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The big cats of the fossil site Château Breccia Northern Section (Saône-et-Loire, Burgundy, France): stratigraphy, palaeoenvironment, ethology and biochronological dating

With 13 figs, 7 tabs

Alain ARGANT, Jacqueline ARGANT, Marcel JEANNET & Margarita ERBAJEVA

Abstract

The Château site, known since 1863, was rediscovered in 1968 and new excavations were carried out there between 1997 and 2006. Bear remains largely dominated the Château Breccia fossil assemblage, but the characteristic peculiarity of this site was the abundance of big cats. The old karstic system, including the Château Breccia fossil site, has been completely destroyed, primarily by erosion, but later by quarrying. During the Pleistocene the cave served as hibernation dens for bears. This was most likely also the birthplace for bear cubs. These bear cubs, whether alive or dead, could be a significant source of food for big cats during the winter. The stratigraphy of the infill (Northern Section) reveals successive phases of occupation. The two main fossiliferous layers were labelled Breccia 4 (Br. 4) and Breccia 2 (Br. 2), the former being the earliest. In both cases, we noticed different, though equivalent, animal associations: a bear (*Ursus deningeri*), a big cat (*Panthera gombaszoegensis*, *Panthera spelaea fossilis*), a canid (*Canis lupus mosbachensis*), and constantly *Arvicola cantianus* (= *A. mosbachensis*). Palynological analysis indicates a milieu of moderately cold temperatures for the two breccias. It suggests an open landscape with grassy areas and a forest of pine, fir, oak and other broadleaved trees.

Thus far, all attempts to obtain absolute dates for the Northern Section of the site have been unsuccessful: ^{14}C and thermoluminescence cannot be used, U/Th and Uranium series dating has failed up to now and ESR is not possible because of the absence of herbivore molars with thick enamel. Therefore, only *Ursus deningeri*, *Panthera gombaszoegensis*, *Panthera spelaea fossilis*, lagomorphs and microfauna with *Arvicola cantianus* biochronologies allow us to suggest an early Middle Pleistocene age for Breccia 4 and a mid Middle Pleistocene age for Breccia 2. The Château Breccia stratigraphy permits biochronologic dating but also the reliable reconstruction of the evolution of two big cats. *Panthera gombaszoegensis* is found in the Breccia 4 sediments, the oldest from the site. *P. spelaea fossilis* and *P. gombaszoegensis* probably coexisted in Breccia 3. Breccia 2 contains only *P. spelaea fossilis*, which conforms exactly to what is known about its first appearance in Europe.

Key words: *Panthera*, *Arvicola*, biochronology, palaeoenvironment, Burgundy, Middle Pleistocene

Introduction

In 1863 during part of the construction of route D165 from Donzy to Valouze in South Burgundy (fig. 1), “an enormous amount of bear and lion bones was exposed” (MONNIER 1869). The bones were embedded in an ancient breccia found in karstic infilling. No study of the bones was made at that time. In 1968 A. and J. ARGANT started a very successful excavation, and continued to excavate from 1997 to 2006. The Château Breccia fossil assemblage provides important information about Middle Pleistocene carnivores, in particular about the genus

Panthera. Any vestiges of the old karstic system were completely demolished by quarrying. However, some coating of breccias on the rock face remained, together with a western gallery filled with sediment sinking under the Garenne plateau.

Three sections have been excavated, shown in fig. 2: Northern Section (with the beginning of the western gallery) and Southern Section, as well as an intermediate explorative excavation between them, “SIPO”, along the western wall. The 2006 excavation showed that the Northern and Southern Sections are not connected. They are simply the vestiges of two close cavities about twenty

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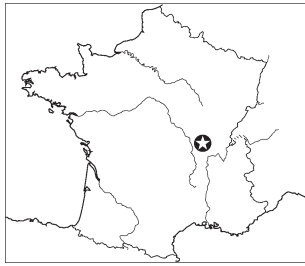


Fig. 1: Location of the Château Breccia.

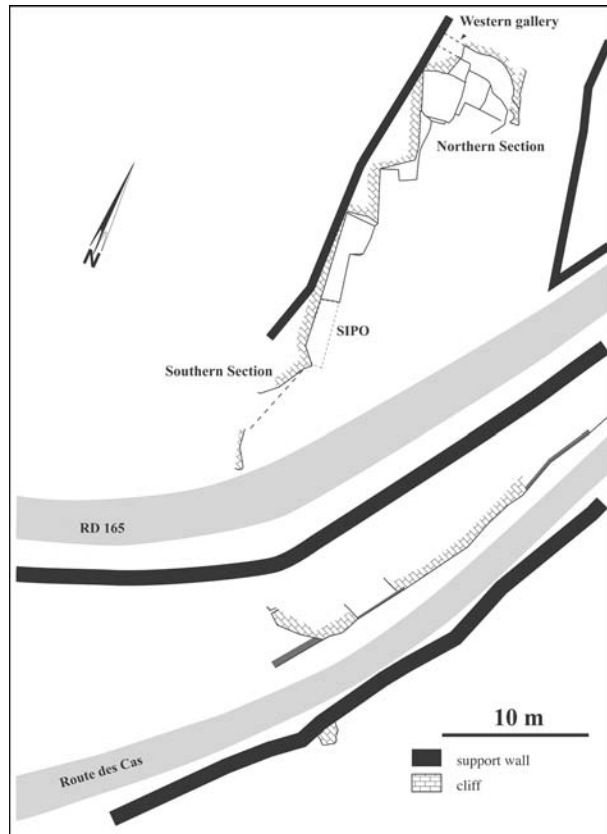


Fig. 2: Château Breccia, map of the site with Northern Section, SIPO (= intermediate explorative excavation) and Southern Section.

meters apart. In the Southern Section a remainder of 14 cm of stalagmitic floor is in place at middle height in the breccia. Its upper part has been dated by B. GHALEB (U/Th-TIMS method): GEOTOP lab # U.6381–Th.6383: 176.795 + 9337–8540 years. This date is incompatible with the biochronologic datings of the Northern Section. The palaeontological material used for this article comes only from the Northern Section. Figure 3 provides an overview on the large mammal and microvertebrate taxa distribution (tab. 2) in each stratigraphic unit (= US) of the three fossiliferous layers (Br. 2, 3 and 4).

Light beige coloured, the palaeontological material is well preserved, strongly mineralized and speckled with manganese dioxide. It is very fragmented because of the superficial tree roots breaking up the bones. This was caused by strong pressure exerted while growing into the

nutrients holes or fissures. Some bones seem to have been slightly rolled.

A three-dimensional documentation of each bone has been collected since 1968 applying a method similar to that used in prehistoric excavations. This allows an accurate taphonomic study of the accumulation (fig. 4). Although the analysis is still under way, the bones seem to have been shifted by mighty, destructive mudflows. These mudflows sometimes carried large rocks, broken speleothems, isolated bones as well as articulated carcasses. For instance, Br. 2 contained many articulated elements of *Panthera spelaea fossilis*, as well as large portions of an individual skeleton. In Br. 4, most of a carcass of *Panthera gombaszoegensis* was lying where the western gallery twists south, while its skull and some of its postcranial bones were trapped in an ancient pothole. Each mudflow removed all the bones and carcasses from the gallery, while the anterior layers were gullied by its force.

In Château, *Ursus deningeri* largely dominates the successive taphocoenoses. The cave was a hibernation den for females and a birthplace for bear cubs, as indicated by the high concentration of milk teeth. In both breccias the taphonomic characteristics rule out any human interference. In fact, the cave contains no artifacts nor herbivore remains, but carnivore bones.

The big cats

Being morphologically similar to one another, the remains of the different felids are sometimes not easy to determine. In contrast, the two *Panthera* species from Château are of quite different size. The jaguar ancestor, *Panthera gombaszoegensis*, was as large as a small living lion, while the cave lion ancestor, *Panthera spelaea fossilis*, was a giant cat. Table 1 shows the abundance of big cat remains, whose study is under way (A. ARGANT 1980, 1991, 2000). All the parts of the skeleton are represented in both species (fig. 5).

Panthera gombaszoegensis

Order C a r n i v o r a BOWDICH, 1821

Family F e l i d a e GRAY, 1821

Subfamily F e l i n a e SIMPSON, 1945

Genus *Panthera* OKEN, 1816

Panthera gombaszoegensis (KRETZOI, 1938)

Synonymy: *Panthera onca gombaszoegensis* (KRETZOI, 1938)

Panthera gombaszoegensis is without a doubt the cat most similar to the present day jaguar although not as much as to consider it conspecific with *Panthera onca*. *Panthera gombaszoegensis* represents the ancestor of *Panthera onca*, which was once spread worldwide, and

STRATIGRAPHY	US	SEDIMENT	FAUNA	DATE
Surface				
SOIL	101	Brown forest floor	Sterile	Present
BRECCIA 1	102	Yellow ochre breccia	Sterile	
BRECCIA 2	103	Yellow pinkish breccia with stones and blocks	<i>Ursus deningeri</i> <i>Panthera spelaea fossilis</i> <i>Canis mosbachensis</i> <i>Felis silvestris</i> <i>Sus scrofa</i> (1 molar) <i>Arvicola cantianus</i> [group A*]	Mid Middle Pleistocene OIS13
	104	Yellowish breccia with stones and blocks		
BROWN PRISMATIC CLAY	105	Deep karst brown red prismatic clay with concretions	Sterile	
BRECCIA 3	106	Yellowish sandy clay	<i>Ursus deningeri</i> <i>Ursus arctos</i> (1 molar) <i>Panthera gombaszoegensis</i> <i>Arvicola cantianus</i> [group B*]	Mid Middle Pleistocene OIS 13
	107	Yellowish breccia with 'chaille' pebbles		
BRECCIA 4	115	Yellowish breccia with 'chaille' blocks	<i>Ursus deningeri</i> <i>Ursus arctos</i> (1 molar) <i>Canis mosbachensis</i> <i>Panthera gombaszoegensis</i> <i>Arvicola cantianus</i> [group C*]	Early Middle Pleistocene OIS 14 or 15
Indet. BRECCIA	116	Reworked ?	<i>Mimomys hintoni</i> ? <i>Oryctolagus cf lacosti</i> ?	Upper Pliocene ? 2 to 2.4 My

Fig. 3: Château Breccia, stratigraphic synthesis of the Northern Section. Infill of the Western Gallery (US = Stratigraphic Unit; *Groups A, B, C refer to microfauna *A. cantianus*).

