



Human Palaeontology and Prehistory

Fauna, environment and human presence during MIS5 in the North of Spain: The new site of Valdavara 3



Faune, environnement et présence humaine pendant la période MIS5 dans le Nord de l'Espagne : le nouveau site de Valdavara 3

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ABSTRACT

Valdavara 3 is a new early late Pleistocene paleontological and archeological cave site in northwestern Iberia. Over 1400 fossils have been collected, representing about 40 species. The fauna is of interglacial aspect and is in accordance with the OSL dates from the fossiliferous layer, which indicate an age of 103–113 ka. The great taxonomical diversity indicates a varied landscape. A small collection of lithic artifacts was found associated with the fossils, demonstrating presence of humans and suggesting short non-residential visits to the cave. The fossiliferous site was predominantly formed by natural processes. Many fossil localities have short or biased faunal lists, but the fossil fauna recovered from Valdavara 3 is remarkably diverse and may reflect the fauna which once lived there.

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R É S U M É

Valdavara 3 est un nouveau site paléontologique et archéologique du début du Pléistocène supérieur dans le Nord-Ouest de l'Ibérie. Plus de 1400 fossiles ont été collectés, représentant environ 40 espèces. La faune est d'aspect interglaciaire et correspond aux dates OSL de

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la couche fossilifère, qui indiquent un âge de 103–113 ka. La grande diversité taxonomique caractérise un paysage varié. Une petite collection d'artéfacts lithiques a été trouvée, associée aux fossiles témoignant de la présence humaine, et suggère de courtes visites non résidentielles à la grotte. Le site fossilifère a été principalement formé par des processus naturels. Nombre de localités fossilifères ont des listes fauniques courtes ou biaisées, mais la faune fossile retrouvée à Valdavara 3 est remarquablement diverse, et peut refléter celle qui y vivait autrefois.

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1. Introduction

The study of the faunal associations of the past is a fundamental aspect to know the evolution of the landscape and environmental conditions throughout the Pleistocene. In addition to providing information on the evolution and distribution of the different species of macro- and microvertebrates, it allows us to characterize the conditions to which human populations had to adapt. However, one of the main problems that research in this field has to face is that of the biases affecting the paleontological record. The first bias is related to the uneven distribution of the fossil record in space and time: some periods and regions are well-known and others virtually unknown. The second major bias has to do with the site formation processes affecting the degree of representativeness of the record. In many archeological sites, the bias is produced by human activities, such as hunting. Other predators introduce similar biases in the representation of species. On the other hand, bear remains are overrepresented in many cave sites because these animals usually hibernate inside the cavities. Due to the frequency of these biases, the assemblages that have a wide diversity of species have a special significance.

The Iberian Peninsula is a good example of the biases affecting the paleontological record. The northwestern corner of Iberia is one of the European regions that have less information on the evolution of species and faunal communities throughout the Pleistocene. The few paleontological assemblages known to date are of relatively recent age and show a low diversity of species. This lack of information is even more pronounced in some time intervals, especially the last interglacial stage (MIS 5). This is a period generally little known in the whole of the Iberian Peninsula. Most of the Peninsular deposits from MIS 5 are in the Mediterranean basin and the Central Plateau and only a few have a wide diversity of species, such as Cueva del Camino (Arsuaga et al., 2012), Bolomor Cave (Blasco and Fernández Peris, 2012) or Cova del Rinoceront (Daura et al., 2015). This scarcity of biotic records from MIS 5 limits our ability to study the paleoenvironmental conditions during this interglacial stage and evaluate the effects of this climatic optimum in the different regions and ecosystems. Therefore, it would be important to have MIS5 faunal assemblages from northern Iberia and especially from the northwestern region, which now is characterized by particular conditions due to the Atlantic influence. The new site of Valdavara 3 helps fill this gap and opens the possibility

of comparing the faunas of the different regions of Iberia during MIS5.

Work in a stone quarry in northwestern Spain led to the discovery of abundant fossils of large mammals with a good preservation. The fossils come from a layer in a cave filling, from which lithic tools and fossils were recovered. The fossils are remarkably diverse indicating the presence of about forty different species of large and small mammals, birds, reptiles, amphibians, and fish. Such diverse fossil fauna is not only rare in this part of Spain. Many fossil sites have shorter or biased faunal lists and do not reflect well the fauna which lived there. In the formation of many late Pleistocene sites human hunting played an important role, resulting in biased faunal association. It seems that in Valdavara 3, humans did not play an important role in the site formation. As a result, the very diverse faunal list reflects better the environment in which these humans lived.

It is the aim of this paper: (1) to describe the locality of Valdavara 3, the fauna and the stone tools, (2) to discuss the preliminary results on the taphonomy and site formation processes, (3) to interpret the environment and human activities.

2. The site, stratigraphy, and radiometric dates

Valdavara 3 is located in the village of Becerreá, 37 km southeast of Lugo (NW Spain; Fig. 1), in the foothills of the eastern mountain ranges of Galicia. Its geographical coordinates are 42°50'24" N, 7°08'02" W. It is situated at 672 m a.s.l., on a hilltop at the right margin of the Cruzul River, 180 m above the current riverbed. The Cruzul is one of the tributaries of the Navia, which flows into the Cantabrian Sea after a course of 83 km. From a geological point of view, the site is located within the Mondoñedo Mantle Domain, one of the units of the Iberian Massif. This zone is made up of Early Paleozoic formations, with a predominance of slates and sandy rocks, although the presence of calcareous formations stands out. Valdavara 3 is one of the cavities belonging to the karst system developed in the Lower Cambrian limestones (Vegadeo formation). The limestones of Vegadeo appear along a wide strip of NNW-SSE direction. In the Becerreá area, three members have been identified in this formation. The lower one is made up of an alternation of slates, limestones, and dolomites. The middle member shows a succession of dolomitized and bedded limestones. Finally, the upper member is composed of dark gray fine-grained limestones and yellowish slates. This limestone formation contains numerous caves, some of them showing

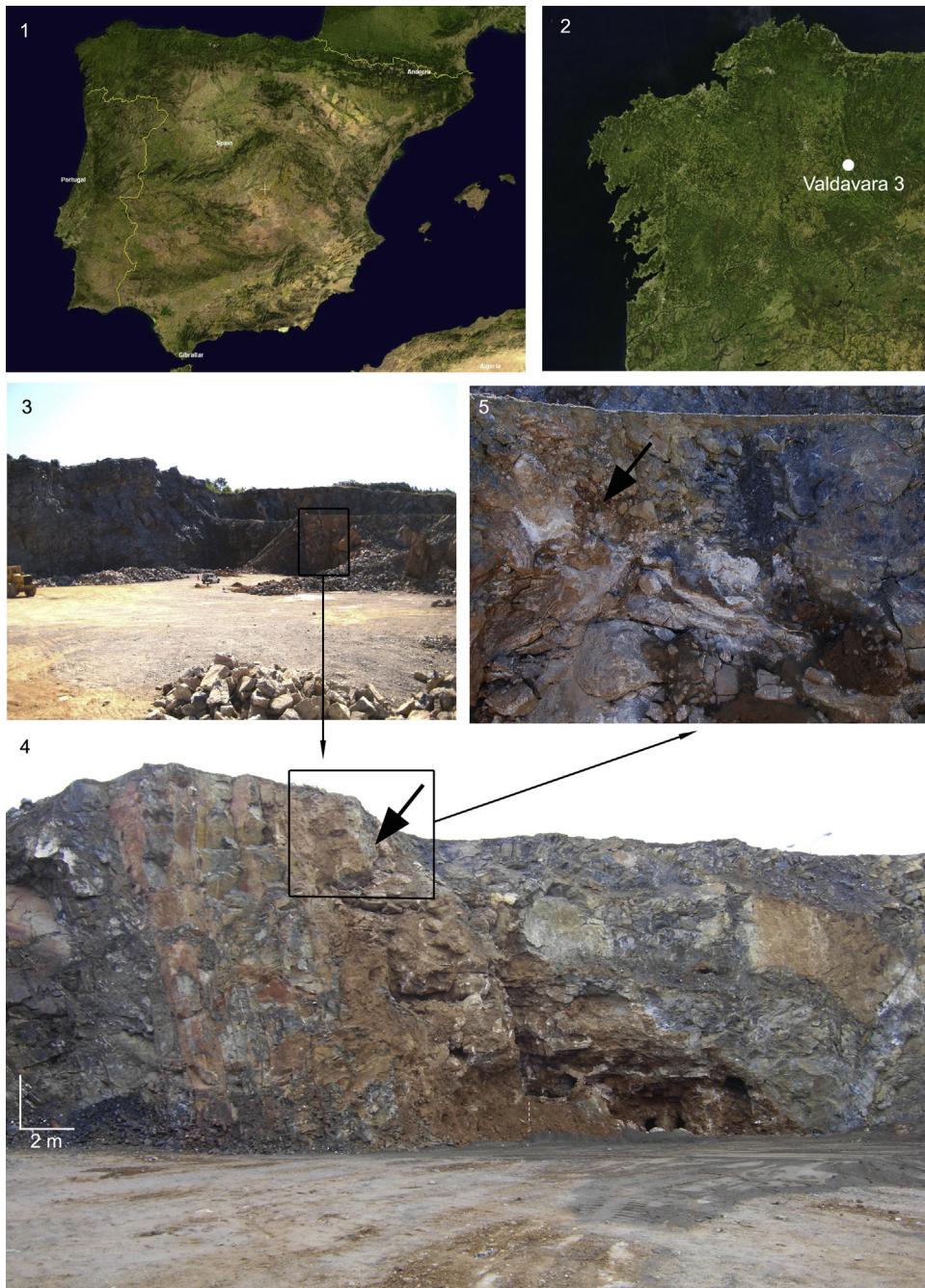


Fig. 1. Location and general view of the site. 1, 2. Maps showing the location of Valdavara 3 in the Northwestern corner of the Iberian Peninsula. 3. General view of the limestone quarry in which the site is located. On the right you can see the section in which the cavity containing the archeo-paleontological remains appeared. 4. Image of the section showing the karstic cavity open in the Cambrian limestones. The big black arrow indicates the location of the archeo-paleontological layer. 5. Close-up view of the upper part of the deposit. The big black arrow indicates the location of the archeo-paleontological layer.

Fig. 1. Emplacement et vue générale du site. 1, 2. Cartes montrant l'emplacement de Valdavara 3 dans le coin nord-ouest de la péninsule Ibérique. 3. Vue générale de la carrière de calcaire dans laquelle se trouve le site. Sur la droite, on peut voir la section où est apparue la cavité contenant les vestiges archéo-paléontologiques. 4. Image de la coupe montrant la cavité karstique ouverte dans les calcaires cambriens. La grosse flèche noire indique l'emplacement de la couche archéo-paléontologique. 5. Vue rapprochée de la partie supérieure du gisement. La grosse flèche noire indique l'emplacement de la couche archéo-paléontologique.

evidence of prehistoric occupations, like Valdavara Cave, an Upper Paleolithic site located 500 m from Valdavara 3 and probably pertaining to the same karstic system.

Valdavara 3 is located in a stone quarry and was discovered in 2009 during quarrying operations. A large part of the cave was destroyed because of blasting, which produced the collapse of most of the sedimentary deposit. A 14-m-thick section was exposed, showing a vertical shaft completely filled by sediments. A preliminary examination indicated that faunal elements were abundant in the sediments detached from the section. Therefore, archeological works started immediately after the discovery and were extended until 2011. The out-of-context remains from the collapsed sediments were recovered during the 2009 field season. The excavation of the in situ sedimentary remnant took place in 2010 and 2011. The excavation showed that most of the site had been destroyed, and only an area of less than 9 m², corresponding to the back of the cave, was preserved (Fig. 2). Three main units were recognized in the 14-m-thick stratigraphic sequence. At the bottom of the sequence, the oldest deposits were composed of sands and gravels. Above this unit, a huge stalagmitic formation extended over most of the sequence. These units were archeologically and paleontologically sterile. At the top of the section, a 0.7 m thick clayey layer (layer B),

enclosed between two stalagmitic crusts, was identified. This was the only clear archeo-paleontological unit recognized in the sequence and was excavated in the 2010–2011 field seasons. This layer was composed of a red-brown clayey matrix, along with abundant limestone blocks and stalagmite fragments. Millimeter-sized schist and quartz gravels were also identified. Neither the limestone and stalagmite fragments nor the gravels showed preferential orientations. Bone remains were homogeneously distributed throughout the layer and discrete horizons were not observed. Although a part of the assemblage was found out of context in the collapsed sediments, the excavation of the preserved deposit proved that lithics were stratigraphically associated with the faunal remains (Fig. 2/4). The faunal lists from the out-of-context assemblage and layer B are very similar, particularly those of macromammals. Moreover, some bone refits between the two assemblages have been identified. These data suggest that both assemblages correspond to the same faunal association.

Two sediment samples from the fossiliferous layer have been dated by OSL in the Laboratorio de Datación y Radioquímica of the Universidad Autónoma de Madrid. The results are coincident ($103,414 \pm 6956$ and $112,837 \pm 8903$ yr BP) and confidently situate the assemblage within MIS 5 (Table 1).

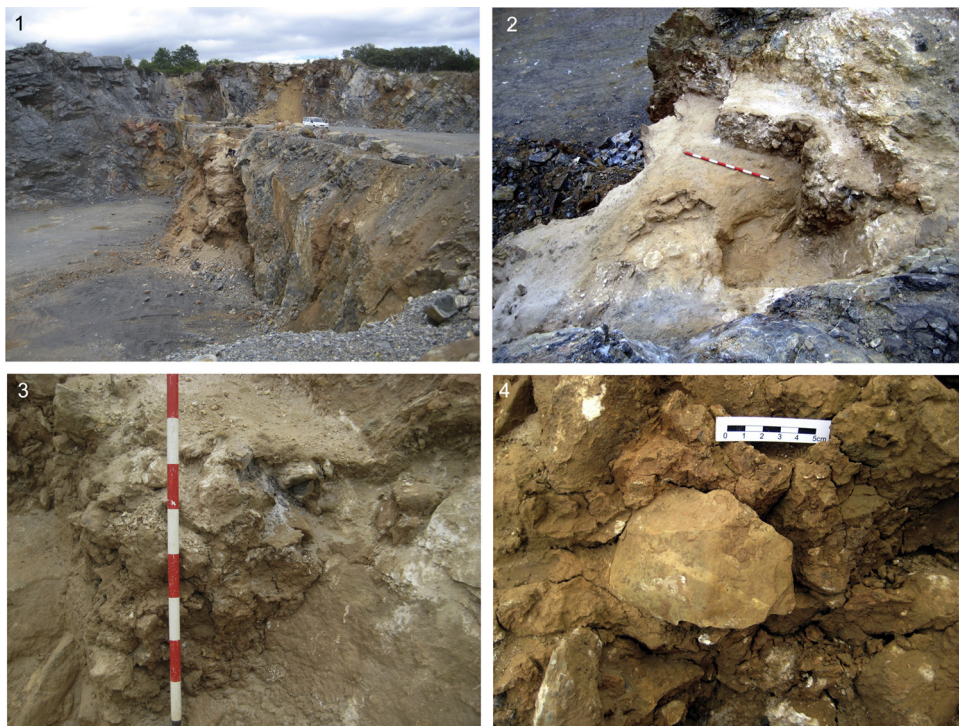


Fig. 2. Valdavara 3 excavation. 1. The site during the 2011 excavation season. 2. The excavated area at the end of the 2010 excavation season. Most of the preserved archeo-paleontological layer was already excavated, but a remnant can be seen at the upper right corner of the photograph. 3. Close-up view of a section of layer B. 4. Photograph showing a quartzite core in situ.

Fig. 2. Excavation de Valdavara 3. 1. Le site pendant la saison de fouilles de 2011. 2. La zone excavée à la fin de la saison des fouilles de 2010. La plus grande partie de la couche archéo-paléontologique conservée a déjà été excavée, mais on peut voir un témoin dans le coin supérieur droit de la photographie. 3. Vue rapprochée d'une section de la couche B. 4. Photographie montrant un nucléus de quartzite in situ.

Table 1

OSL ages for sediment samples from Valdavara 3.

Tableau 1

Âge OSL pour les échantillons de sédiment de Valdavara 3.

Sample code	U (ppm)	Th (ppm)	K ₂ O (%)	H ₂ O (%)	Equivalent dose	Annual dose (mGy/yr)	Age (years BP)
MAD-5948BIN	2.77	10.03	1.75	10.69	271.98 ± 17.09	2.63	103,414 ± 6956
MAD-6025rBIN	3.12	7.46	1.24	18.53	200.85 ± 16.77	1.78	112,837 ± 8903

3. Materials and methods

During the 2009–2011 field seasons, more than 1400 fossils of complete or fragmentary bones and teeth and 18 lithic artifacts were recovered. In 2009, only blasted sediments were studied in the field. The list of the identified specimens and the analytical data are presented in the [Supplementary data](#).

The dental nomenclature and the way of measuring of the Equidae, Rhinocerotidae and Artiodactyla follow Eisenmann et al. (1988), Van der Made (2010a), Van der Made (1996) and Van der Made and Tong (2008). The measurements of the carnivore remains follow largely the same method. The measurements are indicated by acronyms and numbers as explained in the [Supplementary data](#). Where comparisons are made with other material, the collections where that material was studied are indicated by acronyms (see [Supplementary data](#)).

Birds and lagomorphs have been considered as very small animals, following the classification by weight categories of Andrews (1995). Our taxa would correspond to the categories A/B (0.1–1 kg) and C (1–10 kg). The methodology is based on paleontological and taphonomic criteria for the anatomical and taxonomical identification and the analysis of bone structural and surface modifications. For the identification of some bird remains, we have used the collection from the Archeozoology Laboratory of the Universidad Autónoma de Madrid and the corvid identification keys of Tomek and Bochénski (2000). The Minimum Number of Individuals (MNI) was calculated. Surface modifications produced by biological agents have been treated at both macroscopic and microscopic level. For microscopic study, a stereomicroscope Olympus SZ was used. Carnivore damage has been classified into punctures and scores (Binford, 1981; Blumenshine and Selvaggio, 1988; Bunn, 1981; Stiner, 1994), and the location on the anatomical element indicated. Post-depositional modifications include the action of bacteria characteristic of humid environments that produce deposits of manganese on the bones.

The small-vertebrate remains consist of disarticulated bone fragments collected by water screening. All the sediment was water-screened using superimposed 5 and 0.5 mm mesh screens. The fossils were processed, sorted and classified at the IPHES (Tarragona, Spain). The microvertebrate assemblage includes 155 fragments that represent at least 18 species and a minimum of 88 individuals (Table 2). The fragments were identified following the general criteria of systematic paleontology (e.g., Bailon, 1991; Blain, 2005, 2009; Cleef-Rodgers and van den Hoek Ostende, 2001; Corbet, 1988; Pasquier, 1974; Reumer, 1984; Sevilla, 1988; Van der Meulen, 1973) and comparison

with our osteological collections. The specimens have been compared with Iberian forms. Given the age of the site, many identified species are still found in the Iberian Peninsula. Specific attribution of the small mammals is based on the best diagnostic elements: isolated teeth for hedgehogs; humerus for moles; mandibles for shrews; mandibles and isolated teeth for bats; first lower molars for the Arvicolinae subfamily; and isolated teeth for Murinae subfamily. The fossils were grouped using the MNI method, by means of which we determined the sample (i.e. from each level) by counting a diagnostic element, taking into account the side (sin./dext.) whenever possible. The taphonomic study of the small mammals is based on the descriptive and systematic method developed by Andrews (1990), paying special attention on the alterations caused by digestion with the aim of identifying the action of predators.

4. Results

4.1. Systematics

Fish – Actinopterygii indet.

The centrum of an amphicoelous vertebra (Fig. 3/1) demonstrates the presence of an actinopterygian fish, and suggests the nearby presence of a permanent water body.

Spiny toad – *Bufo* cf. *spinosus*

The Mediterranean common toad is represented by one humerus, two radioulnae and 2 phalanges. The humerus (Fig. 4/1) shows a straight and strong diaphysis with a humeral condyle lacking here but that may have been displaced radially. The other elements display the general morphology of the genus *Bufo* like the radioulnae with a wide collum antibrachii (Fig. 4/2) and the short and robust phalanges. Cautious attribution among bufonids to *B. spinosus* can be done based on the size and robustness of the remains: *B. spinosus* reaches generally a larger size than *B. bufo* and especially *B. calamita*. The spiny toad is currently restricted to Iberia and southern France, and inhabits all environments, but with a preference for stable, cooler and woody biotopes (Lizana, 2002; Masó and Pijoan, 2011).

Indeterminate lizard – Lacertidae indet.

A small and somewhat elongated procoelous trunk vertebra (centrum length: CL=2.1 mm) is attributed to a lacertid lizard. The interzygapophyseal constriction is very poorly marked. The neural spine is long, thin and low. Posteriorly, it ends as an interzygapophyseal point that does not project back beyond the postzygapophyses. In ventral view, the centrum is cylindrical with a haemal keel more or less wide and with indistinct lateral edges. The cotyle and condyle are slightly flattened dorsoventrally. Vertebrae are

Table 2

The classification of the taxa identified in Valdavara 3.

