

THE FOSSILS OF CASTOR FIBER FROM THE MIDDLE PLEISTOCENE SITE OF GRUTA DA AROEIRA (PORTUGAL) AND HUMAN-BEAVER INTERACTION

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ABSTRACT

Here we analyze the fossil remains of *Castor fiber* from the Middle Pleistocene site of Gruta da Aroeira, in the Almonda karst system, Tagus basin (Torres Novas, Portugal) and discuss the archaeological implications of the presence of beavers in the region. The Almonda karst system has been the backdrop for human evolution in Portugal, because there are different localities, of different ages, from the Middle Pleistocene to the Holocene, with fossil remains of hominins as well as faunal and archaeological remains. Beaver fossils have been found in the archaeological deposits of at least three cavities of the karst system: the Gruta da Aroeira, the Gruta da Oliveira and the Galeria da Cisterna. Here, for the first time, we describe the fossils of *Castor fiber* from Gruta da Aroeira. The beavers from Aroeira are remarkable because they are the westernmost fossil record of *Castor fiber* in Europe dated to Marine Isotope Stage (MIS) 11, around 420 ka. The aim of the present article is twofold, firstly to study the fossils of beavers from the Aroeira locality, and secondly to discuss the palaeoecological and palaeoenvironmental implications of the presence of this rodent in the Almonda karst sites. This allows us to discuss the hominin-beaver interactions.

Keywords: fossil beavers, skull, mandible, teeth, archaeology, human-beaver interactions, Portugal

RÉSUMÉ

LES FOSSILES DE CASTOR FIBER DE GRUTA DA AROEIRA (PORTUGAL) ET L'INTÉRACTION ENTRE HUMAINS ET CASTORS

Ici, nous analysons les fossiles de *Castor fiber* du site Pléistocène moyen de Gruta da Aroeira, dans le système karstique de Almonda, bassin du Tage (Torres Novas, Portugal), et les implications archéologiques de la présence de castors dans la région. Le karst d'Almonda est un cadre de référence pour l'étude de l'évolution humaine dans la partie occidentale de l'Europe, du Pléistocène moyen à l'Holocène, avec aussi bien des restes d'hominidés fossiles, que de faunes et de vestiges archéologiques. Des fossiles de castors ont été trouvés dans les gisements archéologiques d'au moins trois cavités du système karstique : la Gruta da Aroeira, la Gruta da Oliveira et la Galeria da Cisterna. Ici, pour la première fois, nous décrivons les fossiles de *Castor fiber* de Gruta da Aroeira. Les castors d'Aroeira sont remarquables car ils sont la trace fossile la plus occidentale de *Castor fiber* en Europe; ils sont datés du Stade Isotopique Marin (MIS) 11, autour de 420 ka. Le but de cet article est double, d'une part de présenter l'évolution des castors à travers les fossiles d'Aroeira, et d'autre part de discuter des implications paléoécologiques et paléoenvironnementales de la présence de ce rongeur dans le karst d'Almonda. Cela nous permet de discuter des possibles interactions entre humains et castors.

Mots-clés : castors fossiles, archéologie, interactions humains-castors, Portugal

1 - INTRODUCTION

The Eurasian beaver, the species *Castor fiber*, is a large and semiaquatic rodent with a sparse fossil record. Since the emergence of the family Castoridae, during the Eocene, beavers were tiny to giant, and semiaquatic or burrowing rodents (Crusafont *et al.*, 1948; Freye 1978; Aldana Carrasco, 1992; Huguene y & Escuillie 1996; Meentemeyer *et al.*, 1998; Huguene y, 1999). The family Castoridae was diverse during the Tertiary, but in the Quaternary only two genera of beavers survived in

Europe: the extinct *Trogotherium* (Fostowicz-Frelik, 2008) and the current genus *Castor* (Barisone *et al.*, 2006).

The single extant genus, *Castor*, comprehends two species, the eurasiatic beaver, *Castor fiber* and the American beaver, *Castor canadensis*. Fossils of the genus *Castor* are present in Eurasia since the late Miocene, ca. 10 Ma (Aldana Carrasco, 1992; Huguene y, 1999).

The first record of beavers in the Iberian Peninsula occurs in Spain, in the late Pliocene fluvio-lacustrine layers of the Granada basin (García-Alix *et al.*, 2007), while the first fossil representatives of the species

