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PALEOECOLOGICAL FIRST RESULTS FROM THE MIDDLE PLEISTOCENE SEQUENCE OF COUDOULOUS I (QUERCY, LOT, FRANCE).

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ABSTRACT: The Coudoulous I (Lot, France) sequence has yielded abundant fossil associations dated to the end of the Middle Pleistocene. The total sample consists of 102 taxa corresponding to 75 species of mammals (53 small and 22 large mammals), 11 species of amphibians and 16 species of reptiles distributed in five faunal units (FUs). After evaluating the sample quality with completeness indices (CI and CI_{bda}), we established rarefaction curves that were discussed at length together with Shannon-Wiener diversity (H'), Margalef species richness (D), and the Sørensen-Dice similarity index. In order to better understand structural changes in the mammal associations as well as the climate trends we built the body mass distribution with cenograms in the different FUs. Concurrently, we investigated the whole community using a more analytical approach with the "bioclimatic model" based on a climatic restriction index for each species to infer paleoclimatic proxies (i.e. temperatures, precipitation, aridity) and finally to assign each faunal unit to a dominant type of climate. Our results clearly indicate that the FUs could be systematically associated with a typical temperate climate with sub-Mediterranean temperate species for the largest part of the sequence, which is consistent with the dates obtained (U/Th, ESR/U-series, TT-OSL) and Marine Isotope Stage 7. Nevertheless, cold elements from a Boreal type climate component were also found in the sequence indicating possible climate oscillations in FUs. The upper part of the stratigraphy (FU_{II}) is probably related to MIS 6 while the lowest part of the sequence (FU_{VII}) could correspond to a cold phase of the MIS 7 or earlier (MIS 8?).

Keywords: Vertebrate community, diversity, cenograms, bioclimatic model, climate reconstruction, MIS 6-7.

1. INTRODUCTION

Less than a dozen sites in the French Mediterranean region are dated to the Middle Pleistocene, and perhaps only twenty in southern France (see fig. 2 *in* Brugal et al., 2020). Among them, the Coudoulous sites show one of the most well-constrained chronostratigraphical sequences, yielding very rich and diversified fossil vertebrate and invertebrate associations (Jaubert et al., 2005). The Quercy region, where Coudoulous is situated, exhibits numerous and varied archeological and/or paleontological sites covering the last 0.3 Myr within a wide range of environmental and climatic contexts (Jaubert et al., 2013; Jeannet et al., 2013; Brugal et al., 2013). This region is located at the periphery of the Mediterranean ecological area, subject to the Atlantic conditions of the Aquitaine basin and bordered by the low mountainous area of the Massif Central. We propose in this contribution to depict the succession of fossil associations throughout the complete sequence of Coudoulous I, attributed to the end of the Middle Pleistocene, with the aimof characterizing paleoecological and climatic dynamics.

2. THE COUDOULOUS SITES

The Coudoulous (Coud) sites are located in the Quercy area (44°28'40"N, 1°39'50"E), not far from the Paleolithic cave art site of Pech-Merle (Cabrerets), a region of small Jurassic limestone plateaus divided by more or less narrow valleys and rivers. These sites are in a high position (280m asl) at the junction of the river Lot and its tributary, the Célé (Fig. 1), and correspond to two distinct karstic cavities, namely Coud I and Coud II. First explored with a rescue excavation in 1978-1980 (Bonifay & Clottes, 1981; Jaubert, 1984), the sites were investigated between 1994 and 2003 by J. Jaubert (for Coud I) (Jaubert et al., 2005) and J.P. Brugal (for Coud

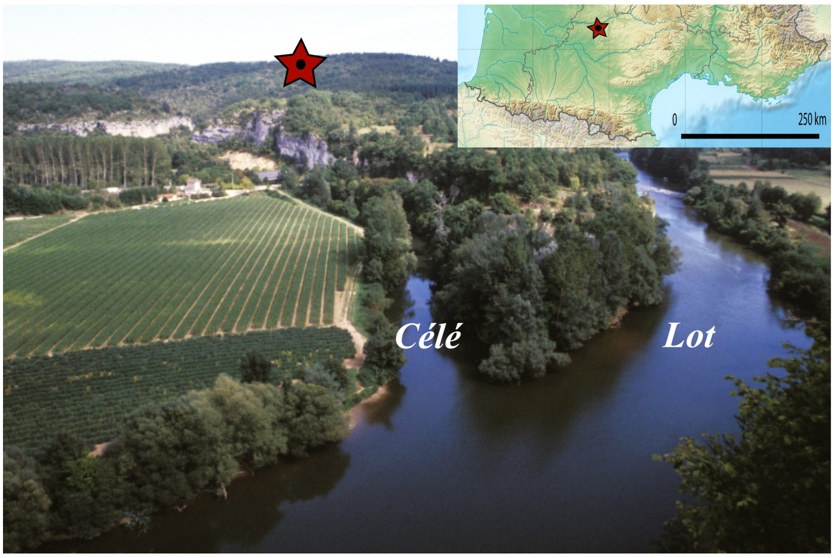

Fig. 1 - Location of Coudoulous sites. Photo J. Jaubert and map reworked from Electronic reference (18).

II) (Brugal et al., 1998; Costamagno, 1999; Brugal, 2006). Here we focus on the Coudoulous I site, with a brief overview and synthesis of the different studies made of this site and its chronological sequence.

2.1. The Coudoulous I sequence

The karstic cavity represents a pitfall (*aven*), with a main vertical entrance after the collapse of the roof above a large room (15-20 m diameter) presently completely filled with detrital (clays, sands, angular limestone rocks) or carbonate (speleothems) deposits, to a total of ca.10 m in thickness (Jaubert et al., 2005). The sequence is divided into 10 stratigraphic layers grouped into 4 main units/formations but only the lower and middle units yield lithic artefact and fossil remains (Fig. 2). Several levels (from 3 at the top to 8 at the bottom) and sub-levels (at least 31) are distinguished within these units. The sequence is bracketed by two speleothems dated by U/Th (Fig. 2): the upper one (between levels 2 and 3) is assigned to MIS 5 (126[+20/-46] and 139[+13/-11] kyr) and, the thick basal one (level 8g-e) at the limit of the method (229[+78/-42] and 202[+78/-39] kyr) is less accurate (Quinif *in* Jaubert et al., 2005; Couchoud, 2006). Two other stalagmitic floors are observed in the sequence (respectively levels 8a and 8c) and all are important periods of sedimentation with a pause in fossil

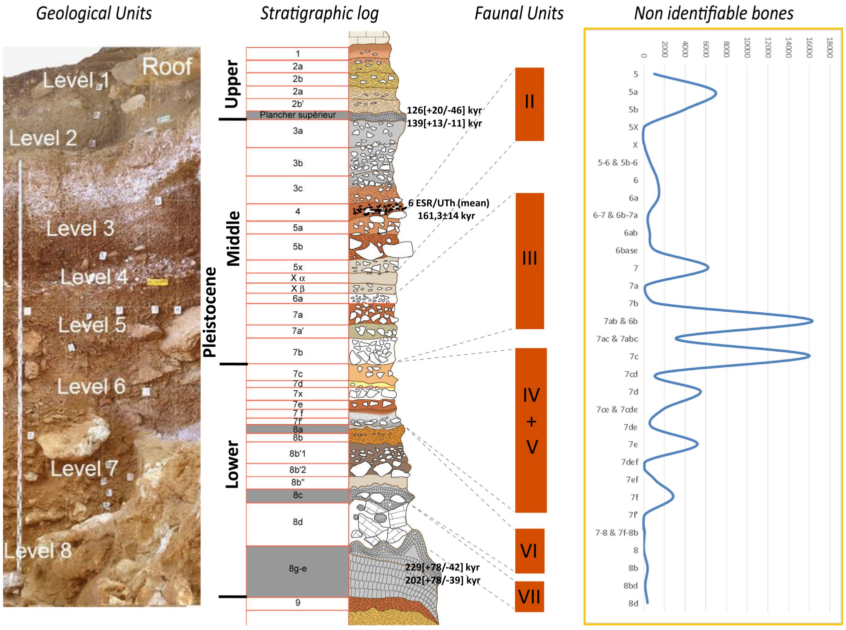

Fig. 2 - Coudoulous I, from left to right: Photo of the geological units (black arrow=2 m); Stratigraphic log with datations (grey bar=speleothems); Faunal Units; Distribution of non-identifiable bone remains (n total=80.452) throughout levels 5 to 8.

deposition, and should be considered as natural limits or cut-offs. The sequence has been dated by U/Th, ESR/U-series and TT-OSL on teeth and bone and sedimentary quartz samples (Hernandez et al., 2015) giving correlations from MIS 7 to MIS 6.

A very rich archaeological level (level 4) occurs at the top of the Coudoulous I sequence, and the levels (3 to 1) above it are sterile. Level 4 yielded abundant lithic artefacts (flint, quartzite), with Levallois core reduction, reported as Early Middle Paleolithic (EMP: stage 6.5) (Jaubert, 1995; Mourre, 1996), associated with a dominant species, the bison (98%), with very few horse and wolf remains. The bison record includes a minimum of 232 individuals, represented by all skeletal parts, but strongly affected by taphonomic processes, which have preferentially removed axial and cephalic bone elements. Teeth are good zooarchaeological and paleoclimatic indicators and demonstrate a catastrophic mortality pattern (juveniles and young adults dominant) and a late spring-early summer seasonality (Brugal, 1999a, 1999b; Brugal & Jaubert, 2006; Hélène Martin, pers. comm.). Oxygen isotope analysis of phosphate in tooth enamel (δ 18Op) shows contrasted seasons with a minimal annual temperature of 9±3 °C, which is about 4 °C lower than at present (Bernard et al., 2009).