Tableau 2

Classification des taxons identifiés à Valdavara 3.

				MNI
Class				
Actinopterygii			sp indet.	1
Class Amphibia				
Linnaeus, 1758	Order Anura Fischer von Waldheim, 1813	Family Bufonidae Gray, 1825	Genus <i>Bufo</i> Laurenti, 1768	
			<i>Bufo</i> cf. <i>spinosus</i> (Daudin, 1803)	5
Class Squamata				
Oppel, 1811	Order Squamata Oppel, 1811			
	Suborder Sauria	Family Lacertidae Batsch, 1788		
		Lacertidae indet.		1
		Family Anguidae Gray, 1825	Genus <i>Anguis</i> Linnaeus, 1758	
			<i>Anguis fragilis</i> Linnaeus, 1758	1
	Suborder Serpentes Linnaeus, 1758	Family Colubridae Oppel, 1811	Genus <i>Coronella</i> Laurenti, 1768	
			<i>Coronella</i> cf. <i>austriaca</i> Laurenti, 1768	1
		Family Viperidae Oppel, 1811	Colubridae indet.	
			Genus <i>Vipera</i> Garsault, 1764	
			<i>Vipera</i> sp.	1
Class Aves				
	Order Falconiformes, Sharpe, 1874	Family Accipitridae, Vieillot, 1816	Genus <i>Haliaeetus</i>	
			<i>Haliaeetus albicilla</i> , Linnaeus, 1758	1
	Order Passeriformes, Linnaeus, 1758	Family Corvidae, Vigors, 1825	Genus <i>Pyrrhocorax</i>	
			<i>Pyrrhocorax graculus</i> , Linnaeus, 1766	1
			Corvidae indet.	1
Class Mammalia				
Linnaeus, 1758	Aves indet.			
	Mammalia indet.			1
	Order Lagomorpha Brandt, 1855	Family Leporidae Fischer de Waldheim, 1817	Genus <i>Oryctolagus</i> Lilljeborg, 1873	
			<i>Oryctolagus cuniculus</i> (Linnaeus, 1758)	1

Table 2 (Continued)

				MNI	
Order Rodentia Bowdich, 1821	Family Castoridae Gray, 1825	Genus <i>Castor</i> Linnaeus, 1758	<i>Castor fiber</i> Linnaeus, 1758	1	
			Family Arvicolidae Gray, 1821	Genus <i>Arvicola</i> Lacépède, 1779	<i>Arvicola sapidus</i> Miller, 1908
		Genus <i>Microtus</i> Schrank, 1798			<i>Microtus agrestis</i> (Linnaeus, 1761)
				<i>Microtus arvalis</i> (Pallas, 1779)	3
		Subgenus <i>Terricola</i> Fatio, 1867		<i>Microtus (Terricola)</i> sp.	13
	Family Muridae Illiger, 1811	Genus <i>Clethrionomys</i> Pallas, 1811		<i>Clethrionomys</i> <i>glareolus</i> (Schreber, 1780)	1
			Genus <i>Pliomys</i> Méhely, 1914	<i>Pliomys coronensis</i> Kormos, 1933	9
		Genus <i>Apodemus</i> Kaup, 1829		<i>Apodemus</i> sp.	1
			Family Erinaceidae Bonaparte, 1838	Genus <i>Erinaceus</i> Linnaeus, 1758	<i>Erinaceus</i> cf. <i>europaeus</i> Linnaeus, 1758
		Order Erinaceomorpha Gregory, 1910			Family: Soricidae Fischer von Waldheim, 1817
Family: Talpidae Fischer von Waldheim, 1817	Genus <i>Talpa</i> Linnaeus, 1758		<i>Talpa</i> sp.	2	
			Order Soricomorpha Gregory, 1910	Order Chiroptera Blumenbach, 1779	

Table 2 (Continued)

		MNI
Order Carnivora Bowdich, 1821	Suborder: Microchiroptera Dobson, 1875	
	Family: Rhinolophidae Gray, 1866	Genus <i>Rhinolophus</i> Lacépède, 1779 <i>Rhinolophus ferrumequinum</i> (Schreber, 1774) 1
	Family: Vespertilionidae Gray, 1821	Genus <i>Myotis</i> Kaup, 1829 <i>Myotis</i> sp. 1
	Family Canidae Fischer de Waldheim, 1817	Genus <i>Vulpes</i> Frisch, 1775 <i>Vulpes cf. vulpes</i> (Linnaeus, 1758) 1
		Genus <i>Canis</i> Linnaeus, 1758 <i>Canis lupus</i> Linnaeus, 1758 1 + 1 juv.
	Family Ursidae Fischer de Waldheim, 1817	Genus <i>Ursus</i> Gray, 1825 <i>Ursus arctos</i> Linnaeus, 1758 2 <i>Ursus spelaeus</i> (Rosenmüller- Heinroth, 1794) 1
	Family Mustelidae	Genus <i>Lutra</i> Brunnich, 1772 <i>Lutra lutra</i> (Linnaeus, 1758) 1
	Family Hyaenidae Gray, 1821	Genus <i>Crocota</i> Kaup, 1828 <i>Crocota crocota</i> (Erxleben, 1777) 1
	Family Felidae Fischer de Waldheim, 1817	Genus <i>Panthera</i> Oken, 1816 <i>Panthera pardus</i> (Linnaeus, 1758) 1 <i>Panthera spelaea</i> (Linnaeus, 1758) 1
	Order Perissodactyla Owen, 1848	Family Equidae Gray, 1821
Family Rhinocerotidae Gray, 1821		Genus <i>Stephanorhinus</i> Kretzoi, 1942 <i>Stephanorhinus hemitoechus</i> (Falconer, 1859) 1

Table 2 (Continued)

				MNI	
Order Artiodactyla Owen, 1848	Family Suidae Gray, 1821	Genus <i>Sus</i> Linnaeus, 1758	<i>Sus scrofa</i> Linnaeus, 1758	1 + 1 juv.	
	Family Cervidae Goldfuss, 1820	Subfamily Capreoli- nae Brookes, 1828	Genus <i>Capreolus</i> Frisch, 1775	<i>Capreolus</i> sp.	2
		Subfamily Cervinae Goldfuss, 1820	Genus <i>Cervus</i> Linnaeus, 1758	<i>Cervus elaphus</i> Linnaeus, 1758	1
	Family Bovidae Gray, 1821	Tribe Caprini Gray, 1821	Genus <i>Rupicapra</i> Frisch, 1775	<i>Rupicapra</i> sp.	1
		Tribe Bovini Gray, 1821	Genus <i>Bison</i> Smith, 1827	<i>Bison</i> sp.	1 + 1 juv.
Order Primates Linnaeus, 1758	Family Hominidae Gray, 1825	Genus <i>Homo</i> Linnaeus, 1758	<i>Homo</i> <i>neanderthalensis</i> King, 1864 (lithic industry)		

not diagnostic to make a separation between the different lacertids (Barahona Quintana, 1996), besides the small size of our fossil preventing an attribution to large lizards as *Timon lepidus*, *Lacerta schreiberi*, and *Lacerta bilineata*. The size of the Valdavara 3 material fits the species *Iberolacerta monticola*, *Podarcis muralis*, *Podarcis hispanica* s.l., and *Podarcis bocagei*, which live today in the North of the province of Lugo (Masó and Pijoan, 2011).

Slow worm – *Anguis fragilis*

The two fossil vertebrae are small (CL < 3.6 mm) and procoelous, with a posterior condyle and anterior cotyle that are dorsoventrally flattened. In ventral view, the centrum, which is much longer than wide, has a flat ventral surface and has lateral margins that are parallel. One of the most complete vertebrae (Fig. 4/3) shows the bases of the hemapophyses fused to the centrum on its posterior

half, and transverse processes that are well-developed and dorsoventrally flattened. The other fragments correspond to a posterior and an anterior part of a caudal vertebra (very probably the two parts of the same vertebra) divided at the level of the autotomy line. These vertebrae can be distinguished from those of other anguines (*Dopasia* and *Pseudopus*) mainly by their smaller size (CL < 5 mm), but also by their relatively elongated shape and the lateral margins of the centrum, which are more or less parallel. The fossil vertebrae do not display any morphological difference from those of the present-day species *A. fragilis*.

The slow worm is a Eurasiatic species with a wide European distribution, with the exception of Ireland, a large part of Scandinavia, the south of the Iberian and Balkan Peninsulas. In Iberia, its southern limit corresponds to the Ebro valley, Central System and Portugal (Galán, 2002a). It

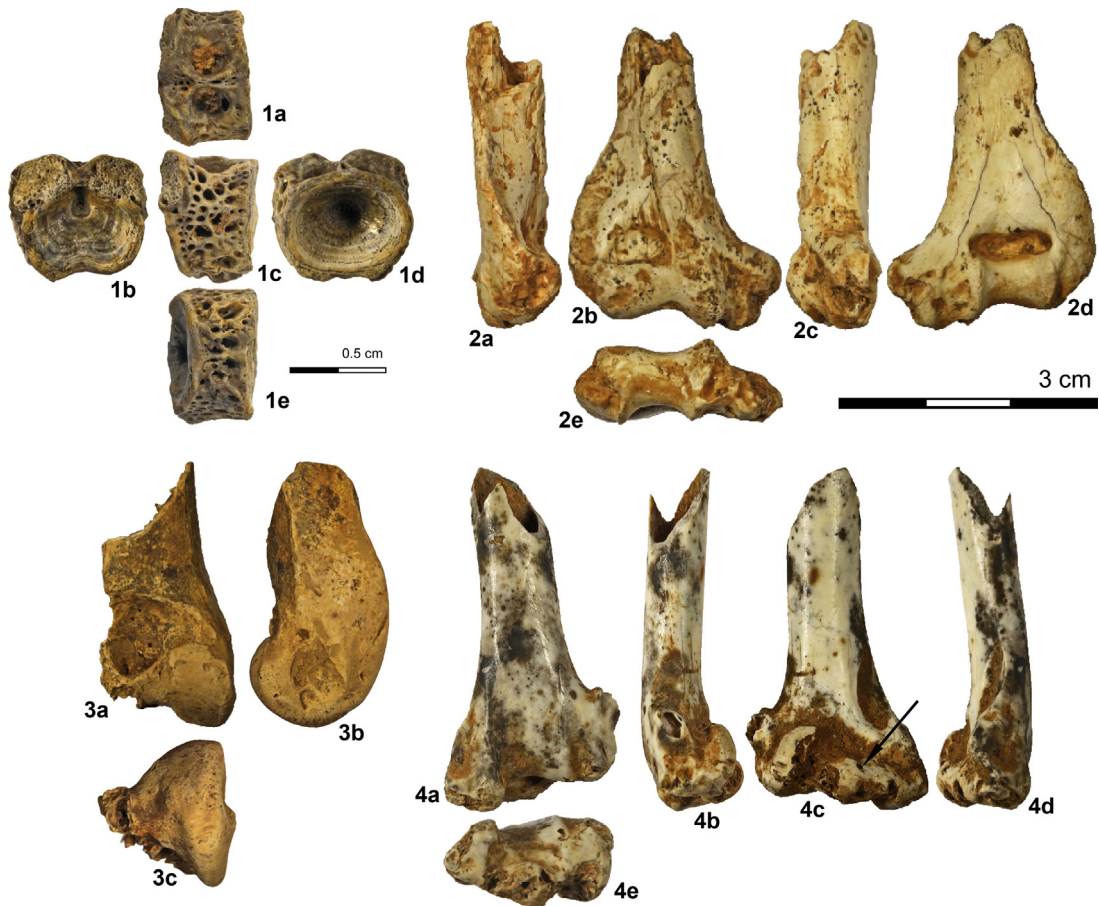


Fig. 3. Fish, avian and beaver remains. 1. Vertebra of a fish (Val-3, 2010, level B, 110): dorsal, anterior, lateral, posterior, and ventral views. 2. Distal humerus of *Castor fiber* (Val-3, 2011, lev. B, 113): a) medial, b) anterior, c) lateral, d) posterior, and e) distal views. 3. Distal femur dext. of *Haliaeetus albicilla* (Val-3, 2009, 602): a) caudal, b) lateral, and c) distal views. 4. Distal epiphysis and part of the diaphysis of a humerus dext. of *Pyrrhocorax graculus* (Val-3, 2009, lev. sup., 2): a) anterior, b) medial, c) posterior, d) lateral, and e) distal views. The black arrow in image 4c indicates a puncture probably associated with the action of a nocturnal raptor.

Fig. 3. Restes de poissons, d'oiseaux et de castors. 1. Vertèbre d'un poisson (Val-3, 2010, niveau B, 110) : vues dorsale, antérieure, latérale, postérieure et ventrale. 2. Humérus distal de *Castor fiber* (Val-3, 2011, niv. B, 113) : a) vues médiale, b) antérieure, c) latérale, d) postérieure et e) distale. 3. Fémur distal droit d'*Haliaeetus albicilla* (Val-3, 2009, 602) : vues a) caudale, b) latérale, et c) distale. 4. Épiphysse distale et partie de la diaphyse d'un humérus droite de *Pyrrhocorax graculus* (Val-3, 2009, niv. sup., 2) : vues a) antérieure, b) médiale, c) postérieure, d) latérale et e) distale. La flèche noire dans l'image 4c indique une ponction probablement associée à l'action d'un rapace nocturne.

is a species with crepuscular and nocturnal habits, whose presence seems to be linked with a high degree of environmental moisture. It lives in areas with a dense vegetal cover, on the edges of the forest and clearings, but even in humid meadows, with loose soils.

Smooth snake – *Coronella cf. austriaca*

The only fossil vertebra (Fig. 4/4) is small (CL = 2.3 mm), bears an incomplete hypapophysis (character of anterior trunk vertebrae), and has a wide neural arch that is markedly depressed dorsoventrally but with a slightly convex dorsal margin and does not show a well-developed interzygapophyseal constriction, as in the genus *Coronella*. The precondylar constriction is somewhat marked, a characteristic of the genus *Coronella* that differs from the juveniles/adults of the other Iberian colubrids (Blain, 2005). According to several authors, *C. austriaca* has prezygapophyseal processes that are wide at the base and shorter than *C. girondica*; the parapophysis is also

longer in relation to the diapophysis in the former species (Bailon, 1991; Blain, 2005; Szyndlar, 1984). However, these characters may show a certain degree of variability, and the attribution is made with caution.

The smooth snake is a medium to southern European species. In Iberia, it mainly lives in the northern half, in particular in northern Portugal, Galicia, Asturias, Cantabria, Basque Country and Pyrenean region. In the Euro-Siberian bioclimatic area, it occurs in the collinean and mountain bioclimatic levels (Galán, 2002b). Its distribution in the North of Iberia seems to be correlated with mean annual precipitation higher than 600–800 mm (Galán, 2002b). It lives in humid-cool environments and in particular in the beech grove and Atlantic oak grove, taking refuge in stony or bushy areas.

Ladder snake – *Rhinechis scalaris*

The only trunk vertebra (Fig. 4/5) is the largest of the vertebrae attributed to snakes in Valdavara 3 (CL = 4.1 mm),

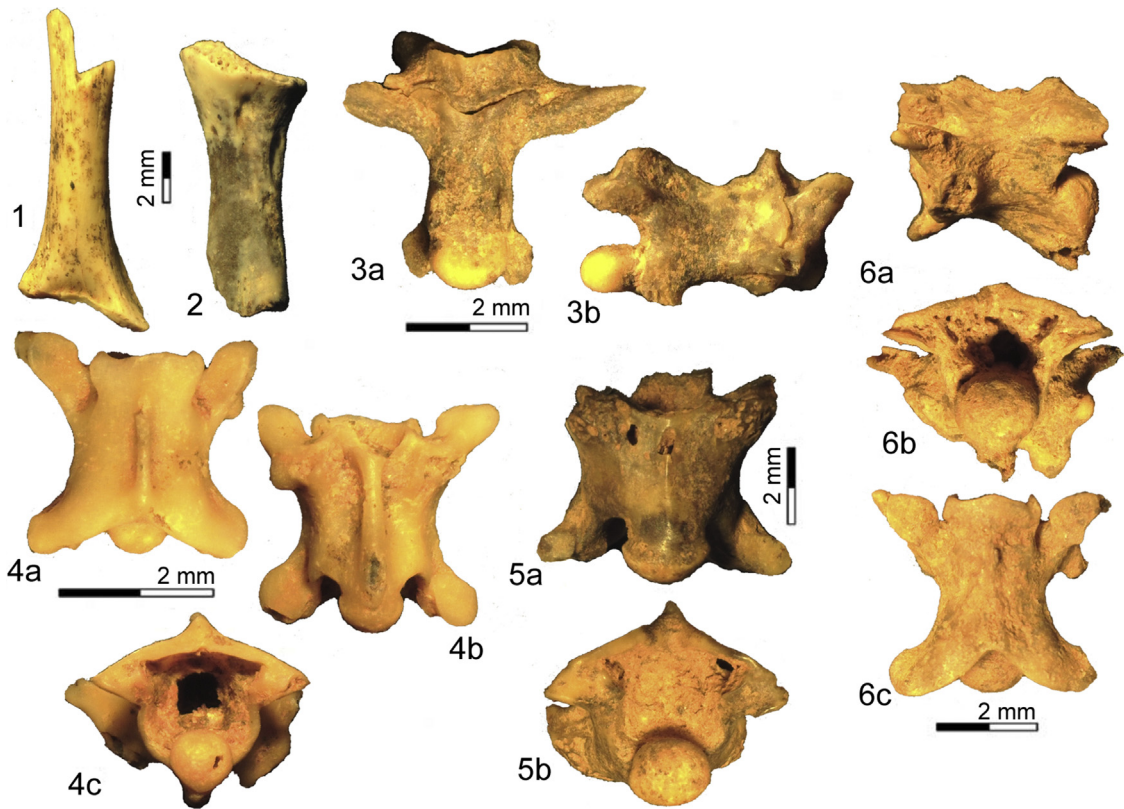


Fig. 4. Some amphibians and reptiles from Valdavara 3. 1, 2. *Bufo cf. spinosus*, 1: right humerus in ventral view; 2: radioulna in lateral view. 3. *Anguis fragilis*, caudal vertebra in ventral (a) and right lateral (b) views. 4. *Coronella cf. austriaca*, cervical vertebra in dorsal (a), ventral (b) and posterior (c) views. 5. *Rhinechis scalaris*, trunk vertebra in ventral (a) and posterior (b) views. 6. *Vipera* sp., trunk vertebra in left lateral (a), posterior (b) and dorsal (c) views. Scale: 2 mm.

Fig. 4. Quelques amphibiens et reptiles de Valdavara 3. 1, 2. *Bufo cf. spinosus*, 1: humérus droit en vue ventrale ; 2 : radioulna en vue latérale. 3. *Anguis fragilis*, vertèbre caudale en vues ventrales (a) et latérale (b) droites. 4. *Coronella cf. austriaca*, vertèbre cervicale en vues dorsale (a), ventrale (b) et postérieure (c). 5. *Rhinechis scalaris*, vertèbre du tronc dans les vues ventrale (a) et postérieure (b). 6. *Vipera* sp., Vertèbre du tronc en vues latérale gauche (a), postérieure (b) et dorsale (c). Échelle : 2 mm.

robust and rather short (CL/centrum width NAW=0.98). The neural arch is not so dorsoventrally depressed as in genus *Coronella*. The precondylar constriction (CNW) is well marked with a ratio CNW/CL=0.46: larger than in adults of genus *Coronella* and concordant with a sub-adult of larger Iberian colubrid snakes. The haemal keel, poorly discernable because of the probable action of gastric juices, seems to have been rather wide and not well delimited laterally. Among Iberian colubrids, this vertebra is consistent with *Rhinechis scalaris*; all other colubrids generally show longer trunk vertebrae.

Rhinechis scalaris is currently present in the province of Lugo, one of its current northernmost occurrences in Iberia (Pleguezuelos and Honrubia, 2002). It lives in Mediterranean environments of rocky bushlands and woodland edges. In northern Iberia, it frequents sunny, dry and opened areas with an orientation facing to the south (Masó and Pijoan, 2011).

Viper – *Vipera* sp.

One incomplete trunk vertebra (CL=3.2 mm) documents a viper (Fig. 4/6). It bears, although broken, a straight hypapophysis. The neural arch is posteriorly depressed, and the centrum is ventrally convex in cross section with

indistinct lateral margins. The condyle and cotyle are rather large and the zygapophyseal articular surfaces inclined. Unlike the vertebra attributed to *Coronella cf. austriaca*, this vertebra is much more gracile with a well-pronounced interzygapophyseal constriction, the zygosphene is much slenderer, the dorsal margins of the neural arch in posterior view are rather straight, and show at least one preserved long and slender parapophyseal process. No more precise attribution is possible among Iberian vipers.

There are currently three species of vipers in Iberia: *V. latastei*, *V. aspis* and *V. seoanei*, but only the latter is represented today in the province of Lugo. *Vipera seoanei* lives in areas with an Atlantic or mountain climate, with not very harsh winters and short and rainy summer and frequents open woodlands, bushlands, and humid meadow edges with a good low vegetal cover, but where insolation is possible (Braña, 2002; Masó and Pijoan, 2011).