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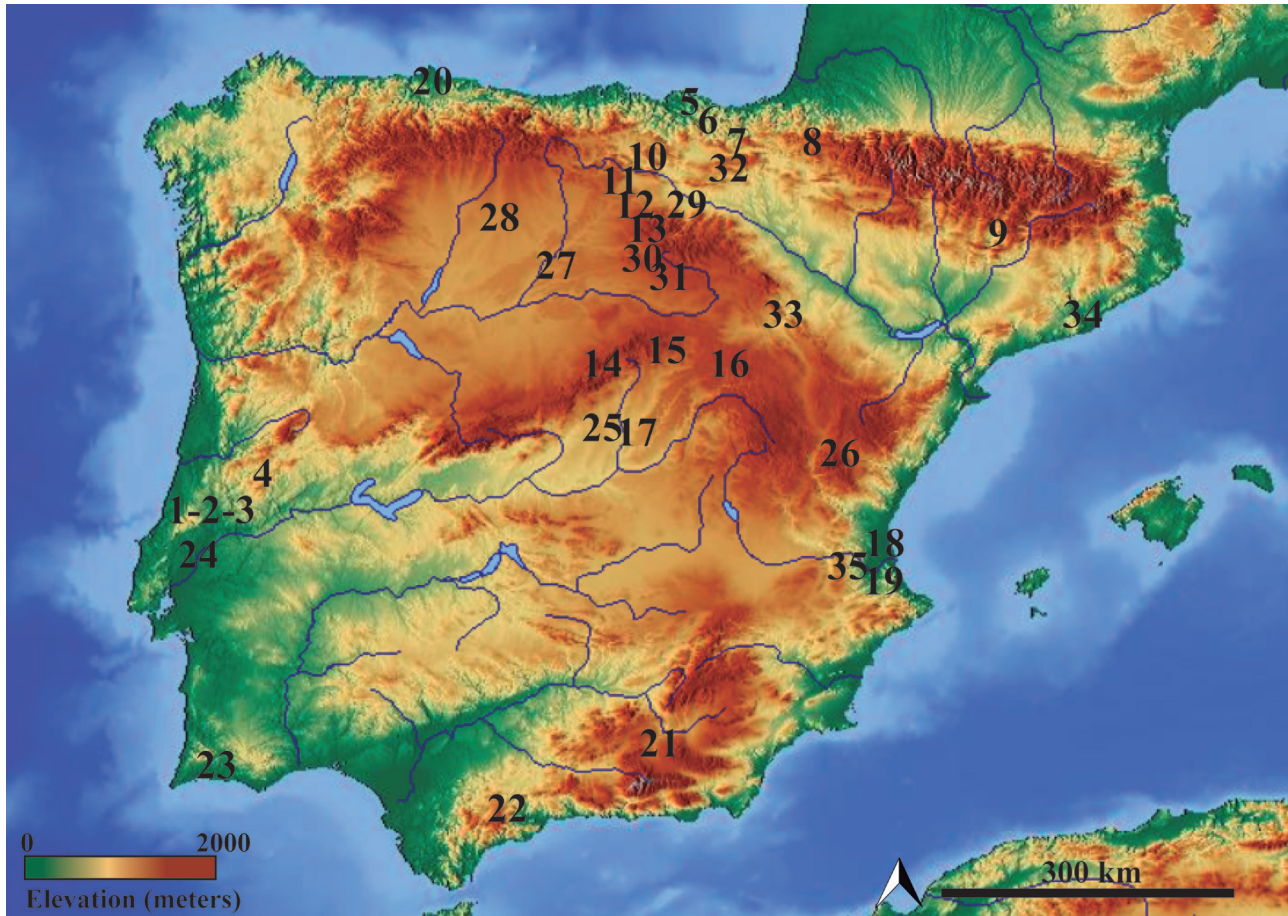


Fig. 1: Localities from the Iberian Peninsula with beaver remains.

Pleistocene localities: 1/ Gruta da Aroeira, 2/ Galeria da Cisterna, 3/ Gruta da Oliveira, 4/ Caldeirão, 5/ Arlanpe, 6/ Lezetxiki, 7/ Olazagutía, 8/ Zatoya, 9/ Els Muricecs, 10/ La Blanca, 11/ Valdegoba, 12/ Atapuerca (Sima del Elefante and Gran Dolina), 13/ Cueva Millán, 14/ Pinilla del Valle, 15/ Cueva de las Figuras, 16/ Cueva de los Casares, 17/ Aridos I, 18/ Bolomor, 19/ Cova Negra, 20/ Las Hienas. **Holocene localities:** 21/ Cuesta del Negro, 22/ Ronda, 23/ Alcaria de Arge, 24/ Vila Nova de São Pedro, 25/ Perales del Río, 26/ Sima del Ruidor, 27/ El Soto de Medinilla, 28/ Era Alta, 29/ Atapuerca (Portalón), 30/ Clunia, 31/ Ucero, 32/ La Peña, 33/ Bilbilis, 34/ Sant Pere de Gavà, 35/ Barranc Fondo. Map extracted from OpenStreetMap.

Fig. 1 : Sites de la Péninsule Ibérique avec fossiles de castor. Sites pléistocènes : 1/ Gruta da Aroeira, 2/ Galeria da Cisterna, 3/ Gruta da Oliveira, 4/ Caldeirão, 5/ Arlanpe, 6/ Lezetxiki, 7/ Olazagutía, 8/ Zatoya, 9/ Els Muricecs, 10/ La Blanca, 11/ Valdegoba, 12/ Atapuerca (Sima del Elefante and Gran Dolina), 13/ Cueva Millán, 14/ Pinilla del Valle, 15/ Cueva de las Figuras, 16/ Cueva de los Casares, 17/ Aridos I, 18/ Bolomor, 19/ Cova Negra, 20/ Las Hienas. *Sites holocènes :* 21/ Cuesta del Negro, 22/ Ronda, 23/ Alcaria de Arge, 24/ Vila Nova de São Pedro, 25/ Perales del Río, 26/ Sima del Ruidor, 27/ El Soto de Medinilla, 28/ Era Alta, 29/ Atapuerca (Portalón), 30/ Clunia, 31/ Ucero, 32/ La Peña, 33/ Bilbilis, 34/ Sant Pere de Gavà, 35/ Barranc Fondo. Carte extraite de OpenStreetMap.

Castor fiber appear in the Early Pleistocene levels of the Atapuerca site complex: “Trinchera-TE; TD”, Sima del Elefante (level TE9, 1.2 Ma) and Gran Dolina (TD4-TD6, 0.9-0.78 Ma) (Cuenca-Bescós *et al.*, 1999, 2001, 2017) (fig. 1).

Here, we describe *Castor fiber* remains from Gruta da Aroeira, one of the scarce contexts in the Iberian Peninsula containing Acheulean-bearing hominins (Daura *et al.*, 2017, 2018; López-García *et al.*, 2018; Sanz *et al.*, 2018, 2020). The site has yielded a rich assemblage of beaver remains dated to MIS 11, the earliest evidence of the species in Portugal. The aim of this paper is to provide the description of the beavers from Aroeira, and enable us to discuss the palaeoecological and palaeoenvironmental implications in relation to the human presence.

