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HOMININ-CARNIVORE INTERACTION DURING THE PLEISTOCENE: DEVELOPMENT OF NEW METHODS FOR THE STUDY OF HUMAN BEHAVIOR THROUGH A TRANSDISCIPLINARY AND EVOLUTIONARY APPROACH

Edgard Camarós Pérez

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Tarragona 2016

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Hominin-carnivore interaction during the Pleistocene:
Development of new methods for the study of human behavior
through a transdisciplinary and evolutionary approach
(Doctoral Thesis, Universitat Rovira i Virgili, Tarragona)

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Printed by: Tratamiento Gráfico del Documento, S.L.
Avda. de los Castros s/n (Edif. Interfacultativo)
39005 Santander
tdg@edicionesTDG.com

Printed in Santander, Spain

First Edition: November 2016.
ISBN 978-84-608-3696-4

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DOCTORAL THESIS

Dr. Florent Rivals, Principal Advisor
Dr. Jordi Rosell, Advisor

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I STATE that the present study, entitled "Hominin-carnivore interaction during the Pleistocene: Development of new methods for the recovery of human behavior through a transdisciplinary and evolutionary approach", presented by Edgard Camarós for the award of the degree of Doctor, has been carried out under my supervision at the *Department d'Història i Història de l'Art* of this university and at the *Institut Català de Paleoecologia Humana i Evolució Social* (IPHES).

Doctoral Thesis Advisors,

Florent Rivals, PhD Principal Advisor	Jordi Rosell, PhD Advisor

Tarragona, 10th November 2015

A en Teo.
El meu petit homínid.
La millor co-evolució.

La unión en el rebaño obliga al
león a acostarse con hambre
(Proverbio africano)

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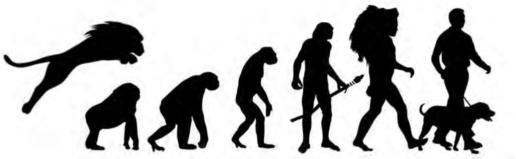

Agraïments

A l'hora d'agraïr l'ajut o el suport rebut al final d'una Tesi Doctoral, un ha de pensar molt bé quin ha estat el camí que l'ha portat fins al dia de la lectura. Un ha de saber identificar quines han estat les variables que han fet possible el camí. Tot i així, segur que n'hi ha que se'ns obliden però que han contribuït de manera especial.

Primer de tot m'agradaria agraïr als directors de la Tesi, els Professors Florent Rivals i Jordi Rosell de l'Institut Català de Paleoecologia Humana i Evolució Social, el seu suport i mestratge al llarg de tot el procés. El seu ajut ha estat total i ha fet possible la recerca que ha culminat en aquesta Tesi. També agraeixo al director de l'IPHES, el Prof. Eudald Carbonell, el seu suport i sincer interès en la meva investigació, i l'haver creat un context ideal per a fer ciència.

La Tesi és un compendi d'articles i no puc més que agraïr tot l'ajut i col·laboració dels co-autors per a desenvolupar la nostra recerca. Especialment a la Marián Cueto i a en Luis Teira, amb qui més estretament he col·laborat.

Aquesta Tesi s'ha dut a terme gràcies a una beca predoctoral FI (DGR2013) de la Generalitat de Catalunya i AGAUR a l'IPHES, en el marc del Doctorat de la Universitat Rovira i Virgili. També gràcies a una beca per a estades a l'extranger BE-AGAUR a la Eberhard Karls-Universität Tübingen *(Alemanya) (2012 BE 00971). He rebut el suport econòmic dels projectes finançats pel MINECO HAR2010-19957/HIST i HAR2013-48784-C3-1-P, i dels projectes de l'AGAUR 2014-SGR-900 i 2014/100573. Agraeixo els IP del projectes la seva confiança, ja que sense l'ajut econòmic d'aquest projectes no hagués pogut dur a terme la recerca.*

La Tesi s'ha desenvolupat a l'IPHES, i agraeixo la col·laboració de tot els col·legues i companys del centre. També he realitzat dues estades fora de sis mesos cadascuna. Una a la Universität Tübingen *amb el Prof. Nicholas J. Conard, i l'altra a la* Universidad de Cantabria *amb el Prof. Pablo Arias. A tots dos i a tothom amb qui he col·laborat d'aquestes universitats els hi agraeixo tot el que he après.*

Vull agraïr també a diverses institucions que m'hagin permès analitzar diferents contextos i materials arqueològics. Gràcies al Museu de València, Museo de Huesca, Museo de Altamira, Instituto Internacional de Investigaciones Prehistóricas de Cantabria (IIIPC), Museo de Arqueología y Prehistoria de Cantabria (MUPAC), Universidad de Cantabria, Consejería de Cultura del Gobierno de Cantabria*, Família Plassard de la Grotte de Rouffignac de França, Museu Etnogràfic de la* Universität Tübingen, Ulmer Museum *i* Institut fur Naturwissenschafliche Archäeologie (Universität Tübingen) *d'Alemanya i al* Royal Belgian Institute of Natural Sciences *de Bèlgica.*

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Agraeixo al Parque de la Naturaleza de Cabárceno *(Cantàbria) haver-me permès realitzar els experiments vinculats amb aquesta Tesi en el marc d'un conveni amb l'IPHES.*

*A les persones que m'han ajudat en algun moment de la meva recerca. Gràcies al Dr. Santiago Borragán (*Parque de la Naturaleza de Cabárceno*), a la Prof. Katerina Harvati, Prof. Hervé Bocherens i Dra. Dorotheé Drucker (*Universität Tübingen*), Prof. Valentín Villaverde (Universitat de València), Prof. Carlos Díez (*Universidad de Burgos*), Prof. Jesús Jordá Pardo (UNED), Dr. Alfred Sanchis (Museu de Prehistòria de València), Prof. Pilar Utrilla i Prof. Lourdes Montes (*Universidad de Zaragoza*) i Dr. Fréderic Plassard. Segur que m'oblido d'algú.*

Però no em puc quedar aquí.

Vull agrair-li als Drs. Florent Rivals i Jordi Rosell que m'acollissin aquell estiu a Teixoneres amb els braços oberts i m'ajudessin quan estaba literalment penjat, i establissin les bases reals del que és aquesta Tesi Doctoral. Ells saben que els hi dec molt. No puc desvincular d'aquest procés a la Dra. Ruth Blasco, que allà on jo veia pessimisme, ella veia una oportunitat. Gràcies als tres per deixar-me formar part del que heu construït. Gràcies també a l'Alexandra Canet, que era allí en aquell moment.

No puc deixar d'agraïr a certes persones la meva passió per la Prehistòria, l'Arqueozoologia i la Tafonomia. Sobretot a aquells amics de sempre del Laboratori d'Arqueozoologia de la Universitat Autònoma de Barcelona com la Dra. Ester Verdún (la meva amiga cargol), la Dra. Lídia Colomines, el Dr. Carlos Tornero, la Dra. Federica Moreno o el Dr. André Colonesse amb els que hem compartit somnis, alguns dels quals s'han fet realitat. A la Prof. Maria Saña li dec l'oportunitat d'haver pogut aprendre d'ella. Gràcies també, al Dr. Ferran Borrell amb qui he compartit no només bons moments sinó també pis.

També agraeixo les hores de recerca viscudes amb els col·legues del Centro Austral de Investigaciones Científicas (CADIC), *de* Tierra del Fuego *(Argentina), fent una recerca apassionant. Gràcies Vanesa Parmigiani, Dr. Henrán de Angelis i un llarg etcètera.*

Però sobretot d'aquella època de formació inicial, li dec al Dr. Jordi Estévez hores de conversa i formació, i la meva passió per l'Arqueozoologia. Aprendre i treballar amb ell va ser tot un plaer i la millor de les experiències personals i professionals. No m'oblido ni dels bons moments ni dels mal moments, que en el fons són l'origen de la meva recerca actual.

Moltes gràcies als companys de l'IPHES, tan d'administració com de recerca, en especial a Vanessa Altés, amb els que he col·laborat més estretament i amb els que no, l'oportunitat de formar part d'un projecte que m'ha fet madurar a nivell científic i personal.

*Agraiexo tot el que he aprés de la Dra. Susanne C. Münzel (*Universität Tübingen*), que va contribuïr a que els sis mesos que varem passar a Tübingen fossin dels millors que mai hem* *viscut. Gràcies també als col.legues d'aquesta universitat dels grups de recerca de l'*INA *i de* Paläeobiologie*.*

També als col.legues i amics de l'IIIPC de la Universidad de Cantabria.

Als amics i col·legues d'Estrat Jove, que vam aprendre junts. A en Pau Sureda, amb qui compartim en una illa perduda de la Mediterrània penes i glòries que fan que aprenguem a marxes forçades.

Als amics de Sitges: Xavier, Marta, Maria i Guillermo. Però sobretot a l'Andrea, que varem nèixer sent ja amics. A l'Edu, a qui em lliga una gran amistat. Als amics de San Ciprián*, on varem viure un any.*

He d'agraïr a la meva família la seva paciència, el suport moral i econòmic en moments durs, però sobretot l'haver plantat la llavor del meu interès pel que passa al món, ja sigui en el passat, el present o en el futur. Tot compta, i sé el que ha implicat per aquesta Tesi cada viatge, cada museu, cada conversa però sobretot cada consell. Gràcies per molt.

I com diu el poem: Gràcies moltíssimes a molts innombrats, ja anònims uns, més evidents citats, l'agraïment romàn amorós.

Per últim, vull agraïr moltes coses a les dues Marián.

Primer a la Marián Cueto li agaraeixo les incomptables hores de recerca que hem compartit, en les que he aprés d'ella moltíssim. Li agraeixo també tot el que ha contribuit a la meva formació i a la investigació relacionada amb aquesta Tesi Doctoral. La recerca que he compartit amb ella ha estat essencial.

Per últim vull agraïr-li a la Marián la resta d'hores que hem compartit més enllà de la investigació. Unes hores que hem dedicat a riure, compartir i a crear una família sense la qual no m'imagino la vida. Tot el que hem viscut junts ho tornaria a viure.

I gràcies Teo per fer-me entendre que es pot estimar algú incondicionalment, que més enllà de tot el que més estimo, estàs tu. I perdona per les hores de més que li he dedicat a la Tesi quan les hauria d'haver dedicat a tu.

A tothom, gràcies!

Edgard

Santander, 10 de Novembre de 2015

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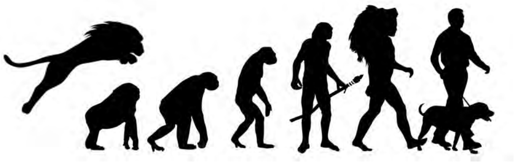
ABSTRACTS
(English, Catalan and Spanish)



Abstract

The aim of this doctoral thesis is to study the interaction between hominins and carnivores during the Pleistocene. The main research objective is to use this interaction to understand and recover modern and complex behavior from archaeological data. In this sense, several forms of past hominin-carnivore interaction are approached from different scopes and using different methods. This is presented as a Dissertation consisting of published scientific papers, to provide a general vision of the complex relation developed between hominins and carnivores during the Pleistocene. A further aim is to build a methodological framework for recovering human behavior from the archaeological record.

The forms of interaction analyzed, using experimental, actualistic, and archaeological approaches, are: a) alternate use of caves; b) carnivore hunting; c) carnivores as a resource for hominins; d) hominins as victims of carnivore attacks; and e) domestication, and all consequences this form of interaction generates (e.g., primary or secondary access to animal carcasses, or hominins as carnivore prey).

From a historical standpoint, this dissertation provides an original vision of the evolution of the interaction between hominins and carnivores from the Middle to the Upper Paleolithic, and develops the idea of how complex and important this interaction is concerning human evolution.

The different archaeological materials analyzed for the present research were discovered at different sites in Western Europe (Spain, France, Belgium, Germany, and Greece).

(Extended abstract in page 345)

Resum

La present Tesi Doctoral versa sobre l'estudi de la interacció entre hominins i carnívors durant el Pleistocé. L'objectiu principal de la recerca és utilitzar aquesta interacció per a entendre i recuperar arqueològicament el comportament humà modern i complex. En aquest sentit, les diferents formes d'interacció que els humans varen desenvolupar en el passat amb els grans carnívors és analitzada mitjançant diferents enfocs i mètodes. Tot això, presentat com a una Tesi per compendi d'articles científics publicats, proporciona una visió general de la complexa relació entre hominins i carnívors durant el Pleistocé, així com una proposta metodològica per a recuperar arqueològicament el comportament humà.

Les formes d'interacció analitzades, ja sigui mitjançant una aproximació experimental, actualita o arqueològica són: a) l'alternança en l'ús de les coves com a hàbitat; b) la cacera de carnívors; c) l'ús dels carnívors com a recurs àmpli; d) els hominins com a víctimes d'atacs de carnívor i e) la domesticació, així com les conseqüències que cada forma d'interacció implica (p.ex., accès primàri o secundàri a les carcasses animals o els hominins com a pressa dels carnívors).

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A nivell històric, la Tesi Doctoral aporta una visió original sobre l'evolució de la interacció entre hominins i carnívors del Paleolític Mitjà al Superior, així com la idea de com de complexe i constant és aquesta interacció i el que implica en l'evolució humana.

Els diferents materials arqueològics analitzats per a la present investigació provenen de diferents jaciments de l'Europa Occidental (Espanya, França, Bèlgica, Alemanya i Grècia).

(Resum ampliat a la pàgina 349)

Resumen

La presente Tesis Doctoral versa sobre el estudio de la interacción entre homininos y carnívoros durante el Pleistoceno. El objetivo principal de la investigación es usar dicha interacción para comprender y recuperar arqueológicamente el comportamiento humano moderno y complejo. En este sentido, las diferentes formas de interacción que los humanos desarrollaron en el pasado con los grandes carnívoros es analizada a través de distintos enfoques y métodos. Todo ello, presentado como una Tesis por compendio de artículos científicos publicados, proporciona una visión general de la compleja relación entre homininos y carnívoros durante el Pleistoceno, así como una propuesta metodológica para recuperar arqueológicamente el comportamiento humano.

Las formas de interacción analizadas, ya sea mediante una aproximación experimental, actualista o arqueológica son: a) la alternancia en el uso de las cuevas como hábitat; b) la caza de carnívoros; c) el uso de los carnívoros como recurso amplio; d) los homininos como víctimas de los ataques de carnívoro y e) la domesticación, así como las consecuencias que cada forma de interacción implica (p.ej., acceso primario o secundario a las carcasas animales o los homininos como presa de los carnívoros).

A nivel histórico, la presente Tesis Doctoral aporta una visión original sobre la evolución de la interacción entre homininos y carnívoros del Paleolítico Medio al Superior, así como la idea de cuán compleja es esta constante relación y lo que implica en la evolución humana.

Los diferentes materiales arqueológicos analizados para esta investigación proceden de diferentes yacimientos de Europa Occidental (España, Francia, Bélgica, Alemania y Grecia).

(Resumen extendido en la página 355)

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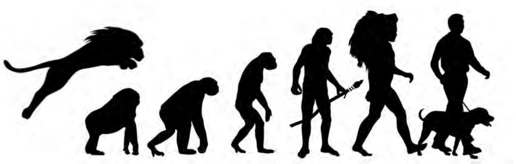

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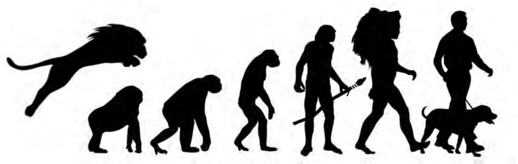
OBJECTIVES AND STRUCTURE 1



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1. Objectives and Structure

A doctoral dissertation presented in the form of published scientific papers must justify its adequacy with respect to doctoral research criteria. In this sense, the objectives must be clear and the presentation of the research must demonstrate a united study and consistent argumentation in the context of a scientific problem. This task is easy when this type of dissertation modality has been planned from the beginning, as has been done with the present thesis.

Nevertheless, a doctoral dissertation designed as a compendium of papers requires explanation regarding the workings of its structure and the organization of the scientific argumentation of the whole thesis. Therefore, this chapter explains the objectives (section 1.1) and structure (section 1.2) to aid in understanding the connection between the different papers and thereby justify its unity as a ddoctoral dissertation. Much effort has been dedicated to provide a connected research flow, where all the papers follow a solid, clear, and related scientific argument. Additional notes reinforce these ideas (section 1.3).

1.1 Objectives

The objectives of the present doctoral thesis are clear and well defined. The main aim of the research is to analyze and understand the interaction between hominins and carnivores during the Pleistocene, and how this interaction changed through time. We have also approached this past relationship in order to recover hominin behavior through it.

Doing this has required the development of new methods to generate a new frame of research work. A transdisciplinary approach to hominin-carnivore interaction has been taken, in the sense that experimentation, actualistic studies (related with ethological observations or forensic surveys), and paleontological and archaeological research have been all integrated to analyze this interaction from different perspectives.

The general objective of understanding the relation between hominins and carnivores during the Pleistocene as a way to study human behavior has been divided into different secondary objectives for study before reaching a general overview. These secondary objectives are questions to be answered in relation to different forms or scenarios of the interaction shared by hominins and carnivores in the past (see Figure 1). These questions are:

> How does the alternate use of caves as dwellings by hominins and carnivores affect the archaeological study of human behavior?

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> How did the interaction between hominins and carnivores evolve from the Middle Paleolithic to the Upper Paleolithic?
>
> Did carnivores attacked hominins, and if positive, can we differentiate between carnivore attacks and carnivore scavenging events on hominins?

Beyond these very specific questions, other issues derived from them are approached as a direct consequence of searching for useful answers. In this sense, when analyzing the evolution of the interaction, other aspects, such as hominin carnivore hunting or the role of carnivores as resources for hominins, are also studied.

Although the aim of the research is a generalist approach to hominin-carnivore interaction during the Pleistocene, specific examples have been used as proofs of concept to build new methods. Examples provide within the doctoral thesis contribute to the debate using the archaeological evidence from the Neanderthal world, as this is a period relatively short

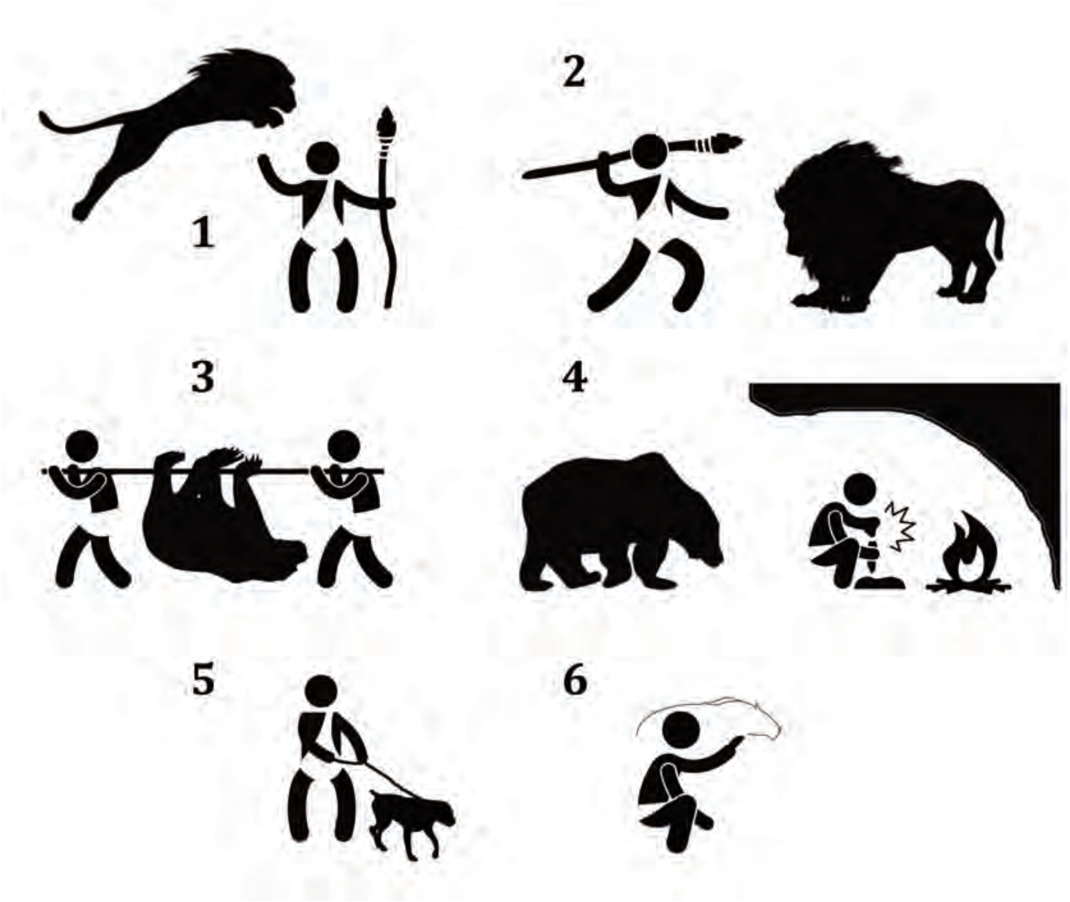

Figure 1. Different forms of hominin-carnivore interaction analyzed in the present doctoral thesis. 1) Carnivore attacks to hominins; 2) Hominins hunting humans; 3) Use of carnivores as a resource by hominins; 4) Alternate us of caves by hominins and carnivores; 5) Domestication of carnivores and 6) The role of carnivores in hominin culture (symbolic and cognitive implication).

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and affordable in order to test our methods and try to answer our specific questions. Middle Paleolithic sites and related-data is abundant, and therefore this sample is a good one for studying hominin behavior through the interaction they developed with large carnivores. Furthermore, in order to analyze how the interaction evolved from the Middle to the Upper Paleolithic, a specific case is approached. In this sense, the geographical area of the Swabian Jura, where an outstanding archaeological record of the relation between humans and carnivores is preserved, also feature in the dissertation. These are case studies added as good proofs to demonstrate the approach and recovery of human behavior through hominin-carnivore interaction.

The examples provided are related to *Homo neanderthalensis* and *H. sapiens*, but the way in which the study of their behavior is analyzed through the relation they had with carnivores can be applied to other human forms. In this sense, our final interest is to build a useful framework for human evolution studies.

The present doctoral thesis is coherent and united research with clear objectives, presented as a compendium of scientific published papers.

1.2 Structure

Structure is an important issue, as it plays a central role in making a doctoral thesis understandable (Witcher, 1990). Although the structure of the present dissertation follows the classic presentation of scientific research, it has some particularities because it is a compendium of papers.

In this sense, Chapter 1, *Objectives and Structure*, is focused on justifying the present document as adequate research for consideration as a doctoral dissertation, by presenting the structure and clarifying and explaining its particularities. Chapter 2, *Metrics: Papers, authors, and institutions,* is a section dedicated to the presentation of the information related to the scientific papers, co-authors, and institutions involved in the compilation. This chapter consolidates this information to visualize the metrics related with the number of papers presented and those authors and institutions that have taken part.

Chapter 3, *Materials, methods, and techniques*, is the part of the dissertation where this information can be found as a unity. In this sense, although in each scientific paper has its own section on Materials and Methods where this information is explained in detail, Chapter 3 aims to visualize all materials and sites used for the dissertation, as all the methods and techniques approached during the research.

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The presented scientific papers form Chapter 4, where all the papers have been organized into different sections depending on their subject, with the aim of providing organized argumentation. Therefore, the papers have been divided into 4 sections:

4.1 *Introduction: Hominin-carnivore interaction during the Pleistocene*
4.2 *Methods and techniques*
4.3 *Experimental approach to hominin-carnivore interaction*
4.4 *Case studies of hominin-carnivore interaction during the Pleistocene*

In section 4.1, the papers provided are related to introductory data concerning hominin-carnivore interaction and to the dissertation hypotheses and objectives. General and background information is provided in order to introduce the subsequent research. Section 4.2 provides information related with methods used and developed. Section 4.3 is dedicated to those papers with a particular focus on the development of taphonomic experimentations related to the study of hominin-carnivore interaction. These experiments provide new insight into the study of the interaction and they are later used to generate results in other sections. Finally, section 4.4 analyses particular case studies of hominin-carnivore interaction to provide insights into the different forms of interaction developed during the Pleistocene, and the evolution of the hominin-carnivore interaction.

Although all the papers have been divided into four sections for a better organization of the thesis, they all provide original perspectives and approaches to hominin-carnivore interaction for the study of human behavior during the Pleistocene.

Furthermore, published or unpublished supplementary information is added, with the aim of complementing the research conducted in the papers of each section. This allows us to include data, information, and results that have been not published within the paper or as individual papers, for space or timing reasons. Supplementary material is relevant to a full understanding of the research and thesis, and provides a way of making our data available to the scientific community.

Finally, Chapter 5 is dedicated to the Discussion, conclusions, and future perspectives of the doctoral thesis. This is an unpublished chapter that discusses the implications of the research in the context of the existing knowledge and published investigations on human evolution. The conclusions summarize the main doctoral thesis argument and the main results obtained in each paper as unique and unified research. Chapter 5 also focuses on the meaning of our results and the new and open questions we have reached that will promote future research.

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Information related to the references used in the dissertation (except for published papers) is added at the end of the text. Annexes are also provided (an economic report of the public investment to the thesis, and original papers and other documents), as is a list of figures.

1.3 Particularities, terminology, and chronology

The present doctoral thesis is a compilation of published scientific papers; thus, in this sense, is has certain particularities concerning some of its parts.

The papers are not presented in the dissertation exactly as they have been previously published in the journals. The texts and the paper structure have been not modified, but contain several changes and particularities, as follows:

1) The papers are not presented in any order referring to their publication date. They are placed in relation to the structure and order designed for the dissertation.

2) The figures are not placed in the exact position found in the original published paper.

3) The figures maintain their original published numeration; therefore, they do not follow a consecutive numerical series in the Dissertation.

4) The citation style or referencing system of each paper maintains the original style required by the journal where the paper is published. Therefore, papers follow different citation styles (e.g., Harvard Referencing, CSE Style, Vancouver System, etc.). Nevertheless, the References (Chapter 6) are cited following the same citaion system used in Queternary International.

5) The figures, tables, and authors are cited in the text in the style required by the journal where the paper is published (e.g., Figure or Fig., AUTHOR & AUTHOR, or Author and Author, Author et al. 2016, or Author et al., 2016, etc.).

6) Regarding the language, depending on the paper, American or British English has been used. Nevertheless, in the doctoral thesis, in general, American English has been used (e.g., title, introductory, and final chapters).

7) Prior to each paper, a cover information page is provided that contains publishing information, such as authors' names, authors' institution, abstract, keywords, and publication specifications (e.g., journal name, volume, and pages).

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8) Published supplementary material is referenced using the same terms as in the published paper (e.g., Online Resource Material, Online Supplementary Material, etc.).

9) A non-published supplementary material section is added as part of the Dissertation to provide more information and data regarding the research.

Furthermore, published papers 5 and 7–10 use the term hominins instead of hominids, which was used in Paper 1. According to scientific convention, the term hominins refers to the group consisting of modern humans, extinct human species, and our immediate ancestors (genera *Homo*, *Australopithecus, Paranthropus*, and *Ardipithecus*), whereas the term hominids refers to the group consisting of all modern and extinct Great Apes (including modern humans, chimpanzees, gorillas, and orangutans, as well as all their immediate ancestors).

The term interactions (in plural), in reference to the relation between hominins and carnivores, is only used in first published paper (Paper 1). In all other papers, this relation is referred as interaction (in singular), as we now think that there is only one interaction between hominins and carnivores during the Pleistocene, but with different forms (carnivore hunting, alternate use of space, domestication, etc.). The idea of citing this relation in the singular form provides unity to the concept of a constant and evolving relationship with many forms of a common process.

Concerning the chronology of the research, we have analyzed archaeological, paleoanthropological, and paleontological evidence belonging to different periods from the Late Pleistocene. The term Pleistocene is used following the major published time scale, in which the base of the Pleistocene is defined by GSSP of the Gelasian Stage at 1.806 (1.8) Ma according to Gradstein and colleagues (2004). Whenever possible, direct dating has been provided (e.g., C14 or Uranium Thorium dates).

The terms Lower, Middle, and Upper Paleolithic have been used.

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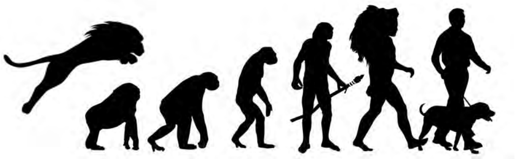
METRICS: PAPERS, AUTHORS AND INSTITUTIONS

2



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2. Metrics: Papers, authors and institutions

The present PhD dissertation is composed by 10 scientific papers. A total of nine papers have been published in peer-reviewed international journals and monographs, and one has been submitted (still in revision).

The papers presented as the *corpus* of the PhD are listed below:

- **Paper 1.** Rosell *et al.* (2012). New insights on hominid-carnivore interactions during the Pleistocene. *Journal of Taphonomy*

- **Paper 2.** Camarós and Cueto (2013). New methodologies for the recovery of human behaviour through the evolution of hominid-carnivore interaction during the Pleistocene. *Antiquity*

- **Paper 3.** Camarós *et al*. (accepted). Make it clear: Molds, transparent casts, and lightning techniques for stereomicroscopic analysis of taphonomic modifications on bone surfaces. *Journal of Anthropological Sciences*

- **Paper 4.** Camarós *et al*. (2013). Aproximación experimental a la modificación de hogares por parte de carnívoros durante el Pleistoceno. Metodología y primeros resultados. *Estudio y difusión del pasado*, Sèrie Monogràfica del MAC-Girona, 25.2

- **Paper 5.** Camarós *et al*. (accepted). Walking with carnivores: Experimental approach to hominin-carnivore interaction. *Playing with the time. Experimental Archaeology and the study of the past*, Servicio de Publicaciones de la UAM

- **Paper 6.** Camarós *et al*. (2013). Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications. *Journal of Archaeological Science*

- **Paper 7.** Camarós *et al*. (accepted). The evolution of Paleolithic hominin-carnivore interaction written in teeth: Stories from the Swabian Jura (Germany). *Journal of Archaeological Science: Reports*

- **Paper 8.** Camarós *et al*. (accepted). Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behavior. *Quaternary International*

- **Paper 9.** Camarós *et al*. (2015). Large carnivore attacks on hominins during the Pleistocene: A forensic approach with a Neanderthal example. *Archaeological and Anthropological Sciences*

- **Paper 10.** Camarós *et al*. (submitted) Neanderthal fossils with carnivore implications: Taphonomic approach and behavioral implications. *Journal of Human Evolution*

All of them except one (Paper 1) have been signed by the PhD candidate as first author. Furthermore, almost all of them contain the words *carnivore, interaction* and *Pleistocene* in the title as an effort to show a common relation among them.

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Concerning the authorship of the papers, a total of 22 different co-authors from 14 different institutions have contributed in different ways to the papers. Below, a list of the co-authors and their academic filiation (the one they signed the paper with) is provided:

- **Pablo Arias.** *Instituto Internacional de Investigaciones Prehistóricas de Cantabria, Universidad de Cantabria* (Spain) (Paper 8)

- **Enrique Baquedano**. *IDEA (Instituto de Evolución en África), Museo de los Orígenes and Museo Arqueológico Regional* (Paper 1)

- **Ruth Blasco.** *The Gibraltar Museum (UK)* (Paper 1) and *Institut Català de Paleoecologia Humana i Evolució Social and Universitat Rovira i Virgili* (Spain) (Paper 6) and *Universitat Autònoma de Barcelona* (Spain) (Paper 10)

- **Nicholas J. Conard**. *Institut für Naturwissenschaftliche Archäologie and Institut für Ur-und Frühgeschichte und Archäologie des Mittelalters, Universität Tübingen* (Germany) (Paper 7)

- **Miriam Cubas.** *Instituto Internacional de Investigaciones Prehistóricas de Cantabria, Universidad de Cantabria* (Spain) (Papers 3, 6)

- **Marián Cueto**. *Instituto Internacional de Investigaciones Prehistóricas de Cantabria, Universidad de Cantabria* (Spain) (Papers 3, 4, 5) and *Laboratori d'Arqueozoologia, Universitat Autònoma de Barcelona* (Spain) (Papers 5, 7-10)

- **Andreas Darlas**. Ephoreia of Paleoanthropology and Speleology of Northern Greece (Paper 10)

- **Carlos Díez**. *Universidad de Burgos* (paper 10)

- **Corine Duhig**. *University of Cambridge* (Paper 10)

- **Katerina Harvati**. *Senckenberg Center for Human Evolution and Paleoecology, Eberhard Karls University of Tübingen* (paper 10)

- **Carlos Lorenzo.** *Universitat Rovira i Virgili and Institut Català de Paleoecologia Humana i Evolució Social* (Paper 9)

- **Lourdes Montes**. *Área de Prehistoria, Universidad de Zaragoza* (Paper 10)

- **Susanne C. Münzel**. *Institut für Naturwissenschaftliche Archäologie, Universität Tübingen* (Germany) (Papers 7, 8)

- **Andreu Ollé**. *Institut Català de Paleoecologia Humana i Evolució Social and Universitat Rovira i Virgili* (Spain) (Paper 9)

- **Jesús F. Jorá Pardo.** *Departamento de Prehistoria y Arqueología. Universidad Nacional de Educación a Distancia* (Paper 10)

- **Florent Rivals.** *ICREA at Institut Català de Paleoecologia Humana i Evolució Social and Universitat Rovira i Virgili* (Spain) (Papers 3-10)

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- **Jordi Rosell.** *Universitat Rovira i Virgili and Institut Català de Paleoecologia Humana i Evolució Social* (Spain) (Papers 1, 6, 10)

- **Frédéric Plassard.** *UMR5199 PACEA, Université Bordeaux 1* (France) (Paper 8)

- **Carlos Sánchez-Hernández**. *Institut Català de Paleoecologia Humana i Evolució Social and Universitat Rovira i Virgili* (Spain) (Paper 3)

- **Jesús Tapia.** *Sociedad de Ciencias Aranzadi* (Spain). (Papers 4, 6)

- **Luis C. Teira.** *Instituto Internacional de Investigaciones Prehistóricas de Cantabria, Universidad de Cantabria* (Spain) (Papers 3, 4, 6, 8)

- **Valentín Villaverde**. *Departament de Prehistòria i Arqueologia, Universitat de València* (Spain) (Paper 9-10)

All of them contributed to this PhD as co-authors of the published papers and I am grateful and in debt with them due to all comments, corrections and positive suggestions they made in order to improve our research. I acknowledge the work and the time they dedicated to the papers.

Furthermore, all papers have been revised by many anonymous reviewers. I am also grateful with them and I acknowledge their suggestions and observations to our work. I appreciate also the work of the editors of the journals and special monographs where the papers have been published.

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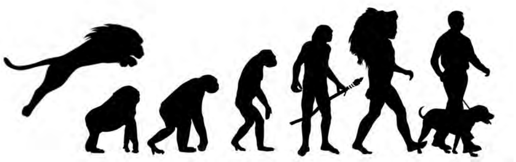
MATERIALS AND METHODS 3



3. Materials and methods

Different types of materials and contexts have been analyzed during the present doctoral thesis research. All were selected to provide new insights into the interaction between hominins and carnivores. Materials used come from different archaeological and paleontological contexts from Western Europe. Sites involved in the dissertation are La Garma, Valdegoba, Jarama VI, Moros de Gabasa, El Castillo, and Cova Negra in Spain; Hohlenstein-Stadel, Vogelherd, Hohle Fels, and Geissenklösterle in Germany; Fonds de Fôret and Spy in Belgium; and Rouffignac in France (see Figure 1). Although materials studied are presented in the 'Materials and methods' section in each paper, the materials analyzed in the present dissertation span from single bone specimens to complete archaeological collections. Nevertheless, experimental materials were also studied, as were paleontological contexts (e.g., intact Pleistocene bear beds).

Figure 2. Location of the sites where the materials and contexts analyzed for the doctoral thesis come from.

In this sense, the materials analyzed come from both old and modern excavations, and are conserved at different institutions. Therefore, many museums, universities, research centers, and even Natural Parks had to be visited to analyze our material or develop taphonomic experiments (Figure 3). Other types of research, such the ones developed in Rouffignac (Dordogne, France) and La Garma (Cantabria, Spain) (Figure 2), were conducted directly inside the cavities (Figures 5 and 7).

Figure 3. Museums, universities, research centres and institutions visited during the doctoral thesis.

Materials involved in the present dissertation are hominin fossils, animal bones, lithic tools, and experimental and paleontological contexts. All share the common feature of being outstanding materials for conducting research related to hominin-carnivore interaction.

Concerning the methods applied, a transdisciplinary approach has been developed in the doctoral dissertation. In this sense, methodological specifications related with disciplined such as paleoanthropology (e.g., Paper 10), archaeozoology (e.g., Paper 8), paleontology (e.g., Paper 7) or even forensic medicine (e.g., Paper 9), have been used to study our material. Of these, taphonomy was the most used discipline.

In other cases, it was necessary to develop methods to study our interaction scenarios. Therefore, in the cases of Rouffignac and La Garma, for example, we designed the study with the aim of measuring the bear beds to characterize them (Figure 5d). Furthermore, we have also studied bone surfaces using the technique of molding and casting with high-resolution silicone applied for this purpose (Figure 6). The techniques and methods used for each study are explained in each paper, and are, in some cases, accompanied with supplementary material (published and non-published). Nevertheless, in the dissertation, two papers are provided that focused only on the methodological aspects of the research (Papers 3 and 4), and these are placed in Chapter 4.2, *Materials and techniques*.

Technique devices used during the dissertation, beyond tools such as calipers, cameras, and others, have included total stations (Figure 5a and 5c) to produce topographic planimetries (Figure 5e, e.g., Papers 5 and 8), portable scanners to scan wall and floor surfaces (Figure 7a-b, e.g., Paper 8), microscopes to analyze bone and stone surfaces (Figure 7c-d, Papers 5, 8), and SEM (Figure 7e, Paper 6 and Unpublished Supplementary Material).

Figure 4. A: Hominin fossils with carnivore damage: 1) Cova Negra; 2) Jarama VI; 3) Moros de Gabasa; 4) Kalamakia; 5-7) Valdegoba; 8) Fonds de Fôret and 9) Hohlenstein-Stadel. B: Hominin fossils without carnivore damage: Spy collection (see Figure 2 for detailed geographical location).

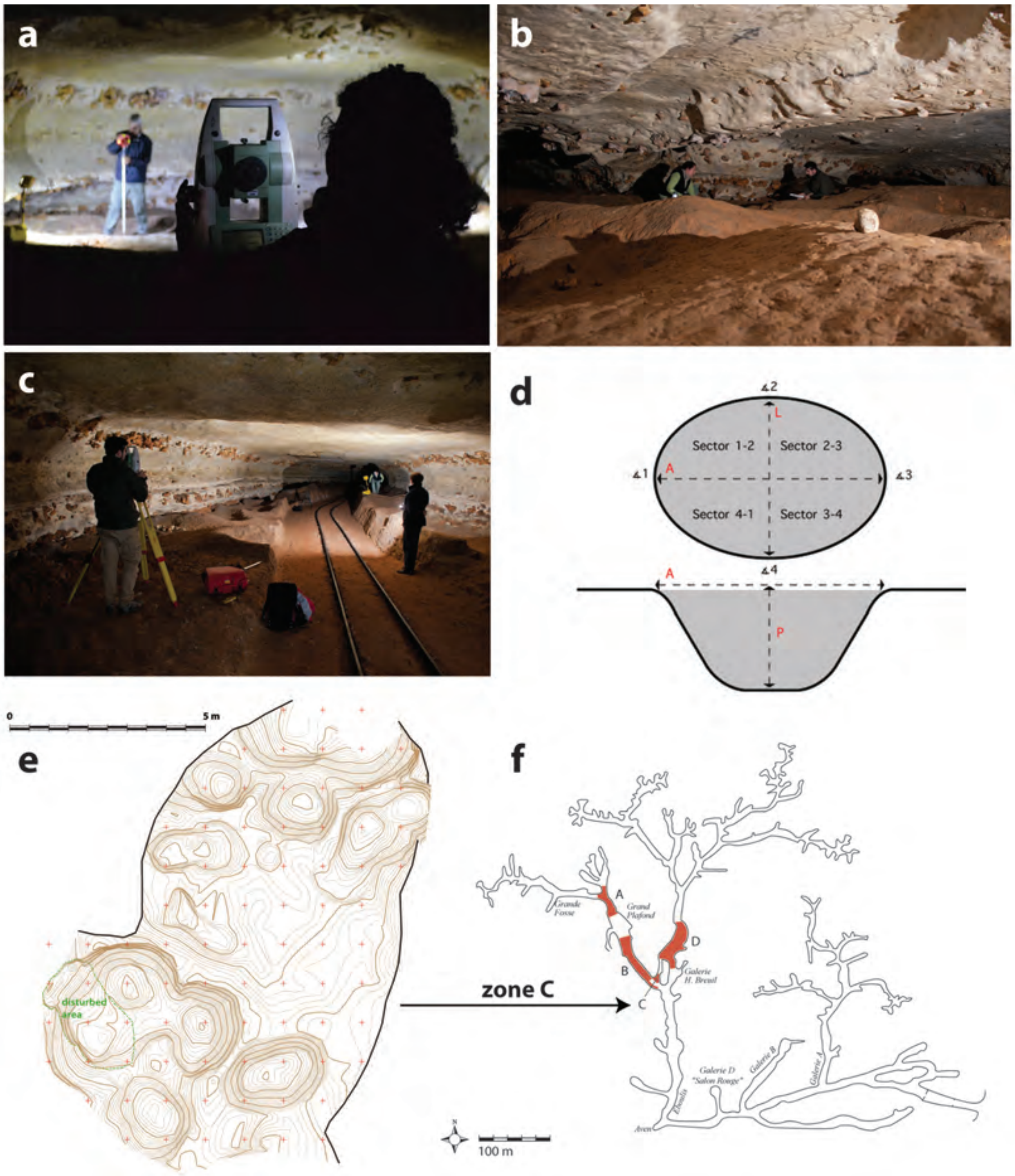


Figure 5. Rouffignac Cave (Dordogne, France): a-c) topography and measurements of the bear beds; d) measurements of the bear beds taken during the field work; e) resulting topography where the bear beds are clearly visible and e) plan of the cave with the research zone highlighted in red, including zone C (e).

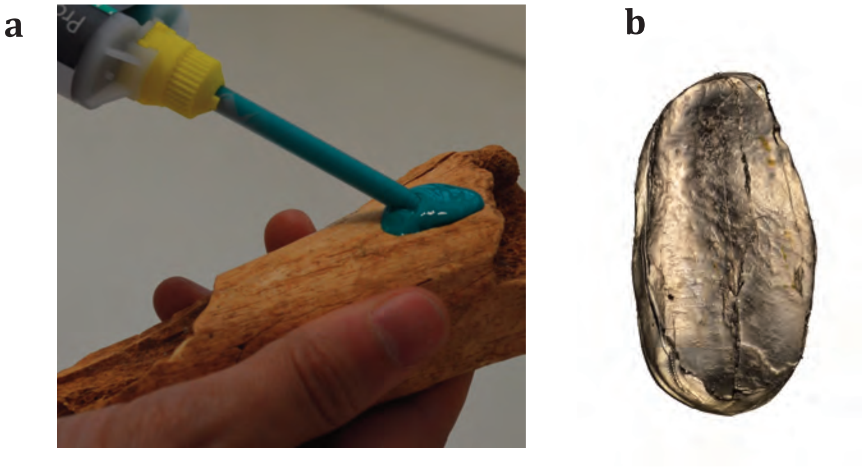


Figure 6. a) Molding process and c) example resulting cast (from a carnivore canine from the Swabian Jura used as a retoucher).

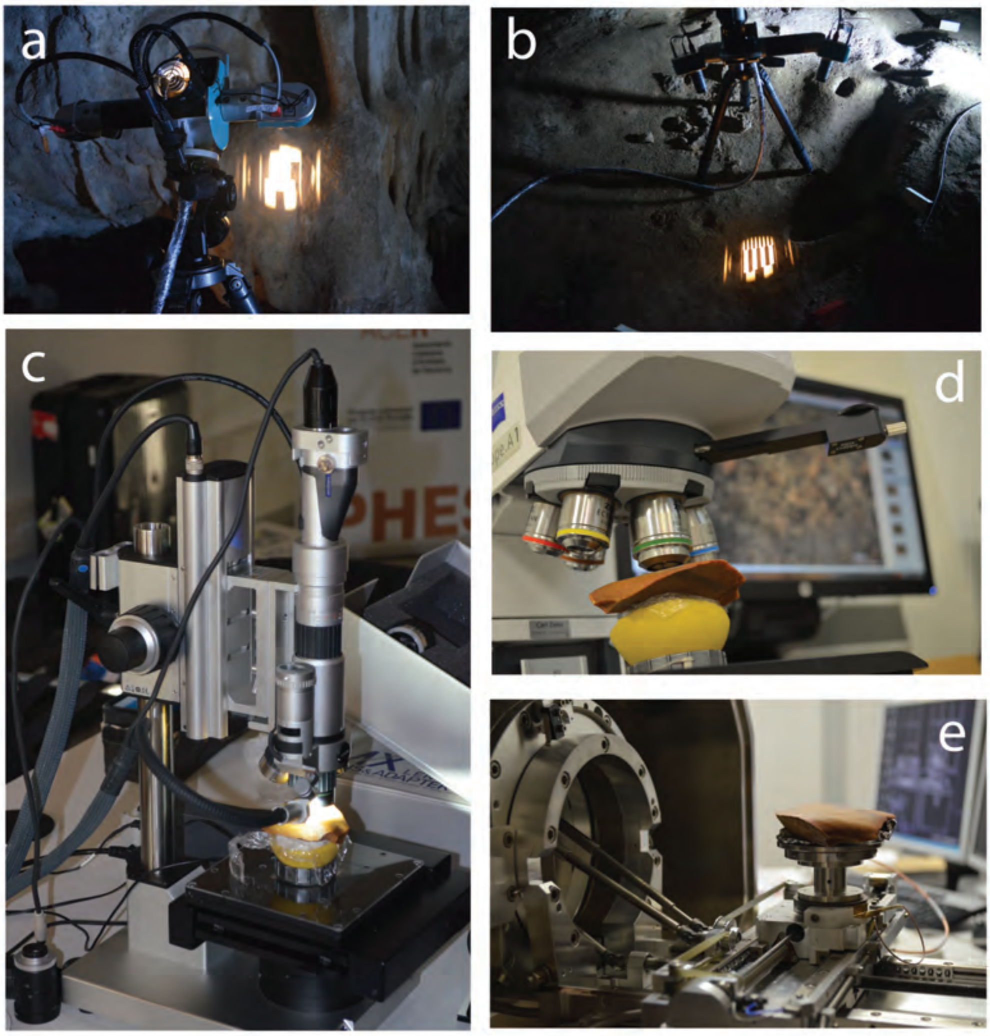


Figure 7. Example of some of the equipments used during the doctoral thesis research to scan cave surfaces (a-b) and observe archaeological material with different optical devices such as microscopes (c-d) and SEM (e).

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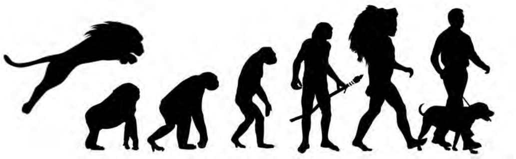
PRESENTED SCIENTIFIC PAPERS 4



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INTRODUCTON: HOMININ-CARNIVORE INTERACTION DURING THE PLEISTOCENE

4.1

PAPER 1

New insights on hominid-carnivore interactions during the Pleistocene

PAPER 2

New methodologies for the recovery of human behaviour through the evolution of hominid-carnivore interaction during the Pleistocene

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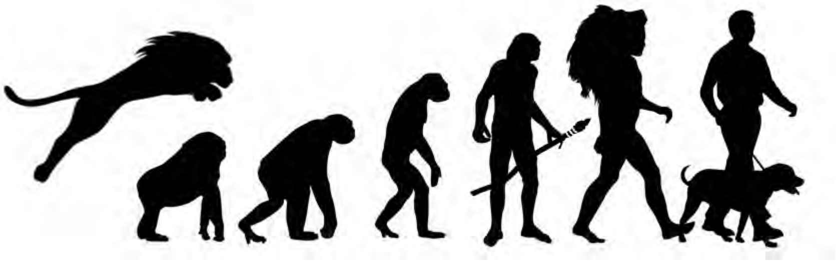
4.1.1

PAPER 1

New insights on hominid-carnivore interactions during the Pleistocene



Chapter 4.1 *Introduction: Hominin-carnivore interaction during the Pleistocene*

Paper 1

New insights on hominid-carnivore interactions during the Pleistocene

Jordi Rosell (1, 2)
Enrique Baquedano (3,4)
Ruth Blasco (5)
Edgard Camarós (2,1)

(1) Àrea de Prehistòria, Universitat Rovira i Virgili
(2) Institut Català de Paleoecologia Humana i Evolució Social
(3) IDEA (Instituto de Evolución en África), Museo de los Orígenes
(4) Museo Arqueológico Regional
(5) The Gibraltar Museum

Journal of Taphonomy, 10 (3-4) (2012), 125-128

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Carnivores are present in the majority of the Pleistocene sites. Apart from their skeletal remains, activities of these predators can be recognized in form of bone damage (toothmarks, bone breakage and digested bones), coprolites and spatial disturbances (moved objects or dug holes and burrows) (Camarós et al., 2013). The role played by these animals in the archaeological sites and their significance in the human behaviour was not ignored by the first researchers during the XIX century and the first half of XX. However, the studies of this period were more focused on distinguishing chrono-cultures and the items associated with them and, therefore, the problem remained in the background. This situation was changing progressively during the second half of the XX century. In the 80s, when the bases of modern Taphonomy and Zooarchaeology were established (Binford, 1981; Brain, 1981; Shipman, 1981; inter alia), the relationships between hominids and carnivores during the Pleistocene became a recurrent topic in the archaeological literature. The main aim of the discussion was to check the human capacities in different periods, linking hominids directly with their most direct competitors for prey and habitat space (Chase, 1988; Binford, 1988; Cruz-Uribe, 1991; inter alia). Today, after more than thirty years of debate, some aspects seem to have been overcome, such as the human access modalities to the carcasses (Domínguez- Rodrigo & Pickering, 2003), but they were replaced by new issues to solve.

In this context, the aim of the congress "Hominid-carnivore interactions during the Pleistocene" (25-28 October 2011, Salou, Tarragona, Spain) was to join the researchers from all the disciplines involved in this subject. More than 200 participants manifested the significance of this issue in the archaeological record. The meeting was divided into three sessions, with the objective to cover all the questions about relationships between hominids and carnivores in the past.

1. Carnivore dens: past and present

In order to recognize the activities of the carnivores involved in the archaeological sites and the role played by these animals in the ecosystems of the past, studies about actual, subactual and prehistoric dens and refuges have multiplied in the last decades. Some actualistic examples are the studies that involve animals in wild state, such as Iberian bears (Sala et al., in this issue) or wolves (Fosse et al., in this issue; Yravedra et al., in this issue) and comparative neo taphonomic studies of the accumulations generated by different predators in Africa, as lions, hyenas and canids (Domínguez-Rodrigo et al., in this issue).

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With the same aim, Pleistocene carnivores are also analysed, such as hyenas or dholes from archaeological sites of Western Europe (Fourvel et al., in this issue; Mallye et al., in this issue; Morales Pérez et al., in this issue). Nevertheless, there are some characteristics which don't allow us to understand, with total clarity, the behaviour of past carnivores in relation to actual carnivores. In the first place, many of the Pleistocene carnivores are nowadays extinct, as are cave bears, sabertooth cats or giant hyenas. Their specific behaviour can only be inferred from specific techniques, from the study of their remains, the contexts were they appear or from the Ethology of their most proximate living biological relatives (Viranta & Grandal d'Anglade, in this issue). In the second place, the range of carnivores of the Pleistocene was much larger than the actual. The coexistence in the past between animals is tied today to specific areas (wolves, bears, lynxes and dholes in the Palearctic and lions, leopards and spotted hyenas in the Sub- Saharan Africa) suggests different ecological relationships and pressures (Martínez-Sánchez et al ., in this issue; Rodríguez-Gómez et al ., in this issue). Therefore, this session tried to put in common data, obtained from both actualistic and archaeological studies, intending to draw the different scenarios in which hominids will later appear.

2. Hominid-carnivore interactions in the archaeological record

Between the most pure dens and anthropogenic campsites, there exists a wide range of intermediate models, which suggests the possible contacts between hominids and carnivores during the Pleistocene (Daujeard et al., in this issue; Martín et al., in this issue; Patou-Mathis et al., in this issue). Taking up again the classic discussion which raises the constant competence relationships, not only for prey, but also in habitat areas, the relationship diversity can be reduced to five principal types:

1. Hominids as regular scavengers of remains stored by other carnivores, both in their hunting areas as in their dens.

2. Carnivores as scavengers of remains stored by hominids in their shelters or campsites.

3. Carnivores as prey of hominids.

4. Hominids as prey of carnivores .

5. Coexistence, commensalism and domestication.

From an archaeological point of view, Model 2 (carnivores as scavengers) is the most frequent one (Rosell & Blasco, 2009; Blasco & Rosell, 2009). On the contrary, some of the oldest works related to Model 1 have been recently revised and the initial interpretations have been questioned (Domínguez-Rodrigo & Pickering, 2003). In this regard, relationships of competence between hominids and predators and the periodicity in the use of spaces is the subject of several works related to archaeological sites (Brugal et al., in this issue; Discamps et al., in this issue; Enloe, in this issue; Smith, et al., in this issue; Morales et al., in this issue; Smith, in this issue; Villaluenga et al., in this issue). Model 3 is difficult to check, especially in more ancient chronologies. Nevertheless, recent publications of occasional hunting of large carnivores during the Middle Pleistocene show the human capacities to affront successfully large predators (Blasco et al., 2010), a behaviour that seems to have been most regular in Upper Palaeolithic (Kitagawa et al., in this issue). Model 4, although much more restricted to Plio-Pleistocene chronologies is also a form of relation between hominid and carnivores (Baquedano et al., 2012). From this perspective, the aim of this session was to evaluate the different types of contacts which are established between hominids and carnivores in the past: their proof, their periodicity and the influence they could have in phenomena of commensalism or domestication of some species (Model 5), as is the case of wolf, now 30 kyr ago (Germonpré et al., 2009).

3. Hominid-carnivore co-evolution

The regular inclusion of meat and fat in the diet of the first hominins, as a consequence, had significant behavioural transformations. New subsistence strategies based on obtaining animal resources emerged, which generated changes in the ecological relationships between hominins and the other predators. However, in this competence, hominins took advantages quickly from two main elements: 1) omnivorism and, 2) technology. This evolutionary process has been seen by some researchers as a phenomenon of co-evolution, which can be explored in various key moments (Stiner, 2002, in this issue). From a biological point of view, maybe the most known must be the one, related to the first migration from Africa and the dispersal of genus Homo all through Eurasia next to various carnivore species, which also have an African origin. From a cultural or social point of view, more recent events, as is domestication, would be the most paradigmatic example. But these co-evolutionary phenomena must be revised from various perspectives (Caparrós et al., in this issue). On the first hand, it is important to evaluate the real grade of pressure to which hominids (omnivores) are submitted by part of these more direct competitors, carnivores, through all their evolutionary history. On the second hand, key elements in human history must be evaluated, as is rapidly developing technology or the existence of social nets, each time more complexes. And, finally, it is necessary to discuss which has been the

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influence of these animals on the development of our social organization and on the diversity of the current behaviour. In summary, the congress revealed that hominid-carnivore interaction continues being a significant topic for understanding the evolution of human behaviour in the past. Currently, the discussion is including new disciplines and techniques involved not only in exploring the different modalities of contacts between hominins and carnivores, but also the reconstruction of the different ecological scenarios where hominids were present. So, the debate is still alive.

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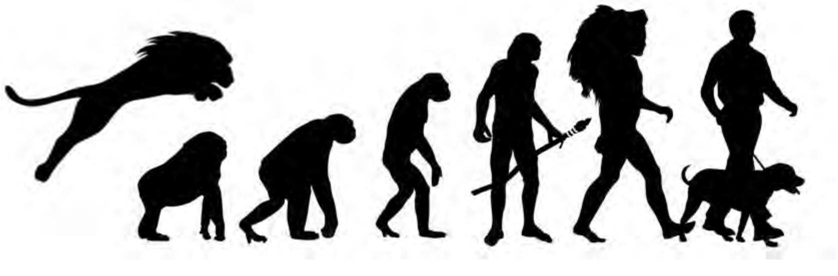
4.1.2

PAPER 2

New methodologies for the recovery of human behaviour through the evolution of hominid-carnivore interaction during the Pleistocene



Chapter 4.1 *Introduction: Hominin-carnivore interaction during the Pleistocene*

Paper 2

New methodologies for the recovery of human behaviour through the evolution of hominid-carnivore interaction during the Pleistocene

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Antiquity, Vol. 087 Issue 335 March 2013 (Project Gallery)

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Introduction

Throughout human evolution, carnivores have played an important role in the shaping of human behaviour (Brain 1981) and some scholars even talk about a co-evolutionary process shared by genus Homo and large carnivores (e.g. Brantingham 1998). During the Pleistocene, hominids interacted with large carnivores in a variety of ways, such as dependency (scavenging) (Blumenschine 1988), confrontation (hunting) (Chase 1988), competition for the use of caves as dwellings, the exploitation of common prey (Pettitt 1997) and, eventually, domestication (Germonpré et al. 2012) (Figure 1). In this sense, a profound analysis of the interaction between hominids and carnivores is a positive way of studying the evolution of human behaviour, as previous studies have proved (e.g. Stiner 2002).

Figure 1. Image of Zone IV in the Lower Gallery of La Garma Cave (Omoño, Cantabria). It is possible to observe in the same picture (due to the preservation of the Lower Gallery, where there is no sedimentation) how carnivores and humans have used caves for different purposes, such as hibernation in the case of bears or for painting in the case of human groups during the Magdalenian. Alternation in the use of caves is one of the most common forms of interaction during the Pleistocene. (Picture by L. Teira/IIIPC)

The project: objectives and approaches

The project entitled 'Development of new methodologies for the study of Neanderthal behaviour through hominid-carnivore interactions' aims to generate methodologies for the analysis of human behaviour by studying the relationship between hominids and large carnivores. To achieve this, we have designed experiments with extant large carnivores such as bears, hyenas, lions and wolves in Cabárceno Nature Park (Santander, Cantabria, Spain) with the aim of recreating potential Pleistocene scenarios of hominid-carnivore interaction (Figure 2). From the results, we will build a methodology with which Palaeolithic archaeological contexts can be better understood. Experimentation will address spatial aspects of complex human behaviour, e.g. the systematic use of fire, the development of scavenging or hunting strategies, direct confrontation between hominids and carnivores , or the achievement of modern cognition related to inhumation rituals . The project also studies osteological collections and archaeological contexts from northern Spain (Figure 3) in order to test the results obtained in the experimental phase.

Figure 2. The research team inside the bears' enclosure preparing an experiment to investigate how large carnivores modify anthropic spatial contexts.

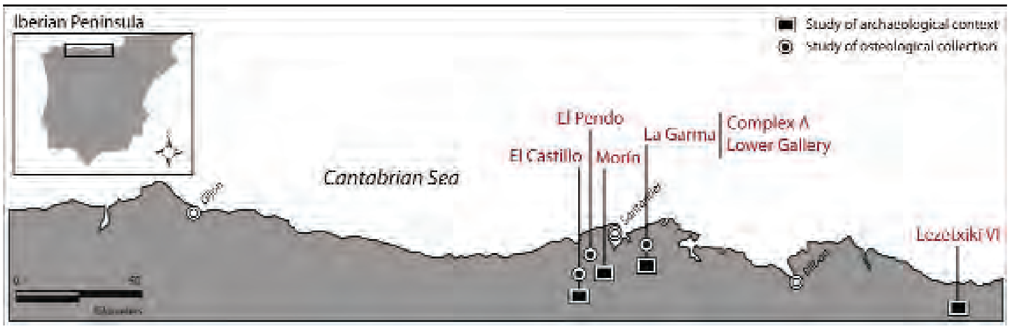

Figure 3. The Cantabrian coastline with the location of archaeological sites involved in the project.

Preliminary results: erased behaviour

The study of human evolution towards modern behaviour is closely related to intra-site spatial analysis. Through the study of artefact distributions, it is possible to reconstruct spatial organisation and thus behaviour. In Lower and Middle Palaeolithic sites, this is important because there is the possibility of observing modern cognition through such spatial patterning. For example, the presence of a hearth reveals the specific organisation of social activity around it (Binford 1978) and indicates a formal conception of domestic space (McBrearty & Brooks 2000). Therefore, the identification of spatial patterns is central to understanding human behaviour and evolution (Vaquero & Pastó 2001). In particular, spatial analysis is an important element for the study of when and how complex behaviour and modern cognition develops. In this sense, spatial analysis is an essential tool for debates on those periods when the presence of modernity and complexity is questioned.

Figure 4. Images of how carnivores modified spatially structured scenarios during experiments, in this case complex combustion structures. A: *Ursus arctos*; B: *Crocuta crocuta*; C: *Panthera leo;* D: *Canis lupus*.

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However, are there any taphonomic agents capable of erasing such evidence of complex human behaviour? There are many. Most of them relate to geological or sedimentological processes such as water erosion and bioturbation. Anthropic processes such as trampling, intentional re-cycling or cleaning activities can also modify or erase spatial patterns. Carnivores, however, have never been directly considered as taphonomic agents capable of the modification of structured human spaces. Due to varied hominid-carnivore interactions, we argue that large carnivores can act as agents of taphonomic modification and erase some or all of the anthropic evidence of modern and complex spatial organisation during the Pleistocene (Figure 4).

For example, one of our experiments aimed to analyse how carnivores (bears, hyenas, lions and wolves), in their alternation with hominids in the use of caves, may have modified anthropic contexts. Through previous studies, we assumed that the most common situation since the Middle Pleistocene was that carnivores arrived at a cave after human groups had abandoned it (Blasco & Rosell 2009). Our research has proved experimentally that when carnivores interact with such abandoned structured spaces (including hearths) they are capable of modifying them to a point where no spatial patterns can be recognised (Camarós et al. 2013). This suggests that carnivores' actions could be responsible for perceptions of hominid behaviour during the Palaeolithic. This could be the reason why, for example, Neanderthals are considered by some scholars as a hominid with the same essential spatial patterns as carnivores (i.e. non-human ones) (Pettitt 1997).

Understanding the processes by which carnivores may have modified archaeological evidence may help us to recover the evidence of modern human behaviour in the Pleistocene. This can be done by statistically modelling carnivores' actions based on our experimentation and comparing the results with known archaeological patterns. As our first results show, the experimental and archaeological study of hominid-carnivore interaction is a positive approach for the development of new methodologies to demonstrate and understand human behaviour and complexity during the Pleistocene.

Acknowledgements

The project is owned and managed by IPHES and (IIIPC), in cooperation with Sociedad de Ciencias Aranzadi, the Gibraltar Museum, Parque de la Naturaleza de Cabárceno (Cantur, S.A.) and Project HAR 2010-19957 (MINECO), and is supported by the Government of Cantabria. Project members are E. Camarós (Project leader), M. Cueto (Project leader), R. Blasco, F. Rivals, J. Rosell and L. Teira. We would like to thank M. Cubas, J. Tapia and P. Arias for their support.