White-tailed eagle – *Haliaeetus albicilla*

Due to the fracture, the recovered portion does not allow us to take exact measurements (Fig. 3/3). Nevertheless, we have measured the width of the lateral condyle (18 mm) and it is within the parameters established for this species taking into account its sexual dimorphism. Its morphology

coincides with the skeletons of this species in the reference collection from the Universidad Autónoma de Madrid. The white-tailed eagle tends to be an over-wintering species (Sánchez-Marco, 2008; Van der Made et al., 2003) that lives on coastal cliffs or close to inland deep water bodies.

Alpine chough – *Pyrrhocorax graculus*

Two fragments, a right humerus (Fig. 3/4) and a left ulna represent the alpine chough. The measurement of the diagonal distal width of the ulna (7.04 mm) is within the parameters defined for *P. graculus* by Tomek and Bochenski (2000). According to the same authors, the humerus distal width (12.2 mm) is within the parameters of this species. The alpine chough lives in the mountains, and usually does not go down to the lowlands nor present in the coasts.

Crow – Corvidae indet.

A right immature tibiotarsus is ascribed to an indeterminate corvid. It has been compared to other immature specimens from other sites and current collections. The measurements of both the distal width (6 mm) and the depth of the distal lateral condyle (5 mm) are within the parameters established for the small corvidae. These birds live in very diverse habitats, especially in extensive forests and rocky areas. Their diet is very varied and they look for areas where they can find everything they need.

Indeterminate birds – Aves indet.

The bird remains are mostly distal epiphyses with a part of the diaphyses. The remains are too poor for a precise identification.

Hedgehog – *Erinaceus cf. europaeus*

The P⁴ is large with a tall protocone, the metacone oriented to back, a short heel and three roots. The M¹ and M² are broken labially, but both have a quadrangular contour in occlusal view. These characteristics allow us to ascribe our remains to the genus *Erinaceus*. There is only one *Erinaceus* species living in Iberia (*Erinaceus europaeus*) and the remains from Valdavara 3 are similar in size to this species. However, because of the scarcity of the remains we prefer assign them to *Erinaceus cf. europaeus*. *Erinaceus europaeus* is distributed over almost all of Iberia and has a very diverse range of habitats, both open and wooded. However, it prefers wet areas.

Shrew – *Sorex* sp.

The fragmented mandibles recovered are characterized by being medium-sized and by the pigmentation of the molars, typical of the genus *Sorex* (Fig. 5/1). Given the scantiness of the remains, we have assigned this specimen to *Sorex* sp. Three species of the genus *Sorex* live in Iberia: *S. araneus*, *S. coronatus*, and *S. granarius*. They are distributed across the northern half of the Peninsula and are characteristic of humid environments with good herbaceous or shrub vegetation cover (Cuenca-Bescós et al., 2008; Pemán, 1990a; Pokines, 1998; Zubeldia Garmendia, 2006).

Mole – *Talpa* sp.

There are currently two species of this genus in Iberia: *Talpa europaea* and *Talpa occidentalis*. According to Cleef-Rodgers and van den Hoek Ostende (2001), the differences in size of the humerus are useful to separate both species. The four *Talpa* humeri identified have a small size more typical of *Talpa occidentalis* than *Talpa europaea*, but due to the

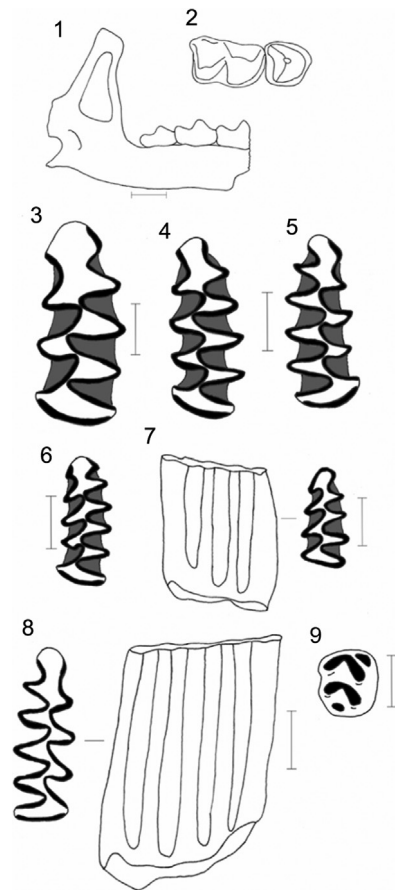


Fig. 5. Some small mammals from Valdavara 3. 1. Left mandible of *Sorex* sp. (lingual view). 2. Fourth lower right premolar (P₄) and first lower right molar (M₁) of *Rhinolophus ferrumequinum* (occlusal view). 3. Left M₁ of *Arvicola sapidus* (occlusal view). 4. Left M₁ of *Microtus arvalis* (occlusal view). 5. Right M₁ of *Microtus agrestis* (occlusal view). 6. Left M₁ of *Terricola* sp. (occlusal view). 7. Left M₁ of *Clethrionomys glareolus* (labial and occlusal views). 8. Right M₁ of *Pliomys coronensis* (labial and occlusal views). 9. Right M₂ of *Apodemus* sp. (occlusal view). Scale: 1 mm.

Fig. 5. Quelques petits mammifères de Valdavara 3. 1. Mandibule gauche de *Sorex* sp. (vue linguale). 2. Quatrième prémolaires inférieure droite (P₄) et première molaire inférieure droite (M₁) de *Rhinolophus ferrumequinum* (vue occlusale). 3. M₁ gauche d'*Arvicola sapidus* (vue occlusale). 4. M₁ gauche de *Microtus arvalis* (vue occlusale). 5. M₁ droite de *Microtus agrestis* (vue occlusale). 6. M₁ gauche de *Terricola* sp. (vue occlusale). 7. M₁ gauche de *Clethrionomys glareolus* (vues labiale et occlusale). 8. M₁ droite de *Pliomys coronensis* (vues labiale et occlusale). 9. M₂ droit d'*Apodemus* sp. (vue occlusale). Échelle : 1 mm.

scarcity of remains we preferred to assign our specimens to *Talpa* sp. The joint distributions of *Talpa europaea* and *T. occidentalis* cover nearly all of the Iberian Peninsula. Their habitat requirements are linked to soft soils, mainly dealing grasslands, from sea level to 2000 m.

Greater horseshoe bat – *Rhinolophus ferrumequinum*

The fourth lower premolars are characterized by a triangular shape with a convex lingual edge, a concave distal edge and a thin cingulum (Fig. 5/2); the M₁ and M₂ have a thin cingulum and show a nyctalodont pattern (the hypoconulid connected with the entoconid), typical of the genus *Rhinolophus*. This combination of characters and the big size of the teeth coincide with *R. ferrumequinum*, a

species with a broad distribution over the Peninsula. This species is found in a wide range of environments. However, it has a preference for wooded areas with open spaces.

Mouse-eared bat – *Myotis* sp.

The only well-preserved tooth is the M₃, characterized by a myotodont pattern, a thick and regular cingulum, a closed trigonid and an open and slightly reduced talonid. This combination of characters suggests that the mandible belongs to genus *Myotis*. The scarcity and poor preservation of the remains do not allow us to identify the species, but the small size of the mandible suggests a small-sized *Myotis*, like *Myotis nattereri* or *M. daubentoni*. The genus *Myotis* is widely distributed in Iberia and occurs normally in forest environments.

Rabbit – *Oryctolagus cuniculus*

The anatomical elements mainly correspond to basipodia and acropodia. Bones and teeth with morphology typical of the Lagomorpha have a small size. This small size indicates the rabbit *Oryctolagus cuniculus*, rather than a hare (*Lepus*), which tend to be larger. Rabbits may live in forests, although they prefer extensive fields covered by shrubs where they can hide. They build burrows in the ground for their shelter. Their main source of food is herbaceous plants or herbs. They prefer warm, dry climates, where sandy areas abound, although this species has successfully adapted to other ecological contexts.

Beaver – *Castor fiber*

The humerus (Fig. 3/2) has a very wide distal end with a wide articulation, wide olecranon fossa, wide medial and lateral epicondyles and wide epicondylar crests. There is no epicondylar foramen. The specimen is much smaller than a humerus of *Meles* and *Lynx* with which we compared it and differs also in not having an epicondylar foramen. The humerus of *Lutra* also has an epicondylar foramen. The humerus of *Vulpes* is much smaller and narrower. The humerus of *Hystrix* is slenderer. The medial and lateral epicondyles are much wider than in *Macaca*. The greatest resemblance is with *Castor fiber*. *Castor fiber* lives in north and eastern Europe, while its distribution in western Europe is discontinuous. Historically beavers were more widespread and there are geographic names referring to them in areas where today they do not live (e.g., Beverwijk in the Netherlands). In historic times, they went extinct in Spain, but have been reintroduced (Ceña et al., 2004). Their fossils are known from a number of localities, such as Atapuerca TE8-14 and TD6 (Rodríguez et al., 2011).

Southwestern water vole – *Arvicola sapidus*

The acute angulation of the lingual re-entrant angle 4 (LRA4) in the two lower first molars, together with the presence in molars of an enamel thicker in the posterior than the anterior parts of the triangles allows us to ascribe the material to *Arvicola sapidus* (Fig. 5/3). *Arvicola sapidus* is a semi-aquatic rodent represented throughout Iberia and associated with flowing or stationary bodies of water.

Field vole – *Microtus agrestis* and Common vole – *Microtus arvalis*

The M₁ assigned to *M. agrestis* are characterized by their reduced size and by the presence of three closed triangles in the posterior complex (TTC) and four triangles that are closed or minimally confluent in the anterior complex (ACC) (Fig. 5/4–5). There is also a marked asymmetry and

alternation in the T4/T5 and T6/T7 triangles, as well as marked alternation in the re-entrant angles; the salient angles are pointed in shape and curved towards the anterior part of the tooth, and the T9 triangle is strongly developed. These features distinguish it from the *M. arvalis* specimens, which are characterized by the almost symmetrical and parallel arrangement of T4/T5 and especially of T6/T7, as well as the corresponding re-entrant angles, giving a rounded shape to the ACC by contrast with the angular form in *M. agrestis*.

The field vole lives in the northern third of Iberia, from the Pyrenees to Galicia, but it is absent in the Mediterranean area. It inhabits open spaces close to deciduous woodland, in humid areas with abundant grass, such as ponds and riverbanks up to altitudes of 1900 m. The common vole displays a similar distribution, although it is a more generalist species and more widely distributed. In Iberia, it is more extensively spread over the southern region and may be found in many environments, from pasture to deciduous and coniferous woodland. Its most frequent habitat is subalpine and alpine meadows; it prefers open, not very humid spaces without high vegetation, and it does not live in closed woodland and swampy areas. It is found at altitudes between 900 m and 2000 m, with an annual rainfall greater than 800 mm (Palomo et al., 2007).

Pine vole – *Microtus (Terricola)* sp.

The characteristics that distinguish the subgenus *Terricola* from other *Microtus* are basically the presence in the first lower molar of an open T4 triangle, as well as T4 and T5 forming what is known as the pitymyan rhombus (Fig. 5/6). At present, there are three species belonging to this subgenus in Iberia: *M. (T.) duodecimcostatus*, *M. (T.) pyrenaicus gerbei*, and *M. (T.) lusitanicus* (Brunet-Lecomte and Chaline, 1993). Morphological differentiation of the species is complicated (Brunet-Lecomte, 1988; Brunet-Lecomte and Chaline, 1990, 1993; Brunet-Lecomte et al., 1987) and due to the scarcity of remains from Valdavara 3 we prefer to ascribe our specimens to the subgenus *Terricola*. The living *Microtus (Terricola)* species have diverging geographical distributions in Iberia, but all are associated with open spaces and stable, moist soils that are easy to dig and that have abundant herbaceous cover.

Bank vole – *Clethrionomys glareolus*

The M₁ has roots, cement on the labial and lingual re-entrants of the triangles, enamel that is continuous and with same thickness over the entire occlusal perimeter, except for a small enamel-free area on the labial part of the posterior lobe (PL), and confluence of the triangles. These characteristics allow us to distinguish our specimen from the extinct genus *Pliomys* and assign it to the living species *Clethrionomys glareolus* (Fig. 5/7). The bank vole is one of the few extant arvicoline species that live in more or less open deciduous woodland or in areas of shrubs or high grasses. It is a good indicator of the presence of vegetation cover in a temperate climate with a humid atmosphere (Cuenca-Bescós et al., 2008; Pemán, 1985, 1990a, 1990b). Within Iberia, its current distribution is northern (Pokines, 1998; Ventura et al., 1993), although it may be found in mountainous massifs of Euro-Siberian climate in eastern Iberia (Arrizabalaga et al., 1986).

Extinct vole – *Pliomys coronensis*

The presence of roots, the absence of cement on the labial and lingual triangles, the enamel-free areas in the mesial anterior cusp (AC) and the labial and lingual part of the posterior lobe (PL) and its relative big size in relation with other arvicolid (with the exception of *Arvicola* species) allow us to ascribe our material to the extinct vole *Pliomys coronensis* (Fig. 5/8). The fossil genus *Pliomys* is probably related to the extant Balkan endemic species *Dinaromys bogdanovi* (Chaline et al., 1999). *D. bogdanovi* is a high mountain species ecologically comparable with *Chionomys nivalis*.

Field mouse – *Apodemus* sp.

The presence in the lower molars of a low occlusal surface with six main cusps, the anterolingual and anterolabial cusps confluent in an X-shape and separated by a deep, narrow groove, in conjunction with a posterior cusp (cp) that is low, rounded and well-developed and the presence of secondary cusps (c) on the labial face of the m1 and of a mesial tubercle (tma) allow us to assign our specimens to the genus *Apodemus* (López-García et al., 2011), but due to the scarcity of the remains we can not assign our material to a species (Fig. 5/9). There are two extant species of this genus in Iberia (*A. sylvaticus* and *A. flavicollis*), both living in

areas with good shrub or tree cover. In regions of homogeneous woodland, however, they prefer the marginal areas.

Red fox – *Vulpes* cf. *vulpes*

The P⁴ (Fig. 6/1–3) has a small protocone, situated anteriorly. There is no parastyle. This is a typical morphology in the Canidae. The size is smaller than in the species of the genera *Canis* and *Cuon*, larger than in most species of foxes and similar in size to *Vulpes praeglacialis* and the living red fox *V. vulpes* (Fig. 6). The former seems unlikely because of the age of the remains and therefore these are assigned to *Vulpes* cf. *vulpes*. *Vulpes* appeared probably during the early middle Pleistocene (*Vulpes “angustidens”* in Przletice and Hundsheim and *Vulpes jansonii* in L’Escale – Bonifay, 1971; Fejfar, 1995; Thenius, 1954; Von Koenigswald and Heinrich, 1999).

Wolf – *Canis lupus*

These remains have a homogenous size and the morphology of a carnivore. The M₁ (Fig. 7/5) is the most indicative fossil. It has a high protoconid, unlike Ursidae and large Mustelidae, and a talonid, which is larger than in Felidae and Hyaenidae. Its morphology is as in the Canidae. It has an entoconid, as in *Canis* and *Vulpes* and unlike in *Cuon* and *Xenocyon lycaonoides*, which lost this cusp. The

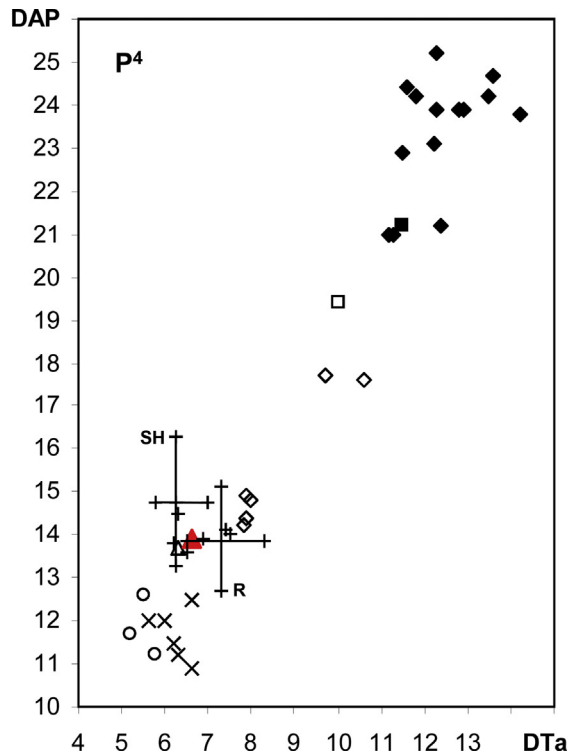
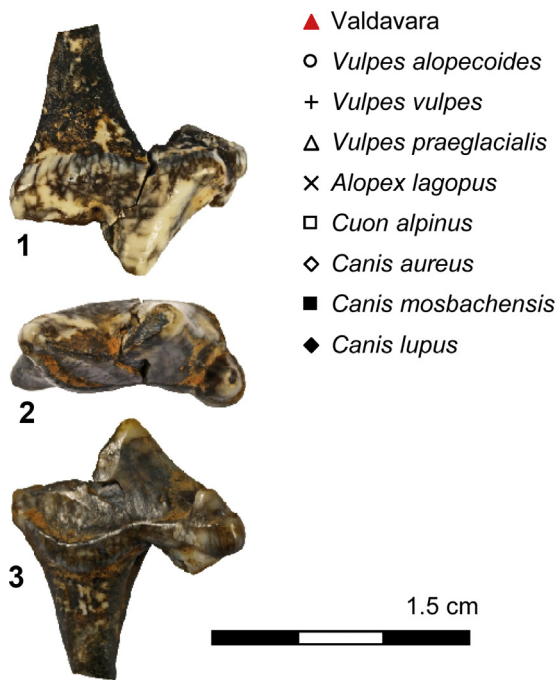


Fig. 6. P⁴ dext. of *Vulpes* cf. *vulpes* (Val-3, 2010, lev. B, 61 + 128): 1) buccal, 2) occlusal, and 3) lingual views. Bivariate diagram comparing length (DAP) and width (DTa) of the specimen from Valdavara 3 with the P⁴ of *Vulpes alopecoides* from Infierno, Villaroya, and Saint-Vallier (Bonifay, 1971); recent *Vulpes vulpes* ($n = 48$ – average and extremes) and from Sima de los Huesos ($n = 13$) (García García, 2003) and from L’Escale and Lunel-Viel (Bonifay, 1971); *Vulpes praeglacialis* from Kalkberg (Bonifay, 1971); recent *Alopex lagopus* (NBC); recent *Cuon alpinus* (NBC); recent *Canis aureus* (NBC); *Canis mosbachensis* from Mosbach (NMM); recent *Canis lupus* from Spain (MNCN).

Fig. 6. P⁴ droite de *Vulpes* cf. *vulpes* (Val-3, 2010, niv. B, 61 + 128) : vues 1) buccale, 2) occlusale et 3) linguale. Diagramme bivarié comparant la longueur (DAP) et la largeur (DTa) de l’échantillon de Valdavara 3 avec la P⁴ de *Vulpes alopecoides* d’Infierno, Villaroya et Saint-Vallier (Bonifay, 1971); *Vulpes* récentes ($n = 48$ – moyennes et extrêmes) et de Sima de los Huesos ($n = 13$) (García, 2003) et de L’Escale et Lunel-Viel (Bonifay, 1971); *Vulpes praeglacialis* de Kalkberg (Bonifay, 1971); *Alopex lagopus* (NBC) récent; *Cuon alpinus* (NBC) récent; *Canis aureus* récent (NBC); *Canis mosbachensis* de Mosbach (NMM); *Canis lupus* récent d’Espagne (MNCN).