EMP or Lower Paleolithic artefacts are scarce and dispersed in the middle to lower units (levels 5a to 8d), and made on quartz, quartzite, metamorphic and volcanic rocks. The techno-typological analysis places this industry within the variability of the Acheulean despite the absence of typically bifacial tools, but with some large cutting tools (LCTs) present (Jaubert, 1995; Jaubert & Servelle, 1996). An interdisciplinary study has demonstrated that the cavity was used for marginal scavenging by Lower Paleolithic hominid groups and as a kill-butchery site during the EMP (Brugal & Jaubert, 1991, 2021; Jaubert et al., 2005).

2.2. Material

This contribution is the first paleoecological analysis of the vertebrate associations from the middle and lower units (levels 5 to 8) of Coudoulous I (Fig. 2). This site represents one of the rare stratigraphic sequences of the Middle Pleistocene yielding a very rich and diversified fauna (NISP=9864). Moreover, a total of more than 80 000 splinters and bone shaft fragments (non-identifiable remains) were also collected during the excavations. Following geological and stratigraphical observations (Kervazo et al., 2021) and the distribution and abundance of faunal remains (Brugal, 2021), 6 faunal units (FU) were identified. According the stratigraphic log in Fig. 2, FUI includes only level 4. FU_{II} and FU_{III} correspond to the middle units, with levels 5 and 6a to 7b, respectively. The two lower speleothems are used as limits in the distinction of the subsequent FUs (FU_{IV+V} to FU_{VII}). FU_{IV+V} have been regrouped here and correspond to level 7c to 7f'. FU_{VI} includes levels 8a to 8c and FU_{VII} corresponds to level 8d.

For the paleoecological purposes of this study the taxonomic determinations were realized at species level in five faunal units (FU_{II}, FU_{III}, FU_{IV+V}, FU_{VI}, FU_{VII}) thanks to detailed studies (Jeannet, 2021, for microvertebrates; Argant, 2021, for felids and ursids; Mallye, 2021, for mustelids; Boudadi-Maligne, 2021, for canids) and our own studies (equids, bovids, caprids, cervids, rhinocerotids, proboscids). The remains with marking errors or that might have been shuffled between different stratigraphic levels were not included. We took into account 9864 Number of Identified Specimens (NISP) from 102 species including small mammals such as rodents (n=35), lagomorphs (n=4), and chiropters (n=14), but also large mammals including ungulates (n=10) and carnivores from small to medium size (n=12), and respectively 16 and 11 species of reptiles and amphibians (Tab. 1).

3. METHODS

Ever since the work of Leonard and Jones (1989) concerning the concept of "diversity", methodological and theoretical approaches have continued to be topical in paleobiological contexts for studying animal communities (rarefaction, richness, sample size, sample unit of measurement, appropriate diversity indices, etc.). Here we present the paleoecological analysis of the Coudoulous I mammals, applying and sometimes cross-referencing different methods (concept, mathematical formulations, limits) to see if they lead to similar results in the different faunal units of this site.

3.1. Completeness indices (CI) and (CI bda)

Natural taphonomic processes as well as carnivore activity and anthropogenic modifications are the key factors that explain biased samples from original deposits. Nevertheless, completeness indices (CI) and (CI_{bda}) (Maas & Krause, 1994; Maas et al., 1995) make it possible to evaluate the quality of the sample in the faunal units, starting with the presence (1) absence (0) of species (Palombo et al., 2008). Completeness indices are based on the assumption of the range-through of the species represented, meaning that a given species, which is present before and after, but not during an interval of time is supposed to have been in continuous existence from its first to last appearance in the stratigraphy. In this particular case, missing species probably result from taphonomic bias, poor sampling or bad preservation of the fossil remains. It should be added that between their first and last appearances, some missing species could have diffused to new landscapes or different habitats in response to strong climate changes.

The completeness indices CI and CI_{bda} are calculated as follows (see details in Maas et al., 1995; Palombo et al., 2008; Fernandez, 2009):

Eq. (1) $CI = [N_t / (N_t + N_{rt})]*100$

Eq. (2) $CI_{bda} = [N_{bda}/(N_{bda}+N_{rt})]*100$

N_t is the number of species known before, during and after the faunal unit considered, including taxa having their first or last occurrences in the interval.

N_{rt} is the number of species known before and after, but not during the faunal unit interval. To calculate N_{rt} in the last and the first faunal units respectively FU_{II} and FU_{VII}, we used species' chronological extension