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METHODS AND TECHNIQUES 4.2

PAPER 3

Make it clear: Molds, transparent casts, and lightning techniques for stereomicroscopic analysis of taphonomic modifications on bone surfaces

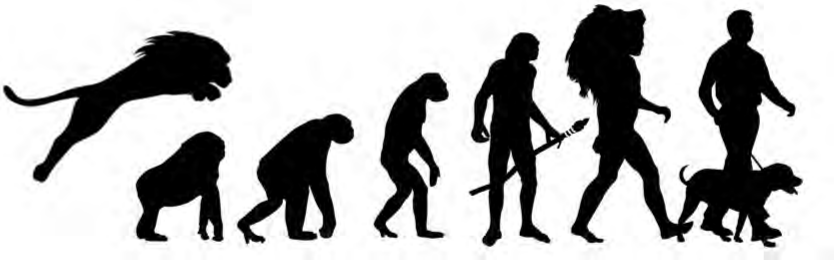
PAPER 4

Aproximación experimental a la modificación de hogares por parte de carnívoros durante el Pleistoceno. Metodología y primeros resultados

4.2.1

PAPER 3

Make it clear: Molds, transparent casts, and lightning techniques for stereomicroscopic analysis of taphonomic modifications on bone surfaces



Paper 3

Make it clear: Molds, transparent casts, and lightning techniques for stereomicroscopic analysis of taphonomic modifications on bone surfaces

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Keywords: Molding, Casting, Bones, Taphonomy

Journal of Anthropological Sciences (accepted)

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Introduction

Molds and casts of archaeological remains are commonly used to produce high-resolution replicas for studying tooth microwear (Solounias & Semprebon, 2002; Rivals *et al.*, 2009; Sánchez-Hernández *et al.*, 2014), for lithic use-wear analysis (Ollé & Vergés, 2014), and on some occasions, for casting bone surfaces (Bello *et al.,* 2009, 2011). Molding of specimens has some advantages over the direct study of the original remains. It permits (1) the sampling of specific part(s) of larger remains, which sometimes cannot fit into the equipment employed for their analysis [a scanning electron microscope (SEM), for example]; (2) easy transport of samples from the collection to the analytical facilities; (3) the exportation of molds abroad for specific studies without requiring any permits; and 4) better observation, in some cases, of taphonomic damage present on the bone surfaces.

The technique of molding is relatively standardized, with the use of high-resolution dental silicon (principally Provil® novo by Heraeus or President® Jet by Coltène Whaledent) to produce the mold. The casting process, depending on the method of analysis, uses a wide diversity of resins (araldite, epoxy, polyurethane, etc.). These resins permit the analysis of the samples using a wide range of techniques, from low magnification using a stereomicroscope to high magnification at the SEM level. Previous studies demonstrated that molds and casts produce highly reliable replicas of surfaces, even for use at high magnification using scanning electron microcopy (Galbany *et al*., 2004, 2006) or focus variation microscopy (Goodall *et al.*, 2015).

We provide guidelines for producing high-resolution molds and casts for the observation of taphonomic modifications on bone surfaces, including those made by anthropic activity, carnivores, or other post-depositional modifications. The high quality of the resulting transparent epoxy casts allows their analysis by light microscopy to produce detailed microphotographs of bone surfaces. The technique proposed here is based on the protocol of Solounias & Semprebon (2002) devised for the study of tooth microwear, which we have modified for its application to the analysis of bone surfaces.

Method

We describe the technique of molding and casting of bone surfaces (Fig. 1). The full process, from cleaning to production of the cast, and then the observation at the light microscope level, is illustrated with pictures and with a video, available as Online Supplementary Material.

The aim of the whole process is to obtain molds that accurately replicate the original bone surface at both the macro- and microscopic levels. We follow the protocol developed by Solounias & Semprebon (2002) for the study of tooth microwear.

The cleaning process

The first step is the cleaning of the bone surface to be analyzed. This process requires removal of any dirt or dust present, or any chemicals used during the excavation or conservation of the bones. If the bone surface is not properly cleaned, the resulting cast might not be suitable for observation. It is preferable to work in a stable environment where the temperature and humidity are not too extreme. The cleaning process is composed of three steps:

Step 1. ***Cleaning with acetone.*** The bone surface is cleaned by swiping with cotton swabs moistened with acetone. The drying time of acetone is very fast; thus, in a few minutes, the surface will be sufficiently dry and ready for the next step.

Step 2. ***Cleaning with ethanol*****.** We eliminate any residue of acetone that could remain on the bone surface using ethanol (>95%) and a cotton swab.

Step 3. ***Drying.*** The surface to be sampled must be totally dry (ca. 5 minutes) before applying the high resolution silicone. Specific temperature conditions will influence the drying (e.g., extreme cold and humid conditions will delay the process).

The molding process: Producing high-resolution molds

As mentioned previously, the technique is a non-destructive and conservation-friendly method for the study of archaeological materials. Creating negative impressions requires a product with high plasticity and non-aggressive chemical composition. For this purpose, high-resolution dental vinylpolysiloxane silicone (e.g., Heraeus Provil® novo light regular set) is used. The kit used comes as a cartridge that is divided into two independents tubes: one contains the base (silicone) and other the catalyst. A mixing tip is attached to the cartridge to provide automatic mixing of the silicone and the catalyst. The cartridge is loaded into a dispensing gun.

Vinylpolysiloxane silicone is characterized by an impressive detail resolution of up to 1 μm, a high recovery after deformation (99.7%), a low linear dimensional change (shrinkage 0.2%), and a high temporal stability. The setting rate of the silicone is fast—5 to 10 minutes, depending on the environmental conditions—which allows repetition of the process several times in a short period. Therefore, when a large number of samples need

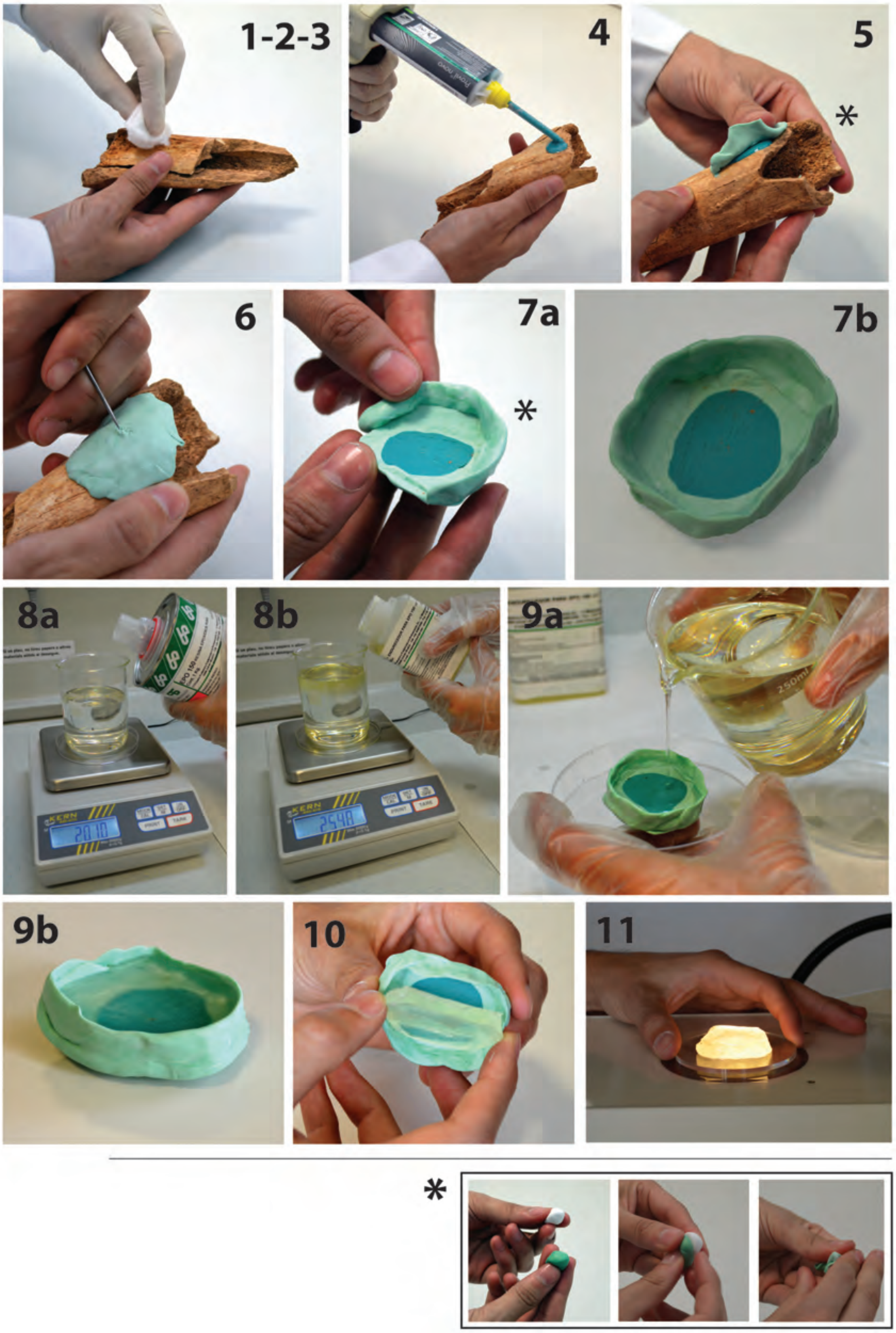

Figure 1. Molding and casting process described in the text. A detailed video of the process is available as Online Supplementary Material S1.

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to be molded, we recommend cleaning them all first before starting the molding process. This will speed up the whole process and conserve silicone components (the mixing tip easily gets blocked due to progressive setting of the silicone). Temperature and humidity will influence the efficiency of the process. From our experience, optimal conditions are a temperature between 18 and 22°C and a humidity of ca. 50%.

Step 4. The silicone is directly applied to the bone surface with the dispensing gun. Before starting this process, we recommend discarding the first amount of mixed silicone. The mixing tip must be as close as possible to the bone surface to avoid the formation of air bubbles, and the spreading has to be constant—making circles provides a better distribution of the silicone.

Once the high resolution negative impression (silicone) has set, a new layer of silicone putty is added to cover it, with the aim of providing support to the mold. The product required is a low-resolution silicone (Heraeus Putty Regular Set), which has a high recovery after deformation (99.7%) and low linear dimensional change (shrinkage) (0.3%). This kit is also composed of a base and a catalyst, which are mixed in a dosing ratio of approximately 1:1 by volume. Specific temperature conditions will influence the timing of the process (e.g., cold and hot temperatures will delay or accelerate the process, respectively). A recommendation under high-temperature conditions is to place the silicone into a refrigerator before starting the process.

Step 5. The same volume of silicone and catalyst is taken (e.g., the size of a chickpea each for a surface of about 10 cm^2). The two components are quickly mixed manually until the mixture has a homogeneous color. The mixture is then flattened to form a surface, which is used to cover the negative impression and an area of about 1 cm around it.

Step 6. While the silicone is still soft, it is recommended to write, as soon as possible, the reference of the sample onto the mold surface (e.g., register, museum or field number). A stylus can be used to scratch the surface. This step allows the direct identification of the mold without using paper labels or individual bags, thereby avoiding any future error concerning the management of large samples. In addition, as in Step 4, the same advice regarding refrigeration related to high-temperature conditions applies here.

Step 7. When the silicone is totally set, it is carefully removed. The high-resolution impression in direct contact with the bone surface is now adhered to the overlying putty silicone. A wall needs to be built around the mold in order to form a recipient, which will be used to create the positive casts (Fig. 1, 7a). The low-resolution resolution silicone putty is used to build a wall about 1 cm high to hold the epoxy resin (Fig. 1, 7b). Before continuing with the process, we recommend to clean the bone as in steps 1, 2 and 3.

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The casting process: Producing high-resolution transparent casts

The molds are filled with epoxy resin to produce transparent casts. Transparent epoxy resin (e.g., CTS Epotek EPO 150) and a catalyst (e.g., K 151 for EPO 150) are required. EPO 150 is a transparent liquid epoxy resin with very low viscosity (500-800 mPas) and high resistance and stability. Both the resin and the catalyst are toxic; therefore, the use of plastic gloves, security mask, and safety glasses is required. The work should also be conducted in a fume hood. A glass container must be used for mixing the epoxy resin and the catalyst, due to the exothermic reaction produced when they are combined (i.e., a regular plastic container might melt).

The epoxy and catalyst need to be mixed in precise proportions, as indicated by the manufacturer. In the case of EPO 150, the components are measured by weight. The proportion of the catalyst is 25% of the total epoxy utilized. For example, 200 g of epoxy requires 50 g of catalyst (Fig. 1, Step 8a and 8b).

Step 8. The weight of the components is measured with a digital scale. A wooden stick is used to mix the components, with constant changes in the direction of motion to ensure a homogeneous mixture. Special attention needs to be taken to avoid the formation of air bubbles. If excessive bubbles are present, they can be removed by centrifugation or use of a vacuum pump.

Step 9. The mixture is poured carefully into the mold (Fig. 1, 10a) and left to harden for 1–2 days at ambient temperature under the fume hood (Fig. 1, 10b). High temperatures should be avoided as they accelerate the catalysis and might reduce the resolution of the cast.

Step 10. Once the epoxy is set, the positive cast is carefully separated from the mold. The sample reference can be scratched on the back of the cast.

Observation of transparent casts

Step 11. The resulting epoxy cast is transparent and uncolored, permitting observation of the surface. The observation is typically conducted using a stereomicroscope with transmitted light (e.g., Zeiss Stemi 2000C). The correct use of the transmitted light is a very important aspect of the observation. In cases where the observation is not sufficiently clear, the light can be changed to a different intensity or angle of transmission (with an incorporated mirror in the base of the microscope) to improve resolution. The clarity of the visualization of different features present on the cast maybe enhanced by manipulating lighting parameters.

Application of the technique: Proof of concept

The technique described can be applied to both experimental and fossil bone surfaces containing taphonomic modifications commonly found in archaeological sites. The aim is to provide examples and a proof of concept regarding the utility and benefits of the method described. The molding and casting technique can be applied to almost all bone surfaces, excluding those with deep fissures and/or exposed spongy tissue. Surfaces displaying those characteristics should not be molded because silicone percolates through the gaps and holes of the bone, making extraction of the mold impossible without damaging the bone specimen. Nevertheless, all other surfaces can be successfully molded. For instance, our examples provided here are related to both human activities and natural agents, such as:

- Chemical damage (e.g., roots and soil acidity) (Fig. 2a)
- Weathering damage (e.g., exfoliation) (Fig. 2b)
- Carnivore damage (e.g., scores) (Fig. 2c)
- Anthropic modifications, such as scraping with lithic tools (Fig. 2d) and polished surfaces (Fig. 2e)
- Experimental superposition of anthropic lithic cutmarks over carnivore scores (Fig. 2f)

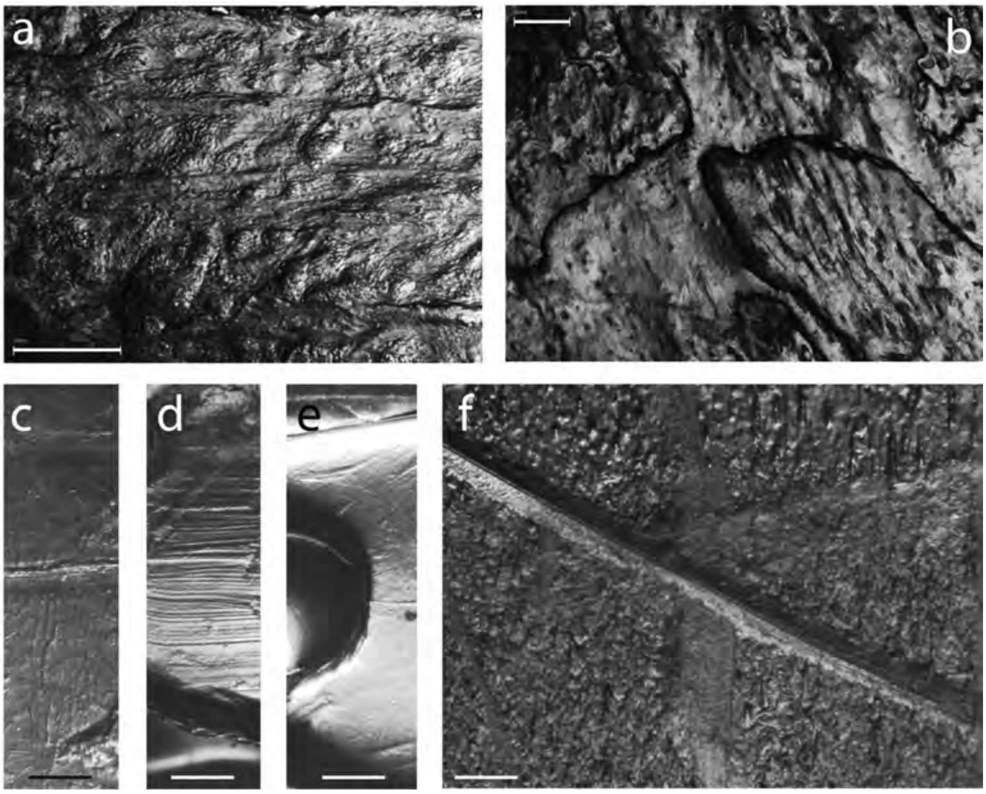

Figure 2. Casts displaying different taphonomical modifications on bone surfaces: a) Chemical damage (roots and soil acidity); b) Weathering damage (exfoliation); c) Carnivore damage (scores); d) Anthropic scraping; e) Polished surface; f) Superposition of cutmark over carnivore score.

As the examples show, the application of the technique described represents an improved approach for the study of different types of taphonomic damage. In this sense, taphonomic damage that is defined by characteristic irregular surfaces, such as vermiculations or exfoliation (Fig. 2a and 2b), can be easily observed. Anthropic modifications are also easily observed as they display complex surfaces composed of regular, flat, and angulated modifications. Scraping traces and cut-marks, for instance, are perfectly visualized as they contrast with the bone surface (Fig. 2c-d and 2f). Furthermore, polished surfaces, which present no difference in relief, also reflect light in a way that allows easy identification (Fig. 2e). All these characteristics are related to the fact that the light is located beneath the transparent cast. The angle of transmitted light can be changed to improving the resolution of the observation. As Figure 3 shows, moving the mirror in different directions highlights different features (Fig. 3a-d). This allows the researcher to focus on different variables present in a single case study. This type of observation is better than the traditional observation of the original bone surface under direct incident light. An advantage of using transparent casts is that the surface need not be metalized (with gold or graphite), unless observation of the cast by SEM is planned. This type of observation has been described previously by other authors (Fiorenza *et al.*, 2009).

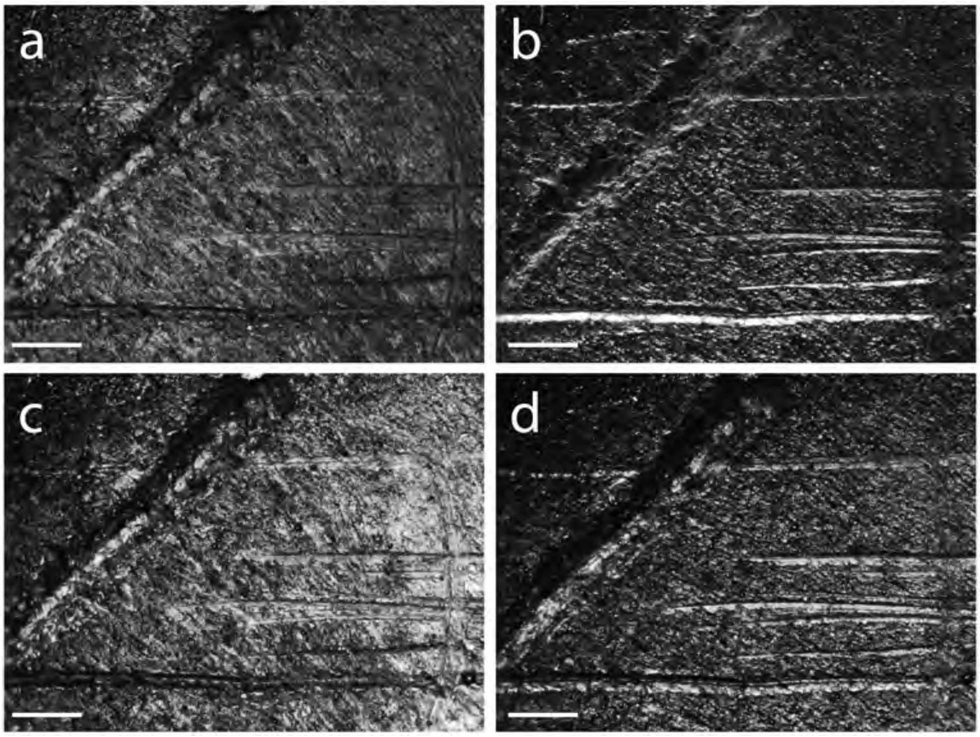

Figure 3. Epoxy cast displaying carnivore scores over anthropic cutmarks observed with light directed from different angles at same intensity (using a stereomicroscope Zeiss Stemi 2000C with transmitted light).

The benefits of silicone casts for analysis of bone surfaces are also related to their high resolution. In this sense, the sampled bone surfaces are perfectly replicated, allowing macro- and microscopic observations. Therefore, the analysis of the casts with devices such as ESEM/SEM is possible without losing information present on the original bone surface.

The present technique has other benefits for analyzing taphonomic modifications on bone surfaces. It is a low-cost, low time-consuming, and nondestructive method that provides a cast with the dimensions of a specific area of the bone rather than the dimensions of the entire bone (case of Fig. 1). In this sense, the casts can be easily stored as reference, teaching, and scientific collections, and can also be easily transported and introduced into specific devices, such as ESEMs/SEMs and others.

The technique also facilitates experimental research protocols aimed at observing before and after scenarios, such as have been applied for the study of lithic tool marks (Ollé & Vergés, 2014; Camarós *et al*., submitted). More benefits can be listed, such as the possibility of rapidly sampling large collections and studying the casts at greater leisure later. This provides the future option of analyzing the bone surfaces from different points of view, which is generally not possible in museum collections due to time and permit limits (e.g., SEM/ESEM analysis, direct measurements, high-quality microphotography, etc.). Furthermore, molds and casts can be stored for many years, allowing their study in the future; for example, when an advance occurs in an existing techniques or new scientific agenda develops. The molding technique is a useful method when working in museums and conducting fieldwork, where materials cannot be easily exported overseas.

In addition, casts can be reproduced several times (Galbany *et al.,* 2006) for observations with different devices that require specific treatment (e.g., SEM) or for teaching purposes (thereby reducing the risks of handling original specimens).

Conclusion

The preparation of molds and casts of bone surfaces improves the stereomicroscopic analysis of taphonomic modifications. It is a non-destructive, low-cost, and low-time consuming method that is easy to replicate and provides important benefits related to different scientific agendas and objectives. In this sense, the high-resolution quality of the surface replicated, the size of the casts, and the intrinsic properties (e.g., the transparency and durability, among others cited here) are positive aspects to take into account when facing a taphonomic study of a bone specimen or collection. The case studies presented here are proofs of concept of this improvement when approaching different taphonomic studies.

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Acknowledgements

This research has been partially founded by the Ministerio de Economía y Competitividad (HAR2013-48784-C3-1-P). E. Camarós is beneficiary of a FI/AGAUR (DGR2013) grant from the Catalan Government. C. Sánchez-Hernández is beneficiary of a pre-doctoral grant (FPI) from the Ministerio de Economía y Competitividad (BES-C-2014-0034).

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4.2.1.1

PUBLISHED SUPPLEMENTARY MATERIAL

PAPER 3

Make it clear: Molds, transparent casts, and lightning techniques for stereomicroscopic analysis of taphonomic modifications on bone surfaces

Video S1

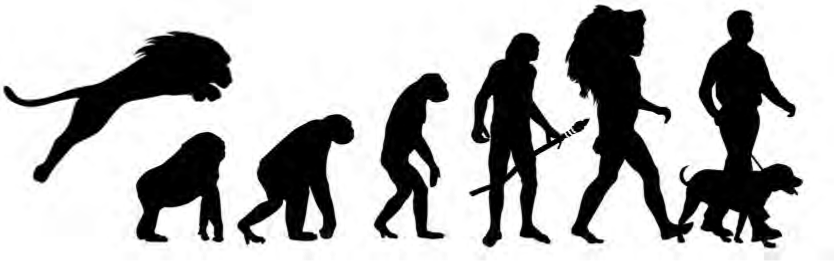
A video describing the technique of molding and casting bone surfaces was attached as online supplementary material.

The video S1 is available as a video archive inside Annex 1.

4.2.2

PAPER 4

Aproximación experimental a la modificación de hogares por parte de carnívoros durante el Pleistoceno. Metodología y primeros resultados



Paper 4

Aproximación experimental a la modificación de hogares por parte de carnívoros durante el Pleistoceno. Metodología y primeros resultados

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The controlled use of fire (by the construction of hearths) is essential to understand the modern human behavior. For the period of time were such control is debated, the alternation in the use of caves by humans and carnivores is common. In the present preliminary paper we focus on the methodology and first results of the experimentation carried out with brown bears (*Ursus arctos*), with the aim of providing new data to the mentioned debate.

Keywords: Carnivores, combustion structures, Pleistocene, experimentation, taphonomy

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1. Introducción

El uso sistemático del fuego y su gestión de manera controlada es uno de los aspectos extrasomáticos más importantes en la evolución del género *Homo* (James 1989). No obstante, para unas cronologías anteriores a 1 ma, dicho comportamiento con el fuego se pone en duda (Karkanas et al. 2007). Para Europa, se aceptan unas cronologías relativamente recientes que se sitúa en torno a 300-400 ka (Roebroeks/Villa 2011). En cuanto a los hogares complejos (aquellos que disponen de una estructura asociada y a los que llamaremos hogares estructurados) no aparecen hasta el final del Pleistoceno medio vinculados a la forma humana *Homo neanderthalensis* (Kelly 1995). Sin embargo, algunos investigadores ponen en duda que los neandertales fueran capaces de gestionar el fuego de manera controlada (Wynn/Coolodge 2008; Sandgathe et al. 2011), pese a las pruebas que existen de ello (cf. Vaquero/Pastó 2001; Cliquet/Lautridou 2009; Jiménez-Arenas et al. 2011).

El control del fuego es un hito importante en la evolución humana, no solamente porque proporciona claras ventajas como cocinar, calentarse, iluminar, cazar o protegerse (Bar-Yosef/Weiner 1996), sino porque implica una nueva organización del espacio social (Gamble 1986). Alrededor de un hogar se estructura la práctica de diferentes actividades sociales (Wünch 1996) y ello va conformando una concepción del espacio doméstico particular (Mcbrearty/Brooks 2000; Henshilwood/Marean 2003). En torno a las estructuras de combustión, las sociedades de cazadores-recolectores se reúnen e interactúan socialmente, producen herramientas, consumen alimentos e incluso celebran rituales (Alperson-Afil/Goren-Inbar 2006). Esto provoca que en torno al hogar se articule toda una serie de materiales relacionados con ciertas actividades, en lo que se ha llamado en la literatura anglosajona hearthrelated assemblages (Vaquero/Pastó 2001; Henry et al. 2004; Alperson-Afil/Goren-Inbar 2006). Esto quiere decir que un hogar (en sentido amplio, junto a sus actividades relacionadas) y el conocimiento pirotecnológico que requiere, están íntimamente relacionados con una organización social compleja y por consiguiente con una cognición moderna (Binford 1989; Stringer/Gamble 1993; Wynn 2009).

El control del fuego abarca diferentes grados de conocimiento pirotecnológico, que van desde el mero aprovechamiento y control de fuegos provocados por fenómenos naturales, hasta el aprendizaje de diversas técnicas de obtención artificial (Collina-Girard 1998; Roussel 2005), o el diseño de estructuras especializadas (Pétrequin et al. 2000). Las evidencias de obtención artificial de fuego son muy difíciles de identificar debido a problemas de conservación, siendo más escasas conforme aumenta la antigüedad del contexto.

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Se asume que la realización recurrente de hogares por parte de un grupo humano puede indicar un conocimiento técnico suficiente para la obtención artificial de fuego, o al menos para su mantenimiento y transporte. En cualquier caso, las actividades en torno a los hogares que reflejan un comportamiento humano moderno, pueden realizarse independientemente de que el fuego haya sido obtenido artificialmente o de que haya sido aprovechado/ transportado, y son los hogares en sí, por tanto, los indicadores de tal avance en la conducta humana. Pero en el registro arqueológico la identificación de las estructuras de combustión, ya sean simples o complejas, tampoco es fácil. La mayoría de evidencias del uso del fuego en yacimientos del Paleolítico inferior, y en menor medida del Paleolítico medio, son restos óseos e industria lítica quemada, carbones aislados o sedimentos rubefactados (Roebroeks/Villa 2011). Esto es debido a los diferentes procesos tafonómicos que afectan a los hogares (Backhouse/Johnson 2007) como la acción de las raíces, de las Corrientes de agua, de la lluvia o el viento (Barbetti 1986; Mallol et al. 2007). Incluso procesos antrópicos como el trampling o la limpieza de hogares pueden afectar a la preservación de una estructura de combustion (Barbetti 1986; Sergant/Crombé/Perdaen 2006). Estos procesos no sólo actúan sobre hogares simples, sino que los hogares estructurados también son susceptibles de sufrir modificaciones hasta el punto de no reconocer su estructuración original (ya sean en forma de disposición de piedras o de depresiones cavadas) (Olive 1989; Texier 2001).

Hasta ahora, los procesos tafonómicos citados anteriormente eran los que se apuntaban como agentes modificadores de hogares. En este trabajo planteamos la posibilidad de que la acción de los grandes carnívoros sea otro agente modificador a tener en cuenta, ya que existen ciertos indicios en el registro arqueológico que nos hacen plantearnos esta posibilidad.

Durante el Pleistoceno medio y superior la alternancia entre homínidos y carnívoros es algo muy común en las cuevas, donde tienen lugar diferentes actividades y acondicionamientos tanto por unos como por otros (Rosell/Blasco 2009). Cuando esto ocurre en un lapso de tiempo muy corto, puede generarse un palimpsesto difícil de interpretar coherentemente. A la luz de las investigaciones recientes sabemos que incluso en el Pleistoceno medio son los carnívoros, en la mayoría de los casos, los que acceden a las cavidades en Segundo lugar buscando aprovechar aquello que los grupos humanos han abandonado (Rosell/Blasco 2009; Blasco 2011). Además, teniendo en cuenta la superposición de las diferentes marcas que dejan tanto carnívoros como humanos en los huesos (mordeduras los primeros y marcas de corte los segundos), podemos apuntar que en algunos casos la alternancia es inmediata puesto que los carnívoros mordisquean restos óseos en estado fresco (Blasco/Rosell 2009).

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El hecho de que los carnívoros ocupen aquellas cavidades abandonadas por los grupos de homínidos nos lleva a preguntarnos cómo interactúan con las estructuras de combustión. Nos centramos en las estructuras de combustión porque son elementos susceptibles de llamarles la atención debido a los restos de carne, grasa y otros tejidos que pueden quedar en los hogares y en las zonas circundantes.

Por tanto, en este trabajo partimos del supuesto de que los grandes carnívoros pueden considerarse como agentes capaces de alterar o suprimir la articulación entre un hogar y sus conjuntos relacionados, puesto que existen evidencias arqueológicas que apuntan en esta dirección. Nuestra hipótesis es que estos animales modifican considerablemente el espacio antrópico y especialmente las hogueras.

2. La experimentación: Objetivos, metodología y desarrollo

Los planteamientos expuestos en la introducción nos han llevado a diseñar un programa experimental con grandes carnívoros en el Parque de la Naturaleza de Cabárceno (Penagos, Cantabria). La elección de este parque guarda relación con su modelo de gestión, cuya política es interferir lo menos posible en la vida de los diferentes animales. Esto, junto con el hecho de disponer de unas infraestructuras adecuadas para el buen desarrollo de los experimentos (asesoramiento veterinario, seguridad, puestos de observación y una amplia gama de especies de carnívoros), hacen de Cabárceno un sitio perfecto para el desarrollo del proyecto bajo unas condiciones de control excepcionales.

El objetivo es desarrollar un proyecto de estudio taxonómico experimental que nos permita evaluar cómo los grandes carnívoros más presentes en los yacimientos arqueológicos del Paleolítico (hienas, lobos, leones y osos) modifican el espacio antrópico una vez abandonado, especialmente los hogares. El protocolo experimental ha sido puesto a prueba con osos, una de las especies cuya alternancia con los humanos en la ocupación de cuevas está mejor documentada (Villaluenga 2009).

Antes de realizar el experimento se ensayó una prueba piloto fuera del recinto en el que se iba a trabajar con los animales. Por cuestiones de seguridad, se requería permanecer el menor tiempo posible dentro del recinto por lo que el diseño de un protocolo adecuado y su posterior ensayo fue esencial. El propósito era generar un protocolo de trabajo válido para llevar a cabo en todos los experimentos futuros con las diferentes especies de carnívoros.

El protocolo diseñado y ensayado es el que se describe en la figura 1. En primer lugar (Fig. 1 paso 1) se recoge de manera aleatoria 12 piedras calizas del mismo Parque de Cabárceno con unas dimensiones de entre 10 y 20 cm. El empleo de calizas angulosas del entorno trata de

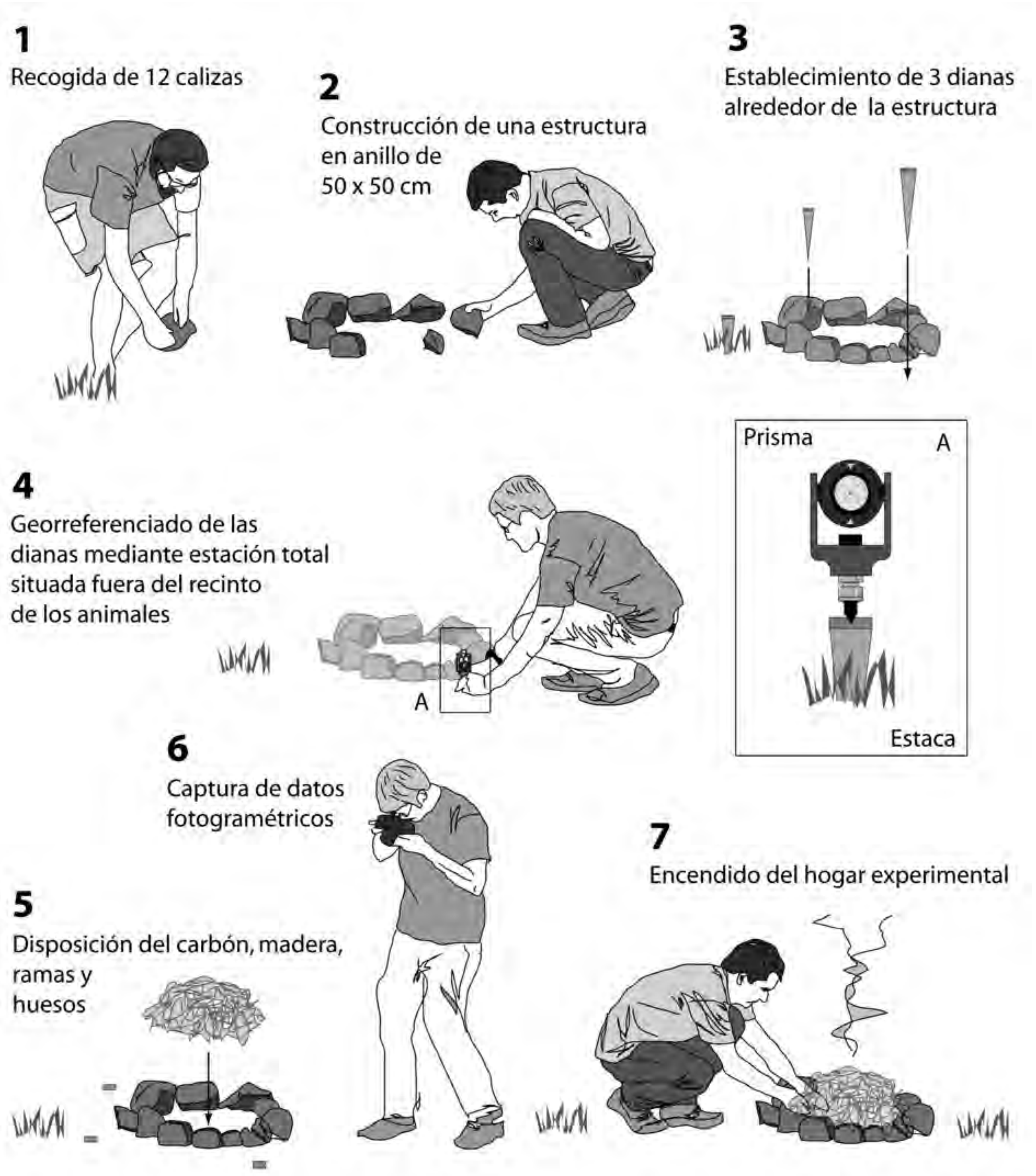

Figura 1. Protocolo experimental desarrollado para la construcción y documentación del hogar.

minimizar la introducción de materiales extraños y de evitar la selección de formatos que puedan exagerar los desplazamientos laterales. Posteriormente (Fig. 1 paso 2) se construye con esas piedras una estructura circular con un diámetro de 50 cm, numerando las piedras de modo que puedan ser identificadas en diferentes fases del experimento (Fig. 2a). Las dimensiones del hogar se han establecido tenido en cuenta las medidas máximas y mínimas de los hogares estudiados en yacimientos del Paleolítico inferior y medio, que oscilan entre los 20 y 100 cm de diámetro (Farizy 1990, 1994; Mellars 1996; Barton 2000; Soler 2001; Cabrera/Pike-Tay/Quirós 2004; Cain 2005; Daujeard/Moncel 2010; Slimak et al. 2010). Una vez la estructura está construida, colocamos en torno al anillo una serie de útiles líticos con una disposición específica (Fig. 2a), ya que toda una serie de elementos (y actividades) van

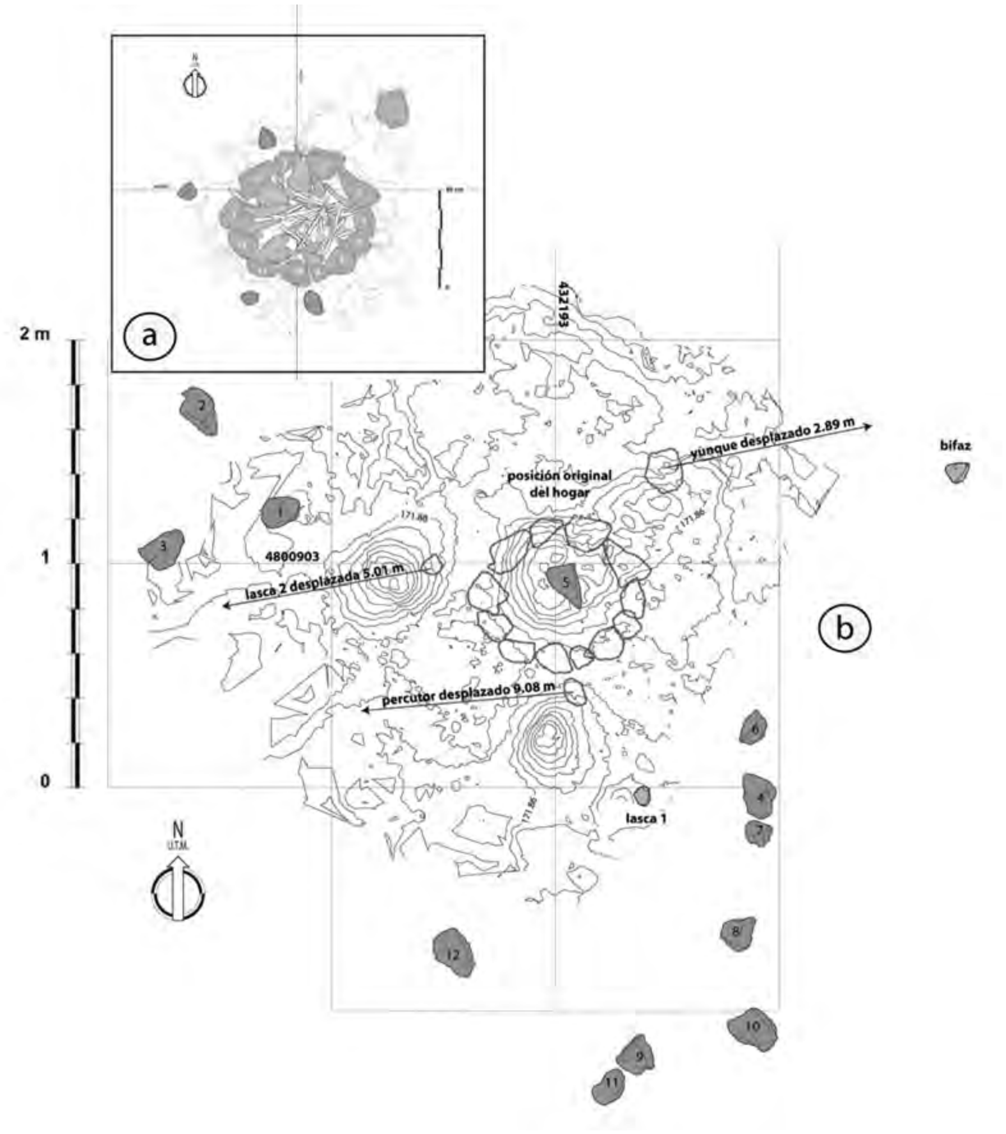

Figura 2. Hogar experimental original (a) y modificado por los osos (b).

relacionadas a las hogueras (Binford 1983). Nuestro objetivo es ver también si los carnívoros pueden romper esa asociación entre el hogar y las actividades generadas a su alrededor. Las herramientas líticas escogidas son un bifaz de cuarcita, un yunque de caliza, dos lascas de sílex y un percutor de cuarcita, todas ellas utilizadas en el procesado de los huesos.

Una segunda fase (Fig. 1 paso 3) comprende la documentación fotogramétrica y topográfica de la disposición original del hogar y de los artefactos asociados. Para ello se disponen tres estacas de madera en torno al hogar y sus elementos asociados, con una señal en su zona superior que actuará a modo de diana. La superficie del triángulo imaginario ha de englobar tanto la estructura como los útiles asociados. Las dianas se georreferencian (Fig. 1 paso 4) con una estación total situada en el exterior del recinto. Ésta está orientada a favor de un sistema de coordenadas local provisional que posteriormente y mediante la red GNSS de Cantabria y un GPS centimétrico (doble frecuencia RTK) se vinculará al sistema ETRS89. La finalidad es obtener una documentación detallada del estado original del espacio diseñado, que sirva de comparación con el resultado del experimento. A continuación disponemos en el siguiente orden el combustible: carbón vegetal (400-600g), hojas de roble para ayudar en el inicio de la combustión (50-100g), pequeños troncos de roble (500-1000g) y finalmente se deposita sobre ello un fémur y una tibia de vaca (*Bos taurus*) (4 kg) fracturados y descarnados.

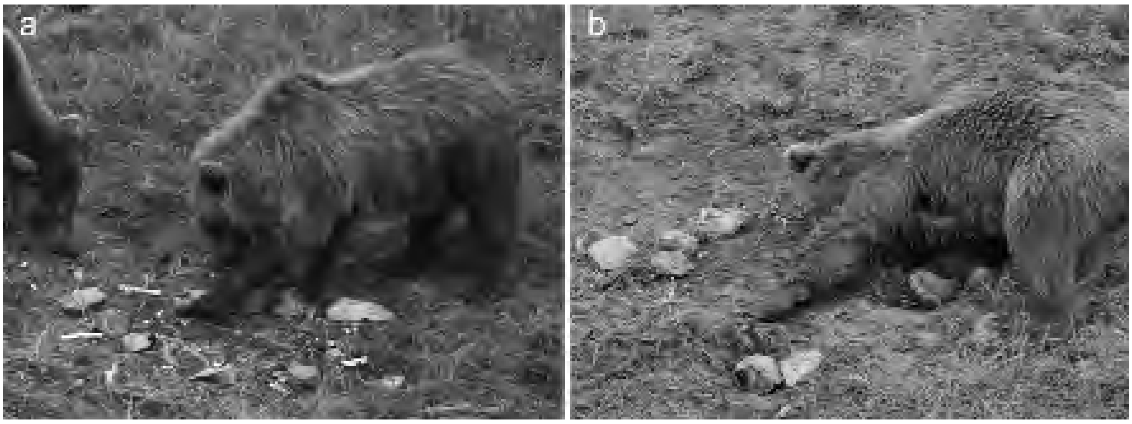

Figura 3. Proceso de modificación de la estructura por parte de los osos.

El tiempo de control del experimento es de 8-9 horas a partir de nuestra salida del recinto, sin proceder a apagar la hoguera, y se realiza un seguimiento permanente de los tiempos y tipos de intervención por parte de los osos, registrados mediante fotografías y tomas de vídeo. Transcurrido este período, volvemos a entrar para registrar las posibles modificaciones mediante la misma técnica de captura fotogramétrica –repetición de los pasos 4 y 6 de la Fig. 1-, y el posicionamiento de los elementos desplazados fuera del encuadre fotogramétrico se realiza mediante estación total de topografía.

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3. Primeros resultados

Las modificaciones causadas por los carnívoros se evalúan a través de la observación directa de su comportamiento, y mediante la comparación entre las posiciones original y final de los distintos componentes de la estructura. El primer procedimiento registra la secuencia y el tipo de acciones realizadas por los carnívoros a lo largo del tiempo de control, mientras que en el segundo procedimiento se contrastan los planos y los modelos 2D de las escenas original y final, identificando los diferentes componentes del hogar y calculando sus desplazamientos.

La estructura de combustión resultante y la disposición de los artefactos asociados puede apreciarse en la figura 2a. La hoguera ardió durante diez minutos más después de nuestra salida del recinto (es decir, un total de 40 minutos), manteniéndose después la combustión en forma de ascuas sin llama. El tiempo de reacción de los osos fue inmediato, y a los 11 minutos (cuando ya estaba sin llama pero seguía humeando) el macho dominante se acercó a la hoguera y empezó a modificarla intentando acceder a los huesos quemados.

A lo largo de las ocho horas siguientes y hasta que volvimos a acceder al recinto, los osos fueron acercándose por orden jerárquico, modificando la estructura de combustión y dispersando la industria lítica asociada ella. Las alteraciones registradas abarcan desde la extracción de huesos del interior del hogar hasta la práctica eliminación de toda la estructura. De hecho, removieron con las manos todas las piedras de la estructura para rebuscar entre las cenizas (Fig. 3a), y otro comportamiento recurrente fue revolcarse en ellas, probablemente para impregnarse del olor (Fig. 3b). Esta acción hizo que todas las cenizas desaparecieran de la zona y que todos los fragmentos de huesos quemados fueran desplazados más allá de nuestra zona de control.

Pasadas las ocho horas, se observa que las modificaciones causadas por los osos son importantes (Fig. 2b). Ninguna de las piedras que conformaba la estructura está en su emplazamiento original, al igual que los útiles asociados a ella, observándose desplazamientos de hasta 9 metros (véase el caso del percutor). El grado de modificación es tal que resulta imposible reconocer el hogar, y su relación espacial con el resto del conjunto es aparentemente irrecuperable.

Los osos, además, cavaron diversos agujeros. Dos de ellos fueron practicados con la intención de desenterrar dos de las estacas (Fig. 2b) empleadas en la fotogrametría, y un tercer hoyo se cavó justo en el emplazamiento original del hogar experimental, debido al olor a grasa que impregnaba el sedimento.

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4. Breve discusión y perspectivas de trabajo

A la luz de los resultados obtenidos podemos apuntar que los osos son un posible agente de modificación de los espacios antrópicos. Por tanto consideramos validada nuestra hipótesis de partida, al menos en el caso de los osos. Los objetivos de esta primera experimentación eran poner a prueba una metodología y un protocolo válido para llevarlo a cabo con más especies de carnívoros. En este sentido, pensamos que tal metodología y el protocolo de actuación es el adecuado. No obstante, hemos decidido introducir un cambio en nuestro proceder para una mejora de las experimentaciones futuras. Hemos optado por extraer las estacas una vez realizados los trabajos fotogramétricos para no insertar elementos de distracción, como lo fueron en el caso de los osos.

Consideramos que la experimentación llevada a cabo es muy positiva y se ha podido desarrollar bajo buenas condiciones de control. Es por esta razón que se ha decidido seguir adelante con el proyecto experimental y replicar la experiencia con otras especies de carnívoros: los lobos, los leones y las hienas.

Un experimento como el descrito aquí tiene implicaciones arqueológicas que pueden resultar de interés. Observamos que los carnívoros (por el momento los úrsidos) son agentes de modificación espacial capaces de borrar aquellas evidencias que nos pueden aportar información sobre el comportamiento y las actividades de los seres humanos. La construcción de hogares implica a nivel de organización del espacio un comportamiento moderno, así como el control y conocimiento pirotecnológico se relaciona con una cognición moderna (Wynn 2009).

Consideramos, a modo de hipótesis para las experimentaciones futuras y a raíz de los resultados aquí descritos, que los carnívoros son un agente taxonómico importante a tener en cuenta, capaz de borrar importantes evidencias de comportamientos humanos. Observamos que pueden alterar, hasta el punto de no reconocer, estructuras (y entre ellas los hogares de tipo complejo) y romper la relación entre un hogar y otras actividades relacionadas espacialmente. En otras palabras, el estudio de la organización social a través del análisis espacial puede ser algo completamente inútil en el caso de que los carnívoros hayan ocupado con posterioridad e inmediatez (y por supuesto hayan modificado) los contextos antrópicos. En este sentido, consideramos necesario continuar con los experimentos mediante la metodología de trabajo aquí descrita para profundizar en estos fenómenos y obtener nuevos modelos de interpretación tafonómica que permitan abordar problemáticas arqueológicas relacionadas con el estudio del comportamiento en evolución humana.

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Agradecimientos

Gracias al Parque de la Naturaleza de Cabárceno y a CANTUR, S.A. la oportunidad para la realización de experimentos tafonómicos. Queremos agradecer a S. Borragán (Jefe de los Servicios Veterinarios del Parque de la Naturaleza de Cabárceno) su inestimable ayuda y asesoramiento. M. Prieto, también de Cabárceno, nos ha ayudado en el recinto de los animales. P. Manrique nos ha asesorado sobre la etología de los osos. Así mismo otras personas han contribuido a que esta investigación sea posible. Agradecemos la ayuda de Á. Armendariz (UC), C. García-Moncó, A. Teira e I. Pastó (IPHES). Sin la colaboración de Carnicería Tito (Santander) tampoco hubiera sido posible realizar este y el futuro proyecto experimental. F. Rivals es beneficiario del proyecto HAR2010-19957 concedido por el Ministerio de Economía y Competitividad.

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4.2.2.1

UNPUBLISHED SUPPLEMENTARY MATERIAL

PAPER 4

Aproximación experimental a la modificación de hogares por parte de carnívoros durante el Pleistoceno. Metodología y primeros resultados

Figure S1. Bears interactingduring the first minutes with the experimental hearth and hearth-related assemblage: a) Bear smelling the experimental scenario; b) Modifiyng the scenario with the hand; c) A bear pulling out of the hearth a burned bone; e) A bear rolling on the ashes, a behavior related with prevention of parasites (*continues in next page*)

(*continued from previous page*): f) A bear digging a hohle where the centre of the hearth was; g-h) Different bears rolling on the erased hearth; i) Resulting scenario.

Video S1

A video containing a 3D model on the resulting experimental scenario is available in the attached CD (Annex 1).

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EXPERIMENTAL APPROACH TO HOMININ-CARNIVORE INTERACTION 4.3

PAPER 5

Walking with carnivores: Experimental approach to hominin-carnivore interaction

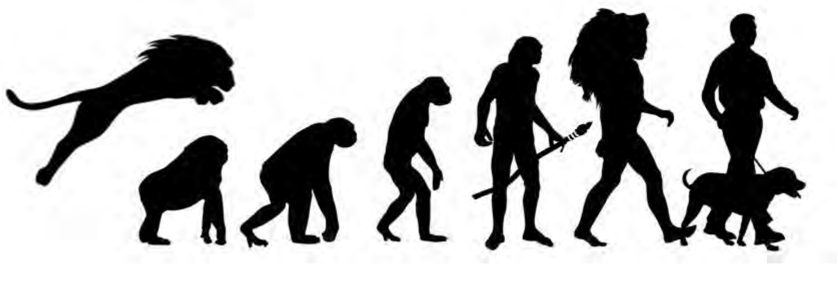
PAPER 6

Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications

4.3.1

PAPER 5

Walking with carnivores: Experimental approach to hominin-carnivore interaction



Chapter 4.3 *Experimental approach to hominin-carnivore interaction*

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Paper 5

Walking with carnivores:
Experimental approach to hominin-carnivore interaction

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The study of the interaction between hominins and carnivores is essential to understand the development of human behavior. Therefore, understanding this relation is one of the most positive approaches to recover behavioral information preserved or destroyed in the archaeological record. In this paper, we present a general overview of our experimental approach with extant carnivores to the study of modern and complex behavior through the development of experimental scenarios with archaeological implications. Our results attest the importance of the use of experimental archaeology for understanding the interaction between hominins and carnivores with the aim of recovering human behavior.

Keywords: Hominins, carnivores, interaction, experimental series, hominin behavior

Playing with the time. Experimental archaeology and the study of the past. R. Alonso, D. Canales, J. Baena (Eds.). Servicio de Publicaciones de la Universidad Autònoma de Madrid (in press)

1 Introduction

The relation between hominins and carnivores is probably one of the most constant interactions present in Human Evolution (Rosell et al., 2012). In this sense, it is also one of the relations with the ecosystem that most has influenced human behavior, and even some scholars have pointed a co-evolution between hominins and large carnivore during our evolutionary history (Brantingham, 1998). By studying different archaeological contexts it is possible to reconstruct some aspects related with such interaction during the Pleistocene. Nevertheless, most of the questions are not completely answered by only approaching the problematic from a strict archaeological point of view and interpretation change when experimentation is developed in order to find new questions and new answers. This way, experimentation is revealed as one of the best research strategies to face the problematic (Camarós and Cueto, 2013).

Our taphonomic experimental research has the aim of recovering human behavior by reconstructing controlled hominin-carnivore scenarios, which can help us understanding Pleistocene contexts where such interaction has been present in different ways. The experiments have been developed in Cabarceno's Nature Park (Cantabria, Northern Spain) with large carnivores such as lions, hyenas, wolves and bears (**IMAGE 01.1**). The animals in Cabárceno live in a semi-free state (**IMAGE 01.2**). Each animal group has enclosures of several hectares limited by natural barriers (cliffs), which are enclosed by artificial integrated fences. The park policy is to interact as little as possible with the animals and therefore they live according to their instincts. This makes Cabárceno as a perfect place to develop experimental scenarios with carnivores due to its possibilities to control variables related to ethological observations.

In the present contribution we provide a general overview on how the different experiments developed can help in the advancement of new methodologies to approach Pleistocene modern human behavior. Issues approached here are related with inhumation practices, specialized use of space, achievement of pirotechnological knowledge, use-wear patterns and subsistence strategies.

2 Experimental hominin-carnivore scenarios

The study of human evolution towards a modern behavior has a lot to do with intrasite spatial analysis. Through the study of the artefacts distribution, it is possible to reconstruct

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spatial organization in relation with activities developed in an area. In Lower and Middle Paleolithic sites, this is a very important issue because it is possible to observe a modern cognition through the spatial organization patterns. For example, the presence of hearths reveals a specific organization of the social activity around it (Binford, 1978), and evidences a formal conception of domestic space (MacBrearty and Brooks, 2000).

Therefore, identifying spatial units is something necessary to understand and demonstrate spatial organization patterns (Vaquero and Pastó, 2001). Using different spaces to develop different activities generates an occupation floor where identifiable and delimited areas can be recognized, and this is something related with behavioral patterns that reveal complexity.

Spatial analysis appears then as a very important element to study when and how complex behavior and modern cognition appears in human evolution, in relation with this recurrent spatial organization patterns. In this sense, spatial analysis is an essential tool for the debates of those periods were the presence of this way of being human is questioned.

Furthermore, interaction between hominins and carnivores are well documented during the Pleistocene. Along human evolution, carnivores have played an important role (Brantingham, 1998). It is well known that during the Middle and Late Pleistocene, Neanderthals have shared alternately with carnivores the same ecological niche to inhabit, hunted common preys in the same habitats, and generated other mutual pressures that have influenced human behavior or difficult its archaeological study (e.g., Stiner, 1994). During the Late Pleistocene, hominins and carnivores did not just shared space at a macro level, they also literally shared same places to live (Rosell et al., 2012). During this period, the occupation of karstic contexts by both hominins and carnivores is a well-documented phenomena (Skinner, 2012). Obviously, they did not shared same cavities at the same time, caves were used alternalty in time to develop different activities.

Evidences of anthropic activity is overlapped or mixed with evidences of carnivore activity causing problems in understanding the assemblage formation process or the isolation of archaeo-stratigraphic units. This so called palimpsests present in caves derived from sharing common places to live, may result in problems related with the study of intra-site anthropic spatial organization.

In this sense, the aim of our experimental project with extant large carnivores such as bears, hyenas, lions and wolves at the Cabárceno Nature Park (Santander, Cantabrian Spain) (**IMAGE 01.1**), is to recreate potential Pleistocene scenarios of interaction between

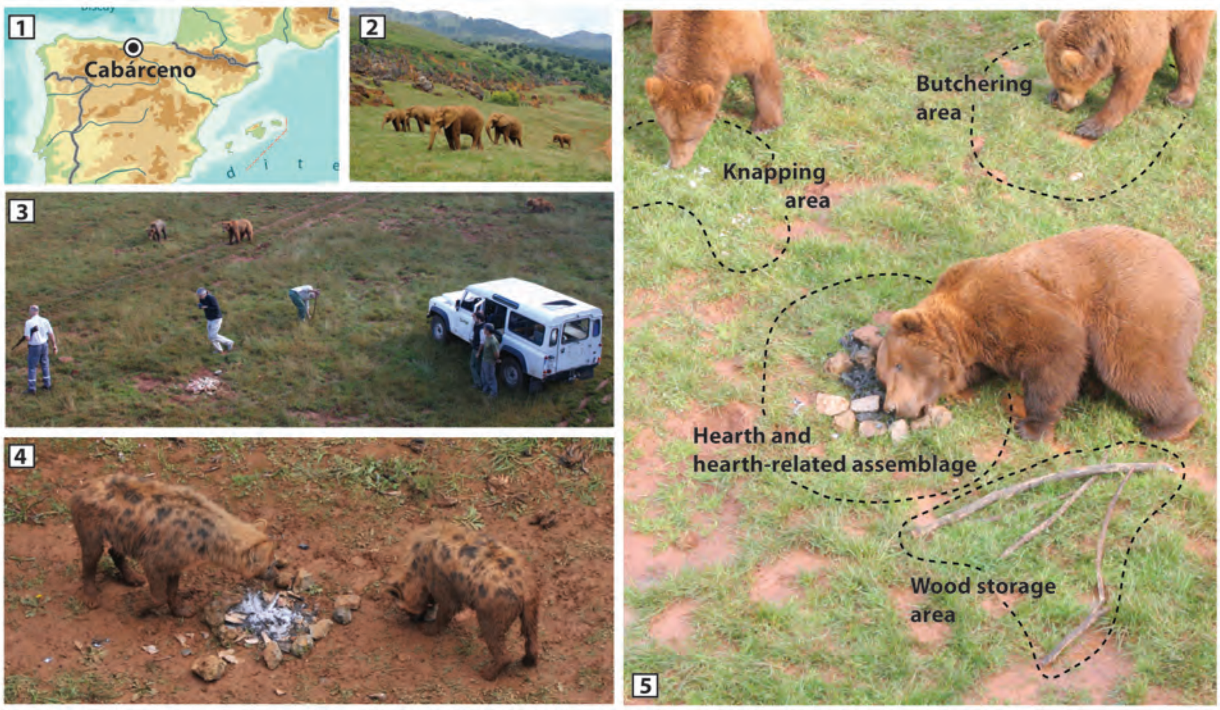

IMAGE 01. Cabarceno's Nature Park location and images of the development of experiments: 1) Location; 2) Animals in the Park; 3) Photogrammetric registering of experimental scenarios; 4) Hyenas modifying a combustion structure; 5) Bears modifying experimental scenarios revealing complex hominin behavior.

hominins and carnivores to develop a methodology to later study Paleolithic archaeological contexts. To do so, different experimental scenarios where developed with the objective of answering specific questions:

> How carnivores modify specialized spatial anthropic distributions?
>
> How they modify lithic objects?
>
> Can we understand the order of the superposition present on bones?
>
> Do carnivores modify and erase structured inhumations?

All questions were designed in order to observe how carnivores are able of modifying and erasing evidences of hominin behavior. Questions derived from a previous experiment (Camarós et al., 2013a; 2013b), where it was proven that carnivores modify space and erase spatial associations which reveal complex and modern behavior (**IMAGE 01.4**).

The first of the experiments was designed in order to build an experimental scenario were different activity areas were reflected in the space (**IMAGE 01.5**). In this sense, different areas were settled reflecting butchering, knapping, wood storage and hearth and hearth related activities.

The experiment was successful in the sense that carnivores highly modified the experimental scenario, erasing almost all evidences of specialized spatial distribution, and therefore, complex and modern behavior. But an additional observation related with spatial modifications by carnivores was registered. It was a recurrent thing that when carnivores moved experimental objects they chewed on lithic assemblage (**IMAGE 02.a**). They were probably attracted to this objects as they presented traces of fat and meat. This was something observed in the previous experiment (Camarós et al., 2013a; 2013b), and therefore during the derived experiments all lithic tools were subjected to previous observation controlled with a resin cast before carnivores could modify them. This control allowed us to identify which marks were developed by carnivores (**IMAGE 02.b**). We observed bear trampling, bites and manipulation of stone artifacts that generated surface modifications such as edge damage, micro-fractures, rounding and striations (**IMAGE 02.c**).