2 - SITE DESCRIPTION

Gruta da Aroeira (39°30'20"N, 08°36'57"W) is a cave located in the Central Limestone Massif of Estremadura (municipality of Torres Novas, Santarém), in central

Portugal (fig. 2). It forms part of the Almonda karst system (fig. 2) (Zilhão *et al.*, 1991, 1993; Daura *et al.*, 2017, 2018). Fieldwork was first conducted in an area external to the site between 1997 and 2002, where erosion had already exposed the sediments of the cave (in the so-called Brecha das Lascas locus), and in the reopened cave entrance (Gruta da Aroeira). In the published studies of these initial excavations, Gruta da Aroeira was designated as “Galerias Pesadas” (Marks *et al.*, 2002a,b; Trinkaus *et al.*, 2003). Archaeological excavations resumed in 2013 in a 6 m² area at the back of the cave (squares H-J/6-8) (fig. 2), with the aim of reaching the base of the stratigraphic succession, assess the depth of the archaeological sequence and determine its chronological range. In this area, the stratigraphic succession spans a thickness of 4 m and comprises three major units. The uppermost one, Unit 1, is a brecciated infill capped by flowstone. Unit 2 (fig. 2) is a 2.2 m-thick mud-supported breccia, rich in angular and sub-rounded clasts, corresponding to Acheulean layer X and capped by a second flowstone dated to 418 +37/- 27 ka (2 σ). Layer X is divided into sub-layers X and Xb/c

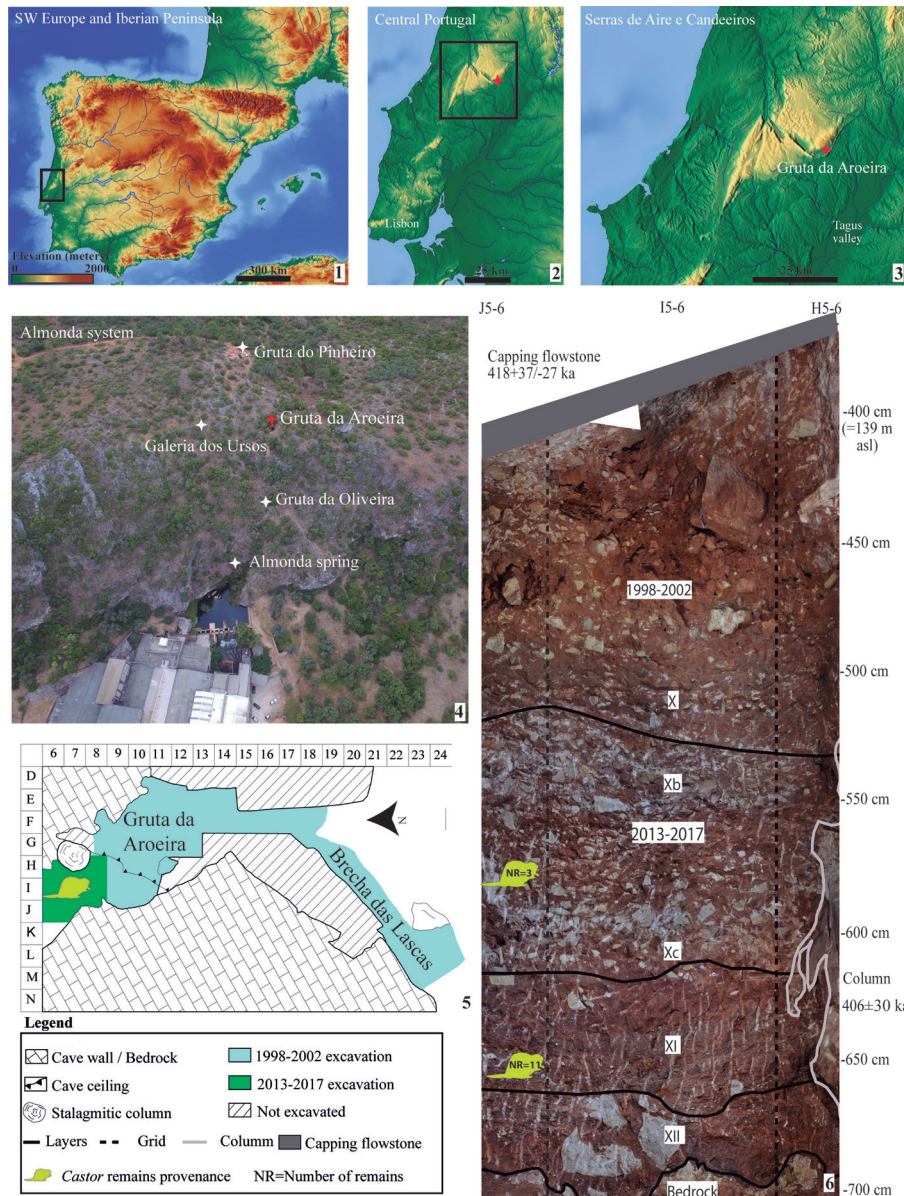


Fig. 2: The site.

(1-3) Geographical location of the Gruta da Aroeira site in the Central Limestone Massif of Estremadura (municipality of Torres Novas, Santarém), in central Portugal, Iberian Peninsula. The site is a cave forming part of the Almonda karst system, in the Tagus basin. Maps are extracted from OpenStreetMap. (4) The Almonda escarpment with the position of Aroeira and the other caves mentioned in the text (image from Pedro Souto). (5) Gruta da Aroeira plan and excavation grid. (6) Gruta da Aroeira stratigraphic profile. Layer X is divided into sub-layers X and Xb/c excavated between 1997-2002 and between 2013-2017. Fossils of beaver remains are signalled with the animal's silhouette. Note the flowstone capping the deposit containing the beaver remains.