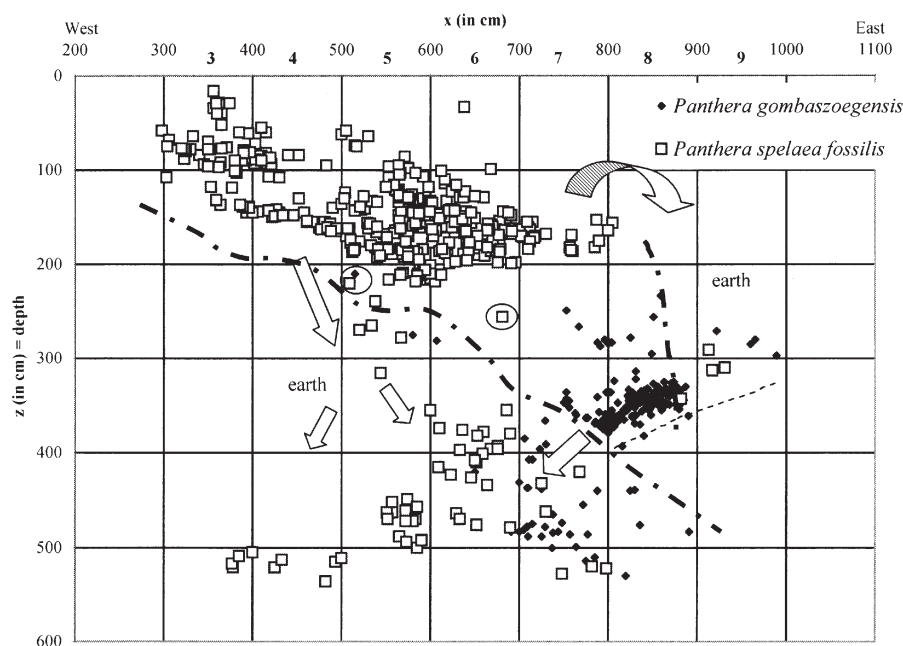


Fig. 4: Château Breccia, position of the bones of *Panthera spelaea fossilis* and *Panthera gombaszoegensis* projected on a vertical west-east cross section, within C squares alignment.
 - · - · - limit of the Breccia;
 → earth extracted from the quarry; O Br. 3.

Table 1: Château Breccia Northern Section, *Panthera gombaszoegensis* and *Panthera spelaea fossilis*: Number of skeletal remains.

element		<i>P. gombaszoegensis</i>		<i>P. spelaea fossilis</i>	
		N	%	N	%
1	skull				
	complete	2	0.52	4	0.43
	fragments	5	1.30	13	1.40
	isolated teeth	12	3.11	28	3.01
2	hemimandibles				
	complete	5	1.30	8	0.86
	fragments	5	1.30	15	1.61
	isolated teeth	15	3.89	36	3.88
3	vertebrae				
	cervical	1	0.26	6	0.65
	thoracic	1	0.26	2	0.22
	lumbar	11	2.85	11	1.18
	sacrum	2	0.52	3	0.32
	caudal	24	6.22	41	4.41
	sternum	2	0.52	5	0.54
indet.	19	4.92	1	0.11	
4	girdle				
	scapula fragm.	9	2.33	8	0.86
	pelvis fragm.	4	1.04	1	0.11
5	forelimb				
	humerus	1	0.26	1	0.11
	humerus fragm.	8	2.07	11	1.18
	radius	1	0.26	3	0.32
	radius fragm.	6	1.55	16	1.72
	ulna	1	0.26	2	0.22
	ulna fragm.	16	4.15	35	3.77
	carpals	16	4.15	76	8.18
metacarpals	6	1.55	42	4.52	
	metacarpals fragm.	7	1.81	18	1.94
6	hindlimb				
	femur	1	0.26	1	0.11
	femur fragm.	9	2.33	21	2.26
	patella	5	1.30	9	0.97
	tibia	1	0.26	1	0.11
	tibia fragm.	5	1.30	15	1.61
	fibula fragm.	5	1.30	20	2.15
tarsals	36	9.33	72	7.75	
metatarsals	6	1.55	22	2.37	
	metatarsals fragm.	15	3.89	33	3.55
7	varia				
	penile bone	0	0.00	0	0.00
	hyoid bone	0	0.00	0	0.00
	sesamoids	27	6.99	68	7.32
	phalanx 1	34	8.81	120	12.92
	phalanx 2	37	9.59	106	11.41
	phalanx 3	26	6.74	54	5.81
8	ribs				
	fixed ribs	0	0.00	1	0.11
	floating ribs	0	0.00	0	0.00
TOTAL		386		929	

whose current Central and South American relatives are now the only survivors. The evolutionary potential of this ancient ancestor cannot be compared with that of its modern descendants. We prefer calling *Panthera toscana* the ancient late Villafranchian representatives and *Panthera gombaszoegensis* the more recent Middle Pleistocene ones, recognising direct links between these

two chrono-species, which incontestably belong to the same evolutionary lineage. The crossing of the Bering Strait at the beginning of the Irvingtonian (KURTÈN & ANDERSON 1980) required a widely ubiquitous species, able to survive the cold temperatures of the intervals of sea level low stand, and to ultimately adapt to the Central and South American settings.

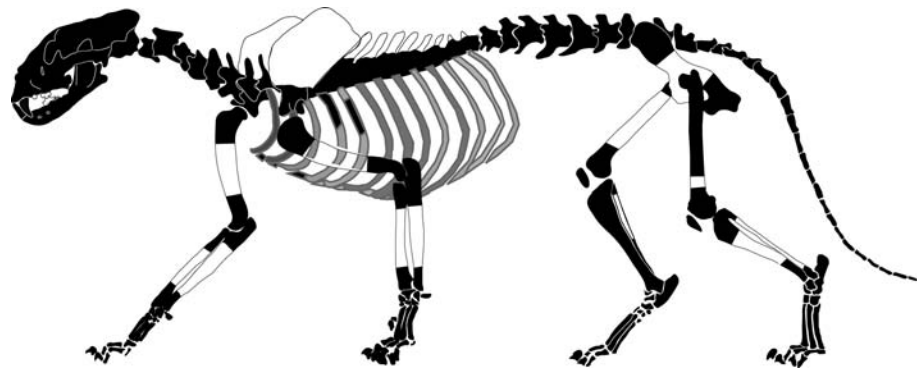


Fig. 5: Château Breccia, *Panthera gombaszoegensis*: Elements of a complete skeleton found in Breccia 4 (after TURNER & ANTÓN 1997: 71, figs 3.27).

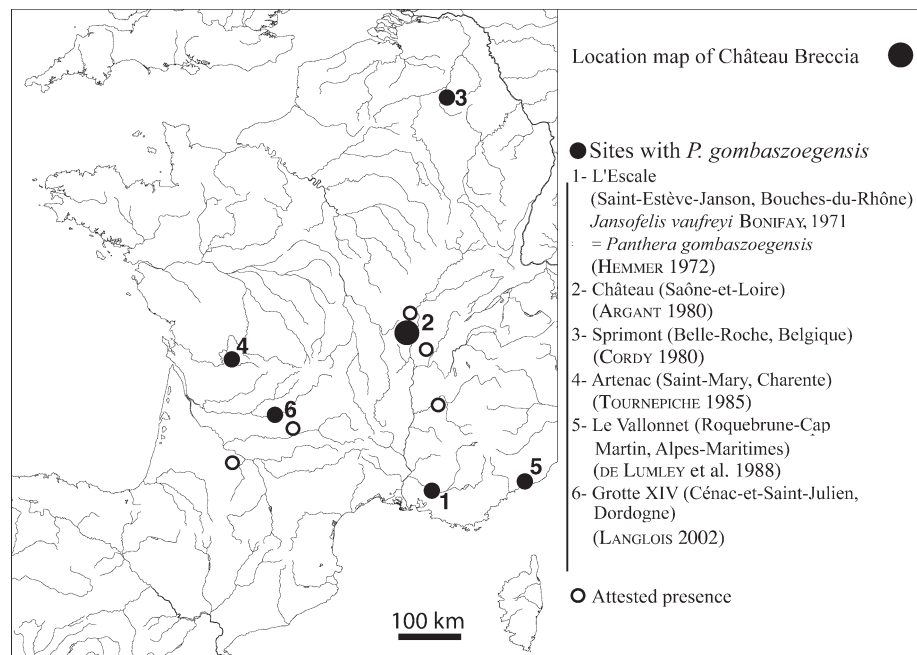


Fig. 6: Distribution of the *Panthera gombaszoegensis* sites in France and in Belgium.

Jaguars were first discovered in France in the cave of L'Escaie (Saint-Estève-Janson, Bouches-du-Rhône), where four individuals were found. Though acknowledging a possible link with *Leo gombaszoegensis* KRETZOI, 1938, from Gombasek in Slovakia (isolated teeth), BONIFAY created a new species she called *Jansofelis vaufreyi* BONIFAY, 1971. HEMMER (1972) showed that *Jansofelis vaufreyi* was synonymous with *Panthera gombaszoegensis* (KRETZOI, 1938) and distinguished two subspecies, i.e. *P. gombaszoegensis toscana* and *P. gombaszoegensis gombaszoegensis*. Bones excavated from 1968 on at the Château Breccia, which is the second jaguar-bearing site discovered in France, are attributed to *Panthera gombaszoegensis* (A. ARGANT 1980, 1991). Successively, the finds from Artenac (Saint-Mary, Charente) (TOURNEPICHE 1985, DELAGNES et al. 1999) as well as those from Belle-Roche (Sprimont, Liège, Belgium) (CORDY 1980, 1995) proved that the species was widely distributed both in and outside France. Since then, records of this species are becoming even more numerous in France (fig. 6): Grotte XIV at Cénac-Saint-Julien (Dordogne) (LANGLOIS 2002), Marignat (Presles, Isère)

(A. ARGANT, personal observation), Coudoulous II (Tour-du-Faure, Lot) (A. ARGANT, personal observation), Azé-Aiglons? (Saône-et-Loire) (A. ARGANT, personal observation), and Villereversure? (Ain) (MARTIN 1968). According to its morphology and size, the third metatarsal bone of La Nauterie (layer 13–14) (Romieu, Gers) (PRAT & THIBAUT 1976: pl. 1–5) attributed by PRAT to *Panthera* sp. is very likely to belong to *Panthera gombaszoegensis* as well.