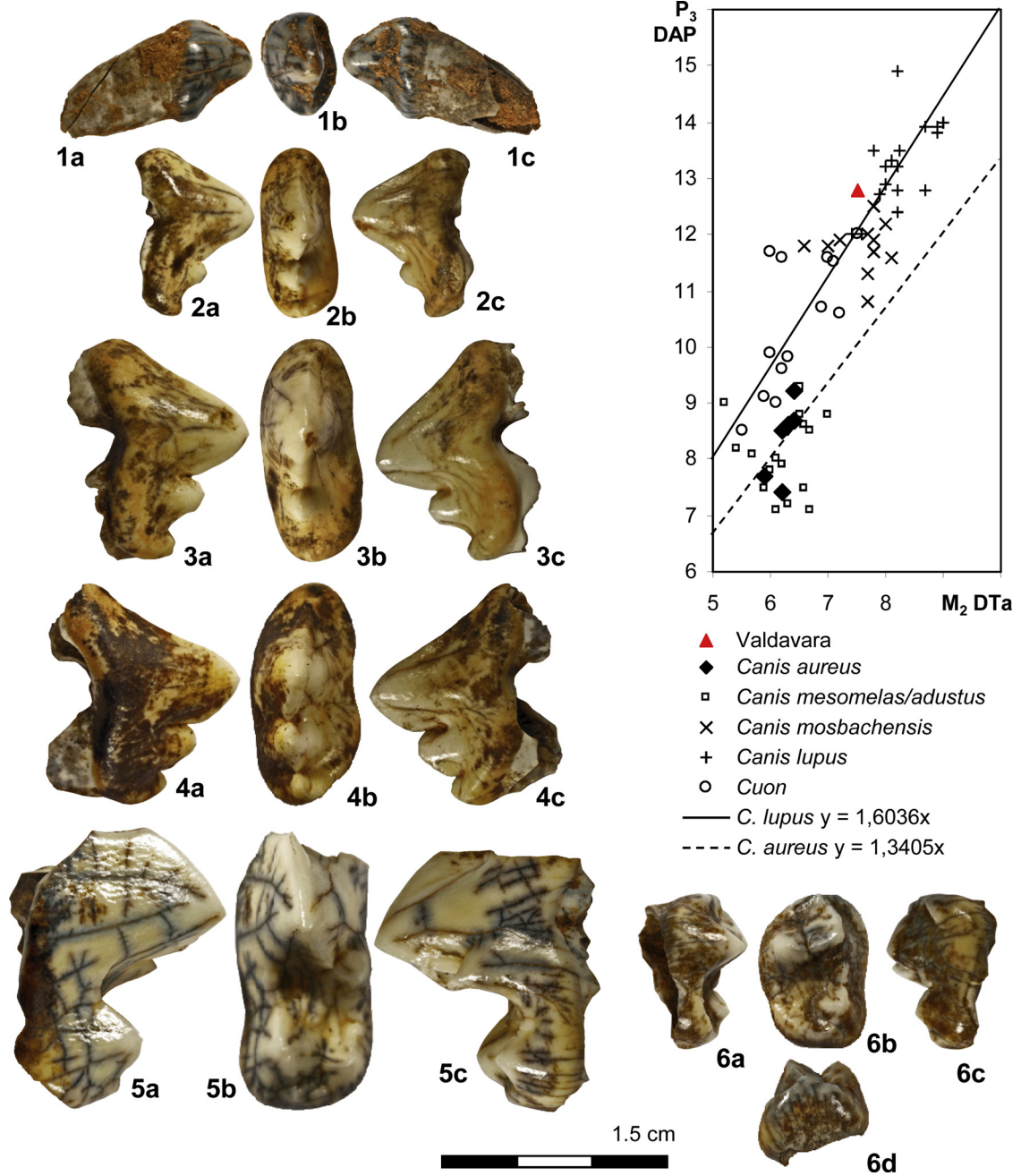


Fig. 7. *Canis lupus* from Valdavara 3. 1. P₁ sin. (Val-3, 2010, lev. B, 52): a) buccal, b) occlusal, and c) lingual views. 2. P₂ sin. (Val-3, 2010, lev. B, 90): a) buccal, b) occlusal, and c) lingual views. 3. P₃ sin. (Val-3, 2010, lev. B, 87): a) buccal, b) occlusal, and c) lingual views. 4. P₄ sin. (Val-3, 2010, lev. B, 50): a) buccal, b) occlusal, and c) lingual views. 5. M₁ sin. (Val-3, 2010, lev. B, 48): a) buccal, b) occlusal, and c) lingual views. 6. M₂ dext. (Val-3, 2010, lev. B, 49): a) lingual, b) occlusal, c) buccal, and d) posterior views. Bivariate diagram comparing the length (DAP) of the P₃ and anterior width (DTa) of the M₂ in the same mandible (the same individual in the case of Valdavara 3) in different Canidae: recent *Canis aureus* (NBC); recent *C. mesomelas* and *C. adustus* (NBC); *C. mosbachensis* from Untermassfeld (Sotnikova, 2001), Atapuerca TD6 (IPHES) and Hundsheim (Thenius, 1954); *C. lupus* from Valdavara 3, Jakinia Naciekowa Cave (ZPALUWr) and Lazaret (cast IPHES) and recent *C. lupus* (MNCN); *Cuon* from Yunxian (HPMW) and Hundsheim (Thenius, 1954) and recent *Cuon alpinus* (NBC).

Fig. 7. *Canis lupus* de Valdavara 3. 1. P₁ gauche (Val-3, 2010, niv. B, 52) : vues a) buccale, b) occlusale et c) linguale. 2. P₂ gauche (Val-3, 2010, niv. B, 90) : vues a) buccale, b) occlusale et c) linguale. 3. P₃ gauche (Val-3, 2010, niv. B, 87) : vues a) buccale, b) occlusale et c) linguale. 4. P₄ gauche (Val-3, 2010, niv. B, 50) : vues a) buccale, b) occlusale et c) linguale. 5. M₁ gauche (Val-3, 2010, niv. B, 48) : vues a) buccale, b) occlusale et c) linguale. 6. M₂ droite (Val-3, 2010, niv. B, 49) : vues a) linguale, b) occlusale, c) buccale et d) postérieure. Diagramme bivarié comparant la longueur (DAP) de P₃ et la largeur antérieure (DTa) de M₂ dans la même mandibule (le même individu dans le cas de Valdavara 3) chez différents Canidae : *Canis aureus* récent (NBC) ; *C. mesomelas* et *C. adustus* (NBC) ; *C. mosbachensis* d'Untermassfeld (Sotnikova, 2001), Atapuerca TD6 (IPHES) et Hundsheim (Thenius, 1954) ; *C. lupus* de Valdavara 3, la grotte de Jakinia Naciekowa (ZPALUWr) et Lazaret (moulage IPHES) et *C. lupus* récent (MNCN) ; *Cuon* de Yunxian (HPMW) et Hundsheim (Thenius, 1954) et *Cuon alpinus* (NBC).

M₂ (Fig. 7/6) has the hypoconid on the buccal side of the talonid, while in *Cuon* and *X. lycaonoides* it is larger and situated more in the middle. In side view, the cusps of the premolars tend to be blunt as in *Canis lupus*, and unlike most other species, including *Canis mosbachensis*, *Canis aureus* or the foxes. This is reflected in these teeth being more elongate, or longer relative to the molars (for the P₄ see Fig. 7). The teeth are larger than in raccoon dogs and jackals, tend to be in the ranges of *Canis mosbachensis*, the earlier *Canis lupus* and the living wolves from Spain, but are small compared to the large latest middle and late Pleistocene wolves and *Xenocyon* (Figs. 7 and 8). Other remains have the morphology and size of a small wolf. The European Pleistocene Canidae include the small foxes (*Vulpes* and *Alopex*), the raccoon dog (*Nyctereutes*), wolves and jackals (*Canis*), a large wolflike dog (*Xenocyon*) and the dhole (*Cuon*) (Crégut-Bonnoure, 1996a). Morphology and size indicates that the dog from Valdavara 3 belongs to the wolf lineage (*C. mosbachensis-lupus*).

Small species of the genus *Canis* appeared about 2 Ma ago. One of these gave rise to *Canis mosbachensis*, which was common in the late early and middle Pleistocene. Around 400–300 ka ago, size started to increase, the premolars became blunter and *Canis lupus* appeared (García García, 2003; Van der Made, 2010b; Van der Made et al., 2017). Bonifay (1971) named the not yet very large wolves *Canis lupus lunellensis*. The recent wolves of Spain are again relatively small. The dog from Valdavara 3 is close in size to *C. mosbachensis* and the living *C. lupus* in Spain, but it is small compared to the late Pleistocene *C. lupus*. Clot and Duranthon (1990) mentioned similar small late Pleistocene *Canis* from the Magdalenian of Isturitz, from the Azilian from Tourasse and various other localities of this age or younger. Some of the small remains have been attributed to a domestic dog. Here we have abundant remains of an adult and some of a juvenile individual, most of them collected in situ from a layer dated to the early late Pleistocene. While the final size of the juvenile bones was not yet reached at the age of death, the teeth show that the adult individual was smaller than other wolves of the same geological age, just like the remains discussed by Clot and Duranthon (1990). In this case, the explanation that the remains belonged to a domestic dog, does not apply, since domestication occurred much later (Thalmann et al., 2013). The premolar morphology is different from that in *C. mosbachensis* and similar to that in *C. lupus*: we interpret this individual as a small wolf.

Brown bear – *Ursus arctos*

The upper fourth premolar (P⁴) has a simple morphology. The tooth is narrow, with an oval outline, and with the protoconid as the only relief (Torres, 1988). Small enamel spikes (Argant, 1991) flank the protoconid. The lower canine is small. The three specimens identified are among the smallest brown bears (Fig. 9/2). The lower fourth premolar (P₄) also has a simple morphology, with three well-separated cusps (Torres, 1988). The deutocone is clearly separated from the metacone and is positioned at the level of the metacone. The specimen fit within the range of variation of the European brown bears (Fig. 9/3). The lower third molar (M₃) of *U. arctos* has a crown with symmetrical edges. The hypoconid displays a single relief and

the ornamentation of the talonid is relatively weak (Torres, 1988). Although rare, the brown bear known in Europe since the early middle Pleistocene (Argant, 2009) becomes more abundant during the late Pleistocene (especially MIS 5) and it is a common species in the Pleistocene NW Iberian record (García-Vázquez et al., 2011).

Cave bear – *Ursus spelaeus*

All the specimens assigned to this species correspond to very large individuals. Only the canines could be measured and compared to other populations. The two lower canines are significantly larger than the largest specimens from the European late Pleistocene (Fig. 9). The cave bear appeared at the end of the middle Pleistocene (MIS 6) (Argant, 2009). During the late Upper Pleistocene (MIS 3) some specimens reached impressive sizes. The extinction of the species in Europe occurred at the end of the last glacial. In Galicia, it is one of the most abundant species (Grandal-d'Anglade and Vidal-Romaní, 1997).

Otter – *Lutra lutra*

A lower canine (Fig. 10/2) had a low crown, unlike in the fox (*Vulpes*) and wild cat (*Felis silvestris*). Female monkeys have canines with the lower border of the crown curving down much on the buccal side and there is a depression on the buccal wall where the upper canine fits. The Valdavara 3 specimen has a straighter lower border and lacks that depression. It resembles the canines of mustelids and is a little smaller than the canines of *Meles* and similar to those of *Lutra* (Fig. 10). A broken upper canine (Fig. 10/1) matches the lower canine in size and in crown height. The fossil record of the Mustelidae is not well-known. From the early or early middle Pleistocene, some relatively large mustelids are known, but the later large mustelids seem to have been *Meles*, *Gulo* and some other species (Crégut-Bonnoure, 1996b). The fossil *Meles* seem to have been similar to the living species (Wolsan, 2001). The known otters of the European main land either belong to *Lutra* and are of similar size as the living species, or to smaller species (Crégut-Bonnoure, 1996b; Willemsen, 1992). The material from Valdavara 3 fits the living species *L. lutra*.

Spotted hyaena – *Crocuta crocuta*

The P₄ (Fig. 11/1) does not have a large paraconid, which is unlike in Felidae and it is also less developed than in *Pachycrocuta* and *Hyaena*. Several bones fit the spotted hyaena and this is also the case for some incisors, but the latter are also not very different from those of *Ursus*. The Pleistocene Hyaenidae from the mainland of Europe include *Chasmaporthetes* (until about 2 Ma), *Pachycrocuta brevirostris* (about 2 Ma till the early middle Pleistocene), *Hyaena* (similar) and *Crocuta* (about 0.9 Ma till the latest Pleistocene). Earliest Pleistocene hyaenas have been placed in *Hyaena perrieri* or *Pliocrocuta perrieri* and in *Hyaena brunnea*. A similar hyaena appeared from the beginning of the Middle until the beginning of the Late Pleistocene and has been assigned to *Hyaena prisca*, *Hyaena striata* (= *H. hyaena*), *H. hyaena* or *P. perrieri* (Bonifay, 1971; Crégut-Bonnoure, 1996c; García and Arsuaga, 2001; Kurtén, 1968; Varela et al., 2010; Von Koenigswald and Heinrich, 1999). The small paraconid on the P₄ from Valdavara 3 is as in *Crocuta* and smaller than in the other European Pleistocene hyaenas. Within Europe, there was a minor gradual increase in the size of *Crocuta*, reaching a size much superior to that of

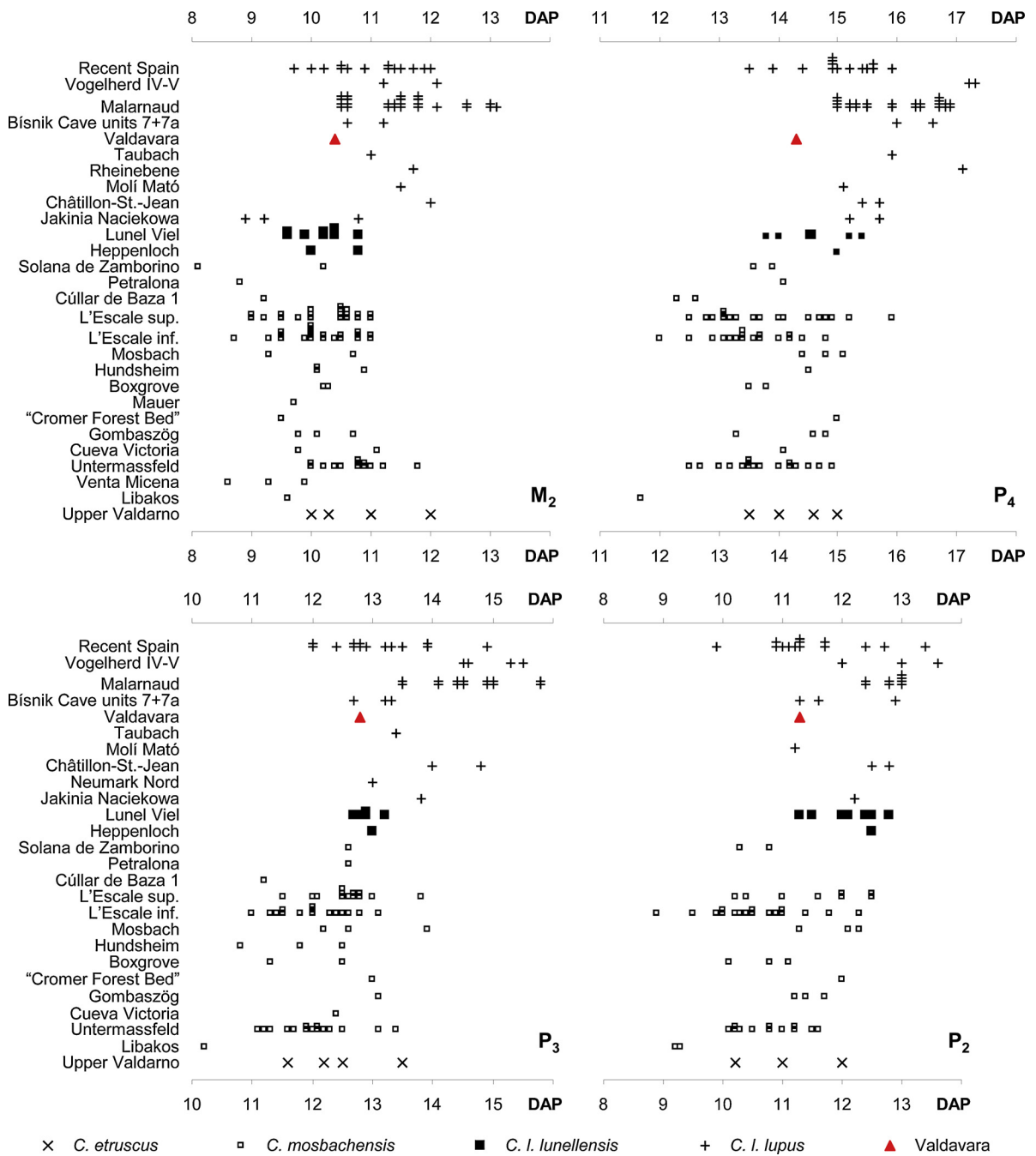


Fig. 8. The variation in size through time in *Canis*, as indicated by the lengths (DAP) of the M₂ and P₂₋₄. The localities are arranged from old (bottom) to young (top): Upper Valdarno (Freudenberg, 1914), Libakos (TUC), Untermassfeld (Sotnikova, 2001), Cueva Victoria (MAC), Gombaszög (Kretzoi, 1938), "Cromer Forest Bed" (Freudenberg, 1914), Mauer (RKUH), Boxgrove (Parfitt, 1999), Hundsheim (Thenius, 1954), Mosbach (NMM), L'Escale (Bonifay, 1971), Cúllar de Baza (Alcalá and Morales, 1989), Petralona (Tsoukala, 1989), Solana de Zamborino (Martin Penela, 1988), Heppenloch (Freudenberg, 1914), Lunel-Viel (Bonifay, 1971), Jakinia Naciekowa (ZPALUWr), Neumark Nord (FBFSUJ), Châtillon-Saint-Jean (Bonifay, 1971), Molí Mató (Alcoi), Taubach (Hemmer, 1977), Valdavara 3 (IPHES), Bísnik Cave (ZPALUWr), Malarnaud (Dufour, 1989), Vogelherd (Lehman, 1954), recent Spain (MNCN).

Fig. 8. Variation de la taille dans le temps chez *Canis*, comme indiqué par les longueurs (DAP) des M₂ et P₂₋₄. Les localités sont classées de la plus ancienne (bas) à la plus jeune (haut) : Valdarno supérieur (Freudenberg, 1914), Libakos (TUC), Untermassfeld (Sotnikova, 2001), Cueva Victoria (MAC), Gombaszög (Kretzoi, 1938), « Cromer Forest Bed » (Freudenberg, 1914), Mauer (RKUH), Boxgrove (Parfitt, 1999), Hundsheim (Thenius, 1954), Mosbach (NMM), L'Escale (Bonifay, 1971), Cúllar de Baza (Alcalá et Morales 1989), Petralona (Tsoukala, 1989), Solana de Zamborino (Martin Penela, 1988), Heppenloch (Freudenberg, 1914), Lunel-Viel (Bonifay, 1971), Jakinia Naciekowa (ZPALUWr), Neumark Nord (FBFSUJ), Châtillon-Saint-Jean (Bonifay, 1971), Molí Mató (Alcoi), Taubach (Hemmer, 1977), Valdavara 3 (IPHES), grotte de Bísnik (ZPALUWr), Malarnaud (Dufour, 1989), Vogelherd (Lehman, 1954), Espagne récente (MNCN).

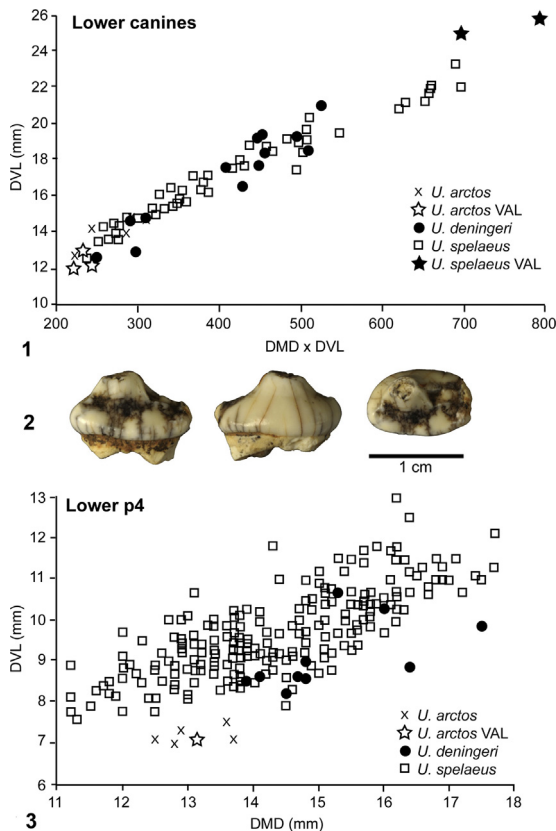


Fig. 9. 1. Measurements on the lower canine of *Ursus spelaeus* and *U. arctos* from Valdavara 3 compared to *Ursus spelaeus*, *U. arctos*, and *U. deningeri* (from Quilès, 2003). 2. Right P_4 of *U. arctos* from Valdavara 3 (Val-3, 2009, 59). 3. Measurements on the lower P_4 of *U. arctos* from Valdavara 3 compared to *Ursus spelaeus*, *U. arctos*, and *U. deningeri* (from Quilès, 2003). Abbreviations: DMD: mesio-distal diameter; DVL: vestibulo-lingual diameter.

Fig. 9. 1. Mesures sur la canine inférieure d'*Ursus spelaeus* et d'*U. arctos* de Valdavara 3 par rapport à celles d'*Ursus spelaeus*, *U. arctos* et *U. deningeri* (d'après Quilès, 2003). 2. P_4 droite d'*U. arctos* de Valdavara 3 (Val-3, 2009, 59). 3. Mesures sur la P_4 inférieure d'*U. arctos* de Valdavara 3 comparées à celles d'*Ursus spelaeus*, *U. arctos* et *U. deningeri* (d'après Quilès, 2003). Abréviations : DMD : diamètre méso-distal ; DVL : diamètre vestibulo-lingual.

the living spotted hyaenas. The specimen from Valdavara 3 is relatively large.