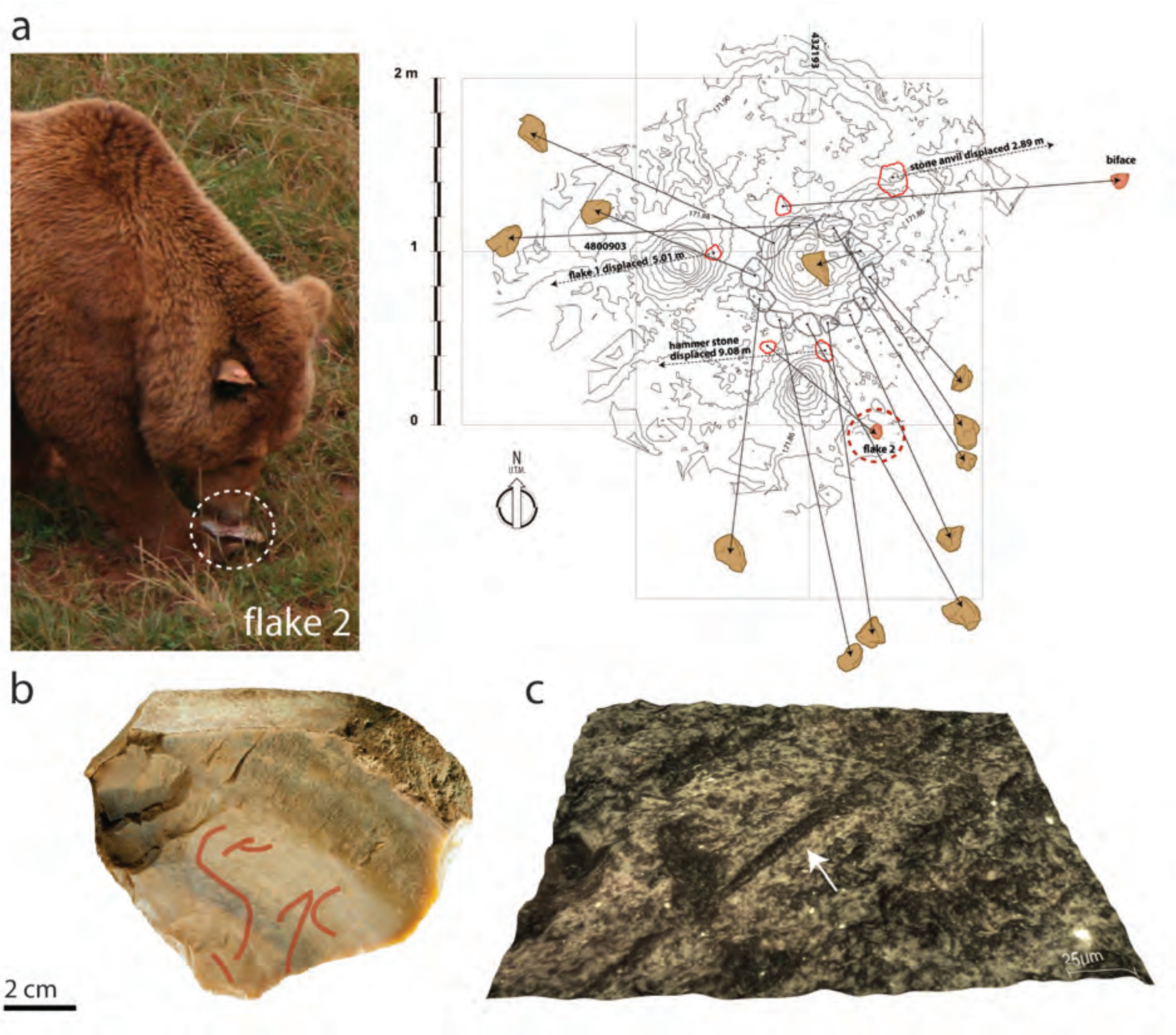

IMAGE 02. Experimental modification of lithic tools: a) Bear biting flake 2 from the hearth-related assemblage; b) flake 2 with bear scores on lithic Surface (highlighted in red) and c) 3D microscopic image of one of the scores produced by a bear biting on flake 2 (3D model obtained with Helicon Focus software after a series of metallographical extended focus images (Zeiss Axioscope A1)).

Furthermore, it is well known that one of the most modified items by carnivores are animal bones (Binford, 1981). We have also conducted experiments with the aim of understanding the order of the superposition of marks generated by both hominins and carnivores (e.g., bite marks over cutmarks) (**IMAGE 03**). Experiments have been previously developed with the same objective with dogs (Blasco and Rosell, 2009). The importance of understanding and characterize such common phenomena in the archaeozoological assemblage (e.g., Krönneck, 2012), is to evidence which agent developed a primary or a secondary access, as one could reflect hunting hominin strategies or on the contrary, scavenging strategies.

A different experiment also conducted with the objective of analyzing how carnivores destroy evidences of hominin behavior, was the one related with how carnivores interact with an structured inhumation. A rectangular experimental inhumation was excavated with a clear inhumation-related objects displaced in the base (**IMAGE 04.1**). A dead deer (*Cervus elaphus*) was placed inside and buried more than 50 cm deep.

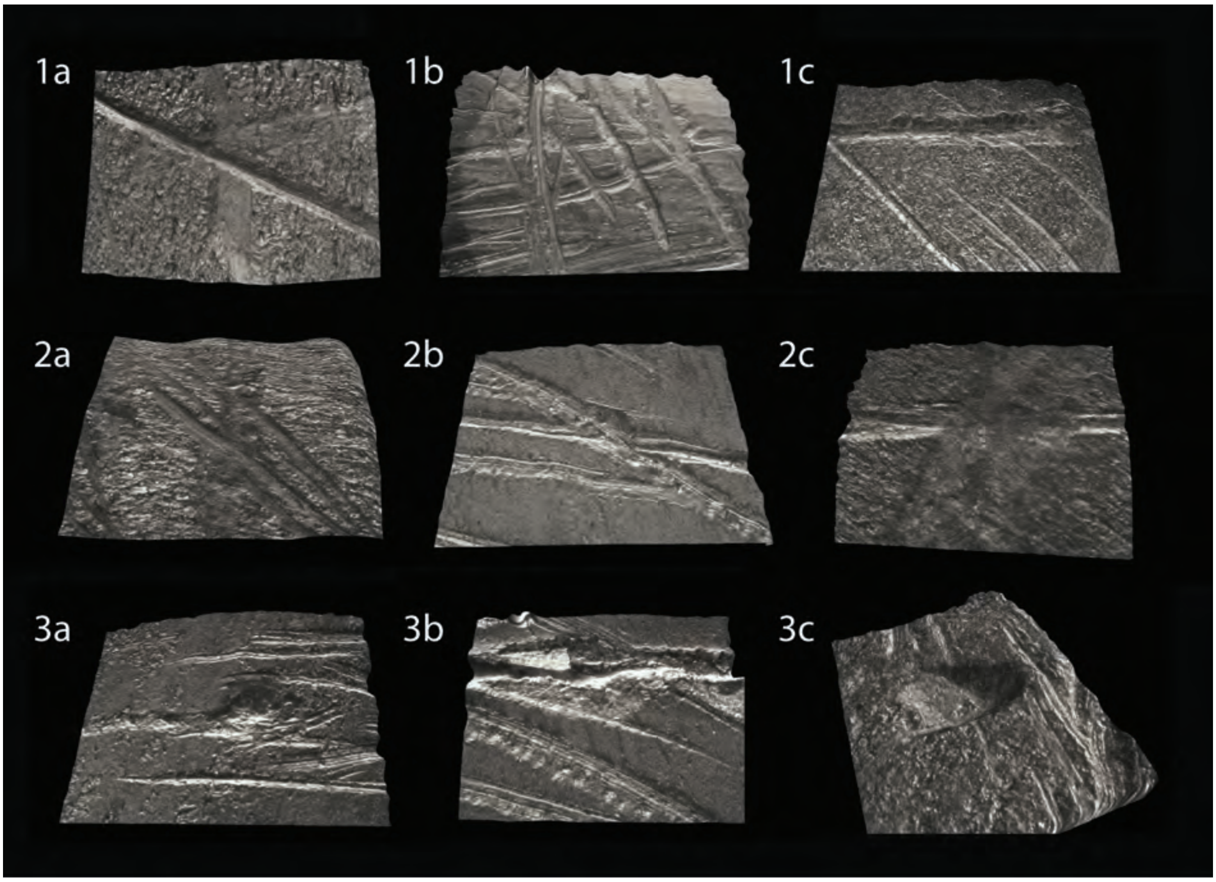

IMAGE 03. Experimental 3D microscopic images of cutmarks and carnivore scores and punctures on bones produced by lions (1), bears (2) and hyenas (3). All images are a cutmark-carnivore mark sequence (1a-3b), except 3c. 3D models obtained with Helicon Focus software after series of stereomicroscope extended focus images (Zeiss Stemi 2000C).

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This experiment has been just conducted with bears and hyenas. Nevertheless, results pose that both of them are animals capable of destroying the evidences of a structured intentional inhumation, such as the burial pit and objects placed inside (**IMAGE 04.1**).

Overall, the aim of the present contribution is to demonstrate the high potential that hominin-carnivore interaction experimental scenarios have when facing the study of hominin modern and complex behavior. In this sense, it is possible to face spatial distributions destroyed by carnivores as taphonomic agents. Understanding this, can help us approach why for example in some sites Neanderthals develop a similar spatial pattern to carnivores (Pettit, 1997). We must assume that in some cases, the action of carnivores may have been the responsible of the destruction of key social practices to infer modern and complex behavior, such as inhumation practices.

Furthermore, carnivores do not only destroy hominin behavioral evidences, they can also generate taphonomical signals that can be misinterpreted. One of them is lithic surface modification. This can be an important confusing factor when analyzing use-wear traces to infer past activities. Therefore, futures research will have to characterize this surface modifications in order to distinguish them from use-wear features.

Although the present contribution is not a conclusive research, it allows us to confirm how important experimental scenarios with extant large carnivores can be when approaching the study of human behavior trough the interaction between hominins and carnivores.

3 CONCLUSIONS AND FUTURE PERSPECTIVES

Our experiments are proving the importance of developing experimental archaeology related with the study of the interaction between hominins and carnivores. The experimental scenarios designed and presented here show how it is possible to approach aspects related with the study of modern and complex behavior and the understanding of as carnivore actions as postdepositional taphonomic agents. First, it is possible to observe how carnivores modify space linked to modern and complex behavior, as hearth and hearth-related assemblages or complex spatial distributions and inhumation contexts. Second, experiments allow us develop new criteria when facing archaeological materiality with taphonomic modifications, such as bones with superposed marks from both hominins and carnivores. This is helping in the understanding of which agent had the primary and the secondary access, what implies many issues related to subsistence strategies (e.g., hunting or scavenging). And finally, experiments developed are showing how carnivores are able of modifying elements that can confuse us when interpreting hominin activities (e.g., use-wear present in lithic tools).

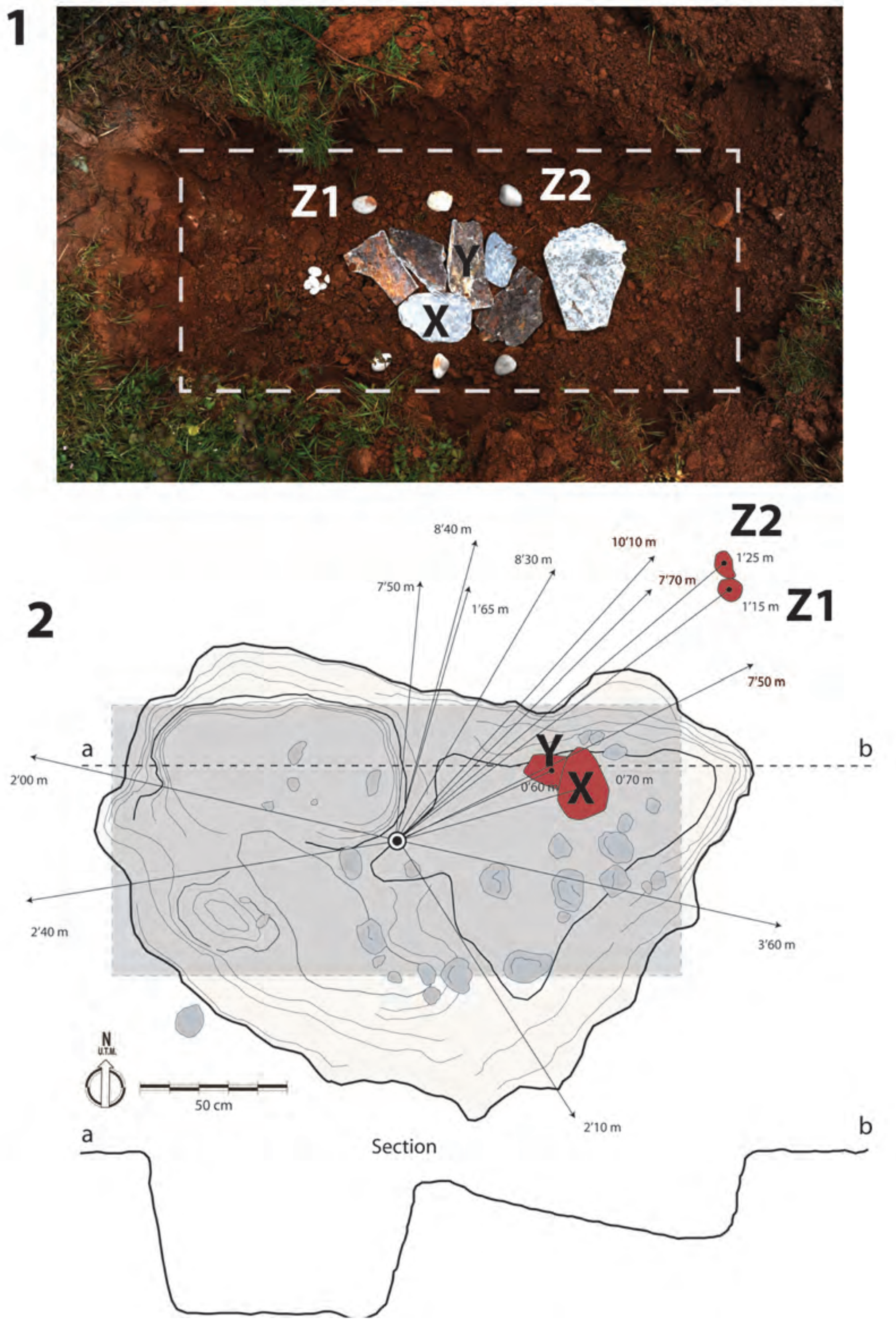

IMAGE 04. Experimental inhumation (bears case): 1) Structured inhumation before carnivore modification and 2) after modification. Objects referred as X,Y, Z1 and Z2 can be seen in previous and after experimental scenes (1 and 2),

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In conclusion, experiments with extant carnivores are providing important and useful information related with the study of human behavior through hominin-carnivore interaction. Furthermore, we are now building a methodology from a multidisciplinary perspective capable of the recovery of behavioral related-information that 1) has been erased due to the activity of carnivores as taphonomic agents (e.g., spatial distributions), 2) that was difficult to recover (e.g., superpositions) and 3) that can confuse us (e.g., use-wear traces).

At the moment, experimental results are giving important information to afford the study of complex anthropic spatial organization and the systematic use of fire (Camarós et al., 2013a; 2013b), scavenging or hunting strategies (primary or secondary access to animal resource), or the isolation of a modern cognition related to inhumation rituals. As experiments developed prove, the interaction between hominins and carnivores has a lot to do in the study of the evolution of human behavior during the Pleistocene.

The aim of this methodology is to provide new insight into the study of human behavior through the analysis of hominin-carnivore interaction during the Pleistocene. Future studies will consist in applying all these results to the study of archaeological assemblages.

ACKNOWLEDGEMENTS

We would like to thanks S. Borragán (Chief of the Veterinary Service of Cabárceno) for his help in the development of all phases of the experiment. M. Prieto, also from Cabárceno has helped us in the animal enclosures. Thanks also to Cabárceno Nature Park and Cantur, SA. This project has been developed with funding from project SGR 2014-SGR-900 (AGAUR) and MINECO project HAR2013-48784-C3-1-P. EC is beneficiary of a FI Research Grant (AGAUR).

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4.3.1.1

UNPUBLISHED SUPPLEMENTARY MATERIAL

PAPER 5

Walking with carnivores: Experimental approach to hominin-carnivore interaction

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HOMININ-CARNIVORE INTERACTION DURING THE PLEISTOCENE: DEVELOPMENT OF NEW METHODS FOR THE STUDY OF
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4.3.1.1 Unpublished Supplementary Material

(This research was presented in the AWRANA 2015 meeting in Leiden, the Netherlands, and will we published in a recent future)

Identification of Post-Depositional Surface Modifications (PDSM) generated by carnivores on stone tools

The present data is included in the Doctoral Thesis as supplementary material associated to Paper 5. It is a non-published research developed in collaboration with Dr. Andreu Ollé (Institut Català de Paleoecologia Humana i Evolució Social), and provides new insight on how carnivores modify the archaeological record and are able of generating confusing evidences.

During the experiments with extant carnivores from Cabárceno (Cantabria, Spain) explained in Paper 5 and 6, we observed that the lithic material from the hearth-related assemblage was bitten and touched constantly by all carnivores (see Figure S1). Some animals bitted the stone tools and others only touched them. This was previously said in Paper 6, and now we are conducting research in order to evidence if carnivores also modified the lithic surfaces.

As part of the experiment with carnivores explained in Papers 4, 5 and 6 lithic tools were molded and casted following same methodology explained in Paper 3 with high-resolution silicon. The aim of this procedure was to isolate all evidences of carnivore modification to the experimental materials. Furthermore, lithic material was impregnated with animal fat to attract carnivores attention and emulate the traces of use, although material was not used after casting.

In order to prove carnivore modification on lithic surfaces, two lithic tools (a flint flake and a quartzite biface) were selected from the experiment with brown bears (*Ursus arctos*) with the aim of identifying and characterizing bears modification of stone surfaces (Figure 2). These lithic tools can be located in the space regarding the experimental scenario by looking Figure 2 from Paper 6 (Stone 6006 is Flake 2 and 6007 is the Biface).

Positive results were obtained, and traces that were not present on the lithic surfaces before the experiment were observed (Figure S3). Different types of modifications were identified and isolated in both Stone 6006 and Stone 6007. In this sense, we observed polished surfaces (e.g., Figure S3, 6006 P1) and striations (e.g., Figure S3, 6007 P1) as the most common ones, among others.

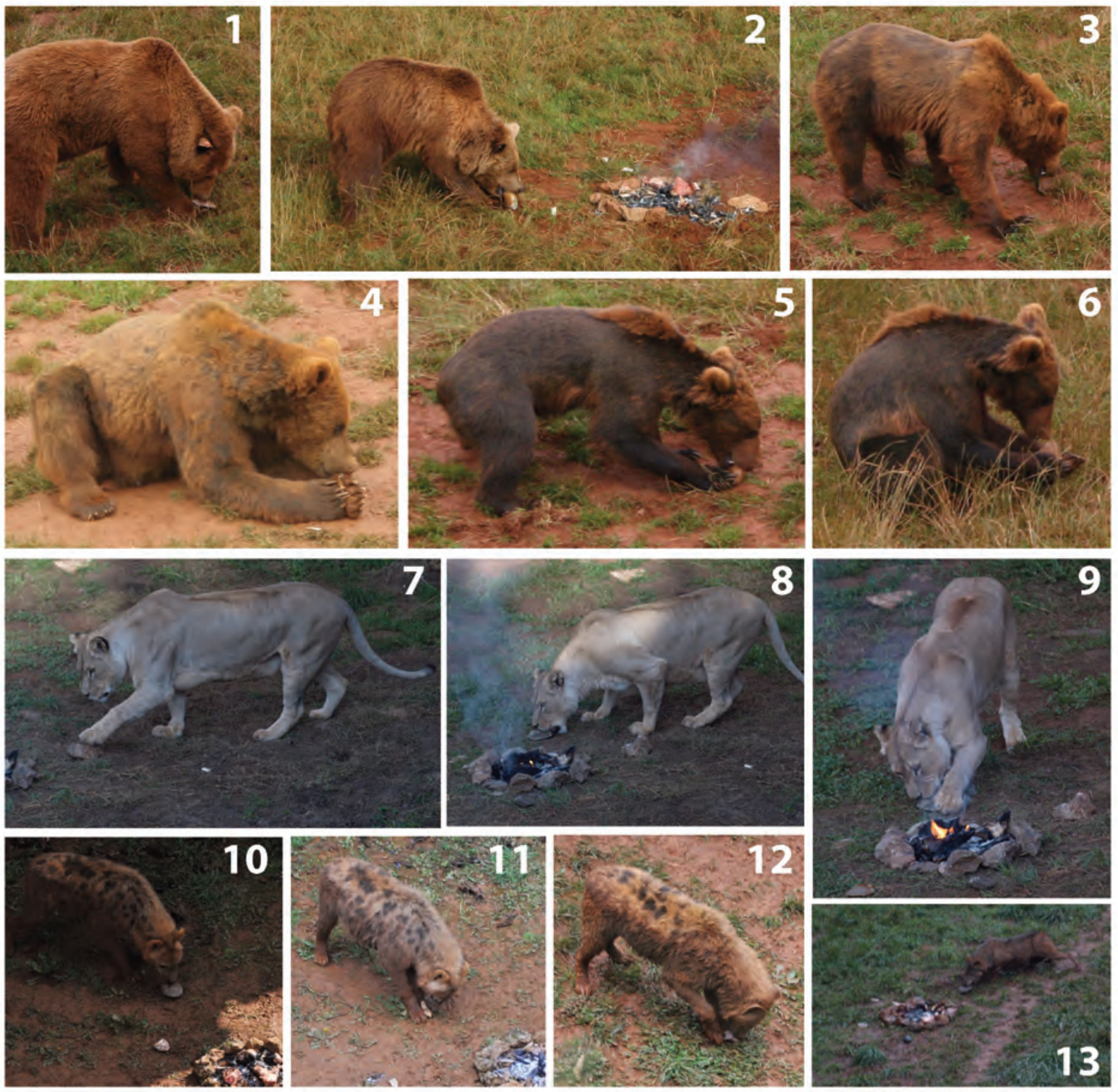

Figure S1. Carnivores from Cabárceno (Spain) interacting with the hearth-related assemblage (lithic tools): 1-6) Bears (*Ursus arctos*); 7-9) Lions (*Panthera leo*); 10-12) Hyenas (*Crocuta crocuta*) and Wolves (*Canis lupus*).

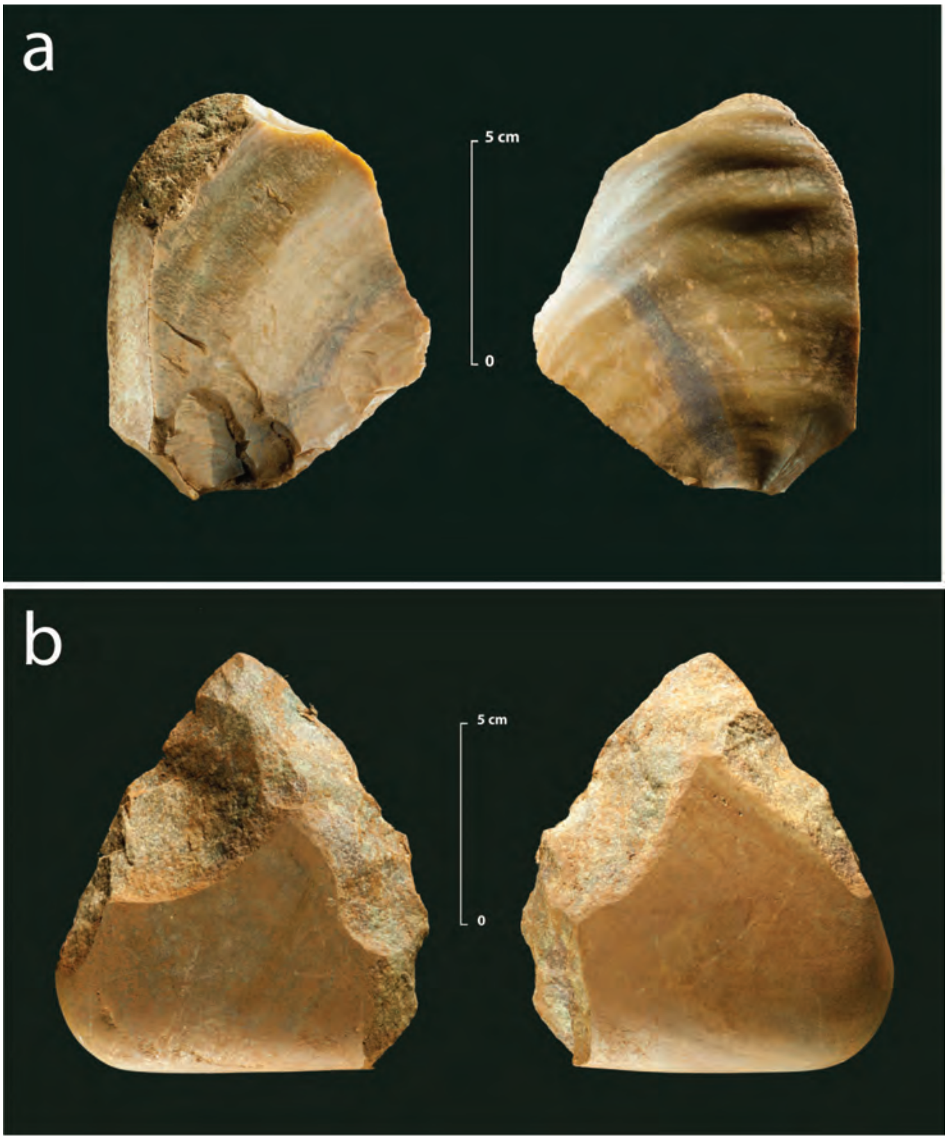

Figure S2. Lithic tools selected to identify and characterize carnivore modifications of stone surfaces. a) Stone 6007 and b) Stone 6006. Spatial location of the lithic material during the experiment can be seen in figure provided in Papers 4, 5 and 6.

With the aim of providing a deeper analysis of the characterization of bear modification of stone surfaces, we have been working on the study of the traces identified on Stone 6006 (a quartzite biface) Point 2 and Point 3 (Figure S2b) as a first approach to these type of carnivore modifications on lithic tools since now never analyzed.

Point 2 is a polished surface with clear internal microstiation that has been observed using different optics, magnifications and devices (e.g., Zeiss Axioscope A1, Hirox KH-8700 or SEM) (Figure S4 and S5). The polished surface can be easily identified due to its brightening condition and silver color, which contrast with the reddish zone in the image, specially on the upper left side, which is related with Cabáceno's sediment (with a high content of iron) (Figure S5).

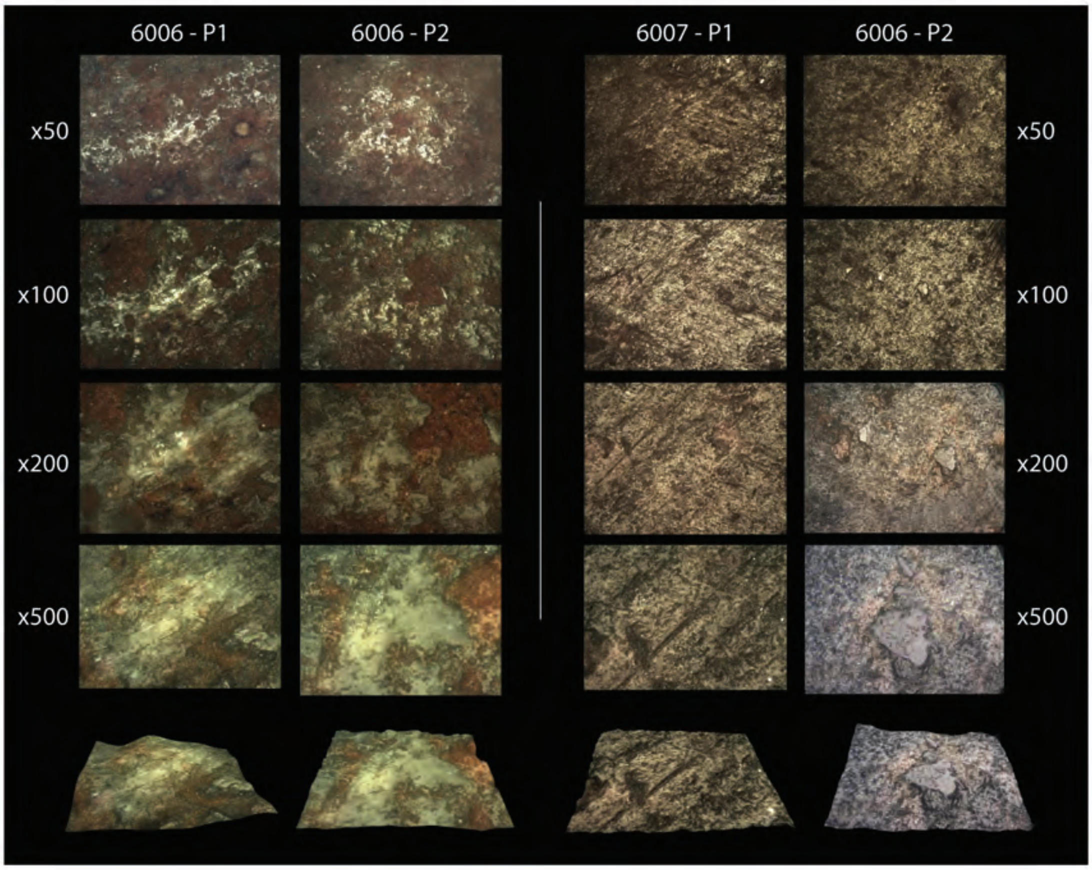

Figure S3. Different types of traces observed on lithic surfaces from Stones 6006 and 6007 (images have been taken using a Zeiss Axioscope A1 microscope, and lower 3D images have been obtained with Helicon Focus software after a series of metallographical extended focus images with the same microscope).

In order to discard that the observed zone interpreted as a polished surface of the quartzite was stuck sediment, we cleaned the zone. The area was introduced in a plastic bag and a solution of water and Derquim (2%) was introduced and left for 12 hours. Later the stone in the bag was placed in a ultrasound machine for 15 minutes. The process was repeated twice.

Cleaning process show that the zone with the polished surface remains intact (Figure 6), while the zone that appear in reddish in Figure 5 and associated with sediment, suffers modification. Nevertheless, to definitely prove that the polished zone was the biface quartzite surface, we conducted a chemical composition analysis at the SEM. Results show how the zone inferred as a polished surface is an area with a high content of silica (Si), and the reddish area with iron (Fe) (Figure S7). This analysis proves that the polished surface is certainly the lithic surface and not sediment or dentine stuck on the stone. Therefore, bears are able of generating a plastic modification (e.g., polished surfaces) on lithic tools (e.g., quartzite).

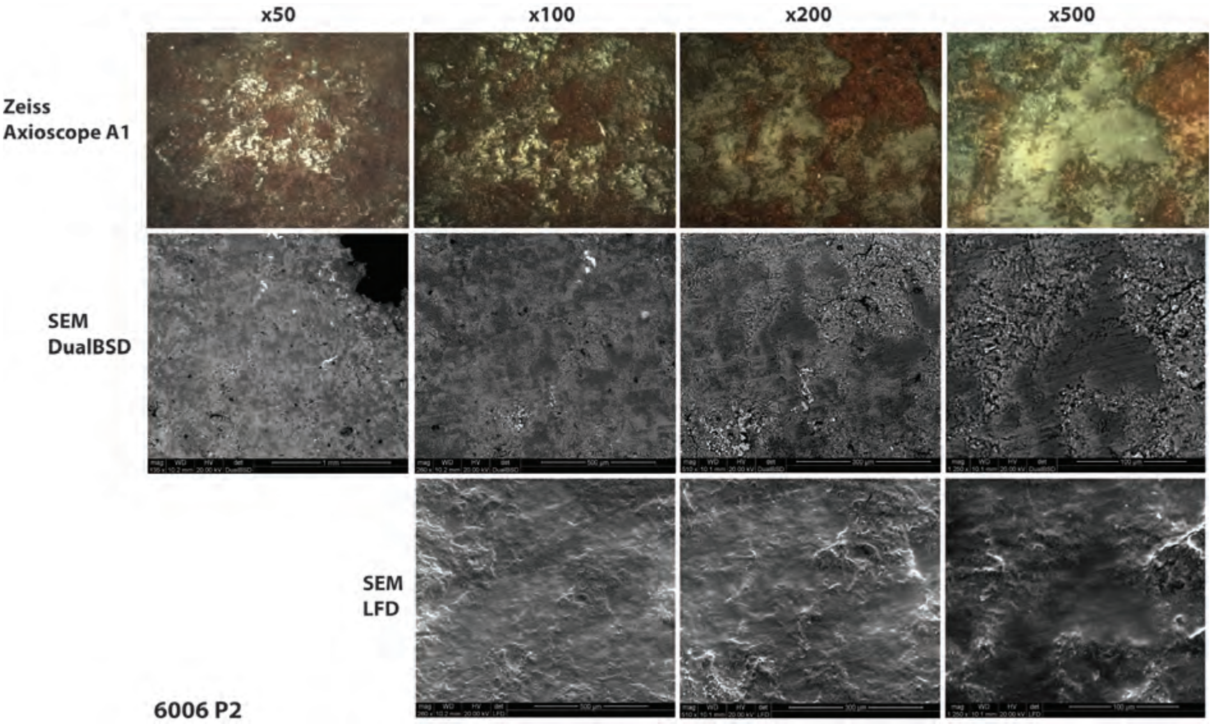

Figure S4. Point 2 of Stone 6006 observed with a microscope and SEM.

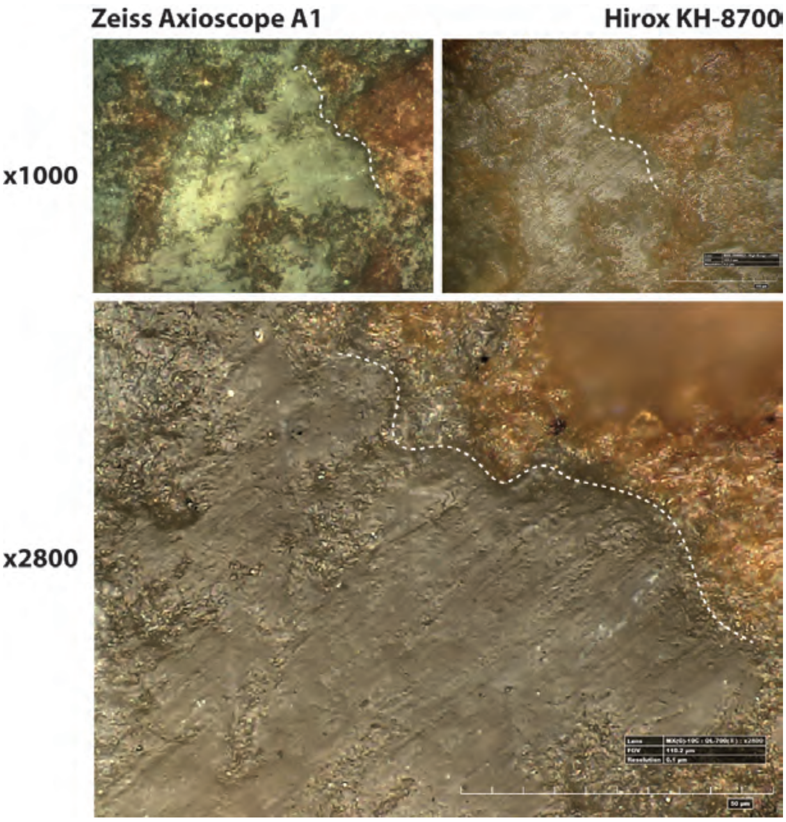

Figure S5. Detailed image of Point 2 of Stone 6006 taken with a microscope Hirox where the polished surface can be appreciated.

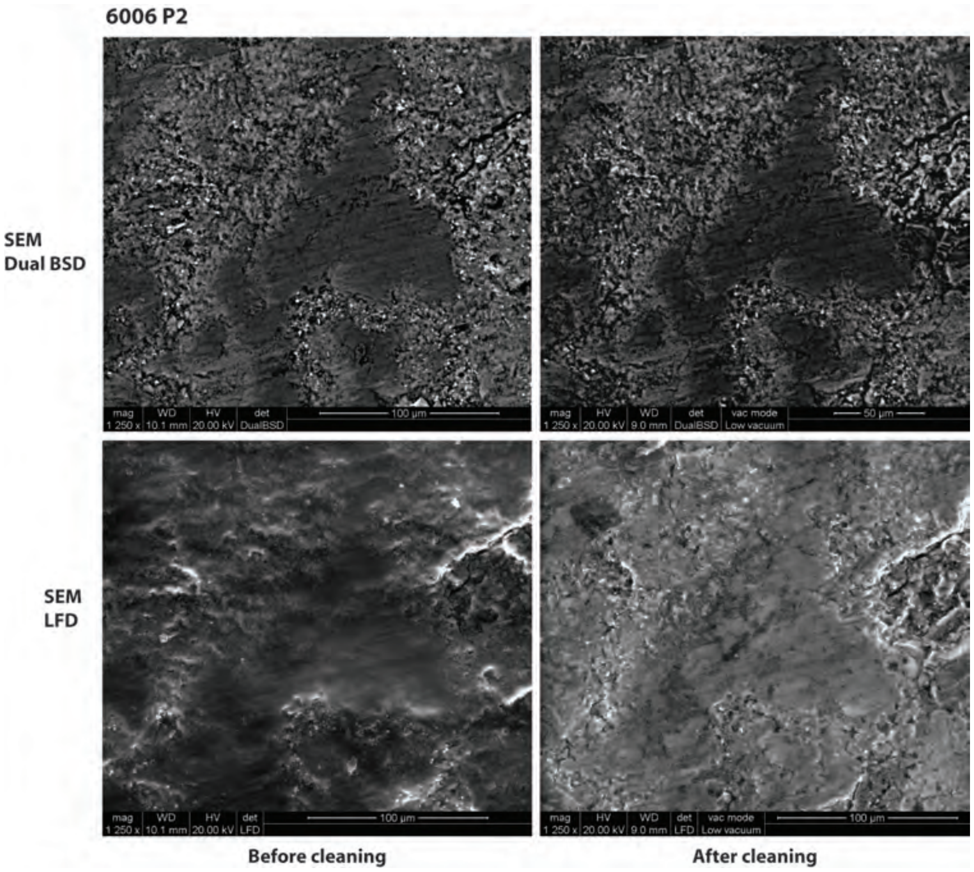

Figure S6. Point 2 of Stone 6006 observed with SEM Dual BSD and SEM LFD, before and after the cleaning process.

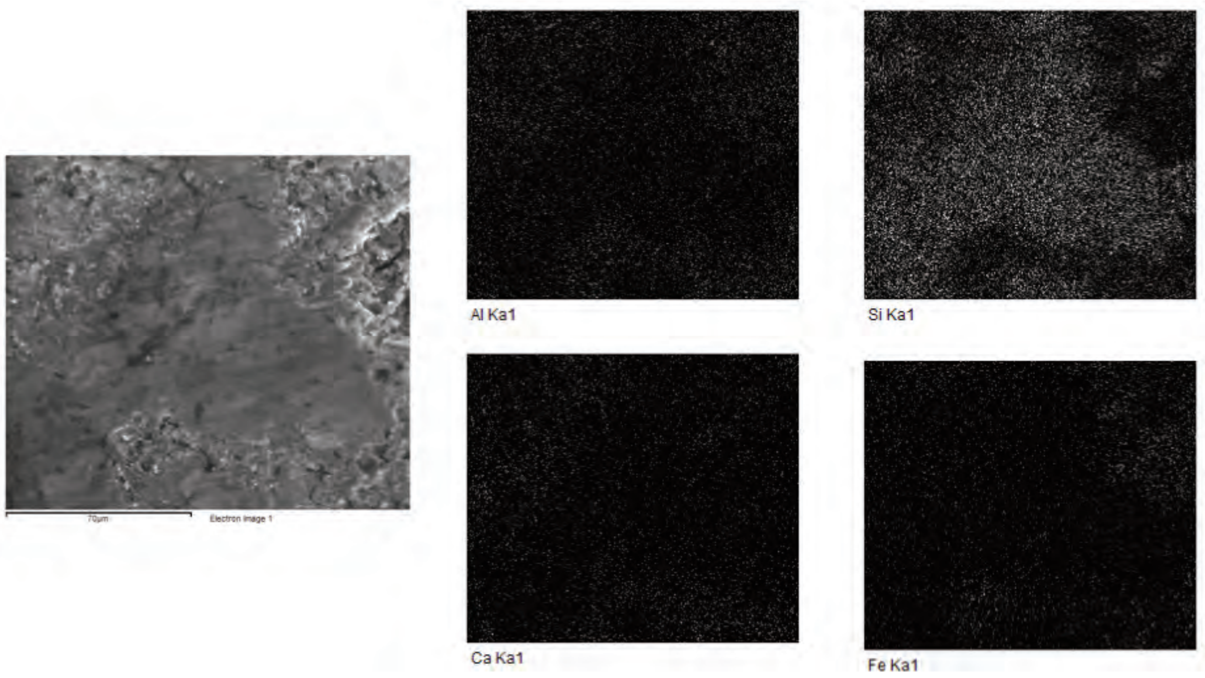

Figure S7. Chemical composition analysis conducted at the SEM on Point 2 of Stone 6006.

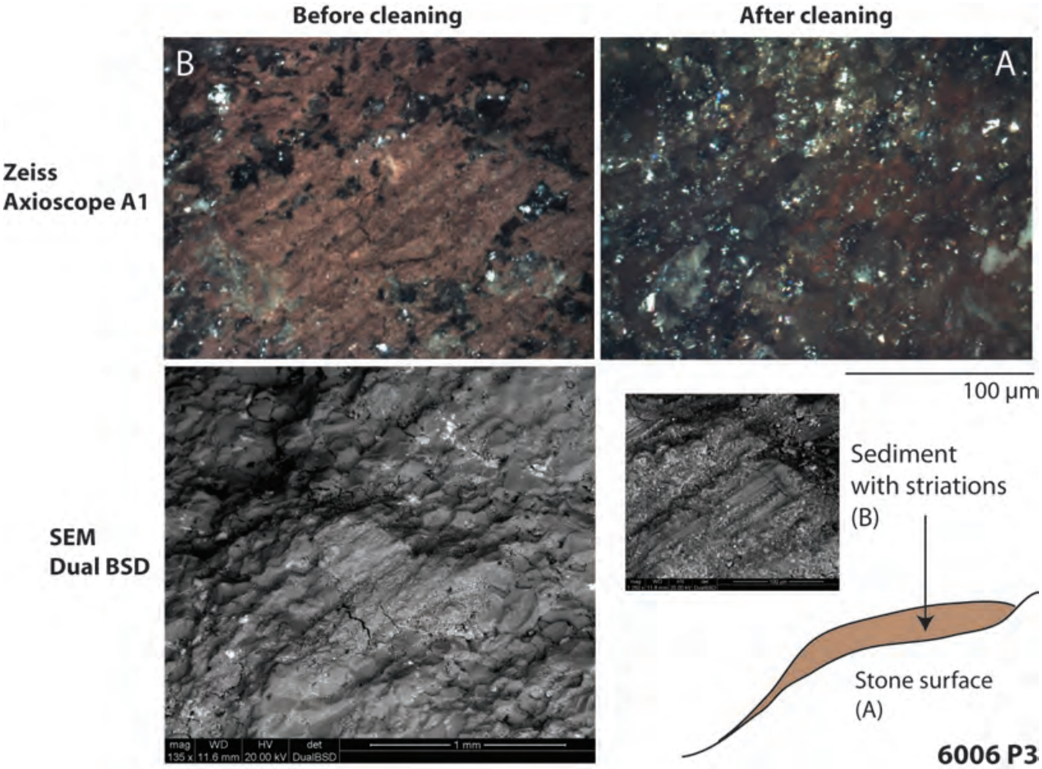

Figure S8. Point 3 of Stone 6006 before and after being cleaned.

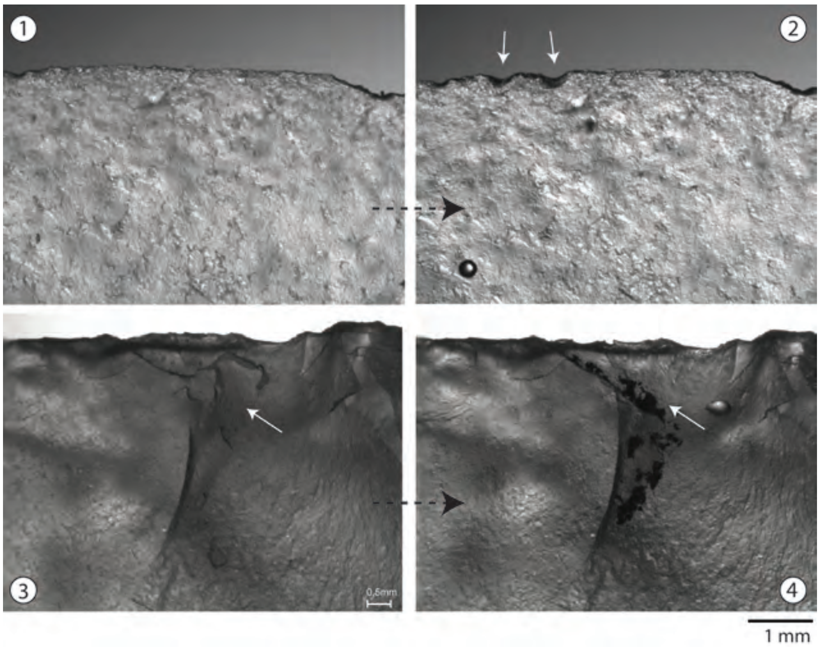

Figure S9. Micro-fractures identified in the edges of the lithic tools. Before (1 and 3) and after (2 and 4) scenarios can be appreciated in the image.

Nevertheless, we have also evidenced the scenario of stuck sediment on the stone surface (Figure S8b). This sediment displays striations as it has been stuck by pressure of the carnivore teeth on the sediment located on the stone. When cleaned with our procedure previously describe, the sediment disappears of the stone surface (Figure S8a).

Other modifications have been also identified in the archaeological record. As all lithic tools introduced in the bears enclosure were casted, we can search for edge modifications. In this sense, we have identified edge damage such as micro-fractures on some of the material involved in the experiment conducted in Cabárceno with bears published in Paper 8.

As we have seen, bears are able of producing PDSM such as edge damage, micro-fractures, rounding, polished surfaces and striations. All these PDSM are been currently characterized in order to distinguish them from use-wear features in the archaeological material. Nevertheless, it has been the first time that it has been proven that carnivores modify lithic tools and a first approach of its characterization is provided. This research will be published in a recent future and other carnivores cases (e.g., lions, hyenas and wolves) will be also analyzed.

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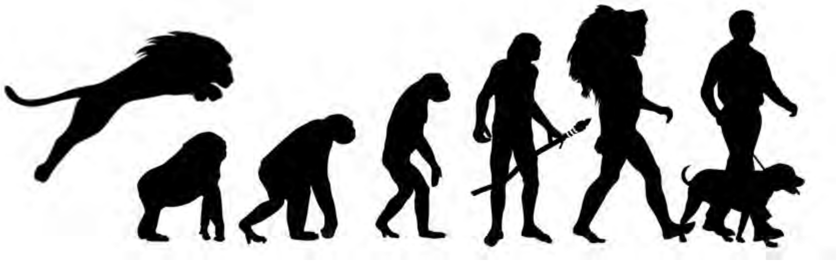
4.3.2

PAPER 6

Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications



Chapter 4.3 *Experimental approach to hominin-carnivore interaction*

Paper 6

Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications

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At most Pleistocene archaeological sites it is difficult to observe structured complex spatial behaviour. This common phenomenon could be a taphonomic issue. Problems in the preservation of the original spatial intra-site distribution could be related to hominidecarnivore alternation in the use of space. In the present paper we analyse the results of our experimentation with large extant carnivores (bears, wolves, hyenas and lions) and propose these animals acted as hearth and hearth-related assemblage modifiers. In this sense, the role of carnivores in the modification of these elements can cause problems in the interpretation and visibility of modern and complex behaviour in the conception of space in the archaeological record.

Spatial distribution, Hearths, Experimental series, Carnivores, Taphonomy

Journal of Archaeological Science, 40: 1361-1368.

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1. Introduction

Researchers agree that not all carnivores behave in a similar way or have the same impact on animal carcasses. Each species has its own ethology and physical characteristics which influence the accumulations that they produce and the intensity with which they act on bone remains. Ethological studies focused on understanding the consumption sequence of carnivores allow us to establish significant differences in carcass handling (e.g., Blumenschine, 1988; Domínguez-Rodrigo, 1994, 2001; Capaldo, 1997; Selvaggio, 1994; Pickering, 2002).

The type of prey, skeletal representation, age at death, superficial and structural modifications on bone remains and spatial distribution are elements commonly used to recognize the degree of carnivore intervention. This degree seems to depend on the activity that these non-human predators perform at a site, i.e. the use that carnivores make of the site.

In Pleistocene contexts, the occupation of karstic areas by carnivores and hominids is well documented (Skinner, 2012). This phenomenon provides a scenario of alternation with remains left by both biological entities that often causes problems in understanding the processes of assemblage formation or isolating specific episodes within the same archaeostratigraphic unit. Then, it is often difficult to differentiate the contributions of each predator due to the frequent palimpsest nature of most Pleistocene archaeological sites.

However, carnivores not only act as accumulators; the smells from the remains left by human groups are attractive for them. For this reason, it is common for scavengers to access these places in search of potentially consumable elements (Binford, 1981; Rosell and Blasco, 2009). Different observations and experimental reproductions have been made, with both wild animals and animals in captivity, attempting to document the modifications made by carnivores on the faunal assemblages generated by human groups (e.g., Sutcliffe, 1970; Bunn, 1986; Bunn and Kroll, 1986; Bunn et al., 1980, 1988; Blumenschine, 1986a, 1986b, 1988; Marean et al., 1992). For instance, several experiments with spotted hyenas in the Serengeti National Park (Tanzania) were conducted by Blumenschine (1988) with the aim of identifying the timing of hominid and carnivore influence on Plio-Pleistocene archaeological bone assemblages. This author reproduced several archaeological contexts using bovid limb bones previously broken while fresh, which were exposed to the hyenas. The first observation was the preference of these scavengers for the fat contained in the epiphyses. The degree of destruction and tooth-marks produced on these bone por-

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tions were very high (of the order of 90% or more in several cases). Similarly, the shafts remained in their original position, but some epiphyses were transported several metres and partially or integrally consumed. Marean and Spencer (1991) and Marean et al. (1992) carried out reproductions of hominid discarded assemblages subjected to the action of captive spotted hyenas to interpret several assemblages from Olduvai. During the series, the carnivores acted on the skeletal parts with a higher proportion of fat: vertebrae, ribs and epiphyses. The common resulting pattern was an assemblage with a predominance of limb bones, similar to those generated by the anthropogenic transport of cranial and limb bones (Marean et al., 1992) or, as Blumenschine (1991) suggested, to the accumulations generated by the human scavenging of carcasses abandoned by large felids (collecting bones with marrow).

These studies were mainly focused on the damage and destruction caused by carnivores. However, other archaeological evidence, such as lithic artefacts, wood, hearths, or spatial repartition and structuring, was not used, nor discussed in depth. The role of nonhuman scavengers on the abandoned camps was also observed in some ethnoarchaeological studies (Binford, 1978, 1981; Binford et al., 1988; Bartramet al., 1991; Yellen, 1991; O'Connell et al., 1992).

All of the researchers coincide in that displacement of material is not common, and that this phenomenon is only produced in the cases of tension among animals. In these cases, some bones can be moved to the peripheral areas of the site. Coprolites are common and are usually found in the ash of the hearths (Bartram and Marean, 1999; Klein et al., 1999).

On this basis, carnivores do not only destroy or modify the bones, but they can also affect the original position of the remains, altering significantly the spatial distribution left by human groups (Binford et al., 1988). This situation has made us question how large carnivores react to a recently abandoned structured hearth with a hearthrelated assemblage, an element that can attract their attention powerfully (smells of meat, organic tissues or fat remains). This variable has not been contemplated by previous studies and is an important factor to value the degree of alteration or loss of spatial and behavioural information after a secondary access of carnivores.

To study this idea, we have carried out an experimental series with large extant carnivores in the Parque de la Naturaleza de Cabárceno (Cantabria, Spain) with the objective of tackling a casespecific archaeological problematic using experimental archaeology as understood by Domínguez-Rodrigo (2008) and as part of "middle-range" theory, based on the testing of alternative hypotheses (Binford, 1981; Gifford, 1981).

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2. Experimental series: methodology

The animals in Parque de la Naturaleza de Cabárceno (Penagos, Cantabria, Spain) live in a semi-free state. Each animal group has enclosures of several hectares limited by natural barriers (cliffs) except for the visitors' observation points, which are enclosed by artificial integrated fences. The park policy is to interact as little as possible with the animals, which live in extensions and only food is provided for them. Consequently, animals live according to their instincts and no population control or other human interference is developed. Probably, animals living in a non-free state present misbehaviour in some aspects compared to wild animals. Nevertheless, the aim of our experiment is to prove capacities, which are not erased in semi-free state animal populations.

The experimental series consisted of the reproduction of a structured hearth (with associated stone blocks in a circular form) with faunal remains, wood and wood charcoal and a hearth-related lithic assemblage, inside four different carnivore enclosures in the park. The large carnivores selected for the experiment were those that were most common in the alternation in the use of caves with human groups in European Pleistocene. Namely bears, lions, wolves and hyenas. These animals in consensus with the Veterinary Service of the Park, were not fed the day before the experiment so the game factor could be eliminated.

A team of three archaeologists and two guards (for safety reasons) entered the animal enclosures and constructed a hearth with a ring of local Cabárceno limestone (n: 12). These rocks were between 10 and 20 cm in size and were angular in shape (to avoid false increased displacements). The dimension of the combustion structure was 50 cm in diameter following the average size of some of the recorded Pleistocene hearths, which vary between 20 cm and 100 cm in diameter (e.g. Farizy, 1990, 1994; Mellars, 1996; Barton, 2000; Soler, 2001; Cabrera et al., 2004; Cain, 2005; Daujeard and Moncel, 2010; Slimak et al., 2010). Inside the experimental structure, a first layer of oak charcoal was deposited (0.4-0.6 kg), a second layer of dry oak leaves followed to help the combustion (0.05-0.1 kg) and finally oak wood was deposited over (0.5-1 kg). On top of all these layers, different fractured fresh cow limb bones (Bos taurus) were deposited. These bones were previously defleshed but contained traces of meat and fat, specially located on the epiphyses. The hearths were lit using ecological fuel briquettes (made of wood chips, paraffin and resin), so non-chemical additives were present.

Surrounding the combustion structure, five lithic tools (two flakes, a biface, one hammer stone and one stone anvil), where placed to observe if these hearth-related elements were spatially perturbed by the carnivores. All the lithic elements were documented, using silicon moulds and 3D scanning technology before and after the experimentation. The objective was to register all the kinds of modifications these materials might suffer. All these lithic artefacts were not used to deflesh the bones in order to not modify tools morphology before animals interact with them. Nevertheless, they were slightly impregnated with fat to generate the same effect as if they have been used to process the carcasses.

Before the hearths were lit, the structure and surrounding elementswere documented with photogrammetry so future changes were observable in comparison with the non-modified hearth (NMH) during the experimental series.

The mapping in the present experimental reproduction has been developed by photogrammetric techniques. The georeferencing process was established with a total station and GPS positioning techniques. The main objective was to record two scenes in detail in the shortest time (before and after the intervention of the animals).

Using stereoscopic pairs taken with calibrated optical cameras, we obtained 3D pointclouds that were combined and triangulated to acquire a high-resolution surface of the scene. All data obtained was processed with PhotoModeler Scanner v.6 software. The pointclouds were georeferenced by using targets measured with total station (Leica TCRM1205) that linked them to a provisional local system. Inside this system, other points strategically distributed in the near landscape were measured. Their position was also calculated in ETRS89 global reference system coordinates with a dual frequency RTK GPS (Leica GPS900) connected to the Cantabrian GNSS net. This way, it was possible to transfer all positions to the already mentioned reference system.

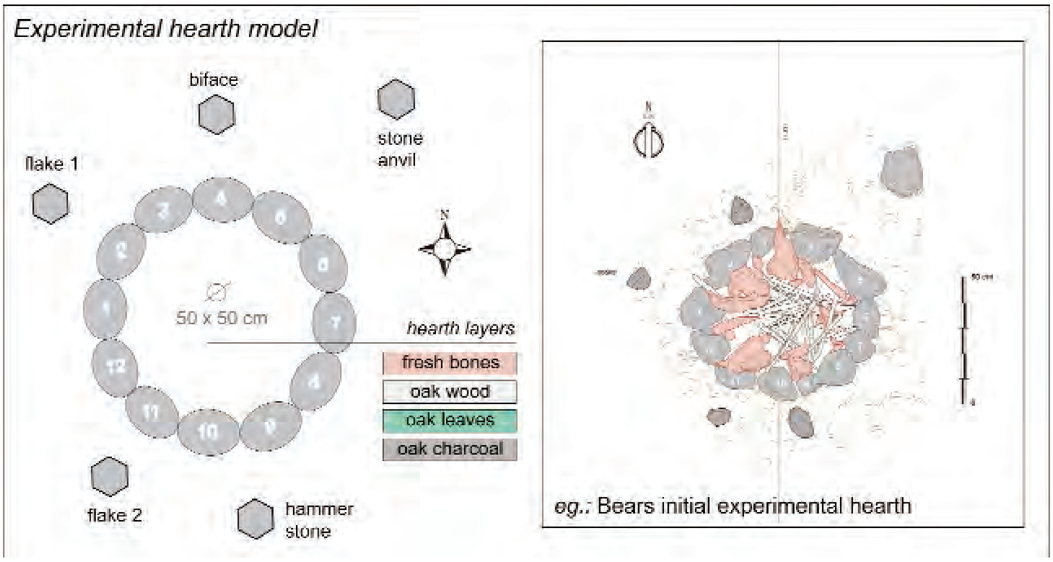

Fig. 1. Experimental hearth (EH) and hearth-related assemblage model used in the experimental series and example of the initial scene generated in Experimental Series 1 (bears).

The experimental hearth (EH) burned in all cases for more than 40 min and less than 100 min. After this, the enclosure was abandoned for safety reasons and also to recreate the conditions of a combustion structure related to a short-term human occupation, where possibly a hearth cannot cause visible thermoalterations in the associated stones and sediment. There are examples of hearths with associated stones with no visible rubefaction (Soler, 2001).

After 8-9 h (except for the wolf experiment), the team entered the enclosures again and repeated the photogrammetric recording with the carnivore-modified hearth (MH).

3. Results

3.1. Experimental series 1: bears (*Ursus arctos*)

The population density of bears in the enclosure at Cabárceno is high, around 70 individuals living together in an area of 7.32 ha. These are animals that had never been in contact with fire in any sense. We entered in the enclosure at 9:00 h, and constructed the EH following our protocol (Fig. 1). This EH contained a fractured B. taurus tibia and femur, 0.8 kg of wood, 0.05 kg of oak leaves and 0.5 kg of charcoal. The lithic artefacts placed around the hearth as a hearth-related assemblage were a local limestone stone anvil, a quartzite biface, 2 flint flakes (one from the Ebro Valley and other from Bergeracois) and a quartzite hammer stone (Online Supplementary Fig. S1). The enclosure was abandoned at 09:40 h. Inline supplementary Figure S1 can be found online at http://dx.doi.org/10.1016/j.jas.2012.09.037.

The EH burned for 42 min and the first bear reacted immediately (1 min after the EH stopped burning). This first animal was the dominant male, and after him different individuals interacted with the hearth in different degrees in order of social hierarchy. Nevertheless, the main destruction (where no association of elements can be recovered) was caused by just two of the male bears (see the Video Data 1 from supplementary material for more information on the ethological behaviour of bears related to the EH modification process). Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.jas.2012.09.037.

The resulting MH by bears (Fig. 2 and Table 1) had been highly disturbed. The original stone ring structure at the end of the experiment was no longer recognisable. Absolutely all the stones and lithic tools that formed the hearth and the hearth-related assemblage were displaced from their original emplacement.

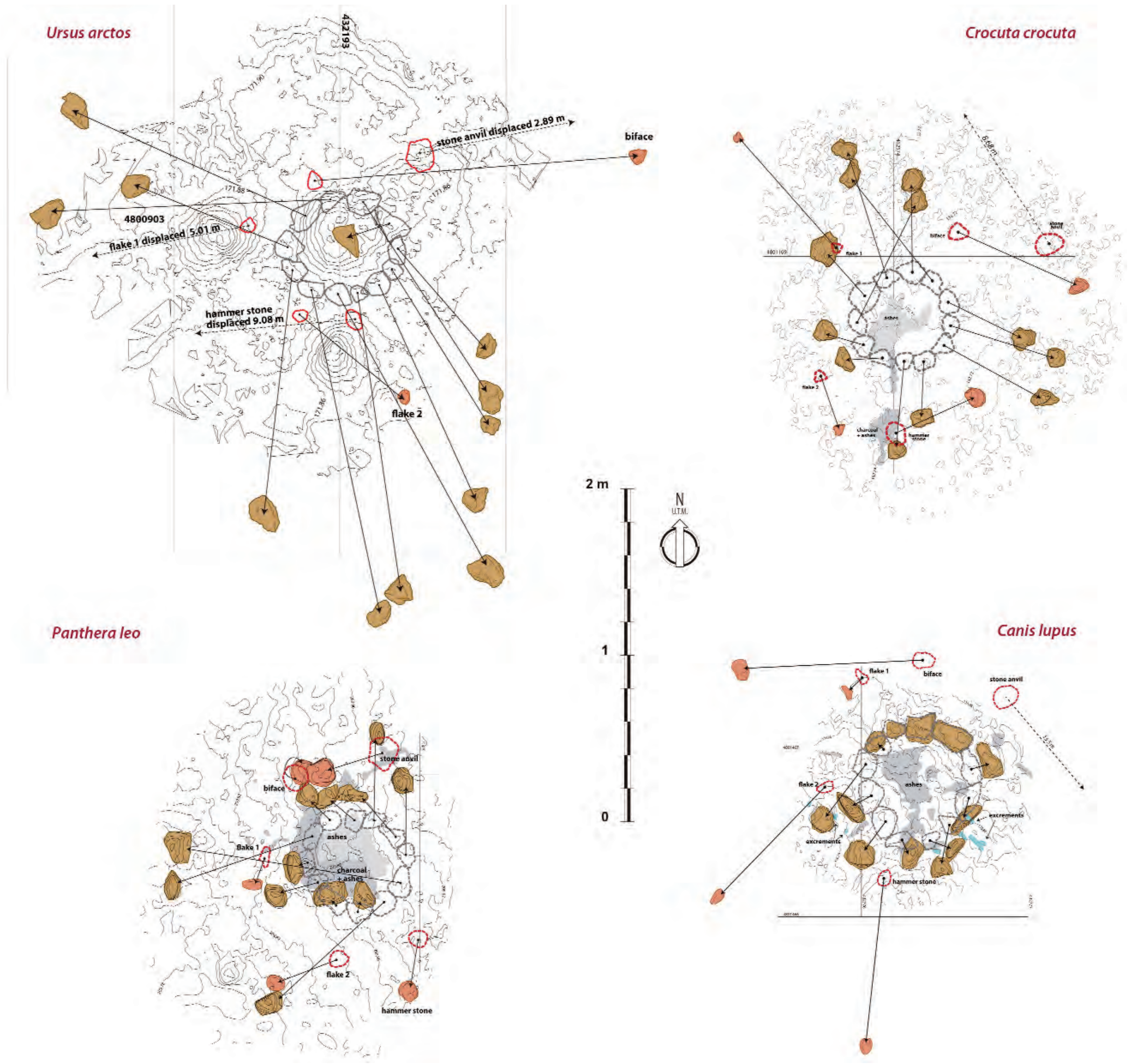

Fig. 2. Experimental hearths and hearth-related assemblages modified by different carnivores.