Unless we imagine that the genus *Dinofelis* first evolved in Europe and then spread widely throughout the world, and that *Panthera* is closely related to *Dinofelis* (Balaruc II, Sète, Hérault, France, Villafranchian about 3 Myr; BEAUMONT 1983), the big *Panthera* cats likely originated in East Africa, as indicated by the earliest records dated to about 3.5 Myr (EWER 1956, DIETRICH 1968, PETTER 1973, TURNER & ANTÓN 1997). We assume the presence of *Panthera* aff. *gombaszoegensis* also in Africa is possible. Figure 7 shows the sites that actually yielded fossil remains of *Panthera* together with the areas of historical distribution of the present day *Panthera onca* (MEDELLIN et al. 2002).



Fig. 7: World distribution of *Panthera toscana*, *P. gombaszoegensis* and *P. onca* (fossil and historical distribution; after VERESH-CHAGIN 1969, KURTÉN 1973, KURTÉN & ANDERSON 1980, SOTNIKOVA 1989, HEMMER et al. 2001, 2003).

Europe: • France: 1 – L’Escale; 2 – Château; 3 – La Nauterie; 4 – Artenac, ensemble I; 5 – Vallonnet; 6 – Cénac-et-Saint-Julien, Grotte XIV; 7 – Villereversure; 8 – Azé-Aiglons; 9 – Marignat; • Spain: 10 – Atapuerca Gran Dolina; 11 – Huéscar I; • Italy: 12 – Olivola; 13 – Val d’Arno sup.; 14 – Perugia; • England: 15 – Westbury-sub-Mendip; • Belgium: 16 – Sprimont/Belle-roche; • The Netherlands: 17 – Maasvlakte; 18 – North Sea; • Germany: 19 – Mosbach 2; 20 – Würzburg-Schalksberg; 21 – Untermaßfeld; 22 – Süßenborn; 23 – Rabenstein; • Austria: 24 – Hundsheim; • Czech Republic: 25 – Koněprusy C 718; 26 – Stránská skála; 27 – Holštejn 1/Chlum 6; • Slovak Republic: 28 – Gombasek; • Hungary: 29 – Vértesszőlös II; 30 – Villány 3; 31 – Somssich-hegy 2; 32 – Kövesvárad; 33 – Uppony 1; • Romania: 34 – Betfia 5; • Bulgaria: 35 – Slivnica; • Greece: 36 – Volos; 37 – Gerakou 1; 38 – Petralona; • Georgia: 39 – Akhalkalaki; • Ukraine: 40 – Zimbal.

Asia: • Azerbaidjan: 41 – Palan-Tiukan; • Tadjikistan: 42 – Lakhuti 2; • Israel: 43 – Oubéidiyeh.

North America: • USA: 44 – Port Kennedy Cave (Pennsylvania); 45 – Cumberland Cave (Maryland); 46 – Edisto Beach (South Carolina); 47 – Vero (Florida); 48 – Melbourne (Florida); 49 – Coleman II A (Florida); 50 – Stickney Point (Florida); 51 – Seminole Field (Florida); 52 – Waccasassa (Florida); 53 – Devil’s Den (Florida); 54 – Florida; 55 – Ladds (Georgia); 56 – Craighead Caverns (Tennessee); 57 – Little Airplane Cave (Tennessee); 58 – Saltpeter Cave (Tennessee); 59 – Big Bone Cave (Tennessee); 60 – Salt River Cave (Tennessee); 61 – Crevice Cave (Missouri); 62 – Moore Pit (Texas); 63 – Laubach Cave (Texas); 64 – Clamp Cave (Texas); 65 – Longhorn Caver (Texas); 66 – Friesenhahn Cave (Texas); 67 – Central Cave (Texas); 68 – Cragin Quarry (Kansas); 69 – Niobrara River (Nebraska); 70 – Gordon (Nebraska); 71 – Mullen (Nebraska); 72 – Curtis Ranch (Arizona); 73 – Smith Creek Cave (Nevada); 74 – Fossil Lake (Oregon); 75 – Delight (Washington); 76 – Irvington (California); • Mexico: 77 – San Josecito Cave (Nuevo León).

Panthera (Leo) spelaea fossilis

Order *Carnivora* BOWDICH, 1821

Family *Felidae* GRAY, 1821

Subfamily *Felinae* SIMPSON, 1945

Genus *Panthera* OKEN, 1816

Panthera (Leo) spelaea fossilis (VON REICHENAU, 1906)

Synonymy: *Panthera leo fossilis* (VON REICHENAU, 1906)

Panthera (Leo) mosbachensis DIETRICH, 1962, not valid

The cave lion has always fired the imagination. There has been considerable debate about whether it was actually a lion or a tiger. For a long time a great number of palaeontologists have admitted that this big cat (genus *Panthera*) is a true lion (sub-genus *Leo*), but of a different species than the modern lion, *Panthera leo*, which is of African origin and which afterwards spread into Asia (*Panthera leo persica*). Studies of ancient DNA (BURGER et al. 2004) corroborate the palaeontologists’ opinion (for instance BOULE 1906,

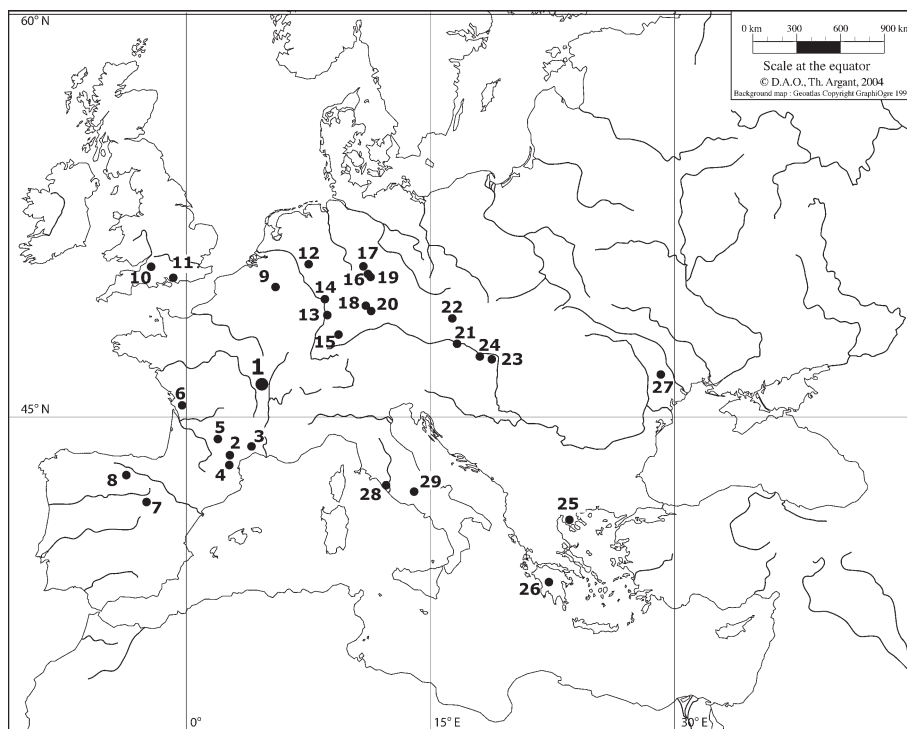


Fig. 8: European distribution of *Panthera spelaea fossilis*.

- France: 1 – Château; 2 – Aldène I. K.; 3 – Lunel Viel; 4 – Tautavel, Caune de l’Arago CMI St. Is.14; 5 – La Fage; 6 – Artenac, ensemble I; • Spain: 7 – Torralba-Ambrona; 8 – Atapuerca Gran Dolina • Belgium: 9 – Sprimont/Belle-Roche; • England: 10 – Westbury-sub-Mendip; 11 – Boxgrove; • Germany: 12 – Dechenhöhle; 13 – Mauer; 14 – Mosbach 2; 15 – Heppenloch, Gutenberg Höhle; 16 – Süßenborn; 17 – Bilzingsleben; 18 – Moggaster Höhle; 19 – Taubach; 20 – Hunas/Hartmannshof; • Austria: 21 – Deutsch-Altenburg I; • Czech Republic: 22 – Stránská skála; • Hungary: 23 – Várhegy; 24 – Vértesszőlös II; • Greece: 25 – Petralona; 26 – Megalopolis; • Moldova: 27 – Tiraspol; • Italy: 28 – Torre in Pietra; 29 – Isernia.

HILZHEIMER 1922, HELLER 1953, LEHMAN 1954, KABITZSCH 1960, MARTIN 1968, VERESHCHAGIN 1969, BONIFAY 1971, BALLESEO 1975, A. ARGANT 1980, 1991 and many others). In fact, *Panthera spelaea fossilis*, which is the name given to the ancient cave lion, is first reported in Europe from the early Middle Pleistocene (Isernia, Mauer, Forest-Bed, Mosbach, Vértesszőlös). These animals were very large “The Cromerian lion in Europe may be the largest felid that ever existed” (KURTÉN 1968: 85). The material from the Château Breccia is very similar (in morphology, size, and degree of fossilization) to that of Mosbach 2, which we had the opportunity to examine at the Museum of Mainz. Size drops steadily in the course of time (with some exceptions, however) until it reaches that of the living lion when the fossil species became extinct, at the end of last Lateglacial. Several ¹⁴C dates confirm that the latest specimens of *Panthera spelaea* are dated to 12,248 ± 66 BP in the Paris Basin, and 11,150 ± 220 BP in southwestern France. The pre-historic man recorded and communicated his observations using cave engravings or paintings (e.g. Chauvet Cave).

The *Panthera spelaea fossilis* – *P. spelaea spelaea* (chron-subspecies) evolutive lineage could be a valuable biochronological tool. An “ancient” *Panthera spelaea spelaea* can be distinguished from a more “recent” one (A. ARGANT 1991).