Faunal units (FUs)			FU_{II}		FU_{III}		FU_{IV+V}		FU_{VI}		FU_{VII}			
			NISP	(S)	NISP	(S)	NISP	(S)	NISP	(S)	NISP	(S)	(In)	Bibliographic references for the calculation of (In)
Total Species Richness (S) = 102	Rodentia (n=35)	*Microtus arvalis*	1037	1	959	1	553	1	285	1	7	1	3,35	Smith et al. (2003)
		Microtus agrestis	168	1	284	1	74	1	81	1	2	1	3,47	Smith et al. (2003)
		Microtus gregalis	98	1	234	1	265	1	10	1	1	1	3,86	Smith et al. (2003)
		Microtus œconomus	20	1	39	1	43	1	2	1	1	1	3,91	Smith et al. (2003)
		Chionomys nivalis	1	1	0	0	3	1	1	1	0	0	3,99	Smith et al. (2003)
		Microtus brecciensis	88	1	77	1	68	1	28	1	3	1	3,96	Smith et al. (2003) cf. *Microtus cabrerae*
		Microtus multiplex	68	1	54	1	26	1	22	1	1	1	3,14	Smith et al. (2003)
		Microtus pyrenaicus	41	1	39	1	9	1	13	1	0	0	3,04	Giannoni et al. (1997) cf. *Microtus gerbei*
		Microtus subterraneus	42	1	51	1	30	1	19	1	0	0	3,00	Smith et al. (2003)
		Clethrionomys glareolus	7	1	82	1	28	1	28	1	2	1	2,99	Smith et al. (2003)
		Lemmus lemmus	0	0	1	1	1	1	0	0	0	0	3,81	Smith et al. (2003)
		Dicrostonyx torquatus	0	0	0	0	2	1	0	0	0	0	3,86	Smith et al. (2003)
		Pliomys episcopalis	1	1	0	0	0	0	0	0	0	0	4,08	Legendre (1989)
		Pliomys lenki	4	1	26	1	22	1	11	1	0	0	3,70	Legendre (1989) cf. *Pliomys* sp.
		Pliomys chalinei	0	0	0	0	1	1	0	0	0	0	3,89	Legendre (1989) cf. average between *Pliomys* sp. / *Pliomys episcopalis*
		Arvicola terrestris	0	0	4	1	2	1	0	0	0	0	4,87	Legendre (1989)
		Arvicola cantiana	7	1	33	1	15	1	3	1	0	0	5,18	Freudenthal & Martín-Suárez (2013)
		Allocricetus bursæ	32	1	146	1	165	1	4	1	0	0	3,47	Legendre (1989)
		Apodemus sylvaticus	163	1	599	1	293	1	27	1	14	1	3,67	Smith et al. (2003)
		Apodemus flavicollis	10	1	6	1	7	1	0	0	0	0	3,37	Legendre (1989)
		Apodemus uralensis	36	1	47	1	21	1	12	1	0	0	3,62	Freudenthal & Martín-Suárez (2013)
		Eliomys quercinus	44	1	202	1	400	1	27	1	10	1	4,38	Legendre (1989)
		Muscardinus avellanarius	0	0	8	1	4	1	2	1	1	1	3,31	Smith et al. (2003)
		Sciurus vulgaris	1	1	0	0	1	1	0	0	0	0	5,77	Legendre (1989)
		Erinaceus europæus	0	0	0	0	3	1	0	0	0	0	7,08	Legendre (1989)
		Erinaceus davidi	0	0	2	1	4	1	0	0	0	0	7,08	Legendre (1989) cf. *Erinaceus europæus*
		Talpa europæa	4	1	10	1	9	1	5	1	1	1	4,34	Smith et al. (2003)
		Talpa minor	0	0	1	1	1	1	0	0	0	0	4,09	Freudenthal & Martín-Suárez (2013) cf. *Talpa occidentalis*
		Sorex araneus	3	1	7	1	6	1	5	1	0	0	2,12	Legendre (1989)
		Sorex minutus	1	1	8	1	7	1	5	1	0	0	1,63	Legendre (1989)
		Sorex minutissimus	2	1	6	1	1	1	0	0	0	0	1,63	Legendre (1989) cf. *Sorex minutus*
		Crocidura russula	3	1	5	1	6	1	5	1	0	0	2,30	Smith et al. (2003)
		Crocidura leucodon	0	0	0	0	1	1	0	0	0	0	2,46	Legendre (1989)
		Crocidura suaveolens	0	0	0	0	1	1	0	0	0	0	2,01	Legendre (1989)
		Castor cf. *fiber*	0	0	0	0	1	1	0	0	0	0	9,85	Smith et al. (2003)
	Lagomorpha (n=4)	*Oryctolagus cuniculus*	3	1	8	1	6	1	0	0	0	0	7,48	Smith et al. (2003)
		Lepus europæus	4	1	3	1	8	1	2	1	0	0	8,23	Smith et al. (2003)
		Lepus timidus	2	1	2	1	5	1	0	0	1	1	8,02	Smith et al. (2003)
		Ochotona pusilla	3	1	9	1	7	1	1	1	0	0	6,00	Freudenthal & Martín-Suárez (2013)
	Chiroptera (n=14)	*Rhinolophus ferrumequinum*	0	0	0	0	1	1	0	0	0	0	3,05	Smith et al. (2003)
		Rhinolophus hipposideros	0	0	0	0	1	1	0	0	0	0	1,55	Smith et al. (2003)
		Myotis myotis	1	1	1	1	3	1	2	1	1	1	3,12	Smith et al. (2003)
		Myotis blythii	0	0	0	0	2	1	1	1	0	0	3,11	Smith et al. (2003)
		Myotis capaccinii	0	0	1	1	1	1	0	0	0	0	2,25	Electronic reference (1)
		Myotis mystacinus	0	0	0	0	2	1	0	0	0	0	1,79	Electronic reference (2)
		Myotis bechsteinii	0	0	0	0	1	1	0	0	0	0	2,30	Electronic reference (3)
		Vespertilio murinus	0	0	0	0	1	1	0	0	0	0	2,80	Electronic reference (4)
		Eptesicus serotinus	0	0	0	0	1	1	0	0	0	0	3,28	Electronic reference (5)
		Nyctalus noctula	0	0	0	0	1	1	0	0	0	0	3,43	Electronic reference (6)
		Pipistrellus pipistrellus	1	1	1	1	2	1	1	1	0	0	1,70	Electronic reference (7)
		Barbastella barbastellus	0	0	2	1	3	1	0	0	0	0	2,30	Electronic reference (8)
		Plecotus auritus	0	0	1	1	5	1	2	1	1	1	2,30	Electronic reference (9)
		Plecotus austriacus	0	0	0	0	3	1	1	1	0	0	2,30	Electronic reference (10)
	Amphibians (n=11)	*Salamandra salamandra*	0	0	2	1	4	1	0	0	0	0	2,95	Sydlowski R. (2000)
		Triturus helveticus	0	0	0	0	0	0	2	1	0	0	1,10	Haerty et al. (2007)
		Bombina variegata	0	0	1	1	0	0	0	0	0	0	2,08	Matz & Weber (1999)
		Pelobates fuscus	0	0	0	0	2	1	0	0	0	0	2,66	Šukalo et al. (2014)
		Bufo bufo	2	1	2	1	6	1	1	1	1	1	4,25	Electronic reference (11)
		Bufo calamita	4	1	7	1	6	1	0	0	0	0	4,32	Electronic reference (12)
		Bufo viridis	0	0	3	1	0	0	0	0	0	0	3,44	Castellano & Giacoma (1998)
		Hyla arborea	0	0	1	1	2	1	0	0	0	0	1,79	Jacob (2007)
		Rana dalmatina	1	1	6	1	4	1	0	0	0	0	3,14	Lodé (1993)
		Rana ridibunda	1	1	0	0	0	0	0	0	0	0	2,55	Electronic reference (13)
		Rana temporaria	1	1	3	1	3	1	0	0	0	0	3,22	Electronic reference (14)
	Reptiles (n=16)	*Lacerta agilis*	0	0	0	0	2	1	4	1	1	1	2,67	Olsson (1993)
		Lacerta viridis	1	1	4	1	8	1	2	1	0	0	3,56	Zucchi (2021) cf. *Lacerta bilineata*
		Podarcis cf muralis	0	0	2	1	3	1	3	1	0	0	2,20	Electronic reference (15)
		Chalcides chalcides	0	0	0	0	2	1	0	0	0	0	0,12	Bogaerts (2006) cf. *Chalcides lanzai*
		Anguis fragilis	2	1	7	1	8	1	6	1	1	1	3,81	Electronic reference (16)
		Coluber viridiflavus	0	0	0	0	3	1	2	1	0	0	5,68	Lelièvre (2010) cf. *Hierophis viridiflavus*
		Coronella austriaca	2	1	2	1	6	1	1	1	0	0	3,81	Graitson & Jacob (2007)
		Coronella girondica	0	0	1	1	6	1	1	1	0	0	3,28	Stoetzel et al. (2010)
		Elaphe longissima	0	0	0	0	2	1	1	1	0	0	6,58	Edgar & Bird (2006) cf. *Zamenis longissimus*
		Rhinechis scalaris	0	0	0	0	1	1	0	0	0	0	4,97	Tur-Torres (2017-2018)
		Malpolon monspessulanus	1	1	1	1	2	1	1	1	0	0	8,01	Mourgues (1908)
		Natrix maura	1	1	2	1	2	1	1	1	0	0	5,70	Electronic reference (17)
		Natrix natrix	0	0	1	1	6	1	2	1	1	1	5,52	Reading & Davies (1996)
		Vipera aspis	0	0	0	0	3	1	1	1	0	0	5,01	Naulleau (1983)
		Vipera berus	1	1	3	1	5	1	2	1	0	0	6,22	Olsson et al. (1997)
		Vipera ursinii	0	0	0	0	3	1	2	1	0	0	4,96	Baron (1997)
	Ungulata (n=10)	*Cervus elaphus*	15	1	88	1	114	1	7	1	2	1	11,99	Prado et al. (2004)
		Dama dama	0	0	4	1	14	1	0	0	0	0	11,32	Prado et al. (2004)
		Capreolus capreolus	3	1	17	1	15	1	1	1	1	1	10,31	Prado et al. (2004)
		Bison priscus cf. *mediator*	56	1	51	1	99	1	68	1	14	1	12,92	Prado et al. (2004) cf. *Bison priscus*
		Equus cf. *mosbachensis*	11	1	30	1	39	1	7	1	3	1	12,93	Prado et al. (2004) cf. *Equus stenonis*
		Hemitragus cedrensis	10	1	48	1	50	1	14	1	7	1	10,47	Smith et al. (2003) cf. *Hemitragus jemlahicus*
		Palaeoloxodon antiquus	1	1	3	1	23	1	0	0	1	1	15,30	Prado et al. (2004)
		Stephanorhinus cf. *hemitocechus*	0	0	7	1	8	1	0	0	0	0	14,90	Prado et al. (2004)
		Rupicapra sp.	1	1	1	1	0	0	0	0	2	1	10,58	Prado et al. (2004) cf. *Rupicapra rupicapra*
		Sus scrofa	0	0	1	1	1	1	2	1	0	0	11,35	Prado et al. (2004)
	Carnivora (n=12)	*Canis lupus lupus*	1	1	214	1	289	1	18	1	25	1	10,67	Prado et al. (2004)
		Cuon alpinus	0	0	5	1	16	1	0	0	0	0	9,80	Prado et al. (2004)
		**Vulpes vulpes*	2	1	9	1	9	1	1	1	0	0	8,90	Prado et al. (2004)
		**Felis silvestris*	1	1	1	1	2	1	0	0	0	0	8,46	Prado et al. (2004)
		Lynx lynx	0	0	7	1	2	1	6	1	3	1	10,04	Prado et al. (2004)
		Panthera spelaea	0	0	56	1	96	1	2	1	5	1	12,17	Prado et al. (2004)
		Ursus arctos	1	1	56	1	117	1	48	1	0	0	12,36	Prado et al. (2004)
		Panthera pardus	0	0	1	1	2	1	0	0	0	0	10,78	Prado et al. (2004)
		**Mustela erminea*	0	0	0	0	1	1	0	0	0	0	4,77	Prado et al. (2004) cf. *Mustela palerminea*
		**Mustela nivalis*	10	1	60	1	102	1	9	1	5	1	4,92	Prado et al. (2004)
		**Mustela putorius*	0	0	1	1	4	1	0	0	0	0	6,80	Legendre (1989)
		**Meles meles*	0	0	7	1	8	1	3	1	0	0	9,48	Prado et al. (2004)
∑ NISP=9864			2024		3673		3226		823		118			
Species Richness (S)			53		73		96		57		29			
CI (see calculation Eq. 1 in text)			52.88								28.43			
CI_{bda} (see calculation Eq. 2 in text)					81.25		91.66		92.85					
Predator prey ratio (PPR)			0.29		0.60		0.67		0.67		0.43			

*not included in the calculation of PPR (see text) from the works of Palombo et al. (2008) as well as Fernandez (2009). Because N_{bda} is the number of species only known before, during and after a faunal unit interval, CI_{bda} excludes the first and last FU whereas CI allows us to take into account all of the faunal units (Maas et al., 1995; Palombo et al., 2008).