Fig. 2 : Le site. (1-3) Situation géographique de la Gruta da Aroeira dans le massif calcaire central d'Estremadura (commune de Torres Novas, Santarém), au centre du Portugal, péninsule ibérique. Le site est une grotte faisant partie du système karstique d'Almonda, dans le bassin du Tage. (4) L'escarpement de Almonda avec la position de Aroeira (image de Pedro Souto) et des autres grottes mentionnées dans le texte. (5) Plan de Gruta da Aroeira et carroyage. (6) Profil stratigraphique de Gruta da Aroeira. La couche X est divisée en sous-couches X et Xb/c fouillées entre 1997-2002 et entre 2013-2017. Les fossiles de castor sont signalés par la silhouette de l'animal. Remarquez la croûte stalagmitique qui scelle le dépôt où les restes de castor ont été trouvés.

(corresponding to the upper and lower parts of a single unit, excavated between 1997-2002 and 2013-2017, respectively). This layer has provided significant evidence about the Acheulean-bearing hominins of Europe, such as the human cranium Aroeira 3, burned bones and other faunal remains, lithic artefacts, including handaxes, and a Cercopithecoid mandible (Daura *et al.*, 2017, 2018; Conde-Valverde *et al.*, 2018; López-García *et al.*, 2018; Sanz *et al.*, 2018, 2020; Alba *et al.*, 2019).

The basal unit, Unit 3, is a fluvial deposit of endokarst origin comprising two layers: layer XI is a 0.4 m-thick silty sand with scattered gravel and faunal remains but no artefacts, and layer XII is a 0.5 m-thick, archaeologically sterile, slightly gravelly sand. The external layer of a stalagmite column covered by layer XII has been dated to 406 ± 30 ka (2σ), giving a maximum age for layer X and part of layer XI, whose deposition, therefore, can be placed within the 390-436 ka interval. Both layers thus date to MIS 11. The fossil remains of *Castor fiber* described here were recovered during the fieldwork carried out at the site between 2013 and 2017. Most were found in layer XI; a few come from layer X (Xb).

Beaver remains of a younger chronology have also been recovered in other sites of the Almonda karst system: in Late Pleistocene layer 13 of Gruta da Oliveira (Zilhão *et al.*, 2010), and in layer C of the AMD2 locus of Galeria da Cisterna, a fluvial deposit of Tardiglacial age (Antunes, 1989; Zilhão *et al.*, 1991, 1993; Zilhão, 2009, 2016; Trinkaus *et al.*, 2011).

3 - MATERIAL AND METHODS

3.1 - EXCAVATION METHODS

The fossil remains of *Castor fiber* were recovered in layers XI (NR=13) and X (NR=3) of the Gruta da Aroeira. The fossils were completely encased in hard carbonate breccias. The hard material needed to be excavated at the site, using a demolition hammer. The bones were removed in blocks and transported to the laboratory. The fossil bones were detached using a pneumatic microhammer and microchisel (Mod. CTS 178) and restored using a normal air scribe (Mod. W224). Where necessary, bones

were consolidated with an acrylic resin (Paraloïd-B72) dissolved in acetone (C₃H₆O). Some fossil remains are still undergoing restoration. Washing and sieving of the sediments are a common method to recover fossil microvertebrates. However, given the size of beavers, their fossil bones were retrieved in the course of the archaeological excavation work, not during the washing-sieving of the sediments. A study of the microvertebrates from washing and sieving the sediments from Aroeira can be found in Lopez-García *et al.* (2018).

3.2 - ANATOMICAL TERMS

The terms and parameters used in the descriptions of Castoridae are from Repenning (1968), Hugueney (1999), Barisone *et al.* (2006), Korth (2008), Fostowicz-Frelik (2008), Mörs & Stefen (2010), and Cuenca-Bescós *et al.* (2017). The premolars and molars have folds on the lingual and labial sides which are named striids for lower, and striae for upper cheek teeth, following Crusafont *et al.* (1948) and Van de Weerd (1976). The folds become the flexids for the lower and flexae for the upper cheek teeth in the occlusal surface. The isolated enamel islets on the occlusal surface of older individuals are described as fossettids in the lower and fossettes in the upper cheek teeth. A distinction between beavers and porcupines (Family Hystricidae, Genus *Hystrix*) is that the enamel islets are formed early in the ontogeny of the porcupines, whereas in beavers they are formed later and do not appear until the animals are old. In the Castoridae, the striae and striids usually reach the base of the crown, while in the Hystricidae they are shorter.

3.3 - MEASUREMENTS

The measurements of the mandible are: height, from the tip of the digastric eminence to the most mesial alveolar edge of the chewing teeth; total alveolar length; and length of the diastema. The mesio distal length and labio lingual width of the incisor and cheek teeth were taken in the occlusal surface. Measurements were taken with a Mitutoyo digital caliper (model CD-8" CX). Given the large size of some specimens, they were photographed with a digital camera Nikon Coolpix 3100 and then measured again. A scale was photographed for referencing. Measurements are given in mm.

3.4 - ABBREVIATIONS

The letters I, P, M, in capital letters are for the upper dentition, incisor, premolar and molar respectively. Lower case letters (i, p, m) are for the lower dentition; md, mandible. L, W are the maximum length and width of the anatomical elements measured. TD or TE are the localities of the Atapuerca karst system where T means trench or "Trincherá" in Spanish; MIS, Marine Isotopic Stage; ka, kiloannum.