Figure 8 shows the European distribution of *Panthera spelaea fossilis*. The African origin of the genus *Panthera* is largely admitted. It could be present 3.5 Myr in eastern Africa (BARRY 1987). True lions (*Panthera leo*) exist at Olduvai Bed I, Shungara (Fm, Mb. G), between 2.3 and 1.7 Myr (WERDELIN & LEWIS 2005).

Palaeoenvironmental data

Palaeoenvironmental studies define the palaeoecological niches of these two big cat species. Micromammal studies as well as pollen analysis provide useful information on the palaeoenvironmental and palaeoclimatic conditions at the time of *Panthera gombaszoegensis* and *Panthera spelaea fossilis* occurrences.

Microfauna

The microfauna has been systematically sought for since 1997 by sieving all unconsolidated sediments and by crushing the solid breccia blocks. M. JEANNET is in charge of analyzing the relatively abundant material discovered.

Table 2: Château Breccia Northern Section, distribution of the microvertebrates in the excavated squares-meters.

	Breccia 2 Group A						Breccia 3 Group B				Breccia 4 Group C				Out of stratigraphy Group D												
	C3	C4	C5	D3	D4	D5	C6	C7	D6	E7	F6	F7	F8	G8	E3	E4	E5	E6	G6	H4	H5	H6	I7	Z25	EE26		
RODENTIA																											
<i>Microtus arvalis</i>	X	X	X	X	X	X			X	X			X		X											X	X
<i>Microtus agrestis</i>		X	X	X	X																						X
<i>Microtus gregalis</i>	X	X	X	X	X		X						X														
<i>Microtus oeconomus</i>					X																						
<i>Microtus nivalis</i>													cf														
<i>Pitymys multiplex</i>	X			X	X																						
<i>Dicrostonyx torquatus</i>		X			X				X																		
<i>Clethrionomys glareolus</i>	X	X	X	X	X																						
<i>Pliomys lenki</i>		X	X																								
<i>Pliomys episcopalis</i>		X																							X		
<i>Allophaiomys pliocaenicus</i>							X						X														
<i>gregaloides</i>													X														
<i>Mimomys hintoni</i>												X															
<i>Arvicola cantianus</i>	X	X	X	X	X	X	X		X	X	X		X					X							X	X	
<i>Arvicola terrestris</i>	X			X																					cf	cf	
<i>Arvicola sapidus</i>	X								cf																		
<i>Apodemus sylvaticus</i>	X	X		X	X						X																
<i>Alloricetus bursae</i>	X		X																								
<i>Cricetus cricetus</i>			X			X																					
<i>Glis glis</i>				X																							
<i>Eliomys quercinus</i>	X	X			X												X										
<i>Muscardinus avellanarius</i>				X																							
<i>Sciurus sp.</i>									X		X																
<i>Marmota sp., (juv.)</i>																									X		
LAGOMORPHA																											
<i>Oryctolagus cuniculus</i>	X					X				X							X		X		X						
<i>Lepus europaeus</i>															X		X										
<i>Lepus timidus</i>																									X		
<i>Ochotona pusilla</i>	X	X	X	X	X	X			X																		
INSECTIVORA																											
<i>Talpa europaea</i>	X	X	X	X	X	X	X	X	X	X					X	X											X
<i>Talpa minor</i>		X	X	X	X																						
<i>Sorex araneus</i>		X			X	X																					
<i>Sorex runtonensis</i>	X		X	X	X	X									X												
<i>Sorex minutus</i>	X	X	X		cf				X																		
<i>Crocidura leucodon</i>		X	X																								
<i>Crocidura russula</i>		X																									
<i>Neomys fodiens</i>			X			X																					
<i>Beremendia fissidens</i>		X																									
CHIROPTERA																											
<i>Myotis nattereri</i>	sp	X	sp										sp														
<i>Plecotus auritus</i>	cf																										
<i>Miniopterus schreibersi</i>	X		X												X												
CARNIVORA																											
Small Carnivores		X	X		X																						
<i>Mustela nivalis</i>	X	X																									
<i>Mustela erminea</i>		X																									
AVES																											
	X			X	X		X		X	X									X	X							

	Breccia 2 Group A					Breccia 3 Group B				Breccia 4 Group C				Out of stratigraphy Group D											
	C3	C4	C5	D3	D4	D5	C6	C7	D6	E7	F6	F7	F8	G8	E3	E4	E5	E6	G6	H4	H5	H6	I7	Z25	EE26
REPTILIA																									
Lacertidae	X		X												X										
<i>Anguis fragilis</i>			X																						
Ophidia	X		X				X																		
<i>Coluber viridiflavus</i>			X																						
<i>Elaphe longissima</i>				X																					
<i>Vipera ammodytes</i>	X																								
AMPHIBIA	X		X						X																
<i>Salamandra salamandra</i>		X																							
<i>Bufo bufo</i>									X																
<i>Rana temporaria</i>			X																						
Discoglossidae					X																				
PISCES				X																					7

The list of the microvertebrates found in the square-meters which have been excavated, distributed over the sections, is shown in table 2.

The way the sediment was formed (by devastating mudslides) with the early destruction of the roof in the karstic system greatly complicates the interpretation of the microfauna. Several finds are typical Middle Pleistocene species, such as *Allophaiomys pliocaenicus gregaloides* [by other students named *Microtus (Stenocranius) gregaloides*; comment by the eds.], which is an ancestor of some modern Microtinae, furthermore *Pliomys episcopalis*, *Pliomys lenki*, *Allocricetus bursae*, *Arvicola cantianus*, *Talpa minor*, *Sorex runtonensis* and *Beremendia fissidens*. Some of them survived from the Early Pleistocene. The most ancient arvicolid determined is *Mimomys hintoni* (found in Br. 4, but probably reworked from an older breccia), which usually can be found in layers dated between 2.5 and 2.2 Myr. *Arvicola cantianus* as well as its direct descendants, *Arvicola terrestris* and *Arvicola sapidus*, are found in the same sector. The Breccia 2 yields a fauna with elements that are found today in Siberia, up to its extreme north (*Dicrostonyx torquatus*, *Microtus oeconomus*, *M. gregalis*), and in the Central Asian steppes (*Microtus gregalis*, *Cricetus cricetus*, *Ochotona pusilla*, *Citellus* sp.) as well as rodents able to live under a Mediterranean climate (*Apodemus sylvaticus*, *Eliomys quercinus*). *Glis glis* and *Lepus europaeus* are rare in Br. 2 and occur under temperate climates.

Lying so close to the surface for a very long time, the layers might have been exposed to potential mixing. Nonetheless, *Arvicola cantianus* is not only constantly present, but it is also the site's most abundant species with numerous hemimandibles contained in the breccia blocks. Unfortunately, the study of the micromammals from the Château Breccia disclosed scarce palaeoenvironmental information. We can only ascertain that the Middle Pleistocene species still remain dominant. *Arvicola cantianus* is a useful chronological reference for dating Br. 2 and Br. 3.

Pollen data

Although modest, the pollen analysis (J. ARGANT 1980, 1990, A. ARGANT & J. ARGANT 2002) yields the only data available in Burgundy for this period. 28 samples have been collected from the breccia (solid or decomposed), in most cases in contact of a bone or a tooth; only four of them resulted non-sterile (tab. 3). Even such a high number of samples may not be sufficient to intercept fossil pollen. Where the pollen and spores are relatively abundant, they are not particularly corroded.

Breccia 4

CHA.1-01-G.8-21bis: The sample gave us the greatest amount of information. It has been collected under a block, which covered a tooth of a carnivore. The pollen concentration reaches 180 grains per g of sediment, which is unusually high for the site; the number of taxa (n = 30) is also high. The spectra show 45.4 % of arboreal pollen, 48.8 % of herbaceous pollen and 5.7 % of Pteridophytes spores. The best represented trees are *Pinus*, then *Quercus*. *Abies* (2.7 %) followed by broadleaved trees: *Betula*, *Alnus* and *Juglans*. Single grains of the following trees were found: *Corylus*, *Acer*, *Cornus*, *Sorbus* cf. *aria*. The abundant pine pollen, which likely comes from several kilometres around, is rather abundant indicating a wide-open landscape. The conditions were temperate and wet enough for *Abies*. The alder suggests the proximity of water.

The non-arboreal pollen is all heliophilous and is dominated by the Poaceae and Cichorioideae type, accompanied by Ranunculaceae, Brassicaceae, *Plantago* and many other taxa. The presence of *Sanguisorba minor* suggests dry grassland on a limestone substratum. In general, such a spectrum is typical of open grasslands with various ecological niches, which accommodate light

Table 3: Château Breccia Northern Section and SIPO, palynology: Number and relative frequencies of the woody, herbaceous and Pteridophytes taxa.