3.2. Rarefaction, richness (S), Margalef (D), Shannon -Wiener (H') and the Sørensen-Dice index

In this study we used the rarefaction method that was popularized by Sanders (1968) for marine invertebrate communities and which has became a standard method. When applying Sanders's algorithm key assumptions (all met in Coudoulous I) are required such as a similar taxonomical rank between individuals collected from a similar place by using standardised procedures (Tipper, 1979). The brilliant idea of Sanders makes it possible to compare the number of species from different assemblages independently of the size of the initial samples and to see to what extent the sampling can induce a bias in the species richness (S) (i.e. area sampled, non-standardized sampling, catchability, etc.) (Raup, 1975; Tipper, 1979; Ricklefs & Miller, 1999; Gotelli & Colwell, 2001). Given the strong correlation between the number of identified specimens (NISP) and the minimum number of individuals (MNI) put forward by Grayson (1984) and later by Lyman (2008), rarefaction has been used in different paleobiological contexts, whether natural or anthropogenic (e.g. Adrain et al., 2000; Belmaker, 2006; Belmaker & Hovers, 2011; Popov & Marinska, 2007; Davis & Pyenson, 2007; Fernandez, 2009). In Coudoulous I we established rarefaction curves for each faunal unit from all the taxa present in the sequence and determined by the rank of the species (S=102). These curves were built with the "individual-based rarefaction" routine of the PAST program (Version 3.23) (Hammer et al., 2001; Hammer & Harper, 2006, see equations 6.10 to 6.13, p. 205).

In addition to rarefaction, we used species diversity which measures species richness combined with evenness, taking into account not only how many species are present but also how evenly distributed the numbers of each species are (see Eq. 3). It has been demonstrated that diversity varies consistently according to large-scale geographical areas with ▯ and ▯ diversity (Rohde, 1992) but also in more restricted areas or habitats at a more local scale (▯ diversity, Whittaker, 1972). Thus, there are many different indices and mathematical solutions to account for the diversity that can be defined in many ways (Hammer et Harper, 2006). These authors indicate that only the number of individuals should be used to estimate the diversity of a community. Consequently, in nearly all paleobiological contexts diversity indices will always be an approximation because MNI will never be the real number of individuals. As a result of the foregoing and the fact that we used NISP, which is strongly correlated to MNI, we focused on the Shannon-Wiener diversity index (Shannon & Weaver, 1964) as it takes into account proportions for the frequency and it is completely adapted for local area (▯ , the within assemblage diversity). We would like to stress that this index is sometimes erroneously labelled as the "Shannon-Weaver" index (see Spellerberg & Fedor, 2003 for this confusion). The formula implemented in Past (Version 3.23) that we used is as follows:

Eq. (3) $H' = -\sum pi \ln pi$

Where (ln) is the logarithm to the base of e (sometime in the literature base two is used), and where pi is the proportion of individuals that belong to species i.

Because species richness (S) increases with sample size, we used Margalef's species richness index (D) that attempts to compensate for this effect, as defined by the formula (Margalef, 1958):

Eq. (4) $D = (S-1) / \ln n$

To go further in the analysis, we calculated the Sørensen-Dice index, which is a statistical indicator that measures the similarity between two samples and was developed independently in botany by Dice (1945) and Sørensen (1948). The Sørensen-Dice formula is as follows:

Eq. (5) $\text{Sørensen-Dice} = 2J / (A+B)$

A and B represent the number of species in each sample and J the number of species common to the samples A and B. It is indexed from 0, a total absence of common elements, to 1 when two samples are identical (see Fig. 3). We do not go into further detail because the similarity coefficients are numerous and can only be explained by mathematical demonstrations (Shi, 1993). Comparing them to the most widely used such as Simpson's (1943) and Jaccard's coefficients (1912), here we have chosen to put more weight on matches than on mismatches due to the multiplication of J by a factor of two (see Eq. 5). Furthermore, the Sørensen-Dice coefficient normalizes with respect to the average rather than the total number of species in the two samples. Consequently, it is somewhat less sensitive to differences in sample size than Jaccard's index. The Sørensen-Dice index is also different from Simpson's coefficient, which is totally insensitive to the size of the larger sample and also does not take into account absences in the smaller sample of comparison (Hammer & Harper, 2006).

3.3. Body mass and cenograms

The cenograms was proposed by Valverde (1964, 1967) in order to compare body size of non carnivore modern terrestrial mammals from different communities. Given that the weight distributions of species are strongly dependent on their environmental conditions in predictable ways, Legendre (1986, 1989) and Gingerich (1989) extended the method into the fossil record to infer different paleoenvironmental characteristics as climatic

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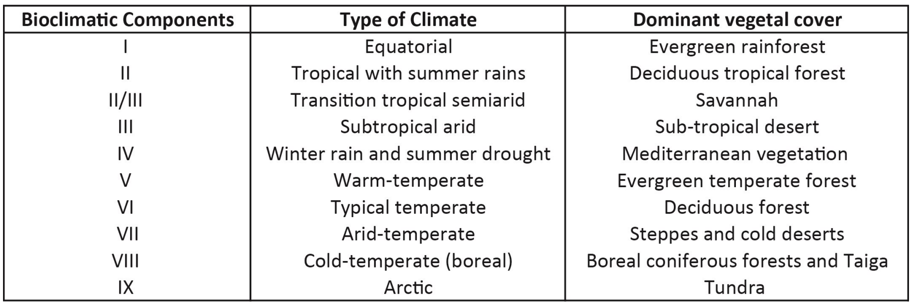
Tab. 1 - Faunal units FU_{II} to FU_{VII} with species richness (S), number of identified specimens (NISP). For each species, log (ln) is given according to their body mass (see bibliographic references including Electronic references). Completeness indices (*CI* and *CI_{bda})* are calculated from Eq. 1 & Eq. 2 in text. For predator prey ratio (PPR=n predator /n prey) see details in text.



Bioclimatic Components	Type of Climate	Dominant vegetal cover
I	Equatorial	Evergreen rainforest
II	Tropical with summer rains	Deciduous tropical forest
II/III	Transition tropical semiarid	Savannah
III	Subtropical arid	Sub-tropical desert
IV	Winter rain and summer drought	Mediterranean vegetation
V	Warm-temperate	Evergreen temperate forest
VI	Typical temperate	Deciduous forest
VII	Arid-temperate	Steppes and cold deserts
VIII	Cold-temperate (boreal)	Boreal coniferous forests and Taiga
IX	Arctic	Tundra

Tab. 2 - Bioclimatic components (BC) according to their type of climate and vegetation cover (from Hernàndez-Fernàndez, 2001a, table 2.1).

changes, namely, humidity or aridity, and types of landscapes, mainly open or closed. Although the initial work of Legendre was controversial on quantitative aspects (see Rodríguez, 1999) other quaternary European paleoenvironmental studies have used the cenogram method (Montuire, 1994, 1999; Rodríguez et al., 1996; Montuire & Desclaux, 1997; Montuire & Marcolini, 2001; Valensi & Psathi, 2004; Hernández Fernández et al., 2006; Palombo & Giovinazzo, 2006; Fernandez, 2009). The initial graphic representation established by Legendre (1986) reports the body mass (ln on the y-axis) according to the rank of the species (on the x-axis from the heaviest to the lightest). Schematically, the plots of points are represented by segments with different slopes (sometimes built by linear regression) and separated by breaks/gaps in the slope (see climatic trends in Fig. 4). Legendre's model (1986, 1989) and Gingerich (1989) who quantified the slopes, gaps and breakpoints, took into account small-sized (500 g<), medium-sized (500 g> 250 kg<) and large-sized mammals (> 250 kg) with two breakpoints around 8 kg and 250 kg. There is a gap (500 g - 8 kg) with greater (steeper) slope for medium-sized species in an open environment (e.g. woodlands and savannas) whereas closed environments have a continuous distribution. In a typical humid environment the breakpoint around 250 kg marks the low regression slope for medium-sized species, with no break for closed landscapes and a gap around 500 g for a more open environment. Gingerich (1989) hypothesized that the relative scarcity of mammals of about 500 g in this type of environment is probably related to the range of size, the density, and the diversity of insects and leaves, both of which are greatest in forests.

3.4. Predator Prey Ratio (PPR)

The PPR is simply the ratio between the number of predators and prey (PPR=n species of predators / n species of prey). For many Pleistocene sites, significant changes in PPR are difficult to interpret. Raia et al. (2007) found evidence for PPR inconstancy through time such as had been pointed out in previous studies (i.e. Van Valkenburgh & Janis, 1993). Here we assume an actualist approach whereby carnivores weighing up 21.5 kg feed mostly on prey that is 45% or less of their own mass (Carbone et al., 1999). Because carnivores above this limit feed mostly on prey that are greater than 45% of their own mass, we excluded from our calculation the mustelids of the sequence as well as *Meles meles*, *Vulpes vulpes* and *Felis silvestris*.

3.5. Bioclimatic analysis

A reconstruction of the climate and the plant environment has been inferred for each Coudoulous I faunal unit from the so-called "bioclimatic model" developed by Hernández-Fernández (2001a, 2001b) and Hernández-Fernández & Peláez-Campomanes (2003, 2005). It has been very recently used on archaeological sites from the Middle Pleistocene with human remains (Lopez-Garcia et al., 2021), and adapted for insectivore and rodent communities from the Last Glacial Maximum to the Holocene (Royer et al., 2020). In the initial work of Hernández-Fernández (2001a, 2001b), 50 associations of present-day mammals were compiled in different latitudes and biotopes corresponding to 10 major bioclimatic components (BC) associated with different types of climates (Tab. 2). A typology adapted from previous works (Walter, 1970; Rivas-Martínez, 1994) made it possible to systematically identify different environmental variables for each BC (e.g. type of vegetation, average annual temperatures, rain rate, thermal amplitude…).

