune.- *In*: H. de LUMLEY, *Le Moustérien de la Baume des Peyrards (Vaucluse).- Bulletin de la Société d'Étude des Sciences naturelles de Vaucluse,* 1952-1956: 34-35.

GAGNIÈRE, S. & GERMAND, L., 1934. Contribution à l'étude de la faune quaternaire dans la vallée du Rhône. La grotte à ossements de la Vallescure (Vaucluse).- *Rhodania*, Vienne, **1615**: 3-11.

GUÉRIN, C., 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaisons avec les espèces actuelles.- *Document des Laboratoires de Géologie de Lyon*, **79(1-3)**: 1-1185.

HELMER, D., 1979. *Recherches sur l'économie alimentaire et l'origine des animaux domestiques d'après l'étude des mammifères post-paléolithiques (du Mésolithique à l'âge du Bronze) en Provence*. Thèse de 3° Cycle, U.S.T.L., Montpellier: 165 pp. (unpublished).

HERVET, S., 2000. Tortues du Quaternaire de France: critères de détermination, répartitions chronologique et géographique.- *Mésogée*, Marseille, **55**: 4-47.

LE FAHLER, B. & FRADIN, R., 1995. Aven de Valescure. *In* GAUBERT, G., & LE FAHLER, B. (Dir.), *Les Arcanes de Vaucluse.- Hydrogéologie et spéléologie des territoires alimentant en eau la Fontaine de Vaucluse*. A.R.E.H.P.A. édit., Avignon, **2**: 303-304.

LUMLEY-WOODYEAR, H. de, 1969. *Le Paléolithique inférieur et moyen du midi méditerranéen dans son cadre géologique. I: Ligurie-Provence, II: Bas-Languedoc, Roussillon, Catalogne*. C.N.R.S. edit., Paris: t. I, 433 p., t. II, 443 p.

MOULLÉ, P.-E., 1992. *Les grands mammifères du Pléistocène inférieur de la grotte du Vallonet (Roquebrune Cap Martin, Alpes-Maritimes). Étude paléontologique des Carnivores, Équidés, Suidés et Bovidés*. Thèse de Doctorat, Muséum national d'Histoire naturelle, Paris: 365 p. (unpublished).

MOULLÉ, P.-E., SIMON, P. & ARELLANO-MOULLÉ, A., 2000. Sospel: Grotte de l' Albaréa. *Bilan scientifique, DRAC-PACA*: 59-60.

MOURER-CHAUVIRÉ, C. & RENAULT-MISKOVSKY, J., 1980. Le paléoenvironnement des chasseurs de Terra Amata (Nice, Alpes-Maritimes) au Pléistocène moyen. La flore et la faune de grands mammifères.- *Géobios*, Lyon, **13(3)**: 279-287.

PACCARD, M., 1963. Le gisement préhistorique de Roquefure (commune de Bonnieux, Vaucluse).- *Cahiers Rhodaniens*, Bordighera, **1**: 3-36.

PATOU, M., 1984. *Contribution à l'étude des mammifères des couches supérieures du Lazaret (Nice, A.-M.). Méthodes et résultats paléontolgiques et palethnographiques.* -Thèse de Doctorat de 3° cycle, Muséum national d'Histoire naturelle & Université Pierre et Marie Curie: 419 p. (unpublished).

PSATHI, E., 1996. *Etude paléontologique, paléoécologique et biostratigraphique du site de la Baume Bonne (Alpes-de-Haute-Provence)*. Mémoire de D.E.A., Muséum national d' Histoire naturelle, Paris: 98 p. (unpublished).

QUILES, J., 2003. Les Ursidae du Pléistocène moyen et supérieur en Midi méditerranéen: Apports paléontologiques, biochronologiques et archéozoologiques.- Thèse de Doctorat du Muséum National d'Histoire Naturelle, Paris, 2 tomes, 1307 p. (unpublished).

RABEDER, G., 1999. Die Evolution des Höhlenbärengebisses.- *Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften* **11**: 1-102.

RADULESCU, C., 1995. Les rongeurs.- *In* A. DEFLEUR & CRÉGUT-BONNOURE, E., (Dir.), *Le gisement Paléolithique moyen de la grotte des Cèdres (Var). Documents d'Archéologie française*, Paris, 1995, **49**: 148-152.

RAMBERT, CH., 2000. *Étude dentaire de la faune de la Baume des Peyrards, Buoux, Vaucluse*.- Mémoire de D.E.A., Université de la Méditerranée et Muséum national d'Histoire naturelle: 214 p. (unpublished).

ROUSSELIERES, F., 2006. *Proboscidiens du Pléistocène moyen et supérieur d'Europe sud-occidentale: anatomie et biométrie statistique*.- Thèse de Doctorat, Université de Lyon: 375 p. (unpublished).