Element	Displaced	Distance from origin (meters)	Azimuth orient. of displacement	Type of modification	Recovered	Element	Displaced	Distance from origin (meters)	Azimuth orient. of displacement	Type of modification	Recovered
Experimental series 1: bears (Ursus arctos)						*Experimental series 2: hyenas* (Crocuta crocuta)					
ST1	Yes	1.00	290°	D	Yes	ST1	Yes	0.31	320°	D	Yes
ST2	Yes	1.52	295°	D	Yes	ST2	Yes	0.77	344°	D	Yes
ST3	Yes	1.69	268°	D	Yes	ST3	Yes	0.50	359°	D	Yes
ST4	Yes	1.41	148°	D	Yes	ST4	Yes	0.74	320°	D	Yes
ST5	Yes	0.27	250°	D	Yes	ST5	Yes	0.47	115°	D	Yes
ST6	Yes	0.80	139°	D	Yes	ST6	Yes	0.67	106°	D	Yes
ST7	Yes	1.09	149°	D	Yes	ST7	Yes	0.66	117°	D	Yes
ST8	Yes	1.43	157°	D	Yes	ST8	Yes	0.33	184°	D	Yes
ST9	Yes	1.80	170°	D	Yes	ST9	Yes	0.49	185°	D	Yes
ST10	Yes	1.87	151°	D	Yes	ST10	Yes	0.22	268°	D	Yes
ST11	Yes	1.97	168°	D	Yes	ST11	Yes	0.23	283°	D	Yes
ST12	Yes	1.51	188°	D	Yes	ST12	Yes	0.78	26°	D	Yes
SA	Yes	2.89	780°	D+G	Yes	SA	Yes	0.68	327°	D+G+T	Yes
B	Yes	1.95	86°	D+G	Yes	B	Yes	0.77	114°	D+G+S	Yes
F1	Yes	5.01	260°	D+T+G	Yes	F1	Yes	0.99	319°	D+G+S	Yes
F2	Yes	1.78	129°	D+G	Yes	F2	Yes	0.33	163°	D+G+S	Yes
HS	Yes	9.08	265°	D+G+T+S	Yes	HS	Yes	0.50	67°	D+G+S	Yes
Femur	Yes	> 40.0	280°-75°	D+G+T+F	No	Femur	Yes	-	-	D+G+T+F+CC	No
Tibia	Yes	> 40.0	280°-75°	D+G+T+F	No	Tibia	Yes	-	-	D+G+T+F+CC	No
						Tarsus art.	Yes	-	-	D+G+T+F+CC	No
Experimental series 3: lions (Panthera leo)						*Experimental series 4: wolves* (Canis lupus)					
ST1	Yes	0.28	255°	D	Yes	ST1	Yes	0.07	308°	D	Yes
ST2	Yes	0.11	254°	D	Yes	ST2	Yes	0.03	282°	D	Yes
ST3	Yes	0.92	252°	D	Yes	ST3	Yes	0.03	320°	D	Yes
ST4	Yes	0.22	313°	D	Yes	ST4	No	-	-	-	Yes
ST5	Yes	0.24	308°	D	Yes	ST5	Yes	0.12	75°	D	Yes
ST6	Yes	0.54	2°	D	Yes	ST6	Yes	0.13	194°	D	Yes
ST7	Yes	0.39	317°	D	Yes	ST7	Yes	0.14	190°	D	Yes
ST8	Yes	0.46	1°	D	Yes	ST8	Yes	0.16	111°	D	Yes
ST9	Yes	1.37	280°	D	Yes	ST9	Yes	0.10	155°	D	Yes
ST10	Yes	0.94	238°	D	Yes	ST10	Yes	0.25	117°	D	Yes
ST11	Yes	0.12	14°	D	Yes	ST11	Yes	0.15	248°	D	Yes
ST12	Yes	0.10	315°	D	Yes	ST12	Yes	0.43	119°	D	Yes
SA	Yes	0.39	253°	D+S	Yes	SA	Yes	15.05	141°	D+?	Yes
B	Yes	0.09	41°	D+G+S	Yes	B	Yes	1.09	268°	D+?	Yes
F1	Yes	0.17	200°	D+G+S	Yes	F1	Yes	0.12	226°	D+?	Yes
F2	Yes	0.41	249°	D+G+S	Yes	F2	Yes	0.83	227°	D+?	Yes
HS	Yes	0.38	190°	D+G+S	Yes	HS	Yes	1.03	187°	D+?	Yes
Tibia	Yes	> 20.0	290°-30°	D+G+T+F	No	Femur	Yes	-	-	D+G+T+F	3 frg.
Tibia	Yes	> 20.0	290°-30°	D+G+T+F	No	*Frg.1*	Yes	19.80	22°	D+G+T+F	Yes
Tarsus art.	Yes	> 20.0	290°-30°	D+G+T+F	No	*Frg.2*	Yes	19.00	31°	D+T+F	Yes
						Frg.3	Yes	20.10	32°	D+T+F	Yes
						Tibia	Yes	-	-	D+G+T+F	4 fgr.
						Frg.4	Yes	12.01	201°	D+T+F	Yes
						Frg.5	Yes	12.06	199°	D+T+F+G	Yes
						Frg.6	Yes	13.76	201°	D+T+F	Yes
						Frg.7	Yes	14.03	195°	D+T+F+G	Yes
						Tarsus art.	Yes	-	-	D+G+T	1 fgr.
						Frg.8	Yes	10.92	344°	D+G+T	Yes

Code for element = ST: stone; SA: stone anvil; B: biface; F: flake; HS: Hammer stone
Code for type of modifications = D: displaced; G: gnawed; T: transported; S: scratched; F: fractured; CC: complctly consumed

Table 1. Characterization of the modifications resulting from different experimental series.

Stones were displaced in a more or less circular dispersion in a 9m2 area around the first position, and stone tools displayed a completely different location reaching in some cases distances of over 9 m (Fig. 2). These artefacts were gnawed and scratched by bears, which caused the presence of microscopic traces on the surface of the stones that are currently in the process of being studied to characterize them. In addition, bones were carried by bears out of our security zone; for this reason it was not possible to reference them in the MH final map. Nevertheless, we can point that they were not located in a 40 m2 area around the EH.

Bears removed the patch of charcoal and ashes present after the combustion. These animals rubbed themselves on the patch, and charcoal and ash adhered to their fur and was carried away when the bears abandoned the EH zone. The activity of bears over the EH was also related with the excavation of holes. A 50 cm diameter hole was dug by one male bear (possibly searching for meat attracted by the fat impregnated sediment), just where the hearth was placed (where stone number 5 is placed in Fig. 2). Two other holes were dug by other bears. These pits are related with the emplacement of our wooden stakes (targets) used for the photogrammetric capture of data. The experimentation with bears was the first one we carried out, and in our original protocol the three stakes should remain driven into the ground during all the experiment so they would not need to be geographically referenced again. Nevertheless, bears were also attracted by these elements (which were excavated by them), and we decided to revise our experimental protocol and stop using the wooden stakes in future experimentations after referencing the non-modified EH and replace them to reference the MH.

3.2. Experimental series 2: hyenas (*Crocuta crocuta*)

Cabárceno Nature Park has two female hyenas living in an area of 982.88 m2. These animals have never been in contact with fire. We entered the hyena enclosure at 09:00 h, and set up the EH following the protocol (Fig. 1). This EH contained a fractured B. taurus tibia, femur and tarsus, 1 kg of wood, 0.07 kg of oak leaves and 0.4 kg of charcoal. The lithic artefacts positioned around the hearth as a hearth-related assemblage were a local limestone stone anvil, a flint (Bergeracois) biface, 2 flint flakes (one from the Ebro Valley and the other from Bergeracois) and a pebble used as a hammer stone (Online Supplementary Fig. S1). The hyena enclosure was abandoned at 09:30 h.

The EH burned for 89 min and the hyenas reacted immediately after the team abandoned the enclosure by showing great interest in the hearth. Nevertheless, they made real physical contact with the EH related assemblage 76 min after we exit the enclosure. The first animal showed a shy and restrained behaviour towards the EH but in the end both animals modified its structure considerably (see the Video Data 2 from Supplementary Material for more information on the ethological behaviour of hyenas related to the EH modification process). Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.jas.2012.09.037.

The resulting experimental MH by hyenas (Fig. 2 and Table 1) had suffered considerable changes to its original structure (online Supplementary Fig. S1). All the burned bones were taken away from the hearth without disturbing the original spatial disposition of the other elements. This was one of the first modifications carried out by hyenas. Afterwards, all the elements were moved and it was very difficult to relate the elements that formed the circular hearth with each other and with the related lithic assemblage.

The association between elements had been erased and all the stones in the circular structure and the hearth related assemblage had been displaced. The displacement of the elements followed a circular dispersion.

The stone anvil was transported by one of the hyenas in its mouth 8.68 m from its original position. The rest of the lithic artefacts were displaced shorter distances and all of them were gnawed and scratched by the animals. With the exception of the stone anvil, all the elements that formed the EH where displaced by using their anterior limbs. They moved hearthstones to provide a better access to the centre of the structure, but they also dug in this central zone. This is the reasonwhy part of the ash and charcoal was displaced out of the original stone circle, and formed a second ash patch. These animals also rubbed themselves within the ash and charcoal patch.

With their anterior limbs, both hyenas scratched the central zone of the hearth. This caused a removal of sediment minimum in depth considerable in diameter. Inside this depression it was possible to recognize the scars of the claws in the sediment (see the Video Data 2 from Supplementary Material).

3.3. Experimental series 3: lions (*Panthera leo*)

In Cabárceno there are 7 lions (1 male and 6 females) living in an area of 1.47 ha. They have never been in contact with fire. We entered the lion enclosure at 08:30 h, and set up the EH following the protocol (Fig. 1). This EH contained a fractured B. taurus tarsus and 2 tibias, 0.9 kg of wood, 0.09 kg of oak leaves and 0.6 kg of charcoal. The lithic artefacts placed around the hearth, as a hearthrelated assemblage, were a local limestone stone anvil, a limestone biface, 2 flint flakes (Bergeracois) and an ophite pebble used as a hammer stone (online Supplementary Fig. S1) . The lion enclosure was abandoned at 09:15 h.

The EH burned for 99 min and the lions reacted immediately (when the flames were still present). All the lions interacted with the hearth (with and without flames) for 53 min without modifying it. Although they were not frightened by the fire, they did not move any component elements of the hearth because they were cautious about approaching it (possibly because of the high temperature). Nevertheless, they touched some of the elements that composed the hearth-related assemblage (stone anvil, flake one and two and the biface) with their anterior limbs. After this, they abandoned the zone where the EH was (which was in the shade) and all of them went to lie in the sun. At 15:15 h the sun shone on the EH and the lions started interacting (in the sense of modification) with the hearth (see the Video Data 3 from supplementary material for more information on the ethological behaviour of lions related to the EH modification process). Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.jas.2012.09.037.

The resulting MH by lions (Fig. 2 and Table 1) can still be recognized as a hearth structure but with some changes in comparison with the initial EH. The degree of modification was not as high as in the case of the bears or the hyenas, but was considerable. All the stones that formed the hearth ring structure were displaced different distances never greater than 110 cm. In this sense, the modification was not high, although the circular shape of the structure was erased.

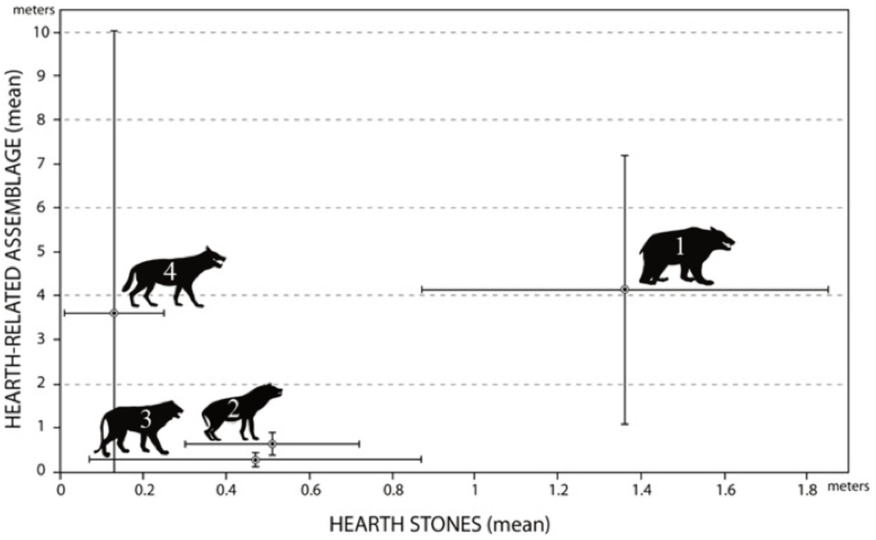

Fig. 3. Bivariate plot of the two main modification variables of the MH. The mean of the hearth-related assemblage distances is plotted in the Y-axis, and the mean of hearth-stones distances is plotted in the X-axis. Error bars show the addition of a standard deviation (s.d.) in each side for each case. 1) Bears; 2) Hyenas; 3) Lions and 4) Wolves.

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Concerning the hearth-related elements, they were all displaced (between 5 and 30 cm from their initial location) and as in the case of bears and hyenas, the lions gnawed and scratched them producing microscopic traces that are currently being analyzed . Bones were consumed and transported out of our security area around the EH (a radius of 20 m2 around the EH).

Lions rubbed themselves over the ash lens and displaced ash and charcoal with their anterior limbs, generating new ash patterning out of the original stone structure.

3.4. Experimental series 4: wolves (*Canis lupus*)

In Cabárceno the population of wolves is 12 individuals (5 males, 7 females). Like the other species, wolves had never been in contact with fire. The experiment began at 08:30 h, when the structure was constructed following the protocol (Fig. 1). This EH contained a fractured B. taurus femur, tibia and tarsus, 0.5 kg of wood, 0.1 kg of oak leaves and 0.55 kg of charcoal. The lithic artefacts displaced around the hearth as a hearth-related assemblage were a local limestone stone anvil, a flint (Bergeracois) biface, two flint flakes (one from Bergeracois and the other from Ebro Valley) and an ophite pebble used as a hammer stone (online Supplementary Fig. S1). The wolf enclosure was abandoned at 09:00 h.

The EH was alight for 57 min. The hearth burned out very quickly due to climatic conditions (wind and rain). During all the time the experiment lasted, the wolves displayed an interested attitude in the experimental hearth and the hearth-related assemblage but they never came into physical contact with it (see the Video Data 4 from supplementary material for more information on the ethological behaviour of wolves related to the EH modification process). Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.jas.2012.09.037.

The experiment lasted nine hours, and after that time the research team confirmed that wolves did not modify the hearth nor the hearth-related assemblage. The Veterinary Service of Cabarceno Nature Park pointed out that wolves are more active at night and we decided to leave the experimental scenario in the enclosure all night and return next morning at 08:30 h. Although this decision was not in accordance with the protocol, we thought that this extraordinary situation would not affect the results of the experiment if wolves modified the EH because we could still prove the capacity of these animals to modify anthropic spatial structures.

The MH was documented during the next day. The modification carried out by wolves was not high compared with the rest of carnivore taxa. The wolves experimental scene presented little changes (Fig. 2). The hearthstone circle was still visible, and just eight stones out of twelve had been displaced more than 5 cm. Inside the hearth an ash patch was still recognisable, but no charcoal was preserved. The hearth-related assemblage was not displaced greatly, despite the stone anvil being 15.5 m away from its original position (Online Supplementary Fig. S2). This large distance was probably influenced by the fact that there was a slope near the hearth and due to its round shape it was susceptible of rolling down this slope. This could have increased the action of wolves towards the displacement of this lithic element. Another interesting modification was the presence of wolf excrements over some hearthstones and others in clear relation with the EH. Inline supplementary Figure S2 can be found online at http://dx.doi.org/10.1016/j.jas.2012.09.037.

All the fresh bones burned in the EH were taken out of the hearthstone ring by the wolves. Some bone flakes where found near the EH, nevertheless other were located far away from the original zone. Bone remains were located distinctively in the highest zone of the enclosure and in the lowest zone, proving that the slope of the terrain did not influence these locations. The distances from the EH reached in some cases nearly 20 m.

4. Discussion

Experimental series indicates that large carnivores are taphonomic agents capable of modifying anthropogenic structured spaces. The example provided in our experimentation, how carnivores modify a hearth and its hearth-related assemblage, suggests that these animals are capable of erasing information at archaeological sites essential to infer behavioural patterns through the analysis of space. This is an important issue with the study of carnivore secondary access to anthropogenic assemblages.

Animals selected for the experiment, bears, hyenas, lions and wolves, modified the experimental anthropic scene to different degrees. All of them displaced or removed elements that form and allow us to identify a combustion structure such as burned bones, charcoal, ash, burned sediment or an association of structural stones. Regarding the stone ring, bears present a higher mean distance of general displacement (1.36 m), followed by hyenas (0.51 m), lions (0.47 m) and wolves (0.13 m). Differences between the way they modified the EH and its hearth-related assemblage are considerable between bears and all other carnivores because all associations of elements were erased. In the other cases, it is possible to recognise the ash and ash/charcoal lens in association with lithic artefacts or displaced structural stones. Nevertheless, if we consider the mean distances for hearthstones and hearthrelated assemblage separately (see Table 1 for data information), we observe clearly differences between carnivores (Fig. 3). Wolves modify hearth-related assemblage the less, followed by hyenas and lions that present similar values. Bears are the carnivores that most modified lithic assemblage. Concerning hearthstones distances similarities and differences, those are similar to the hearth-related values. Wolves present a high value in this case due to the influence of the slope in the movement of the round shaped stone anvil.

A common behaviour that was observed in bears, hyenas and lions, was that many animals interacted with the hearth, rubbed on the patch of charcoal and ashes. This contributed to the dispersal of some remains of charcoal and ash, but in the case of lions, this was not as notorious as in the case of bears or hyenas. In the present case, it was possible to recognise a well-defined charcoal lens and an adjacent ash lens as well as some other dispersed ash patches around.

Specific modifications can be quantified. For example, bears dug in a much intense way than hyenas and no evidence of ash or charcoal was present. While hyenas, lions and wolves did not erase the evidence of combustion traces such as the ash and charcoal lens, and the dispersion of structural stones and hearth-related assemblage was not so high as the one carried out by bears. Wolves were the only carnivores to defecate over the hearth, despite hyena coprolites being commonly found in archaeological hearth ashes (Bartram and Marean, 1999).

The lithic assemblage was scratched and gnawed by all carnivores. It is possible to observe scores in the surface of the lithic elements macroscopically when these are dirty with clay after the experimental series. We are still in the process of trying to characterize these carnivore modifications on the lithic assemblage with the help of silicon moulds and the 3D scanning technology developed before and after the experimentation. This part of the study is still underway and we hope diagnostic and more profound conclusions will be extracted in the near future.

Regarding the resulting spatial distribution, all carnivores followed a resultant centripetal dispersion pattern in different modification degrees and there are general observations on how carnivores modify structured hearths and hearth-related assemblages that can be isolated from other post-depositional agents such as root damage, watercourses, rain, wind (Barbetti, 1986; Mallol et al., 2007) or even anthropic actions like trampling (Sergant et al., 2006) or cleaning events (Dibble et al., 2009). Modifications developed by carnivores follow a centripetal dispersion pattern associated with other characteristic elements such as digging in the sediment or the presence of excrement.

The observations of our experimental series contribute towards the interpretation of carnivore secondary access to anthropogenic assemblages. Our experimentation highlights that carnivores are capable of modifying anthropic structured spaces and that there are elements in the archaeological record such as coprolites, carnivore bone remains and skeletal elements with evidence of carnivore activity (e.g., scores, punctures, gnawing or digested bones), that are clues to spatial taphonomic modification by these agents. In this sense, spatial analysis of artefact distribution considering carnivore activity will help explain taphonomic modifications that affect the interpretation of human behaviour.

5. Conclusions

The experiments presented here provided sufficient information to prove that large carnivores are capable of modifying spatial anthropic structures. Modifications caused by bears, hyenas, lions and wolves to our experimental assemblages are considerable and in some cases (e.g. bears and hyenas) it is difficult to reconstruct the original association between elements.

It has been proven that large extant carnivores have the capacity of modifying combustion structures and their associated assemblages. In this sense, it is possible to assume that non-human carnivores could also have been capable of modifying this kind of anthropic structures in the past. We know by different previous experimental studies that carnivores modify bone assemblages in different degrees (e.g., Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Domínguez-Rodrigo and Piqueras, 2003). In addition, the present paper proves the capacity of large carnivores to disturb anthropic spaces, and highlights the possibility that this scenario happened during the Pleistocene.

The fact that large carnivores modify and alter anthropic spatial structures, in the case of the experiments carried out involving hearths and hearth-related assemblages, proves that carnivores are capable of erasing certain associations of elements in space. In this sense, our results have archaeological implications because behavioural interpretations of archaeological contexts should be made bearing in mind that large carnivores may have been a taphonomic agent of spatial modification. This is important to approach the study of carnivore secondary access to anthropogenic contexts and a consequent potential loss of information that helps researchers to infer modern and complex human behaviour related to space and other cognitive processes.

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Acknowledgements

We would like to express our gratitude to S. Borragán (Chief of the Veterinary Service of Cabárceno) for his help in the development of all phases of the experiment. M. Prieto, also from Cabárceno has helped us in the animal enclosures. Thanks to Cabárceno Nature Park and Cantur, SA for understanding our necessity of experimenting in the Park. I. Pastó, C. García-Moncó, A. Teira and Á. Armendariz helped us in different steps of our research. We acknowledge the generosity of Tito Butcher's (Santander). J. Rosell works within the research projects CGL 2012-38434-C03-03 and CGL 2012-38358. R. Blasco works within the research project CGL2009-12703-C03, CGL2009-7896 and SGR2009 188. F. Rivals works within the research project HAR2010-19957.

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4.3.2.1

PUBLISHED SUPPLEMENTARY MATERIAL

PAPER 6

Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications

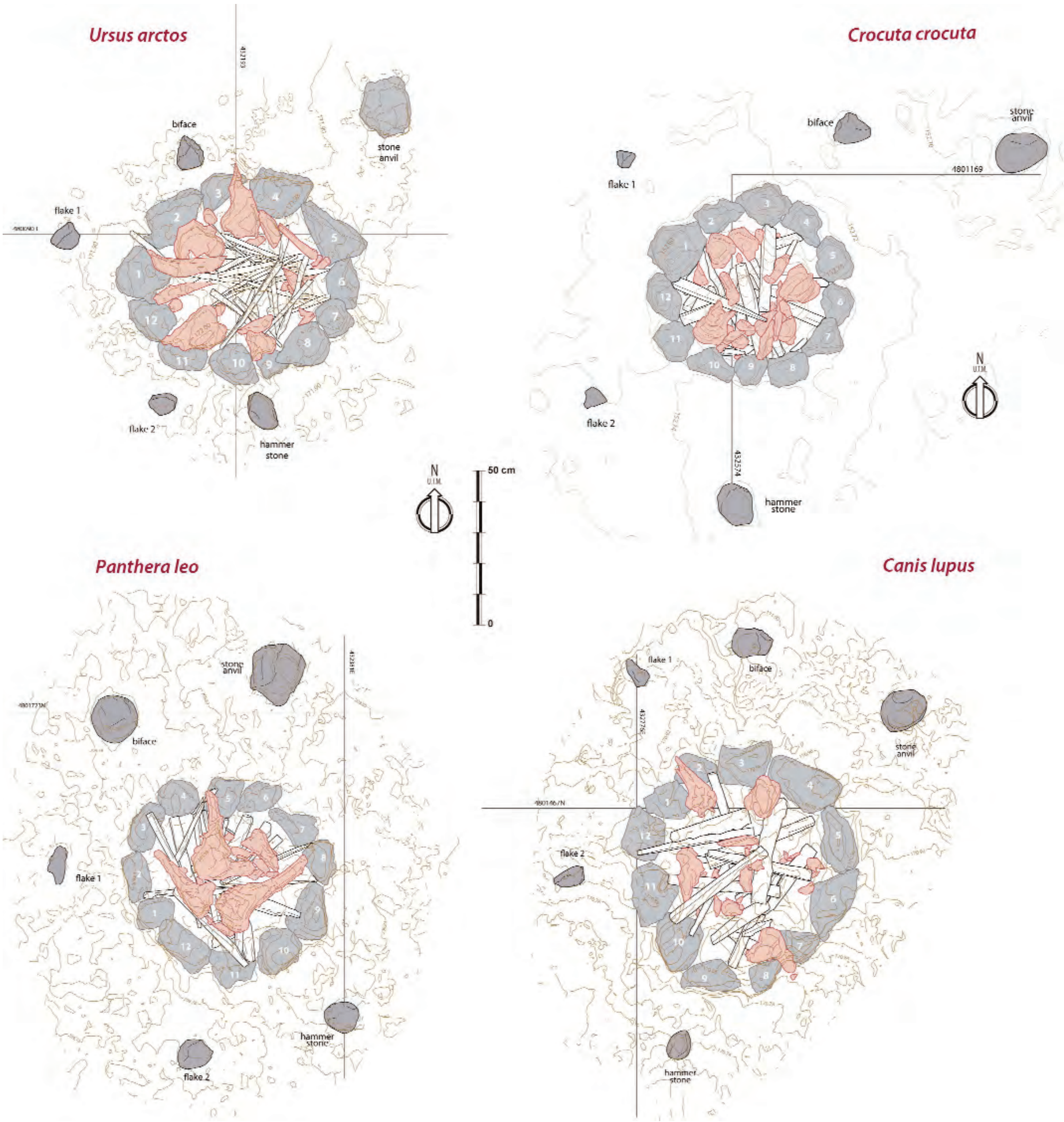

Figure S1

This figure, published as Online Supplementary Material represents previous experimental scenario before carnivores modify it. Original scenario can be compared with the modify it one published as Figure 2 in Paper 6.

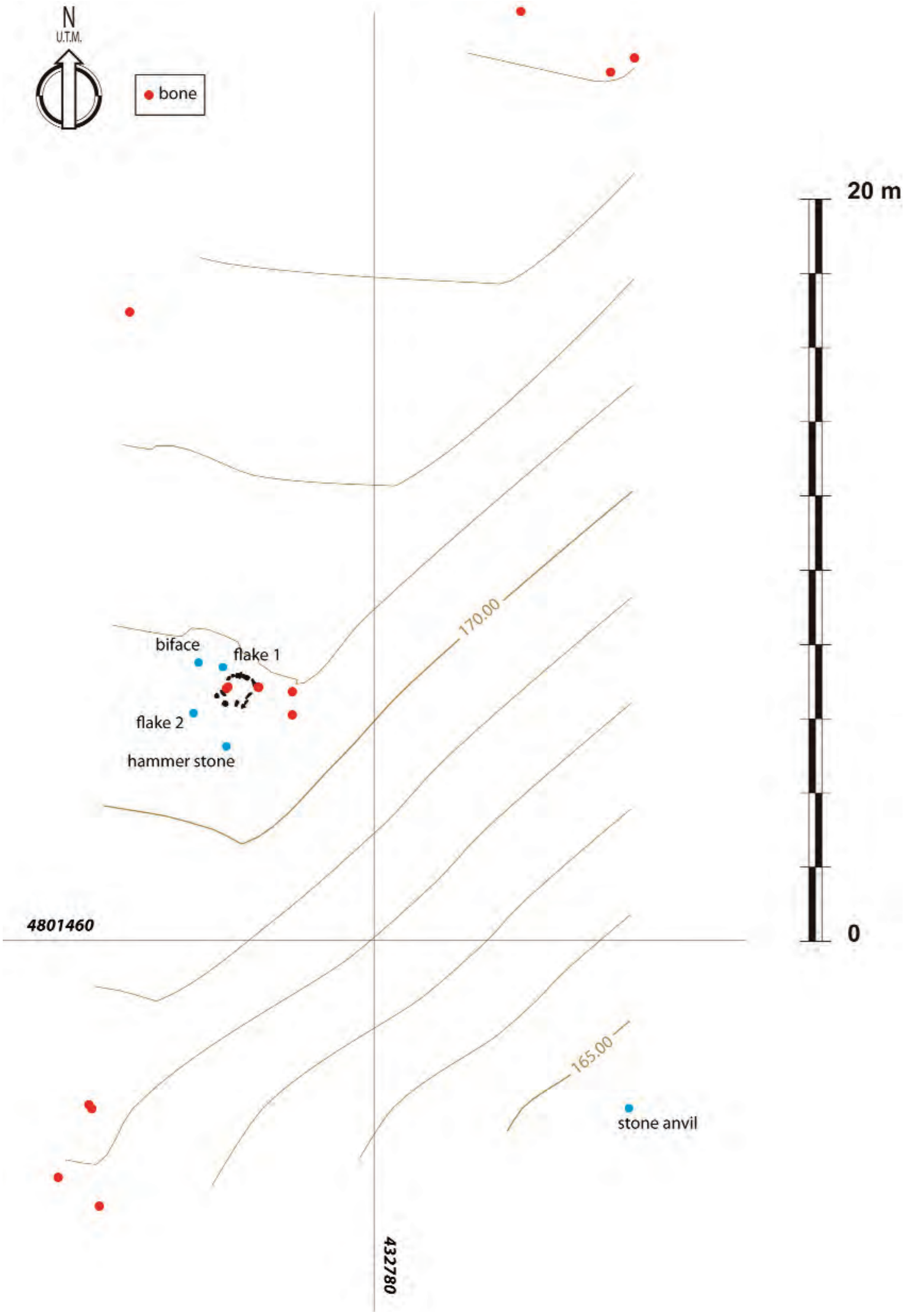

Figure S2

This figure represents general modification related with wolves experimental series 4. Detailed modified scenario has been published as Figure 2 in Paper 2.

Video S1

A video on Experimental Series 1-4 was attached to this paper as online supplementary material. The video can be downloaded from *Journal of Archaeological Science*, also available as a video archive inside Annex 2.

4.3.2.2

UNPUBLISHED SUPPLEMENTARY MATERIAL

PAPER 6

Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications

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HOMININ-CARNIVORE INTERACTION DURING THE PLEISTOCENE: DEVELOPMENT OF NEW METHODS FOR THE STUDY OF HUMAN BEHAVIOR THROUGH A TRANSDISCIPLINARY AND EVOLUTIONARY APPROACH
Edgard Camarós Pérez

Figure S3. Cow remains used.

Figure S4. Preparing the topographic work.

Figure S5. Entring the bears enclosure.

Figure S6. Experimental hearth.

Figure S7. Photogrametric works.

Figure S8. Experimental hearth combustioning.

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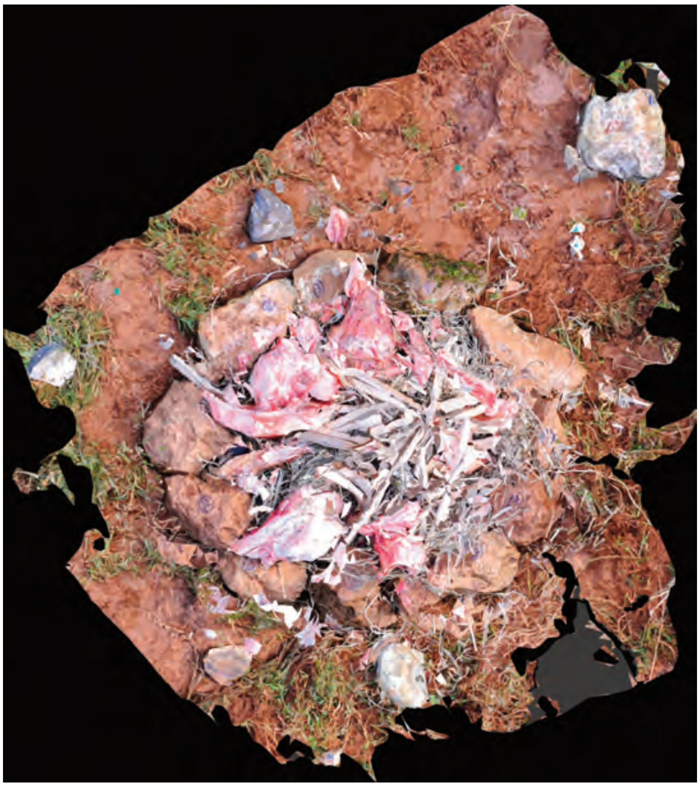

Figure S9. Initial bears experimental hearth with cow remains and wooden sticks. Orthoimage of the scenario used to build the data through photogrametry for planimentry (Image: L. Teira)

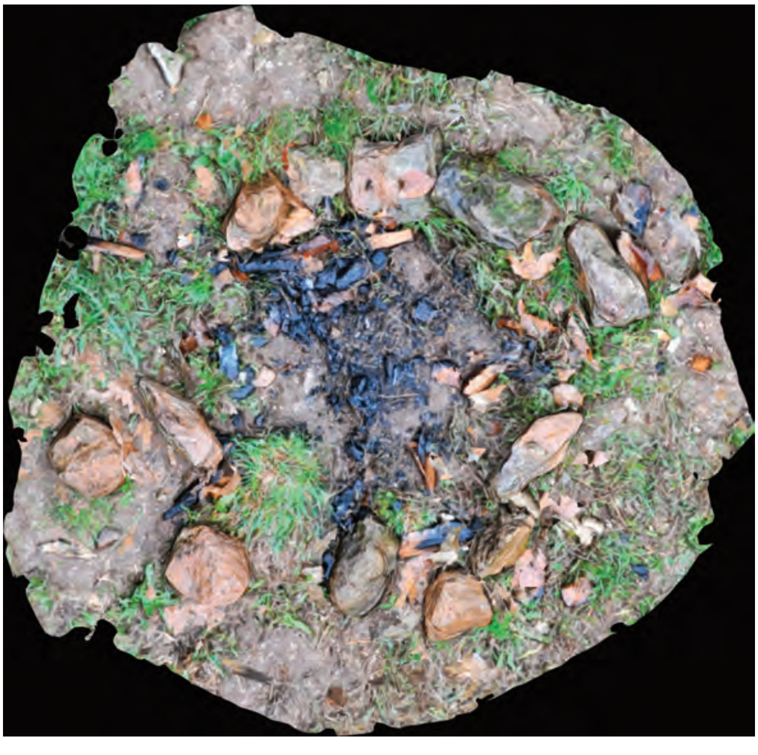

Figure S10. Final wolves experimental hearth with remaing materials. Orthoimage of the scenario used to build the data through photogrametry for planimentry (Image: L. Teira)

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CASE STUDIES OF HOMININ-CARNIVORE INTERACTION DURING THE PLEISTOCENE 4.4

PAPER 7

The evolution of Paleolithic hominin-carnivore interaction written in teeth: Stories from the Swabian Jura (Germany)

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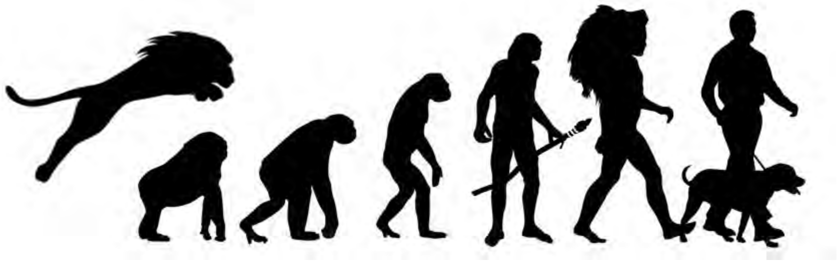
4.4.1

PAPER 7

The evolution of Paleolithic hominin-carnivore interaction written in teeth: Stories from the Swabian Jura (Germany)



Chapter 4.4 *Case studies of hominin-carnivore interaction during the Pleistocene*

Paper 7

The evolution of Paleolithic hominin-carnivore interaction written in teeth: Stories from the Swabian Jura (Germany)

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The interaction between hominins and carnivores during the Paleolithic is a highly dynamic, and the study of these relationships provides key insights into the evolution of human behavior. In this sense, the relations that hominins had with large carnivores can help us address topics that span from subsistence behavior to intra-site spatial organization. Usually, all these studies are developed by analyzing post-cranial faunal remains, including carnivore and non-carnivore anatomical elements. Teeth and activities related to teeth (e.g. bite marks) are additional elements that inform us about hominin-carnivore interactions. In the present paper, we analyze the changing forms of interaction between hominins and carnivores during the Paleolithic of the Swabian Jura (Germany) using carnivore tooth remains and carnivore bite marks. We observe that the relation between hominins and carnivores reflects a dynamic interaction from the Middle to the Upper Paleolithic that is documented trough tooth remains and bones with tooth marks from carnivores. The present multidisciplinary contribution analyzes teeth and tooth marks to understand site formation process, carnivore hunting, tool use, human recycling behavior, the role of ornaments made from carnivore teeth, and domestication process.

Keywords: Interaction, Carnivores, Tooth marks, Swabian Jura, Paleolithic

Journal of Archaeological Science: Reports (accepted)

1. Introduction

The evolving interaction between hominins and carnivores during the Paleolithic is a dynamic issue and its study provides a better understanding of human behavior and its changes through time (Rosell et al., 2012). In this regard, the relationship between humans and large carnivores can provide valuable information on aspects ranging from subsistence strategies to ritual practices (e.g., Stiner, 2012, Conard, 2003). Hominin-carnivore interaction studies are commonly conducted by analyzing post-cranial faunal remains, including carnivore and non-carnivore skeletal elements. However, teeth and their signatures, such as bite marks, also provide key insight into the interaction between hominins and carnivores.

The study of tooth-related characteristics can provide interesting insight into the behavioral patterns of hominins (e.g., Rivals et al., 2009, Saladié et al., 2013, 2015). This potential is related to the application of new methods or the advancement of existing methods that have contributed to improved knowledge of human paleoecology (e.g., Bocherens et al., 2014), subsistence (e.g., Tornero et al., 2013) and social behavior (e.g., Álvarez-Fernández, 2010). Furthermore, teeth are one of the most well-preserved faunal remains at archaeopaleontological sites (Hillson, 2005), and are involved in a wide range of the activities performed by hominin groups (Reitz and Wing, 2008).

In this paper, we analyze the changing interaction between hominins and carnivores during the Paleolithic in the Swabian Jura (Germany) from a transdisciplinary perspective, using carnivore tooth remains and tooth-related signatures. The aim is to provide a general overview of the relationship between hominins and carnivores and its evolution during the Middle and Upper Paleolithic (approx. 50-27 kyrs uncal BP) in this geographical area.

We address aspects such as the alternating use of space by hominins and carnivores, direct interaction, and the use of carnivores as a raw material or as prey. Furthermore, we look at factors related to the cultural significance of carnivores and even wolf domestication, one of the latest forms of hominin-carnivore interaction, using only tooth-related studies.

The Swabian Jura has preserved outstanding evidence for the study of how hominins interacted with carnivores (e.g., Münzel et al., 2011, Kitagawa et al., 2012), and tooth-related studies are crucial to approaching the evolution of such interactions in relation to hominin behavioral changes. Archaeological evidence points to a complex relationship in this singular area, and hominin-carnivore interaction is analyzed in order to establish its importance in relation to the cultural florescence that occurred at the beginning of the Upper Paleolithic (Conard, 2003), as it seems this interaction had a substantial effect on modern behavior.

2. Materials and methods

We used different tooth-related materials to analyze the interaction between hominins and carnivores during the Paleolithic in the Swabian Jura (approx. 50-27 kyrs uncal BP). The materials analyzed do not consist solely of tooth remains, but also include bone remains bearing tooth marks on their surfaces. The bone remains studied are from herbivorous animals, but also from large carnivores and hominins.

The primary faunal collection analyzed was that from Hohle Fels (HF), although other sites were involved in the search for specific scenarios of hominin-carnivore interaction, such as Geißenklösterle (GK), Vogelherd (VH) and Hohlenstein Stadel (HS). All of the sites are located in the Swabian Jura, the largest karst system in southwestern Germany, in both main valleys, the Ach and the Lone (Fig. 1). All of the sites considered have been the subject of previous works and they are well dated and chronologically ascribed (Conard and Bolus, 2003, 2008). Table 1 summarizes the most relevant archaeological characteristics of the sites analyzed and main bibliographical references in relation to hominin-carnivore interaction.

All of the materials analyzed were approached from a taphonomic perspective, and both anthropic and non-anthropic marks were studied through the generation of high-resolution silicon casts. The aim was to better observe all of the marks on the surface by illuminating the cast from underneath (Fig. 2). This method is a useful and economical alternative in the taphonomic study of bone surfaces, and it has been used in previous studies of tooth microwear (e.g., Semprebon et al., 2004).

The benefits of this method have been previously described for the study of tooth microwear in ungulates and carnivores (e.g., Rivals, 2015) and primates (Solounias and Semprebon, 2002). Nevertheless, this is the first time that this method has been applied to the study of bone surfaces and tooth taphonomy beyond paleoecological approaches, although it has been described in detail (Camarós et al., submitted).

Figure 1. Archaeological sites form the Swabian Jura (Germany) considered and cited in the study (Map: Landesmuseum Baden-Württemberg).

Taxa and modifications	GK				HF				VH		HS	
	MP	AUR	GRA	MAG	MP	AUR	GRA/AUR	GRA	MP	AUR	MP	AUR
U. spelaeus/U. arctos	586(1,3)	2972(1,3)	1419(1,3)	28(3)	534(1,4)	1021(1,4)	946(1)	2273(1)	27(4)	122(4)	4069(4)	1935(4)
Butchering	7(4)	10(4)	x(1) 15(4)	-	x(2), 5(4)	38(4)	x(3)	152(4)	-	-	-	2(4)
Tooth pendant	-	-	x(1)	-	-	-	x(5)	x(1)	-	-	-	-
Tools	-	-	-	-	-	x(6)	-	x(1)	-	x(6)	-	-
Canis lupus	39(1) 19(3)	160(1) 91(3)	30(1), 14(3)	-	7(1), 5(4)	44(1) 25(4)	11(1)	54(1) 34(4)	8(4)	38(4)	240(4)	157(4)
Butchering	1(4)	1(4)	-	-	1(4)	4(4)	-	3(4)	-	-	-	-
Tooth pendant	-	-	x(1)	-	-	-	-	x(1)	-	-	-	-
V. vulpes/ A. lagopus	26(1,3)	159(1)	109(1)	28(3)	4(1)	34(1,4)	14(1)	73(1,4)	-	20(4)	-	97(4)
Butchering	-	-	7(4)	-	-	1(4)	-	-	-	1(4)	-	-
Tooth pendant	-	x(4)	x(5)	-	-	x(4)	x(5)	-	-	x(7)	-	4(4)
Crocuta spelaea	7(4)	13(4)	-	1(3,4)	1(4)	5(4)	-	2(4)	10(4)	17(4)	476(4)	44(4)
Tooth pendant	-	-	x(1)	-	-	-	-	-	-	-	-	-
Tools	-	-	-	-	-	-	-	1(4)	-	x(6)	-	-
Panthera leo spelaea	4(3)	1(3)	1(3)	-	1(4)	9(4)	-	6(4)	2(4)	4(4)	80(4)	15(4)
Butchering	-	-	-	-	-	-	-	5(4)	-	-	-	-
Tools	-	-	-	-	-	x(4)	-	-	-	x(6)	-	-
Felis lynx	1(3)	2(3)	-	1(3)	-	-	-	-	-	-	-	-
Butchering	-	-	-	-	-	-	x	-	-	-	-	-
***Felis* sp.**	-	-	-	23(3)	-	-	-	-	-	-	-	-
Indet small carnivore	-	13(3)	4(3)	2(3)	-	-	-	-	-	-	-	-
Indet large carnivore	7(3)	36(3)	7(3)	-	-	-	-	-	-	-	-	-

Table 1. NISP of carnivore remains from archaeological sites and layers from the Swabian Jura and main anthropic modifications. GK: Geißenklösterle; HF: Hohle Fels; VH: Vogelherd; HS: Hohlenstein Stadel. MP: Middle Paleolithic; AUR: Aurignacian; GRA: Gravettian; MAG: Magdalenian. (1) Barth et al. (2006); (2) Münzel et al. (2004a); (3) Münzel et al. (2004b); (4) Kitagawa et al. (2012); (5) Conard and Bolus (2003); (6) Niven (2006); (7) Floss (2007).

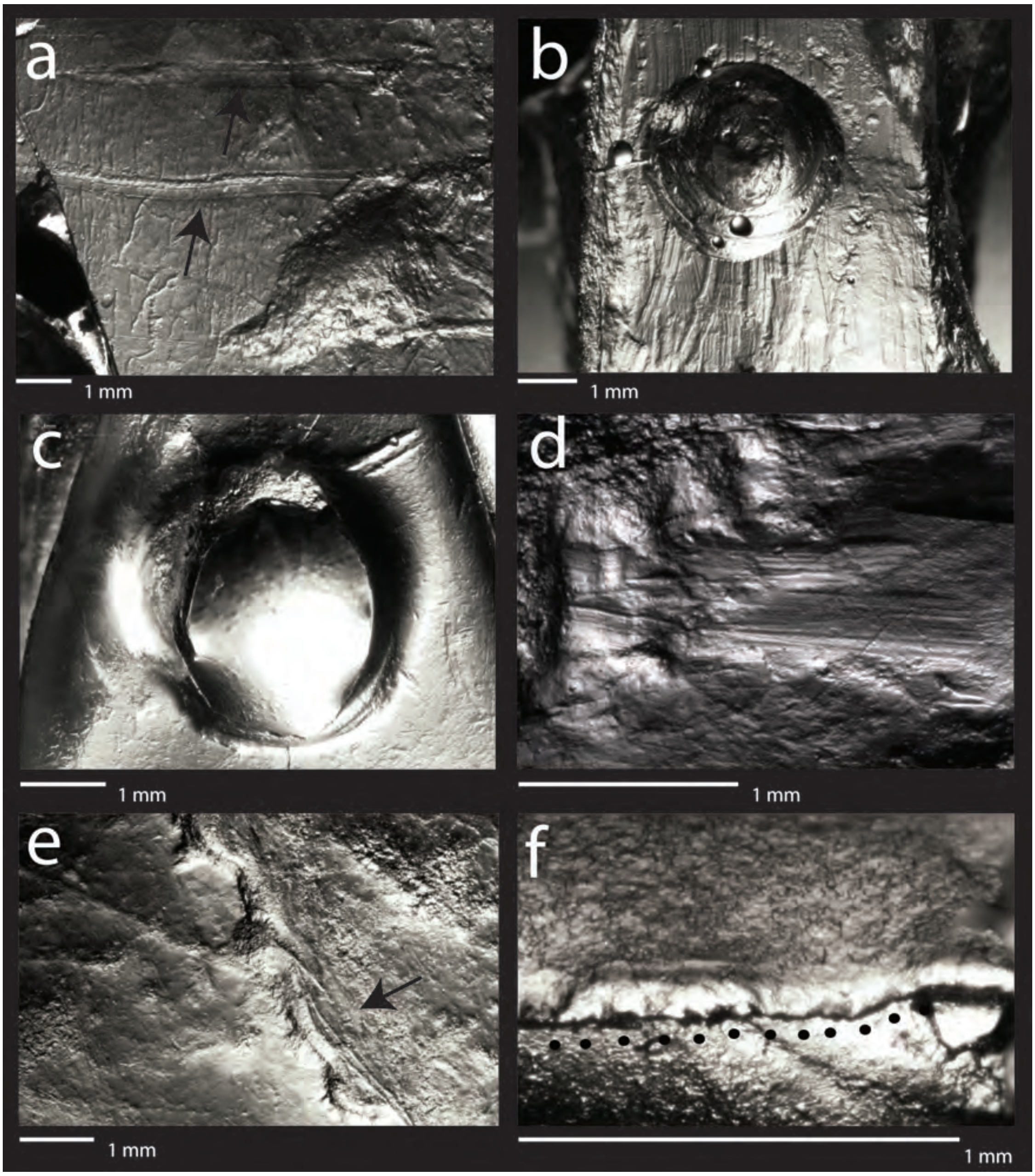

Figure 2. Different examples of high-resolution silicon casts from HF: a) Hominin toothmarks on fox bone; b) Non-finished pendant on bear incisor; c) Pendant on fox canine (detail from Figure 7f); d) Lithic score from a retoucher made on cave bear canine (detail from Figure7d); e) Score beneath a fracture on a cave bear canine retoucher (detail from Figure 7d) and f) Polished surface evidencing use wear traces on a flake of a bear canine (detail from Figure 6c).

3. Results

3.1 Direct interaction

The Swabian Jura is not an area with abundant fossil hominin bones, although some evidence has been recovered from Hohlenstein Stadel, Vogelherd, Sirgenstein, Geißenklösterle and Hohle Fels (see Conard and Bolus, 2003). The cave of Hohlenstein Stadel is the only site at which not only Neanderthal hominin remains have been recovered (Orschiedt, 1999, Street et al., 2006) (Figure 3.1), but also anatomically modern human (AMH) remains dating from the Upper Paleolithic, Mesolithic and Neolithic (Orchiedt, 1998, 1999, Rigaud et al., 2014) (Figs. 3.2 and 3.3).

One of the noteworthy features of some of the specimens recovered from Hohlenstein Stadel is the fact that they exhibit carnivore tooth marks on the bone surface. This evidence reveals a direct interaction between hominins and carnivores. Taphonomic studies have not been able to reveal the nature of this direct interaction and therefore give rise to several different scenarios.

The Neanderthal remain exhibiting carnivore damage consists of an adult male diaphysis of a right femur, unearthed in the archaeological horizon of the *Schwarzes Moustérien* (Völzing, 1938; Kunter and Wahl, 1992). This Neanderthal bone, the only one recovered in the Swabian Jura (Street et al., 2006), presents the typical morphology of a diaphyseal cylinder shaped by intense carnivore chewing (Figure 3.1). Both epiphyses have been consumed and the entire bone surface is covered with pits of a considerable size, according to Domínguez-Rodrigo and Piqueras (2003) and Andrés and colleagues (2012). All these features are related to the activity of a large carnivore such as a hyena or canid (Fosse et al., 2012, Binford, 1981). Both carnivore species have been identified in Middle Paleolithic layers at Hohlenstein Stadel (Kitagawa et al., 2012).

Anatomically modern human remains from the Neolithic *Knochentrümmerstätte* also exhibit carnivore damage on the surface of some of the specimens (Orschiedt, 1998, 1999) (Figs. 3.2 and 3.3). The damage is mainly associated with furrowing and small to medium-size carnivores (Orschiedt, 1998, 1999).

Although the presence of carnivore activity on the surface of hominin bones clearly testifies the direct interaction, it is quite difficult to infer the type of scenario that originated the damage. It is obvious that carnivores modified the bones postmortem, but it is difficult to determine whether the hominins were eaten after death and/or burial or, on the contrary,

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whether they were eaten after a carnivore attack. Both scenarios are highly interesting and have important implications with regard to behavioral interpretations. In the case of the Neanderthal specimen, it is impossible to prove whether the corpse was just scavenged, or whether the individual was hunted by a large carnivore, as has been suggested in other cases with other Neanderthal fossils (Camarós et al., 2015). On the other hand, the Neolithic AMHs were probably modified post-mortem by a small carnivore after having been buried (Orschiedt, 1998, 1999). Previously buried human remains with evidence of carnivore modifications are not uncommon (e.g., Colard et al., 2014, Horwitz and Smith, 1988).

3.2 Alternating use of caves

During the Paleolithic, humans and carnivores alternated in using caves and rockshelters for different purposes (Blasco and Rosell, 2009, Costamagno et al., 2005, Yravedra and Cobos, 2014). In the Swabian Jura, this alternating use of space is reflected in the archaeopaleontological record, as both archaeological and strictly paleontological evidence can be found in almost all Swabian cave stratigraphies. This reveals a scenario of the alternating use of caves between hominins and different carnivores during the Paleolithic (e.g. Conard, 2011).

Different carnivores used Swabian cave sites to carry out their activities. For example, fetal remains point to the use of sites like Hohle Fels and Geiβenklösterle as dens for hyenas and cave bears during winter (Münzel and Conard, 2004, Kitagawa et al., 2012). This activity (among others such as prey transportation to caves) has given rise to assemblages in which the entire surface of the bones is covered with evidence of chewing by those carnivores. The presence of carnivore modifications on bones is reflected in furrowing, digestion traces, pitting, and scores, in addition to puncture marks. The study of the pits may reveal important information on the type of carnivore that occupied the cave.

We measured the carnivore pits (length and breadth) present on the bone surfaces of different ungulate species from the Hohle Fels archaeological horizons, using same criteria as Domínguez-Rodrigo and Piqueras (2003) and Sala et al. (2014). Our aim was to document and characterize the type of carnivore responsible for the modification to the faunal assemblage during each period and to determine whether there were any visible differences. Our results suggest that, within the bone assemblage analyzed, large carnivores were responsible for the pits present on the bone surfaces during the Middle Paleolithic, large to medium-sized carnivores generated the tooth marks during the Aurignacian/Gravettian, and only small carnivores were active during the Magdalenian (Fig. 4).

Figure 3. Hominin bones with evidence of carnivore activity: 1) Neanderthal femur from HS with both ends chewed and detail of proximal zone with pit marks (Archaeological Horizon *Schwarzes Moustérien*) and 2-3) AMH bones from HS (*Knochentrümmerstätte,* Neolithic) (after Orschiedt, 1999).

These results illustrate a clear decrease in the size of the carnivores responsible for the pits, meaning that from the Middle to the Upper Paleolithic different carnivores alternatingly occupied Hohle-Fels. Large carnivores such as cave bears, lions and hyenas are associated with ancient chronologies, and small carnivores like foxes are mostly associated with early Paleolithic chronologies.

This observation is consistent with the pattern observed in many Swabian caves, except for Hohlenstein Stadel, where a decrease in the NISP and %NISP of large to medium-sized carnivores was documented from the Middle Paleolithic to the Gravettian (Kitagawa et al., 2012), while an increase in small carnivores (as well as ungulates and hares) was recorded during this period (Kitagawa et al., 2012).

There is therefore an inverse correlation between the intensified anthropic use of caves during the Upper Paleolithic and the decrease in large to medium-sized carnivore remains at Swabian sites (Conard, 2011, Conard et al., 2006, 2012). This could be explained by an increase in large carnivore hunting activities (e.g. Münzel and Conard, 2004a, 2004b). The result of such hominin activities was that carnivore remains or evidence of carnivore activities (such as bite marks) decreased from the Middle to the Upper Paleolithic. Some clear cases of this phenomenon are the hyena, lion (Kitagawa et al., 2012) and cave bear populations (Münzel and Conard, 2004, Münzel et al., 2011).

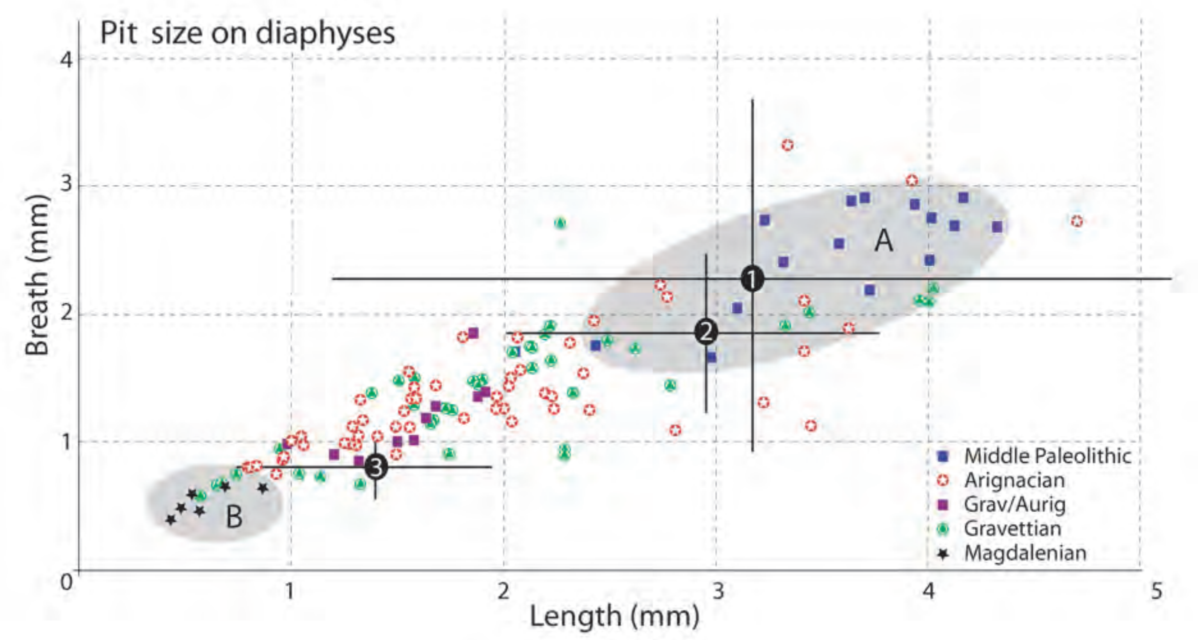

Figure 4. Pits measurements on bone surfaces from HF different Archaeological Horizons (e.g. A: Middle Paleolithic and B: Magdalenian) overlapped with actualistic measurements of carnivore tooth marks provided by Domínguez-Rodrigo and Piqueras (2003): 1 (hyenas), 2 (bears) for large sized animals and Delaney-Rivera et al. (2009): 3 (dogs) for medium sized animals.

3.3 Recycling activities

Bears commonly break their teeth, primarily their canines (Sonne et al., 2007) (Fig. 5b), mainly due to intense male-to-male competition (Ramsay and Stirling, 1986) and other ecological stresses, as seen in other large carnivores (e.g., Rothschild and Diedrich, 2012). In Hohle Fels, many of these broken canines have been found in both Middle and Upper Paleolithic horizons (NR=51) (Figs. 5 and 6). According to their breakage pattern, they are naturally exfoliated teeth associated with dental development and bear ethology. The non-anthropic tooth breakage pattern is always the same (Figs. 6a), although there is variability in size (Fig. 5) and morphology (Fig. 6c compared to 6a).

Interestingly, these naturally broken canines from Hohle Fels were subjected to recycling activities by Upper Paleolithic hominins. In archaeological horizon IIc, dated between 26 kyr and 29 kyr (Hahn, 1995, Housley et al. 1997, Conard and Bolus, 2008), several naturally broken bear canines appear to have been used for different purposes (Fig. 6c-f). Two canine flakes (Fig. 5c-d) present consistent evidence of use wear on their sharp edge (Fig. 2f), and two others (Fig. 6e-f) exhibit evidence of anthropic modification to produce ornamental objects with different suspension techniques, present also in other materials (e.g., Conard and Bolus, 2003).

These kinds of materials provide clear evidence of recycling activities during the Upper Paleolithic, in a context of the alternating use of caves by hominins and carnivores. They prove that hominins gathered, transformed and used carnivore teeth found at the cave as cutting tools or ornaments.

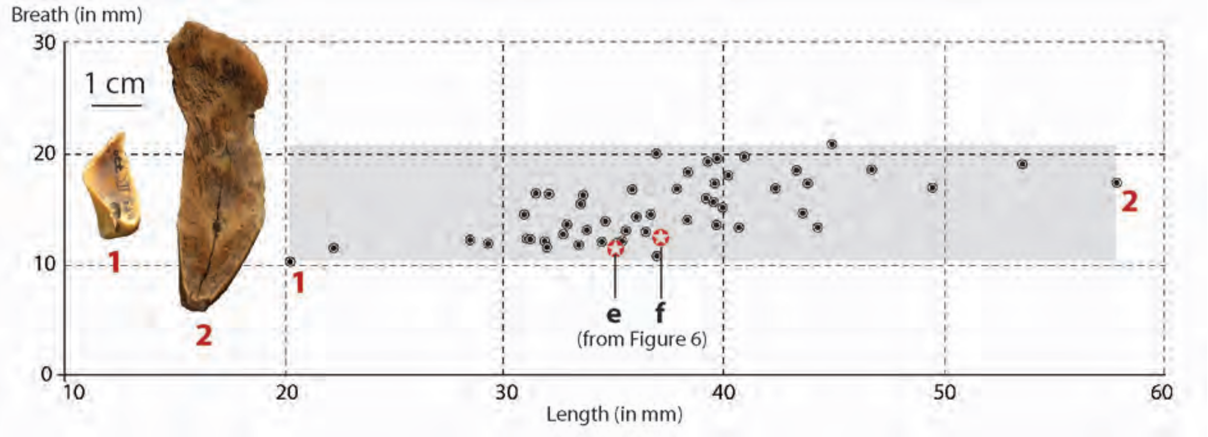

Figure 5. Size of all flakes of naturally broken canines from HF, and the ones re-cycled as ornaments (e and f from Fig. 6).

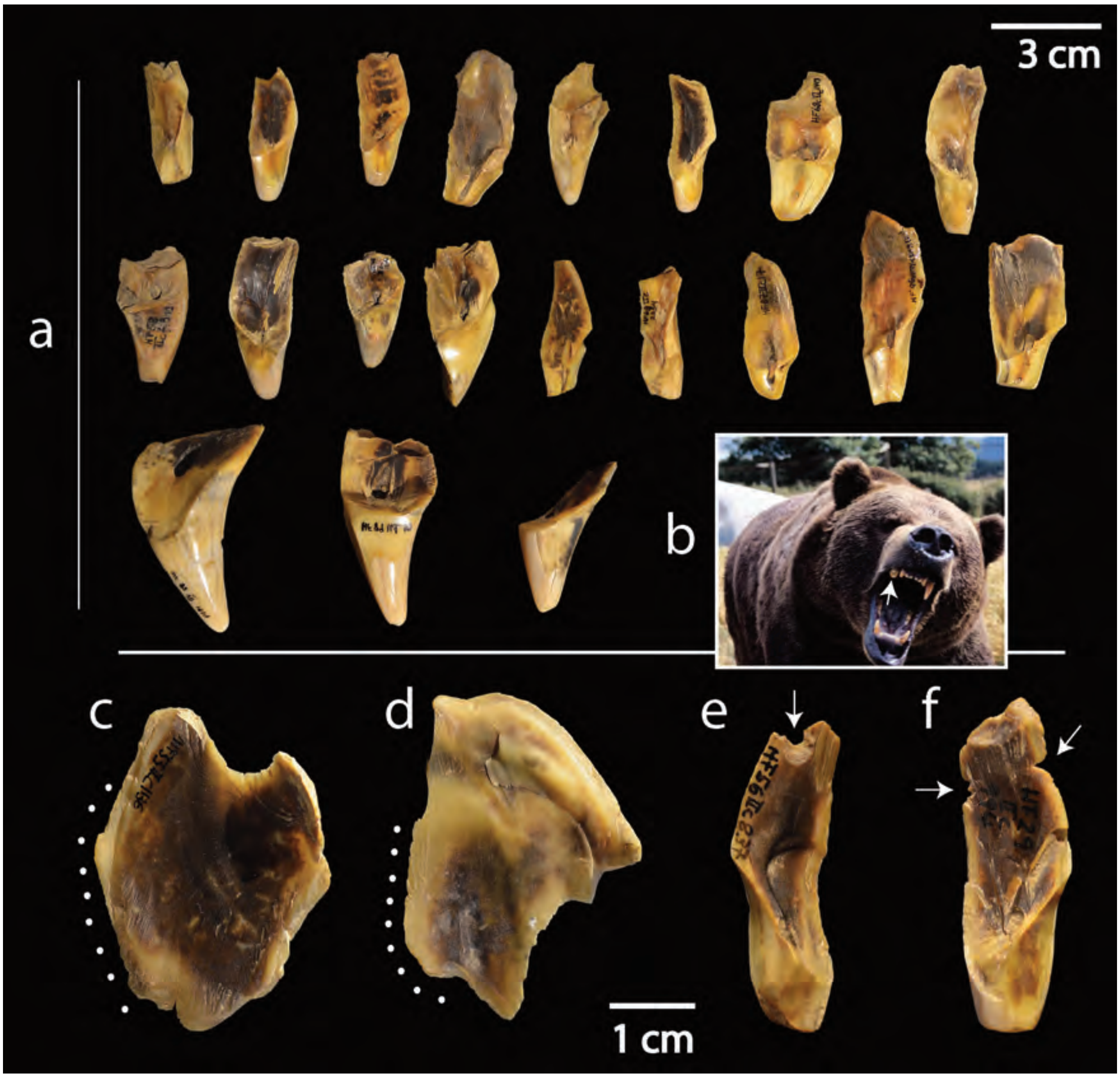

Figure 6. Cave bear flakes from HF: a) Naturally broken canines with different size; b) Brown bear with a broken canine; c-d) Cave bear canine flakes used as tools (see Figure 2f for detail of c) and e-f) Naturally broken canines modified to be used as ornaments.