Thus, each mammalian species is associated with a CRIi (Climatic Restriction Index) value ranging from 0 to 1 which characterizes its climate dependence such that:

Eq. (6) $\mathrm{CRIi} = 1/n$

With n the number of BCs where the species are represented and i the BC where the species appear. For the distribution of species by climatic types we used the work of Hernández-Fernández et al. (2007) and Jeannet (2010, 2021) for microfauna. For large mammals, and in rare cases their nearest living ecological analog species, we used the studies of Bhatnagar & Lovari (2008), Palombo (2015) and Lovari et al. (2016a, 2016b). For example, in Table 3, according to the data from Hernández-Fernández, (2001a, appendix 2), the CRIi value is equal to 1 for *Ochotona pusilla*, in BC VII, which means that all elements of this species are exclusively associated with this Arid-temperate climate. On the other hand, the CRIi of 0.33 for *Microtus oeconomus*, which is associated with bioclimatic components VI, VIII and IX, indicates that this species is more eurioic than the previous one. It is therefore possible to calculate for several mammalian species a probability of association (BC) for each of the 10 bioclimatic components according to the following formula:

FU $_{II}$ **mammalian association**	***Bioclimatic component***									
	I	*II*	*II/III*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*IX*
	Equatorial	Tropical with summer rains	Transition tropical semiarid	Subtropical arid	Winter rain and summer drou	Warm-temperate	Typical temperate	Arid-temperate	Cold-temperate (boreal)	Arctic
Microtus arvalis	-	-	-	-	-	-	1,00	-	-	-
Microtus agrestis	-	-	-	-	-	-	0,50	-	0,50	-
Microtus gregalis	-	-	-	-	-	-	0,50	-	0,50	-
Microtus œconomus	-	-	-	-	-	-	0,33	-	0,33	0,33
Chionomys nivalis	-	-	-	-	-	-	0,33	-	0,33	0,33
Microtus brecciensis	-	-	-	-	-	0,33	0,33	0,33	-	-
Microtus multiplex	-	-	-	-	0,20	0,20	0,20	0,20	0,20	-
Microtus pyrenaicus	-	-	-	-	0,20	0,20	0,20	0,20	0,20	-
Microtus subterraneus	-	-	-	-	-	-	1,00	-	-	-
Clethrionomys glareolus	-	-	-	-	-	-	0,50	-	0,50	-
Pliomys episcopalis	-	-	-	0,20	0,20	-	0,20	0,20	0,20	-
Pliomys lenki	-	-	-	0,20	0,20	-	0,20	0,20	0,20	-
Arvicola cantiana	-	-	-	-	0,20	0,20	0,20	0,20	0,20	-
Allocricetus bursæ	-	-	-	-	0,20	0,20	0,20	0,20	0,20	-
Apodemus sylvaticus	-	-	-	-	0,50	-	0,50	-	-	-
Apodemus flavicollis	-	-	-	-	-	-	1,00	-	-	-
Apodemus uralensis	-	-	-	-	-	-	0,33	0,33	0,33	-
Eliomys quercinus	-	-	-	-	0,50	-	0,50	-	-	-
Sciurus vulgaris	-	-	-	-	0,33	-	0,33	-	0,33	-
Talpa europæa	-	-	-	-	-	-	1,00	-	-	-
Sorex araneus	-	-	-	-	-	-	0,50	-	0,50	-
Sorex minutus	-	-	-	-	0,20	-	0,20	0,20	0,20	0,20
Sorex minutissimus	-	-	-	-	-	-	-	-	1,00	-
Crocidura russula	-	-	-	-	0,50	-	0,50	-	-	-
Oryctolagus cuniculus	-	-	-	-	1,00	-	-	-	-	-
Lepus europæus	-	-	-	-	-	-	1,00	-	-	-
Lepus timidus	-	-	-	-	-	-	-	-	0,50	0,50
Ochotona pusilla	-	-	-	-	-	-	-	1,00	-	-
Myotis myotis	-	-	-	-	0,50	-	0,50	-	-	-
Pipistrellus pipistrellus	-	-	-	-	0,33	-	0,33	0,33	-	-
Cervus elaphus	-	-	-	-	0,33	-	0,33	0,33	-	-
Capreolus capreolus	-	-	-	-	0,50	-	0,50	-	-	-
Bison priscus cf. *mediator*	-	-	-	-	-	0,25	0,25	0,25	0,25	-
Equus cf. *mosbachensis*	-	-	-	-	-	0,25	0,25	0,25	0,25	-
Hemitragus cedrensis	-	-	-	-	0,20	0,20	0,20	0,20	0,20	-
Palaeoloxodon antiquus	-	-	-	-	-	0,33	0,33	0,33	-	-
Rupicapra sp.	-	-	-	-	0,20	0,20	0,20	0,20	0,20	-
Canis lupus lunellensis	-	0,11	0,11	0,11	0,11	0,11	0,11	0,11	0,11	0,11
Vulpes vulpes	-	-	-	0,14	0,14	0,14	0,14	0,14	0,14	0,14
Felis silvestris	-	0,14	0,14	0,14	0,14	0,14	0,14	0,14	-	-
Ursus arctos	-	-	-	-	0,25	-	0,25	0,25	0,25	-
Mustela nivalis	-	-	-	-	0,20	-	0,20	0,20	0,20	0,20
∑CRIi (Climatic Restriction Index)	0,00	0,25	0,25	0,80	7,15	2,76	15,31	5,81	7,84	1,82
BCi=(∑CRIi)*100/S	0,00	0,60	0,60	1,90	17,01	6,57	36,45	13,83	18,66	4,33
S=42 (n species)										

Tab. 3 - Distribution of the mammalian species identified in FU_{II} according to their Climatic Restriction Index (CRIi, see detailed Eq. 6 in text) and Bioclimatic Component (BCi, see detailed Eq. 7 in text) in accordance with Hernàndez-Fernàndez (2001a) for the CRIi.

Eq. (7) BCi = (∑ CRIi)*100/S

(S) being the number of species present in the faunal association (or species richness).

Note also that the BCi value is equivalent to the cumulative rates of Andrews (1990) or to the % THI of Fernández-Jalvo et al. (1998). To end with our example, in Table 4, the highest probability BCi of the UF_{II} mammalian association corresponds to BC VI (Arid-temperate climate) with 36.45%, followed by BC VIII with a probability of 18.66%, and so on.

For each FU, we reported mammalian associations and their most likely BC (Tab. 4). To go deeper into the climate reconstructions, in this table we calculated some paleoclimatic proxies from the BCi values (Eq. 7) using the multiple linear regression coefficients from Hernández-Fernández (2001a, table 4.1 to 4.3). These indices and the parameters of their equations (b=intercept, a1 to a9=regression coefficients) are presented in the table 5 with the following components:

- Mean Annual Temperature (°C) (MAT).
- Mean Annual Thermal Amplitude (°C) (MATA). This expresses the difference (°C) between the mean temperature of the warmest month and that of the

		Associated probabilities for Bioclimatic Component (BC)			**Paleoclimatic proxies**						
FUs	**S**	***Probability 1***	***Probability 2***	***Probability 3***	**MAT (C°)**	**MATA (C°)**	**APTI**	**CTI**	**MAP (mm)**	**MTCM (°C)**	**AI**
FU$_{II}$	42	*36.45* **(BC VI)**	*18.66* **(BC VIII)**	*17.01* **(BC IV)**	6.88	22.73	997.52	44.04	1008.05	-5.64	59.69
FU$_{III}$	56	*36.38* **(BC VI)**	*20.03* **(BC IV)**	*15.39* **(BC VIII)**	8.49	20.87	1113.67	86.81	1042.09	-2.28	56.34
FU$_{IV+V}$	73	*35.03* **(BC VI)**	*20.77* **(BC IV)**	*14.52* **(BC VII)**	8.38	20.70	1110.44	80.02	972.20	-2.18	52.89
FU$_{VI}$	41	*38.64* **(BC VI)**	*16.29* **(BC VII)**	*15.89* **(BC IV)**	7.65	21.65	1010.51	59.16	1085.35	-4.24	61.46
FU$_{VII}$	25	*46.12* **(BC VI)**	*16.80* **(BC VIII)**	*14.80* **(BC IV)**	7.29	20.16	908.21	35.14	1236.79	-3.18	71.50

Tab. 4 - Coudoulous I faunal units and their probabilities (P1 to P3) of association with a Bioclimatic Component (see Table 2 for BC description). (S), species richness (excluding reptiles and amphibians). Paleoclimatic proxies with Mean Average T° (MAT), Mean Annual Thermal Amplitude (MATA), Annual Positive Temperatures Index (APTI), Compensated Thermal Index (CTI), Mean Annual Precipitations (MAP), Mean Temperatures of the Coldest Month (MTCM), Aridity Index (AI) (see text for details). Calculation for some paleoclimatic proxies from multiple linear regression coefficients provided in table 5.

coldest month of the year. According Rivas-Martínez (1994), it is an index of continentality simple.