CHA 1	Breccia 4				Breccia 2		SIPO	
	CHA1.01–G8–21 bis		F8–158–Pg		D4–53	CHA.1–SIPO–US 203		
	n	%	n	%	n	n	%	
<i>Pinus</i>	80	26.94	119	34.90	49	29	7.67	
<i>Abies</i>	8	2.69	4	1.17		3	0.79	
<i>Picea</i>			2	0.59				
<i>Betula</i>	3	1.01	1	0.29		1	0.26	
<i>Quercus</i>	31	10.44	6	1.76	21	22	5.82	
<i>Alnus</i>	4	1.35	2	0.59		1	0.26	
<i>Carpinus</i>			1	0.29				
<i>Juniperus</i>			1	0.29	1			
<i>Juglans</i>	4	1.35	1	0.29		1	0.26	
<i>Corylus</i>	1	0.34	1	0.29		6	1.59	
<i>Acer</i>	1	0.34				2	0.53	
<i>Cornus</i>	1	0.34						
<i>Ephedra</i>	1	0.34						
<i>Sorbus cf. aria</i>	1	0.34						
<i>Hedera</i>					1	2	0.53	
<i>Cedrus</i>						2	0.53	
<i>Fagus</i>						4	1.06	
<i>Prunus</i>						1	0.26	
<i>Castanea</i>						2	0.53	
<i>Ostrya</i>						1	0.26	
AP	135	45.45	138	40.47	72	69	18.25	
NAP	145	48.82	63	18.48	3	300	79.37	
Spores	17	5.72	140	41.06	4	1	0.26	
CYPERACEAE	4	1.35	15	4.40				
RANUNCULACEAE	12	4.04	8	2.35		2	0.53	
POACEAE	46	15.49	2	0.59		24	6.35	
<i>Plantago lanc. type</i>	6	2.02	6	1.76		104	27.51	
<i>Plantago m/m</i>						12	3.17	
LAMIACEAE	5	1.68	7	2.05		1	0.26	
APIACEAE	1	0.34	1	0.29		30	7.94	
CARYOPHYLLACEAE		0.00	3	0.88		2	0.53	
RUBIACEAE		0.00	2	0.59		2	0.53	
BRASSICACEAE	11	3.70	1	0.29		1	0.26	
FABACEAE	4	1.35				3	0.79	
GERANIACEAE	1	0.34						
<i>Polygonum</i>			1	0.29				
<i>Artemisia</i>						21	5.56	
<i>Ambrosia type</i>						22	5.82	
<i>Rumex</i>						4	1.06	
CHENOPODIACEAE	2	0.67	2	0.59		13	3.44	
ASTEROIDEAE	5	1.68				5	1.32	
CICHORIOIDEAE	31	10.44	2	0.59		3	0.79	
<i>Centaurea</i>	1	0.34				2	0.53	
ROSACEAE	3	1.01				1	0.26	
<i>Sanguisorba mi nor</i>	1	0.34						
<i>Calluna</i>	1	0.34				4	1.06	
URTICACEAE						28	7.41	
PRIMULACEAE						2	0.53	
CRASSULACEAE						2	0.53	
SAXIFRAGACEAE						1	0.26	
<i>Filipendula</i>						1	0.26	
<i>Typha latifolia</i>						1	0.26	
<i>Typha angustifolia</i>						1	0.26	
<i>Thalictrum</i>					1	1	0.26	
Unknown	11	3.70	13	3.81	2	7	1.85	
Monolete spores	8	2.69	118	34.60		1	0.26	
Trilete spores	9	3.03	22	6.45	4			
Pollen sum	297		341		79	378		
Number of taxa	30		25		7	41		

pine and fir woods, as well as oaks and other broadleaved trees. The climate was temperate but colder than today.

CHA.1-F.8-158: Though less rich (85 grains per g and 25 taxa), this sample is also worthy of interest because of its position under a skull of *Panthera gombaszoegensis* (F.8-73). Its spectra have been compared with those obtained from CHA.1-01-G.8-21bis. The major differences are: *Pinus* is more abundant (34.9 %) than in CHA.1-01-G.8.21bis, which makes up for the lesser amount of *Quercus*, and the arboreal pollen percentages are very similar in both samples. *Picea* appears for the first time, as well as *Carpinus* and *Juniperus*. In contrast, *Acer*, *Cornus*, and *Sorbus* are missing. The Poaceae and Cichorioideae play almost no part and as a result the amount of herbs is low, while the Pteridophytes dominate.

The landscape appears to be quite open, with fairly dense woods of conifers (pine, fir, picea) and some deciduous trees. The increased abundance of ferns is perhaps due to cooler climatic conditions leading to the reduction of dry grassy areas.

Breccia 2

The clay sampled under the sacrum of a bear (**CHA.1-01-D.4-53**) gives some information about Breccia 2. Unfortunately the limited number of taxa ($n = 7$) prevents an accurate description of the vegetation. There is uncertain presence of grass (cf. *Thalictrum?*). The trees dominate with *Pinus* and *Quercus*. *Hedera* suggests temperate conditions. Although the landscape suggested by this sample is unclear, the woodland areas must have been quite spread.

SIPO

The so called SIPO belongs to the Southern Section. Only a thin stalagmitic floor, interstratified within the sandy clay infilling of the SIPO gave a fairly reliable sample for pollen analysis (**CHA1-Z.24** and **Z.25**). It appeared to be rich in insect debris and in pollen (378 grains, 42 taxa). The excellent conditions for fossilisation were created by the continually wet floor as well as by the fast precipitation of calcite. This proves how reliable the pollen is. The taphocoenosis found at the top of the level includes *Ursus deningeri* (with many very young cubs), *Panthera spelaea*, *Panthera gombaszoegensis*, *Lepus timidus* and *Arvicola cantiana*. The chronological relationship with the Northern Section is not established yet, but both big cats are present. So, whatever the age, the pollen analysis of this stalagmitic floor provides interesting elements for the reconstitution of the felids' environment of life.

Nearly 80 % of the pollen grains belong to grass, widely represented by the plantains (*Plantago lanceolata*, 27.5 % and *Plantago* type *major/media*, 3.2 %), followed by the Apiaceae (8 %), Urticaceae (7.4 %), Poaceae

(6.3 %), Asteroideae (mostly *Artemisia*, 5.6 % and *Ambrosia* type, 5.8 %), Chenopodiaceae (3.4 %), *Rumex* (1 %) as well as by 13 other taxa. Among these, *Typha* (*latifolia* and *angustifolia*) indicates the presence of a water pond. Trees occur. They form 20.3 % of the total amount of pollen. The two dominant taxa, *Pinus* (7.7 %) and *Quercus* (5.6 %), are accompanied by various broadleaved trees, which occur each with one or two pollen grains: *Fagus* (1.2 %), *Corylus* (1.5 %), and *Acer*, *Prunus*, *Alnus*, *Betula*, *Juglans*, *Hedera*, *Castanea*, and *Ostrya carpinifolia*. *Abies* (0.6 %) and *Cedrus* (0.6 %) are the only conifers besides *Pinus*.

Most of the trees are more or less heliophilous (except *Fagus* which needs shade for growing), mesophilous or mesothermophilous (RAMEAU et al. 1989). *Fagus*, *Abies*, *Juglans* need a damp atmosphere. *Alnus* requires permanent water in the soil. In sum, the accumulated evidence indicates important edaphic and atmospheric moisture, under temperate and fresh climatic conditions.

Despite it functioning like a deep karst sinkhole (brown clay, reworked speleothems), in the SIPO area there is a great number of bones of *Ursus deningeri* cubs, likely because of its proximity to the entrance of the cave (less than 10 m) and thus its obvious use as a passage. A large part of the pollen material entered the cave attached to the paws or fur of the animals or incorporated in their dung, or even contained in the intestines of decaying carcasses. Insects were yet another important means of transport. The way sporopollinic material entered the cave can explain the overrepresentation of herbs. The spectra point to an open landscape wherein nitrophilous species prospered, particularly Chenopodiaceae and Urticaceae. The plant assemblage is strikingly similar to those of modern mesohygrophilous or mesoxerophilous meadows, characterized by Poaceae, *Rumex*, *Urtica*, *Ranunculus*, *Plantago lanceolata* (BOURNÉRIAS et al. 2001), which flourish thanks to trampling but also to the enrichment in nitrogen by urine and dung. It was likely the same around the cave, which was frequented by the bears, cats (*Panthera spelaea fossilis* and *P. gombaszoegensis*), and smaller mammals (*Meles* sp., *Lepus timidus*, *Arvicola cantianus*). Sediments of the same kind and of a clearly colder cycle lie on both sides of the cave's thin floor (3 cm thick). These basal deposits are overlain by the stratigraphic unit US 202, which contains an articulated skeleton of *Lepus timidus*, which also indicates a cold phase. Sandwiched between these two cold periods, the stalagmitic floor represents presumably a stage of climatic warming, indicated by sufficiently well marked forest dynamics. The bottom of a small valley in the SIPO excavation area provided the highest moisture favourable to *Alnus*, *Typha* and most of the herbs, as well as trees.

From a qualitative point of view, the SIPO area is quite similar to Br. 4, but the lack of a complete reference stratigraphic column prevents an exact chronological location of the site. However, the samples suggest a single type of landscape, under similar climatic conditions, which seem to be perfectly in line with the fauna.

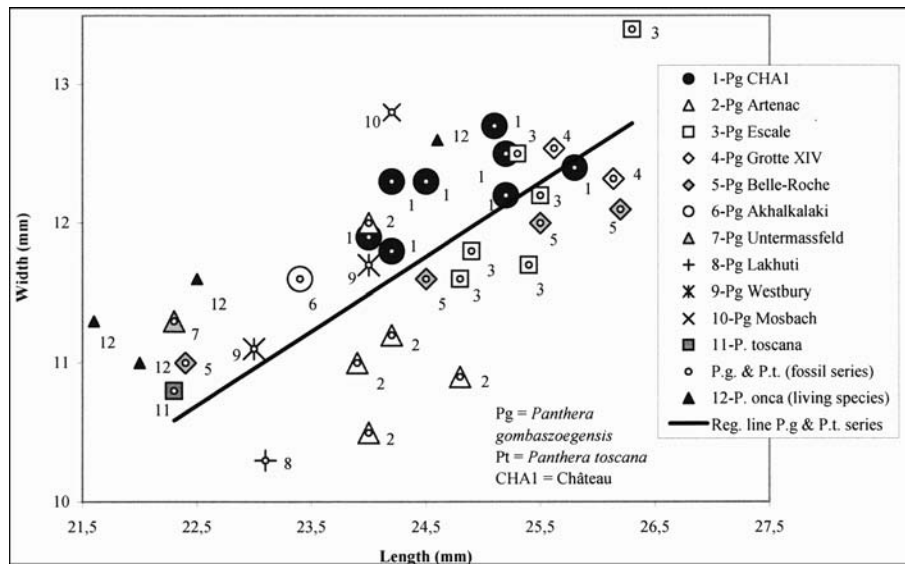


Fig. 9: *Panthera gombaszoegensis*, scatter diagram for the length and width of the m1 from various sites. Empty or white circle inside the symbols = fossil series.