Leopard – *Panthera pardus*

The reduction of the P_{1-2} and M_{2-3} , and the absence of a talonid in the lower carnassial indicate that the material (Fig. 11/3) belongs to a felid. The carnassials are wider than in *Acynonyx* and the Machairodontinae. The European Pleistocene Felinae are small (*Felis*, *Lynx*), or medium size (*Acynonyx*, *Puma*, *P. pardus*) or large (*P. spelaea*, *P. gombaszoegensis* or *P. onca gombaszoegensis*) (Argant, 1996). The cheek teeth from Valdavara 3 have sizes that fit *P. pardus* and *Puma*. There is a large cusp behind the main cusp and behind this one there is a still lower third cusp in P_4 . This is like in *P. pardus*, while in *Puma* the cusp behind the main cusp is lower and placed further backwards; behind it, there is no third cusp. *Panthera pardus* appeared shortly after the early middle Pleistocene transition and lasted

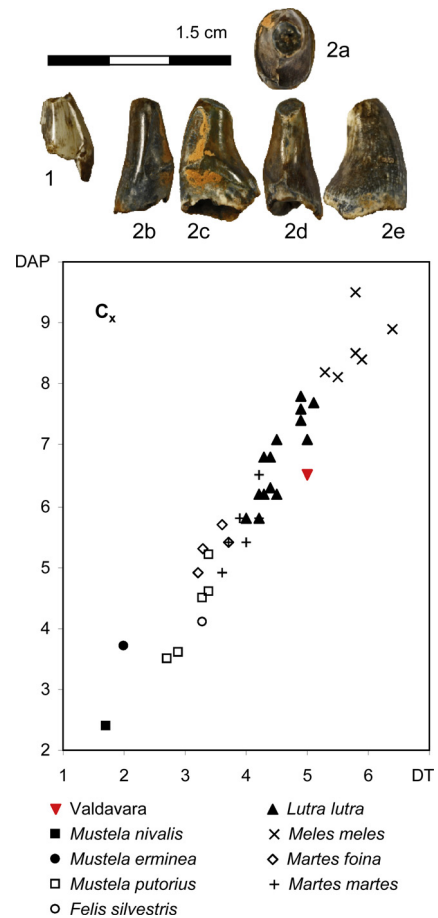


Fig. 10. *Lutra lutra* from Valdavara 3. 1. Canine fragment, possibly C_x dext. (Val-3, 2011, lev. B, 33): lingual view. 2. C_x dext. (Val-3, 2011, lev. B, 32): a) apical, b) anterior, c) lingual, d) posterior, and e) buccal views. Bivariate diagram of length (DAP) against width (DT) of the lower canine (C_x) comparing the specimen from Valdavara 3 with: *Mustela nivalis*, *M. erminea*, *M. putorius*, *Martes foina*, *Lutra lutra*, *Meles meles*, *Felis silvestris* (all recent, all MNCN).

Fig. 10. *Lutra lutra* de Valdavara 3. 1. Fragment d'une canine, peut-être C_x droite (Val-3, 2011, niv. B, 33) : vue linguale. 2. C_x droite (Val-3, 2011, niv. B, 32) : vues a) apicale, b) antérieure, c) linguale, d) postérieure et e) buccale. Diagramme bivarié de la longueur (DAP) par rapport à la largeur (DT) de la canine inférieure (C_x) comparant le spécimen de Valdavara 3 avec : *Mustela nivalis*, *M. erminea*, *M. putorius*, *Martes foina*, *Lutra*, *Meles*, *Felis silvestris* (toutes récentes, toutes MNCN).

until close to the end of the Pleistocene (Sanchis et al., 2015).

Cave lion – *Panthera spelaea*

Two fragments of a P_4 , found in 2010 in level B, fit together and fit in an alveolus in a mandible fragment with remains of a M_1 found not in situ in 2009 (Fig. 11/4). The carnassial does not have a talonid and behind it there is no other tooth or alveolus as in the Felidae. The M_1 and a P^4 (Fig. 11/5) are large and wide as in *Panthera leo*. A metapodial and phalanges are larger than in recent lions (IPHES). Fossil lions are known from Europe under various species or subspecies names, but more recently the name *P. spelaea* is applied (Argant, 1996; Stuart and Lister, 2010). The oldest cave lion may have appeared in isotope stage 17 (Parfitt



Fig. 11. 1. *P4* dext. of *Crocuta crocuta* (Val-3, 2009, 39): a) lingual, b) occlusal, and c) buccal views. 2. Coprolite from Valdavara 3 (Val-3, 2009, 262): two perpendicular views. 3. Mandible with canine and P_{3-4} and M_1 of *Panthera pardus* (Val-3, 2009, 503): left mandible buccal (a), lingual (b) and occlusal views (e), right mandible lingual (c), buccal (d) and occlusal (e) views. *Panthera spelaea* from Valdavara 3. 4. Mandible with remains of P_4 and M_1 (Val-3, 2010, lev. B, 24 and Val-3, 2009, 90): a) occlusal, and b) buccal views. 5. Posterior part of P_4 (Val-3, 2009, 92): a) buccal, b) occlusal, and c) lingual views.

Fig. 11. 1. *P4* droite de *Crocuta crocuta* (Val-3, 2009, 39) : a) vues linguale, b) occlusale et c) buccale. 2. Coprolite de Valdavara 3 (Val-3, 2009, 262) : deux vues perpendiculaires. 3. Mandibule avec canine et P_{3-4} et M_1 de *Panthera pardus* (Val-3, 2009, 503) : vues buccale (a), linguale (b) et occlusale (e) de la mandibule gauche, vues linguale (c), buccale (d) et occlusale (e) de la mandibule droite. *Panthera spelaea* de Valdavara 3. 4. Mandibule avec les restes de P_4 et M_1 (Val-3, 2010, niv. B, 24 et Val-3, 2009, 90) : vues a) occlusale et b) buccale. 5. Partie postérieure de P_4 (Val-3, 2009, 92) : vues a) buccale, b) occlusale et c) linguale.

et al., 2005; Van der Made et al., 2017). The species survived until about 14–14.5 ka (Stuart and Lister, 2010).

Indeterminate carnivore – Carnivora indet.

A coprolite (Fig. 11/2) consists of two pellets stuck together. It is well mineralized. Hyenas and other carnivores may produce droppings with a high mineral content. Carnivore excrements are often sausage-shaped and tend to consist of a series of ball shaped elements stuck together. Diameters are variable, but those of *Cara-cal* (an African cat similar in size to *Lynx*) may be up to 20 mm, *Acynonyx* 25–35 mm, *Panthera pardus* 20–30 mm, *P. leo* >40 mm (Stuart and Stuart, 2000). The diameters of hyaena scat and coprolites (both *Hyaena* and *Crocuta*) range between 15.5 and 44 mm (Horwitz and Goldberg, 1989). *Crocuta* coprolites have diameters from 31 to 44 mm (Fernández Rodríguez et al., 1995). The different pellets in a complete *Crocuta* excrement differ in shape and size according to their position in the defecation sequence, with type A first leaving the gut and type G last (Diedrich, 2012). The two pellets from Valdavara 3 show great similarity to types B and C, situating them somewhere before the middle of the complete excrement. This is where the diameters tend to be largest, but with 20.8–24.7 mm, the diameters of the Valdavara 3 specimen are relatively small. The excrements of *Lynx* may consist also of a series of pellets, with morphologies not very unlike those of *Crocuta* (van Diepenbeek, 1999, fig. p. 251). Sanz et al. (2016) compared shape, length, and width of scat and coprolites of canids, felids and hyaenids. *Canis* scat tends to be more elongated than that of hyenas and felids. The C type pellet from Valdavara 3 have a length of about 25 mm and a somewhat shorter diameter, while the B type pellet have a length of 15–20 mm and a diameter of 24.7 mm. These pellets would be in the lower end of the distribution *Crocuta* (which more likely would correspond to types D–G).

Morphologically, the Valdavara 3 coprolite resembles most those of *Crocuta*, but they are relatively small. It is to be expected that juveniles produce smaller pellets. Alternatively, they could have been produced by a smaller species of carnivore. Since fresh scat, even with a high mineral content, is fragile, this coprolite suggests that a living individual of carnivore was present at this place.

Horse – *Equus* cf. *torralbae*

The remains with the morphology of an equid seem to be homogenous and to belong to a moderately large species. A lower premolar (Fig. 12/2) has a U-shaped linguaflexid, as is common in caballoid horses, while stenonid species have a V-shaped linguaflexid (Forsten, 1992). A complete first phalanx (Fig. 12/1) has a moderately robust aspect. This is confirmed metrically (Fig. 12). *Equus hydruntinus* has much more gracile phalanges. Phalanges assigned to *E. mosbachensis* and *E. taubachensis* are much larger, while specimens assigned to *E. germanicus* and similar species are of similar length, but are on average more robust. The specimen from Valdavara 3 is in the middle of the phalanges assigned to *E. torralbae*. The upper cheek teeth tend to have relatively well-developed styles and a relatively large protocone.

Caballoid horses include the domestic horse (*Equus caballus*), the tarpan (*E. ferus*) and Przewalski's horse (*E. przewalskii* or *E. ferus przewalskii*). The wild forms were

previously included in *E. caballus*, but now the name *E. ferus* is used for the wild ancestor of the domestic horse. There are different opinions on the classification of the fossil European caballoid horses. Azzaroli (1990) recognized a single species (*E. caballus*), Forsten (1988) recognized three species (*E. mosbachensis*, *E. germanicus* and *E. caballus*) and Eisenmann (1991) recognized three types with eleven species. These are still the prevalent options. Eisenmann's (1991) types are primarily based on the relative sizes of the protocones. If protoconal indices are calculated based on the averages in her Table 2, it appears that differences between the samples tend to be small, while the samples that have somewhat more different values tend to be small samples. The average of a sample tends to resemble that of the population from which it is taken, but differences may occur and small samples have a greater chance not to be representative than large samples. This effect may have contributed to the more complex classification by Eisenmann (1991).

All specialists in equids recognize the importance of the size and proportions of the metapodials and the first phalanges. The clearest patterns are seen in the metapodials, but to some extent these are also observed in the first phalanges. Fig. 12 (diagram) shows the proximal width (DTp) and length (L) of the first phalanx. Stenonid horses of the *E. altidens/petralonensis/hydruntinus* group are very gracile. The caballoid horses show much variation in size and robustness (Fig. 12), which is difficult to reconcile with the single species concept of Azzaroli (1990). These horses include a large and robust species to which the names *Equus mosbachensis* and *E. taubachensis* are applied, but which probably all correspond to Forsten's (1988) *E. mosbachensis*. Then there is a group of robust horses of smaller size, to which the names *E. germanicus*, and *E. gallicus* are applied. This group corresponds to Forsten's *E. germanicus*. It is known from France, but no similar horses have been reported from Spain (Maldonado Diaz, 1996). Then there is a group with phalanges of similar length, which are more gracile (Torralba, Atapuerca TD10, TG and TE19, Solana de Zamborino, Pinilla del Valle, Cueva del Buho, etc.), to which the names *E. torralbae* and *E. antunesi* have been applied (Maldonado Diaz, 1996; Martín Penella, 1988), the former being the older name. These could correspond to Forsten's (1988) *E. caballus* (*E. ferus* or *E. przewalskii*). We tentatively assign the Valdavara 3 material to *E. torralbae*, but recognize the need of a more thorough study.

Steppe rhinoceros – *Stephanorhinus hemitoechus*

The P_{3/4} (Fig. 13/2) has smooth enamel, while in *Coelodonta* it is much more rugose. The tooth is within the metrical ranges of the P₃ of *Stephanorhinus kirchbergensis* and of the P₄ of the other species of this genus. The second phalanx of the third toe (Fig. 13/1) is much smaller than in *S. kirchbergensis*, but well in the metrical ranges of *S. hundsheimensis* and close to that of the remaining species (diagram Phal III-2 in Fig. 13). The first phalanges of the side toes are in the ranges for *S. hundsheimensis*, *S. hemitoechus* and the earlier *S. etruscus*, but are clearly larger than the later samples attributed to this species (the two smallest specimens in Fig. 13). The poor remains of a second upper premolar suggest that its crown had a length of about 24.4 mm at the crown base, which is very short.

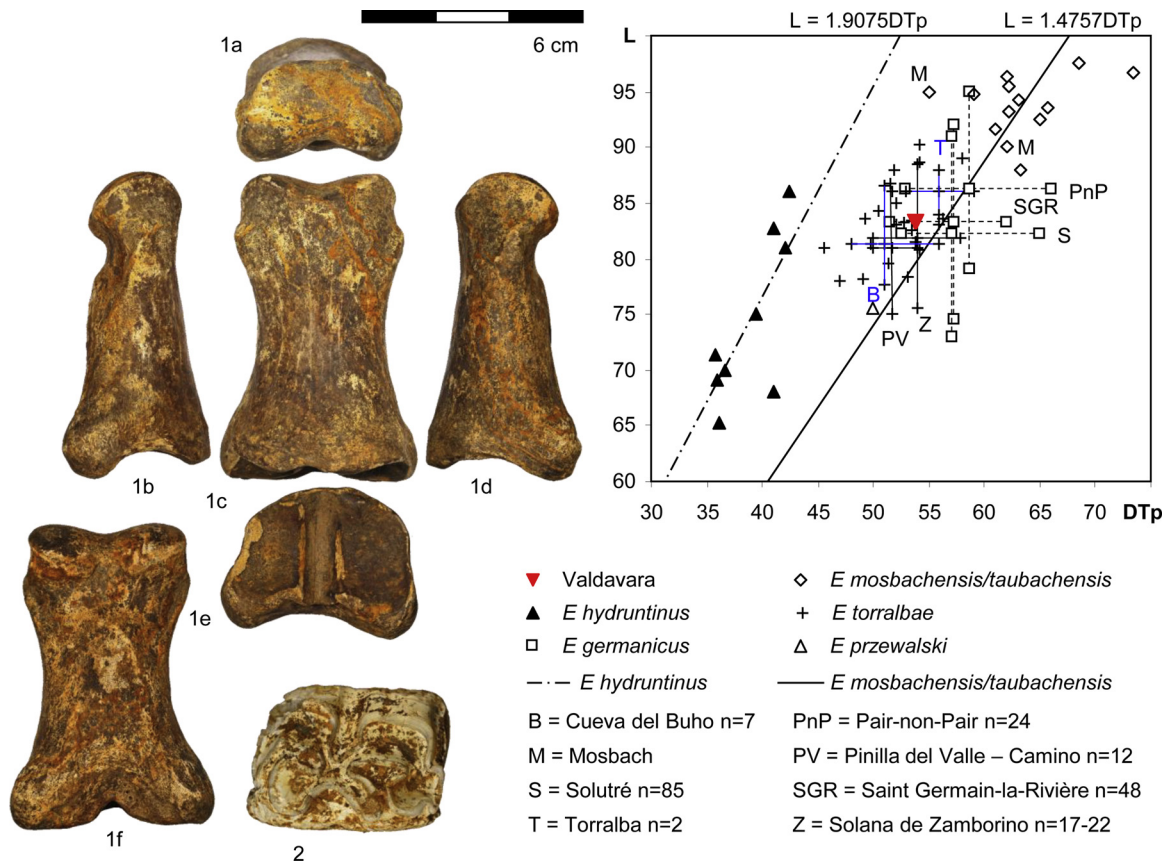


Fig. 12. Bivariate diagram of the proximal width (DTp) and length (L) of the first phalanx of *Equus* comparing the specimen from Valdavara 3 with *E. mosbachensis*/*E. taubachensis* from Ehringsdorf (Musil, 1975) and Mosbach (Von Reichenau, 1915); *E. germanicus*/*E. torralbae* from Atapuerca TD10 (IPHES, CENIEH), Atapuerca TG (MB), Atapuerca TE19 (CENIEH), Torralba (Maldonado Diaz, 1996), Solana del Zamborino (Martín Penela, 1988), Pinilla del Valle – Camino, Cueva del buho, Villacastín, Pedraza, and Valdegoba (all Maldonado Diaz, 1996); recent *E. przewalski* (Prat, 1980); *E. gallicus* from Solutré and Pair-non-Pair (Martin Penela, 1988) and Saint-Germain-la-Rivière (Prat, 1980) and *E. hydruntinus* from Lunel-Viel (Eisenmann and Mashkour, 1999), Arenero Santa Catalina, Madrid (MAN), Carihuela, Romanelli, Achenheim lower loess, Fontéchevade, Pradelles, Agios Georgios (all Maldonado Diaz, 1996). In some cases, minimum, mean and maximum of a sample are indicated. Lines indicate average proportions of the species. 1. Phalanx III-1 sin. (Val-3, 2009, 501): a) proximal, b) lateral, c) dorsal, d) medial, e) proximal, and f) plantar views. 2. P_{3/4} dext. (Val-3, 2011, level B, 66): occlusal view.

Fig. 12. Diagramme bivarié de la largeur proximale (DTp) et de la longueur (L) de la première phalange d'*Equus* comparant l'échantillon de Valdavara 3 avec *E. mosbachensis*/*E. taubachensis* d'Ehringsdorf (Musil, 1975) et Mosbach (Von Reichenau, 1915); *E. germanicus*/*E. torralbae* d'Atapuerca TD10 (IPHES, CENIEH), Atapuerca TG (MB), Atapuerca TE19 (CENIEH), Torralba (Maldonado Diaz, 1996), Solana del Zamborino (Martín Penela, 1988), Pinilla del Valle – Camino, Cueva del Buho, Villacastín, Pedraza et Valdegoba (tous Maldonado Diaz, 1996); *E. przewalski* récent (Prat, 1980); *E. gallicus* de Solutré et Pair-non-Pair (Martin Penela, 1988) et Saint-Germain-la-Rivière (Prat, 1980) et *E. hydruntinus* de Lunel-Viel (Eisenmann et Mashkour, 1999), Arenero Santa Catalina, Madrid (MAN), Carihuela, Romanelli, loess inférieur d'Achenheim, Fontéchevade, Pradelles, Agios Georgios (tous Maldonado Diaz, 1996). Dans certains cas, les valeurs minimales, moyennes et maximales d'un échantillon sont indiquées. Les lignes indiquent les proportions moyennes des espèces. 1. Phalange III-1 gauche (Val-3, 2009, 501) : vues a) proximale, b) latérale, c) dorsale, d) médiale, e) proximale et f) plantaire. 2. P_{3/4} droite (Val-3, 2011, niveau B, 66) : vue occlusale.

The rhinoceroses of the Western European Pleistocene belong to four species of the genus *Stephanorhinus*, to *Coelodonta* or to the giant *Elasmotherium* (Guérin, 1980, 1982). The Valdavara 3 material differs from: *Coelodonta* in having smoother enamel; *S. kirchbergensis* and the giant *Elasmotherium* in being smaller; the very small *S. etruscus* in being larger; and *S. hundsheimensis* in having a very small second premolar. The best fit is with *S. hemitoechus*. *Stephanorhinus hemitoechus* replaced *S. hundsheimensis* between about 500 and 450 ka. Initially the species may have been more gracile (*S. hemitoechus falconeri*), while after about 250 ka it was more robust (*S. hemitoechus hemitoechus*) (Van der Made, 2010a). The material from Valdavara 3 does not allow an attribution to one of these

two subspecies. The youngest record of *S. hemitoechus* is around 45 ka (Stuart and Lister, 2012).