3.4 Carnivore exploitation

The Swabian Jura is an outstanding zone for the study of Paleolithic carnivore hunting and consumption. Several sites have provided direct evidence of cave bear hunting during the Upper Paleolithic, such as Hohle Fels (Münzel and Conard, 2004). However, there is also tentative evidence of carnivore hunting during the Middle Paleolithic (Kitagawa et al., 2012).

Upper Paleolithic carnivore hunting is related to the use of hides and the consumption of meat, primarily inferred through cut marks on bones (Münzel and Conard, 2004a, 2004b) (e.g., Fig. 7c), but also through evidence of tool and ornament production (e.g., Kitagawa et al., 2012, Conard and Bolus, 2003, 2008). The species hunted were mainly cave bears (*Ursus spelaeus*), lions (*Panthera leo spelaea*) and hyenas (*Crocuta crocuta spelaea*). Cave bear exploitation in the Swabian Jura is especially interesting; many bones have been found with cut marks related to disarticulation and defleshing activities, and a vertebra with a flint projectile embedded in it has even been recovered, dating to 28,000 uncal BP (Münzel and Conard, 2004, Kitagawa et al., 2012). Evidence of winter cave bear hunting during dormancy has also been found (idem.). Cave bear hunting increased during the Gravettian (Wojtal et al. 2014) and some hypotheses suggest a probable link between the hominin predation of bears and their ultimate extinction before the Magdalenian period (Münzel et al., 2011).

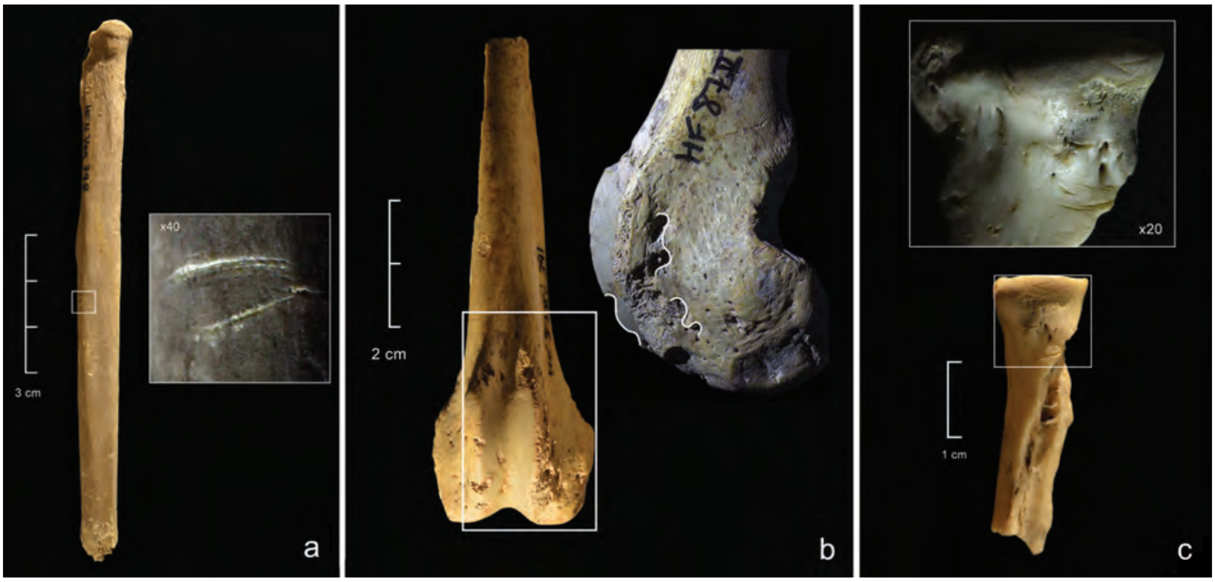

Figure 7. Carnivore bones with different marks from HF. a) Fox radius with human scores on the bone surface (AH Vaa); b) Fox femur with continuous punctures and pits on the diaphysis (AH Vc) and c) Lynx radius with cut marks and impact mark (AH IIb).

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This is a good example of how carnivore hunting and general consumption intensified all throughout the Upper Paleolithic, and provides clear evidence of increasing pressures between hominins and carnivores in the Swabian Jura.

Our contribution is related to small carnivore exploitation. We examined several tooth marks on fox (*Vulpes vulpes*) bone surfaces from the Aurignacian and Gravettian Hohle Fels archaeological horizons (NR 10) (Fig. 7a-b). The marks on the bones present a morphology described by several authors (Fernández-Jalvo and Andrews, 2011, Saladié et al., 2013 among others) as resulting from human biting on at least three bones, and consist of scores with flaking (Figs. 2a and 7a) and double punctures with a characteristic double arch morphology (Fig. 7b).

Therefore, during the Paleolithic, not only were large carnivores hunted and consumed in many ways, small carnivores like foxes or lynxes (e.g., Fig. 7c) were also obtained by means of hunting or other techniques (such as traps) during the Upper Paleolithic. This is an example of another form of interaction between hominins and carnivores in the Swabian Jura.

However, hunting to obtain meat or fur is not the only way hominins used carnivores during the Upper Paleolithic in this area.

3.5 Tools, ornaments and sculptures: beyond exploitation

Carnivores were also used as a raw material for the production of tools and ornaments in the Swabian Jura. Furthermore, carnivores played an important role in Paleolithic production, with great cultural significance (Conard, 2003). In fact, this is an exceptional area in which this use of carnivores and its social significance was developed during the Upper Paleolithic.

The importance of carnivores during the Upper Paleolithic in the Swabian Jura emerged during the Aurignacian and continued through the Gravettian, although in a different form (Kitagawa et al., 2012).

During the Aurignacian, carnivores were used recurrently as motifs in the cultural repertoire. Mammoths tusks (in essence teeth), were worked to produce ivory figurines. Evidence of these figures has been found in different caves along the Ach and Lone Valleys (Conard and Bolus, 2003, 2008) and ivory has been suggested as playing a crucial role as a medium for symbolic expression (Conard, 2003, Conard et al., 2006, 2009). The Aurignacian sculptures from the Swabian Jura belong to one of the oldest traditions of figurative art known in the

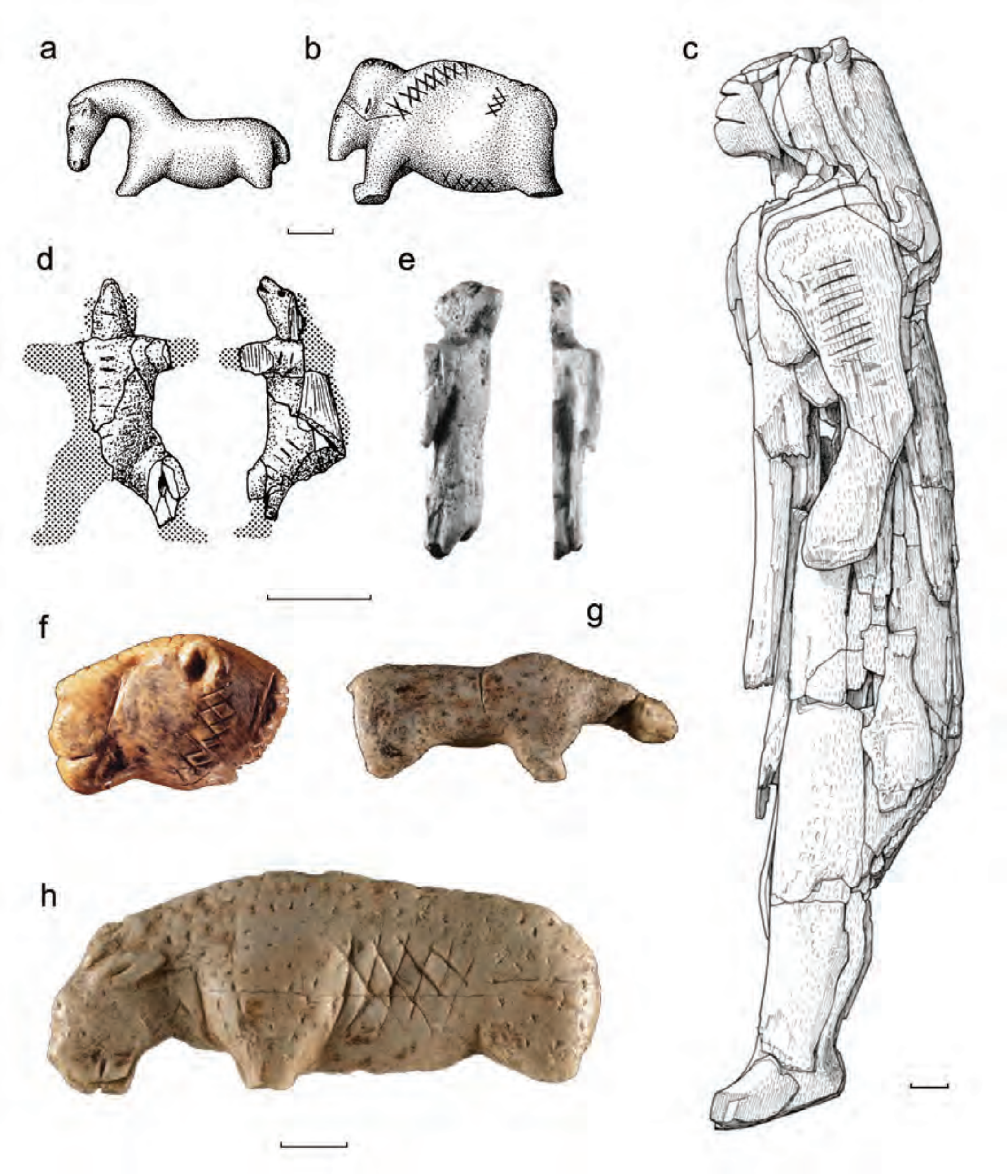

Figure 8. Ivory figurines: a) Horse from VH (IV); b) Mammoth from VH (IV); c) Newly reffitted *Löwenmensch* from HS (Kind et al., 2014); d) Cave bear from GK (AH II) (after Hahn, 1977, 1986, Conard and Bolus, 2003); e) Therianthrope with the characteristics of a felid and human from HF (after Conard, 2003); f) Cave lion head from VH (AH IV/V); g) Cave lion from VH (IV/V) and h) Cave lion from VH (IV/V) (e-h: Photos by H. Jensen, © University of Tübingen). Scale bars, 1 cm.

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world, dating more than 30 kyr (Conard, 2003). Although a wide range of animals were represented by the ivory figures found basically in Hohle Fels, Geiβenklösterle, Hohlenstein Stadel and Vogelherd (e.g., Fig. 8a-b), predators are well represented (e.g., Figs. 8c-h).

One of the most well-known ivory figures from the Swabian Jura is the one known as the 'lion man' (*Löwenmensch*), found in the Aurignacian levels dated to ca. 32 ka BP of Hohlenstein Stadel (Schmid, 1989, Conard and Bolus, 2003, Kind et al., 2014). It is an ivory sculpture of an anthropomorphic figure with the head of a lion (Fig. 8c). However, this is not the only figure representing this hominin-carnivore admixture (Fig. 8e). It seems clear that felids played an important role in the Swabian Jura Aurignacian culture, as they are well-represented (Conard, 2003). Most of them are concentrated in Vogelherd (Niven, 2006) (e.g., Fig. 8f-h).

Nevertheless, during the Aurignacian, carnivores also played an important role as raw materials. An example of this is how large carnivore canines from lions, hyenas as well and cave bears were used as retouchers (e.g., Taute, 1965, Niven, 2006) (Figs. 9a-d).

Bone retouchers are tools used to knap stones (Tartar, 2012). They are mainly made from the diaphyses of the long bones, and the use of carnivore bones is rare (Abrams, 2014). In the Swabian Jura, we have been able to identify several Aurignacian retouchers made of carnivore canines (Figs. 8a-d). The species used were cave lions, hyenas and cave bears. The marks on the surfaces of the teeth are the result of using the canines as soft hammers on lithic artifacts (Mallye et al., 2012). Pits and scores are present, as well as hatched, pitted and scalded areas (e.g., scores on Fig. 2d). The carnivore canines from the Swabian Jura have been intensively used, as there is evidence of breakage with use underneath the fractured area (Fig. 2e).

With regard to teeth worked to create pendants, there are also some examples of perforated fox teeth during the Aurignacian (Floss, 2007). Nevertheless, it is during the Gravettian that carnivore teeth played a significant role as a raw material to produce ornaments, and the practice was more common during this period compared to the Aurignacian (Kölbl and Conard, 2003, Pacher, 2005, Kitagawa et el., 2012). The carnivore teeth used were canines and incisors, and the species represented were mainly bears, foxes, wolves and rarely hyenas (e.g., Figs. 9e-j). The techniques employed to produce ornaments were diverse and include both perforation (Figs. 2b-c; 6e and 9e-j) and lateral incisions to facilitate suspension (Fig. 6f). The production process is well represented by unfinished products (Fig. 2b), which helps us to understand how the canines were perforated: a base was created in order to reduce the surface to subsequently perforate by means of curvilinear movements

Figure 9. Aurignacian retouchers (a-d) and Gravettian pendants (e-j) from the Swabian Jura: a) Vogelherd (cave lion canine); b) HF (cave lion canine); c) VH (cave lion canine); d) VH (cave bear canine); e) GK (fox canine); f) HF (fox canine); g) GK (fox canine); h-j) HF (cave bear incisor, wolf incisor, cave bear milk canine).

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(Fig. 2b). Intensive use has also been documented by means of polished surfaces (Fig. 2c) and broken suspension areas (Fig. 9e, g-j).

Therefore, teeth played an important role during the Upper Paleolithic in relation to both cultural expression and traditional ornament production in the Swabian Jura.

3.6 Early domestication process

One of the latest forms of interaction between humans and carnivores is domestication. Domestication represents one of the most important types of interaction due to its implications for hominin behavior. The domestication of wolves has been described as a veritable revolution in the history of humanity (Boudadi-Maligne, 2012). Wolves are known to be the first domesticated animals, although the chronology of that process is rife with controversy (e.g., Crockford and Kuzmin 2012, Germonpré et al., 2012); however it seems clear that the domestication process begun during the early Upper Paleolithic (Germonpré et al., 2009), possibly during the Gravettian (Germonpré et al., 2012, 2013).

Domestication is a process that generated clear changes in the size and morphology of the bones of biological wolf populations (Morey, 2010). Nevertheless, during the early stages of domestication, distinguishing wolves (*Canis lupus*) from domestic dogs (*Canis familiaris*) is not easy from either archaeozoological or genetic studies. Attempting to differentiate diet composition between domestic dogs and wild wolves through isotopic composition (e.g., Guiry, 2012, Bocherens et al., 2015) is also a challenge. Therefore, finding evidence of the domestication process is not an easy task (Boudadi-Maligne, 2012).).

To date, the archaeological evidence of wolf domestication nearest to the Swabian Jura is that yielded by the Magdalenian site of Kesslerloch Cave (Switzerland) (Napierala and Uerpmann, 2012). Evidence of the domestication process was recovered there through the study of a maxillary fragment directly dated between 12 and 14 kyr uncal BP (ídem). In Hohle Fels, a canid maxillary fragment has also been found in the Gravettian Archaeological Horizon IIb (Fig. 10). What is interesting about this bone is that although the size of the molars matches those from a wolf population (Fig. 11), the dental morphology is much more similar to that exhibited in domestic dogs (Fig. 10). Some morphological features differ from those of wolves and more closely resemble those of dogs, especially when compared with the Kesslerloch specimen.

Specifically, the P4 protocone is located farther back distally and orientated differently from those in wolves, which are orientated toward the mesial side of the tooth, as de-

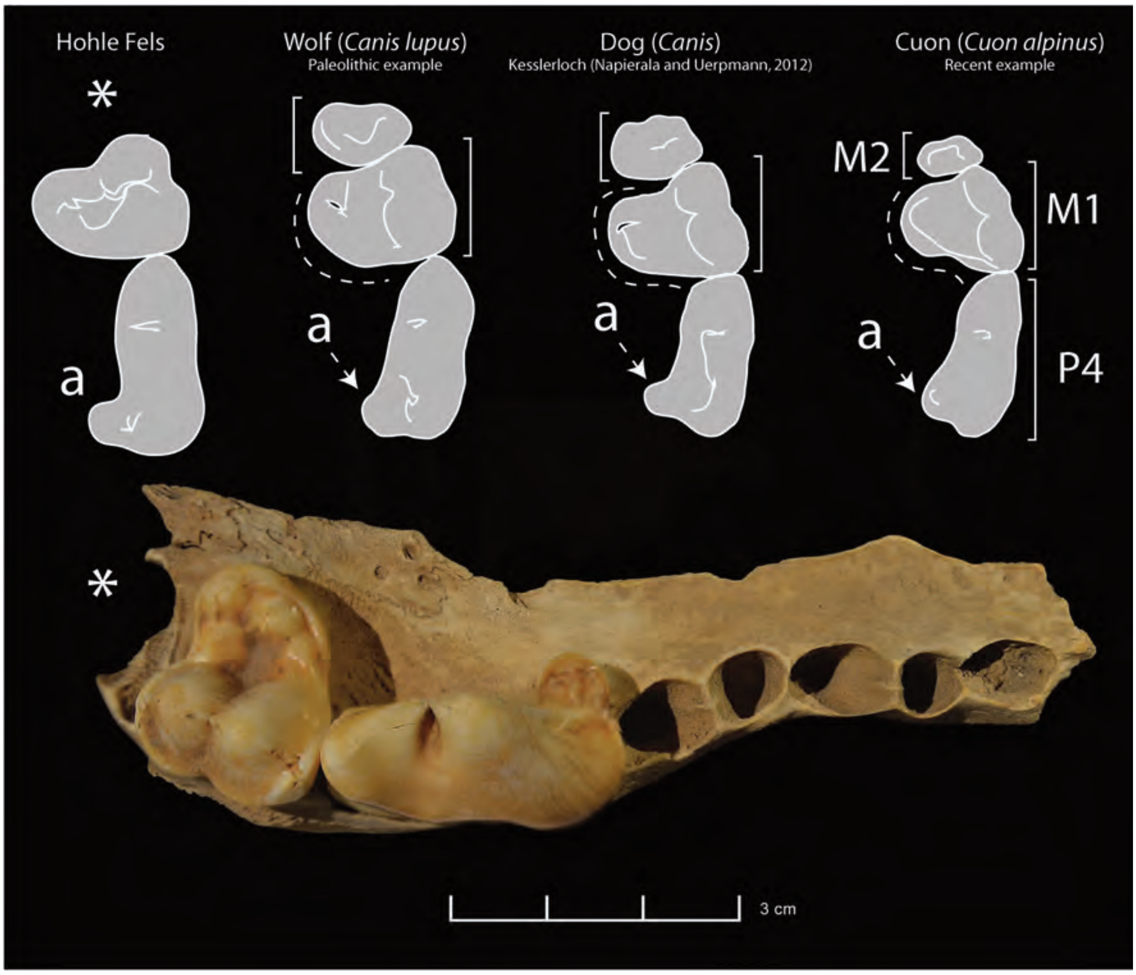

Figure 10. HF M1 and P4 specimens compared with wolf, Kesslerloch dog and cuon teeth morphology (examples obtained after Napierala and Uerpmann, 2012). a) Protocone.

scribed by Napierala and Uerpmann (2012). There are also some wolf morphological characteristics present in the M1, whose shape is also similar to the one from Kesslerloch.

Overall, the morphological dental features present in the Hohle Fels specimen are a mixture of wolf and dog. The specimen is very similar in morphology but not in size to the specimen form Switzerland. This morphological admixture may suggest the wolf domestication process in the Aurignacian period, and the size reveals how similar in some aspects a wild wolf can be to an early-domesticated dog.

Although a single fragment represents little evidence to confirm an Early Upper Paleolithic domestication process at Hohle Fels, it is a first step towards opening our research to new perspectives related to hominin-carnivore interaction.

Hohle Fels is not the only cave site from the Swabian Jura that has potential data for inclusion in the early wolf domestication process debate. In Geiβenklösterle, a single carnassial has been found in geological horizon 17 (dated between the Middle Paleolithic and the Aurignacian), and according to Napierala and Uerpmann (2012), its length and breadth match those from Kesslerloch as well as others provided by Germonpré and colleagues (2009).

Therefore, the Swabian Jura appears to be an area to consider in the analysis of the domestication process. Furthermore, confirming the domestication of wolves during the Aurignacian in this particular area represents further proof of modern and complex behavior during the Early Paleolithic in addition to other Swabian evidence of prehistoric innovation.

4. Discussion

The Swabian Jura is an outstanding area for the study of the interaction between hominins and carnivores. Several sites preserve singular evidence of a constant but changing relation throughout the Paleolithic. Therefore, this area appears to be an excellent place to analyze this evolving interaction, and especially to infer its role in the evolution of complex and modern hominin behavior.

Our contribution to the study of hominin-carnivore interaction is related to the analysis of teeth and their marks on bones. Nevertheless, our results are consistent with previous archaeozoological research and provide new insight into how hominins interacted with carnivores in many different ways during the Paleolithic.

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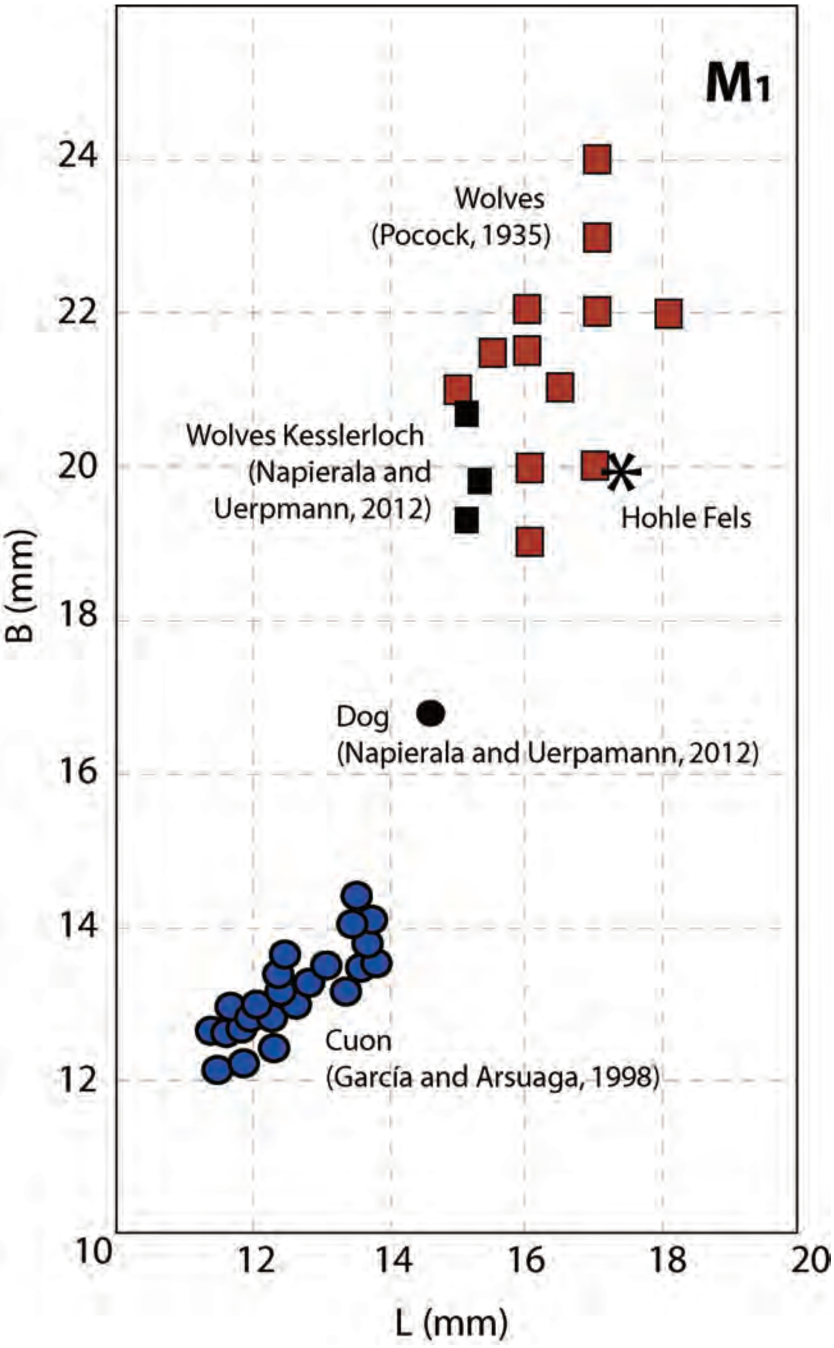

Figure 11. M1 measurements (Length and Breath) from the HF specimen compared with same measurements from wolves (Pocock, 1935, Napierala and Uerpmann, 2012), a dog from Kesslerloch (Napierala and Uerpmann, 2012) and Cuons (García and Arsuaga, 1998)

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The first contribution presented in this paper is related to the study of direct interaction between hominins and carnivores during the Middle Paleolithic. The direct interaction considered here is reflected in hominin remains bearing carnivore damage recovered from Hohlenstein Stadel. Although uncommon, other Neanderthal remains with carnivore damage do exist (see Díez et al., 2010). Some of these rare cases have been inferred as carnivore attacks on hominins (Camarós et al., 2015). However, most of them reveal postdepositional taphonomic carnivore damage in a context of alternating use of space. It is impossible to discern whether the Hohlenstein Stadel Neanderthal was attacked prior to its consumption although more recent human bones from the Neolithic period at the same cave (Orschiedt, 1999) are undeniably the result of postmortem scavenging by carnivores.

Carnivore damage is also present in many other animal bones from the Swabian Jura (Kitagawa, 2012). This damage is made up of scores, furrowing, depressions and punctures and reflects both secondary access to animal carcasses transported by hominins (e.g., Krönneck, 2012) and primary access and the posterior transportation of prey by carnivores to caves (e.g., Niven, 2006). This points to the alternating use of the caves by hominins and carnivores, as in other European contexts (e.g., Straus, 1982, Lindly, 1988, Yravedra and Cobos, 2014), which provided a scenario of competition for the use of the space, but also the basis for hominins to develop recycling activities with the remains they found in the caves. Examples of this type of situation are the worked naturally broken bear canines described above.

Nevertheless, pressure related to the use of space changes trough the Upper Paleolithic. As tooth marks measurements prove, the role of carnivores in the accumulation of fauna in caves diminishes throughout the Paleolithic (Conard, 2011). There is a clear difference in the size of the carnivores present in the caves between the Middle and the Upper Paleolithic, observable in both tooth marks studies and the archaeozoological record from previous research (Conard, 2011, Kitagawa et al., 2012). This can be explained by both the intensified use of sites (Conard, 2011, Conard et al., 2006, 2012) and carnivore hunting (Münzel and Conard, 2004, Münzel et al., 2011) by humans during the Upper Paleolithic.

The Swabian Jura also preserves outstanding evidence of carnivore exploitation. Neanderthals occasionally hunted bears in this area (Conard et al., 2012, Kitagawa et al., 2012), as they did in other geographical areas (David, 1997, Wojtal et al., 2014) and with other carnivore species (Stiner, 1994, Arribas et al., 1997, Yravedra, 2005). However, it is during the Upper Paleolithic that this type of scenario deserves particular attention, as it is during this period that extraordinary evidence of carnivore hunting, including cave bears

(Münzel and Conard, 2004), and of clear carnivore exploitation for purposes such as hide procurement (Kitagawa et al., 2012) has been recovered. In this respect, not only were large and medium-sized carnivores exploited, but also small animals like foxes were obtained for meat consumption.

Therefore, carnivores are included as a versatile resource in Upper Paleolithic economic strategies. Evidence of such versatility is also related to the use of carnivore remains as raw materials to produce not just ornaments, but also tools such as retouchers. Although the type of carnivore exploitation is different during the Upper Paleolithic cultural periods, especially characterized by the different use of carnivore teeth, it is clear that increasing carnivore exploitation occurred (*idem*).

In parallel to all of this evidence of increasing and diversified carnivore exploitation during the Upper Paleolithic, carnivores were also included as motifs in the ivory sculpture tradition (Conard, 2003). They played an important role, especially the felids, in the Aurignacian cultural tradition (Conard, 2003, Conard and Bolus, 2003, 2008).

Thus, the general scenario of Upper Paleolithic hominin-carnivore interaction is related to increasing carnivore exploitation in many forms and to the inclusion of carnivores as raw materials in the Paleolithic economy, as well as an important motif in their cultural tradition. Beyond this, the pressure between the two groups was constant, derived from macro and micro space sharing, and the systematic hunting of carnivores was likely intended to reduce this competition for space and resources. Certainly, Swabian hominin-carnivore interaction has been previously described as a scenario that spanned from competition to predation and later to active exploitation (Kitagawa et al., 2012).

The evidence of early wolf domestication discussed here for the Swabian Jura is proof of yet another form of complex carnivore exploitation. Hominin strategies related to how to deal with carnivore pressures were not limited only to elimination (e.g. active hunting) (Münzel et al., 2011), inclusion (domestication) was also developed as a way of taking advantage of a conflict.

Overall, and taking in account all evidence of interaction, it seems clear that the Swabian Jura is a zone of complex sympatry between hominins and carnivores. Furthermore, it is also evident that the type of interaction developed during the Upper Paleolithic had a higher impact on the environment than the interactions that occurred in the Middle Paleolithic (Conard, 2011). A relationship defined by much higher pressure and the extinction of the cave bear before the LGM, an increase in hominin population densities, and wolf domestication are good examples of such a change. However, we must also look to the archaeological record about the role that hominin-carnivore interaction had in relation to the development of modern and complex behavior as evidenced through unique proof of prehistoric innovation in the Swabian Jura.

There is consistent evidence of a coevolutionary interaction between hominins and carnivores in the Swabian Jura. Future research must think about how these mutual pressures influenced hominin behavior and contributed to making the Upper Danube an important centre of innovation during the Early Upper Paleolithic.

5. Conclusion

Based on our observations from assemblages from the Middle and Upper Paleolithic, the relationship between humans and carnivores was a dynamic and changing interaction preserved in tooth remains and bones bearing carnivore tooth marks. Archaeological sites such as Hohle Fels, Geißenkösterle and Vogelherd, among others in the Swabian Jura, are settings of interaction, where the great diversity of this relationship during the Paleolithic can be documented.

In the present paper we have provided insight into the complex relationship between hominins and carnivores by analyzing tooth remains and tooth marks. We found that studies of teeth and the modifications they cause provide important information about hominin behavior, including carnivore hunting, tool production, human recycling activities, the production of ornaments, the alternating use of caves by hominins and carnivores, and even the domestication process.

Our observations are consistent with previous approaches and illustrate how this interaction spans from a competitive relationship with bidirectional pressures during the Upper Paleolithic, to a relation defined by active hominin predation and exploitation of carnivores during the Upper Paleolithic. Both extinction and domestication processes act as proof for how complex this interaction was in this area.

In conclusion, the study of teeth in their diverse contexts is a powerful approach towards understanding hominin-carnivore interactions during the Paleolithic and their changes over time. Furthermore, it is clear that the Swabian Jura is an outstanding area for the study of such interaction, and future studies will have to take on the role of this interaction in relation to cultural innovation during the Upper Paleolithic, as it seems there is a connection.

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Acknowledgements

EC is beneficiary of a FI/AGAUR (DGR2013) grant of the Catalan Government and a BE/AGAUR Grant (2012 BE 00971) at the Eberhard Karls-Universität Tübingen. EC and FR received funding from *Ministerio de Economía y Competitividad* (projects HAR2010-19957/HIST and HAR2013-48784-C3-1-P) and *Agència de Gestió d’Ajuts Universitaris i de Recerca* (projects AGAUR 2014-SGR-900 and 2014/100573). We would like to acknowledge Maria Malina her support in the field and laboratory. We would also like to thank the comments of the anonymous reviewers.

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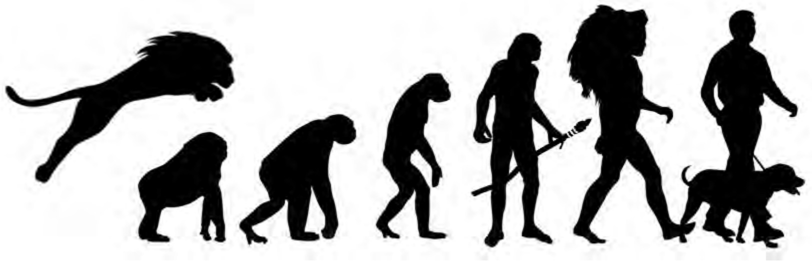
4.4.2

PAPER 8

Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behavior



Chapter 4.4 *Case studies of hominin-carnivore interaction during the Pleistocene*

Paper 8

Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behaviour

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The evidence of modern and complex behavior is a key debate in human evolution. Neanderthals have been excluded from this debate from many years, until new insight have provided a new conception of the neanderthal behavior. Nevertheless, although archaeological data of complex and modern behavior has been inferred, this is not a generalized scenario in Middle Paleolithic sites. In the present paper, we point taphonomical issues as the responsible for this misconservation of cognitive markers. Furthermore, we highlight the action of ursids as one of the agents that has most modified the archaeological record. Nevertheless, bears not just erase behavioral evidences, their action may also generate material realities that can be misinterpreted by archaeologist as neanderthal behavioral markers. In the present paper we analyze issues related to organized use of space and symbolic behavior such as inhumation practices and graphical expression. We approach this issue from a multidisciplinary research based mainly in actualistic, experimental, paleontological and ethological observations.

Keywords: Neanderthals, Bears, Interaction, Pleistocene, Behavior

Quaternary International (accepted)

1. Introduction

Modern and complex behavior has been discussed widely in the scientific literature. The "package" related to modernity and complexity includes evidence associated with technological, social, and cognitive innovations in relation to hunting methods and diet, hafting procedures, and heat treatment, among others (see McBrearty and Brooks, 2000, Villa and Roebroeks, 2014). All these are key cognitive markers that allow differentiation of modern humans from archaic hominins (Marean et al. 2007, Conard, 2010). Conventional explanations relate all these innovations as evidence of the modernity and complexity usually assigned to *Homo sapiens* (Li et al., 2014).

For many years, Neanderthals have been excluded from the debate related to the display of modern behavior (D'Errico, 2003). Nevertheless, recent research has provided evidence of archaeological data indicating complex Neanderthal behavior and modern cognition (summarized in Villa and Roebroeks, 2014). This evidence points towards a new conception of Neanderthal behavior, related to new insights associated with symbolic issues (e.g., Zilhao et al., 2010, Roebroeks et al., 2012, Morin and Laroulandie, 2012, Peresani et al., 2013), subsistence strategies (e.g., Scott, 1980, Blasco et al., 2014, Rufà, 2014, Yravedra et al., 2014, Fiorenza et al., 2015), intra-site spatial organization patterns (e.g., Chacón et al., 2012) and technological innovations (e.g., Soressi et al., 2013, Yravedra and Uzquiano, 2013, Abrams, 2014). Nevertheless, despite all this behavioral evidence, the debate on Neanderthal cognitive and behavioral evolution remains largely unresolved (Taborin, 1998, White, 2002, Higham et al., 2010).

Some archaeological data do support Neanderthal behavioral modernity, but the number of examples is not large, and they are considered by many as exceptions or acculturation evidence (Mellars, 1999, 2005). Nevertheless, we believe this is an issue related to taphonomic damage and post-depositional site preservation. Preservation has been pointed out previously as a key factor in structuring the present state of knowledge on cultural complexity and innovation (Langley et al., 2011).

Among all agents that may have changed archaeological site preservation (e.g., water, weathering, sedimentation, etc.) (e.g., Barbetti, 1986, Mallol et al., 2007), carnivores can be acknowledged as one of the most active (Lindy, 1988, Binford et al., 1988, Lyman, 1994). Their modification actions can be contextualized in the alternate use of caves by both agents (hominins and carnivores) for development of different activities (Straus, 1982,

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Blasco, 1997, Stiner, 2002, Enloe, 2012, Yravedra and Cobos, 2015). Modification may be related to bone damage and spatial modifications (Camarós et al., 2013a, Arilla et al., 2014) that render palimpsests difficult to study (Egeland et al., 2004, Baena et al., 2012 vs. Yravedra and Gómez-Castanedo, 2014). Among all carnivores that may have been responsible for such damage, ursids can be identified as animals that developed a close interaction with Neanderthals (e.g., Estévez, 2004, see Rosell et al., 2012a).

Bears developed direct interactions with Neanderthals, as confirmed by evidence that they, together with other carnivores (Pérez Ripoll et al., 2010, Blasco et al., 2010), were hunted (Auguste, 1995, David, 1997) for meat and fur (Tillet, 2002) and for other resources (e.g., Abrams, 2014). Bears also presumably instigated attacks on Neanderthals, in the context of constant pressures arising from sharing the same ecosystem (Camarós et al., 2015). In this sense, the alternate occupation of the same caves is one of the most common forms of indirect interaction between Neanderthals and bears (Viranta and Grandal, 2012).

In the present paper, we examine different perspectives to show how bears may have served as taphonomic agents in the study of Neanderthal behavior. Specifically, we analyze issues related to the organized use of space and symbolic behaviors such as inhumation practices and graphical expression. Taphonomic experiments and archaeopaleonthological analyses related to bears are developed to provide a proof-of-concept of the degree of complexity of the interaction that occurred between hominins and carnivores during the Pleistocene and the implications it has concerning the study of Neanderthal behavior.

2. Materials and methods

A multidisciplinary approach based on hominin-carnivore interaction has been used in the present paper. In this sense, experimentation and archaeopaleontological and ethological approaches have been developed in order to provide new insight into the study of Neanderthal behavior through the relationship Neanderthals had with bears.

To do so, several experiments have been developed with extant bears (*Ursus arctos*) in the Nature Park of Cabárceno (Cantabria, Spain). This is an excellent context for developing experiments, due to the Park's policy of interfering as little as possible with animals that live in a semi-free state of liberty. In this sense, animals preserve their natural instincts in a perfect context for scientific observation. Experiments were developed following a methodology we used previously (Camarós et al., 2013b), which consisted of the performance of an experimental scenario inside the bears' enclosure. Places with no slope were preferentially selected. The spatial distribution of the bears' actions is then registered with photogrammetric techniques using targets measured with Total Station software (Leica TCRM1205) that linked them to a provisional local system. The aim of this is to control all spatial changes due to the animals' actions. One of the experiments required specific particularities, and an excavation machine was used to excavate in the soil (see Supplementary Material Fig. S1). Other methodological particulars of each experiment are described in section 3.1.

Archaeological sites were also studied. The selected sites were those that presented traces of ursid action according to our needs (e.g., bear scratches and bear beds) and that displayed an outstanding state of preservation. We analyzed the archaeopaleontological contexts of Rouffignac (France) and La Garma (Spain). At both sites, we measured the length, breadth, and depth of the bear beds present (see Supplementary Material Fig. S2). We also analyzed other bear traces, such as scratches on the walls and soil, using scanning technology.

Our results, both experimental and paleontological, were compared with recently published research related to the study of modern and complex Neanderthal behavior. In this sense, sites such as La Chapelle-aux-Saints (France) and Gorham's Cave (Gibraltar) are cited and discussed.

3. Results

3.1 Erased behavior

The identification of structured and specialized spaces in the archaeological record reveals modern and complex behavior (Lombard, 2012). Nevertheless, identification of original hominin spatial distributions is not always possible, due to taphonomic processes. Post-depositional processes, such as sediment movement or water action, among others (Goldberg and MacPhail, 2006), are responsible for the destruction of the original spatial connection between archaeological artifacts. Previous experiments that we developed also pointed to large carnivores as taphonomic agents capable of erasing specific spatial distributions that would reveal modern and complex behaviors to archaeologists (Camarós et al., 2013a).

An experimental series, previously developed with bears, hyenas, lions, and wolves, consisted of generation of an experimental hearth and hearth-related assemblage. Although all carnivore species interacted with the combustion structure and modified it, bears were the ones that most changed the original spatial distribution (Camarós et al., 2013a). The re-

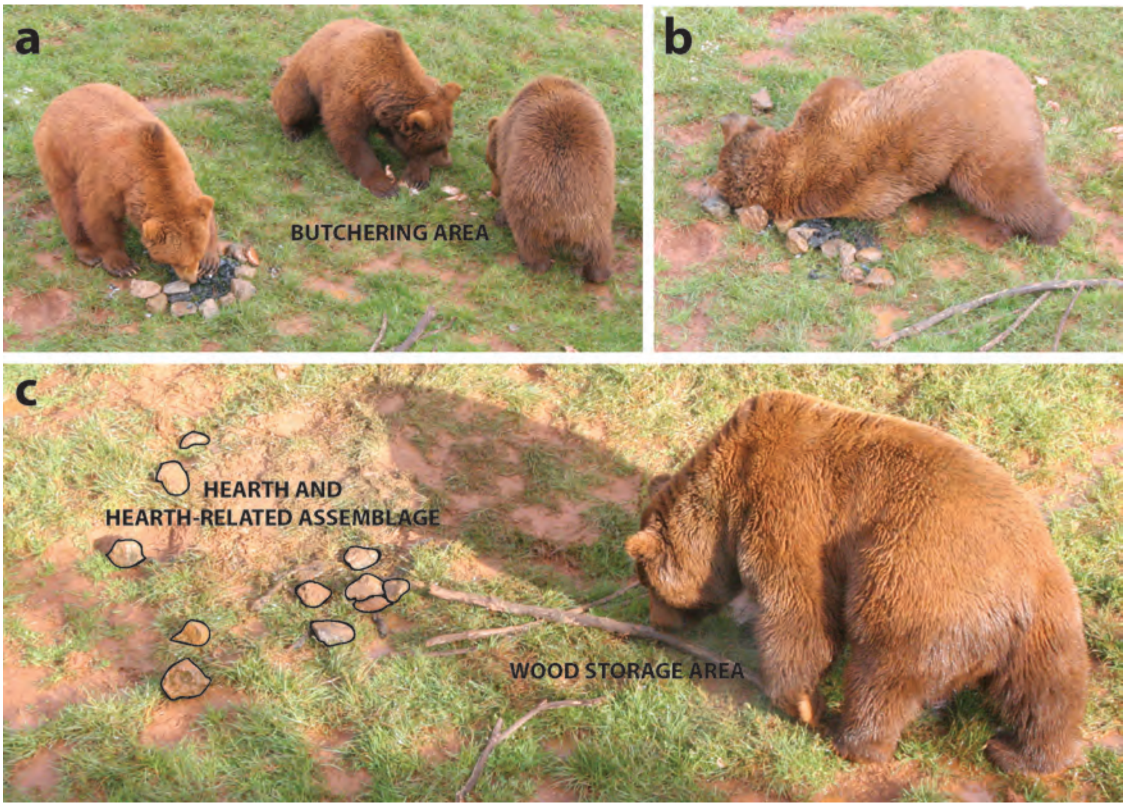

Figure 1. Different images taken during the experiment with bears in Cabárceno (Spain): a) Male bears interacting with the combustion structure and the butchering area; b) Male bear modifying the hearth and c) Spatial distribution of stones from the hearth (highlighted) and wood storage area during the experiment.

sulting spatial distribution revealed complete destruction of the initial experimental scenario. These results motivated the experiments presented here, with the aim of extending our knowledge of how bears have acted as taphonomic agents of spatial modification in the past.

The first experimental scenario consisted of the investigation of a spatial distribution, which revealed several aspects associated with the display of modern and complex behavior. The specialized spatial organization was composed of a unique experimental scenario, with areas linked to specific activities, such as a knapping area, a butchering area, a hearth and hearth-related assemblage zone, and a wood storage area (Figs. 1 and 2). This scenario was based on some of the best-known Neanderthal sites with a complex spatial distribution that revealed modern behavior (see Henry et al., 2004, Jaubert and Delagnes, 2007).

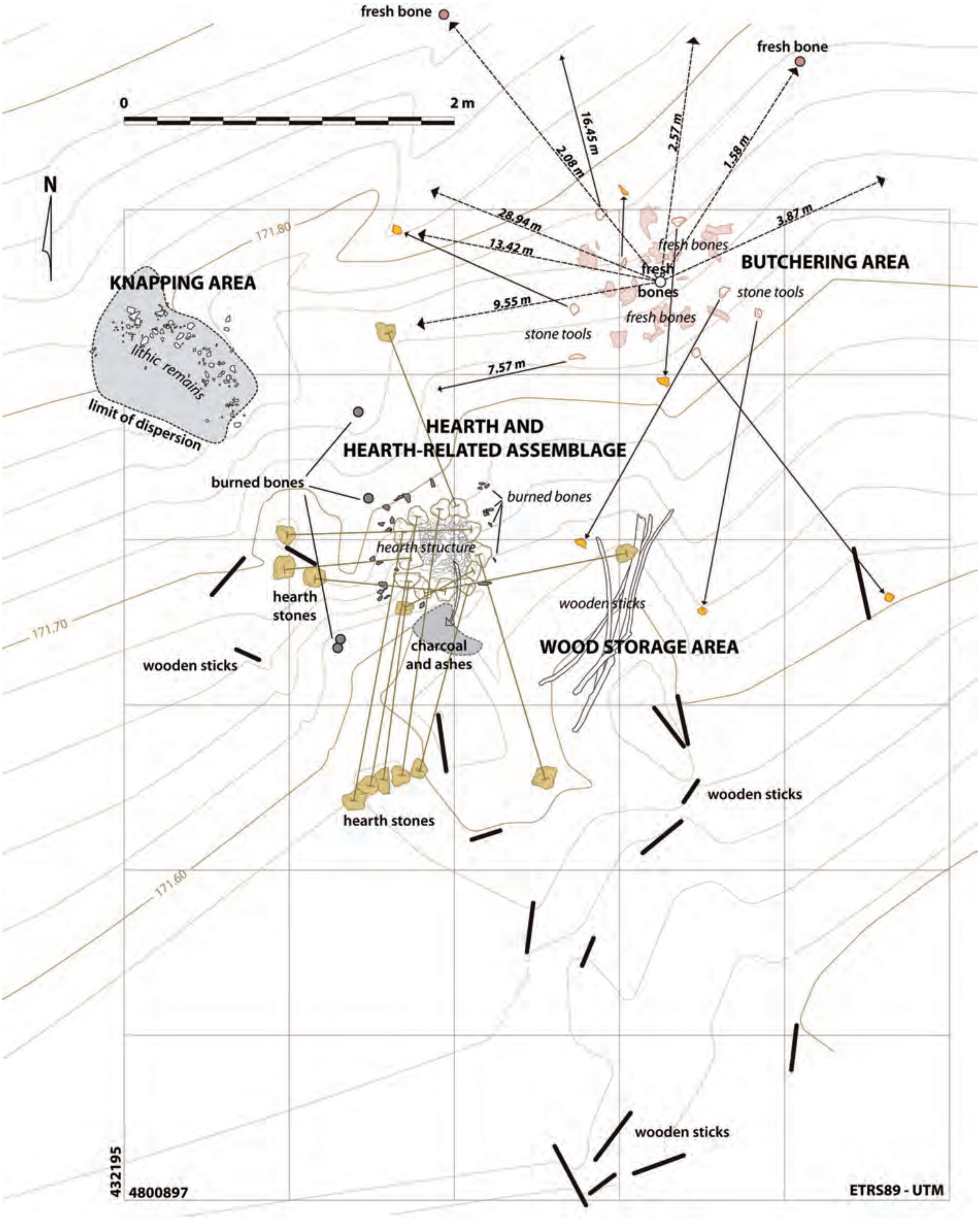

Figure 2. Experimental scenario with four specialized areas with its spatial distribution before and after the bears action (highlighted).

The results were clear and significant. Bears highly modified the experimental scenario, interacting with all areas constructed in a time lapse of four hours. During this period, a total of 10 bears modified the original structure, although the first four bears (males) were responsible for most of the spatial damage (Fig. 1). All items that composed each area were moved from their original positions, following a general radial pattern (Fig. 2).

Concerning the knapping area, the lithic “arch” disposition, composed of flint flakes and microflakes emulating the spatial result of knapping, was erased. The new spatial disposition generated a complete different shape (Fig. 2). The butchering area, consisting of fresh cattle bones and used lithic flakes, was also modified. Bones are the items that were distributed in a bigger spatial range, with distances between 1.58 m to 28.94 m, following a radial pattern. The wood storage area was highly modified, as wood sticks were not just spatially dislocated, but also broken as a result of biting and manipulation of these items. Sticks were distributed basically to the south and none of them maintained their original length. Finally, the hearth and hearth-related assemblage zone were also modified. The area was composed of a stone hearth, with charcoal and ashes inside, and burned bones around the combustion structure. The spatial distribution generated by bears differed slightly from the one observed in previous experiments (Camarós et al., 2013a), as dispersion was not strictly radial and new stone associations were generated and a linear association of the five stones was generated south of the original position. Furthermore, a new cluster of charcoal and ashes was displayed 50 cm from the initial location.

Overall, the spatial distribution of the experimental scenario by bears resulted in a clear mixture of items belonging to different areas, which complicates the inference of the original specialized spatial distribution. Nevertheless, bears are also capable of destroying other spatial distributions that are important in the study of modern and complex behavior, such as burials.

As part of our experimental series on how bears modify spaces, we carried out an experiment with the aim of studying how ursids interact with a structured burial (Fig. 3). A burial pit was excavated 50 cm deep inside the bears’ enclosure and seven slate stones with pebbles around them were deposited at the base (Fig. 3a). Afterwards, red deer (*Cervus elaphus*) remains (basically internal organs) were deposited over the stones and the experimental burial pit was covered and compacted with an excavator machine (a detailed figure of the process can be found as Supplementary Material Fig. S1).

Immediately after the team abandoned the zone where the burial pit was located, a male bear started an inspection of the area (Fig. 3b). Bears interacted with the experimental scenario for two hours, and they dug, attracted by the animal remains. Observation after

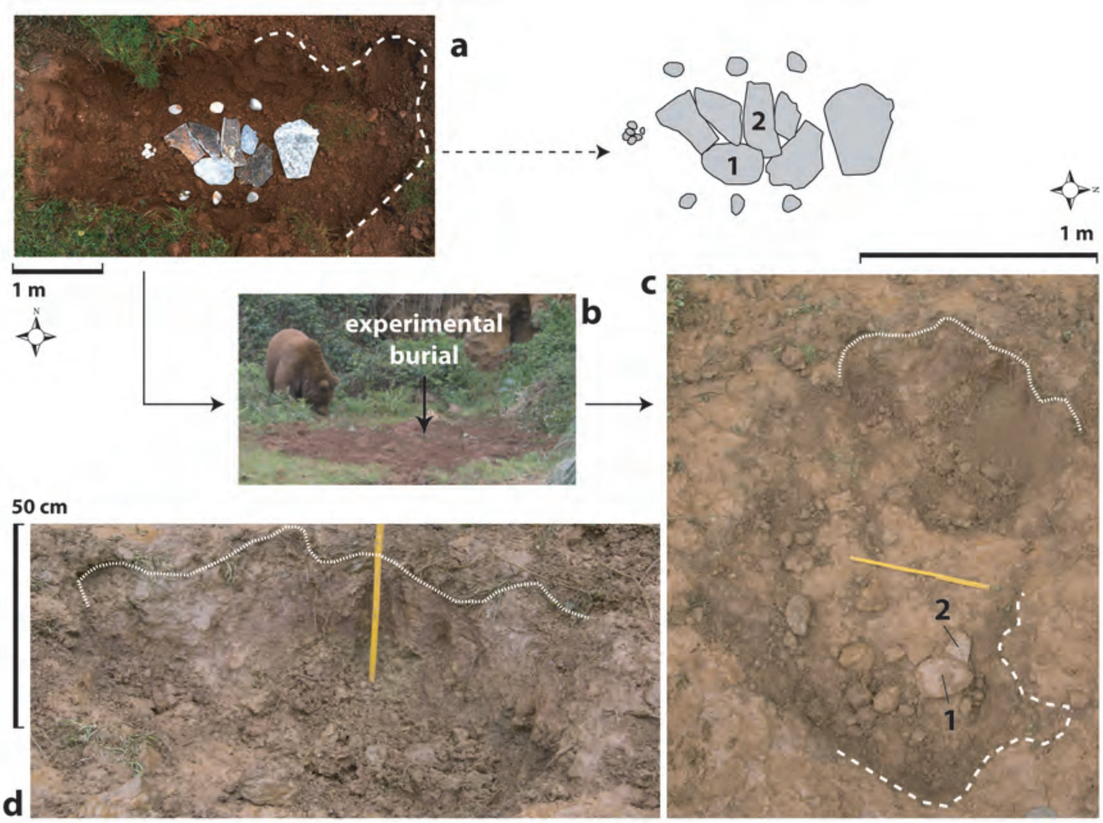

Figure 3. Brown bears destroying evidences of experimental intentional inhumations: a) Experimental structured inhumation (without the flesh on it); b) Bear approaching the covered experimental inhumation; c and d) Experimental inhumation modified by bears (it is possible to appreciate how stones 1 and 2 have been moved in image c compared to image a)

the bears' intervention showed the bears to be highly capable of modifying a burial pit (Fig. 3a-b). The rectangular burial shape was changed and the new limits of the pit contained scratches on the vertical walls (Fig. 3d). Even the internal stone disposition was changed and the original disposition was completely modified (Fig. 3c) (more images of the resulting experimental scene can be found as Supplementary Material Fig. S2). Only the slate stones designated as one and two (Fig. 3a) were located inside the pit; all other stone elements from the base were found outside, at distances between 1.15 m and 10.10 m away (Fig. S2). Some of these stone plaques were broken and fragmented into many pieces and presented evidence of clear notches and scores (Fig. 4).

3.2 Emulated behavior

Bear action in relation to the study of human behavior is not restricted only to destruction of archaeological evidence. These animals may also generate evidence that emulates hominin behavior. The first case presented here is related to the study of inhumations, and the second one with graphical expression. Both cases presented are crucial when discussing modern and complex Neanderthal behavior.

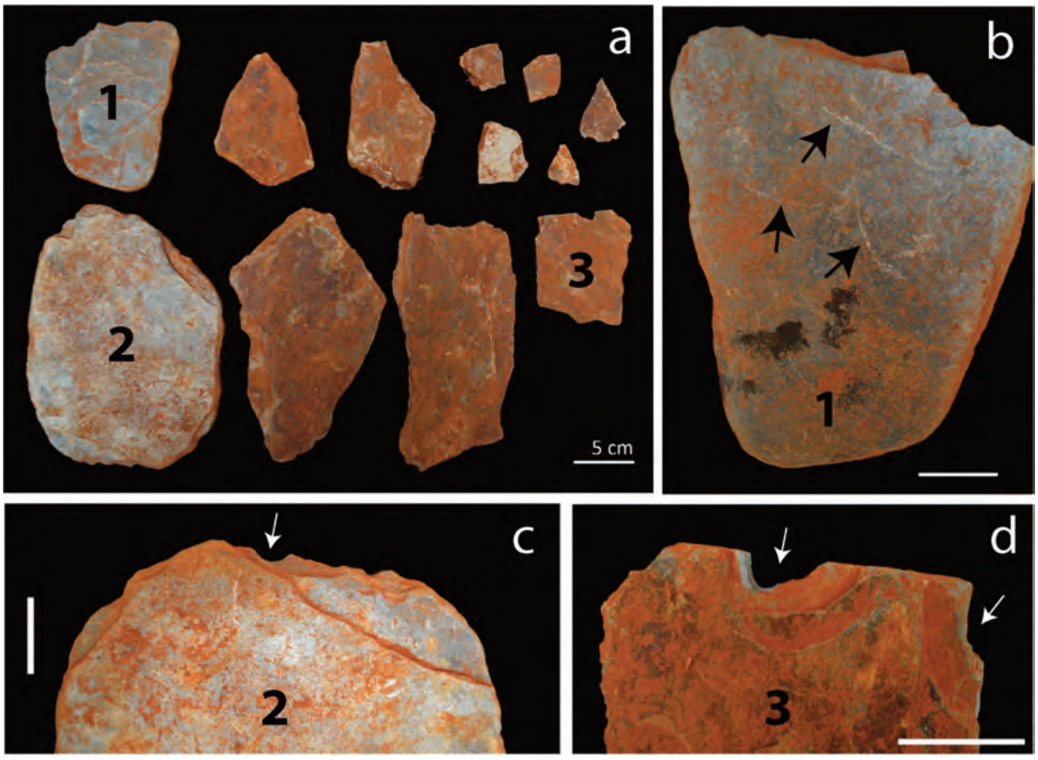

Figure 4. Slate stones from the base of the burial pit with carnivore damage: a) Fragmentation of stones; b) Scores on stone 1 and c-d) Notches on stones 2 and 3 (scale in b,c and d is 5 cm).

La Chapelle-aux-Saints (France) is one of the classic archaeological sites with evidence of a probable Neanderthal inhumation, as claimed by Bouyssonie and colleagues (1908) during the first decade of the twentieth century. Recently, due to current excavation work, new evidence has been published that supports the interpretation of an intentional burial at the site (Rendu et al., 2014). The paper presents excellent research where an old problem is approached from a well-planned, multidisciplinary archaeological strategy to finally provide evidence supporting the presence of a Neanderthal burial at the Bouffia Bonneval in La Chapelle-aux-Saints. The research is opportune because it provides results that can be added to the new conception of Neanderthals in current science, a viewpoint that reflects a complex and modern behavior.

Nevertheless, the conclusions by Rendu and colleagues (2014) regarding the Bouffia Bonneval context as an intentional burial have been criticized by Dibble et al. (2014), with strong arguments. Therefore, a debate is emerging in relation with the interpretation of La Chapelle-aux-Saints archaeological context. Thus, a new look at the evidence is needed, from a perspective that takes into account hominin-carnivore interactions, as this would provide an alternative and much more complex vision to the debate.

We measured a total of 66 bear beds from Rouffignac (France) (N = 59) and La Garma (Spain) (N = 7) and compared these to published measurements of the burial pit from La Chapelle-aux-Saint by Rendu et al. (2014) and Bouyssonie et al. (1908) (see Supplementary Material Fig. S3). In addition, we compared brown bear bed measurements provided by Fosse and colleagues (2004) from Arriutort and Zazpigagna (France) (Fig. 5). Our observations indicate that the pit morphologically resembles a cave bear bed.

As shown in Figure 5, the burial pit from La Chapelle-aux-Saints provided by Rendu et al. (2014) matches in size the measurements for a cave bear (*Ursus spealaeus*) bed. This included not only the transverse and longitudinal profiles, but also its depth.

Despite inhumations, one of the clearest pieces of evidence for modern and complex behavior is the capacity for the production of graphical expression (MacBrearty and Brooks, 2000), traditionally associated with Anatomically Modern Humans (AMH). Nevertheless, recent research has confirmed that Neanderthals had the capacity for such production, as seen in Gorham's Cave (Gibraltar) (Rodriguez-Vidal et al., 2014), where an abstract pattern, engraved into the bedrock dated between 38.5 and 30.5 cal kyr BP, has been identified. In this sense, an old paradigm has been overcome, and the interpretation and publication of new evidence is anticipated based on this new discovery. Nevertheless, archaeologists must be aware that bears may again generate similar confusing traces.

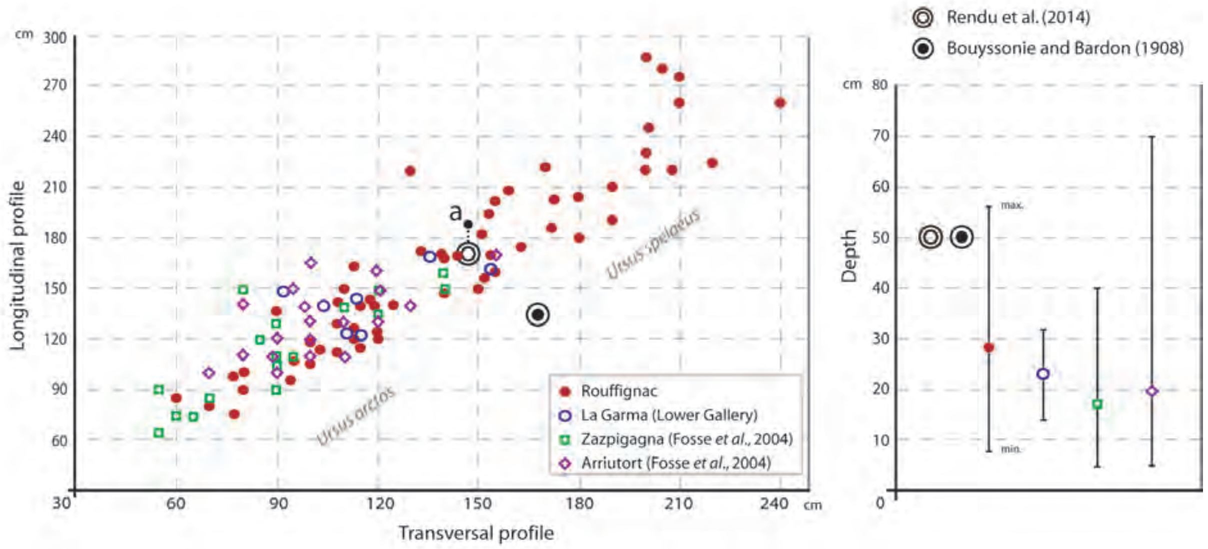

Figure 5. Cave and brown bear bed measurements compared with the burial pit from Bouffia Bonneval at La Chapelle-aux-Saints (measurements inferred from Rendu et al., (2014), Fig. 1 and 2; and Bouyssonie and Bardon, 1908).

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Bear behavior inside caves usually leaves its traces as scars in the cave. These scratches, due to the bears' actions of clawing the walls, are preserved and can also be associated with rock art due to the alternate use of caves (Bocherens et al., 2006). The morphology and spatial distribution of these phenomena need analysis, as they can be similar to the ones produced by hominins when developing graphical expression in caves.

In this sense, we have analyzed different archaeopaleontological contexts with clear evidence of bear behavior inside caves. We have studied the Lower Gallery of La Garma (Spain) and Rouffignac (France). Both are well-known sites that preserve exceptional material evidence of both hominin and bear behavior. Our main goal has been to observe the variability among bear scratches in order to achieve preliminary characterization, for later comparison of them with abstract pattern engravings, particularly with the ones found in Gorham's Cave (Gibraltar) (Fig. 6j-k) (Rodríguez-Vidal et al., 2014).