3.5 - HOUSING OF THE MATERIAL

The archaeozoological material from Aroeira is currently housed at the *Centro de Arqueologia da Universidade de Lisboa* (UNIARQ) in Lisbon, Portugal. The remains are labelled using the site acronym ARO followed by the inventory number.

4 - RESULTS: SYSTEMATIC PALAEOLOGY

Order RODENTIA Bowdich, 1821

Family CASTORIDAE Hemprich, 1820

Genus Castor Linnaeus, 1758

The physical appearance of the two species, *Castor fiber* and *C. canadensis* is comparable, but their karyotypes make them separate species (Ducroz *et al.*, 2005).

Species Castor fiber Linnaeus, 1758

STUDIED SPECIMENS

The studied specimens of *Castor fiber* from layers X and XI are: right mandible with the complete tooth row, i to m3 (ARO #682); left mandible with i, p4, m1 and m2 and isolated M1-2 (ARO #740); right maxillary fragment (ARO #131); right maxilla P4 to M3 (ARO #158); right maxilla I-P4 (ARO #663); left maxilla I-M1 (ARO #173); isolated P4 and M1 (ARO #171); metapodial (ARO #665); and cemented bones, formed by humerus, radius, ulna, rib, femur and pelvis (ARO #677). The studied specimens of *Castor fiber* from layer Xb are: left maxilla with P4 to M3 (ARO #1299); left mandible i-m1 (ARO #930); and left scapula (ARO #1220).

MANDIBLE

There are seven mandibular fragments in layers XI and X from Gruta da Aroeira (pl. 1). The mandible is robust, the articular condyle is large (pl. 1, cls. 1b & 1c). The mandible has a strong digastric eminence, seen in the ventral part in both lateral and medial views (pl. 1, cls 4a & 4b); the anterior part of fma is between the alveolus of the p4 and m1. The upper maseteric crest is prominent. In broken mandibles, the long alveolus of the incisor is visible (pl. 1, cls 1c, 2a & 3b).

THE INCISOR

The lower incisor is a long tooth of continuous growth and never develops roots. The long alveolus extends distally into the vertical ramus of the mandible, behind the alveolus of the m3 (pl. 1, cls. 1c, 2a & 4b). The labio lingual width of the incisor varies slightly along the tooth decreasing to the base, as shown in the table 1 measurement of i#682.

THE CHEEK TEETH, P4, M1, M2, M3

All the teeth present the typical striids of lower cheek teeth in the genus *Castor* in the labial and lingual sides



Pl. 1: *Castor fiber* mandibles, with their preserved teeth: premolar (p) and molars (m), from Aroeira.

(1) Right mandible (ARO#633), in (1a) occlusal, (1b) lateral and (1c) medial views; (1d) occlusal view of the only tooth preserved, the p4. (2) Left mandible (ARO#740) in (2a) medial and (2b) lateral views; (2c) occlusal view of p4- m2. (3) Right mandible (ARO#158) in (3a) lateral and (3b) medial views; (3c) occlusal view of p4-m3. (4) Right mandible (ARO#682) in (4a) lateral and (4b) medial views; (4c) occlusal view of p4-m3.

*Pl. 1 : Mandibules de *Castor fiber*, avec leurs dents conservées: prémolaires (p) et molaires (m), d'Aroeira. (1) Mandibule droite (ARO # 633), en vues (1a) occlusale, (1b) latérale et (1c) médiale ; (1d) vue occlusale de la seule dent conservée, la p4. (2) Mandibule gauche (ARO # 740) en vue (2a) médiale et (2b) latérale ; (2c) vue occlusale de p4- m2. (3) Mandibule droite (ARO # 158) en vues (3a) latérale et (3b) médiale ; (3c) vue occlusale de p4-m3. (4) Mandibule droite (ARO # 682) en vues (4a) latérale et (4b) médiale ; (4c) vue occlusale de p4-m3.*

Tab. 1: Mandibular specimens and measurements of the fossil beaver remains, *Castor fiber*, from Aroeira.

Lower case letters are used for the lower dentition: i, incisor; p4, fourth premolar, m1, first molar; m2, second molar; m3, third molar; ≈ almost equal to; two values separated by - means that the same parameter was measured in different areas, usually anterior-posterior. Measurements are given in mm.

*Tab. 1 : Spécimens mandibulaires et mesures de restes de castor fossile d'Aroeira, *Castor fiber*. Des minuscules sont utilisées pour la dentition inférieure: i, incisive; p4, quatrième prémolaire, m1, première molaire; m2, deuxième molaire; m3, troisième molaire; ≈ presque égal à; deux valeurs séparées par - signifie que le même paramètre a été mesuré dans différentes zones, généralement antérieur-postérieur. Les mesures sont données en mm.*

Specimen ID	Anatomical location	Mandibular elements preserved	Length	Width	High at alveolus p4	High end diastema
# 663 ARO2014 XI-I6	Rigth	Nearly complete	92.66	17.03		
		i	6.58	8.96		
		p4	7.51	7.04		
# 682 ARO2014 XI-I6	Rigth	Horizontal ramus		17.45	28.47	25.68
		i	7.93	7.72-8.53		
		p4	9.84	7.82		
		m1	8.52	≈8.19		
		m2	8.09	7.62		
		m3	7.84	≈5.48		
# 158 ARO2014 XI-I7 adult	Rigth	Horizontal ramus	≈65.49	18.93		
		p4	10.82	7.31		
		m1	8.12	7.35		
		m2	7.75	7.99		
		m3	8.16	6.7		
# 928 ARO2014 XI-I7	Rigth	Horizontal ramus				
		p4	partially encased by carbonate			
		m1				
		m2infd	idem	8.25		
# 665 ARO2014 XI-I6	Left	Fragmen alveolus and i		≈9.01		
# 740 ARO 2014 XI-I6	Left	Horizontal ramus		16.85		
		i		6.9		
		p4	8.95	7.02		
		m1	8.53	7.75		
		m2	6.72	8.6		
# 930 ARO 2014 Xb-h6	Left	Horizontal ramus	51.84	16.97	28.91	
		i	7.75	8.64	9.77-8.65	
		p4	11.32	8.86		
		m1	9.93	8.51		