- Annual Positive Temperatures Index (APTI). This provides a measure of the intensity of the summer heat.
- Compensated Thermal Index (CTI). In extratropical zones, the CTI is designed to equilibrate the cold “excess” that occurs during winter in the continental climates (average temperature of the coldest month of the year minimum), or the excessively mild winter in the marked oceanic territories, so that these index values can be significantly compared (Rivas-Martínez et al., 2011).
- Mean Annual Precipitation (mm) (MAP)
- Mean Temperatures of the Coldest Month (°C) (MTCM)
- Aridity Index (AI). We calculated this index from De Martonne (1926) which is still used with good results (Pellicone et al., 2019). It is simply the ratio between the mean annual precipitation (mm) (MAP) and the mean annual temperature (°C) (MAT) weighted by 10 such that: (AI) = MAP / MAT + 10. This index should be read carefully because the higher the AI, the lower the aridity.

4. RESULTS AND DISCUSSION

4.1. Sample quality

In Coudoulous I, *CI* indicates a low-quality sample for FU$_{II}$ (52.88) and FU$_{VII}$ (28.43) whereas CI$_{bda}$ corresponds to a very slightly modified sample in FU$_{III}$, FU$_{IV+V}$ and FU$_{VI}$ respectively with 81.25, 91.66 and 92.85 (Tab. 1). An index value higher than 70 usually reflects very little disturbance in a faunal unit interval (Maas et al., 1995; Palombo et al., 2008). Biases are often related to lower values in shorter chronological intervals, which is clearly the case in FU$_{VII}$ with only one archaeological level (8d). The *CI* of this faunal unit (28.43) reflects the lowest quality sample in the whole sequence. On the other hand, the overlying FU$_{VI}$ shows a very high CI$_{bda}$ index (92.85). FU$_{IV+V}$ (CI$_{bda}$=91.66) and FU$_{III}$ (CI$_{bda}$=81.25) also both indicate very good quality samples mainly associated to the subdivisions of level 7, probably contemporary with MIS 7, which is supported by biomarkers (mammal species and/or evolutive stage) and absolute dates (e.g. Jaubert et al., 2005, 2013; Boudadi-Maligne, 2010; Hernandez et al., 2015). Finally, in the most recent FU$_{II}$ *CI*=52.88 indicates a poor-quality sample. This faunal unit, beneath level 4, is related to the first part of MIS 6 (Jaubert et al., 2005; Hernandez et al., 2015), a glacial period known for involving dramatic drops in temperature (Mokeddem & McManus, 2016). The relatively low species richness of this faunal unit might coincide with this climate cooling.

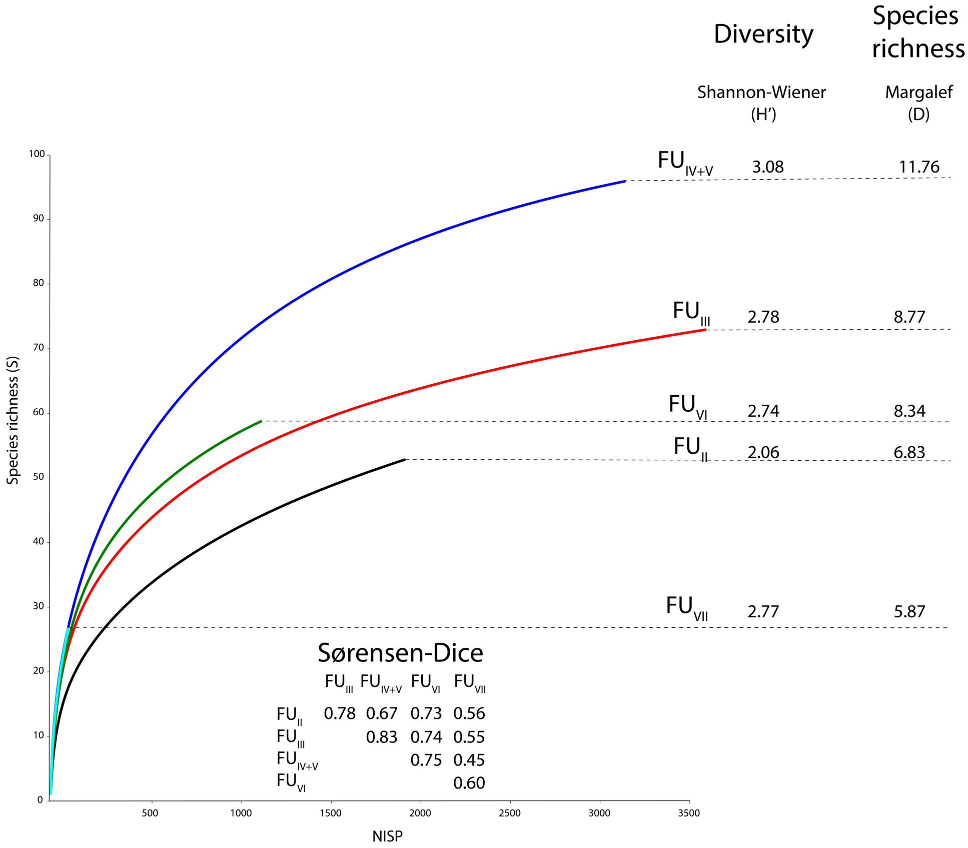
4.2. Diversity (*s.l.*)

In Coudoulous I, rarefaction curves illustrate the expected number of species whatever the initial sample size in each faunal unit (Fig. 3). The number of rarefied species in FU$_{IV+V}$ is higher than in the lower FU$_{III}$, FU$_{VI}$, FU$_{II}$ and FU$_{VII}$, respectively. In the same way the decreasing values of the Margalef index (D) are totally in line with the rarefaction curves. Although the calculations are quite different, both rarefaction and the Margalef index (D) reach the same result. The latter also compensates for the sample size effect by dividing the number of species in a sample by the natural log of the number of individuals (see Eq. 4). Furthermore, the curve from FU$_{VII}$ does not reach the asymptotic plateau, indicating a significant bias in this sample (lowest *CI*), also shown by the weakness of the NISP and the species richness (NISP=118 and S=29) which correspond to the single archaeological level 8d.

Interestingly enough, the species-rich communities may have a greater number of trophic levels than species-poor communities (Briand, 1983). It is in light of this evidence that Yachi & Loreau (1999) formulated the “insurance hypothesis” stating that high species rich-

	b	**a1**	**a2**	**a3**	**a4**	**a5**	**a6**	**a7**	**a8**	**a9**
Mean Annual Temperature °C (MAT)	24.296	0.159	-0.103	0.032	-0.038	-0.145	-0.11	-0.217	-0.372	-0.451
Mean Annual Thermal Amplitude °C (MATA)	-2.02	0.072	0.171	0.058	0.203	0.218	0.008	0.456	0.659	0.165
Annual Positive Temperatures Index (APTI)	2920.208	18.761	-12.514	2.845	-5.054	-14.783	-21.896	-21.833	-26.537	-35.444
Compensated Thermal Index (CTI)	655.351	4.591	-4.331	0.434	-1.831	-4.425	-5.719	-6.958	-9.651	-15.534
Mean Annual Precipitation (mm) (MAP) (mm)	3240.41	19.416	37.247	37.435	38.442	7.015	5.144	32.647	35.223	30.164
Mean Temperatures of the Coldest Month (°C) (MTCM)	26.441	0.153	-0.243	0.081	-0.044	-0.371	-0.068	-0.586	-0.853	-0.578
Aridity Index (AI) = MAP/MAT+10										

Tab. 5 - Paleoclimatic proxies with equation parameters (b=intercept, a1 to a9 = regression coefficients) from Hernández-Fernández (2001a, table 4.1 to 4.3) (see details in text).



	FU_{III}	FU_{IV+V}	FU_{VI}	FU_{VII}
FU_{II}	0.78	0.67	0.73	0.56
FU_{III}		0.83	0.74	0.55
FU_{IV+V}			0.75	0.45
FU_{VI}				0.60

Fig. 3 - Rarefaction curves, Shannon-Wiener diversity (H'), Margalef species richness (D) and Sørensen-Dice similarity for each faunal unit (FU_{II} to FU_{VII}). NISP in Table 1 is used for calculation with Past 3.23, (Hammer et al., 2001). For rarefaction see details in text for "individual-based rarefaction" routine from PAST. For calculation of Shannon-Wiener (H') see Eq. 3, for Margalef species richness (D) see Eq. 4 and for Sørensen-Dice similarity see Eq. 5 and Table 1.

ness increases community stability with species that respond differently to environmental fluctuations (see also Ives et al., 2000). If we accept this hypothesis, the rarefaction curves associated with the highest Margalef indices could be good indicators of a stable community in Coudoulous I (respectively FU_{IV+V}, FU_{III}, FU_{VI}, FU_{II}, FU_{VII}).

In Figure 3, the Shannon-Wiener diversity index (H') values are almost correlated to the species richness (S) and Margalef's values (D). Nevertheless, in FU_{VII} the diversity is higher with H'=2.77 whereas the number of species is much less important (n=29) than in FU_{II} (n=53) which has the lowest diversity H'=2.06. It means that independently of both species richness and the lowest *CI* (discussed above), the Shannon-Wiener index is very sensitive to the individual distribution frequency among species in FU_{VII}.

In all faunal units the H' values are comprised between 2.06 and 3.08. It is difficult to compare these values with other sites, knowing that diversity is strongly dependant on multiple local factors (e.g. climate, taxonomical groups, ecosystem involved, etc.). Nevertheless, it is now widely accepted that high species diversity indicates a highly complex community with more species interactions (Whittaker, 1972). It is worth noting that in nature, whatever the taxonomic group studied, H' often ranges between 1.5 and 3.5 according to Gaines et al. (1999).