Similarities between the bear scratches and the abstract pattern engraved in Gorham's cave are evident. First, observation is possible of how bears are able to produce permanent scratches on karstic cave walls, defining patterns of parallel lines (Fig. 6a-g) and even superposed ones (Fig. 6d-f). Furthermore, ursid marks also display a pointed start and a pointed or fringed end (Fig. 6a-i), as described by Rodriguez-Vidal et al. (2014) for the Neanderthal engraving (Fig. 6j-k). Overall, bear scratches may also produce associations of parallel scratches (engraved lines), which can generate a non-intentional abstract pattern similar to that intentionally created by hominins.

When comparing space between parallel "lines," we can also observe how similar this interspace can be in both different realities (Fig. 7). Gorham's engraving certainly contains parallel internal microstriation in each section; nevertheless, this microtopography may not always be preserved due to taphonomic processes occurring in karstic systems, such as water action (Goldberg and MacPhail, 2006).

4. Discussion

The interaction between hominins and carnivores during human evolution has influenced human behavior in many ways (Stiner, 2012). Since *Homo* added meat to his diet and entered the predatory guild 2-3 millions years ago (Isaac and Crader, 1981; Domínguez-Rodrigo et al., 2012), carnivores played an important role during the Pleistocene concerning hominin evolution (Rosell et al., 2012b), in what can be seen as a co-evolutionary process (Brantingham, 1998).

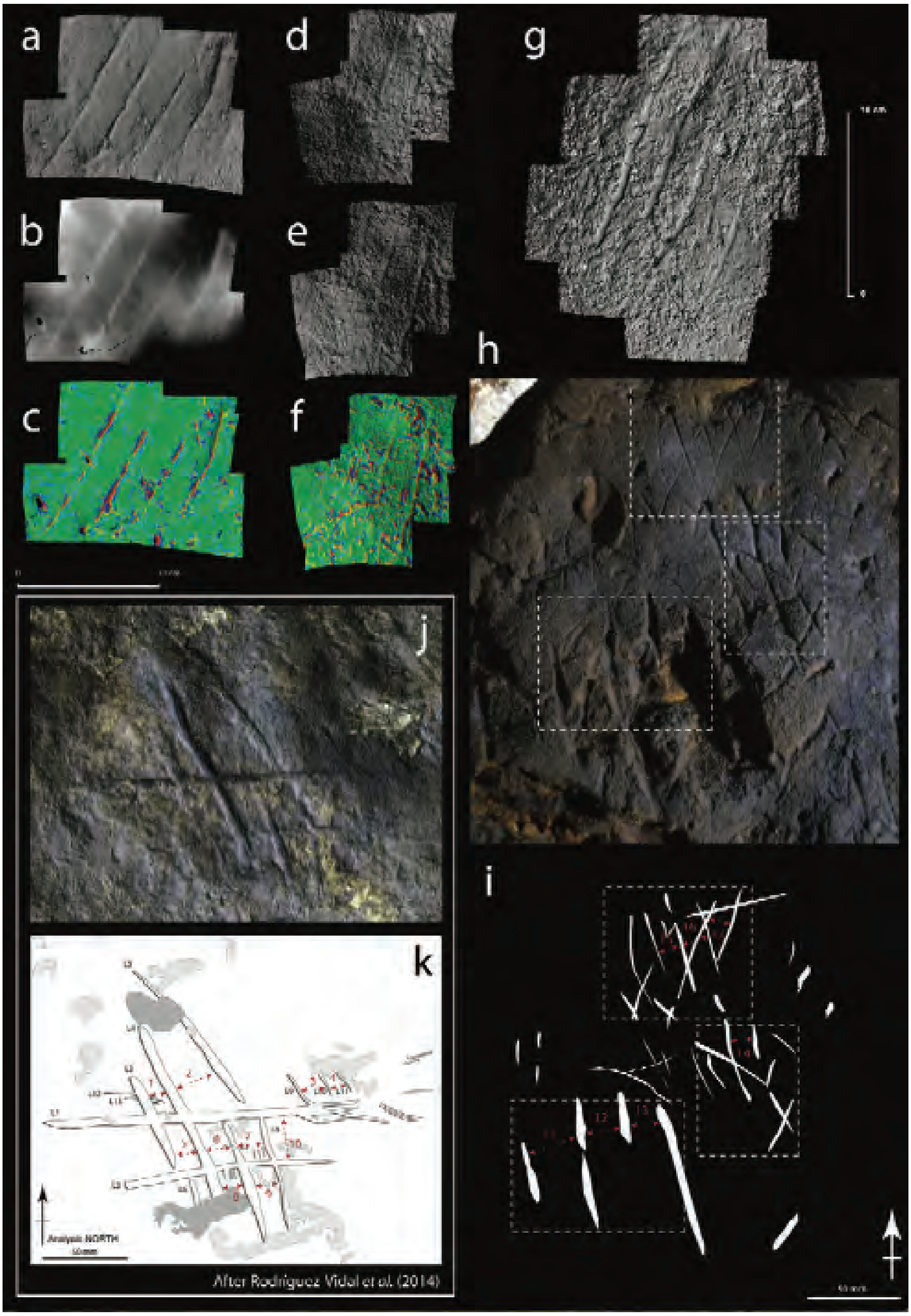

Figure 6. A-g) Structured light scanned bear scratches from La Garma (Spain) viewed with different light filters; a-c) Scratches made on the ground (soil); d-f) Crossed parallel scratches made on the karstic cave wall; g) Parallel scratches made on the karstic cave wall; h) Associated bear scratches on the soil near the cave wall in Rouffignac (France) and i) selected scratches and measurements taken to compare with j-k) neanderthal engraving from Gorham's Cave (Gibraltar) and measurements taken (j-k modified after Rodríguez-Vidal *et al.*, 2014).

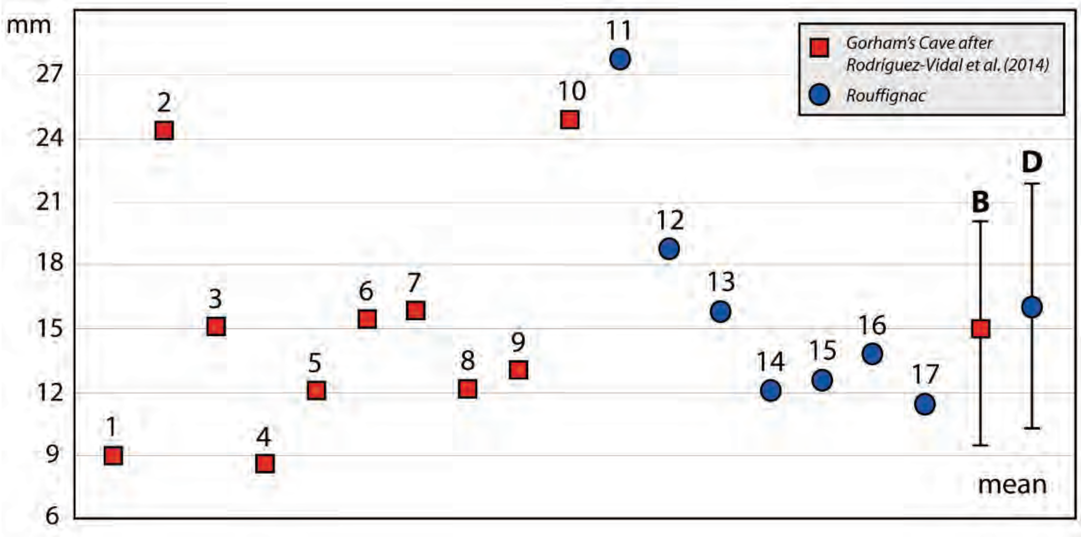

Figure 7. Measurements of the spaces between "lines" from Gorham's Cave engraving (red squares) and Rouffignac's bear scratches (blue circles) from Figure 6. Means with maximum and minimum sizes are also provided (b and d).

Neanderthals were also subjected to interaction with large carnivores. Compared to other hominins, they developed a close relationship with bears (Estévez, 2004). Their interaction with bears and other carnivores was defined by their hunting activities (e.g., David, 1997, Tillet, 2002, Pérez Ripoll et al., 2010, Blasco et al., 2010), as the same prey was shared in a common ecosystem (Beauval et al., 2005) and both carnivores and Neanderthals alternately occupied the same caves (Blasco, 1997, Skinner, 2012, Yravedra and Cobo, 2015). This alternate use of caves to develop different activities by both agents is one of the most common hominin-carnivore interactions occurring during the Paleolithic (Straus, 1982, Blasco and Rosell, 2009). As our research has shown, this has implications concerning the study of modern and complex Neanderthal behavior, as previously discussed, for example, with the case of the Divje Babe I flute (d'Errico et al., 1998).

The experiments presented here show how extant bears are capable of destroying spatial connections and structured space (Camarós et al., 2013a). These experiments showing how ursids modify a space with defined areas now indicate that bears can erase all evidence of a specialized space. In this sense, our results are useful as positive analogical observations for understanding what could have happened to hominin-abandoned spaces, in a context of alternate use of caves. The original organized use of space was probably modified by bears, as one of the most common carnivores present in archaeological sites, especially in Neanderthal occupation layers (Stiner, 2002). The mixture of areas observable as a result of the experiment (Fig. 2), and the impossibility of recognizing specialized spatial distributions, must make us think of the consequences this could have had during the Paleolithic.

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In addition, if we consider the results of the second experiment with bears, we must discuss the possibility that carnivores were also responsible for burial site destruction. In this sense, carnivore modification of intentional inhumations, by attraction to the smell of corpses, may be the reason why so little evidence exists of Neanderthal burials, and why burial capacities have been denied for the Neanderthals (e.g., Gargett, 1989), as a trait indicating no presence of modernity and complexity in their behavior. Carnivore destruction of Neanderthal burials has been previously hypothesized (Gargett, 1999), and probable related evidence of carnivore damage to hominin fossils has been identified (Diedrich, 2014).

Bear destruction, as a taphonomic agent of Neanderthal evidence of complex and modern behavior, may be the reason why AMH sites seem to display a level of complex organization that cannot be found in the Middle Paleolithic. According to several authors (e.g., Stringer and Gamble, 1993, see Villa and Roebroeks, 2014), these sites held a) numerous well defined structures, b) hearths, and c) differential use of habitation space (summarized in Wolpoff and Caspari, 1996). Carnivore modification may then be the reason why some Neanderthal sites display a simple spatial organization that does not differ from that of non-human carnivores (Pettitt, 1997), although we have consistent evidence of structured use of domestic space (e.g., Henry, 1998, Vallverdú et al., 2010, Chacón et al., 2012, Villa and Roebroeks, 2014).

However, the action of bears is not only restricted to destruction of spaces. On the contrary, their activity inside caves may generate modification that, like destruction, can influence behavioral archaeological interpretations. This could be the case for the Neanderthal burial site at La Chapelle-aux-Saints. As we have previously indicated, the interaction between Neanderthals and carnivores was quite complex during the Middle Paleolithic. At La Chapelle-aux-Saints, this complexity could be the basis for a difficult interpretation of the Neanderthal inhumation, but also a good alternative viewpoint for contributing to the debate in order to discuss the intentional burial at the site.

The identification of Neanderthal burials is not common, although several examples of such phenomena exist (see Gargett, 1989, 1999). The inference of intentional burials is essential when discussing aspects related to modern and complex patterned behavior in Neanderthals. For the excavation team at La Chapelle-aux-Saints, the attribution of an anthropic origin to the burial pit seems essential for accepting an intentional Neanderthal burial at Bouffia Bonneval. Therefore, after a logical and solid interpretation, Rendu at al. (2013: 83) rejected the hypothesis of an endokarstic origin of the burial depression. Nevertheless, a brown or cave bear origin was also rejected because:

1) Bear beds have a different morphology, according to Fosse et al. (2004) and Hellgren and Vaughan (1989),

2) Ursid faunal remains are quasi absent, and

3) The shallow depth and relatively small opening of the burial depression makes it unlikely to have been used for bear hibernation.

Nonetheless, all these arguments for rejecting an ursid origin of the burial pit can be rebutted. First, concerning the different morphology between the pit and bear beds, this comparison is made only by providing bed measurement for brown bear (*U. arctos*) (Fosse et al., 2004) and black bear (*U. americanus*) (Hellgren and Vaughan, 1989). When comparing it with the cave bear (*U. spelaeus*) bed dimensions that we measured from Rouffignac (France), the distinction is no longer as clear (Fig. 5) and the pit is revealed to be similar to hibernation nests of this species. This interpretation may differ when taking into account the measurements of transverse and longitudinal profiles provided by Bouyssonie and colleagues (1908). The measurements and shapes described from the burial pits during the first excavations do not overlap with cave or brown bear bed measurements (Figs. S2 and 5).

Moreover, despite the statement that ursid remains are *quasi absent* (Rendu et al., 2014: 83), the presence of bear remains is a fact, although identification of the ursid species is difficult. However, due to the chronological and geographical attribution of Bouffia Bonneval, the most probable ursid is the cave bear. Rendu et al. (2014: 83) also argue that the burial context, due to its shallow depth and open conditions, is not a good place for bear hibernation, although *U. americanus*, for example, is well known to use a wide range of hibernation den types (Hellgren and Vaughan, 1989, Haynes, 1994) and remains of the Pleistocene *U. spelaeus* have been found in rock shelters (e.g. Dimitrijević, 1991).

Therefore, and considering our results, we suggest that the burial pit from La Chapelle-aux-Saints is in fact a cave bear bed and not a brown bear bed as was suggested by Dibble et al. (2014: 3), based on the measurements provided by Fosse et al. (2004) and Stiner et al. (1996). Nevertheless, the fact that the pit could be interpreted as a bear bed does not mean that Bouffia Bonneval is not an intentional burial. Actually, evidence has been presented for the re-use of bear beds as inhumation bases during the Upper Paleolithic in La Grotte de Cussac (France) (Aujoulat, 2001). This would reveal Neanderthal recycling activities in the context of an alternate use of caves with carnivores and a much more complex hominin-carnivore relationship during the Middle Paleolithic.

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Finally, our research goes further, by relating bear activity that may be confused with intentional Neanderthal actions. In this sense, we have provided the example of how similar an abstract patterned engraving, in this case the one from Gorham's cave (Rodríguez-vidal et al., 2014), can appear to a bear's scratches. Furthermore, this is not the only case of similar graphical expression, since another has been reported in the Upper Paleolithic that also resembles ursid scratches (e.g., Cueva de Ardales in Spain, see Ramos et al., 2014). Therefore and taking in account that new evidence provide arguments to accept a Neanderthal capacity for graphical production, we should confirm first that what we face in the archaeological record is not the result of bear activity.

Bears occupied caves alternately with Neanderthals in many regions of Europe, and their activity can be associated with archaeological remains and contexts. Our research provides strong evidence for a need for caution when interpreting Neanderthal modern and complex behavior, especially in those archaeological sites where a clear carnivore presence is observed. There is no doubt that Neanderthals possessed such behavior (Villa and Roebroeks, 2014). Nevertheless, Pleistocene Neanderthal-carnivore interactions (in this case, with bears) are a much more complex issue than previously thought, and therefore we must learn how this may had affected our own behavioral interpretations.

5. Conclusions

No evidence exists for a superiority complex of Modern Humans over Neanderthals (Villa and Roebroeks, 2014), as evidence reveals that Neanderthals displayed a complete "package" of behavioral modernity and complexity (e.g., Henry et al., 2004, Chacón et al., 2012, Rodriguez-Vidal et al., 2014). Nevertheless, our research proves that bears, one of the most common carnivores in archaeological sites (e.g., Stiner, 2002, Viranta and Grandal, 2012, Arilla, 2014), can generate confusion when approaching behavioral issues.

On the one hand, bear actions can erase hominin spatial distributions and spatial structurations, such as specialized use of spaces or burial contexts. On the other hand, bears can also generate structures or materiality that can be confused with hominin ones, such as burial pits or abstract pattern engravings. In this sense, the present paper shows how bear actions can serve as a taphonomic confusion factor when approaching the study of Neanderthal behavioral modernity and complexity. This is especially the case when analyzing issues related with symbolic behavior such as inhumation practices, the display of graphical expression, and the organized use of space.

Future research will have to face analysis related to the transfer of the resulting knowledge of experimentation to archaeological research that display Neanderthal-carnivore in-

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teractions. Future research needs to continue the characterization of materialized actions of bears (and other carnivores) in caves, in order to provide data that aim to differentiate between carnivore activity and hominin intentional actions.

In conclusion, our research verifies how complex the interaction between hominins and carnivores could have been during the Pleistocene, and the important consequences it may have concerning the study of Neanderthal modern and complex behavior.

Acknowledgements

We would like to thank help received by *Parque de la Naturaleza de Cabárceno* (Cantabria) and CANTUR, S.A. to develop our experiments in Cabárceno. This research was carried under an IPHES and IIIPC/UC project supported by the Government of Cantabria and by two research projects founded by *Ministerio de Economía y Competitividad* (HAR2010-19957/HIST and HAR2013-48784-C3-1-P) and *Agència de Gestió d'Ajuts Universitaris i de Recerca* (AGAUR 2014-SGR-900 and 2014/100573). E. Camarós is beneficiary of a FI/AGAUR (DGR2013) grant of the Catalan Government.

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4.4.2.1

PUBLISHED SUPPLEMENTARY MATERIAL

PAPER 8

Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behavior

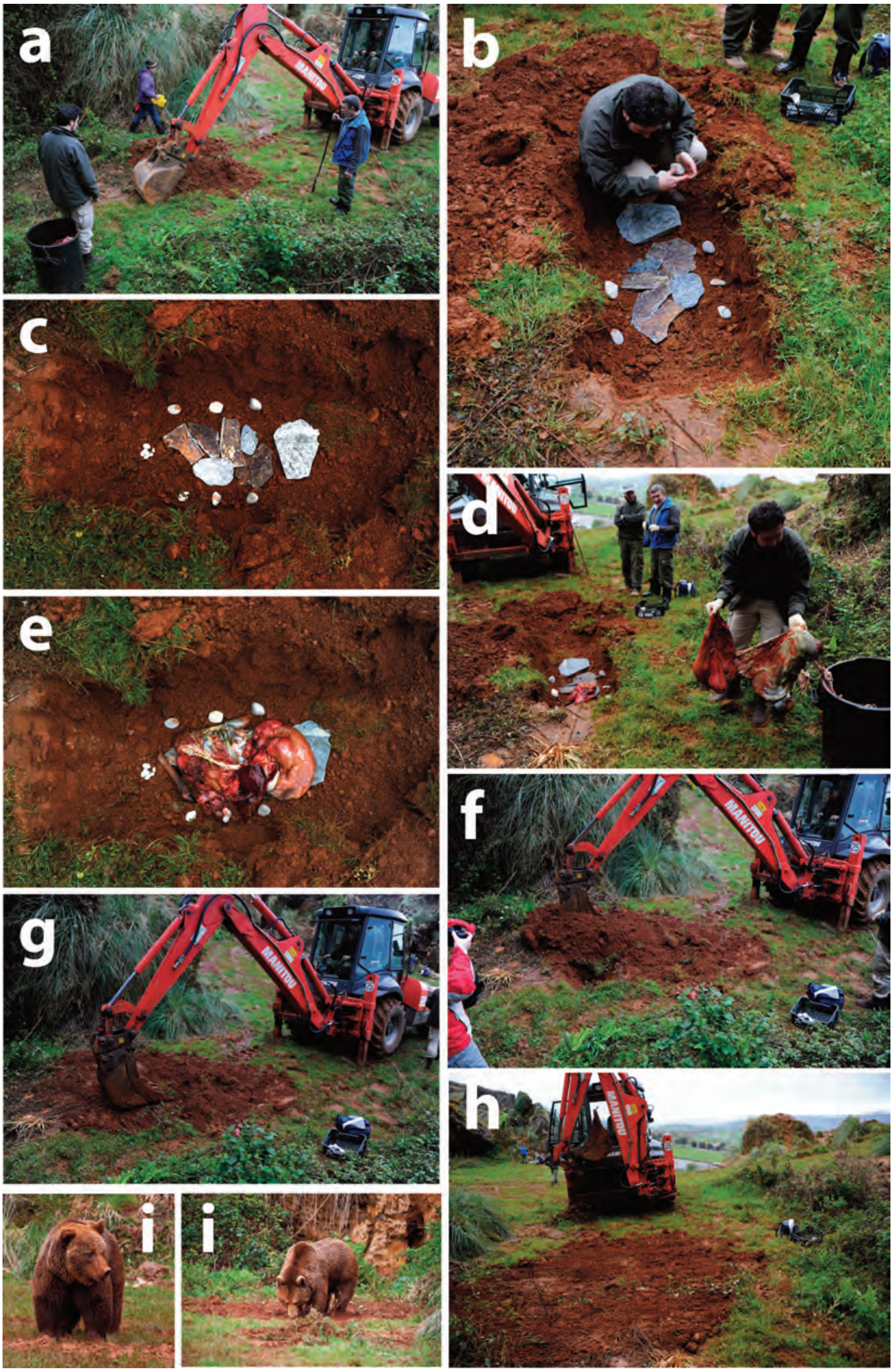

Figure S1. Experimentation with bears concerning the study of carnivore modification of inhumations: a) Excavating the burial pit; b) Placing a structured stone base; c) Resulting spatial distribution of the stone base; d) Placing deer bones and soft tissue in the burial pit; e) Resulting burial base with deer remains; f) Covering the burial pit; g) Compacting the earth on the pit; h) Experimental scenario before bears intervention; i) First bears interacting with the experimental scenario.

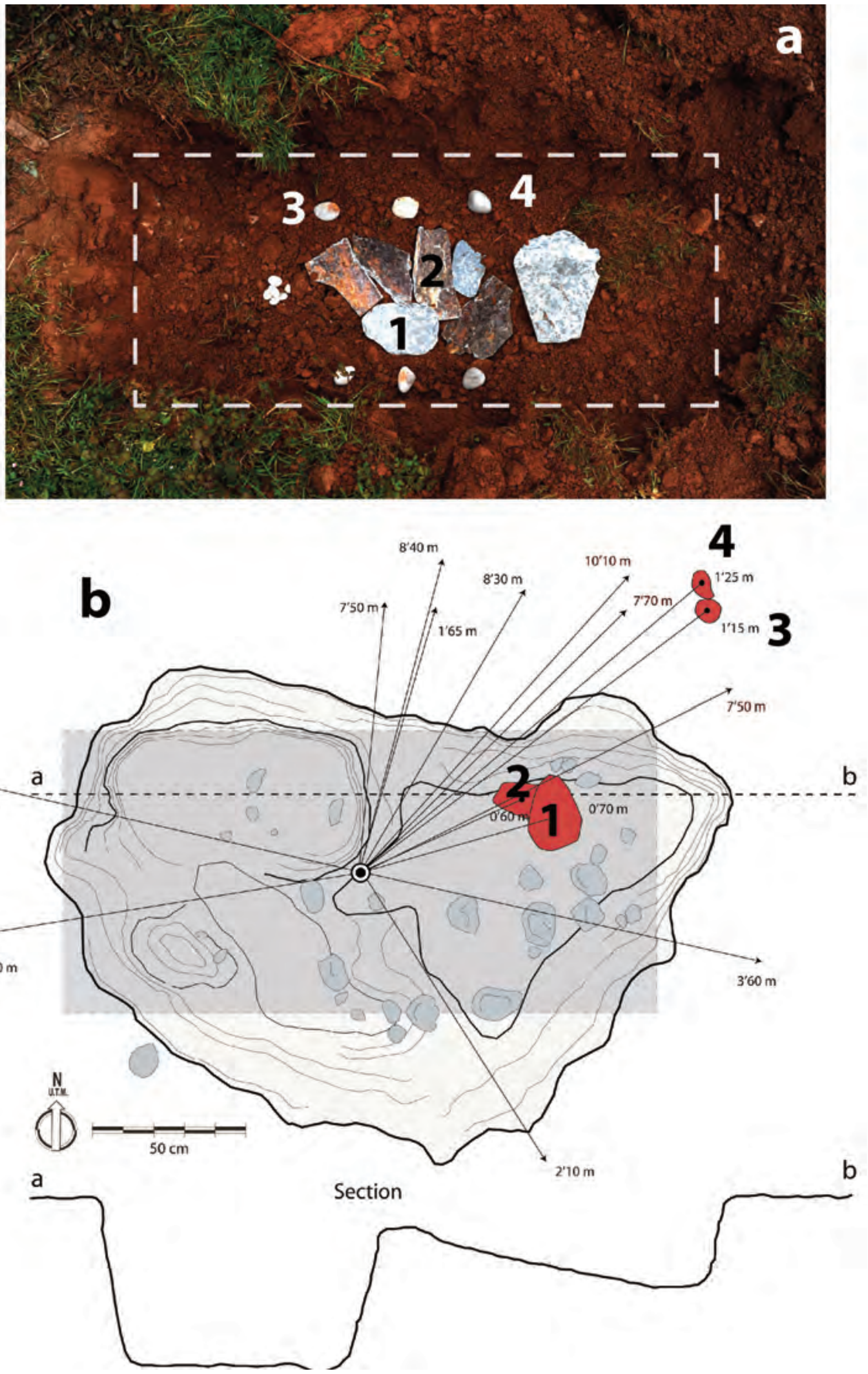

Figure S2. Comparison of the experimental scenario (structured burial pit) before (a) and after (b) the bears modification.

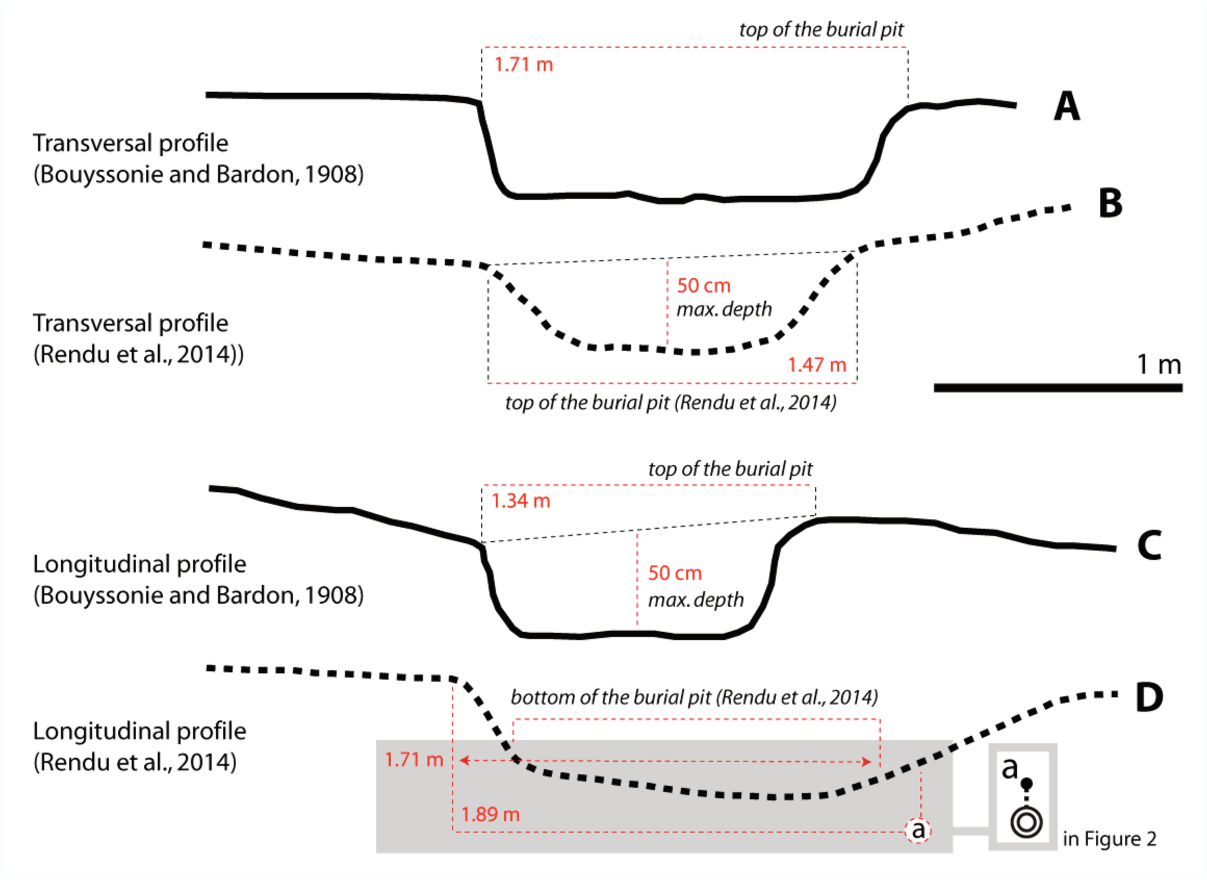

Figure S3. Measurements taken from La Chapelle-aux-Saints burial pit provided by different authors and used in Figure 5 of Paper 8.

4.4.2.2

UNPUBLISHED SUPPLEMENTARY MATERIAL

PAPER 8

Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behavior

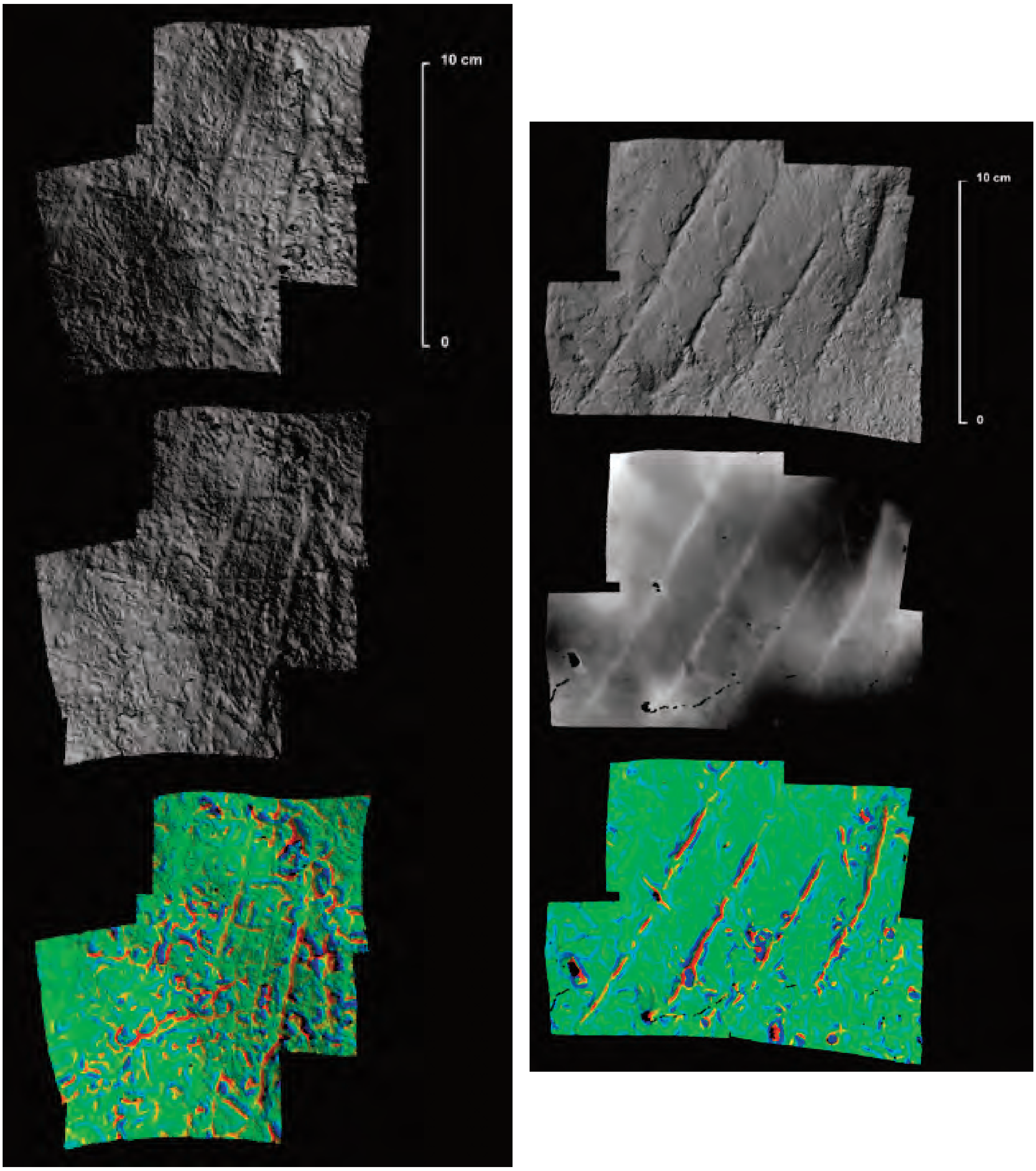

Figure S4. Structured light scanned bear scratches on the floor of the Lower Gallery of La Garma (Spain). Detailed images published in Figure 6 (a-f) of Paper 8 with different light filters in order to a better visualization of the scratches.

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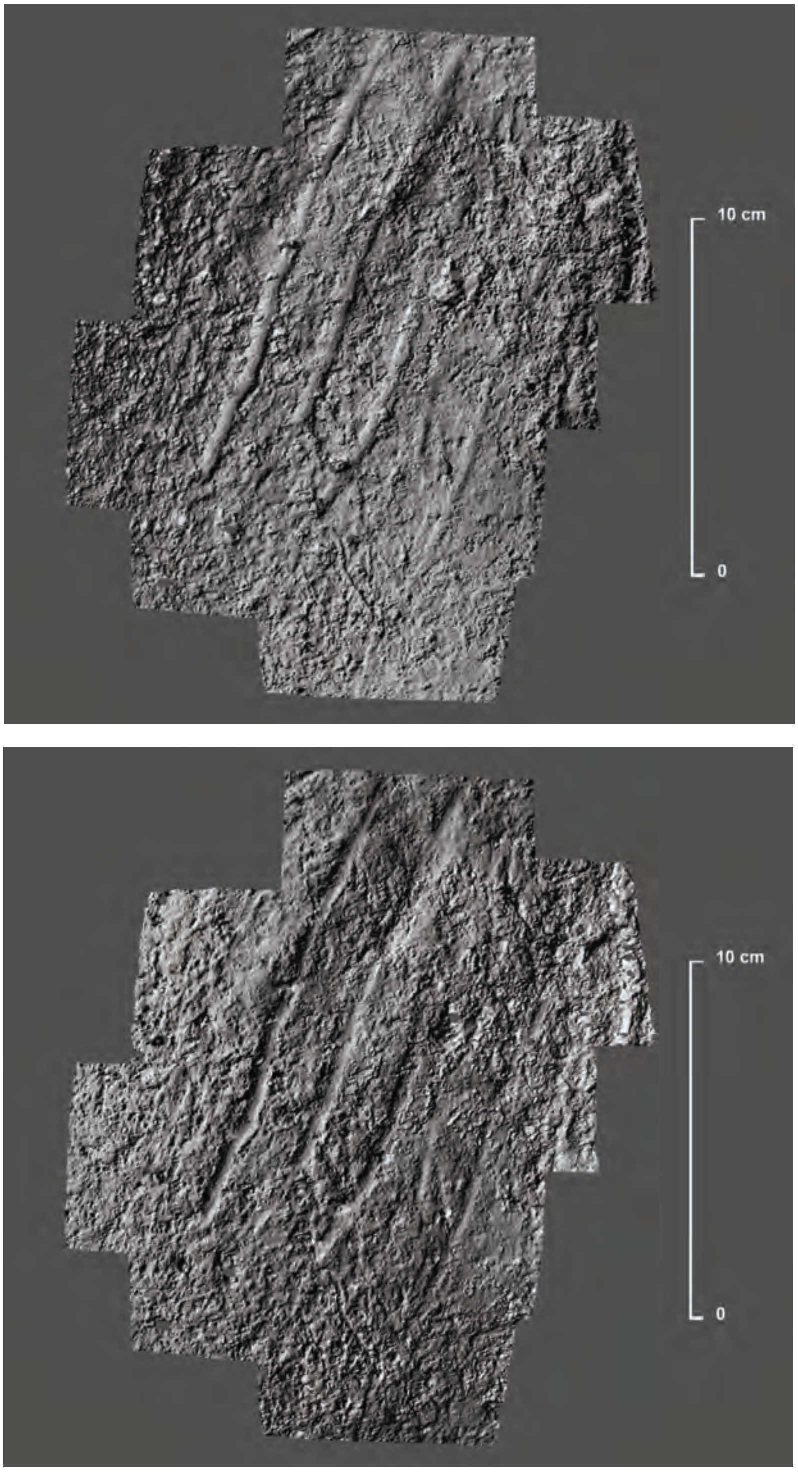

Figure S5. Structured light scanned bear scratched on the wall of the Lower Gallery of La Garma (Spain). Detailed image of the scratch published in Figure 6 (g) of Paper 8 with different light filters in order to a better visualization of the scratches.

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Figure S6. The experiment has also been developed with hyenas (*Crocuta crocuta*) at Cabárceno Nature Park (Cantabria, Spain): a) Excavating the experimental burial pit; b) Placing the structured burial base; c-d) Placing the deer (Cervus elapus) soft tissue and bone remains; c) Covering and compacting the experimental burial pit before the experiment.

Figure S7. Female hyenas (*Crocuta crocuta*) during the experiment: a-b) Digging the experimental burial pit to recover the deer remains placed at a depth of 50 cm.

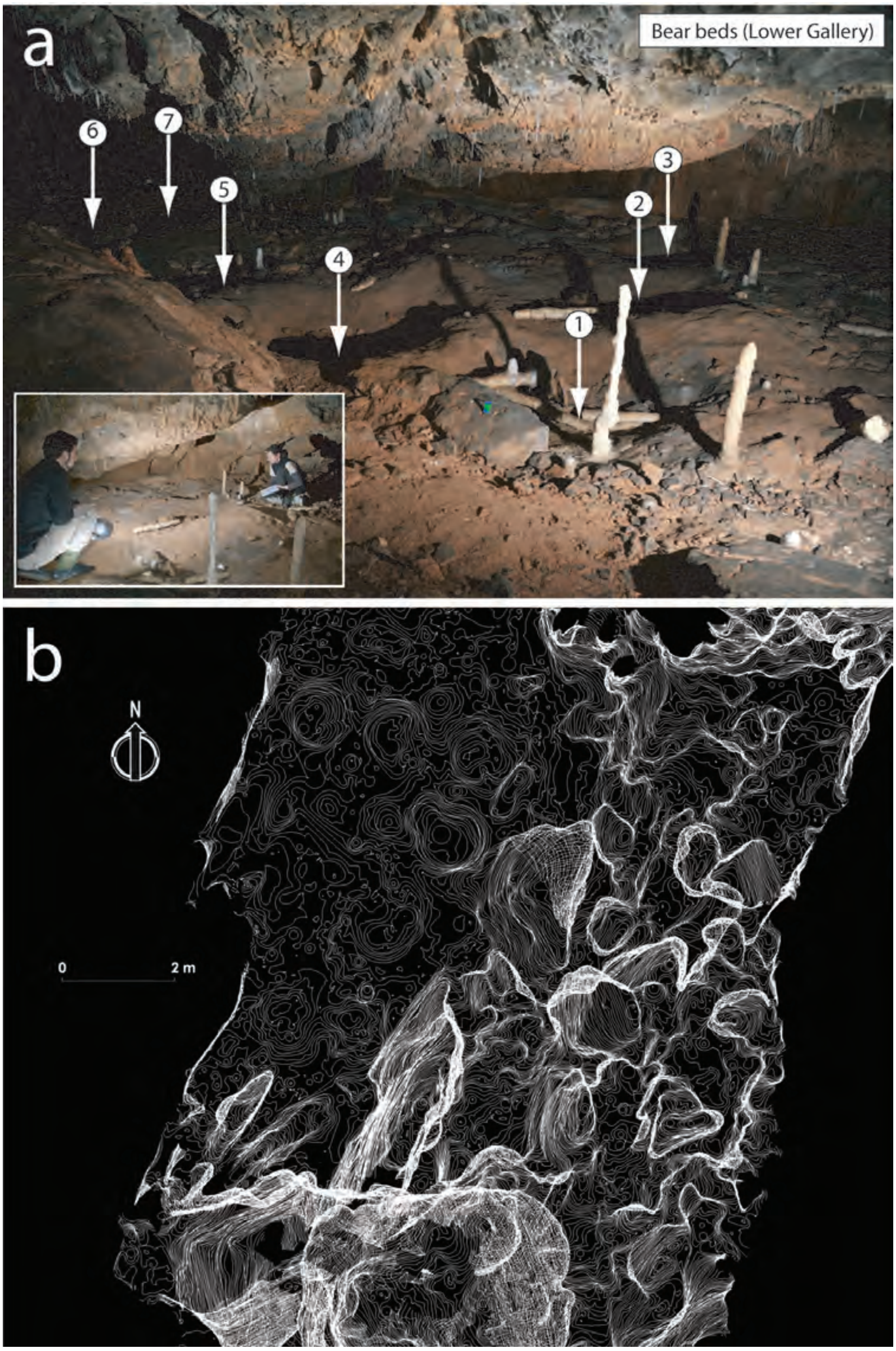

Figure S8. Zone IV of the Lower Gallery of La Garma (Cantabria, Spain): a) Image and numeration of the bear beds used for the research; b) Plan of Zone IV where bear debs are located (and appreciated).

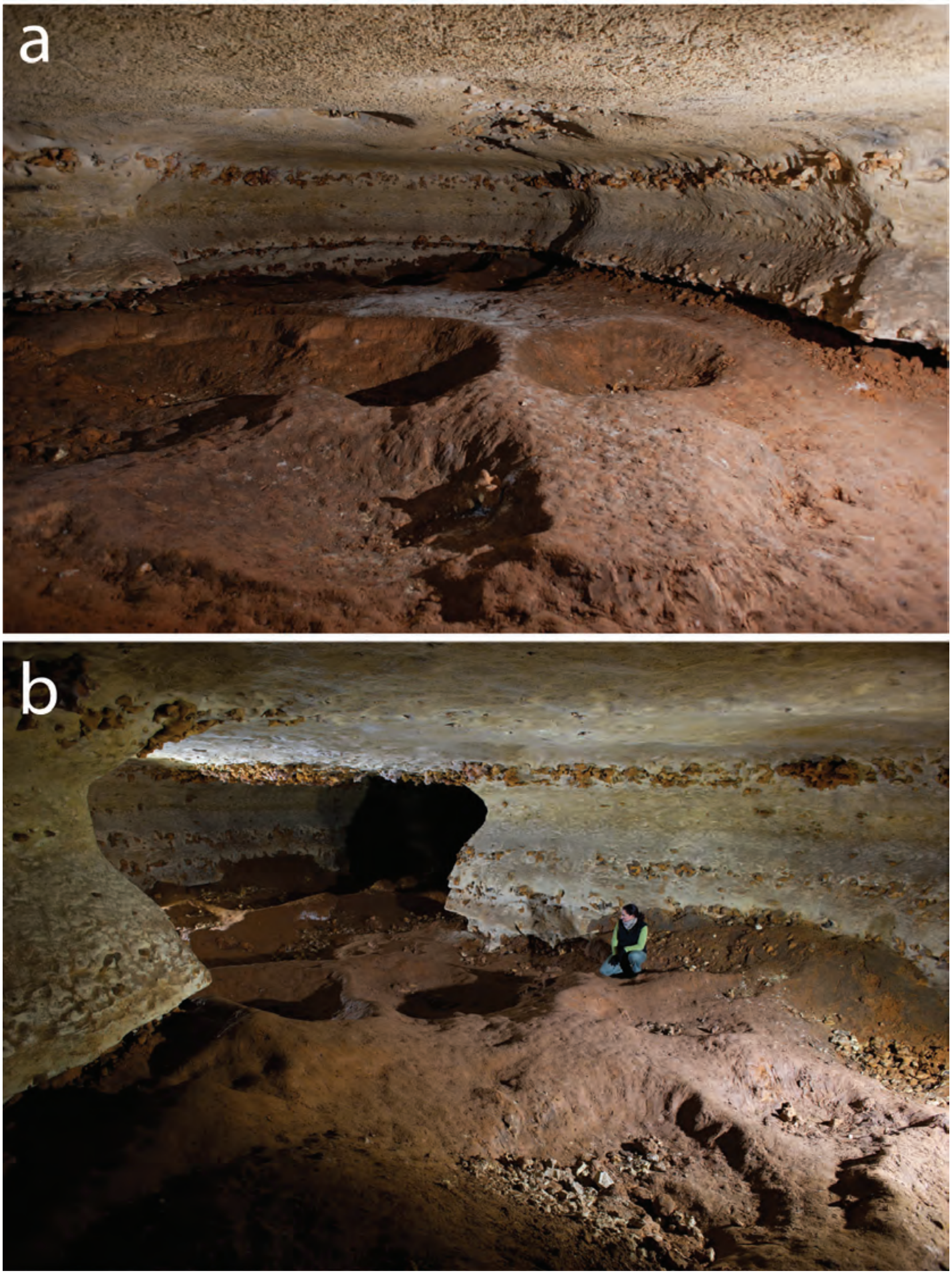

Figure S9. Rouffignac Cave (Dordogne, France): a) Bear beds from Rouffignac used for the research and b) image with a human scale in order to appreciate how big they are.

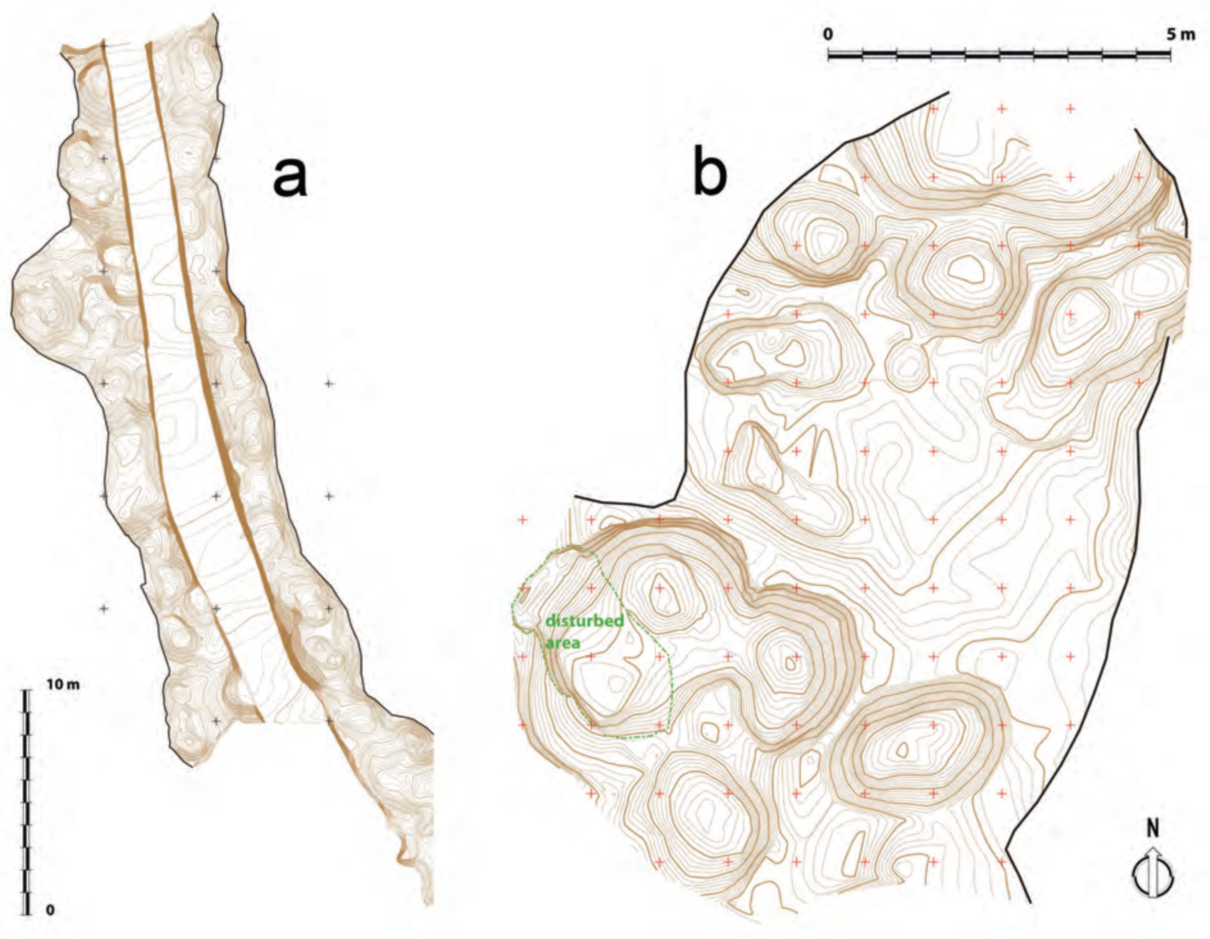

Figure S10. Rouffignac Cave (Dordogne, France): a and b) Plan of the zones where the bear beds used for the research are located. The trench for the touristic train can be appreciates in a. The location of the zones can be found in Figure 5 from section Materials and methods.

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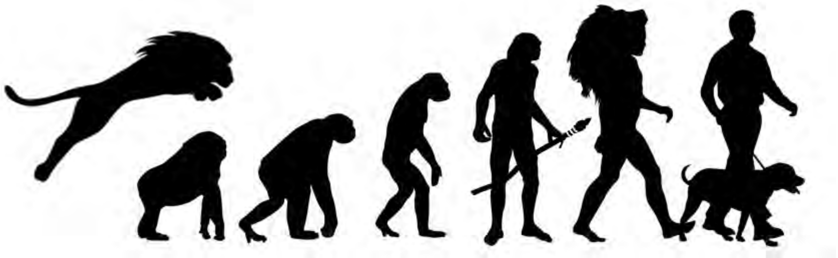
4.4.3

PAPER 9

Large carnivore attacks during the Pleistocene: A forensic approach with a Neanderthal example



Chapter 4.4 *Case studies of hominin-carnivore interaction during the Pleistocene*

Paper 9

Large carnivore attacks on hominins during the Pleistocene: A forensic approach with a Neanderthal example

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Interaction between hominins and carnivores has been common and constant through human evolution and generated mutual pressures similar to those present in worldwide modern human-carnivore conflicts. This current interaction is sometimes violent and can be reflected in permanent skeletal pathologies and other bone modifications. In the present paper, we carry out a survey of 124 forensic cases of dangerous human-carnivore encounters. The objective is to infer direct hominin-carnivore confrontation during the Pleistocene, which is important to understand behavioral changes during human evolution. In addition, the case of Neanderthals is analyzed in order to find evidence of past attacks using forensic observations. The results obtained pose that Neanderthals could potentially have been involved in dangerous encounters during the Pleistocene, validating our methodology to approach past attacks from a forensic perspective.

Keywords: Carnivores, interaction, confrontation, forensic medicine, neanderthals

Archaeological and Anthropological Sciences, DOI: 10.1007/s12520-015-0248-1

Introduction

Predation is assumed to be a fundamental influence in the evolution of primate behavior (Cheney and Wrangham 1987). Consequently, deterrence of predation has been described as an element with a high sociobiological impact on the origin of the human condition (Fay et al. 1995). Brain (1981) once asked "Who killed the Australopithecines?" as he recognized that the interaction between hominins and carnivores had enormous potential for the study of human behavioral changes; he pointed out that humans could effectively handle these interactions simply by increased intelligence and development of technology (Brain 1981).

Research on direct confrontation between hominins and large carnivores is clearly important (Hart and Sussman 2005), and yet this subject has not been extensively explored, largely due to the difficulty of approaching the topic using only archaeology and/or paleoanthropology. Nevertheless, dangerous encounters between carnivores and archaic forms of genus Homo have been inferred (e.g., Brain 1981; Bunn and Ezzo 1993; Treves and Naughton-Treves 1999; Boaz et al. 2004; Baquedano et al. 2012). The interactions between hominins and large carnivores have occurred at high frequency and taken different forms that generated mutual pressures (Rosell et al. 2012). Scenarios emerging from these pressures include dependency (scavenging) (Binford 1989; Stiner 1994), confrontation (carnivore hunting) (Auguste 1995; Arribas et al. 1997; Tillet 2002; Pérez Ripoll et al. 2010), competition for the use of caves as dwellings (Blasco and Rosell 2009), and the exploitation of common prey (Pettitt 1997). One of the latest documented scenarios is domestication during the Late Pleistocene (Germonpré 2013).

Today, similar pressures result globally in conflicts between different wild large carnivore species and humans (Treves and Karanth 2003; Pettigrew et al. 2012). For example, conflicts are mainly related with snow leopards (*Uncia uncia*), leopards (*Panthera pardus*), tigers (*Panthera tigris*) and Asian black bears (*Ursus thibetanus*) in Asia (e.g., Hussain 2003; Mishra 1997; Sekhar 1998; Dhar et al. 2008); lions (*Panthera leo*), African hunting dog (*Lycaon pictus*) and hyenas (*Crocuta crocuta*) in Africa (e.g., Patterson et al. 2004; Gusset et al. 2009; Kolowski and Holekamp 2006); wolves (*Canis lupus*), cougars (*Puma concolor*) and bears (*Ursus arctos horribilis, Ursus americanus*) in North America (e.g., Musiani et al. 2003; Conrad 1992; Herrero and Fleck 1990); jaguars (*Panthera onca*) and pumas (*Puma concolor*) in South America (e.g., Polisar et al. 2003; Mazzolli et al. 2002); dingoes (*Canis lupus dingo*) in Australia (e.g., Allen and Sparkes 2001); or brown bears (*Ursus arctos*) and wolves (*Canis lupus*) in Europe (e.g., Swenson et al. 1999; Linnell et al. 2002). The reasons for these conflicts are mainly associated with the similar resource use patterns of people and wild animals (Ahmed et al. 2012) and with their overlapping habitats (Agarwal and Mumtaz 2009). These conflicts have generated a rising incidence of attacks that constitute an increasingly serious form of human-wildlife confrontations conflict (e.g., Herrero and Higgins 2003; Conover 2008; Brown and Conover 2008; Neto et al. 2011), related to shrinking wild carnivore habitats (Skuja 2002), loss of their prey (Thakur et al. 2007) or wildlife hunting (Inskip and Zimmermann 2009). As such, they present a scenario of mutual pressures between humans and wildlife that may be comparable to the relationships that existed between large carnivores and hominins during the Pleistocene. Fossil humans could have been involved in direct confrontation scenarios (dangerous encounters) with large carnivores similar to those seen today,

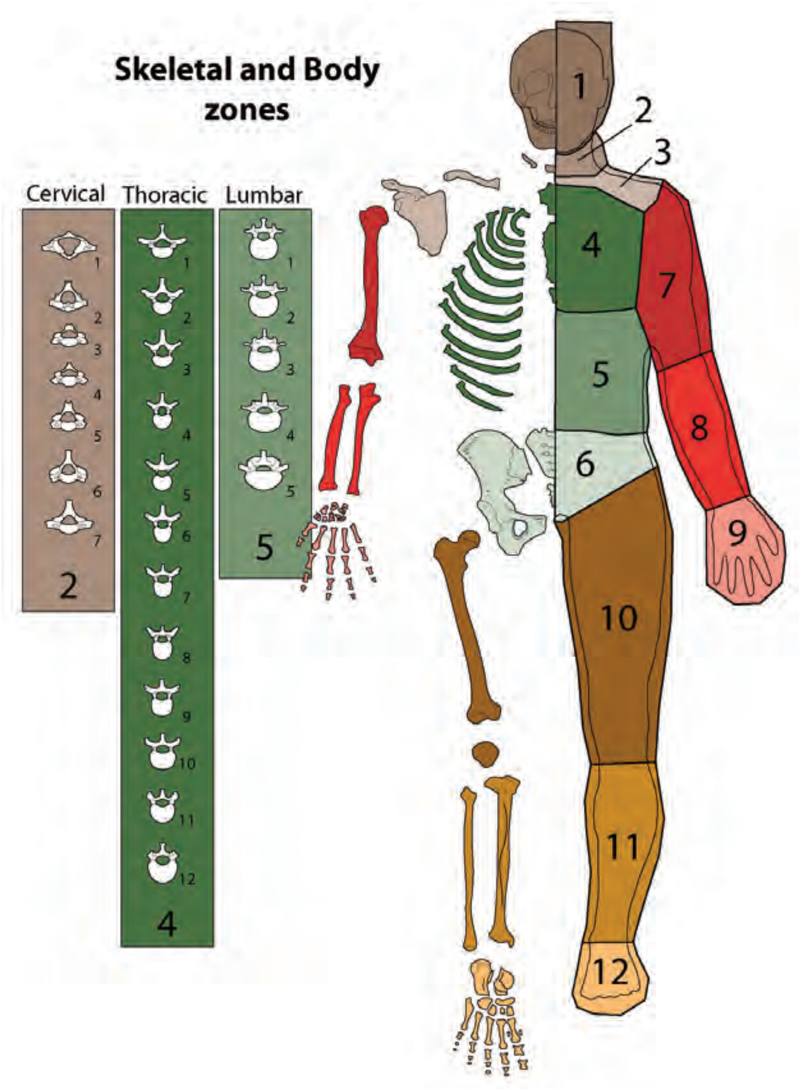

Figure 1. Classification of skeletal and body zones used in the forensic survey.

which then have the potential to provide insight into hominin behavior and even inferences regarding social organization (e.g., Dhar et al. 2008; Nabi et al. 2009a; 2009b; Rasool et al. 2010).

For this reason, we carried out a forensic survey with the objective of developing a comparative methodology aimed at identifying direct confrontations between hominins and carnivores during the Pleistocene. An application example is provided for the case of Neanderthals as a proof of concept, as these hominins are assumed to be a human form that had a close relationship with large carnivores (e.g., Estévez 2004; Dusseldorp 2011).

Materials and methods

Forensic information of carnivore attacks on humans was obtained by carrying out an intensive bibliographic survey. The data selected were obtained in specialized medical journals involving forensic cases where victims and injuries caused by carnivores could be clearly documented. The carnivores selected were members of the ursid, felid, and canid families. Although few well-described forensic cases exist for hyenids, this carnivore is also included in our survey (except for statistical observations).

All information has been transferred to a database where individual characteristics either of the victims and/or the attacking carnivores can be examined. Each case has been individualized so specific aspects of the resulting injuries inflicted by the animals could be overviewed. All injuries (including bone damage and general body wounds) are clustered depending on their location in skeletal and body zones (Fig. 1). A total of 124 cases are studied, and of these 92 are considered for the quantitative analysis as the damage can be isolated. All information related to each case is available as Online Resource Material (the forensic cases database is also related to the bibliographic list provided) (Online source 1 and 2).

Observations are applied to the study of a Neanderthal bone fragment from the site of Cova Negra and to the register of traumatic lesions observable on the Neanderthals skeletons provided by Berger and Trinkaus (1995).

Forensic information is evaluated and patterns for each carnivore family in direct confrontation with humans are presented. A statistical approach is developed with the objective of observing major and minor injuries inflicted by each carnivore family. Nevertheless, our main interest is documentation of bone damage caused by all carnivores.

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Results and discussion

Forensic survey of carnivore attacks to humans

Interaction between humans and wild animals has increased in recent decades (Ambarli and Bilgin 2008; Inskip and Zimmermann 2009), with a high proportion of these contacts being violent (Dhar et al. 2008). Carnivore attacks are characterized by the combined occurrence of injuries (including puncture wounds, lacerations, avulsions, and bone fractures (Baliga et al. 2012)), crushing, and penetrating trauma (Agarwal et al. 2011). Humans attacked by large carnivores are consequently at risk of suffering blunt and penetrating trauma caused by teeth, paws, and claws, which may lead to a local infection (Capitini et al. 2002; Kunimoto et al. 2004; Lehtinen et al. 2005; Turkmen et al. 2012) because wounds are often contaminated with a variety of pathogens (polymicrobial infection) such as *Pasturella multocida* and others (Kizer 1989; Isotalo et al. 2000; Linnell et al. 2002; Abrahamian and Goldstein 2011). Fatal attacks are common, especially in Africa and Asia (Conrad 1992), although many cases are reported in which victims survive a violent encounter with a carnivore (Agarwal et al. 2011). After a carnivore attack, victims may develop future specific pathologies such as arthritis (e.g., Burdge et al. 1985) or others (see Papadoulos et al. 1999).

Although these are general trends observed in carnivore attacks, specific patterns can be identified in the forensic survey resulting from different carnivore families.

Ursidae

Direct confrontation between humans and bears is relatively common in different parts of the world (Lathrop 2007), and must be considered either as predatory or defensive (Herrero 1985; Herrero and Fleck 1990). Subspecies involved in these dangerous encounters are the black bear (*U. americanus*) (Murad and Boddy 1987), grizzly bear (*U. arctos horribilis*) (Cardall and Rosen 2003; Kunimoto et al. 2004), Asian black bear (*U. thibetanus*) (Agarwal et al. 2011), and less commonly the polar bear (*U. maritimus*) (Herrero and Fleck 1990) and brown bear (*U. arctos*) (Ambarli and Biglin 2008). Although other subspecies are involved in attacks on humans (Rajpurohit and Krausman 2000; French 2001), only those cited here were studied in our forensic research. A total of 45 cases were analyzed.

In general, death is not common after a bear attack (Herrero and Fleck 1990), although serious injuries are generated by teeth, claws, and paws (French 2001). The bear attack pattern is one of the best studied in forensic medicine (e.g. Rasool et al. 2010). Bears tend

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to rear up on their hind legs and strike victims with their claws (Dhar et al. 2008). Biting the victim is also common and a bear attack ends with different degrees of minor and major injuries, predominantly located in the upper half of the body (Dhar et al. 2008; Rasool et al. 2010; Agarwal et al. 2011; Baliga et al. 2012), especially in the head and face (Thakur et al. 2007).

The present observation of a total of 45 forensic cases is commensurate with this known attack pattern of bears. Figure 2.1 shows that within the 38 case studies with bone modifications, the main bone damage is located in the head zone (skull and mandible) and upper limbs (clavicle, humerus, radius, ulna, metacarpals, and hand phalanges). Bears tend to attack the victim's head, causing wounds and fractures in that zone; and humans react by protecting themselves with their arms, causing damage in that region. Long-bone diaphyseal linear, comminuted, and segmental fractures in the upper limb are not rare, and finger amputation is also common (Dhar 2008). All these bony injuries are frequently associated with general soft-tissue wounds (Fig. 2.2), as observed in other cases (Rasool et al. 2010). Therefore, bone modification after a bear attack would appear to occur in the body areas where other general non-bony wounds are inflicted by the animal.

Felidae

Feline attacks on humans reflect a predatory behavior in nearly all cases and follow the same pattern employed for predation on other large mammals (Cohle et al. 1990) in both wild and captive contexts (e.g., Henja 2010). These encounters may not always be fatal for humans (Wright 1991), but due to large cats' attack pattern, they can result in very serious wounds caused by teeth and claws. Feline-human conflicts that end in dangerous encounters are increasingly common occurrences in different parts of the world (Nyhus and Tilson 2004; Inskip and Zimmermann 2009).