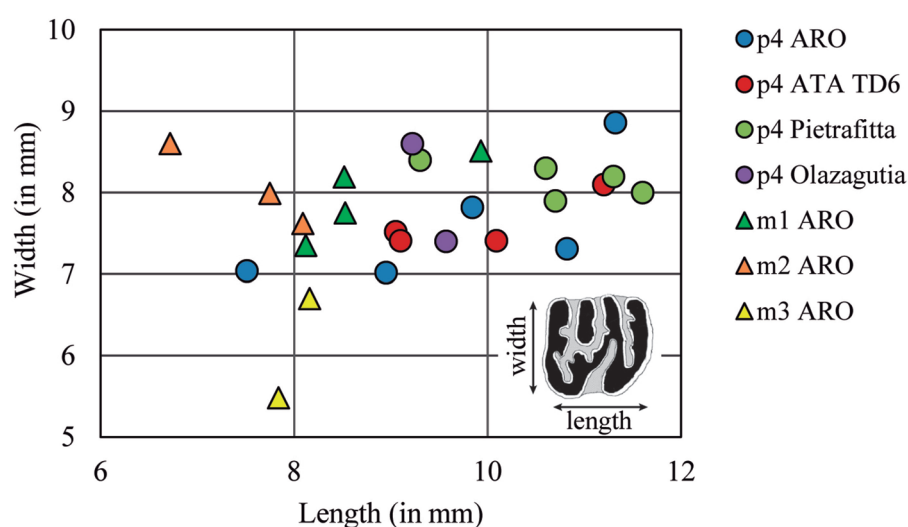


Fig. 3: Measurements of beaver lower teeth (p4-m3) from Gruta da Aroeira (ARO), this work, compared to other fossils from the Early Pleistocene TD6 of the Trinchera Dolina in the Sierra de Atapuerca (ATA TD6) and Late Pleistocene Olazagutia, in Navarra, Spain, and Early Pleistocene Pietrafitta in Italy (Cuenca-Bescós *et al.*, 2017).
Fig. 3 : Mesures des dents inférieures du castor (p4-m3) de Gruta da Aroeira (ARO), ce travail, comparées à d'autres fossiles du Pléistocène inférieur TD6 de la Trinchera Dolina dans la Sierra de Atapuerca (ATA TD6) et du Pléistocène tardif Olazagutia, en Navarre en Espagne et Pietrafitta du Pléistocène précoce en Italie (Cuenca-Bescós *et al.*, 2017).

(pl. 1, cls. 1a, 1b, 1c, 2a, 2b, 3a, 3b, 4a & 4b). The occlusal surfaces present also the typical folds or flexids of beaver molars (pl. 1, cls. 1d, 2c, 3c & 4c). The p4, m1, m2 and m3 of mandible ARO #682 present a noticeable crenulated paraflexid, unfolding in two or more folds on its anterior side (pl. 1, cl. 4c). The flexids of the premolars and molars in the rest of specimens are smooth. The fossettids in the p4 of mandible ARO #158 (pl. 1, cls. 3a & 3c), shows that it is a senile beaver. The rest of the mandibles have cheek teeth of juvenile to young adult beavers, not reaching the “fossetid” stage. The size of the teeth is given in table 1. Note the great variability of the length (L) of the p4, while the width (W) is less variable (fig. 3). Some cheek teeth lack fragments of enamel; in the tables, the symbol \approx indicates that the parameter may be a bit larger than the measurement obtained because the enamel wall is damaged.

MAXILLAE

Fragments with teeth as well as isolated upper teeth are the only maxillary remains (pl. 2 & tab. 2). The cheek teeth have the striae and folds typical of *Castor fiber*.

POSTCRANIAL REMAINS

The postcranial remains of *Castor fiber* are mostly incomplete (pl. 3). From layer XI, the remains are: the proximal articulation and part of the shaft of a right humerus (ARO #677; 40.01x23.65x16.59; pl. 3); part of the ilium and acetabulum of the left pelvis (22.95x16.12). There are also several fragments of ulna, radio and autopodials. From layer Xb, the remain is a fragment of the left scapula (ARO#1220; 96.33x60.41x6.53; pl. 3).



Pl. 2: Fragments of *Castor fiber* maxillae with their preserved teeth: premolar (P) and molars (M), from Aroeira.

(1) Left maxilla (ARO#1299) in (1a) lateral, (1b) medial and (1c) occlusal views; (1d) occlusal view of P4-M3. (2) Left maxilla (ARO#173) in (2a) medial and (2b) occlusal views; (2c) occlusal view of M1-P4 (2c).

*Pl. 2 : Fragments de maxillaires de *Castor fiber* avec leurs dents conservées: prémolaires (P) et molaires (M), d'Aroeira. (1) Maxillaire gauche (ARO # 1299) en vues (1a) latérale, (1c) médiale et (1c) occlusale ; (1c) vue occlusale du P4-M3. (2) Maxillaire gauche (ARO # 173) en vues (2a) médiale et (2b) occlusale ; (2c) vue occlusale de M1-P4.*

Specimen ID	Element and side	Upper dentition preserved	Length	Width
ARO #740	Rigth	M1-2	6.09	6.49
ARO #173	Left maxilla	I	9.16	8.4
		P4	9.36	7.81
		M1	6.78	8.24
ARO #171	Left maxilla	P4	8.91	8.08
		M1	6.08	5.62
ARO #173	Rigth maxilla	P4	9.93	0.34
		M1	7.42	8.45
ARO #188	Rigth maxilla	M1-2	6.67	6.44
ARO #666	Rigth maxilla	M1-2	6.09	6.11
ARO #1299	Left maxilla	P4	8.67	8.72
		M1	6.87	6.8
		M2	6.08	6.25
		M3	5.88	6.15

Tab. 2: Maxillary specimens and measurements of Aroeira fossil beaver remains, *Castor fiber*.