Wild boar – *Sus scrofa*

The fossils with the morphology of a suid include a maxilla with a M³ with elongate shape and complex talon (Fig. 14/2). The P³ (Fig. 14/1) has a narrow paracone with high parapre- and parapostristas and relatively well-developed pre- and poststyles. There is a low protocone with its protopre- and protopostcristas, enclosing a fossa, which separates the proto- and paracone. A primocone (nomenclature of Van der Made, 1996) with well-developed pre- and postcristas projects a little lingually. This morphology occurs in *Sus scrofa*, while *Sus strozzi* tends to have a paracone that is conical and

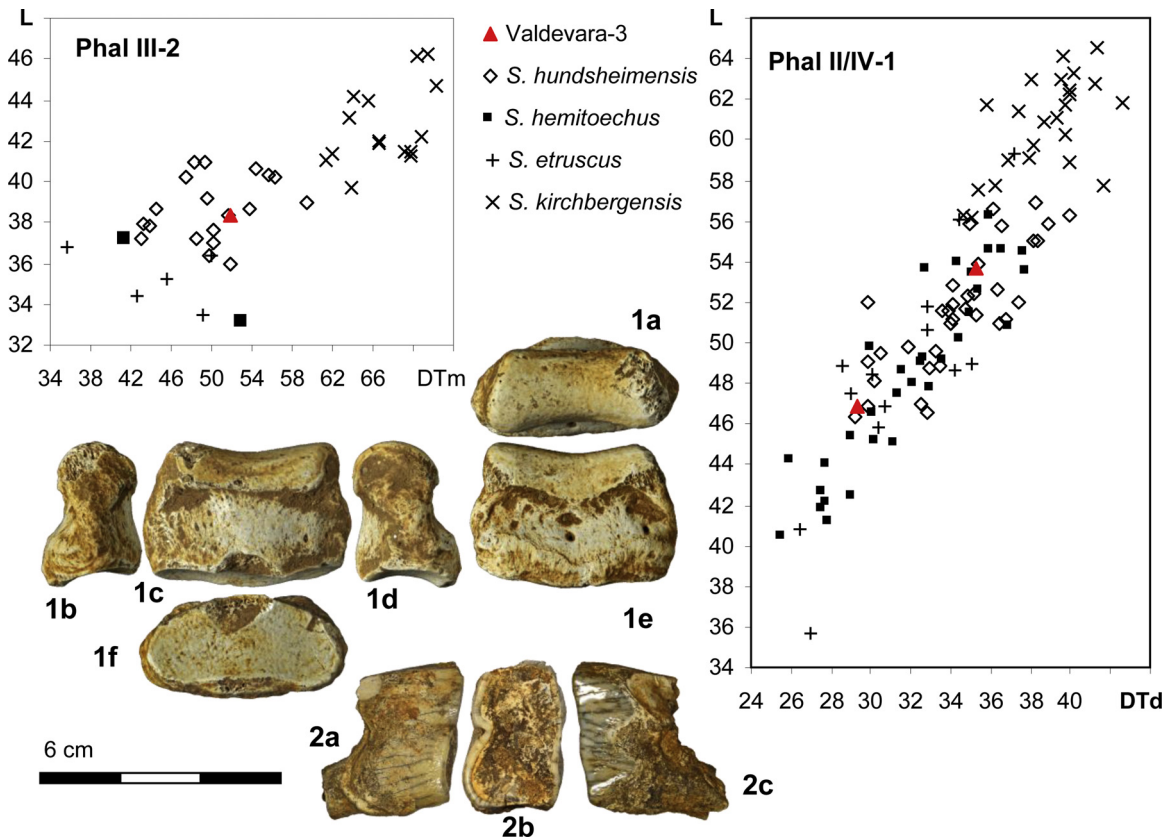


Fig. 13. Bivariate diagrams of the length (L) and maximal width (DTm) of the second central phalanx (Phal III-2) and the distal width (DTd) and length (L) of the first abaxial phalanx (Phal II/IV-1) comparing the phalanges of Valdavara 3 with those of different species of *Stephanorhinus*: *S. kirchbergensis* from Bilzingsleben (FSBFSUJ); *S. hemitoechus* from Arago (LPTUP), Bilzingsleben (FSBFSUJ), Atapuerca TD10 and TG (IPHES), Neumark Nord (FBFSUJ), *S. etruscus* from Valdarno (IGF), Atapuerca TD4, TD6 and TD7 (MB, CENIEH; IPHES), *S. hundsheimensis* from Hundsheim (NMW, IPUW), Mauer (SMNK), Miesenheim (RGZSM), *Stephanorhinus hemitoechus* from Valdavara 3. 1. Phal III-2 sin. (Val-3, 2009, 98): a) distal, b) lateral, c) dorsal, d) medial, e) plantar, and f) proximal views. 2. P₃ sin. (Val-3, 2009, 536): a) buccal, b) occlusal, c) lingual views.

Fig. 13. Diagrammes bivariés de la longueur (L) et de la largeur maximale (DTm) de la deuxième phalange centrale (Phal III-2) et de la largeur distale (DTd) et de la longueur (L) de la première phalange abaxiale (Phal II/IV-1) comparant les phalanges de Valdavara 3 avec celles de différentes espèces de *Stephanorhinus*: *S. kirchbergensis* de Bilzingsleben (FSBFSUJ); *S. hemitoechus* d'Arago (LPTUP), Bilzingsleben (FSBFSUJ), Atapuerca TD10 et TG (IPHES), Neumark nord (FBFSUJ), *S. etruscus* de Valdarno (IGF), Atapuerca TD4, TD6 et TD7 (MB, CENIEH, IPHES), *S. hundsheimensis* de Hundsheim (NMW, IPUW), Mauer (SMNK), Miesenheim (RGZSM), *Stephanorhinus hemitoechus* de Valdavara 3. 1. Phal III-2 gauche (Val-3, 2009, 98) : vues a) distale, b) latérale, c) dorsale, d) médiale, e) plantaire et f) proximale. 2. P₃ gauche (Val-3, 2009, 536) : vues a) buccale, b) occlusale, c) linguale.

much more massive, a protocone that is more conical and with less developed crests and a fossa that opens antero-lingually and a less well-developed primocone. The P₃'s from Valdavara 3 are narrow as in *Sus scrofa*, while those of *Sus strozzi* are wider (Fig. 14). One of the Valdavara 3 specimens is the longest one in the graph, the next longest one being from the early middle Pleistocene of Koneprusy, while the other fossils are from late Pleistocene or Holocene localities.

At present two species of Suidae are recognized from the Pleistocene of the European mainland, *Sus strozzi* from the early Pleistocene and *Sus scrofa* from the latest early Pleistocene onwards (Faure and Guérin, 1984; Van der Made, 1992; Van der Made and Moyà-Solà, 1989). These differ in various features, including the width of their premolars (Van der Made, 1999a). The narrow P₃ indicates that the pig from Valdavara 3 is the common wild boar *Sus scrofa*. How and when *Sus scrofa* replaced the earlier pigs in Europe is still a matter of discussion, but it was present shortly after

1 Ma (Van der Made et al., 2017). *Sus scrofa* was subject to significant changes in its body size. The earliest populations had large body sizes (Parfitt et al., 2010), while later it was generally small, though in Taubach and Jaurens it was also large (Faure and Guérin, 1983; Hünermann, 1977) and at present it is very small. Though sample sizes are small in the comparison (Fig. 14), the wild boar from Valdavara 3 seems to have been very large.

Roe deer – *Capreolus* sp.

The pedicle of an antler fragment (Fig. 15/A1) is wholly situated on top of the brain case and not partially over the orbita. This is common in the Capreolinae, where the posterior limit of the frontals and antler base, moved backwards. The antler itself has a strongly perlated burr and surface of the main beam. This is typical of *Capreolus*. The upper molars (Fig. 15/A2) are small. However, the P₂ is not outside the ranges of the earlier samples (Fig. 15/B). A maxilla with two molars, which is part of the first collection and has not been found in situ, seems to fit a molar

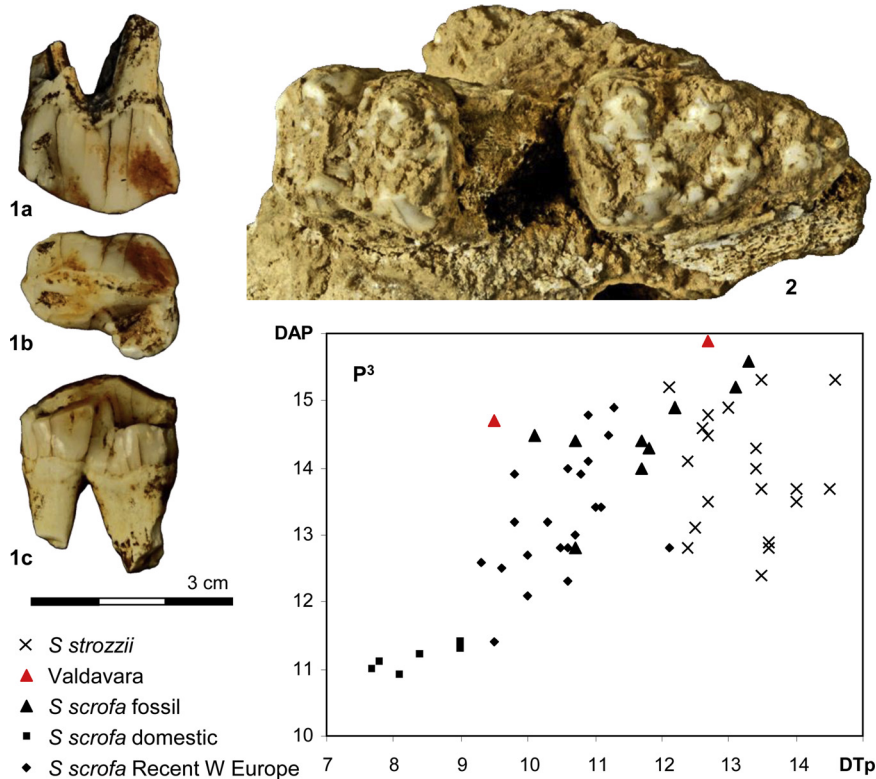


Fig. 14. Bivariate diagram comparing posterior or maximal width (DTP) and length (DAP) of the specimens from Valdavara 3 with the upper third premolars of *Sus strozzi* from Gerakarou (AUT), Senèze (cast NMB), Upper Valdarno (IGF, AVP), Ceyssaguet (MNPE); fossil *Sus scrofa* from Koneprusy (NMP), Mosbach (NMM), Taubach (IQW), Pinilla del Valle (UCM), Cueva de Saldarañao (ETSI), (sub)fossil domestic pig from Cueva de Saldarañao (ETSI), recent *Sus scrofa* from Spain (MNCN, UPVB), the Netherlands (NBC), Germany (NBC, HUJ). *Sus scrofa* from Valdavara 3. 1. P³ sin. (Val-3, 2010, lev. B, 33): a) buccal, b) occlusal, and c) lingual views. 2. M²⁻³ sin. (Val-3, 2010, lev. B, 152): occlusal view.

Fig. 14. Diagramme bivarié comparant la largeur (DTP) et la longueur (DAP) postérieure ou maximale des spécimens de Valdavara 3 avec les troisièmes prémolaires supérieures de *Sus strozzi* de Gerakarou (AUT), Senèze (NMB), Upper Valdarno (IGF, AVP), Ceyssaguet (MNPE); *Sus scrofa* fossile de Koneprusy (NMP), Mosbach (NMM), Taubach (IQW), Pinilla del Valle (UCM), Cueva de Saldarañao (ETSI), porc domestique (sub) fossile de Cueva de Saldarañao (ETSI), *Sus scrofa* récent d'Espagne (MNCN, UPVB), des Pays-Bas (NBC), d'Allemagne (NBC, HUJ). *Sus scrofa* de Valdavara 3. 1. P³ gauche (Val-3, 2010, niv. B, 33) : vues a) buccale, b) occlusale et c) linguale. 2. M²⁻³ gauche (Val-3, 2010, niv. B, 152) : vue occlusale.

that was excavated from level B (Fig. 15/2). While some recognize only one species, *C. capreolus*, up to four species are recognized by other authors, which differ in size and body proportions (Kahlke, 2001; Pfeiffer, 1998). The size of *Capreolus* decreased in time and this is documented for the M₃, astragalus, metatarsal and first phalanx (Van der Made, 1998; Van der Made et al., 2017). The exact moment when the present small size was reached is not clear, but this may have been very late. Here the size changes in the P₂ are documented (Fig. 15B), but it is difficult to see a size trend. Maybe this is so because this tooth is more variable than other teeth. We assign the material to *Capreolus* sp.

Red deer – *Cervus elaphus*

A lower premolariform tooth (Fig. 15/3) has the morphology of a D₂, rather than a P₂. The low and elongate tooth is comparable in size to the *Cervus elaphus* D₂ while the P₂ of this species are wider and the P₂ of *Dama* shorter (Fig. 15/B). *Cervus elaphus* appeared in western Europe around 1 Ma (Van der Made et al., 2017). Initially it had antlers with no crown, but after about 500 ka, it developed a crown. It had significant fluctuations in size (Van der Made, 2011; Van der Made et al., 2014): it was small from the later part of

MIS5 until MIS3, large in MIS2 and at present it is small, but there is overlap between the populations with large and small sizes. The Valdavara 3 material is insufficient to estimate the average size of the bones or teeth of the population.

Chamois – *Rupicapra* cf. *pyrenaica*

A horn core (Fig. 16/2) is straight with a small diameter as in *Rupicapra*, while other small bovids of the European Pleistocene tend to have larger and curved horn cores with flattened or triangular sections. The upper molars and premolars (Fig. 16/1) are worn, but must have had high crowns. The molars have no lingual interlobular columns. This morphology occurs in the Caprinae. The molars have well-developed paraexocristas. The size is smaller than in *Ovis*, *Capra* and *Hemitragus*, but fits *Rupicapra*. The small straight and round horn core and the small dentition of caprine morphology clearly indicate *Rupicapra*. Two living species are recognized: *R. pyrenaica* from the Cantabrian Mountains, the Pyrenees and central Apennines and *R. rupicapra* from the Alps, central Europe, Balkans, Caucasus, and NE Turkey (Aulagnier et al., 2009). It has been suggested that *R. pyrenaica* dispersed during the middle Pleistocene into

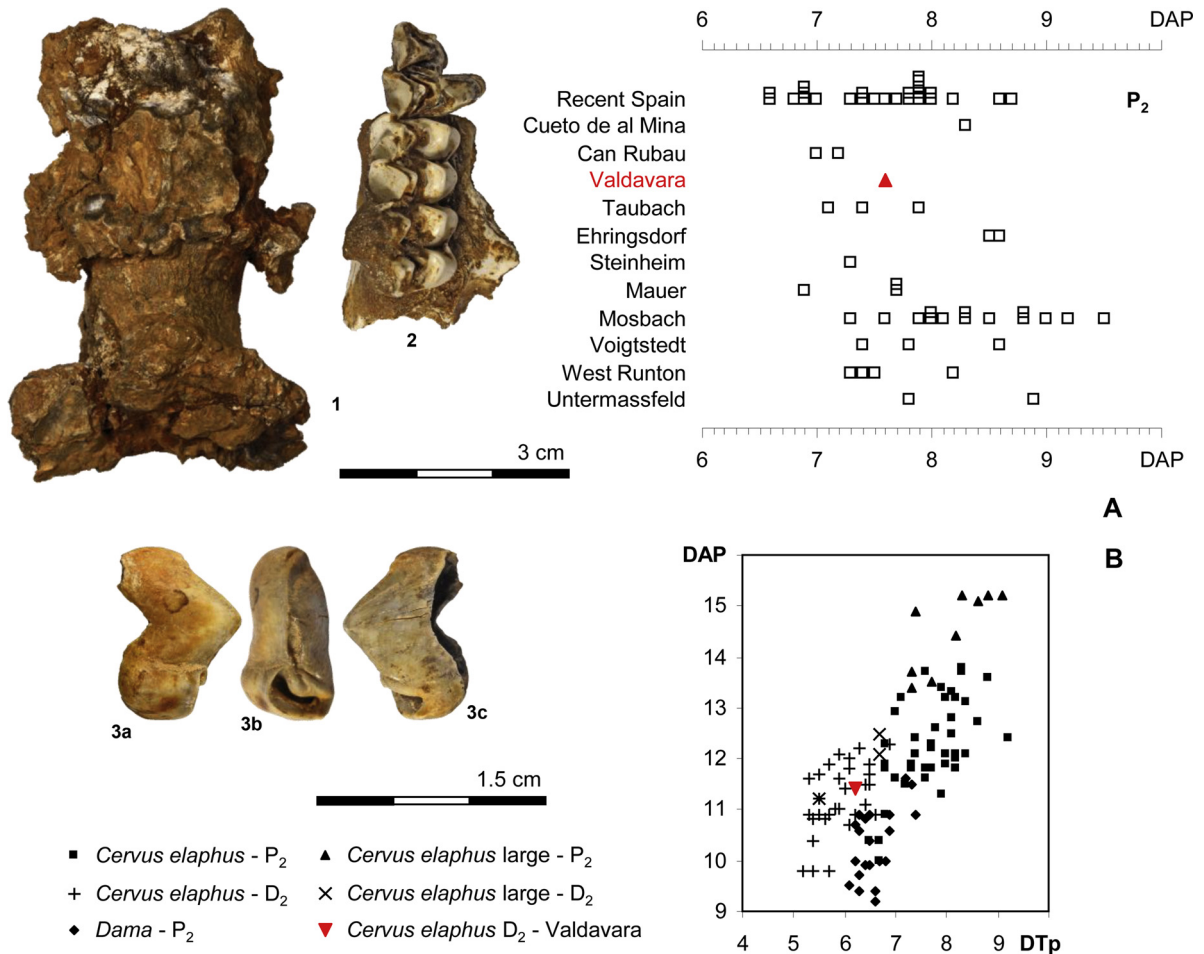


Fig. 15. *Capreolus* from Valdavara 3. 1. Frontal and antler base sin. (Val-3, 2010, lev. B, 514): medial view. 2. Maxilla dext. with M²⁻³ (Val-3, 2009, 255) and right M¹ (Val-3, 2010, lev. B, 23) fit together: occlusal view. *Cervus elaphus* from Valdavara 3. 3. D₂ sin. (Val-3, 2011, 21): a) buccal, b) occlusal, and c) lingual views. A. The variation in size of *Capreolus*, as indicated by the length (DAP) of the second lower premolar (P₂). The localities are ordered from old (bottom) to young (top): Untermassfeld (IQW), West Runton (NHM), Voigtstedt (IQW) and Mosbach (NMM), Mauer (SMNK), Steinheim am Murr (SMNS), Ehringsdorf (IQW), Taubach (IQW), Valdavara 3, Can Rubau (CIAG), Cueto de la Mina (MNCN), Spain – recent (MNCN). B. Bivariate diagram comparing the *C. elaphus* tooth from Valdavara 3 with the P₂ of *Dama* from Atapuerca TG10 (Van der Made, 1999), Azokh (MUB), and Spain (recent; MNCN); the P₂ of small-sized *C. elaphus* from Atapuerca TG10 (Van der Made, 1999b), Azokh (MUB), Abric Romaní (IPHES), Cueva de la Paloma (MNCN), Spain (recent; MNCN); the D₂ of small-sized *C. elaphus* from Atapuerca TG10 (Van der Made, 1999b), Azokh (MUB), Abric Romaní (IPHES), Cueva de la Paloma (MNCN), Mosbach (NMM), Mauer (SMNK), Miesenheim (RGZSM), Arago (LPTUP), Bilzingsleben (FBFSUJ), Las Majolicas (MNCN), Murr (SMNS), Pinilla del Valle (UCM); and the P₂ and D₂ of large sized *C. elaphus* from Neumark Nord (LVH).

Fig. 15. *Capreolus* de Valdavara 3. 1. Base et frontal de bois de cervidé gauche (Val-3, 2010, niv. B, 514) : vue médiale. 2. Maxilla droite avec M²⁻³ (Val-3, 2009, 255) et M¹ droite (Val-3, 2010, niv. B, 23) : vue occlusale. *Cervus elaphus* de Valdavara 3. 3. D₂ gauche (Val-3, 2011, 21) : vues a) buccale, b) occlusale et c) linguale. A. Variation de la taille de *Capreolus*, comme indiqué par la longueur (DAP) de la deuxième prémolaire inférieure (P₂). Les localités sont classées de la plus ancienne (en bas) à la plus jeune (en haut) : Untermassfeld (IQW), West Runton (NHM), Voigtstedt (IQW) et Mosbach (NMM), Mauer (SMNK), Steinheim am Murr (SMNS), Ehringsdorf (IQW), Taubach (IQW), Valdavara 3, Can Rubau (CIAG), Cueto de la Mina (MNCN), Espagne – récent (MNCN). B. Diagramme bivarié comparant la dent de *C. elaphus* de Valdavara avec la P₂ de *Dama* d'Atapuerca TG10 (Van der Made, 1999), Azokh (MUB) et Espagne (récente, MNCN); le P₂ de *C. elaphus* de petite taille d'Atapuerca TG10 (Van der Made, 1999b), Azokh (MUB), Abric Romaní (IPHES), Cueva de la Paloma (MNCN), Espagne (récent, MNCN); le D₂ de *C. elaphus*, de petite taille, d'Atapuerca TG10 (Van der Made, 1999b), Azokh (MUB), Abric Romaní (IPHES), Cueva de la Paloma (MNCN), Mosbach (NMM), Mauer (SMNK), Miesenheim (RGZSM), Arago (LPTUP), Bilzingsleben (FBFSUJ), Las Majolicas (MNCN), Murr (SMNS), Pinilla del Valle (UCM); P₂ et D₂ de *C. elaphus* de grande taille de Neumark nord (LVH).

Europe and *R. rupicapra* in the late Pleistocene, displacing the former in most of Europe, but leaving relict populations in Spain and Italy (Crégut-Bonnoure and Guérin, 1996). Analyses of the DNA and microsatellites suggest the existence of one to three species (Pérez et al., 2014, 2017; Rodríguez et al., 2009). Pleistocene fossils from Iberia have recently been assigned to *R. pyrenaica* (Arceredillo-Alonso, 2015). We cannot discuss the taxonomy of the Pleistocene

Iberian chamois based on the Valdavara 3 material, and therefore assign those specimens to *R. cf. pyrenaica*.