The felines (basically leopards (*Panthera pardus*) (Nabi et al. 2009a), jaguars (*Panthera onca*) (Neto et al. 2011), lions (*Panthera leo*) (Packer et al. 2005), tigers (*Panthera tigris*) (Langley and Hunter 2001) and cougars (*Puma concolor*)) attack humans in the same way in most cases. They carry out a solitary surprise attack motivated by a predatory behavior that can be stimulated by the quick erratic movements of the victim (e.g., jogging or running) (Conrad 1992; Rollins and Spencer 1995). Prey size is considered by felines in their solitary hunting (Atwood et al. 2007); thus, children are commonly attacked (Chum and Pui 2011). Felines rarely employ a head-on attack, but prefer to approach the victim from behind or over the shoulder (Chapenoire et al. 2001). This results in major injuries in the head, nape, and neck regions, especially from penetrating bites that cause skull damage,

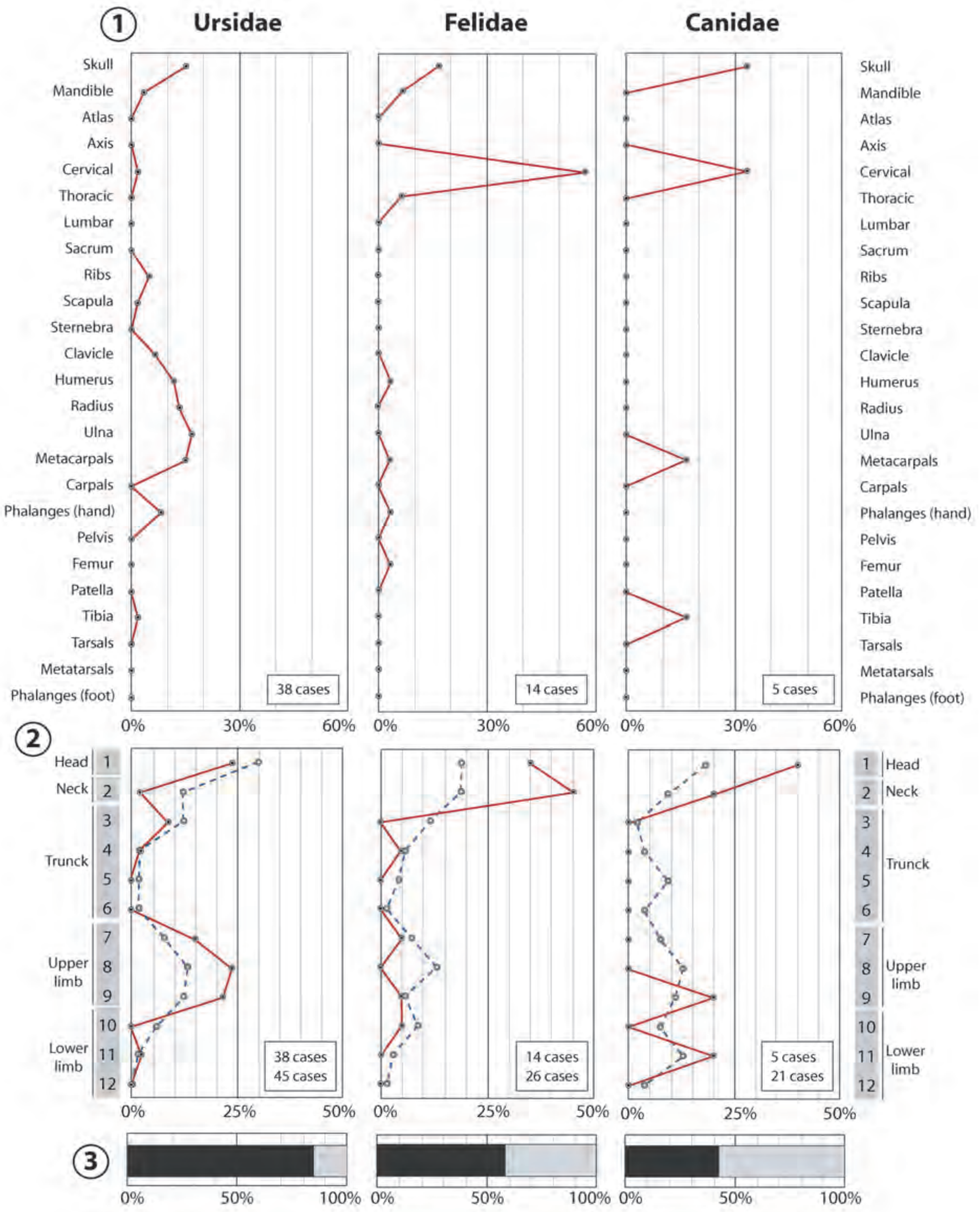

Figure 2. Different patterns observed in carnivore attacks on humans by Ursidae, Felidae and Canidae. 1) Bone damage (fractures/scores/punctures) observed in different cases for each skeletal element; 2) Bone damage (fractures/scores/punctures) (red line) compared to general wounds (blue dashed line) in different cases for each body zone (numbers refers to Fig. 1); 3) Average of bone damage compared to general wounds present in all cases. Source data provided as Online Resource Material (see Online Resource 1 and 2).

cervical vertebral fractures, and/or damage to the anterior neck structure (Conrad 1992; Henja 2010; Emami et al. 2012). Claws usually cause deep lacerations in the back. Other body regions, although represented by a minimum number of cases, can also be damaged (e.g., Burdge et al. 1985).

Bone damage on humans is basically defined by the feline's particular attack pattern. The predatory attack involves shaking the prey by the neck region (Bury et al. 2012), causing subsequent cervical lesions (Bock et al. 2000; Murphy et al. 2007; Nabi et al. 2009b; Chum and Pui 2011). This is usually defined by compound fractures of the cervical bodies (Chapenoire et al. 2001). Nevertheless, skull surface damage can also be caused by a big cat attack, and modifications such as scores, punctures, perforations, or cortical fractures caused by several bites may occur (Conrad 1992; Neto et al. 2011).

Our observations of 26 cases (14 with bone damage) corroborate previous studies, as bone damage is located in the head and neck area (Fig. 2.1). Cervical vertebrae are the principal bone elements that suffer modification after a feline attack on a human. Other skeletal elements can also be affected, resulting from a defensive reaction by the person being attacked. Extremities are not the primary region where felines attack, but limbs are involved in rare cases (Conrad 1992) and exhibit comminuted bone fractures (Prayson et al. 2008) (Fig. 2).

Comparison of bone damage with other wounds not related with osteological modification by body zone (Fig. 2.2) shows good association in 26 cases. However, the upper limbs show more general wounds that do not include bone damage (specifically on the forearm). Wounds are located in this zone because the victims try to defend themselves from the attack with their arms.

Canidae

Currently, canids (essentially foxes, dingoes, wolves, and domestic dogs) account most frequently for cases of animal-related fatalities, with a very high number of attacks on humans (see Langley 2005). Our interest in canid-related fatalities was restricted to canid pack attacks and to single wild wolf attacks. Due to their ethology, most canids develop group hunting (Borchelt et al. 1983), and therefore a single animal attack is somewhat rare in nature with wild specimens, although it happens (Linnell et al. 2002). In the present time, attacks by single canids on humans are rather more common (Weiss et al. 1998; Macbean et al. 2007) but are represented by *Canis familiaris*, and this is related to domestication and the consequences of living with these animals. Therefore, we have mainly

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focused on canid pack attacks, a situation where even domestic dogs, as social animals, have an inherent pack instinct that can cause them to become excited to a frenzy by the smell and taste of blood (Kneafsey and Condon 1995). Furthermore, since domestic dog pack attacks are very similar in pattern to those seen with wolf groups in the wild (Butler et al. 2011), they are also included in our survey.

Pack behavior will generate an attack pattern directed toward humans that consists of immobilizing the prey by striking at the limbs. Once the prey has been brought down, canids will attack all parts of the body (Fonseca and Palacios 2013), especially the head and neck area (Kneafsey and Condon 1995; Avis 1999; Linnell et al. 2002; Bury et al. 2012), followed by extremities (Wright 1990). Defensive marks can also appear on the upper and lower extremities (de Munnynck and van de Voorde 2002), and the victim's movements will simultaneously stimulate the attack (Lauridson and Myers 1993), even leading to amputation of portions of a limb (Avis 1999). Biting, clawing, and crushing forces to the head, neck, and hindquarters will produce a combination of wounds, described as punctures, lacerations, and avulsion of skin and soft tissue (Santoro et al. 2011). Bone damage also occurs to those zones (Bury et al. 2012). In the case of wolves, a predominance of injuries on the dorsal aspect of the body has been observed by Nabi and colleagues (2009a).

As with felines, canids select their prey by size; thus, children are very often targets of attacks (Fouriel and Cartilidge 1995). Because of a child's relatively soft and vulnerable skull, serious penetrating injuries of the cranium have been described (idem.).

A total of 21 cases have been analyzed; five were pack attacks. The canid collective attack strategy leads to the appearance of bone damage on different parts of the body such as the head (skull), the neck (cervical vertebrae), and the arms (metacarpal) and legs (tibia) (Fig. 2.1).

Comparison of the body regions where bone damage appears with the location of general wounds (Fig. 2.2) after a canid attack indicates that soft tissue injuries are not highly related with osteological modification. In this sense, a canid attack can generate serious wounds all over the body, especially in the trunk region (Nabi et al. 2009a), but this does not mean that bone damage is associated.

Hyenidae

Hyena attacks are not well reflected in forensic literature and thus are not included in the database and quantitative study of carnivore attack patterns. Nevertheless, this section has been added to illustrate that hyena attacks on humans are common today, just as they could have been in the past.

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In Africa, hyenas coexist with humans at a high density in some countries (Yirga et al. 2012) and this situation may lead to dangerous encounters. In situations of hunger, hyenas can attack humans, perceiving small children and the elderly as vulnerable and easier prey (Brain 1981; Gade 2006). Nevertheless, although predatory attacks on people occur, hyenas much more commonly feed on humans by scavenging human tombs in cemeteries (Horowitz and Smith 1988; Yirga et al. 2012).

The scarcity of forensic literature on hyena attacks complicates any inference regarding an attack pattern towards humans. In spite of this situation, Mitchell and others (2011) have recorded an attack on a 27-year-old female in Tanzania that reveals a probable pattern. In this case, a single hyena followed a pattern similar to the one employed by large cats, by attacking the head and neck region of the victim in an attempt to cause prey submission, and probably damaging the cervical spine zone (Mitchell et al. 2011). Although hyenas look like canids, genetically they are similar to felines, and in this sense, hyenas probably follow a similar pattern to that of one of the large cats (idem.)

This single case is not sufficient to infer a pattern, especially considering the pattern that hyenas follow to hunt other non-human mammals. Hyenas develop both lone and cooperative prey captures, although individual hunting has a much higher average of success (Watts and Holekamp 2007). The hyena hunting strategy reveals no significant preference for any species and its behavioral opportunism allows the capture of anything it can overpower (Hayward 2006). Concerning prey size, a single hyena can capture a prey three times its body weight (Watts and Holekamp 2007).

Comparison between carnivore attacks

Similarities and differences both exist among carnivore attack patterns on humans. The evidence suggests that carnivores, when attacking humans, follow the same pattern as when hunting non-human prey (Herrero and Fleck 1990), especially if the attack is predatory. In these cases of attacks on humans, prey size again seems to be an important factor (Gade 2006), and is the reason why so many attacks on children have been recorded, especially in cases related with canids, felines, and even hyenas (e.g., Brain 1981; Conrad 1992; Fouriel and Cartilidge 1995; McKee 2003; Gade 2006).

The patterns followed by different carnivores when attacking humans permit the inference that carnivores can be grouped by family, rather than by species, depending on their ethology.

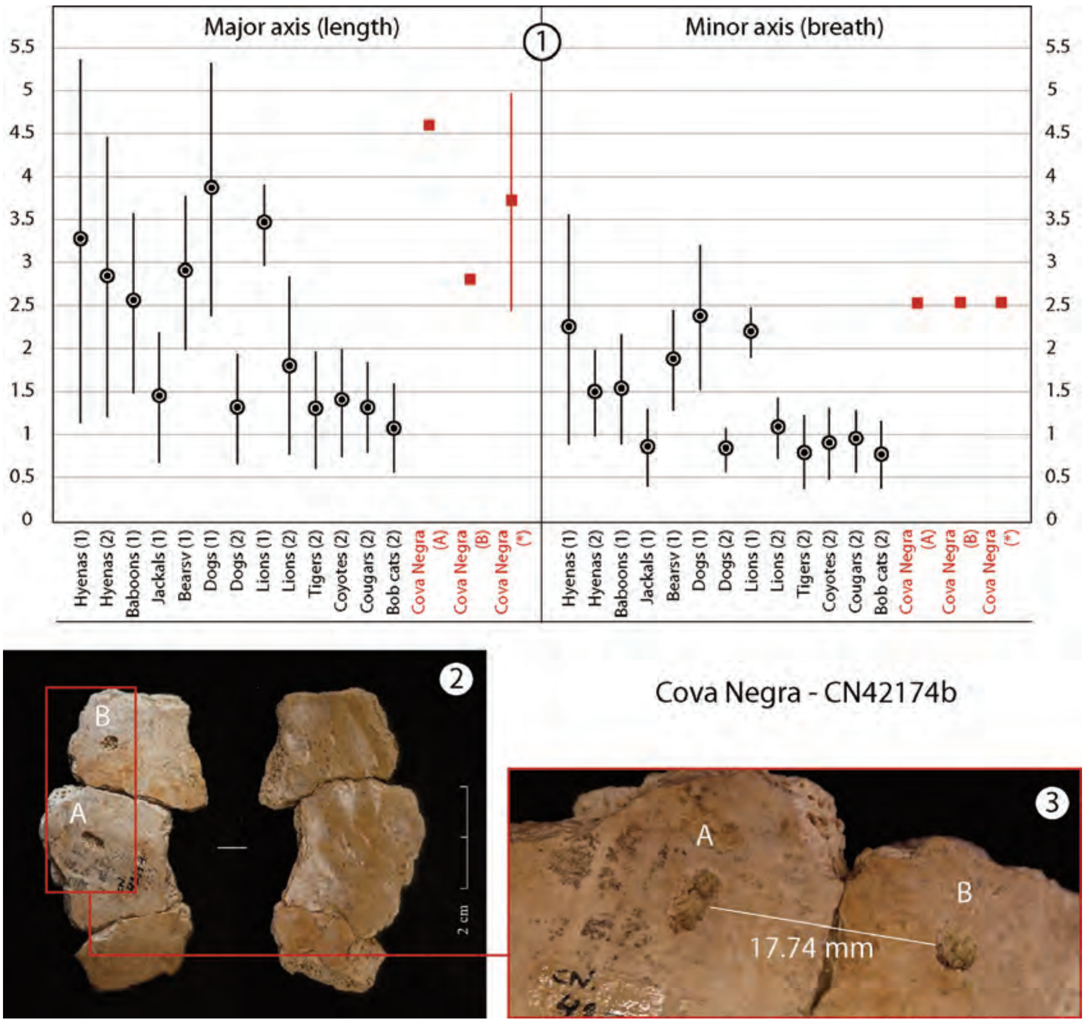

Figure 3. Cova Negra puncture sizes compared to the mean percentages of tooth pit sizes on diaphyses produced by different carnivores, according to Dominguez-Rodrigo and Piqueras (2003) (1) and Delaney Rivera et al. (2009) (2); 2) Cova Negra right parietal CN42174b with punctures A and B highlighted and 3) detail of the punctures with the interpuncture distance measured.

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In general, carnivore attacks result in minor or major injuries, and only a relatively small proportion are fatal (Agarwal et al. 2011). However, this depends on the type of carnivore species. In the case of felines, the average number of attacks that lead to death is extremely high when compared to bears (Nabi et al. 2009a). This is probably because most cases related to felines are predatory (Neto et al. 2011), in contrast with bear attacks, which may often be related to defensive attacks (of their cubs or their territory) (Ambarli and Bingin 2008). This is also something that can be inferred in the way a human is attacked. Ursids usually attack their victims from the front and as a dissuasive action (increased by a defensive reaction of the person, understood by the bear as a fighting response) (French 2001). Felines, on the other hand, tend to attack the victim/prey from the rear or over the shoulder (Chapenoire et al. 2001). The case of canids can be also classified as predatory or defensive attacks, and their attack pattern is similar to that of felines in the sense that they target the neck region, shaking the prey into submission (Bury et al. 2012). Nevertheless, the main difference is that canids usually attack in packs and therefore other pack-members would help bring down the victim by biting the upper and lower extremities. As in bear attacks, death is not as common in canid attacks as it is following feline attacks.

One common feature of nearly all the carnivore attack cases, whether they are predatory or defensive, is that the victim was alone at the precise moment of the encounter with the attacking animal. Regarding the number of animals attacking, in the wild, felines (except for lion prides) and bears attack alone (although they can be accompanied by their cubs) and canids usually attack in packs.

The behavior of the animal attacking a human will determine the general injury pattern and, because the attack behavior is different for each carnivore family, the injury pattern will differ (Fig. 2). Among all carnivore families studied in the present paper, bears generate much more bone damage in cases of attacks (85 %), followed by felines (58 %), and canids (42 %) (Fig. 2.3).

Our observations indicate that each carnivore has a different attack pattern that at the same time generates a different injury pattern, including differences in bone damage. These observations can be a general forensic base for differentiating between different carnivores responsible for an attack on a human, which may be difficult to identify on some occasions (Kiuchi et al. 2008).

Proof of concept: The Neanderthal case

The present paper has a clear forensic application and interest due to the characterization of the damage caused by carnivore attacks. Nevertheless, the aim of the research was to

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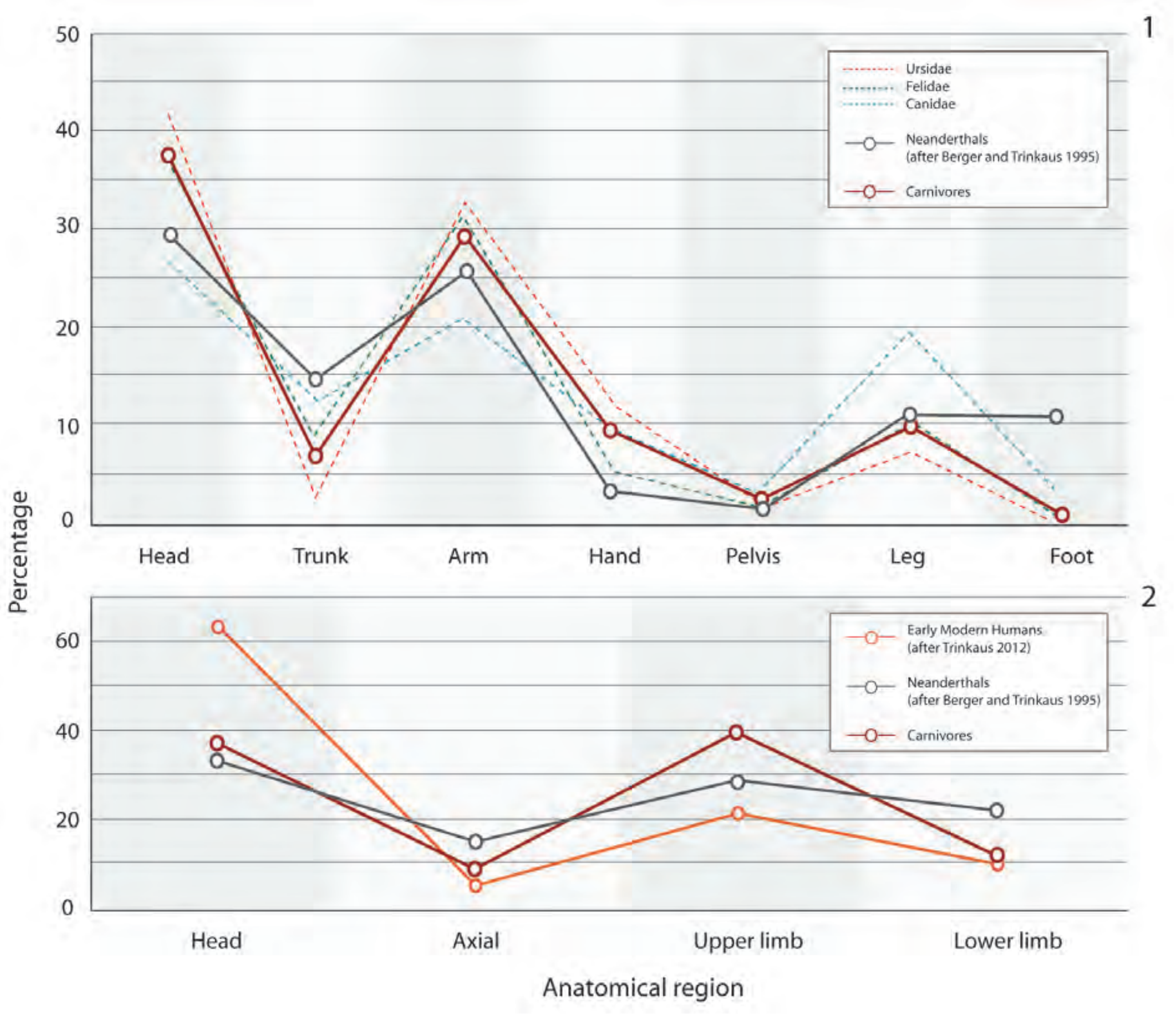

Figure 4. Percentage distributions of traumatic lesions by anatomical region caused by carnivores compared to 1) Neanderthal lesions sample (Berger and Trinkaus 1995) and 2) Neanderthals and Early Modern Humans (Trinkaus 2012).

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propose a methodology for collecting evidence for the reconstruction of past attacks. The comparison of a present scenario with a past one is valid because direct confrontation between hominins and carnivores during the Pleistocene, as in the present, involve mutual pressures derived from a conflictive relationship where common interests overlap (e.g., Schuette et al. 2013). Therefore, we use the modern relationship between humans and carnivores as a valid analogy (Treves and Naughton-Treves 1999) in order to approach the study of carnivore attacks on humans.

Providing evidence for this issue is not an easy task, and as a proof of concept, we have selected Neanderthals to validate our methodology. The Neanderthals developed intense interactions with large carnivores (Gamble 1993) due to mutual pressures arising from conflicts where competition was an inherent factor. Many pressures existed between top-carnivore Neanderthals (Bocherens et al. 2001) and carnivores, as both competed directly for resources (e.g., Dusseldorp 2011) and used the same caves (e.g., Straus 1982). The Neanderthals also hunted large carnivores (see Blasco et al. 2010). Moreover, it is not uncommon to find a good representation of carnivore remains in the archaeological sites where Neanderthals are documented, confirming their presence in the same territories (Straus, 1992; Mussi 2001; Brugal and Fosse 2002) This scenario provides a context where direct confrontation existed and therefore it is an excellent case for applying our forensic observations in order to confirm past carnivore attacks on humans.

The Cova Negra (Spain) site, a well-known cave occupied during the Middle and Upper Pleistocene (Villaverde et al. 1996; Villaverde et al. 2004), contained 24 Neanderthal bone remains belonging to cranial, dental, and postcranial elements (Arsuaga et al. 2007). We have analyzed one of them (CN42174b), a cranial fragment belonging to the central part of a right parietal (idem.), due to its high similarity with the punctures present at cranial fragment SK-54 from Swartkrans (South Africa) described as a fossil reflecting a leopard attack to an Australopithecus by Brain (1981). The parietal fragment bone CN42174b (Fig. 3) presents two measurable punctures on the exocranial surface, produced by a large carnivore (Fig. 3.2 and 3.3), although the damage was interpreted as the action of a small carnivore by Arsuaga et al. (2007). The length and breadth have been measured and compared with data available from experimental samples provided by Domínguez-Rodrigo and Piqueras (2003) and Delaney Rivera et al. (2009). The results show how the size of both punctures matches the largest ones visible on Figure 3.1, comparable with bears, large canids, or hyenas.

The punctures have been produced by both canines (left and right) of a carnivore with an intercanine width of 17.74 mm, which would correspond to a medium-sized carnivore, according to Murmann et al. (2006). If we take in account our forensic observations (Fig. 2) and the probable size orientation provided by neotaphonomic studies (Fig. 3.1), we can propose that the Cova Negra Neanderthal represented by the CN42174b fragment reflects an attack by a large felid. This is something coherent in relation with the faunal spectrum present at Cova Negra Mousterian levels, where *Panthera pardus* has been identified (Villaverde et al. 1996). This interpretation is different to the one provided by Arsuaga and colleagues (2007), where they argued that the carnivore damage was generated postmortem by a fox size carnivore. This new interpretation is related to our present taphonomic analysis of the fossil specimen.

Nevertheless, application of our forensic observations to the paleoanthropological record is not the only strategy available to verify past carnivore attacks on Neanderthals. Proof can also be obtained by paying attention to the paleopathologies displayed by Neanderthal skeletons.

Berger and Trinkaus (1995) studied traumatic lesions and post-traumatic degenerative changes in a large Neanderthal skeleton assemblage obtained from different archaeological sites. These authors recognized a high incidence of Neanderthal head and neck trauma (Berger and Trinkaus 1995: 845), and considered that anatomical distribution of traumatic lesions could provide an insight into Neanderthal behavioral patterns (Berger and Trinkaus 1995: 841); we would agree with this. They attempted to understand these lesions by comparing trauma among Neanderthals with lesion distributions from different recent human samples. The Neanderthal traumatic lesion pattern appears to be extremely similar to the one presented by North American professional rodeo athletes (Berger and Trinkaus 1995: 848). Berger and Trinkaus's main conclusion was that this general pattern was the result of frequent close encounters between Neanderthals and dangerous prey, due to their hunting strategy (defined by their available body-to-body technology) (Berger and Trinkaus 1995: 850).

The anatomical distribution pattern of traumatic lesions generated by carnivore attacks on modern humans is plotted in Fig. 4.1, together with the one provided by Berger and Trinkaus (1995). A close match is evident between the Neanderthal distribution and attacked humans, providing an alternative explanation to the "rodeo rider" hypothesis and a plausible scenario that could explain Neanderthal trauma.

The similarity of the trauma pattern between Neanderthal and Early Anatomically Modern Humans (EAMH) has led to recent questioning of the "rodeo rider" analogy (Trinkaus 2012). New alternatives, such as inter-human violence, are now proposed to explain the persistence of a similar traumatic injury pattern in the Upper Paleolithic (Trinkaus 2012: 3693). Results of a foraging mobility can also be an explanation for this common pattern (Trinkaus 2012: 3692), as has already been proposed (Berger and Trinkaus 1995).

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The injury pattern of humans attacked by carnivores has also been compared with the anatomical distribution of traumatic injuries in EAMH provided by Trinkaus (2012), and it also showed a close match (Fig. 4.2).

In this sense, direct confrontation between Neanderthals and carnivores could represent an alternative and plausible explanation for the injury pattern found on Neanderthal anatomical remains. Dangerous encounters between Neanderthals and large carnivores would be reflected in their skeletons in the form of fractured bones or injuries derived from post-traumatic degenerative osteological changes, as happens with modern cases (e.g. arthritis, see Burdge et al. 1985).

Furthermore, we can propose direct confrontation as a form of interaction between hominins and carnivores that also affected EAMH during the Upper Paleolithic. This would give an idea of the long duration of conflict between hominins and carnivores during the Pleistocene, which continues even in the present time due to mutual pressures.

The scenario of hominins as carnivore preys appears to be much more common than it was previously thought. Predation among hominins is not just restricted to Neanderthals and EAMH as we have discussed, early ancestors were also attacked (e.g., Brain 1981; Bunn and Ezzo 1993; Boaz et al. 2004; Eppinger et al. 2006; Baquedano et al. 2012; Curnoe and Brink 2010). Therefore, confirming predation on hominins through past attacks, especially in early moments of our evolution, is an essential task to accomplish in order to analyze the development of hominin behavior as it is an influence for cooperation emergence (Hart and Sussman 2011) or technological development (Brain 1981).

The effort to confirm past carnivore attacks is important because it is possible to extract social aspects of this specific relationship. The study of social factors related with modern carnivore attacks on humans can give ideas about behavioral inferences derived from direct confrontation during the Pleistocene. An interesting issue is the fact that, in Tanzania, for example, risk factors are recognized that can result in a lion attack, such as poorly constructed huts, walking long distances to resources, sleeping outdoors at night, or sightings of bush pigs (Kushnira et al. 2010). In India, bear attacks are more related with territoriality and villagers try to avoid attacks from bears by using a dog for protection and/or carrying weapons (Ambarli and Bilgin 2008). Another technique used in India to avoid bear attacks has been to travel in groups and avoid isolation (Agarwal et al. 2011), as nearly all attacks occurred when a person was alone collecting firewood in the forest (Dhar et al. 2008).

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In North America, activities that involve carrying dead ungulates, such as hunting, may attract grizzly bears, and this could end in a dangerous encounter (Fleck 1990). Concerning felines like cougars, jogging is an activity that may motivate a predatory attack (e.g., Neto et al. 2011). In the case of wolves, being accompanied by a dog may generate an aggressive behavior by wolves towards the dog (Linnell et al. 2002), although a common recommendation is to be accompanied by a dog to avoid carnivore attacks (see French 2001). In this sense, domesticated canids would provide security, although co-existing with dogs also has a high price due to the large number of domestic attacks recorded (Dhar et al. 2008).

Another significant factor related with social organization issues is the age and gender observed in a very high average of carnivore attacks in Asia. Rasool and colleagues (2010) report that the bear attack cases they studied (n=417) showed a predominance of middle-aged (96.8%) male victims (80.33%), which is attributed to the outdoor activities undertaken predominantly by men, rather than by women, in Indian society. This was also observed in Sumatra (Indonesia) with tiger attacks, where the typical victim is a middle-aged male working in his fields near the forest edge during the day (Nyhus and Tilson 2004). This pattern is also similar in Africa and may reflect a sexual division of labor or sex-differentiated ranging patterns among humans, as has been pointed out by Treves and Naughton-Treves (1999). A gender connection is also apparent in the confrontation between Maasai and lions, where spearing a male lion is part of a manhood ritual that provides immense prestige and a public display of bravery (Hazzah 2009), as well as an inherent risk.

In summary, examples of current direct confrontation between humans and large carnivores can help explain past carnivore attacks on humans and contribute ideas about how to recover human behavior by analyzing this complex relationship (Treves and Naughton-Treves 1999).

Conclusion

The conflict between humans and large carnivores has been present and constant throughout human evolution, enduring even to modern times. This conflict made direct confrontation during the Pleistocene an inherent factor in the relationship between hominins and carnivores. We provide a forensic methodology that is useful in diagnosing carnivore-related damage on human bones and allows discernment of the type of carnivore responsible for lesions found on fossil hominins based on the anatomical patterning. Therefore, bone damage resulting from a current-day carnivore attack can be used in a positive manner to recover information about past carnivore attacks by comparing it with fossil hominin traumas.

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In the present paper, we have applied our forensic observations to Neanderthal traumatic lesions provided by Trinkaus and Berger (1995) as a proof of concept, and provide an alternative explanation to the paleopathologies present on the Neanderthal skeletons related to carnivore attacks. Although evidence of attacks on Neanderthals by carnivores has been gleaned by just studying paleoanthropological remains (Cova Negra is one example discussed here), we postulate that comparison of bone damage with current forensic records is also a positive strategy for recovering this information as an actualistic framework to generate new approaches. Furthermore, we have observed that EAMH lesions are also explainable in a context of attacks on humans by large carnivores. In this sense, we prove with our forensic methodology that not just Neanderthals were attacked by carnivores, also EAMH were. This scenario seems to have been common during the Pleistocene and continues today due to similar mutual pressures.

Therefore, predation on hominins appears to be a common scenario during the Pleistocene and it has to be assumed as a constant influence in human evolution, and much more attention must be paid to this. In this sense, our methodology provides new insight in order to develop new perspectives concerning the role of predation in our evolution.

Understanding the dimensions of the conflict between hominins and carnivores and providing evidence of its consequences, such as carnivore attacks on fossil hominins, is an important issue due to its deep social and cultural implications. If we consider the current relationship between hominids and carnivores as a valid analogy (Treves and Naughton-Treves 1999; Hart and Sussman 2005), we will understand to the necessity of understanding the interaction between hominins and carnivores during the Pleistocene. Confirming past carnivore attacks is an important improvement on the knowledge of this issue, although more research is needed in future to calibrate its sociobiological implications in human evolution.

Acknowledgements

We would like to express our gratitude to R. Vallender (Canadian Wildlife Service), V. Santucci (National Park Service, USA), A. Sanchis and Museu de Prehistòria de València for their facilities so this paper could be developed. We would also like thank the comments of the anonymous reviewers. This research was carried under an IPHES and IIIPC/UC project supported by the Government of Cantabria and by two research projects founded by Ministerio de Economía y Competitividad (HAR2010-19957/HIST and HAR2013-48784-C3-1-P) and project 2014-SGR-900 (AGAUR). E. Camarós is beneficiary of a FI/AGAUR (DGR2013) grant of the Catalan Government and a BE/AGAUR Grant (2012 BE 00971) at the Eberhard Karls-Universität Tübingen. C. Lorenzo works under the research projects funded by Ministerio de Economía y Competitividad (CGL2012-38434-C03-01 and 03) and AGAUR (2014 SGR 899).

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4.4.3.1

PUBLISHED SUPPLEMENTARY MATERIAL

PAPER 9

Large carnivore attacks during the Pleistocene: A forensic approach with a Neanderthal example

Online Resource material 1

This document can be found in Annex 1.

Online Resource Material 2

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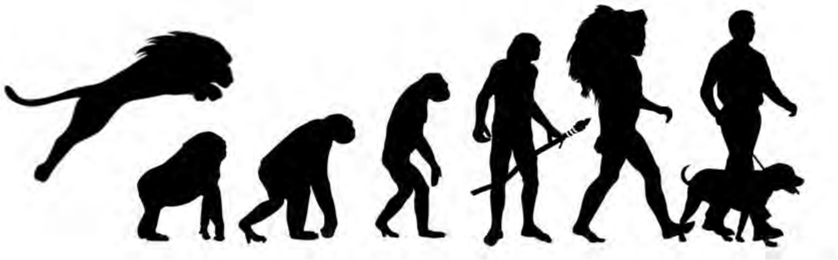
4.4.4

PAPER 10

Neanderthal fossils with carnivore damage: A taphonomic approach and behavioral implications



Chapter 4.4 *Case studies of hominin-carnivore interaction during the Pleistocene*

Paper 10

Neanderthal fossils with carnivore damage: A taphonomic approach and behavioral implications

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Carnivore damage on Neanderthal fossils is a much more common taphonomic modification than previously thought. Its presence could have different explanations, including predatory attacks or scavenging scenarios, which are both situations with important implications concerning Neanderthal behavior. In the present paper, we analyze several Neanderthal hominin fossils from a taphonomic and forensic perspective in order to infer the nature of the modifications observed on the bone surfaces. Fossils studied from Spain, Germany, Belgium, and Greece that display carnivore modifications are evaluated from a taphonomic perspective for the first time in a significant sample of hominin specimens. The results show that the materials analyzed have been modified by small to large carnivores and that both attacks and strictly carnivore scavenging events can be inferred. This study also points out the importance of developing taphonomic approaches to the analysis of hominin bone surfaces to study behavioral aspects in human evolution.

Keywords: Neanderthals, Middle Paleolithic, carnivores, taphonomy, hominin fossils

Journal of Human Evolution (submitted)

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HOMININ-CARNIVORE INTERACTION DURING THE PLEISTOCENE: DEVELOPMENT OF NEW METHODS FOR THE STUDY OF HUMAN BEHAVIOR THROUGH A TRANSDISCIPLINARY AND EVOLUTIONARY APPROACH
Edgard Camarós Pérez

1. Introduction

The study of Neanderthal hominin fossil taphonomy, although only superficially developed and infrequently conducted, is essential for understanding aspects related to bone preservation and conservation, as well as for inferring behavioral aspects. The range of taphonomical damage on Neanderthal fossils is represented by both anthropogenic and natural modifications, including tooth marks (hominin and other animals), cut marks, thermoalteration, percussion marks and/or the use of their bones as bone retouchers (e.g., Russell 1987; Defleur et al., 1999; Beauval et al., 2005; Barroso et al., 2006; Rosas et al., 2011; Verna and d'Errico, 2011). Some of these bone modifications can be linked with behavioral particularities displayed by Neanderthals that are related to ritual or symbolic behaviors, such as cannibalistic events (e.g., LeMort 1987; Rosas et al., 2006; Garralda et al., 2014), but they also can reflect site formation and post-depositional processes that affected hominin assemblages (Gargget, 1999; Sala et al., 2014).

Other common taphonomical features are identifiable on Neanderthal bone surfaces, such as the ones related to hominin-carnivore interactions, as indicated by hominin fossils with carnivore modifications. In this sense, several Neanderthal fossils display carnivore damage (e.g., White and Toth, 1991; Quam et al., 2001; Beauval et al., 2005; Barroso et al., 2006; Trinkaus et al., 2007; Lorenzo et al., 2012; Puymerail et al., 2012; Harvati et al., 2013), which can represent carnivore attacks on these hominins (Camarós et al., 2015) or strictly carnivore scavenging activity (Arsuaga et al., 2007; Díez et al., 2010). Nevertheless, carnivore damage on Neanderthal (and other hominin) fossils is commonly only cited as side information or is linked to debate due to the difficulty of inferring the nature of the modification (predation vs. scavenging) (Camarós et al., 2016a) and the carnivore responsible for the damage (e.g., Andrews and Fernández-Jalvo, 1997; Sala et al., 2014). Overall, carnivore modification on human fossils, with few exceptions, has not been an issue of intense interest in many scientific agendas (Njau and Blumenschine, 2012).

Nevertheless, carnivore damage on hominin remains has been identified on more than just Neanderthal fossils. The fossils of hominins—such as Australopithecines (Brain, 1981; Berger, 2006) and other Pliocene hominins (Davidson and Solomon, 1990), *Homo erectus* (Boaz et al., 2004), and others, including *Homo sapiens* (Orschiedt, 1999; Kuzmin et al., 2009; Curone and Brink, 2010)—show carnivore damage that has been related with predatory events (e.g., Njau and Blumenschine, 2012) and postmortem carnivore modifications (e.g., Baquedano et al., 2012).

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In the case of Neanderthal, the carnivore damage observed on bone surfaces beyond predation (see Camarós et al., 2015) also points to the possibility that Neanderthals corpses were scavenged by carnivores from erased intentional burial pits (Gargaett, 1999; 1989; Dierdirch, 2011; Camarós et al., 2016b), as happened with several *H. sapiens* inhumation contexts from different periods (e.g., Colard et al., 2014; Marían-Arroyo, 2014). Therefore, understanding the nature of carnivore modifications on Neanderthal fossils remains an unresolved and controversial issue—with important implications for the study of Neanderthal behavior—that has not been approached to date.

In the present research, we analyze different Neanderthal fossils from archaeological sites in Western Europe with the aim of searching for carnivore damage on their bone surfaces. Among the bones studied, several displayed carnivore damage. These fossils were studied from a taphonomic and forensic perspective, in order to understand and characterize the nature of the damage (predation vs. scavenging), the agent responsible, and the underlying behavioral implications.

2. Materials and methods

In total, 55 specimens of hominin fossils (see Table 1) were analyzed from nine different archaeological contexts in Western Europe, with the aim of searching for carnivore damage on their bone surfaces. The hominin specimens came from well-known archaeological sites in Spain [Cova Negra (Valencia) (Villaverde et al., 1996), Valdegoba (Burgos) (Díez, 1991), Jarama VI (Guadalajara) (Jordá Pardo, 2001) and Los Moros de Gabasa (Huesca) (Utrilla and Montes, 1989)], Belgium [Spy (Namur) and Fonds de Fôret (Liège) (Toussaint and Pirson, 2006)] Germany [Hohlenstein Stadel (Swabian Jura) (Völzing, 1938)] and Greece [Kalamakia (Laconia) (Darlas and de Lumley, 2004)] (Figure 1). Not all fossils display carnivore damage (e.g., the Spy hominin assemblage) (Table 1); therefore, only specimens with observed carnivore modifications are presented in the results section.

Hominin fossils examined for the study consisted of mandible fragments, a parietal, a clavicle, metatarsals and phalanxes, femora, and a navicular, all identified as *Homo neanderthalensis* by previous paleoanthropological research (see Kunter and Wahl, 1992; Arsuaga et al., 2007; Quam et al., 2001; Lorenzo et al., 2012; Lorenzo and Montes, 2001; Twiesselmann, 1961; Harvati et al., 2013).

For the observation of human remains, a taphonomic approach has been developed that takes into account all evidence of carnivore activity. The observation of human bones followed standard methods for identifying human bones modified by animals such as carni-

Specimen	Site	Anatomical part	Taxonomic affiliation	Carnivore Damage	Image
CN42174b	Cova Negra	Parietal R	Neanderthal (Arsuaga et al., 2007)	Yes	Fig. 2 (1)
VB4	Valdegoba	Fourth metatarsal R	Neanderthal (Quam et al., 2001)	Yes	Fig. 2 (2a)
VB5	Valdegoba	Fifth metatarsal L	Neanderthal (Quam et al., 2001)	Yes	Fig. 2 (2b)
VB1	Valdegoba	Mandibular fragment + R I2–M2 and L P3–M3	Neanderthal (Quam et al., 2001)	Probable	Fig. 2 (2c)
VB3	Valdegoba	Distal fragment of a proximal manual phalanx	Neanderthal (Quam et al., 2001)	Yes	Fig. 2 (2d, 2e)
F-4 II	Jarama VI	Proximal fragment of a first metatarsal L	Neanderthal (Lorenzo et al., 2012)	Yes	Fig. 2 (3)
Ga1.4D':150.5	Moros de Gabasa	Diaphyseal fragment of a clavicle R	Neanderthal (Lorenzo and Montes, 2001)	Yes	Fig. 2 (4)
Ga1.6A-200-137	Moros de Gabasa	First phalanx foot L	Neanderthal (Lorenzo and Montes, 2001)	No	-
Ga1. Rev.439	Moros de Gabasa	First metatarsal R	Neanderthal (Lorenzo and Montes, 2001)	No	-
Ga1.4A.245.26	Moros de Gabasa	P3 (Maxilar)	Neanderthal (Lorenzo and Montes, 2001)	No	-
Ga1.Rev.303	Moros de Gabasa	M1 (Manibular R)	Neanderthal (Lorenzo and Montes, 2001)	No	-
Ga1.8.260.5	Moros de Gabasa	M2 (Madibular R)	Neanderthal (Lorenzo and Montes, 2001)	No	-
HS37 3668	Hohlenstein Stadel	Diaphysis of a femur R	Neanderthal (Kunter and Wahl, 1992)	Yes	Fig. 5
-	Fonds de Fôret	Femur with distal epiphysis R	Neanderthal (Twiesselmann, 1961)	Yes	Fig. 6
KAL14	Kalamakia	Navicular L	Neanderthal (Harvati et al., 2013)	Yes	Fig. 7
-	Spy	Hominin collection (NR 40)	Neanderthal (Thoma, 1975; Trinkaus, 1978)	No	-

Table 1. Analyzed hominin fossils from different archaeological sites.

Figure 1. Neanderthal fossils showing carnivore damage: archaeological sites analyzed in this study and cited in the paper.

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vores (e.g., Haglund et al., 1992; Botella et al., 1999; Stodder, 2008; Sala et al., 2014) or rodents (Haglund, 1988), among other modifications. A standard archaeozoological approach to bone taphonomic modifications was also applied (e.g., Binford, 1981; Klein and Cruz-Uribe, 1984; Lyman, 1994; Egeland, 2012) and the fractures were classified according to Villa and Mahieu (1991). Teeth nomenclature was taken from Hillson (2005). Bone surface modifications were treated at both macroscopic and microscopic levels and included carnivore bone damage, such as bone breakage, notches, scores, crenulated edges, gnawing, furrowing, and pits.

The length and breadth of pits on the bone diaphyses were measured with a stereomicroscope and a digital caliper. These measurements were then compared with those of experimental non-human predator tooth marks provided by several authors (Domínguez-Rodrigo and Piqueras, 2003; Delaney Rivera et al., 2009; Andrés et al., 2012) in order to infer the probable carnivore agent.

A computed-tomography scanner from the Senckenberg Center for Human Evolution and Paleoecology (Universität Tübingen, Germany) was also used to obtain CT images of the Kalamakia specimen, to obtain a better characterization of the carnivore damage observed on this specimen.

3. Results

Cova Negra, Spain

The site at Cova Negra (Valencia, Spain) has a well-dated stratigraphy ascribed to the Late Pleistocene (MIS 5 to MIS 3) (Villaverde et al., 1996; 2004). Over 24 cranial, dental, and postcranial hominin fossils have been discovered that belong to the Neanderthal type (Arsuaga et al., 2007).

One of these fossils, a cranial fragment of a central part of a right parietal (CN42174b) (Figure 2: 1), displays carnivore modifications. The specimen corresponds to a parietal bone of a juvenile individual, and it shows two measurable carnivore tooth pits on the exocranial surface (Figure 3: 1 and detail) (Camarós et al., 2015). The size of both pits matches the group of the large carnivores visible in Figure 4, which are compatible with bears and hyenas. Nevertheless, the possibility remains that the pits could have been produced by both canines (left and right) of a carnivore with an intercanine width of 17.74 mm, which would correspond to a medium-sized carnivore, like a felid, according to Murmann et al. (2006).

Figure 2. Fossils from Spain from different views. Cova Negra: 1) CN42174b; Valdegoba: 2a) VB4; 2b) VB5; 2c) VB1; 2d) VB3; 2e) Same specimen as 2c (VB1); Jarama VI: 3) F-4 II and Los Moros de Gabasa: 4) Ga1.4D':150.5.

Valdegoba, Spain

The archaeological site at Valdegoba (Burgos, Spain) is a small cave located in the Southern end of the Cantabrian Mountains. It was excavated during the 80s and 90s, and it has a dilated stratigraphy that extends from the end of the Middle Pleistocene to part of the Upper Pleistocene (Díez et al., 1988). Several human remains were recovered from different archaeological levels from the MIS 5 to MIS 3 (Díez, 1991). To date, as many as five human specimens have been identified as the Neanderthal type (Quam et al., 2001) (Table 1) (Figure 2: 2).

Carnivore damage on one of these fossils was previously observed by Quam and colleagues (2001), and on two of them by Díez and colleagues (2010). Our observations match the previous ones, but we also suggest that the entire collection of the hominin fossils from Valdegoba display carnivore activity.

A fourth metatarsal (VB4) (Figure 3: 2a) shows evidences of gnawing on the medial surface of the base and on the edges of the distal metaphyseal surface. A probable score mark is present near the distal metaphyseal surface. Another bone, a fifth metatarsal (VB5) (Figure 3: 2b), has gnawing marks at the base and distal epiphysis. Furthermore, both mandibular fragments belonging to same specimen (VB1) (Figure 3: 2c and 2d) bear notches that were probably caused by carnivore activity on the inferior edge of the corpus. Finally, a proximal manual phalanx (VB3) (Figure 3: 2d) exhibits gnawing and pitting on the dorsal and plantar surfaces, with the resulting removal of the proximal epiphysis. Tooth pit sizes on this specimen resemble those of a small-sized carnivore, as can be observed in Figure 4.

Jarama VI, Spain

The site of Jarama VI (Guadalajara, Spain) is an archaeological site excavated during the 90s with a well-dated stratigraphy covering MIS 3 (Jordá Pardo, 2001). In Level 2, a single proximal fragment of a left first metatarsal of an adult individual attributed to the Neanderthal type was identified (specimen F-4 II) (Lorenzo et al., 2012) (Figure 2: 3).

This bone presents carnivore damage on its surface. These modifications consist of gnawing on the proximal and distal metaphysis, which resulted in a fracture with crenulated edges, visible in the dorsal, medial, plantar, and lateral views. Scores and pits are also present all over the bone surface located near the distal part of the metatarsal (Figure 3. 3). The measurements of these pits suggest that the agent responsible for the damage could be a relatively small- to medium-sized carnivore (Figure 4), such as a fox or an immature wolf, as also indicated by Lorenzo and others (2012).

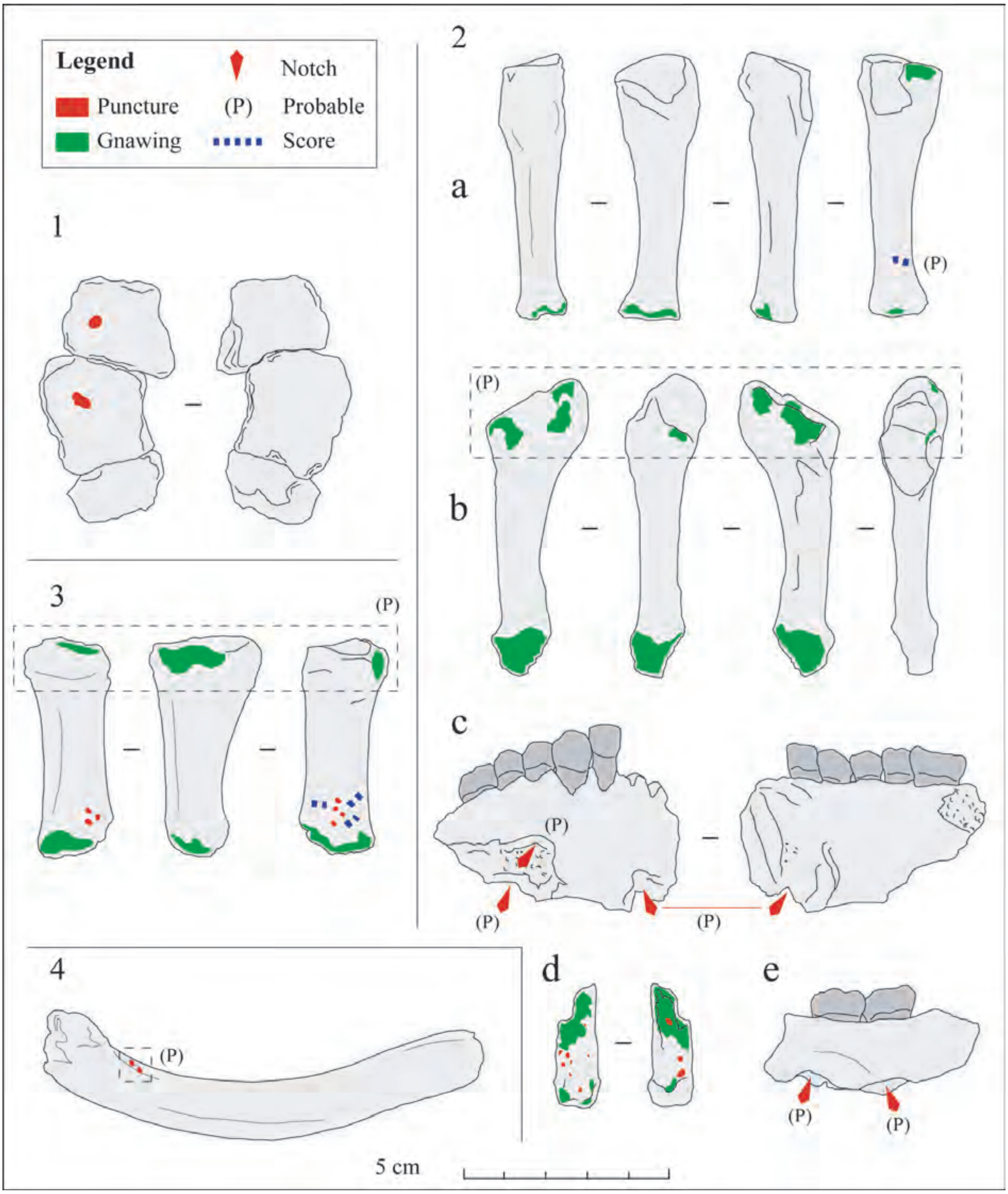

Figure 3. Fossils from Spain with carnivore damage highlighted (the same order and numeration as in Figure 2).

Los Moros de Gabasa, Spain

A total of six human skeletal elements have been identified at Los Moros de Gabasa (Huesca, Spain) (Table 1) which have been attributed to the Neanderthal type (Lorenzo and Montes, 2001). The cave is chronologically ascribed to the Middle Paleolithic, with a radiocarbon dating that situates the human occupation between 40–50 kyr BP, and the hominin fossils to <46.5 Ka BP (Hoyos et al., 1992).

Only one of the recovered elements—a diaphysis of a right clavicle (specimen Ga1.4D':150.5) (Figure 2: 4)—displays probable carnivore damage, identified previously as a single depression on the bone surface that matches with a canid tooth mark (Utrilla, 2000). Taphonomic analysis of the bone surface confirmed the presence of a deep triangular-shaped tooth pit, near another smaller one (Figure 3: 4). The carnivore damage is located on the posterior part of the clavicle, near the attachment site for both the deltoideus and trapezius muscles.According to the comparison with the works of Domínguez-Rodrigo and Piqueras (2003) and Delaney Rivera et al. (2009), both parallel tooth pits,, could correspond to a medium-sized carnivore (Figure 4).

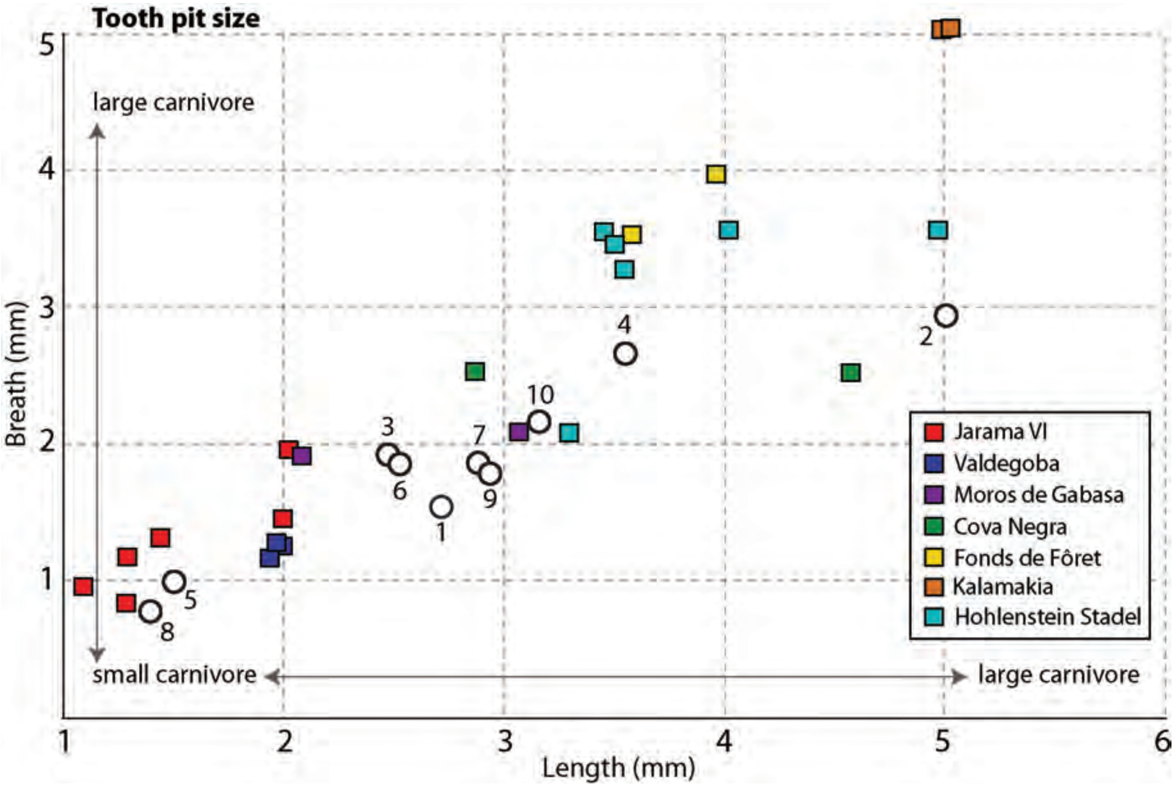

Figure 4. Tooth pit size from Neanderthal fossils, compared with actualistic data (only mean size): 1) Hyena shaft; 2) Hyena end; 3) Wolf shaft; 4) Wolf end; 5) Fox shaft; 6) Fox end; 7) Lion shaft; 8) Dogs; 9) Bears, and 10) Hyenas. Measurements 1-7 from Andrés et al. (2012), 8 from Delaney-Rivera (2009), and 9-10 from Domínguez-Rodrigo and Piqueras (2003).

Hohlenstein Stadel, Germany

The Hohlenstein Stadel cave is the only site from the Swabian Jura (Germany) (Figure 1) where a Neanderthal fossil has been recovered (Street et al., 2006). Located in the Lone Valley, It is a well-known site due to the exceptional find of an Early Upper Paleolithic ivory sculpture of the Lionman (*Löwenmensch*), an anthropozoomorphic figurine with a human body and a lion's head (Conard and Bolus, 2003; Kind et al., 2014). In 1937, an adult male shaft of a right femur was found in the *Schwarzes Moustérien* archaeological horizon (Völzing, 1938) (Figure 5). The specimen can be ascribed to the Neanderthal type (Kunter and Wahl, 1992), and it displays clear carnivore damage (Camarós et al., 2016a).

This femur can be described as a typical diaphyseal *cylinder* (Kerbis Peterhans, 1990) resulting from a very intense carnivore chewing (Figure 5: 1,2). Both epiphyses have been consumed and removed—a carnivore action commonly associated with hyenas and canids in their dens (Binford, 1981; Fosse et al., 2012). Furthermore, the entire bone surface has been heavily tooth-pitted and scored, especially near the distal and proximal zones (Figure 5: 2). Concerning the pits, only six of them were measurable and they seem to show a strong consistence with large-sized carnivores, probably hyenas, bears, lions, or wolves (Figure 4).

Fonds de Fôret, Belgium

The Fonds de Fôret site consists of two caves located in Trooz (Liège), in Belgium. A femur (Figure 6) was found during the old excavations in 1830 by F. Tihon (Toussaint and Pirson, 2006), although F. Twiesselmann did not study it until 1961. The analyzed left femur belongs to an adult Neanderthal and has a shaft with an anteroposterior curvature and a rounded cross section that resembles that of classic Neanderthals (Twiesselmann, 1961). Concerning its taphonomical study a layer of varnish complicates the study of the surface, but a zone with pitting is observable where an oblique fracture is located on the proximal zone of the shaft. The measurements of the angles of the fracture planes (76° and 86°) match better with an oblique fracture generated by pressure force (as occurs with the bite of a carnivore), rather than with a dynamic force (as occurs with an anthropic impact), according to Alcántara et al. (2006). Nevertheless, these authors also point out that fracture planes of less than 90° are difficult to ascribe.

The clearest evidence of carnivore damage is found on the distal part of the bone. The metaphysis has three pits (Figure 6a) on the anterior face of the femur. In the same zone, but on the left side, a large-sized score is present (Figure 6: 3). On the epiphysis, the sur-

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Figure 5. Femur from Hohlenstein Stadel: 1) Different views of the fossil and 2) Detailed image of the proximal zone.

faces of the medial (Figure 6c) and lateral (Figure 6: d) epicondyles show moderate furrowing with defined crenulated edges (Figure 6: 1,2). No damage is evident on the articular facet of the distal epiphysis; thus, the femur was probably in anatomical connection with the tibia when the carnivore accessed it.

Identifying the probable type of carnivore responsible of the damage is not an easy task. Nevertheless, the modifications observed and the dimensions of the large score resemble those ones generated by large carnivores (Binford, 1981), and are consistent with hyenas and canids (Andrés et al., 2012). Furthermore, the tooth pit sizes also point to a large carnivore as the agent responsible of this damage (Figure 4).

Figure 6. Femur from Fonds de Fôret: a) Anterior view; b) Distal view; c) Dorsal view; and d) Medial view.

Kalamakia, Greece

The Kalamakia cave is located on the western coast of the Mani peninsula (Laconia, Greece). It was excavated between 1993 and 2006 and the stratigraphy spans from 100 to >39 Ka BP, where several human remains of the Neanderthal type have been discovered (Darlas and de Lumley, 2004; Harvati et al., 2013). In the uppermost archaeological level, in the upper half of Unit IV (ca. >39 Ka BP), an adult left navicular with carnivore damage was recovered (Harvati et al., 2013) (Figure 7).

The specimen displays intense carnivore modifications. A deep pit (Pit 1) is located on the ridge separating the intermedial and medial articulations surfaces (Figure 7: a-b). This last surface, where the medial cuneiform articulates, also shows modification resulting in crenulated edges on the dorso-medial portion (Figure 7: a-b). Another deep tooth pit can be observed on the non-articular face of the dorsal aspect of the navicular (Figure 7: d-e), just above the medial zone of the talar facet. Measurements of the depressions point to a large carnivore (Figure 4).

A CT-scan of the specimen helps in the characterization of the modifications and in the interpretation of the responsible agent (Figure 7: b,c,e). The pit observable on the distal view can be described as having a pointed, oval-shape with a defined protuberance and with a v-shaped section on its major axis (plantar section a-a') (Figure 7: c). This characterization of the pit shape has been compared with the shapes made by different carnivore species (e.g., *Panthera leo, Crocuta crocuta, Canis lupus* and *Vulpes vulpes*) and their tooth pieces, and the most similar one is the shape of the lower carnassial (Pm4) of a hyenid or a large felid (see an example of the comparison in Figure 7: f-h). Therefore, the shape of Pit 1 is consistent with this species dental piece, and the pit form in KAL14 could be the result of a depression caused by the protocone of a lower carnassial, where the protoconid ridge is also visible (Figure 7: h).

4. Discussion

Taphonomical studies on hominin remains, specifically the ones related to carnivore damage, appear only infrequently (e.g. Njau and Blumenschine, 2012), as the main interest is only paleoanthropological. Nevertheless, the few exceptions that include the taphonomic analysis of carnivore damage on hominin fossils have been essential for understanding the crucial behavioral issues beyond physical anthropology (e.g., Brain, 1981, Berger, 2006, Njau and Blumenschine, 2012, Baquedano et al., 2012). These observations are mainly related to the understanding of predator-prey relationships and environmental pressures among early hominins.

Regarding Neanderthals, carnivore damage on hominin bone surfaces has been identified (cited in Díez et al., 2010), but these appear just as side notes in scientific literature dedicated to taxonomical and/or functional morphology. Nevertheless, in some exceptional cases, the taphonomical analysis of carnivore damage has been the central point of the research (e.g., Díez et al., 2010; Camarós et al., 2015) and even an essential aspect for reevaluating issues such as the cannibalism evidence from Grotta Guattari (Italy) (White and Toth, 1991) or the intentionality of the hominin accumulation of the Sima de los Huesos from Atapuerca (Spain) (Andrews and Fernández-Jalvo, 1997; Sala et al., 2014).