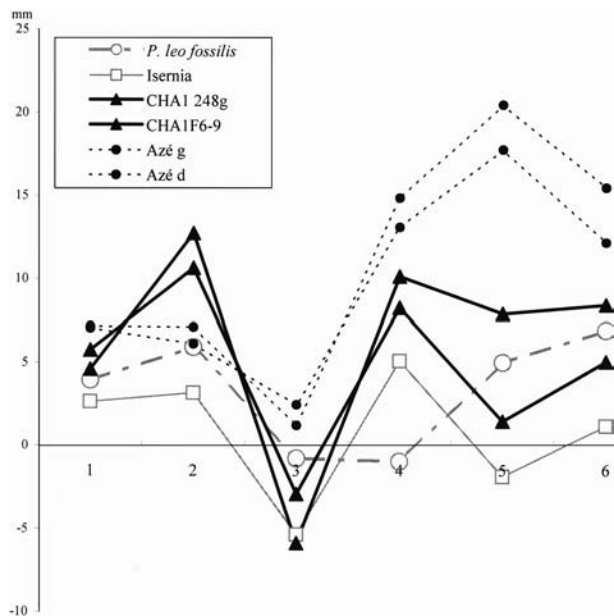


Fig. 10: Comparison of the P4 of *Panthera spelaea fossilis* from Château Breccia (CHA1 248g, CHA1F6-9), measurements from various sites after SCHÜTT & HEMMER (1978), *Panthera spelaea fossilis* from Isernia and *Panthera spelaea spelaea* from Azé (France) with the average of the more recent cave-lion *P. spelaea spelaea* (n = 14), represented by the horizontal axis (0). Measurements: 1 – total length, 2 – paracone length, 3 – metacone length, 4 – protocone width (max.), 5 – posterior width (max.), 6 – width behind protocone (min.).

Results

In the case study, the palaeoenvironment indicated by the pollen analysis of Br. 2, Br. 4 and even of the SIPO's stalagmitic floor, which represents a warming cycle within a cold phase, is virtually the same. Overall, the landscape was open with grasses spread on the uplands, while woodlands of pine and fir, but also of broadleaved trees,

such as oak, birch, walnut tree, distributed in the valley. Alder could grow in the wet zone along the brook nearby. The climate was temperate but colder than today, although it sometimes might have been even markedly cold inferred from the association (if autochthonous) of *Panthera gombaszoegensis* with *Lepus timidus* in the SIPO and *P. spelaea fossilis* with *Dicrostonyx torquatus*, *Citellus* sp. and *Ochotona* sp. in the Northern Section.

Biochronologic dating

All methods to obtain absolute dates for the Northern Section are inadequate for this time period (¹⁴C, thermoluminescence, potassium/argon). The absence of herbivore molars with thick enamel prevents ESR dating. Three attempts of U/Th and Uranium series dating on stalagmitic layers by Y. QUINIF (cerak, Mons) have been unsuccessful until now. The most reliable chronological indications point to an age somewhat lower than 1 Myr. Fortunately though, the assemblages from this section provide helpful biochronologic clues.

Ursid biochronology

Except a single m1 attributed to *Ursus arctos* in Br. 4, the Château bear remains are all assigned to *Ursus deningeri*. The study of the m1 as well as the morphodynamic method on P4 and p4 (RABEDER 1992) indicate a typical Middle Pleistocene *U. deningeri*. Comparison (unfortunately, based on different sample sizes) between the populations from Br. 2 (m1, n = 47 and P4/p4, n = 37/49) and Br. 4 (m1, n = 6 and P4/p4, n = 3/4) shows that the Br. 4 bears, being much older (A. ARGANT & J. ARGANT 2002), were less advanced than the Br. 2 ones.

Felid biochronology

Evolutionary level of *Panthera gombaszoegensis* from Château Breccia Northern Section

Felids' lower carnassial is generally a well-studied tooth. Figure 9 is the diagram of the width vs length distribution of this tooth in *Panthera toscana*, *P. gombaszoegensis* as well as in modern *P. onca*. The Château m1s cluster in the upper part of the diagram near those of l'Escaie, Belle-Roche and Mosbach, and far from *Panthera toscana* (number 11 in the diagram is the average of the Italian Upper Villafranchian specimens). According to the dimensions and proportions of its m1, *P. gombaszoegensis* from Château clusters with the massive and larger-sized mid Middle Pleistocene representatives.

Evolutionary level of *Panthera spelaea fossilis* from Château Breccia Northern Section

The big cats' fourth upper premolar is also generally well studied. Figure 10 shows the comparison of six P4 measurements (total length, paracone length, metacone length, protocone maximal width, posterior maximal width, minimal width behind protocone) of ancient cave lions related to the average of the more recent *Panthera spelaea spelaea* (n = 14). The samples are represented by the average (n = 6) of *Panthera leo fossilis* from Mauer, Mosbach, Obrigheim, und Scharzfeld (Einhornhöhle) (SCHÜTT & HEMMER 1978), the P4 from Isernia La Pineta (Italia) (SALA 1990) and two left P4 from Château (CHA.1-F.6-9, CHA.1-C.5-248). Azé is a locality from the same region as Château (Saône-et-Loire) and included the left and right P4 of a complete skull (AZE-K.13-29) of a more ancient form of *Panthera spelaea spelaea* (A. ARGANT 1988).

The two premolars from Château are very similar to that from Isernia. At present, Isernia La Pineta is the most ancient site containing *Panthera spelaea fossilis*. Isernia La Pineta had been originally dated to an age older than 730 kyr, while more recently (COLTORTI et al. 2005) the site has been dated to the early Middle Pleistocene, at ca. 600 kyr. This new dating is far more consistent with the known age of arrival of *Panthera spelaea fossilis* in Eurasia. Hence, the *Panthera spelaea fossilis* from Château is one of Europe's most ancient representatives of this particularly large subspecies together with the other Cromerian ones from Isernia, Mauer, and Mosbach.

Lagomorph biochronology

Lagomorphs are scarce at Château. They belong to two species: *Oryctolagus cf. lacosti* POMEL, 1853 (family Leporidae), and *Ochotona* sp. (family Ochotonidae). The terminology used here to describe the teeth structures is that

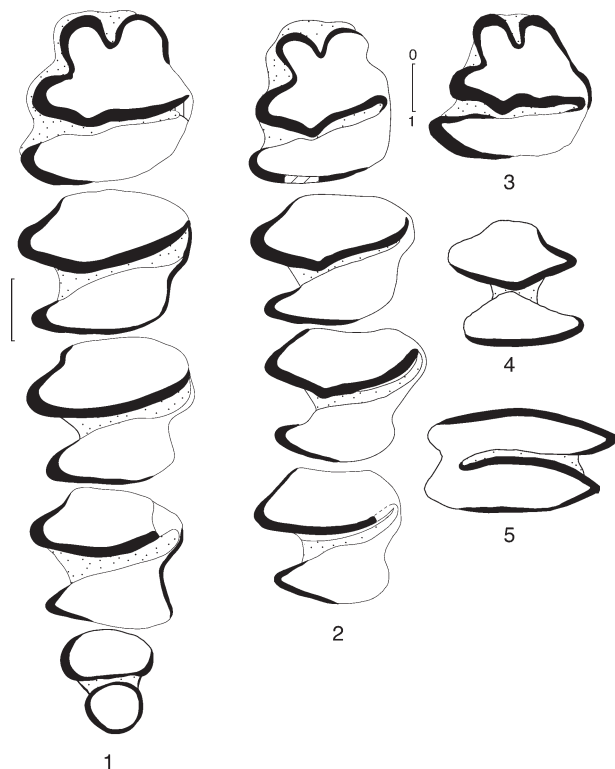


Fig. 11: *Oryctolagus cf. lacosti* POMEL, 1853, lower dentitions (occlusal views): 1 – left p3–m3 (CHA.1–H.6); 2 – left p3–m2 (F-120; Montoussé-5) (after CHALINE et al. 2000: fig. 3A); 3 – left p3 (Aridos-1) (after LOPEZ MARTINEZ 1980: fig. 23a). *Ochotona* sp., lower and upper teeth (occlusal views) (CHA.1–C3): 4 – right m2, 5 – right P4.

of PALACIOS and LOPEZ MARTINEZ (1980) for *Oryctolagus*, and that used by ERBAJEVA (1988) for ochotonids.

Order L a g o m o r p h a BRANDT, 1855
 Family L e p o r i d a e GRAY, 1821
 Subfamily L e p o r i n a e TROUSSART, 1880
 Genus *Oryctolagus* LILLJEBORG, 1874
Oryctolagus cf. lacosti POMEL, 1853

M a t e r i a l : CHA.1–H 6 (out of stratigraphy), left mandible with p3-m3, without incisor; angular process and ascending ramus are broken (tab. 4; fig. 11, 1–3).

D e s c r i p t i o n : Medium size leporid, similar, in the structure of teeth and size, to *Oryctolagus cf. lacosti* POMEL, 1853. The mandible is slender. The root of the lower incisor reaches back almost to the base of p3, forming a small tubercle on the mandible's outer wall. There are two mental foramina, one located anteriorly to p3, the second below p3 halfway the height of the mandible. On the lingual surface of the incisive portion of the mandible there is a rather deep groove near the lower border of the mandible, which continues to p4. The p3 hypoflexid stretches almost to the lingual border of the tooth. It is not plicated, filled with thick cement; the protoflexid and anteroflexid are rather deep and filled as well with thick ce-

Table 4: Measurements (mm) of lower cheek teeth of *Oryctolagus* cf. *lacosti* POMEL from Château, Aridos-1 and Montoussé-5. Length and width are maximum distances on the occlusal surface and include the enamel. All measurements are given in millimetres.

	Château		Montoussé (CHALINE et al. 2000)		Aridos-1 (LOPEZ MARTINEZ 1980)	
	n	x	n	x	n	x
Coronar length p3–m3	1	13.0			1	12.35
Coronar length p3–m2	1	11.2	1	11.9		
Coronar length p3–m1	1	8.4	1	8.9		
Coronar length p3–p4	1	5.6	1	6.0		
Length p3	1	3.1	1	3.25		
Width p3	1	3.3	1	3.25		
Length p4	1	2.7	1	2.7		
Length p4 trigonid	1	1.5	1	1.5		
Length p4 talonid	1	1.0	1	1.25		
Width p4 trigonid	1	3.2	1	3.25		
Width p4 talonid	1	2.5	1	2.75		
Length m1	1	2.8	1	2.6		
Length m1 trigonid	1	1.4	1	1.5		
Length m1 talonid	1	1.15	1	1.3		
Width m1 trigonid	1	3.1	1	3.4		
Width m1 talonid	1	2.5	1	2.55		
Length m2	1	2.75	1	2.8		
Length m2 trigonid	1	1.4	1	1.45		
Length m2 talonid	1	1.25	1	1.3		
Width m2 trigonid	1	2.9	1	3.35		
Width m2 talonid	1	2.5	1	2.55		
Length m3	1	2.0				
Length m3 trigonid	1	0.95				
Length m3 talonid	1	1.0				
Width m3 trigonid	1	1.7				
Width m3 talonid	1	1.1				
Mandible height at p3	1	10.0				
Mandible height at m3	1	12.7			1	11.2

ment, while the paraflexid is shallow and without cement. The lingual border of p3 is rather convex. The lower teeth have a pattern very similar to that of the living species *Oryctolagus cuniculus*. Trigonids and talonids of p4–m2 are connected on the lingual side, while there is a thick cement layer on the labial side of the teeth.