Bison – *Bison* aff. *priscus*

The molars have high crowns, well-developed interlobular columns and well-developed buccal styles and ectocristas or lingual stylids and ectocristids (Fig. 17/2). This is as in the Bovini, while the Caprinae lack interlobular columns and have less pronounced ectocristas and lingual

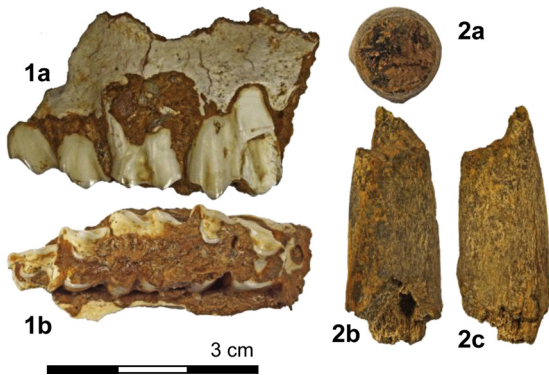


Fig. 16. *Rupicapra cf. pyrenaica* from Valdavara 3. 1. Maxilla sin. P³–M² (Val-3, 2010, 611): a) buccal, and b) occlusal view. 2. Horn core (Val-3, 2009, 506): a) distal, and b–c) side views.

Fig. 16. *Rupicapra cf. pyrenaica* de Valdavara 3. 1. Maxillaire gauche P³–M² (Val-3, 2010, 611) : vues a) buccale et b) occlusale. 2. Cœur de bois de cervidé (Val-3, 2009, 506) : vues a) distale et b–c) latérales.

stylids and ectocristids. Two distal metatarsals (Fig. 17/1) have the lateral and medial side with the shape of a Bordeaux wine bottle as in *Bison* and not of a Bourgogne bottle as in *Bos* (Gee, 1993). In side view, the D₂ (Fig. 17/3) has an anterior edge (the parastylid or precristid), which lowers gradually from the tip to the base. This is as in the P₂ and D₂ of *Bison*, whereas in *Bos* (and *Bubalus*) it extends more anteriorly at midheight (Fig. 17.4). The roots of the tooth are not preserved, but based on its small size, the tooth is interpreted as a D₂ (Fig. 17 bivariate diagrams). The tooth is very small, even for a D₂.

The morphology of the remains indicates *Bison*. Different authors recognize different species or subspecies of *Bison* in Europe (Crégut-Bonnoure and Guérin, 1996; Sher, 1997; Van der Made et al., 2017), which differ in size, robusticity of the metapodials, and in skull and horn core shape. *Bison schoetensacki* survived till the early late Pleistocene, but after its extinction *B. priscus* became the most widespread European bison (Van der Made et al., 2017). Work in progress suggests that this species may have arisen from a smaller middle Pleistocene form. Recently, *B. bonasus* and another similar small form have been interpreted to have arisen from interbreeding of *B. priscus* and *Bos primigenius* (Soubrier et al., 2016). The bison from Valdavara 3 probably represents a still not yet very large stage of the *B. priscus* lineage.

Indeterminate mammal – Mammalia indet.

A phalanx is gracile and curved with a very wide proximal end (Fig. 18). The proximal articular facet has some damage at the dorsal side, because of which it is not possible to observe its shape there. The facet is concave in all directions. Near the plantar side of the facet, there is a furrow in the middle, but it does not continue dorsally. The distal articulation is convex in dorsoventral direction and completely flat in transverse direction. Its size is comparable to that of the central phalanges of a cat. However, it differs from those of small carnivora such as *Felis* and mustelids in that these have a clear furrow in the middle of the distal articulation. In *Vulpes* and the Lagomorpha, the phalanx is straight and its proximal facet is oriented more

vertically with parallel lateral edges. The first phalanges of *Macaca* have a shallower depression in the middle of the distal articular surface and has the proximal surface of a completely different shape and oriented more vertically (in dorsoventral direction). They are also clearly larger. The first phalanges of *Castor* are less curved and those of *Hystrix* tend to be more robust with more vertically oriented proximal facets. Their phalanges have less widened proximal ends. The first phalanges of *Erinaceus*, the largest insectivore in the Pleistocene of Europe, are much smaller. We did not find a taxon with similar features and therefore cannot assign the phalanx from Valdavara 3 to a taxon.

4.2. Preliminary taphonomy

Although a complete taphonomic study has not been performed, some preliminary observations can be made. Punctures and scores associated with biting and chemical corrosion by digestion have been identified in the epiphysis of the immature tibiotarsus and the humerus of *Pyrrhocorax graculus* (Fig. 3/4c). These alterations may be caused by nocturnal raptors, like owls (Andrews, 1990). Evidence of human activity has not been identified on the bird bones, which seem to have accumulated due to the action of non-human predators. The damage on corvid and rabbit bones indicates that carnivores living in the immediate surroundings of the cave were the primary accumulator agent. All the rabbit remains exhibit manganese deposits and fissures produced by humid conditions (Fernández-Jalvo and Andrews, 2016). The tarsal bones show a slight thinning of the articular surfaces produced by digestion. One of the phalanges presents carnivore damage. However, the predator cannot be identified due to the paucity of remains. The fish vertebra indicates a size in the range for a prey of the fish eagle. Alternatively, it could have been brought into the cave by the otter. Except the *Haliaeetus albicilla* bone, all the bird remains show the typical black surfaces associated with manganese deposits. This indicates the presence of water during the formation of the deposit (Fernández-Jalvo and Andrews, 2016).

The taphonomical analysis of the small-vertebrate remains has included 571 elements. The skeletal element frequencies indicate a good representation of small-vertebrate skeleton elements, especially for rodents. The differential anatomical representation, the presence of breakage and, especially, the digestion marks show that the origin of these remains can be related with predation. Although the remains show lower skeletal representation and higher breakage rates than those expected for any predator according to Andrews (1990), it results coherent with fossil assemblages and probably related with post-depositional agents. The percentage of small-vertebrate digested elements is low (21.7%): 22.9% of incisors, 19.8% of molars and 39.1% of postcranial remains. The most significant pattern is the clearly predominant light digestion degree (16.5%), in less proportion the moderate degree (4.4%) and the heavy digestion is rare (0.9%). These few number of digested elements, reinforced by the slight signs of digestion, indicate that the fossils were accumulated by some type of owl, inside the Category 1 or 2 (*sensu* Andrews, 1990; Fernández-Jalvo and Andrews, 1992), probably the

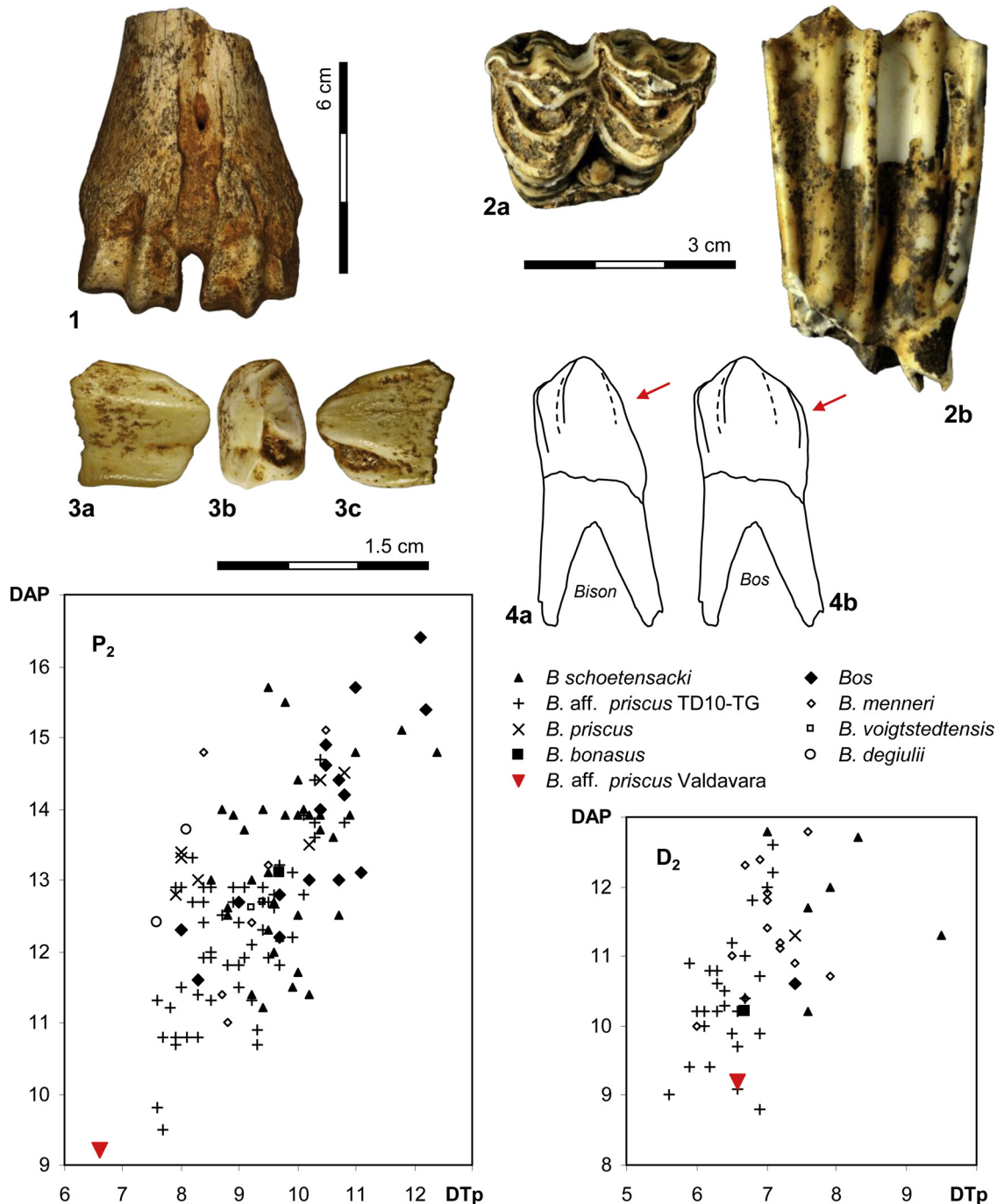


Fig. 17. *Bison aff. priscus* from Valdavara 3. 1. Distal part of metatarsal (Val-3, 2009, 519): dorsal view. 2. $M^{1/2}$ sin. (Val-3, 2009, 91): a) occlusal, and b) buccal views. 3. D_2 sin. (Val-3, 2009, 521): a) buccal, b) occlusal, and c) lingual views. 4. Schematic view of the left P_2 of *Bison* (4a) and *Bos* (4b). Bivariate diagrams comparing width (DTp) and length (DAP) of the tooth from Valdavara 3 with the P_2 and D_2 of: *Bi. menneri* from Untermassfeld (IQW), *Bi. voigtstedtensis* from Voigtstedt (IQW), Mauer (RKUH), Atapuerca TD8 (IPHES); *Bi. degulii* from Pirro Nord (IGF), *Bi. schoetensacki* from Vallonnet (MPRM), Apollonia 1 (AUT), Stránská Skála (MMB), Süßenborn (IQW), Isernia la Pineta (DSGPUF), Mosbach (NMM), Mauer (SMNK), Vértesszölös (HGSB), Bilzingsleben (FBFSUJ), Petralona (AUT), Azokh V (MUB); *Bi. aff. priscus* from Atapuerca TD10 and TG10-11 (MB, IPHES, CENIEH); *Bi. priscus* from Port Katon (AHAPMR); recent *Bi. bonasus* (IPHES, MZSUF), and *Bos primigenius* from Neumark Nord (LVH), Pinilla del Valle – Camino (UCM), Abric Romaní (IPHES), Paglicci (DSGPUF).

Fig. 17. *Bison aff. priscus* de Valdavara 3. 1. Partie distale du métatarse (Val-3, 2009, 519): vue dorsale. 2. $M^{1/2}$ gauche (Val-3, 2009, 91): vues a) occlusale et b) buccale. 3. D_2 gauche (Val-3, 2009, 521): vues a) buccale, b) occlusale et c) linguale. 4. Vue schématique de la P_2 gauche de *Bison* (4a) et *Bos* (4b). Diagrammes bivariés comparant la largeur (DTp) et la longueur (DAP) de la dent de Valdavara 3 avec les P_2 et D_2 de *Bi. menneri* d'Untermassfeld (IQW), *Bi. voigtstedtensis* de Voigtstedt (IQW), Mauer (RKUH), Atapuerca TD8 (IPHES); *Bi. degulii* de Pirro nord (IGF), *Bi. schoetensacki* de Vallonnet (MPRM), Apollonia 1 (AUT), Stránská Skála (MMB), Süßenborn (IQW), Isernia la Pineta (DSGPUF), Mosbach (NMM), Mauer (SMNK), Vértesszölös (HGSB), Bilzingsleben (FBFSUJ), Petralona (AUT), Azokh V (MUB); *Bi. aff. priscus* d'Atapuerca TD10 et TG10-11 (MB, IPHES, CENIEH); *Bi. priscus* de Port Katon (AHAPMR); *Bi. bonasus* récent (IPHES, MZSUF) et *Bos primigenius* de Neumark nord (LVH), Pinilla del Valle – Camino (UCM), Abric Romaní (IPHES), Paglicci (DSGPUF).



Fig. 18. First phalanx of an indeterminate mammal (Val-3, 2011, lev. B, 27).

Fig. 18. Première phalange d'un mammifère indéterminé (Val-3, 2011, niv. B, 27).

Tawny Owl (*Strix aluco*) or the Eurasian Eagle-Owl (*Bubo bubo*). Both species are opportunistic and sedentary predators (Mikkola, 1983). The fossil association is therefore representative of the ecosystem in the vicinity of the cave at the time when the remains were deposited.

No digestion marks are observed in bat teeth, but such marks are not easily detectable because of the high resistance of the enamel (Fernández-Jalvo, 1995). The species identified frequent caves, so it could be related with in situ mortality, but occasional predation by nocturnal birds of prey cannot be discounted (Kowalski, 1995). The same applies to the amphibian and reptiles. Some of them tend to use caves as refuges (Blain et al., 2008; Mikkola, 1983), but some remains exhibit digestion marks that related them directly with the predation. As it happens with fish remains, small mammal, amphibian and reptile remains show manganese and fissures related to humid conditions and flooding, which is coherent with a fossiliferous cave environment.

Eighteen species are represented by a single individual (Table 2). The 11 exceptions are: *Microtus agrestis*, (14), *M. arvalis* (3), *Terricola* sp. (13), *Pliomys coronensis* (9), *Sorex* sp. (4), *Talpa* (2/3?), *Canis lupus* (1 adults, 1 juvenile), *Ursus arctos* (2), *Equus* cf. *torralbae* (2 adult, 1 juvenile), *Sus scrofa* (1 adult, 1 juvenile) and *Bison* sp. (1 adult, 1 juvenile). The small-vertebrates are recovered in a different way and the MNI is thus not comparable to that of the large mammals. The species vary greatly in number of specimens between one or a few to 23 (*Stephanorhinus hemitoechus*), 25 (*Bison* aff. *priscus*), 27 (*Equus* cf. *torralbae*), and 39 (*Canis lupus*). Quite often, a fossil association is dominated by two or three species, which are well represented in numbers of specimens and individuals, but this does not seem to be the case. Generally, it is assumed that species living in larger groups tend to be better represented in a fossil association. The representation in Valdavara 3 might reflect this to some extent.

4.3. Archeology

Human activities in Valdavara 3 are testified by a small but diagnostic lithic assemblage (Fig. 19) and some cut-marks on bone remains. The lithic assemblage is composed of 18 artifacts, twelve from the collapsed sediments and six recovered during the excavation. Quartz is the dominant raw material ($n=11$), but quartzite ($n=5$) and sandstone ($n=2$) are also represented. The absence of flint is noteworthy, since this material is well represented in the Upper Paleolithic assemblage of the nearby Valdavara Cave. Rolled cortical surfaces indicate that these materials were collected in alluvial formations. Flakes and flake fragments are the most abundant artifacts ($n=15$), and three cores have been also identified. Instead, we have not found any retouched artifact. Large flakes are clearly dominant and most of them show cortical surfaces. Neither Levallois nor blade products have been identified. Two of the cores exhibit very expedient reduction sequences and yielded only a few flakes. However, the third one is most significant from the technical point of view. It is a discoidal core that shows a clearly hierarchical structure (Fig. 19/6). One surface was used for flaking, while the opposite surface, which remains mainly cortical, was used to prepare the striking platforms. This reduction strategy is widespread in Middle Paleolithic technologies.

Modifications of faunal remains by humans included cut-marks and bone breakage. We have identified cut-marks on 28 bone fragments (1.9% of the faunal remains) (Fig. 20), including some remains corresponding to bison, red deer, and rhinoceros. They are slicing and sawing marks that are related to different actions, like defleshing, disarticulation and removal of viscera. Carnivore damage is less common. Only six elements showed tooth-marks associated with the action of large carnivores. One bone, a proximal femoral epiphysis of *S. hemitoechus*, showed both cut-marks and carnivore damage. Concerning the non-biological processes, the most common modifications are associated with weathering (30.1% of bone remains), manganese coatings (29.7%) and trampling (24.6%).

5. Discussion

While Spain is rich in paleontological and archeological sites, its northwestern corner, Galicia, is much poorer. Only one pre-Pleistocene fossil mammal locality is known. This is As Pontes, of Oligocene age, and it yielded few remains of two species of rodents, some of an anthracothere (cf. *Elomeryx*), a crocodile, fish, mollusks, and plants (Cabrera et al., 1994; López-Martínez et al., 1993). No early and middle Pleistocene localities and only a few late Pleistocene and Holocene sites with fauna and/or archaeology are known (Grandal-d'Anglade et al., 1997; López-González, 2003).

The majority of the Galician paleontological sites are characterized by reduced faunal spectra, often dominated by bear remains. This scarcity of sites is probably caused by the high elevation and geology of Galicia. Areas with erosion predominate, while areas with sedimentation are less extensive. The Paleozoic granites, quartzites and slates, which acid soils prevent from fossil preservation, are dominant, while limestone formations are uncommon and

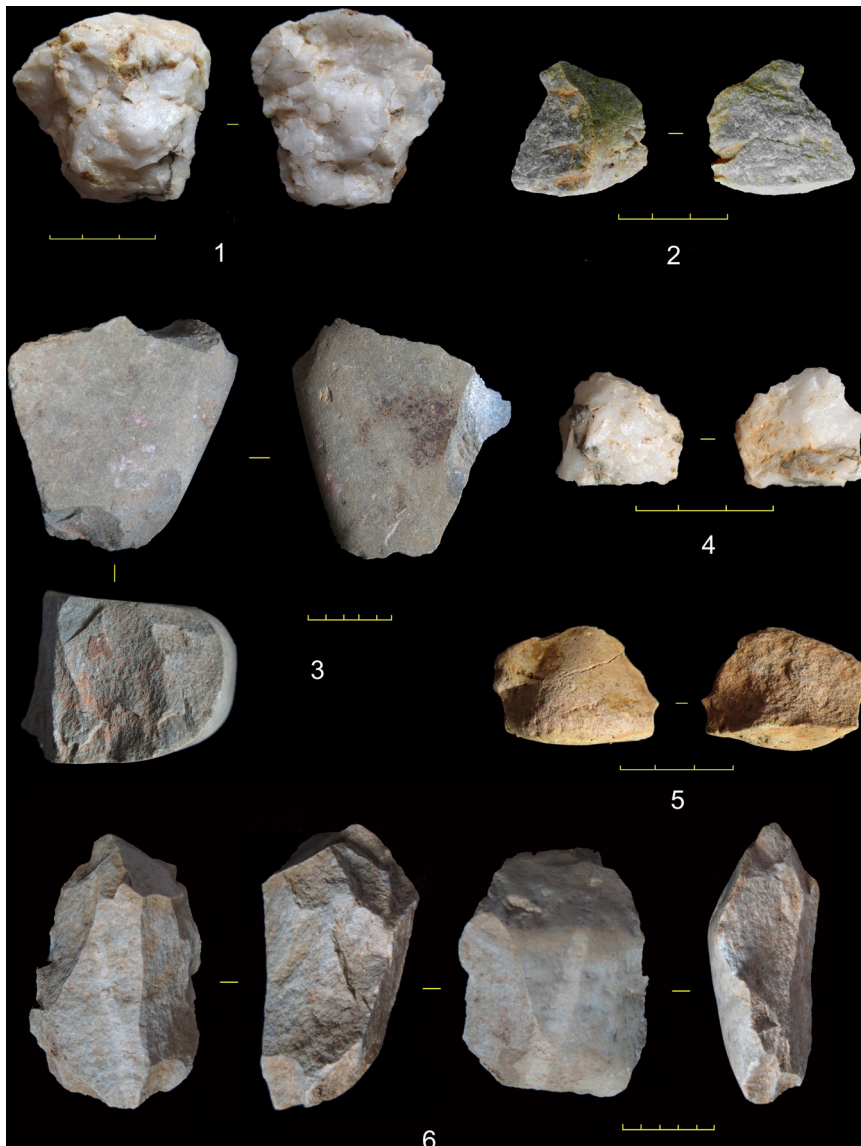


Fig. 19. Lithic remains from Valdavara 3: quartz flakes (1, 4), quartzite flake (2), sandstone flake (5) and quartzite cores (3, 6).
Fig. 19. Restes lithiques de Valdavara 3 : éclats de quartz (1, 4), éclat de quartzite (2), éclat de grès (5) et nucléus de quartzite (3, 6).

karstic systems are therefore rare. Due to the scarcity of caves, Galicia has been relatively neglected by the Spanish researchers interested in the Paleolithic. However, a new research project has recently reported previously unknown late Pleistocene sites (de Lombera-Hermida and Fábregas, 2011), like Valdavara 3.