Upper case letters are used for the upper dentition: I, incisor; p4, fourth premolar; m1, first molar; m2, second molar; m3, third molar. Measurements are given in mm.

Tab. 2 : Mesures des restes de maxillaire de castor fossile d'Aroeira, *Castor fiber*. Les majuscules sont utilisées pour la dentition supérieure: I, incisive; p4, quatrième prémolaire, m1, première molaire; m2, deuxième molaire; m3, troisième molaire. Les mesures sont données en mm.

5 - DISCUSSION

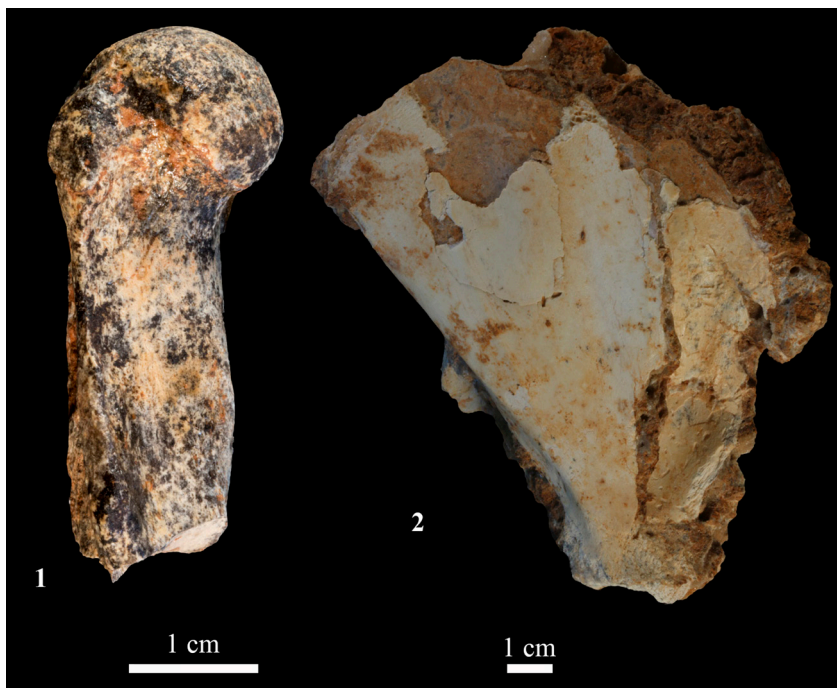
The dimensions and morphology of the *Castor fiber* from Aroeira are not significantly different from Quaternary specimens of *Castor fiber* and extant beavers. Still, the ARO-p4 is slightly shorter and narrower than the p4 of the beavers from the Early Pleistocene of Pietrafitta and Atapuerca Gran Dolina TD6, and the Late Pleistocene from Olazagutia (Cuenca-Bescós *et al.*, 2017). We use the p4 because this tooth is the most complete element in the ARO material, as well as in the other collections and so a sufficient sample can be gleaned from the literature. The smaller dimensions are related to the fact that most Aroeira specimens are juvenile; hence, it is to be expected that their size be somewhat smaller (Stefen, 2009).

In the Iberian Peninsula, *Castor fiber* persists until the Late Pleistocene and the Early Holocene (Sesé & Soto, 1981, Villaverde & Martí, 1984; Antunes, 1989; Zilhão *et*

al., 1991, 1993; Póvoas *et al.*, 1992). Its last appearance datum may correspond to the Late Prehistory to Roman ages at: the Vila Nova de São Pedro hilltop settlement, in the Ribatejo (Antunes, 1989); El Soto de Medinilla (Liesau von Lettow-Vorbeck, 1998), in Valladolid, and El Portalón de Cueva Mayor in Atapuerca (Cuenca-Bescós *et al.*, 2017).

5.1 - TAPHONOMY AND DEMOGRAPHIC COMPOSITION

Most of the mandibular specimens are juveniles or young adults. They present unerupted or recently erupted incisors and the fossetid condition is not present. Compared with the data in Stefen (2009), the length of Aroeira's p4 suggests that they belong to animals of between two and four years of age (25-50 months). The proportion of juveniles to adults is 6/1. Juvenile beavers



Pl. 3: *Castor fiber* postcranial remains from Gruta da Aroeira.

(1) Left humerus, proximal articulation and shaft in lateral-posterior view (ARO #677) from layer XI. (2) Scapula (ARO #1220) from layer Xb.

Pl. 3 : Restes postcrâniens de *Castor fiber* de Gruta da Aroeira. (1) Humérus gauche, articulation proximale et diaphyse en vue latérale-postérieure (ARO # 677) de la couche XI. (2) Omoplate (ARO # 1220) de la couche Xb.

usually leave the family pond after the second year; as a rule, therefore, the family group includes more juveniles than adults (Halley & Rosell, 2002, 2003; Halley, 2011, Campbell-Palmer *et al.*, 2012; Halley *et al.*, 2013). Thus, the composition of Aroeira's *Castor fiber* thanatocenosis is consistent with a natural accumulation.