Comparisons: The teeth and mandibles of *Oryctolagus* cf. *lacosti* POMEL, 1853 from Château are close, in size and morphology, to those of the Montoussé-5 (France) (fig. 11-2) and Aridos-1 (Spain) rabbits (fig. 11-3) (LOPEZ MARTINEZ 1980, CHALINE et al. 2000). However, the Château specimens differ from *Oryctolagus* of Montoussé-5 in the more convex lingual border of p3 as well as in the flatter anterior border of the hypoflexid. They differ from the Aridos-1 specimens in the absence of plications in the hypoflexid of p3. The *Oryctolagus* from Château resembles the “Leporidae indeterminé” from Bagur-2 in Spain (LOPEZ MARTINEZ et al. 1976), in

the structure of the lower teeth, but they exceed the Spanish specimens in size (length and width of the p3 from Bagur-2 are 2.29 mm and 2.42 mm respectively, versus 3.1 mm and 3.3 mm in *Oryctolagus* from Château).

Family *Ochotonidae* THOMAS, 1897
 Subfamily *Ochotoninae* THOMAS, 1897
 Genus *Ochotona* LINK, 1795
Ochotona sp.

Material: Isolated right P4 and right m2, fragment of left I1 (CHA.1–C 3, Br. 2) (fig. 11-4–5).

Description: Small-sized ochotonid; teeth are similar in shape to those of all *Ochotona* species. P4 is wider and shorter anteriorly than posteriorly, the hypostria extends almost to the external border of the tooth, filled with thin cement. The trigonid of m2 is slightly longer and wider than the talonid, the syncline between both conids is

Fig. 12: *Arvicola cantianus*, morphotypes according to the position of the *Mimomys*-fold (definitions of the types see text). Type 1 is closest to *Mimomys*, type 6 is closest to the recent *Arvicola*. → Position of the *Mimomys*-fold.

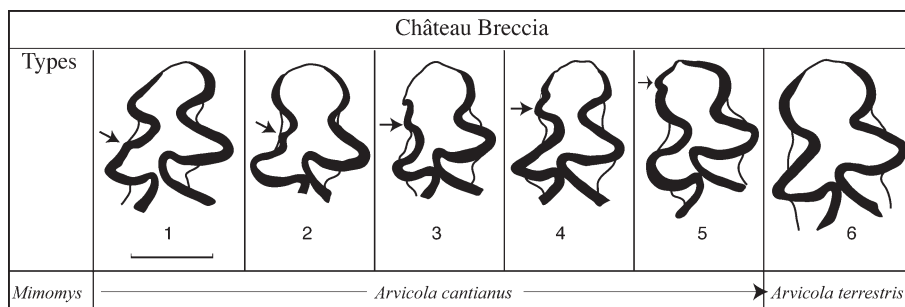


Table 5: Château Breccia Northern Section, *Arvicola cantianus*: SDQ (relative thickness of the posterior cutting edges of all anticlines expressed as a percentage of the corresponding anterior cutting edges) and SZQV (relative thickness of the anterior cutting edges of all anticlines as a percentage of the occlusal length of the m1) for the 4 groups: group A = EN = Br. 2; group B = EN = Br. 3; group C = EN = Br. 4; group D = varia.

	Breccia 2	Breccia 3	Breccia 4	SIPO
Group	A	B	C	D
n	52	43	4	3
mean	130.6	133.3	124.5	110.5
max	157.7	157.2	132.3	114.0
min	105.3	113.4	116.0	105.3
sd	12.11	9.37	7.43	4.57
SDQ				
n	34	24	-	-
mean	196.8	192.3	-	-
max	245.9	222.0	-	-
min	162.9	159.6	-	-
sd	20.2	16.45	-	-
SZQV				

filled with cement. The tooth enamel is thicker on the anterior and lingual borders of the upper teeth as well as on the posterior and labial borders of the trigonids and talonids of the lower cheek teeth. Length and width of P4 and m2 are respectively 1.25 x 2.2 mm and 1.55 x 1.5 mm.

Arvicola biochronology

Biometry of the enamel thickness of the m1

Arvicola cantianus remains have been classified into 4 groups (A–D), originating from different Breccias and unstratified squares (fig. 3, tab. 2):

Group A: 52 m1 from EN, Northern Section, Breccia 2 (US 103, 104). Squares C.3, C.4, C.5, D.3, D.4, D.5;

Group B: 42 m1 from EN, Northern Section, Breccia 3 (US 107 and yellowish clayish silt US 106). Squares C.6, C.7, D.6, E.7;

Group C: 4 m1 from EN, Northern Section, Breccia 4 (US 115, the oldest). Squares F.6, F.7, F.8, G.8;

Group D: 3 m1 from various areas, not in stratigraphy, SIPO square Z.25, and ES square EE.26.

Table 6: Château Breccia, frequency of the presence of the *Mimomys*-fold on the m1 of *Arvicola cantianus* within the 4 groups A, B, C, D.

	Breccia 2	Breccia 3	Breccia 4	SIPO
Groups	A	B	C	D
	20/52	15/42	2/4	1/3
	38.46%	35.71%	50.00%	33.00%
total	n = 38/104			

The progressive change in the thickness of cutting edges in *Arvicola* m1 triangles has long been observed (HINTON 1910). HEINRICH (1978, 1990) calculated the percentage of the thickness of the posterior enamel edges in relation to the anterior edges. On the base of this ratio (the so called SDQ index) a chronological order of sites containing *Arvicola* can be elaborated (HEINRICH 1978, 1990, KOENIGSWALD & HEINRICH 1999: 63, fig. 4, MAUL et al. 2000: 134, text-fig. 3). The results for the Château Breccia are given in table 5. The SDQ values for the group C are not significant because of the small samples size. Group D is too heterogeneous and thus had to be disregarded. A and B are the best represented groups and give a very similar index, which confirms their chronological proximity.

HEINRICH (1978, 1990) devised still another method, based on the calculation of the parameter SZQV (relative thickness of the anterior edges of all anticlines as a percentage of the occlusal length of the m1). The results obtained using this second method on the Château groups A and B are shown in table 5. Also the SZQV two groups are similar and lead to the same conclusion as that obtained calculating the SDQ index. However, we draw attention to the differences between both parameters used as well as to the great individual variability depending on age, sex and environment of life (JEANNET & CARTONNET 2000).

Mimomys-fold

Another criterion to obtain a relative age is the vestigial *Mimomys*-fold in the m1, which is more or less developed in 38 of the 104 molars from the Château Breccia (37.25 %) (tab. 6). This fold is typical of *Mimomys*, while it occurs only accidentally from the appearance of *Arvi-*

Table 7: Château Breccia, *Arvicola cantianus*: Main morphotypes of the anterior loop of the m1 according to the position of the *Mimomys*-fold. Percentages for group A and B only. See morphotypes fig.12; diagram fig.13.

Number		TYPE 1	TYPE 2	TYPE 3	TYPE 4	TYPE 5	TYPE 6	Total
Group A	Breccia 2		7	10	2	5	28	52
Group B	Breccia 3	5	7	7	1	4	18	42
Group C	Breccia 4	1	2			1		4
Group D	Diverse			2			4	6
%		TYPE 1	TYPE 2	TYPE 3	TYPE 4	TYPE 5	TYPE 6	Total
Group A	Breccia 2	0.00	13.46	19.23	3.85	9.62	53.85	100.00
Group B	Breccia 3	11.90	16.67	16.67	2.38	9.52	42.86	100.00

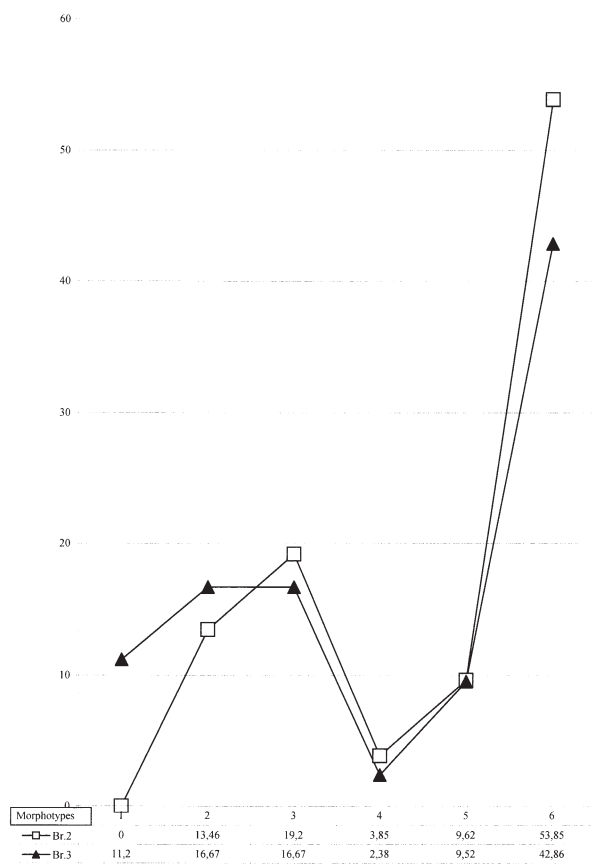


Fig. 13: Château Breccia, *Arvicola cantianus*: Distribution of the morphotypes (position of the *Mimomys*-fold) within group A (Breccia 2) and group B (Breccia 3).

cola onwards. The question is “how” and “how fast” did this structure evolve? The second question would need a comparative study of large populations from many well-dated Middle and Late Pleistocene sites. As to how did the *Mimomys*-fold evolve, we must see how this ephemeral fold on t4 (4th triangle mesial of the posterior loop, or BSA3 after VAN DER MEULEN 1973) changed its position through time. It started in a “subhorizontal” position on the anterior wall of t4, as we find it in *Mimomys*. Success-

sively, it moves to a horizontal position in the external re-entrant angle of the anterior loop (A6 – 6th angle, or BRA3), which turns longer (“*monticola*” type). Finally, it turns into a weak strip, which tends to merge with the rounded extremity of the enamel edge around the external part of the anterior loop (t6, or BSA4).