Another important consideration that should be emphasized is that H' as well as D are completely independent of the temporal gradient in the different FUs whereas the Sørensen-Dice index almost always shows a greater similarity between the closest FUs through time. In other words, the more distant the FUs are, the less species they have in common. This should not be considered as a statistical artefact but most likely as a gradual turnover of species through time, probably due to paleoenvironmental changes.

In southern Africa, Andrews & O'Brien (2000), combining 15 climatic variables with current mammal species (n=285), showed that woody plant species (n=1359) alone explained 75% of the variability in mammal species richness. Nevertheless, large mammals over 90 kg, scansorial, aquatic or fossorial mammals were not significantly correlated with woody plant species richness, unlike small-bodied arboreal frugivores and insectivores.

This led us to test which species were most affected by possible climate and plant cover changes in the different faunal units of Coudoulous I. Therefore, we

a) Species richness (S) for microfauna and macrofauna in FUs

Faunal Units (FUs)	Microfauna (S)	Macrofauna (S)	Total (S)
II	41	12	53
III	52	21	73
IV+V	75	21	96
VI	44	13	57
VII	18	11	29

b) Chi² Test between species richness (microfauna *vs* macrofauna) in FUs

Chi² (Observed value)	3.891
Chi² (Critical value)	9.488
DDL	4
p-value	0.421
alpha	0.05

c) Species richness (S) for herbivores and carnivores in FUs

Faunal Units (FUs)	Prey (S)	Carnivores (S)	Total (S)
II	7	5	12
III	10	11	21
IV+V	9	13	22
VI	6	7	13
VII	7	4	11

d) Chi² Test between species richness (herbivores *vs* carnivores) in FUs

Chi² (Observed value)	1.705
Chi² (Critical value)	9.488
DDL	4
p-value	0.790
alpha	0.05

Tab. 6 - a) Species richness (S) for microfauna and macrofauna in faunal units of Coudoulous I ; b) Chi² Test between species richness (microfauna vs macrofauna) in FUs; c) Species richness (S) for herbivores and carnivores in FUs; d) Chi² Test between species richness (herbivores vs carnivores) in FUs.

tested the proportions of species throughout the sequence according to their size (microfauna vs macrofauna) and their diet (herbivores vs carnivores). The results of the Chi² test indicate no significant differences between microfauna and macrofauna between the FUs. The same is true for the proportion of herbivores and carnivores (Table 6-a to 6-d).

One possible explanation for these results is that regardless of the different types of climate in a small sampling area (e.g. within habitat), there is no significant difference between the richness of small and large size species within animal communities (Brown & Nicoletto, 1991). At larger spatial scales, the pattern is quite different with small species generally far exceeding the number of large species (Bakker & Kelt, 2000).

4.3. Cenograms

The cenograms in Figure 4 illustrate the difference in total species richness (S) between the FUs as a function of their body mass (y-axis): the higher the rank, the lightest the species (x-axis). In all FUs, a very clear break in slopes for species around 100 g can be observed, which has already started at about the limit of 500 g. Medium-sized species (500 g to 250 kg without carnivores) are less represented in all faunal units except in FU_{IV+V}. Finally, the large-sized species (more than 250 kg) are scarce. According Legendre's method, there are two general trends in Coudoulous I: either an open-arid landscape simultaneous with a decrease in small mammals as well as the total species richness (e.g. FU_{VII}), or closed-arid landscapes with an increase in small mammals and highest species richness with possibly more humid climate trend (e.g. FU_{IV+V}). These two opposing profiles should help inform our reading of the evolution of landscapes. For example, FU_{VII} fits well with the results of Gingerich (1989) for open-arid environments. In these typical landscapes, the slope of the cenograms is more pronounced with a larger gap around the limit of 500 g, a scarcity of medium-sized species (500 g to 250 kg) and finally the lowest total species richness. Nevertheless, there are inconsistencies between the general shape of these two opposing cenograms and some paleoclimatic proxies such as MAP and AI (counterintuitively the higher the AI, the lower the aridity) (Tab. 4). Indeed, the latter show a more arid climatic trend in FU_{IV+V} (AI=52.89 MAP = 972.20 mm) than in FU_{VII} (AI=71.50 and MAP = 1236.79 mm). Furthermore, the range of values provided by De Martonne (1926) and reworked by Pellicone et al. (2019) for AI < 50 indicates a humid climate. The results obtained with the paleoclimatic proxies and the cenograms do not invalidate each other. However, they seem to indicate a wetter climate trend than the theoretical pattern of the model suggests, with more pronounced humidity in FU_{VII} than in FU_{IV+V}. Furthermore, we have to keep in mind that AI is a continuous complex gradient difficult to interpret, which spans several biomes (e.g. from tropical rainforest to tropical deciduous woodland, to savanna, to desert) (Hernández-Fernández et al., 2006).

Gómez Cano et al. (2006) have shown that ceno-

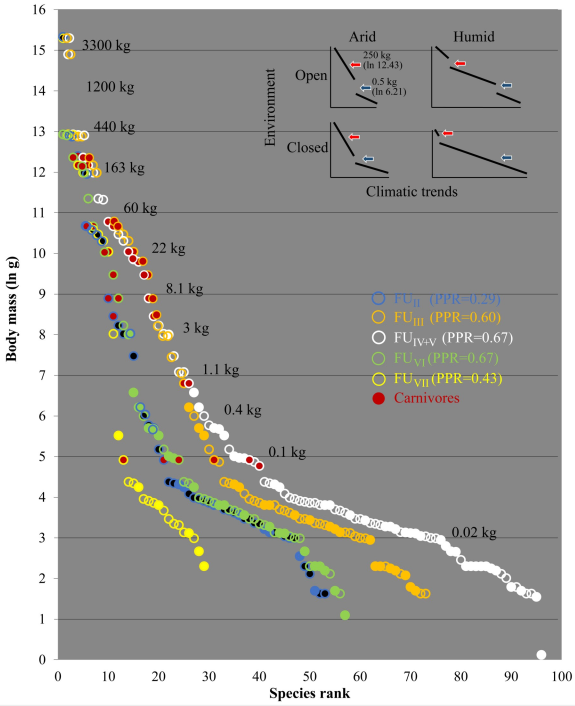


Fig. 4 - Cenograms according to the body mass (in g) for each faunal unit (FU_{II} to FU_{VII}) in Coudoulous I. For predator prey ratio (PPR=n predator /n prey) see details in text. Filled circles for bats, reptiles and amphibians. Red filled circles for carnivores.

a) Body mass (kg) bootstrap confidence interval calculated for prey, predators and small mammals

Faunal units	II	III	IV+V	VI	VII
Prey animals	[59.04 - 578.38]	[73.86 - 598.39]	[75.28 - 512.98]	[67.37 - 683.51]	[59.27 - 686.25]
Predators	[43.00 - 233.51]	[27.18 - 127.00]	[26.56 - 131.09]	[31.44 - 212.35]	[22.99 - 193.10]
Small mammals	[0.036 - 0.098]	[0.033 - 0.078]	[0.030 - 0.066]	[0.031 - 0.070]	[0.032 - 0.091]

b) Kruskal-Wallis test of body mass for prey, predators and small mammals in all faunal units

prey :

Faunal units	II	III	IV+V	VI	VII
II	-	0.995	0.874	0.980	1
III	0.995	-	0.997	0.985	0.995
IV+V	0.874	0.997	-	0.829	0.874
VI	0.980	0.985	0.829	-	0.980
VII	1	0.995	0.874	0.98	-

predators :

Faunal units	II	III	IV+V	VI	VII
II	-	0.864	0.864	0.897	0.521
III	0.864	-	1	0.980	0.994
IV+V	0.864	1	-	0.980	0.994
VI	0.897	0.980	0.980	-	0.900
VII	0.521	0.994	0.994	0.900	-

small mammals :

Faunal units	II	III	IV+V	VI	VII
II	-	0.995	0.912	0.412	0.999
III	0.995	-	0.971	0.631	0.887
IV+V	0.912	0.971	-	1.000	0.068
VI	0.412	0.631	1.000	-	***< 0.0001***
VII	0.999	0.887	0.068	***< 0.0001***	-

Tab. 7 - a) Body mass (kg) bootstrap confidence interval distribution (95%) for prey (ungulates), predators (excluding all mustelids, *Meles meles*, *Vulpes vulpes*, *Felis silvestris*) and small mammals in FUs (calculation with the bootstrap percentiles interval function in R, Version 3.2.1). b) Kruskal-Wallis test for comparing the body mass (kg) of prey (ungulates), predators (excluding all mustelids, *Meles meles*, *Vulpes vulpes*, *Felis silvestris*) and small mammals in all FUs (Calculation from XLSTAT Version 2017.1.1, using multiple pairwise comparisons option for the recalculation of the ranks for each two-by-two combination of the samples, **< 0.0001** is highly significant).

gram analyses work well with a random species loss of up to 60-70% in a fossil assemblage. The unequal sizes of the samples and the possible biases in representation of the species led us to calculate a confidence interval for the body mass of predators (excluding mustelids, *M. meles*, *V. v*ulpes and *F. silvestris*), their prey (ungulates) and small mammals in each FU (Table 7-a). The bootstrap percentiles interval function in R (Version 3.2.1) makes it possible to provide the mean and the 2.5% and 97.5% percentile of the bootstrap distribution as confidence intervals (see details in Efron & Tibshirani, 1993). The predators, their prey and the small mammals showed relatively similar body mass confidence intervals in the different FUs (Table 7-a). To investigate this further we undertook a Kruskal-Wallis analysis, using the multiple pairwise comparisons option (XLSTAT Version 2017.1.1) to detect possible significant changes in their body mass (Table 7-b). Our results are mainly consistent with previous observations about a stable community over time. Only the body mass values for small mammals from FU$_{VII}$ and FU$_{VI}$ are statistically different and should be explored to distinguish between evolutionary aspects (ecomorphology) or more likely sampling bias (s.l.) as discussed for FU$_{VII}$.