No direct carnivore or anthropogenic modification of these bones could be identified. Even though beaver remains are scarce in Lower Palaeolithic sites, the exploitation of this taxon by hominins has been demonstrated in two layers from Caune de l'Arago, where the practice was deemed opportunistic but not rare (Lebreton *et al.*, 2017). In the Middle and Upper Palaeolithic, the evidence that beavers were hunted for their fur and meat is more abundant (Fiore *et al.*, 2004; Slimak *et al.*, 2010; Rendu, 2010). Given that Aroeira layer XI is a fluvial deposit and the beaver bones found therein show no evidence of anthropogenic modification, it is likely that, as with the remains from layer C of Galeria da Cisterna, they relate to natural death events.

However, in layer X of Gruta da Aroeira and layer 13 of Gruta da Oliveira, the *Castor fiber* fossil remains come from archaeological deposits in which they are found in association with the remains of hunted game and abundant stone tools of, respectively, Acheulean and Mousterian affinities. These deposits accumulated once the incision of the underground network and the descent of the phreatic level in the system turned those former karst outlets into open cave entrances available for human occupation; in these cases, the beaver remains were not found in deposits that reflect their natural environment. Therefore, whatever the cause of the animals' deaths — natural or inflicted by a predator — an agent of accumulation must have been involved in the transportation of the carcasses, or elements thereof, from the ponds at spring level to the cave entrances located upslope. In the case of Gruta da Oliveira, coeval use of the site by hyaenas and other carnivores means that an agent other than humans may have been responsible for the beaver remains. In the case of Gruta da Aroeira, however, bear is the only carnivore (scarcely) represented, the faunal assemblage is dominated by anthropogenically accumulated ungulate remains, and so it remains entirely possible that the layer X beavers reflect human hunting of the species, as at the Caune de l'Arago.

5.2 - THE ECOLOGY AND HABITAT OF *CASTOR FIBER* IN AROEIRA

Beavers are specialized mammals with strict ecological preferences - aquatic environments surrounded by abundant arboreal vegetation - and that seems to have been the case in the past as well (Hugué, 2004; Barisone *et al.*, 2006; Erbajeva & Alexeeva, 2014). The habitat of *Castor fiber* is a mix of running and still water. Although European beavers seem to thrive in small rivers, living in shelters constructed along the banks, they can also make big dams. A good habitat for beavers should have perennial running water, be surrounded by forests to secure the supply of food and of wood for shelters and dams. The forests afford an easy access to food during winter seasons and provide the necessary timber for the building of dams, providing

ponds that protected them against predators (Campbell-Palmer *et al.*, 2012, Perfect *et al.*, 2014). These conditions require a regular rainfall and temperate climate, which agrees well with the formation time, MIS 11, of Aroeira layers X and XI.

In recent times, the spring of the Almonda has been dammed to take advantage of its abundant and permanent water source to power watermills and to generate electricity for adjacent factories. The pond thereby formed provides a good analogy for the kind of environment that beavers could have created for themselves during the Quaternary. The animals would have been able to swim between the pond and the underground parts of the river upstream from the spring, explaining why their remains have been found in the basal, river-accumulated sands forming the base of the Aroeira and Cisterna sequences.

5.3 - HUMANS AND BEAVERS

Reduced to about 1200 animals in eight isolated populations by the beginning of the xxth century, *Castor fiber* has recovered strongly in geographical range, populations, and number of individuals. By 2010, stable populations existed in all countries within their former natural range in Europe, except for Portugal, Italy and the southern Balkans. Until recently, it was held that beavers had gone extinct before historical times in many areas of their former natural range in Europe; though recent archaeological discoveries demonstrate that beavers persisted until at least the Middle Age (Bejenaru *et al.*, 2013; Manning *et al.*, 2014; Salari *et al.*, 2020). There is a growing body of literature on the importance of beavers as keystone species and ecosystem engineers (Zavyalov, 2014).

The archaeological evidence from the Almonda karst sites shows that beavers and humans shared the same area and environments from the Middle Pleistocene to the Late Pleistocene. As a line of thought, it is possible that humans in Aroeira used the ponds of *Castor fiber* for fishery. To date, no fish remains have been recovered in Gruta da Aroeira and the water birds recovered were not hunted (Marks *et al.*, 2002a). However, fish remains are abundant in the Upper Magdalenian levels of Lapa dos Coelhos, another of the Almonda karst system sites, and the anthropogenic nature of those remains is corroborated by the bone fishhooks found alongside (Almeida *et al.*, 2004).

There is increasing evidence for the consumption of semiaquatic and small game in the Palaeolithic. The data are scarce for the Lower Palaeolithic, and concern the consumption of tortoises, lagomorphs, marmots, and beavers (Desclaux *et al.*, 2011; Blasco *et al.*, 2016; Lebreton *et al.*, 2017), but abundant documentation exists for the Middle and the Upper Palaeolithic (Stiner *et al.*, 1999). In Portugal, the cave site of Figueira Brava demonstrates the large-scale exploitation of marine resources by Last Interglacial Neanderthals, including large crabs, mollusks, waterfowl and fish (Zilhão *et al.*, 2020). There is little question that aquatic and semiaquatic resources played a role in the diet of Palaeolithic hunter-gatherers.

6 - CONCLUSIONS

Beavers are poorly documented in the Iberian Lower Palaeolithic fossil record. Gruta da Aroeira is one of the few localities where several individuals are represented; the remains date to MIS 11 and are the earliest evidence of beavers in Portugal. Beaver populations expanded during the Upper Pleistocene in the Iberian Peninsula, when their fossils occur more frequently. Their presence in the Atlantic façade of Iberia during the Middle Pleistocene strengthens the notion that, in the past, the peninsula harboured important, well-established populations of beavers.

Indeed, the archaeological evidence strongly suggests that beavers were continuously present in the area around the Almonda spring through the Middle and the Late Pleistocene.

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