Figure 12 shows various morphotypes with different position of the *Mimomys*-fold:

Type 1: on the anterior wall of t4 (BSA3) near the tip of the salient angle (as in *Mimomys*);

Type 2: on the anterior wall of t4 (BSA3), close to the vertex of the re-entrant angle A6 (BRA3);

Type 3: on the anterior wall of A6 (BRA3), close to the vertex;

Type 4: on the anterior wall of A6 (BRA3), far from the vertex of the re-entrant angle. This disposition appears mostly when BRA3 and LRA4 create a narrow neck in the anterior loop. It is the so called “*monticola*” shape, which often occurs in *Arvicola sapidus*, and causes a dissymmetric shape of the anterior loop.

Type 5: on the posterior wall of t6 (BSA4), tends to merge into the antero-external protruding part of the anterior loop. A small re-entering enamel fold still exists in front of the *Mimomys*-fold. It is delimited outwards in its anterior part by a beak-shaped enamel strip.

Type 6: Anterior loop without any *Mimomys*-fold (typical morphology of recent *Arvicola terrestris*).

The occurrence of the different morphotypes of m1 the 3 groups A, B and C of the northern sector is reported in table 7, and shown graphically for the sufficient rich groups A and B in fig. 13. The morphotypes are ordered from the oldest, most primitive ones (i.e., types 1 and 2) with typical *Mimomys* fold, to the most recent ones (i.e., types 5 and 6), represented in modern *Arvicola* and generally lacking a *Mimomys*-fold. The diagram (fig. 13) shows that

- the two curves are almost parallel;
- Br. 2, which is the most recent sample, contains no m1 of type 1;
- Br. 3, which is somewhat more ancient, includes over 11 % of morphotype 1, while type 2 is predominant (3 % more than type 1);

- the curves meet at the centre of the diagram and stay next to each other;
- when type 6 reaches 11 %, the curves finally separate.

Furthermore, the diagram shows the slightly younger age of group A (Br. 2) compared with that of the group B (Br. 3), thus confirming the results of the biometrical analysis. Unfortunately, the small amount of data from the oldest breccia (group C, Br. 4) prevents any reliable result. At least, we can recognise that *Mimomys*-folds are present in two of four cases, which indicates its greater age in comparison with the former groups A and B.

Results

Thanks to the biometry of the m1 and to the study of the presence and position of the *Mimomys*-fold, the bio-chronology of *Arvicola cantianus* permits to date Br. 2 and Br. 3. The average rates of increase of the enamel thickness in the m1 triangles (Group A: n = 52, SDQ mean = 130.6; Group B: n = 43, SDQ mean = 133.3) indicates that these are two Middle Pleistocene populations.

The SZQV index calculated by HEINRICH (1990) for *Arvicola cantianus* specimens from the Central European sites of Přezletice in the Czech Republic, Hundsheim in Austria and Mosbach 2 and Bilzingsleben II in Germany gave values quite close to those obtained from our specimens from Château. The oldest, early Middle Pleistocene species from Château, such as *Pliomys lenki*, *Pliomys episcopalpis*, *Allophaiomys pliocaenicus gregaloides*, *Talpa minor*, *Sorex runtonensis*, *Beremendia fissidens*, coexist with *Arvicola cantianus*. This proves that the faunas from Br. 2 and 3 of Château belong to the group of “older *Arvicola cantianus* faunas” (“Ältere *Arvicola cantianus*-Faunen” sensu KOENIGSWALD & HEINRICH 1999: 63, fig. 4).

Mosbach 2, which contains one of the most ancient *Arvicola cantianus*, presumably correlates with MIS 13, thus dates at the end of the Cromerian at around 500 kyr. Our analysis shows a great resemblance between the *Arvicola* samples from Mosbach 2, Château’s Breccia 3 and the slightly younger Breccia 2. Burgundy is not located in Central Europe. Nonetheless, because of similar altitudes and climatic conditions inferred from the fossil faunas of Mosbach 2 and Château’s Br. 3 and Br. 2 these localities might be comparable.

Because of its cold temperate climatic indications, Château’s Br. 4 might correlate with the early Middle Pleistocene isotopic stage 14 or cooler parts of 15, nearly at 600 kyr.

Conclusions

One of the most interesting results of our study of the Château site is that it reveals the palaeoenvironmental conditions under which big cats lived as well as how they behaved. At

Château big cats found ideal conditions: 385 m above sea level, upstream from a small brook valley, with little caves opening towards the south-east, at the bottom of small cliffs and in the proximity of three permanent springs, the area likely attracted the herbivores on the way towards the granite summits (Mont-Gremoi, 555 m), the Guye valley (Pontot Pass) and the Grosne valley (Les Granges Pass). It is worth mentioning that there were no streams or lakes of any importance in the area, although the living descendant of *Panthera gombaszoegensis*, i.e. *Panthera onca*, is often associated with water bodies. All the pollen records indicate the presence of open, grassy uplands and of sparse woodlands in those valleys. Therefore, the climate was rather temperate but colder than today and sometimes even quite cold: in fact, *P. gombaszoegensis* is associated with *Lepus timidus* in the SIPO, and *P. spelaea fossilis* with *Dicrostonyx torquatus*, *Citellus* sp., and *Ochotona* sp. in the Northern Section.

In spite of the good conditions of conservation of the specimens, as for instance the particularly abundant bear cub remains, no juvenile felid was found. Therefore, *Panthera gombaszoegensis* and *Panthera spelaea fossilis* probably did not use the cave as a reproduction place. Felids sometimes shelter under rocks or in the entrance of caves to cool off in summer. This does not justify such a high mortality of big cats. A karstic system that functioned as a trap may have increased the risks of death. The very large, complete skull of *Panthera spelaea fossilis* (CHA.1.98–C.3–246), with its two half mandibles still articulated, its mouth closed and all the teeth preserved, incisors included, indicates sudden death and rapid post-mortem transport and burial; the specimen was actually caught up by a mud flow, which also carried boulders in the western gallery. Other bones of this individual are also preserved near the skull. The mud flow could have removed carcasses that laid in the gallery as well as it could be directly responsible for the death of this lion. Such cataclysmic flows could be caused by thawing in spring or by summer storms.

Why did these big cats come into the cave? Caves with bears usually also yield some remains of *Panthera spelaea*. For instance, at Azé 1–3 (excavated by A. and J. ARGANT 1982–1985), the distal end of the tibia (AZE. J.15–50) of an adult bear shows the trace of a right P⁴ of *Panthera spelaea*, which corresponds exactly to that of the complete skull (AZE.K.13–29) excavated in the same cavity (A. ARGANT 1988). The lion of Azé moved 200 m on a chaotic ground, in total darkness, to bite the back leg of a bear (dead or alive?). Felids must imperatively feed in winter because they do not hibernate as bears do. With their excellent sense of smell they are able to locate carrion (or hibernating bears) at a long distance.

In Château, there are many remains of young or very young bear cubs (*U. deningeri*), among which many milk teeth. For instance, there are 28 D3 and 31 d3 (right teeth do not pair with left ones). These numbers are presumably lower than in reality. No trace of the teeth of the big felids was observed on their bones, but we cannot exclude ravaging of smaller and more fragile elements. The roots of the deciduous teeth are often broken, which prevents

us from observing if they were resorbed (cubs are about 8 months when the milk teeth fall out as the permanent ones erupt). Intact roots correspond to bear cubs, which died by starvation, disease or by predation. The scarcity of the sample prevents any statistical analysis; nonetheless, the evidence of root resorption is very rare.

The many lines of evidence indicate a dating of the Château Breccia to the Middle Pleistocene. The bear, a full-fledged *Ursus deningeri* is still far from the transitional latest Middle Pleistocene *Ursus deningeri* – *spelaeus* representatives. The teeth of *Panthera gombaszoegensis* are notably larger than those of the more ancient, Late Villafranchian *Panthera toscana* (fig. 9). Château documents the replacement of *Panthera gombaszoegensis* by the earliest *Panthera spelaea fossilis* cats, in Europe. In fact, both cats were found associated in Breccia 3 during the 2006 season of excavation as they had been recovered in other European mid Middle Pleistocene sites (Mosbach 2, Belle-Roche at Sprimont in Belgium, Vértesszőlös in Hungary).

Finally, the microfaunal assemblages, the biometry of the m1 but also the frequent presence of the *Mimomys*-fold on the m1 of *Arvicola cantianus* correlate Château Br. 2 and Br. 3 (being very close chronologically) with Mosbach 2. Our analyses indicate that Br. 4 existed long before Br. 3: the latter, in fact, accumulated against Br. 4 residual lateral coatings along the eastern wall. Breccia 4 is also dated to the Middle Pleistocene because of the presence of a less advanced *Ursus deningeri* (A. ARGANT & J. ARGANT 2002), but far from *Ursus etruscus*. Moreover, the Breccia 4 canid, whose analysis is under way, is *Canis mosbachensis*, a close relative of *Canis etruscus*. *Arvicola cantianus* is still fairly primitive, yet its presence rules out the Early Pleistocene, which is characterized by *Mimomys*. The only big cat that matches the large-sized *Panthera gombaszoegensis* disappeared from Western Europe at the end of the mid Middle Pleistocene.

Unfortunately, the microfauna from Château does not provide more detailed stratigraphic information, except that the *Arvicola cantianus* finds of Br. 3 and B. 2 are at a similar evolutionary level and therefore close in age to finds of such faunas like Mosbach 2, with the oldest known representatives of this species. Br. 4 can be placed in the Early Middle Pleistocene, somewhere between 0.5 and 1 Myr. The degree of evolution of *U. deningeri* rules out any less advanced representative of this period, while the presence of *Arvicola cantianus* indicates horizons not older than 780 kyr. The site records the period of sympatry of *Panthera gombaszoegensis* and *Panthera spelaea fossilis* at the beginning of the mid Middle Pleistocene, as indicated by the finds from Br. 3 and Mosbach 2.

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