4.4. Predation

In present-day ecosytems, terrestrial carnivores are much rarer than most of their prey due to the competition with predators of similar sizes to avoid the overconsumption of the resources on which they depend (Peters & Wassenberg, 1983; Hatton et al., 2015). As expected, the PPR calculated in all of the FUs are always lower than 1 (Fig. 4). They are relatively stable in the sequence at around 0.6, with the exception of FU$_{VII}$ (PPR = 0.43) and FU$_{II}$ (PPR = 0.29). On a longer time scale, PPR ratio seems to be very dependent on the renewal of the Plio-Pleistocene fauna with the arrival or the extinction of certain predators (Raia et al., 2007; Croitor & Brugal, 2010). For now, it is difficult to infer predators-prey interactions including man in Coudoulous I except that the greater PPR, the more important the CI in each FU.

4.5. Bioclimatic analysis

In Coudoulous I, the mean annual temperatures (MAT) in the different faunal units are relatively similar to those established on the exclusive basis of the microfauna by Jeannet (2021) (Tab. 4). Nevertheless, MAT alone does not permit the distinction between bioclimatic components, except in the case of very different ecozones (Rivas-Martínez et al., 1999). This is not the case with the mean annual thermal amplitude (MATA or IC in Rivas-Martinez et al., 1999) that constitutes an excellent indicator of continentality. The MATA values recorded in FU$_{VII}$, FU$_{IV+V}$ and FU$_{III}$ correspond to a semi-continental climate (IC 18 to 21 in Rivas-Martínez et al., 1999, p. 8) and to a subcontinental climate in FU$_{VI}$ and FU$_{II}$ (IC 21 to 28 according to the same authors). In both cases the winters were harsh and the summers hot and rainy. The annual positive temperature index (APTI) calculated at Coudoulous I indicates that the APTI values are all between around 900 and 1100 and correspond to the interval of the sub-Mediterranean temperate bioclimatic variant (800 <APTI> 1400, see Rivas-Martínez et al., 1999). Likewise, the compensated thermal indices of Coudoulous I all have values less than 180 which is consistent with this type of climate (see CTI in Rivas-Martínez et al., 2004). Finally, the most significant result concerns the faunal units, whose highest probabilities are all associated with the bioclimatic component VI, which corresponds to a typically temperate climate (Tab. 4). The vegetation cover of BC VI consists of a nemoral zone dominated by deciduous forests with broadleaf trees (e.g. maple, oak, hickory, beech, chestnut) with several different kinds of plants like mountain laurel, azaleas and mosses. The bryophyte stratum and terrestrial lichens as well as various dwarf plants are very developed, while there are few herbaceous plants. Nevertheless, a poorly diversified or even mono-specific cover cannot be excluded in this type of environment (Hernández-Fernández, 2001a). This kind of vegetation cover is potentially located between the Boreal zone (coniferous forests) and the Mediterranean zone (sclerophyllous forests).

In Table 4, FU_{II} and FU_{VII}, are both associated with BC VIII as second probabilities, with cold Boreal type climate elements. These results completely match the paleoenvironmental conclusions of Jeannet (2021) which indicate much more severe climatic conditions in FU_{II} and FU_{VII}. FU_{II} could be related to MIS 6 with climatic degradation as mentioned previously, and FU_{VII} to a cooler phase of MIS 7 or older (MIS 8?). The existence of large ice caps at the North Pole during ice ages, in conjunction with the Scandinavian anticyclone weather systems, likely generated continental surface winds coming from the East, and caused a decrease in precipitation in Eurasia (COHMAP, 1988). For example, in France during these colder periods, there is a decrease in precipitation (down to a minimum of 600 mm during the Würm), unlike the hottest interglacial periods where precipitation can reach 1200 mm during the Eemian (Hernández-Fernández, 2001a). While it is very likely (Probability 1 and 2) that FU_{II}, FU_{VII} show climatic affinities with continental elements, the combination of aridity (AI) and rainfall pattern (MAP) related with thermal indices (MAT, MTCM, APTI) seems to exclude a typical boreal climate in these faunal units, even in its mildest variant (*sensu* Rivas-Martínez et al., 1999, 2004) (see Tab. 4).

However, in all of the FUs of Coudoulous I the association of some species present today but in environments with very different environmental characteristics raises the question of their ecological plasticity and their contemporaneity. As an example, in FU_{IV+V} we note the presence of *Dicrostonyx torquatus* and *Sorex minutissimus* which live today in very severe climatic conditions, unlike *Oryctolagus cuniculus* or to a lesser extent *Microtus arvalis*, which are generally associated with a much warmer climate. During the Late Pleistocene, the association of *D. torquatus* and *M. arvalis* is not uncommon in southwestern France and reflects the ecological adaption of some taxa that evolved in very specific biomes (Royer et al., 2016). This kind of association is part of the "disharmonious communities" of animals and plants adapted to a climate that has no modern counterpart (Huggett, 2004). It could be explained by refuge areas forming a mosaic of settlements of small populations dispersed in several habitats, known as the "patch -corridor-matrix model", allowing their survival and cohabitation (Huggett & Cheesman, 2002). Regardless of the potential for climate adaptation of species and the plasticity of their ecological niche in the Pleistocene, there is no doubt that the temporal resolution of the faunal units of Coudoulous I corresponds to a grouping of different temporal phases.

5. CONCLUSION

In current ecological studies, species richness has been demonstrated to vary consistently with large-scale geographical factors such as latitude and altitude. The sequence of Coudoulous I allows us to follow an entire animal community and its relationship to paleoenvironmental changes through time at a local scale.

First of all, it appears that FU_{II} and FU_{VII} are different from the other faunal units, with their low-quality samples, unbalanced and low PPR and the lowest species richness values. FU_{II}, which is the most recent faunal unit, may belong to the first part of MIS 6, with new paleoenvironmental conditions. FU_{VII} is the oldest faunal association and is very well individualized as it is composed of a single level (8d) that may correspond to a cooler phase of MIS 7 or older (MIS 8?). FU_{VII} has the lowest species richness and above all an extremely disturbed assemblage as identified by the completeness index (*CI*). Nevertheless, FU_{VII} has a greater diversity than FU_{II} which provides a much larger number of species. This shows that the Shannon-Wiener (H') performs well and is very sensitive to the individual distribution frequency even if there is a great imbalance of the species richness between samples.

In the rest of the sequence, the faunal associations FU_{III} to FU_{VI} show both greater diversity and species richness, thus indicating a greater number of trophic levels and a more stable community. The concept of the "insurance hypothesis", which states that the greater the species richness, the more important are the interactions between species, is supported by the rarefaction curves that are systematically in line with Margalef (D). The number of species, according their body mass and their diet, displays no significant differences between all the FUs, as is usual in a small sampling area (e.g. within habitat). In addition, the Sørensen-Dice index almost always indicates a greater similarity of common species between the closest FUs throughout the sequence. This reveals a gradual turnover of species through time, probably due to paleoenvironmental changes.

The predators, their prey and the small mammals showed no significant changes in their body mass through time, with the exception of the small mammals between FU_{VII} and FU_{VI}, which probably indicates the same pattern of evolution throughout the sequence. We showed clearly for FU_{II} and FU_{VII} that the lower the completeness index, the lower the PPR. This ratio is practically the same in the rest of the sequence but difficult to interpret from the small number of predators and their prey.

Theoretically, body mass distribution analysis in the cenograms should be efficient with a random species loss of up to 60-70% in a fossil assemblage. We established the cenograms in the different FUs and found them consistent with the pattern of a temperate climate corresponding to the bioclimatic component VI. According their theoretical slopes, breakpoints and species richness we identified two general trends corresponding to an open-arid and more closed-arid climate. Nevertheless, a cross reading with paleoclimatic proxies revealed a wetter climate trend than the theoretical pattern arid-open landscape suggests.

In addition to the cenograms, the bioclimatic model based on transfer functions from current mammalian associations clearly showed that the paleoecological requirements of Coudoulous I species were very similar between the different faunal units. While there were significant climatic changes, they remained limited enough to prevent any complete turnover of species. One of the key outputs is the maximum probabilities calculated for each FU that are all systematically associated with the bioclimatic component VI. This component corresponds to a typical temperate climate with a predominance of deciduous forests that could potentially be located between the Boreal zone (coniferous forests) and the Mediterranean zone (sclerophyllous forests). At Coudoulous I, sub-Mediterranean temperate elements dominate throughout the sequence but faunal units such as FU_{VII}, FU_{IV+V} and FU_{III} show affinities with semi-continental or sub-continental conditions (i.e. FU_{VI}, FU_{II}). Finally, the paleoclimatic proxies from the bioclimatic model make it possible to exclude a boreal-type climate.

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