Fig. 21 indicates the presence of the different taxa in the Pleistocene and Holocene faunas of Galicia. As indicated by radiometric dating and biochronology, Valdavara 3 is the oldest of these sites. It is the only one with a varied fauna dating to the early late Pleistocene (MIS5d) and for the first time it is possible to know the fauna of this age from this part of Spain. The fauna from Valdavara 3 consists of at least 40 species of vertebrates: 1 fish, 1 anuran, 5 squamate reptiles, 3 birds and 30 mammal species.

Due to the partial destruction of the site and the small excavated area, interpreting the site formation processes is particularly difficult. We do not know the original morphology of the cavity and the excavated zone seems to be a marginal sector. Nevertheless, the data suggest that different processes contributed to the formation of this assemblage. The scarcity of carnivore tooth-marks on bones, coprolites and juvenile carnivores indicate that the use of the cave as a carnivore den was not the dominant formation process. Whereas the lithic industry and anthropogenic marks indicate that the hominids have been present in the cavity and acted on some bone remains, residential occupations seem unlikely due to the low number of lithic remains. Human activities would be related to sporadic visits in which some artifacts usually transported

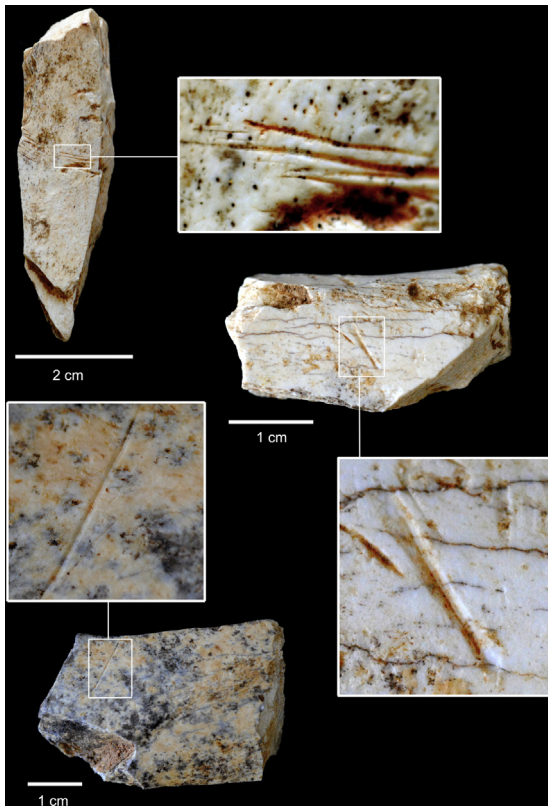


Fig. 20. Examples of cut-marks from Valdavara 3.

Fig. 20. Exemples de marques de coupe de Valdavara 3.

during movements were abandoned. Given the limited role played by humans and carnivores, it is likely that a significant part of the accumulation of large mammal remains was related to the presence of a natural trap in some part of the cavity. This interpretation has been proposed for other sites that show a high taxonomic diversity (Gilbert and Martin, 1984; Gómez-Olivencia et al., 2015; Ollé et al., 2005; Pokines et al., 2011).

5.1. Sites with scarce evidence of human presence

Pre-Pleistocene fossil localities are common and do not have indications of human presence. However, towards the end of the Pleistocene humans became increasingly important in the formation of sites with fossils. Archaeological assemblages characterized by huge amounts of faunal remains and scarce evidence of human presence are common throughout the middle and late Pleistocene. They have been called “paleontological sites with indices of human presence” (Brugal and Jaubert, 1991) and indicate mobility strategies that were frequent in the Lower and Middle Paleolithic. Most assemblages correspond to cave sites, although open-air occurrences are not unknown (Daura et al., 2013).

Two processes are normally used to explain the formation of such bone assemblages. On the one hand, animals may enter the caves by accidental falls in vertical shafts acting as natural traps (see Bar-Oz et al., 2012; Marder

et al., 2011; Moncel et al., 2008; Wolverton, 2006). On the other hand, faunal accumulations may be related to non-human predators using the caves as dens (Baryshnikov and Tsoukala, 2010; Diedrich and Žák, 2006; Fosse, 1996; Fosse et al., 1998; Stiner, 1991; Villa et al., 2010). Among the latter, the caves used by bears for hibernating and denning tend to exhibit huge amounts of bear remains (see Andrews and Turner, 1992; Argenti and Mazza, 2006; Grandal-d’Anglade, 1993; Quilès et al., 2006; Stiner, 1999; Stiner et al., 1996; Torres et al., 2007). However, these natural formation processes are not mutually exclusive and faunal assemblages are normally palimpsests formed by different inputs.

In these sites, human presence is attested to small lithic assemblages and some modified bones, resulting from short visits for exploiting the animal carcasses accumulated by natural agents. In general, introduction of animal resources by humans and residential occupations are discarded. However, some scholars have questioned whether the lithic artifacts found in these sites really indicate human presence. Villa and Soressi (2000) suggested that the lithics from carnivore dens might correspond to redeposited artifacts introduced into the caves by natural processes. The association between bones and lithics would be purely accidental. However, this can hardly be considered as a general explanation and the nature of the bone and lithic association must be considered on a case-by-case basis, taking into account taphonomical data and artifact refitting.

These assemblages are common throughout the middle and late Pleistocene in the Iberian Peninsula: Trincherá Galería (Ollé et al., 2005), Torrejones (Díez et al., 1998), Lezetxiki (Alvarez-Alonso and Arrizabalaga, 2012), Tossal de la Font Cave (Olària et al., 2005), Teixoneres (Rosell et al., 2010), 120 Cave (Terradas and Rueda, 1998), Ermitons (Maroto, 1985), Mollet (Maroto et al., 2012). Some sites have been interpreted as natural traps (Trincherá Galería) and others as hyaena (Torrejones, Teixoneres, Mollet) or bear (Lezetxiki) dens. Most of them have been dated to the end of the middle and the early late Pleistocene. Valdavara 3 is another site with scarce indications of human presence.

5.2. Environment and biogeography

None of the species is indicative of cold or glacial environments. In Europe North of the Pyrenees, the climatic cycles resulted in an alternation of “glacial” and “interglacial” faunas. Initially, this was not the case in Iberia, which was a refugium for the “interglacial” faunas. However, during the latest glacial periods, “glacial” taxa penetrated the Peninsula. This is the case with *Mammuthus primigenius*, which is known from many sites in Spain, the southernmost being Padul in the province of Granada (Aguirre et al., 1973; Álvarez-Lao et al., 2009; Van der Made and Mazo, 2001). Its presence in the gravel pit Arriaga near Madrid (Álvarez-Lao and García, 2011a) shows it was present in Spain during MIS6 (Silva et al., 2013). The woolly rhinoceros *Coelodonta* spread as far south as Madrid and is known from MIS6 in La Parte in the North of Spain (Álvarez-Lao and García, 2011a; Arsuaga Ferreras and Aguirre Enriquez, 1979). Other taxa, which

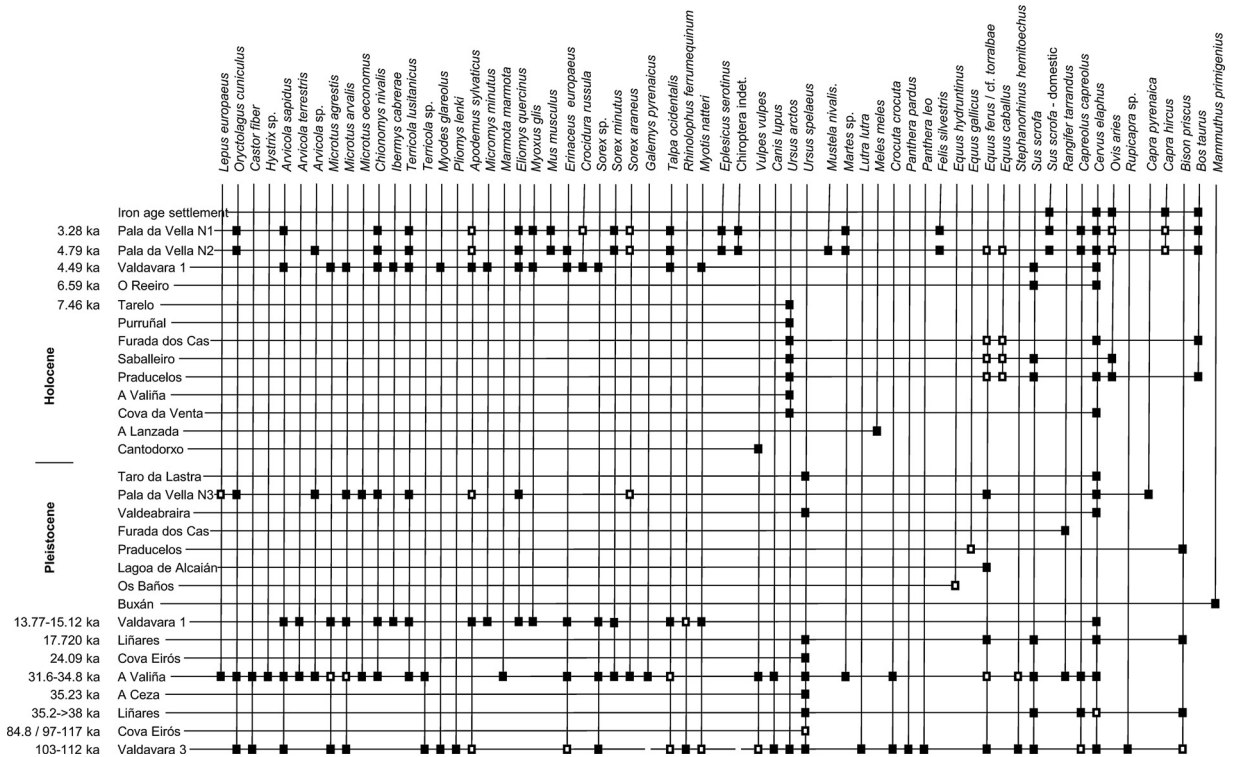


Fig. 21. The mammals identified from Valdavara 3 compared to those of other Pleistocene and Holocene localities from Galicia. Identifications from Valdavara 3 from this paper, Valdavara 1 after López-García et al. (2011) and of the remaining sites after López-González (2003) and Fernández Rodríguez and Villar Quinteiro (1993). In some cases, the taxonomy is updated, notably in the cases of domestic animals. In some cases, it was not clear whether a domestic or wild animal was meant (e.g., *Equus caballus/ferus*).

Fig. 21. Mammifères identifiés à Valdavara 3, comparés à ceux d'autres localités du Pléistocène et de l'Holocène en Galice. Identifications de Valdavara 3 de cet article, Valdavara 1 d'après López-García et al. (2011) et des autres sites d'après López-González (2003) et Fernández Rodríguez et Villar Quinteiro (1993). Dans certains cas, la taxonomie est mise à jour, notamment dans le cas des animaux domestiques. Dans certains cas, l'identification à un animal domestique ou sauvage (par exemple *Equus caballus/ferus*) n'était pas claire.

were widespread during cold periods, such as *Rangifer*, *Gulo*, *Alopex*, and *Saiga*, reached the Cantabrian Mountains and the Spanish Pyrenees (Altuna, 1993; Altuna and Mariezkurrena, 1996; Álvarez-Lao and García, 2011b). The reindeer reached these areas by MIS6 (Álvarez-Lao and García, 2011a). *Rangifer* is known from the Galician sites of Valiña and Furada dos Cas, *Mammuthus primigenius* from Buxán (López-González, 2003), and *Coelodonta* is also present at the Cova Eirós faunal record (Fábregas-Valcarce et al., 2012). On the one hand, "glacial" taxa are thus to be expected in Spanish sites dating to the cold periods as far back as MIS6. On the other hand, the Iberian Peninsula was a refugium for the "interglacial" fauna, but at present it is impossible to know how far these taxa retreated to the south. The low number of taxa of the Pleistocene faunas from Galicia (Fig. 21) might be because many taxa retreated from mountainous and possibly cold areas. For these reasons the interpretation of a faunal association as indicative of glacial or interglacial conditions in this part of Europe is not straightforward. However, the great diversity of "interglacial" taxa and the total absence of "glacial" taxa suggest that Valdavara 3 represents interglacial conditions. Among the large mammals, *Ursus*, *Sus*, and *Cervus* are indicative of more closed and *Stephanorhinus hemitoechus*, *Equus*, *Crocota* and *Panthera spelaea* of more open environments. The

presence of *Lutra* and *Castor* suggests the presence of permanent water bodies.

Although there are few small-vertebrate remains, from a palaeoenvironmental point of view the assemblage of Valdavara 3 is dominated by taxa linked with open wet meadows, as indicate the abundance of *Microtus agrestis* and *Microtus (Terricola) sp.* and the presence of *Erinaceus cf. europaeus*, *Talpa sp.*, *Sorex sp.*, *Anguis fragilis* and *Coronella cf. austriaca*. The presence of *Apodemus sp.*, *Clethrionomys glareolus*, *Rhinolophus ferrumequinum*, *Myotis sp.*, *Bufo spinosus* and *Anguis fragilis* indicates certain open forest coverage. *Arvicola sapidus* is indicative of flowing or stationary bodies of water surrounding the site, although the presence of *Rhinechis scalaris* and *Pliomys coronensis* may suggest the occurrence of somewhat drier open or bushland habitat. Wet conditions were also suggested by the presence of *Haliaeetus albicilla*, since this species indicates that there were deep waters near the cave. The absence of cold-adapted species among the micromammals should be stressed.

The rich Pleistocene fauna reflects the presence of varied habitats to satisfy the needs of all these species. The temperate and wet conditions, indicated by the large and small-vertebrate fauna, are consistent with the MIS 5 chronology indicated by OSL dating.

5.3. Chronology

From a biochronological point of view, the best diagnostic species is *Pliomys coronensis*, an extinct vole whose most ancient record in Iberia are found in the middle Pleistocene layers of Galeria and Zarpazos caves (Cuenca-Bescós et al., 2010a; Galindo-Pellicena et al., 2011) with an age between 430–245 ka (Berger et al., 2008). *P. coronensis* is a relative abundant species in the Iberian sites from the latest middle Pleistocene to the first half of the late Pleistocene (ca. 40 ka) (Cuenca-Bescós et al., 2010a; López-García, 2011; López-García et al., 2012), although we can find it occasionally in some Cantabrian sites until 13 ka (Cuenca-Bescós et al., 2010b). The relative abundance of *P. coronensis* in Valdavara 3 suggests an age of >40 ka. The absence of the small mammals typical of the late Pleistocene, like *Arvicola amphibius* or *Chionomys nivalis*, well represented in the latest Pleistocene layer 4 of Valdavara 1 (López-García et al., 2011), suggests a latest middle to early late Pleistocene (ca. 200–60 ka) age for Valdavara 3.

The origin of *Ursus arctos* is not very well documented, but the species is cited in Heppenloch and Lunel-Viel (Argant, 1996), that is also from about 400 ka onward. The first appearance of *Stephanorhinus hemitoechus* is believed to be around 450 ka (Van der Made, 2010a; Van der Made and Grube, 2010). Stuart and Lister (2007) reported a latest radiometric date for this species of ca. 42 ka cal BP and believed that its extinction could be related to the last glacial maximum. The species is possibly still present in Valiña, dated to 31.6–34.8 ka (López-González, 2003). The large mammal fossils suggest an age of 450 to 31.6 ka for Valdavara 3.

The chronocultural attribution of the lithic assemblage is difficult due to the low number of artifacts. Knapping strategies seem clearly aimed at flake production. In addition, one of the cores and the recovery of *débordant* flakes suggest the use of the discoidal knapping, which is common in Middle Paleolithic assemblages, although it can also be found in other technological contexts. Moreover, no artifacts diagnostic of other technocomplexes (Acheulian, Upper Paleolithic) have been recovered. These features are consistent with a chronology in the time range of the Middle Paleolithic and fall within the Middle Paleolithic variability on northwestern Iberia. Although scarce, these assemblages are characterized by the use of immediate and local lithic resources from secondary deposits, mainly quartz and quartzite. Flint artefacts only appear in the Upper Paleolithic sites, as in the case of Valdavara Cave (de Lombera-Hermida and Rodríguez Rellán, 2010). From the technological point of view, the presence of Levallois technology is scarce, only identified when fine-grained quartzites are available, as in Cova Eirós (de Lombera-Hermida et al., 2014; Rodríguez-Álvarez et al., 2011).

The age ranges indicated by the small and large mammals and lithic assemblage are consistent with the OSL dates of 103.414 ± 6956 and 112.837 ± 8903 years BP, which corresponds to MIS 5d.

5.4. The fauna of Valdavara 3 in a wider context

Of particular interest is the long list of large mammals (ungulates and carnivores) from Valdavara 3. Compared to the recent large mammals of Spain (excluding recent introductions or re-introductions), Valdavara 3 lacks *Dama*, *Capra*, *Felis*, *Lynx* and several of the mustelids (*Mustela*, *Martes*, *Meles*). By comparison, the living fauna from Galicia lacks *Cervus*, *Dama*, *Capra*, *Rupicapra* and *Lynx*, meaning that present ungulate diversity is considerably impoverished. The lack of mustelids in Valdavara 3 is very likely due to an insufficient sample size. However, Valdavara 3 has a number of wild mammals, which are extinct (*Ursus spelaeus*, *Stephanorhinus hemitoechus*, *Bison priscus*) or extinct in Europe (*Crocota*, *Panthera pardus*, *P. spelaea*) or reintroduced (*Equus ferus*). Compared to the temperate taxa of Europe of isotope stage 5, the following large mammals are lacking in Valdavara 3: *Macaca*, *Elephas*, *Cuon*, *Ursus thibetanus*, *Hyaena*, *Equus hydruntinus*, a large *Equus* the size of *E. mosbachensis*, *Hippopotamus*, *Megaloceros*, *Bos primigenius*, as well as the mustelids. Of course, not all European stage 5 species lived in the same place and, in reality, in most places only a selection of these species lived and interacted.

Which species lived together and which did not, depended on the local environment. The fossils found at a site indicate which species lived there, but there are many reasons why species, which lived in that place may not be represented in the fossil collection of that site. In addition to the examples from Galicia (Fig. 21), many well-known sites probably do not represent the true biodiversity, which existed there. The lower layers of Lezetxiki have a high taxonomical diversity, but cave bear is clearly dominant (Altuna, 1972) and represents more than 60% of the identified remains. Similar biases are found in Arlanpe Cave, Labeko Koba Cave and Ekain (Ríos-Garaizar et al., 2012, 2015) and Amutxate Cave, where only 39 of approximately 17,000 bones belong to mammals other than cave bears (Torres et al., 2007).

Aguirre (1989) provided lists of the mammalian species present in 38 sites and levels of the upper Pleistocene of Spain, Von Koenigswald and Heinrich (1999) gave faunal lists of central European localities, including many of Eemian age, and Arribas (2004) gave numerous Pleistocene and Holocene faunal lists, some 25 of them of Spanish sites of the Eemian or MIS5. The recently published fauna from Artazu VII in Basque Country is somewhat younger, but shares many of its elements with Valdavara 3, though there is no indication of human presence and the site is younger (dated to 98.4–88.5 ka; Suárez-Bilbao et al., 2016). Compared to those all those sites, Valdavara 3 is one of the richest in species. Most other sites have much shorter lists and it is not possible to know whether these lists represent a minor part of the fauna that lived there, or whether the fauna which lived there was much less diverse. It is possible that the faunal list of Valdavara 3, at least for the large mammals, approaches the real diversity, which was there.

The European fauna suffered a major extinction event during the end of the Pleistocene and the Holocene.

Whether this event is due to the expansion of *Homo sapiens* into Europe, to climatic change, or to a combination of the two is debated, but the result is that the European fauna is considerably impoverished compared to any previous moment of the Quaternary. Valdavara 3 and other rich MIS5 fossil associations are the closest analogues of what the present European local faunas could have looked like without this extinction event.

6. Conclusions

The study of the fossil association from Valdavara 3 leads to the following conclusions:

- among the > 1400 fossils, remains of 40 species of vertebrates were identified: 1 fish, 1 anuran, 5 squamate reptiles, 3 birds and 30 mammal species (Table 2);
- the fauna includes taxa living in open and in closed environments and taxa adapted to aquatic life, suggesting a varied landscape with the permanent presence of an important water body;
- a small collection of lithic artifacts show that humans lived in this varied landscape and sporadically visited the cave, but did not greatly contribute to the formation of the fossil assemblage;
- the fauna is of interglacial aspect;
- the faunal composition is consistent with the age indicated by OSL dating (103–113 ka; Table 1), corresponding to MIS 5d;
- whereas many fossil localities of similar ages have short or biased faunal lists, the fauna from Valdavara 3 is remarkably diverse and includes many of the temperate species that lived in western Europe at that time and probably represents fairly well the fauna that once lived at that place;
- faunas like the one from Valdavara 3 give us an impression of the local biodiversity could have been, if there had not been a late Pleistocene–Holocene extinction event.

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Appendix A. Supplementary data

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