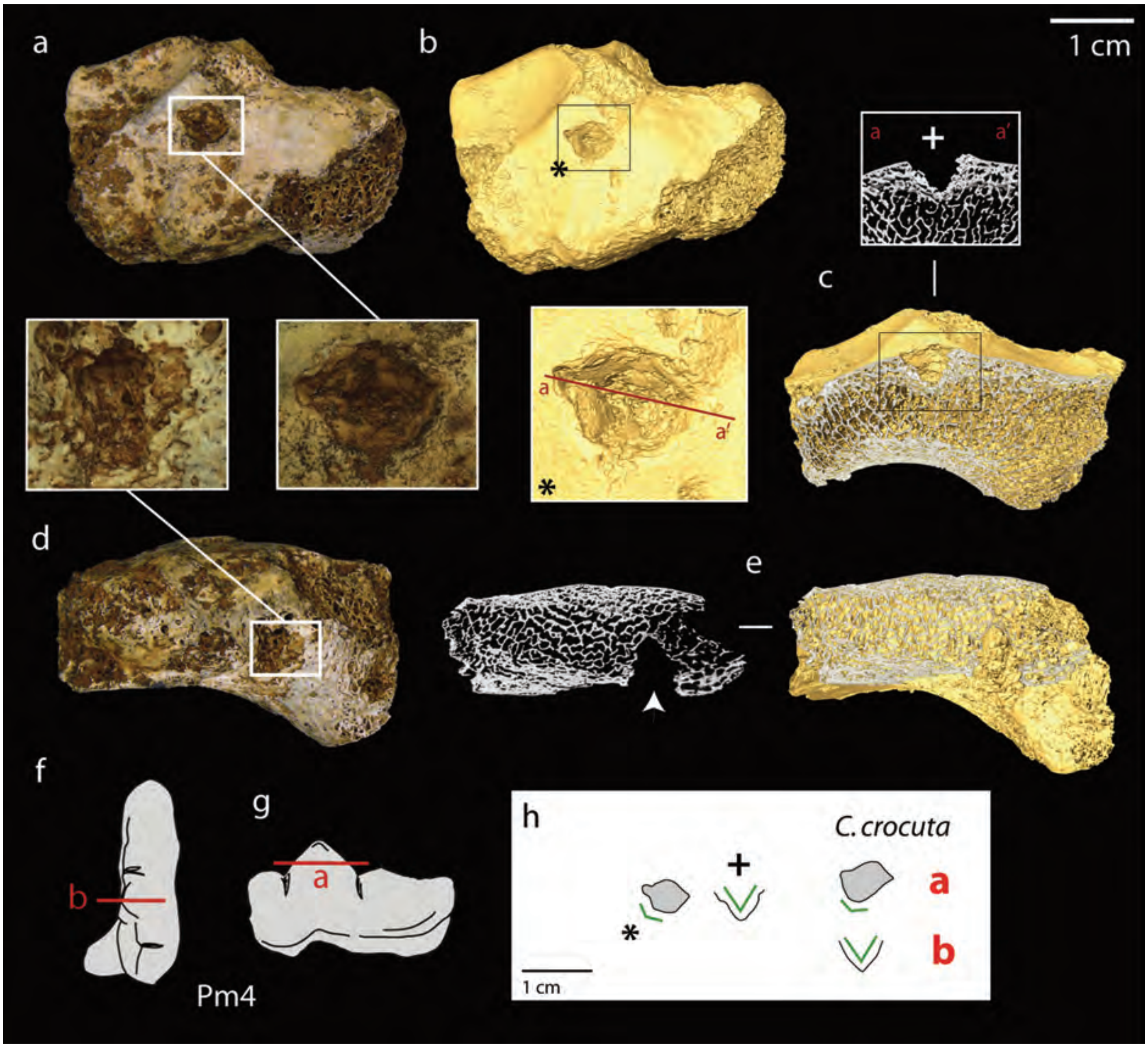

Figure 7. KAL14 navicular from Kalamakia: a) Distal view and detail of the tooth Pit 1; b) CT image from distal view; c) CT image from the plantar view, sectioned; d) Dorsal view and detail of tooth Pit 2; e) CT image of dorsal view, sectioned; f-g) *Crocuta crocuta* lower Pm4 from different views (f: occlusal; g; buccal) and sections analyzed on the paracone; h) Sections * and + from KAL14 tooth pit 1 compared with sections a and b from images f and g.

The hominin assemblage analyzed here displays carnivore damage commonly found on vertebrate skeletal remains (e.g., Binford, 1981; Haynes, 1980; Lyman, 1994). This damage is defined by multiple types of tooth marks (pitting, furrowing, and scoring) and carnivore bone breakage, which indicates different gnawing intensity on Neanderthal bones. In this sense, according to the consumption patterns of a human body by carnivores (Haglung, 1997)—which depends on the condition of the body, cause of death and degree of disarticulation (Stodder, 2008)—our sample displays different consumption stages. The specimens from Cova Negra, Valdegoba, Moros de Gabasa, and Jarama VI show a moderate intensity of carnivore damage, while the Fonds de Fôret fossil displays intense gnawing activity by carnivores, and the Hohlenstein Stadel and Kalamakia specimens show very intense activity.

Identifying the agent responsible for the damage is an important aspect for later distinguishing between strictly scavenging events and predatory attacks. In our analyzed sample, we see a representation of both small (e.g., mustelids, small felids, and canids) and large (e.g., lions, bears, hyenids, and large canids and felids) carnivores (see Figure 4). In this sense, our size interpretations through tooth pit measurements are consistent with the carnivore species present in all sites where archaeozoological information is available (see Feranec et al., 2010; Villaverde et al., 2006; Kitagawa et al., 2012; Harvarti et al., 2013).

Beyond the taphonomical observations on Neanderthal fossils, the behavioral significance of carnivore damage is a controversial issue (Díez et al., 2010). Consumed hominin corpses may indicate different scenarios with important human behavioral implications that can be reached through two taphonomical histories, both ending in a similar result. These are a fatal predatory carnivore attack with consumption or a strictly scavenging event (postmortem modifications). The first one is related to carnivore attacks on Neanderthals, which reveals a high ecological pressure between hominins and carnivores and a specific predator-prey relationship (Camarós et al., 2015). The second type of evidence, which does not imply predation, can also relate to carnivores' actions of modifying Neanderthal inhumations (Gargett, 1999; Diedrich, 2014), as they are capable of digging up burial contexts (Camarós et al., 2016b). Nevertheless, distinguishing between these two scenarios is challenging, and crucial behavioral implications arise concerning the inference of one or the other option.

In our analyzed sample, we can point to the cases of Jarama VI and Valdegoba as scenarios where a small carnivore has been responsible for the modification. Therefore, carnivore damage can be inferred to be the result of a strictly scavenging event. The same consumption patterns have been observed on human corpses scavenged by small carnivores, where moderate gnawing is located on the distal parts of phalanxes, metapodials, and other long bones (Moraitis and Spiliopoulou, 2010; Rippley et al., 2012; Young et al., 2015a).

For the case of the navicular from Kalamakia, the carnivore damage by a hyenid or large felid located on a non-exposed facet of the bone when the foot was articulated, suggests that the animal consumed the hominin remains when advanced disarticulation had occurred (Haglung et al., 1997; 1989). Forensic literature reports that hyenas, for example, are more likely to feed on humans by scavenging tombs in cemeteries (Horwitz and Smith, 1988; Yirga et al., 2012), rather than by attacking. This may suggest scavenging behavior on hominin corpses in the Kalamakia upper half of Unit IV, where carnivore activity on faunal assemblage is more intense (Harvati et al., 2013). However, the idea of a previous predatory attack cannot be completely discarded, as no hyenas have been recorded at the site, but leopards (*Panthera pardus*) have been, which would also be consistent with the modifications.

The same controversy arises for the femura discovered in Hohlenstein Stadel and Fonds de Fôret, as they display damage commonly associated with scavenging of human remains by carnivores, such as the consumption of long bones that resulted in *bone cylinders* and fractured remains (e.g., Stodder, 2008; Milner and Smith, 1989). This is also the most probable case for the Neanderthal fossils with similar carnivore modifications discovered in Gruta da Oliveira, Rochers-de-Villaneuve, Grotte de la Tour, and Zafarraya (Beauval et al., 2005; Barroso et al., 2006; Trinkaus et al., 2007; Puymerail et al., 2012). Nevertheless, as considerably large carnivores have caused the modifications, a predatory attack is also a probable scenario, revealing paleoecological pressures. Today, forensic investigations point towards a wide range of carnivore species that carry out predatory attacks on humans as a result of a complex human-wildlife conflict; these include hyenids (e.g., Brain, 1980, Gade, 2006), felids (e.g., Packer et al., 2005) canids (Langley, 2005), and ursids (e.g., Herrero and Fleck, 1990). Only the case of the Cova Negra parietal, due to its pit size and location on the anatomy, can be inferred as a large carnivore attack (Camarós et al., 2015), possibly by a leopard (*Panthera pardus*), which is consistent with the faunal spectrum in the cave (Villaverde et al., 1996; Sanchís et al., 2015).

All Neanderthal bones analyzed here have been located in isolation from, or in non-anatomical connection with, other hominin fossils also discovered in the same archaeological contexts (see Völzing, 1938; Arsuaga et al., 2007; Quam et al., 2001; Lorenzo et al., 2012; Lorenzo and Montes, 2001; Twiesselmann, 1961; Harvati et al., 2013). As seen in forensic cases, carnivores can also be implicated as being responsible for the transportation of human carcasses and their skeletal disarticulation and/or spatial dispersion (e.g., Young et al., 2015b; Beck et al., 2015). This could be an explanation for the appearance of Neanderthal fossils in caves—as an accumulation by carnivores, as has been suggested for Cova del Gegant (Spain) (Daura et al., 2010).

Taphonomical analysis of human bone surfaces can help in understanding behavioral aspects and site formation processes where hominin fossils are involved (e.g., Brain, 1981; Colard et al., 2014; Sala et al., 2015; L'Abbé et al., 2005). The same needs to be performed with Neanderthal fossils, as carnivore damage seems evident on many of them. Nevertheless, the significance of Neanderthal fossils with carnivore damage is a difficult issue to resolve due to the lack of both a good sample of hominin remains and good archaeological records (Díez et al., 2010). Furthermore, the behavioral aspects, such as the role of predation in Neanderthal evolution or the destruction of inhumation contexts by scavenging carnivores, remain controversial, as both scenarios may result in the same taphonomic modifications. Accordingly, efforts should be taken in the direction of analyzing hominin fossils from a taphonomical perspective that extends beyond paleoanthropology, using forensic evidence, experimentation, and new technologies that can help in approaching this issue. Further research must be conducted on this topic, and new methods developed, in order to distinguish between predatory and scavenging scenarios.

5. Conclusion

Carnivore damage is much more common on Neanderthal bone surfaces than was previously thought. The present research examined this damage in a considerable sample of hominin fossils, and the results confirmed the importance of this approach for studying Neanderthal paleoecology and behavior.

In the sample analyzed here, most of the Neanderthal fossils display damage by small and large carnivores, both moderate and intense. Most of the damage is consistent with scavenging scenarios, according to actualistic, experimental, and forensic observations. Nevertheless, previous predatory attacks cannot be discounted, as this was also common during the Pleistocene (Hart and Sussman, 2005; Camarós et al., 2015).

Taphonomic analysis of hominin bone surfaces must be incorporated into scientific agendas, and fossils should be studied beyond paleoanthropology. Furthermore, new methods and devices (e.g., CT images) should be developed and used to distinguish scavenging and predatory scenarios and their important behavioral implications in human evolution.

Acknowledgements

EC is beneficiary of a FI/AGAUR (DGR2013) grant of the Catalan Government. RB is a Beatriu de Pinós-A post-doctoral scholarship recipient from Generalitat de Catalunya and co-financed by the European Union through Marie Curie Actions, FP7. This research was

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partially funded by *Ministerio de Economía y Competitividad* (projects HAR2010-19957/HIST, HAR2013-48784-C3-1-P, CGL2012-38434-C03-03, CGL2012-38358, CGL-BOS-2012-34717), *Agència de Gestió d'Ajuts Universitaris i de Recerca* (projects AGAUR 2014-SGR-900 and 2014/100573) and SéNeCa Foundation (project ref. 19434/PI/14). Thanks to Ulmer Museum, Museu de Prehistòria de València, Museo de Huesca, Museo de Burgos and Institut Royal des Sciences Naturelles de Belgique for their permission and authorization to analyze their fossils.

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4.4.4.1

SUPPLEMENTARY MATERIAL

PAPER 10

Neanderthal fossils with carnivore damage: A taphonomic approach and behavioral implications

Supplementary Material

Data

Tooth pit measurements, length (major axis) and breath (minor axis), used for Figure 4 (Paper 10):

Tooth pit measurements

Site	Length (mm)	Breath (mm)
Los Moros de Gabasa	2.11	1.97
Los Moros de Gabasa	3.16	2.09
Valdegoba	2.00	1.34
Valdegoba	1.84	1.21
Valdegoba	1.94	1.37
Cova Negra	2.81	2.55
Cova Negra	4.60	2.51
Jarama VI	2.10	1.90
Jarama VI	2.00	1.40
Jarama VI	1.20	0.90
Jarama VI	1.40	1.30
Jarama VI	1.30	1.20
Jarama VI	1.30	0.70
Fonds de Fôret	3.96	3.90
Fonds de Fôret	3.60	3.52
Kalamakia	5.9	5.3
Kalamakia	5.4	5.4

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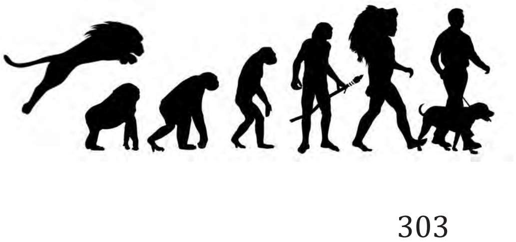
DISCUSSION, CONCLUSIONS AND FUTURE PERSPECTIVES

5



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Discussion and conclusions

The interaction between hominins and carnivores during the Pleistocene is a complex and frequently debated issue (Stiner, 2012). Since the genus *Homo* entered the predatory guild by adding meat to its diet 2–3 Mya (Isaac and Crader, 1981; Domínguez-Rodrigo et al., 2012), carnivores have played an important role in human evolution. As a result of this relationship, new scenarios emerged for hominids in general terms, including the dependency on carnivores for meat food (scavenging events; e.g., Blumenschine, 1988), confrontation (predation in both directions; e.g., Chase, 1988; Njau and Blumenschine, 2006), ecological competition for the use of common prey and caves as living spaces (e.g., Pettitt, 1997), and domestication at the end of Pleistocene (e.g., Germonpré et al., 2012).

The interaction during the Pleistocene was so intense that some scholars talk about a co-evolutionary process between hominins and carnivores (Brantingham, 1998; Stiner, 2012). From this point of view, the studies of the relationships developed between hominins and these animals and their evolution through the time can be used as a positive approach to understand human behavioral changes (Brain, 1981). Despite this, inferring a co-evolutionary relationship between hominins and carnivores is not an easy task: 1) The Plio-Pleistocene is a long period in temporal terms, and 2) throughout this period, hominins experimented with a significant number of changes and transformations, both in biological and in cultural terms. Therefore, our work attempts to contribute to the debate from the perspective of the Neanderthal world. Thus, the study has focused mainly on the European Late Pleistocene.

Neanderthals seem to have developed intense and continuous interaction with carnivores (Gamble, 1993). Due to the abundance of well-excavated sites and archaeological data, the case of the Neanderthals is a good one to analyze to deeply understand their interaction with carnivores and its behavioral implications, while trying to infer co-evolutionary elements in the relationship.

Archaeologically, Neanderthals display several forms of interaction with different carnivore species, including hunting activities (David, 1997), sharing of the same cave alternately (Yravedra and Cobo, 2014), and even sharing common prey in a common exploited ecosystem (Beauval et al., 2005). The most common form of interaction during the Middle Paleolithic was the alternate use of caves to develop different activities by both agents (Straus, 1982; Blasco and Rosell, 2009; Skinner, 2012; Viranta and Grandal, 2012). Our investigation has focused on analyzing the consequences of such alternate use of cavities when considering hominin behavior. Our contribution to the subject has taken an experimental perspective, understanding that experimental archaeology is an excellent approach for tackling case-specific archaeological problems (Domínguez-Rodrigo, 2008) and as part of a middle-range theory based on the testing of alternative hypotheses (Binford, 1981).

The results obtained from our experimental series developed with extant carnivores (*Ursus arctos*, *Panthera leo*, *Crocuta crocuta*, and *Canis lupus*) show that large carnivores are an important taphonomic agent of spatial modification and should be added to the list of agents to be considered when facing the analysis of site modifications. In this sense, the experiments presented in this doctoral thesis show how large carnivores may act as agents with the capacity of erasing spatial connections; this has important archaeological implications.

Although we know that taphonomic experiments with captive animals may be subject to criticism (see Gidna et al., 2013), we must say, first, that our experiments have been developed with animals living in a semi-free state of liberty at the *Parque de la Naturaleza de Cabárceno* (Cantabria, Spain), and second, that our experiments were only intended to prove capacities, which do not differ from those of wild animals in Cabárceno. Therefore, as we have argued extensively in the dissertation, our taphonomic experiments are useful and valid; moreover, they have significant archaeological implications and applications.

Regarding this issue, and with our experimental results, we can enter into the debate on the evidence of Neanderthal modern and complex behavior. Our results demonstrate that carnivores can significantly modify the spaces used by hominins (e.g., hearth and hearth-relates assemblages, specialized use of space, and inhumation contexts) in a particular way that differs from other post-depositional events, such as root damage, watercourses, rain, wind, trampling, or cleaning events (see Barbetti, 1986; Sergant et al., 2006; Mallol et al., 2007; Dibble et al., 2009). In this sense, large carnivores may act as erasing agents of essential evidence of modern and complex behavior as understood by several authors (Binford, 1978; McBrearty and Brooks, 2000; Vaquero and Pastó, 2001) in a context of alternate use of the same caves. Therefore, carnivores could be responsible for the destruction of those spatial connections that define modern and complex behavior (summarized in Villa and Roebroeks, 2014) and those key cognitive markers that allow differentiation of modern humans from archaic hominins (Marean et al., 2007; Conard, 2010) usually assigned to *Homo sapiens* (Li et al., 2014). This could be why Neanderthal sites have been considered to display a spatial organization that does not differ from that of non-human carnivores (Pettit, 1997), although there is consistent evidence of the structured use of domestic space (summarized in Chacón et al., 2012).

Future research will have to consider how to archaeologically recover the information erased by carnivores to demonstrate modern and complex behavior. This will evidence that

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the unresolved debate on Neanderthal cognitive and behavioral evolution (Taborin, 1998; White, 2002; Higham et al., 2010) is an issue of taphonomic damage and post-depositional site preservation. Preservation has been pointed to previously as a key factor influencing the state of knowledge on cultural complexity and innovation (Langley et al., 2011).

The taphonomic experiments that we developed also contribute to the use-wear analysis. Villa and Soressi (2000) pointed toward carnivores as probably responsible for taphonomic damage on stone tools, as they sometimes appear in carnivore dens. Although these authors were the first ones to highlight this, no debate on this issue or any kind of study has been conducted until now. Carnivores do not only modify space and bone remains (e.g., Blumenschine, 1988; Marean et al., 1992; Domínguez-Rodrigo and Piqueras, 2003); our experiments show that carnivores (bears, lions, hyenas, and wolves) also modify lithic surfaces and edges. They alter stone tools through modifications including polished surfaces, striations, and edge-damage in the form of micro-fractures. We have been able to characterize this damage for the case of bears (*Ursus arctos*), and the interesting thing about our results is that in the first stage, these modifications can be confused with use-wear traces. Although we have attempted a first approach to address this issue, more experimental series need to be carried out in this direction.

As seen, carnivores are able of erasing behavioral evidence when entering an abandoned anthropogenic context. Nevertheless, we have also seen that they can emulate anthropogenic evidences of human activity with their own actions. The modifications on the stone tool surfaces are not the only case analyzed in the dissertation. Our research is also focused on how bears specifically are capable of producing more confusing traces.

Among all carnivores, bears seem to be the animals that developed the closest interaction with Neanderthals (Estévez, 2004; Auguste, 1995; David, 1997), including in terms of the alternate use of cavities (Viranta and Grandal, 2012). Our studies point to them as responsible for generating material evidence similar to that allowing archaeologists to infer hominin behavioral innovation and complexity. The cases that we analyzed in the dissertation were the study of inhumations and graphical expression. Both were approached through our own data by discussing the evidence in La Chapelle-aux-Saints (France) and Gorham's Cave (Gibraltar), which are crucial examples when debating modern and complex behavior.

La Chapelle-aux-Saints is a well-known site where the presence of a Neanderthal inhumation has been claimed (Boussonie and Bardon, 1908; Rendu et al., 2014). Although we also agree with this interpretation, our studies reveal a different explanation regarding the origin of the burial pit. When comparing the measurements of the La Chapelle-aux-Saints inhumation pit with those we obtained from bear beds from Rouffignac (France) and La Garma (Spain), in addition to data provided from the French sites of Arriutort and Zazpigagna (Fosse et al., 2004), an alternative explanation to an anthropic origin of the pit emerges.

According to our measurements, the burial pit from La Chapelle-aux-Saints is consistent with those of cave bear beds. In this sense, our interpretation of the burial pit would be related to the reutilization of a pre-existing cave bear (*Ursus spelaeus*) bed by Neanderthals to bury a corpse. This would provide complex dimension to the interaction between Neanderthals and carnivores in the context of alternate use of caves, where hominin reuse of carnivore spaces took place. The reuse of bear beds during the Upper Paleolithic was also evidenced at the site of La Grotte de Cussac (France) in the same way that we propose for the Neanderthals (Aujoulat et al., 2001).

Concerning the study of Neanderthal graphical expression and its relation to carnivore activity, we discussed the case of the engraving from Gorham's Cave (Gibraltar; Rodríguez-Vidal et al., 2014). At the Gorham's site, an abstract patterned engraving was identified and interpreted as resulting from Neanderthal activities, and thus clear evidence of modern and complex cognition as defined by MacBrearty and Brooks (2000).

The finding of this evidence overcomes an old paradigm and points toward Neanderthals as hominins that conducted activities resulting in graphical expression. It is certain that more evidence will be interpreted now that a scientific boundary has been overcome. Nevertheless, bears with their activity can still produce confusing traces.

The analysis of bear scratches from La Garma (Cantabria, Spain) shows how similar they can be to an abstract pattern. Bear scratches may be produced on the floor, on walls, and on sediment but also on karstic rocks or walls. These scars, the product of bear clawing activity in caves, may generate parallel lines resulting in non-intentional abstract patterns. According to this and due to the similarity with the first evidence discovered of Neanderthal graphical expression, future interpretations will require a deep morphological and spatial distribution analysis in order to avoid confusing Neanderthal patterns with bear scratches. In this sense, it is interesting to mention that the alternate use of caves by Upper Paleolithic humans and bears has resulted in the overlapping of scratches and rock art (Bocherens et al., 2006).

In sum, our analysis of potential carnivore activity in cavities provides sustainable evidence for caution when inferring Neanderthal behavioral innovation and complexity.

Therefore, our experimental and paleontological observations must be taken into account, and carnivores during the Pleistocene must be seen as both taphonomic erasing agents and as animals able to generate confusing traces.

As previously mentioned, another form of interaction involves Neanderthals as hunters of carnivores (Auguste, 1995; David, 1997; Pérez Ripoll et al., 2010). These animals were hunted to exploit their meat and fur (Tillet, 2002; Blasco et al., 2010) and other resources (e.g., Abrams et al., 2014). From our point of view, carnivore hunting, the use of the same cave, and exploiting common prey generated a competitive relation among Neanderthals and carnivores with important ecological pressures.

The presence of Neanderthals and large carnivores in specific territories (Straus, 1982), competing directly for the same resources (Dusseldorp, 2011), provided a scenario where direct confrontation had to exist, as happens nowadays when modern societies' interests overlap with those of wild life (Schuette et al., 2013). This origin of present conflict can derive also in the opposite direction—in carnivore attacks toward humans.

Providing evidence to suggest that Neanderthals were the prey of the carnivores is not an easy task. Our contribution to this issue has arisen through the conception that modern relationship between humans and carnivores is a valid analogy (Treves and Naughton-Treves, 1999) to approach the study of past carnivore attacks on hominins. The comparison of a present scenario with a past one is valid because the direct confrontation mentioned involve mutual pressures derived from scenarios such as similar resource use patterns of people and wild animals (Ahmed et al., 2012) including their overlapping habitats (Agarwal and Mumtaz, 2009).

Using modern confrontation between humans and carnivores, we have approached Pleistocene carnivore attacks toward hominins and the development of a useful method to infer such a form of direct interaction. In this sense, the analysis of current forensic cases has been essential, as our results suggest that bone damage resulting from a current-day attack can be used as a positive manner to recover similar past scenarios by comparison with fossil traumas.

The lesion pattern found on Neanderthal fossils has been compared with that resulting from our survey, and we find this to be a useful method for diagnosing carnivore-related damage on human bones that also allows discernment of the type of carnivore responsible for the trauma observed. Our data have been used to explain Neanderthal traumatic lesions, providing an alternative explanation to the paleopathologies analyzed by Berger

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and Trinkaus (1995). Furthermore, our forensic observations allowed us to infer the carnivore damage on a Neanderthal fossil from Cova Negra (Valencia, Spain), a cranial fragment belonging to the central part of a right parietal (Arsuaga et al., 2007), as the result of an attack by a medium-sized feline according to tooth pit size and location in the anatomy. The agent responsible was probably a leopard (*Panthera pardus*), which is a coherent interpretation according to the faunal spectrum of Cova Negra Mousterian levels (Villaverde et al., 1996; Sanchis et al., 2015). It is interesting to mention how similar the damage on this fossil is to that present on the australopithecine cranial fragment SK-54 from Swartkrans (South Africa), inferred by Brain (1981) to be due to a leopard predatory attack.

This study represents an attempt to elucidate carnivore predation toward Neanderthals and a positive proof of concept. Nevertheless, inferring predation is not as easy as it seems because taphonomic modifications resulting from a carnivore attack may be the same as those produced by strictly scavenging scenarios on hominin corpses.

We have tried to address this issue by analyzing several Neanderthal fossils from Western Europe. Neanderthal fossils from Spain (Cova Negra [Valencia; Villaverde et al., 1996], Valdegoba [Burgos; Díez, 1991], Jarama VI [Guadalajara; Jordá Pardo, 2001], and Los Moros de Gabasa [Huesca; Utrilla and Montes, 1989]), Belgium (Fonds de Fôret [Liège; Toussaint and Pirson, 2006]), Germany (Hohlenstein Stadel [Swabian Jura; Völzing, 1938]), and Greece (Kalamakia [Laconia; Darlas and de Lumley, 2004]) have been analyzed from a taphonomic perspective in the search for carnivore damage. This kind of analysis on paleoanthropological remains is not common and seldom conducted (Njau and Blumenschine, 2012). Nevertheless, when developed, they provide new insight into behavioral issues (e.g., White and Toth, 1991; Andrews and Fernández-Jalvo, 1997; Sala et al., 2014).

The results obtained show that two different kinds of interpretations can be carried out for the hominin sample analyzed. We provide evidence to suggest that Neanderthal fossils reflect both small- and large-sized carnivore modifications and therefore reveal strictly scavenging events by small non-human predators and potential predatory attacks by large carnivores. It is assumed that small carnivores are only capable of scavenging human corpses and cannot carry out predatory attacks towards hominins. However, this phenomenon remains unclear for the large carnivores. The resulting scavenging carnivore damage on hominin skeletons can be similar and impossible to differentiate from the evidence of predatory attacking events with following consumption (unless specific damage in specific anatomical parts is evidenced, e.g., the Cova Negra cranial fragment). Therefore, those fossils appearing to have large carnivore damage on their surfaces may have resulted from either a strictly scavenging event or a predatory attack.

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Our experimental results can be related to our taphonomic observations of Neanderthal fossils with carnivore damage. If bone modifications resulted from scavenging scenarios, this could be explained by scenarios of hominin inhumation contexts being modified by carnivores, as has been previously suggested (Gargett, 1999; Diedrich, 2014).

Neanderthal fossils with carnivore damage occur (White and Toth, 1991; Quamet al., 2001; Beauval et al., 2005; Barroso et al., 2006; Trinkaus et al., 2007; Lorenzo et al., 2012; Puymerail et al., 2012; Harvati et al., 2013). In the dissertation, we pose that this is much more common than previously thought, and due to its behavioral implications, the importance of conducting these taphonomic studies in addition to paleoanthropological analysis is highlighted.

Inferences regarding scavenging *versus* predatory events remain controversial. In this sense, our dissertation ends with an open question and clarifies the current difficulty of distinguishing between the two.

Overall, the results obtained suggest that Neanderthals had a complex relationship with carnivores. As seen, these hominins shared the same ecosystem with different carnivores, in turn sharing caves alternately and common prey. This interaction can be described as a competitive relation with features revealing ecological pressure among Neanderthals and carnivores. These pressures, beyond the common use of space and prey sharing, are also reflected with direct interaction (common hunting and confrontation).

We therefore infer an interaction were ecological pressures derived from competing in the same niche for space and resources, resulting in a conflict between Neanderthals and carnivores. Nevertheless, this conflict—similar to that existing nowadays between human societies and wildlife due to overlapping interests—not only provided risk but also opportunity for both. Scavenging can be seen as a positive scenario for hominins and carnivores (Treves and Naughton-Treves, 1999), although Neanderthal scavenging is substantially reduced during the Upper Pleistocene and seldom identified (Blasco and Rosell, 2009).

The immediate alternate use of caves evidenced through the superposition of carnivore marks and anthropic cutmarks demonstrated in archaeozoological assemblages (e.g., Krönneck, 2012) show the rapid occupation dynamic. Nevertheless, the order of the superposition of marks may indicate that although the alternation in occupying caves is immediate, carnivores' access to the cavities occupies a secondary position, suggesting low pressure for hominins. In this sense, our contribution to this debate seeks to provide information on who has primary or secondary access to animal carcasses (and secondary access to caves),

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as defined by our experiments seeking to characterize the order of the overlapping marks. This primary access to the caves by Neanderthals provides evidence of the possibility of a non-competitive scenario for the use of these spaces, which can be explained through short-term occupation of sites as a mechanism that recovered and balanced the ecosystem, thereby reducing additional pressure on the environment (Rosell et al., in press).

One of the main objectives in the dissertation is to analyze how hominin–carnivore interaction evolved. To do so, we studied the case of the evolution of the relationships between these two biological entities during the Paleolithic in the Swabian Jura (Germany). This geographic area preserves outstanding evidence of hominin–carnivore interaction (Münzel et al., 2011; Conard et al., 2012; Kitagawa et al., 2012), and our research brings new insight into the evolutionary process of this relationship. We have analyzed tooth- and tooth–tooth-related archaeological and paleontological evidence from Hohle Fels, Geißenklösterle, Vogelherd, and Hohlenstein Stadel in the Swabian Jura, and our results provide a picture of the evolution of the interaction between hominins and carnivores from the Middle to the Upper Paleolithic.

In the Swabian Jura, we infer a constant alternate use of caves by both hominins and carnivores during the Middle and Upper Paleolithic. Nevertheless, there is a clear difference in the size of the type of carnivores occupying cavities (e.g., Hohle Fels). During the Middle Paleolithic, carnivores occupying caves are large ones like bears (both *U. spelaeus and U. arctos*), felines, and hyenas according to our tooth-mark measurements in the archaeozoological assemblage. In contrast, the carnivore size decreases during the Upper Paleolithic, showing the presence of very small carnivores during the Magdalenian period in caves. This means that throughout the Paleolithic, the presence of large carnivores diminishes in favor of small ones, and in turn, the role of carnivores in the accumulation of fauna in cavities decreases (Conard, 2011). Our results can be explained via two compatible reasons, namely the intensification in the use of sites (Conard et al., 2006; 2012) and carnivore hunting (Münzel and Conard, 2004a; 2004b; Münzel et al., 2011) by humans during the Upper Paleolithic.

Carnivore hunting—which includes many species to exploit different resources derived from these animals—intensifies during the Upper Paleolithic (Münzel and Conard, 2004a; 2004b; Niven, 2006; Kitagawa et al., 2012), as in other European archaeological contexts (e.g., Stiner, 1994; Arribas et al., 1997; Yravedra, 2005; Wojtal et al., 2014). In parallel to increasing and diversified carnivore exploitation, carnivores are included as motifs in ivory sculpture tradition, playing an important role in the Upper Paleolithic cultural tradition (Conard, 2003; Conard and Bolus, 2003; 2008) and providing evidence of innovation. Finally, in the Swabian Jura, we have identified the evidence of probable early wolf domestication during the Gravettian.

In sum, our approach to hominin–carnivore interaction during the Pleistocene shows how complex this relation have been. The case of Neanderthals illustrates that during the Middle Paleolithic competition with carnivores existed, in addition to pressures derived from direct interaction and confrontation that generated mutual ecological pressures in the environment. Nevertheless, during the Upper Paleolithic, the same scenario existed (including direct confrontation) but with increasing competition for resources and space due to different subsistence strategies and much more prolonged site use, as well as a probable increase in hominin population densities (Straus, 1982; Conard, 2011).

To deal with this increasing competition, different strategies were developed during the Upper Paleolithic. First, increased carnivore hunting and the inclusion of carnivores as raw material in the Paleolithic economy developed in order to reduce competition for space and resources. As we have seen, in the Swabian Jura for example, hominin–carnivore interaction spanned from competition to predation and what we can consider active exploitation (Kitagawa et al., 2012). Therefore, the interaction that developed during the Upper Paleolithic had a higher impact on the environment than that occurring in the Middle Paleolithic.

Upper Paleolithic hominin strategies related to how to deal with carnivore pressures were not limited to active hunting (elimination), which even forced several carnivore species towards the extinction before the Late Glacial Maximum (Münzel et al., 2011). Domestication (inclusion) can be seen as a strategy to reduce ecological pressures and a way of taking advantage of a conflict.

This conflict and its pressures could have represented the perfect scenario to motivate innovation beyond domestication, such as a sculptural tradition as in the Swabian Jura, an outstanding area of sympatry between hominins and carnivores. In this sense, hominin–carnivore interaction could be related to the development of hominin behavior, as has been pointed out previously (Brain, 1981).

Finally, having analyzed different forms of interaction between hominins (Neanderthals and Anatomically Modern Humans) and carnivores considered in this doctoral thesis, it is time to address the question raised in the introduction: Is there a co-evolutionary process between hominins and carnivores during the Late Pleistocene? This is not an easy question to answer. First, we must understand what aspects define co-evolution between two species.

In a narrow sense, a co-evolutionary process is defined by reciprocal genetic changes in interacting species, owing to natural selection imposed by each on the other (Futuyama, 2009). Nevertheless, co-evolution includes several types of relations between species (Thompson, 1994). These are *specific co-evolution* (the simplest form), in which two species evolve in response to each other, as in a classic predator-prey relationship, and others such as *guild co-evolution* or *escape-and-radiate co-evolution* (Futuyama, 2009). Co-evolution may also include extreme adaptations in the form of interactions between species defined as *mutualism* (or symbiotic mutualism), where species are intimately associated for much of their lives (idem.).

Concerning human evolution, several authors have suggested that the relation between hominins and carnivores can be defined as a co-evolutionary process (e.g., Brantingham, 1998; Stiner, 2012). In general terms, we agree with this definition. There is much evidence of co-evolution between hominins and large carnivores, at least during the Late Pleistocene. Some of these are discussed in this dissertation, such as humans forcing several carnivore species to extinction, scavenging dependencies, or the domestication of wolves.

Although a few approaches have been taken (e.g., Fay et al., 1995; Hart and Sussman, 2011), not much research exists on the role of predation in hominin evolution, despite its influence on the evolution of primate behavior (Cheney and Wrangham, 1987). As we have demonstrated in this dissertation, predation on hominins is a difficult issue to confirm taphonomically. Furthermore, case studies, such as the one we have mentioned here related to the Swabian Jura, must also be developed in other geographical areas that have similar outstanding archaeological evidence before claiming the existence of a co-evolutionary process between hominins and carnivores during the Late Pleistocene.

A need exists for more case studies with consistent archaeological and paleontological evidence to define hominin–carnivore interaction as a co-evolutionary process, that is, beyond a close relation between species.

When facing the study of human behavior to infer changes attributed to an interaction, and as highlighted here, we will again have to take into account the consequences of hominin–carnivore interaction, such as the carnivores’ capacity to erase or emulate hominin traces of behavior. Overall, this doctoral thesis concludes that the interaction between hominins and carnivores represents a complex, constant, and changing relation during the Pleistocene. As a result, it is a useful issue to address when studying human behavior that cannot be obviated.

Through the analysis of this interaction, we have approached and provided new insights into hominin behavioral issues related to paleoecological pressures and their adaptive re-

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sponses and evolutionary implications (e.g., general hominin-carnivore predator–prey relationships), as well as the evolution of the relationship from the Middle to the Upper Paleolithic. Specific behavioral issues, such as recycling activities, resource management, subsistence strategies, or cognitive features have also been tracked through the analysis of hominin–carnivore interaction. Thus, new methods to approach these behavioral aspects have been developed within the dissertation. Another contribution is the identification of carnivores as an important taphonomic agent that can erase or emulate modern and complex hominin behavior.

Overall, through its transdisciplinary approach, this dissertation has provided new insights and new methods for the analysis of the interaction between hominins and carnivores during the Late Pleistocene for the recovery of human behavior. In this sense, hominin–carnivore interaction is highlighted as an essential topic that should be studied to further elucidate human evolution.

Future Perspectives

The present doctoral thesis has opened a research line concerning the study of human behavior through the analysis of Pleistocene hominin-carnivore interaction. It has confirmed that a transdisciplinary approach to the relation that hominins had with carnivores in the past can generate positive results that can explain and provide an understanding of our evolution. In this sense, future perspectives will be orientated towards the study of more cases of hominin-carnivore interaction to understand the evolution of this relation, as well as the role it had in the development of modern and complex human behavior.

New methodologies have been developed as one of the main aims of the dissertation. Therefore, in some cases, these will be applied to other archaeological contexts, chronologies, and problematics (e.g., molding and casting of bone surfaces). A direct archaeological application will also be developed beyond experimental approaches (e.g., searching for carnivore spatial destruction of hominin contexts) for specific archaeological sites.

Transfer of knowledge will be also carried out, for example, in the case of the forensic study of different carnivore attacks on humans. Our characterization of the resulting osteological trauma after a carnivore attack will be analyzed in depth and published with a forensic perspective and focus in order to transfer our results to other scientific disciplines, such as forensic medicine. In this sense, more collaboration with scientists from other fields is necessary to conduct this kind of research, and this will be useful in places like India or some countries of Africa where carnivore attacks are the reflection of a modern

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conflict between wildlife and people.
Furthermore, open and new questions have been reached during the research. In this sense, a special emphasis of our future investigations will be in trying to answer these questions. Some of them are related to the evidence of a co-evolutionary relation between hominins and carnivores.

The role of predation in human evolution (hominins as carnivore prey) is probably the question that we find most necessary and interesting to answer, as we have seen that much fossil evidence indicates a probable active predation towards the genus *Homo*. Furthermore, addressing this specific scenario of a predator-prey relationship would provide new data for ultimately defining the interaction between hominins and carnivores during the Pleistocene as a co-evolutionary process.

Therefore, new research conducted as the scientific extension of this dissertation, related with the taphonomical analysis of hominin fossils, will include the forensic study of predation, more experimentation with extant carnivores, and other approaches to understand the role of predation in human evolution.

The present doctoral thesis has been the perfect training vehicle for identifying and developing these future post-doctoral research perspectives.

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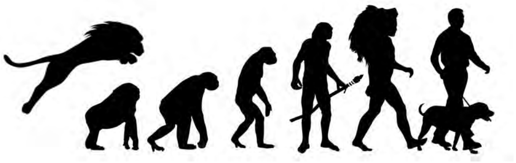

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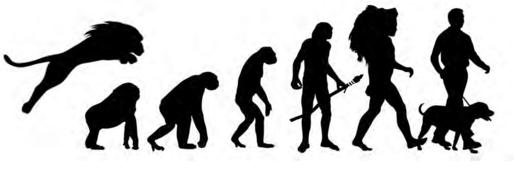
ANNEXES 7



7.1 Annex 1

Original papers and other Supplementary Material

All documents cited in Annex 1 can be found inside an attached CD.

Original published papers in PDF format

- Paper 1
- Paper 2
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- Paper 8
- Paper 9

Other material

- Video S1 (Paper 3)
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- Video S1 (Paper 6)

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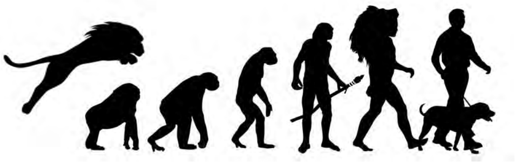

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EXTENDED ABSTRACTS
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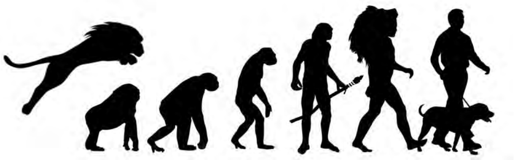

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The present doctoral thesis confirms that the interaction between hominins and carnivores during the Pleistocene is a constant and complex relation, with many forms that can help us understand human behavior.

The forms of interaction discussed span from 1) alternate use of cavities; 2) carnivores as prey; 3) carnivores as a resource; 4) hominins as prey; and 5) the domestication process (see Figure 1 from section *Introduction: Objectives and Structure*).

All these types of interaction, and the consequences that derive from them, were analyzed, such as the discussion on primary or secondary access to animal carcasses or the implication of occupying the same caves, when studying the spatial relations of material to infer behavior.

The aim of Paper 1 (4.1.1) was to introduce the subject and the state of the art of the research by presenting the main forms (*models* in the paper) of hominin-carnivore interaction during the Pleistocene. The open question of whether this relation reflects a co-evolutionary process is also asked. It is a general paper that briefly summarizes all the issues that will be approached in the dissertation. This paper was published as an introductory discussion for the Special Issue “Hominid-Carnivore Interactions during the Pleistocene,” published by *Journal of Taphonomy* and edited by J. Rosell, E. Baquedano, R. Blasco, and E. Camarós (2012).

Once the subject has been presented, another brief article, Paper 2 (4.1.2), introduces the main idea that guides the research presented here. This is that human behavior can be recovered archaeologically through study of the interaction between hominins and carnivores and by developing new methods. This paper introduces the taphonomic experimental project explained later, and it represents the first step towards the constitution of the present thesis research program.

In this sense, we must highlight that the present dissertation was constructed linearly, and that although its aim was to analyze all forms of hominin-carnivore interaction, the results of one paper would stimulate new questions whose answers were addressed in the next one. As an example, if Paper 6 proved that carnivores were capable of modifying anthropic spaces in a context of alternate use of caves that erased modern and complex behavior, Paper 8 analyzed how these animals could act as disturbance agents of inhumations. In turn, this motivated the question of how carnivores modified hominin fossils (Paper 10), and if this scavenging scenario could be differentiated from predatory evidence (Paper 9 and 10).

Although all papers endeavored to contribute new methods to the study of hominin behavior, a specific section can be defined as methodological; this is section 4.2 *Methods and techniques*.

Papers 3 (4.2.1) and 4 (4.2.2) discuss methods used in other papers; techniques are described and presented as new taphonomical advances for the analysis of bone surfaces and carnivore spatial modifications. Therefore, Paper 3 is an article describing in detail the technique of molding and casting of bone surface to analyze taphonomic modifications. There, an existing technique, applied previously for the study of tooth microwear and use-wear traces (Ollé and Vergés, 2014), is adapted for bone surfaces. This paper highlighted that the use of molds and casts improves the stereomicroscope analysis of taphonomical modifications, and provides many benefits beyond strictly bone observation, such as sampling, fieldwork, or teaching improvement through the availability of high-resolution transparent replicas. Concerning the case of the dissertation, this technique helped in the analysis of archaeological materials in Paper 7 (4.4.1). Later, Paper 4 describes the methods used to develop taphonomic experiments with extant carnivores at the Carbárceno Nature Park (Cantabria, Spain). The results of an experiment with bears (*Ursus arctos*), in terms of how they modify experimental scenarios with a hearth and a hearth-related assemblage, were first presented. Nevertheless, the main idea of the paper was to present the method used, with an in-depth discussion of the protocol of the first experiment. In turn, positive results motivated experiments with more carnivores (published in Paper 6) and emphasized the development of methods for productive use of experimental and actualistic observations in the service of archaeological goals.

Therefore, a strong part of the doctoral thesis is section 4.3 *Experimental approach to hominin-carnivore interaction*, where the developed experiments were aimed at building new methods that would provide new insight into this interaction.

In this section, Paper 5 (4.3.1) summarizes the taphonomic experiments we developed, and presents the main questions we endeavored to answer with them. Therefore, the paper discusses results obtained for more than just the experiments explained in detail in Paper 6 or 8 in relation to spatial modification by carnivores. It also provides preliminary data on experiments that we have not been able to publish yet in their entirety. In this sense, we introduce the issue of how to analyze the order of the superposition of marks generated by both hominins and carnivores. This is a commonly observed taphonomical situation in the Pleistocene archaeological record and has been the focus of previous experiments. The aim of our new experiments is to understand this superposition to determine the difference in primary or secondary access to animal carcasses, which reflects hunting or scavenging strategies developed by humans.

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Furthermore, the issue on how carnivores modify stone surfaces is also introduced. Detailed data are not published within the paper, but we have added these results as unpublished supplementary information (4.3.1.1). Here, we approach how carnivores are also capable of modifying stone surfaces providing data for characterizing this damage in order to prevent confusion of this type of damage with use-wear traces.

Paper 6 (4.3.2) focuses on how carnivores modify experimental hearths and hearth-related assemblages. The experiment is published in detail and the archaeological implications of our results are discussed. The first contribution of this research is that it points to large carnivores (ursids, felids, canids, and hyenids) as important taphonomical post-depositional agents of spatial modification. The experiment proves that carnivores are capable of erasing certain associations of elements in spaces, which archaeologically reveal modern and complex behaviors and other cognitive processe. Furthermore, the experiment provides new data for characterization of spatial damage occasioned by different large carnivores; these data, in future, will be modeled in a search for these types of patterns in the archaeological record.

The last chapter is 4.4 *Case studies of hominin-carnivore interaction during the Pleistocene*, and it is dedicated to particular examples. The included case studies span from chronologically and geographically ascribed examples to specific interaction forms approached through new perspectives, such as through the use of our taphonomic experiments or a forensic perspective.

First, with Paper 9 (4.4.1), we have provided an example of how the relation between hominins and carnivores evolved from the Middle to the Upper Paleolithic. The example used is the case of the geographical area of the Swabian Jura (Germany). This is an excellent location for analysis, as this area is full of sites, such as Hohle Fels, Geißenklösterle, Vogelherd, or Hohlenstein Stadel, among others, that preserve outstanding archaeological evidence for understanding how hominins interacted with all types of carnivores. Our study is a multidisciplinary contribution that addressed hominin-carnivore interaction by analyzing teeth and tooth marks from different archaeological sites in the Swabian Jura; the study was included in a Special Issue published by the *Journal of Archaeological Sciences: Reports,* edited by F. Rivals, E. Camarós, and C. Sánchez-Hernández (2015-2016). This research contributed to the understanding of several human behavioral aspects, such as carnivore hunting, tool use, human recycling activities, the role of ornaments made from carnivore teeth, and the domestication process. Furthermore, we provided a view into the evolution of the interaction that indicated an increasing complexity and active exploitation of carnivores from the Middle to the Upper Paleolithic in this region, which generated mutual pressures and competition for space and resources.

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Another publication from this section, Paper 8 (4.4.2), is the one focused on how bears (both *Ursus arctos* and *Ursus spelaeus*) developed a complex interaction with Neanderthals during the Pleistocene that has implications for the study of their behavior. This multidisciplinary research was based mainly on actualistic, experimental (our own results previously discussed), paleontological, and ethological observations. The results proved that bears are responsible for erasing evidence of complex and modern behavior (as defined by McBrearty and Brooks, 2000; Villa and Roebroeks, 2014). Nevertheless, the research also addressed the evidence for the bears' capacity of emulating what has been archaeologically inferred as Neanderthal behavior. In this sense, we provided new interpretations for understanding and approaching behavior related to the organized use of space, inhumation practices, or graphical expression.

The next form of interaction, discussed in Paper 9 (4.4.3), is the one related to hominins as carnivore prey, approached through carnivore attacks on hominins. The issue has been addressed from a forensic perspective, analyzing current forensic cases of humans attacked by large carnivores worldwide, to confirm this type of scenario in the Pleistocene through the fossil record. In this sense, modern day forensic cases are used to build a valid frame of reference for use in explaining past evidence. We confirm the validity of our approach using the case of Neanderthals as a proof of concept. Our results show how carnivores could have been responsible for the pathologies reflected on the Neanderthal traumatic lesion pattern by carrying out predatory attacks on these hominins, thereby providing an alternative scenario to the "*rodeo riders*" hypothesis suggested by Berger and Trinkaus on 1995 (1995). Furthermore, the case of traumatic patterns on Early Anatomically Modern Humans is also discussed, in order to show how common carnivore attacks towards humans are during evolution, as they are in different parts of the world today.

Paper 10 (4.4.4), the last publication that composes the dissertation, is focused on the taphonomic analysis of Neanderthal human fossils from Western Europe (Cova Negra, Valdegoba, Jarama VI, Moros de Gabasa in Spain; Spy and Fonds de Fôret in Belgium; Hohlenstein Stadel in Germany; and Kalamakia in Greece). This represents original taphonomical research that is seldom conduct. A large paleoanthropological sample is analyzed and conclusions are reached regarding behavioral implications. First, we distinguish between modifications caused by small and large carnivores, and then, second, relate this evidence to strictly scavenging scenarios and predatory attacks. Our conclusions point out that some of the analyzed fossils show modifications that reflect only scavenging activities, while others, although they indicate carnivore consumption of corpses, could also imply a previous predatory attack (e.g., the Cova Negra specimen, also discussed in Paper 9).

This paper highlights the importance of conducting these kind of taphonomical studies on hominin fossils, although in the present dissertation the origin of the carnivore damage (scavenging vs. predatory scenarios) is not identified, and therefore the sissertation ends with an open question. In turn, this defines our future perspective in relation to the study of predation in human evolution.

Results are discussed in a wider context and global debate in section *5, Discussion and Conclusions.*

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La present Tesi Doctoral, definida per compendi d'articles científics publicats, confirma que la interacció entre hominins i carnívors durant el Pleistocé és quelcom constant i complexe, amb múltiples formes d'interacció que poden ajudar a entendre el comportament humà.

Les formes d'interacció analitzades han estat 1) l'alternança en l'ús de les cavitats; 2) els carnívors com a presa; 3) els carnívors com a recurs; 4) els hominins com a presa i el procés de domesticació (veure Figura 1 de la secció *Introduction: Objectives and structure*).

Totes aquestes formes d'interacció han estat analitzades, així com les conseqüències que en deriven, com l'accés primari o secundari a les carcasses animals o les implicacions que té el fet d'ocupar les mateixes coves a l'hora d'estudiar el comportament.

L'objectiu de l'Article 1 (4.1.1) ha estat el d'introduir el tema d'estudi de la Tesi, així com l'estat de la qüestió mitjançant la presentació de les principals formes d'interacció entre hominins i carnívors durant el Pleistocé (anomenades *models* a l'article). La pregunta oberta sobre si aquesta relació reflecteix un procés co-evolutiu roman introduïda aquí. Es tracta d'un article general que resumeix breument tots els temes que seran tractats a la Tesi. Aquest article va ser publicat com a una discussió introductòria del volum especial *Hominid-Carnivore Interactions during the Pleistocene* a la revista *Journal of Taphonomy* editat per J. Rosell, E. Baquedano, R. Blasco i E. Camarós (2012).

Una vegada el tema ha estat introduit, l'Article 2 (4.1.2) presenta la idea que guiarà la recerca de la Tesi. Aquesta idea és que el comportament humà pot ser recuperat arqueològicament a partir de l'estudi de la interacció entre hominins i carnívors desenvolupant nous mètodes per aproximar-nos a la comprenssió de la relació entre els agents. Aquest article introdueix el projecte tafonòmic que s'explicarà i s'ampliarà després, i representa el primer pas vers el programa de recerca de la present Tesi Doctoral.

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En aquest sentit, hem de subratllar que la Tesi ha estat construïda linealment, i malgrat que el principal objectiu ha estat el d'analitzar totes les formes d'interacció entre hominins i carnívors, els resultats d'un article han estimulat noves preguntes que han estat tractades en el següent. D'aquesta manera, si l'Article 6 demostra que els carnívors són capaços de modificar els espais antròpics en un context d'alternança per les cavitats que elimina les evidències de comportament modern i complex, l'Article 8 analitza com aquest animals poden actuar com a agent de destrucció d'inhumacions. Al mateix temps, aquesta idea motiva la pregunta de com els carnívors modifiquen els fòssils d'hominins (Article 10), i si aquest escenari carronyaire pot èsser diferenciat de les evidències de la depredació (Article 9 i 10).

Tot els articles contribueixen amb el desenvolupament de nous mètodes per l'estudi del comportament dels hominins, no obstant, s'ha afegit una secció que podem definir com a metodològica. Aquesta és la secció 4.2 *Methods and techniques*.

En aquest sentit, els Articles 3 i 4 (4.2.1 i 4.2.2 respectivament) estan destinats a la discussió dels mètodes emprats en els altres articles. Les tècniques descrites estan presentades aquí com a nous avenços en el camp de la tafonomia per a l'estudi de les superfícies òssies i les modificacions de l'espai per part dels carnívors. Així doncs, l'Article 3 descriu en detall la tècnica per a la realització de motllos i rèpliques de les superfícies òssies per a estudiar les modificacions tafonòmiques. Aquí s'explica com una tècnica ja disponible per a l'anàlisi del microdesgast dentari i les traçes d'ús, es adaptada per a poder estudiar les superfícies òssies. L'article subratlla la importància de l'us dels motllos i rèpliques per a un anàlisi esteromicroscòpic de les modificacions tafonòmiques. Així mateix, també es posa de manifest els beneficis que aquesta tècnica adaptada té pel mostreig, el treball de camp o la docència a través de les rèpliques transparents d'alta ressolució. Pel que fa a la Tesi, el mètode ha estat aplicat a l'Article 7 (4.4.1).

Dins la mateixa secció l'Article 4 descriu la metodologia emprada per a desenvolupar els experiments tafonòmics amb carnívors al *Parque de la Naturaleza de Cabárceno* (Cantàbria, Espanya). Aquí, els resultats d'un experiment amb l'espècie d'ós bru (*Ursus arctos*) sobre com modifiquen aquests animals un escenari experimental, són discutits. L'objectiu d'aquest article és debatre en profunditat el protocol dut a terme en aquest primer experiment amb carnívors. Els resultats positius de l'experiència són els que motiven el desenvolupament dels experiments presentats posteriorment a l'Article 6.

En aquest sentit, un aspecte fonamental d'aquesta Tesi és la secció 4.3, *Experimental approach to hominin-carnivore interaction*, on els experiments que s'hi descriuen busquen la contrucció d'un marc de treball metodològic de referència per a aproximar-nos a la interacció des de una nova perspectiva.

A la secció, l'Article 5 (4.3.1) resumeix els experiments tafonòmics duts a terme en el marc de la Tesi Doctoral, així com també s'especifiquen les preguntes i les problemàtiques que es vol contestar i tractar amb aquests. Així doncs, aquest treball aprofundeix en la discussió dels experiments descrits en l'Article 6 o aplicats al casos arqueològics de l'Article 8. També es proporcionen resultats preliminars d'alguns experiments que encara no s'han pogut publicar de manera extensa i en detall. En aquesta línea s'introdueix el tema de com abordem l'estudi de les superposicions de marques de carnívors i d'hominins. Aquest tipus de solapament és de presència comú entre els contextos arqueofaunístics. L'objectiu d'aquest experiment és generar una metodologia que permeti entendre l'ordre de la superposició per a determinar quin agent és el responsable de l'accés primari i quin del secundari, amb importants inferències sobre el tipus d'estratègia d'adquisició dels recursos practicada al passat (p.e., cacera vs. carronyeig).

La qüestió de com els carnívors modifiquen superfícies lítiques també es tractat en aquesta secció, presentada a mode de material complementari no publicat (4.3.1.1). Aquí demostrem com els carnívors són capaços de modificar la industria lítica, caracteritzem aquestes modificacions i resaltem la importància d'aquesta recerca a l'hora de no confondre-les amb traces d'ús degut a la seva semblança.

A continuació, l'Article 6 (4.3.2) es centra en com diferents carnívors modifiquen fogueres i el seu conjunt associat. L'experiment és presentat en detall i les seves implicacions arqueològiques discutides. En primera instància, aquest treball apunta als carnívors (úrsids, fèlids, cànids i hiènids) com a importants agents post-depositacionals de modificació espaial. L'experiment demostra que el carnívors són capaços de la destrucció d'associacions de certs elements en l'espai, que arqueològicament permeten inferir el comportament modern i complex, així com d'altres marcadors de processos cognitius. Finalment, aquesta recerca proporciona dades per a la caracterització de la modificació tafonòmica de l'espai per part dels carnívors, que en un futur haurà de ser modelitzada per a localitzar aquest mateixos patrons al registre arqueològic.

L'última secció és la 4.4, *Case studies of hominin-carnivore interaction during the Pleistocene*, dedicat a l'anàlisi de casos concrets. Els exemples tractats són casos d'estudi que provenen de diferents contextos geogràfics i amb una adscripció cronològica variada.

En primer lloc, l'Article 9 (4.4.1) analitza l'evolució de la interacció entre hominins i carnívors del Paleolític Mitjà (PM) al Paleolític Superior (PS). L'exemple emprat és el cas arqueològic del Jura de Suàbia (Alemanya). Aquesta àrea és idònïa per a desenvolupar-hi aquest estudi ja que preserva un registre excepcional a jaciments com Hohle Fels, Geißenklösterle, Vogelherd o Hohlenstein Stadel. La nostra aproximació ha estat efectuada a partir d'un enfoc multidisciplinar que parteix de l'estudi estrictament de les restes i marques dentàries conservades als jaciments citats. Aquesta recerca ha estat publicada en un volum especial de la revista *Journal of Archaeological Science: Reports*, editat per R. Rivals, E. Camarós i C. Sánchez-Hernández. L'estudi permet entendre aspectes comportamentals en relació a la interacció hominins-carnívors com les estratègies de cacera, activitats de reciclatge, el rol dels ornaments confeccionats en restes dentàries o el procés de la domesticació per part dels grups humans paleolítics. A partir de l'anàlisi es conclueix que l'explotació de carnívors evoluciona vers una complexitat i una intensificació durant el periode tractat (PM-PS), que genera dins la regió pressions mútues i competició pels mateixos recursos que portarà fins i tot alguns carnívors a l'extinció.

Un altre treball d'aquesta secció, l'Article 8 (4.4.2) està focalitzat en l'estudi de l'acció dels úrsids a les cavitats, i les implicacions que aquesta té a l'hora d'estudiar el comportament Neanderthal. Aquesta recerca multidisciplinar està basada en estudis actualístics, experimentals, paleontològics i etològics. Els resultats demostren que els úrsids són capaços d'eliminar les evidències arqueològiques que permeten inferir comportament modern i complex. A més a més, la recerca també apunta vers els óssos com a agents responsables d'emular inintencionalment amb la seva activitat el que pot ser inferit com a evidències comportamentals Neanderthals. En aquest sentit, s'han obtingut interpretacions novedoses per a aproximar-nos a l'estudi de l'espai estructurat, contextos d'inhumació (p.e., La Chapelle-aux-Saints) i fins i l'expressió gràfica (p.e., Gorham's Cave).

A l'Article 9 (4.4.3) es tracta un tema controvertit, com és l'estudi del hominins com a presa, a partir del atacs de carnívors a aquestos. El tema ha estat enfocat a partir d'una perspectiva forense, analitzant casos actuals d'atacs de carnívors sobre humans en tot el mòn, per a intentar a la vegada trobar aquest mateix escenari al registre fòssil. En aquest sentit, els casos forenses moderns s'empreen per a desenvolupar un marc de referència vàlid per a explicar les evidències del passat. Pensem que la nostra aproximació es vàlida, i presentem el cas Neanderthal a mode de prova de concepte. Els nostres resultats demostren que els carnívors poden haver estat els responsables de les paleopatologies reflectides en el patró traumatològic Neandertal. Aquests resultats plantegen una explicació alternativa a la hipòtesi dels "*rodeo riders*" publicada per Berger i Trinkaus el 1995. A més a més, el patrò traumatològic dels Humans Anatomicament Moderns també és discutit per a mostrar que l'atac de carnívors sobre hominins és un fet comú al llarg de l'evolució humana.

L'article 10 (4.4.4), és l'ultim treball presentat a la Tesis i consta de l'anàlisi tafonòmic de diferents fòssils Neandertals Europeus (Cova Negra, Valdegoba, Jarama VI, Moros de Gabasa d'Espanya; Spy i Fonds de Fôret de Bèlgica; Hohlenstein Stadel d'Alemanya; i Kalamakia de Grècia). Aquesta aproximació tafonòmica és original i ha estat poques vegades desenvolupada. A partir del conjunt paleoantropològic i s'obtenen conclusions amb importants implicacions comportamentals. Primer, es distingeix entre la identificació de petits i grans carnívors com els responsables de les diferents modificacions dels fòssils, que en segon lloc indiquen per una banda activitats animals estrictament de carronyeig, però també d'atacs depredatoris. La nostra recerca apunta vers diferents escenaris que queden reflectits als fòssils humans. Per una banda, escenaris on únicament els carnívors han accedit a un cos i l'han carronyejat. Aquesta situació es pot posar en relació amb les nostres investigacions experimentals sobre la modificació d'inhumacions per part dels carnívors. Però per altra també poden reflectir atacs predatoris. La contribució d'aquest article roman en la necessitat de desenvolupar aquest estudi, malgrat que en aquesta Tesi, la identificació de l'origen de la modificació dels carnívors no obté resposta. En aquest sentit la Tesi tanca amb una pregunta oberta i defineix les perspectives futures, en relació amb l'estudi de la depredació en evolució humana.

Tots els resultats són valorats i discutits en un context i debat més àmpli en la secció 5, *Discussion and Conclusions*.

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La presente Tesis Doctoral, definida por compendio de artículos científicos publicados, confirma que la interacción entre homininos y carnívoros durante el Pleistoceno es algo constante y complejo con múltiples formas de interacción que pueden ayudar a entender el comportamiento humano.

Las formas de interacción analizadas fueron 1) la alternancia en el uso de las cavidades; 2) los carnívoros como presa; 3) los carnívoros como recurso; 4) los homininos como presa y el proceso de domesticación (ver Figura 1 de la sección *Introduction: Objectives and structure*).

Se han analizado todas estas formas de interacción además de las consecuencias que derivan de ellas, como es el acceso primario o secundario a las carcasas animales o las implicaciones que tiene el hecho de ocupar las mismas cuevas a la hora de estudiar el comportamiento.

El objetivo del Artículo 1 (4.1.1) es introducir el tema de estudio de la Tesis, así como el estado de la cuestión mediante la presentación de las principales formas de interacción entre homininos y carnívoros durante el Pleistoceno (denominadas *models* en el artículo). La pregunta abierta sobre si esta relación refleja un proceso co-evolutivo queda introducida aquí. Se trata de un artículo general que resume brevemente todos los temas que serán

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tratados en la Tesis. Este artículo fue publicado como una discusión introductoria del volumen especial *Hominid-Carnivore Interactions during the Pleistoceno* en la revista *Journal of Taphonomy* editado por J. Rosell, E. Baquedano, R. Blasco y E. Camarós (2012).

Una vez introducido el tema, el Artículo 2 (4.1.2) presenta la idea que guiará la investigación de la Tesis. Esta idea es que el comportamiento humano puede ser recuperado arqueológicamente a partir del estudio de la interacción entre homininos y carnívoros desarrollando nuevos métodos para aproximarnos a la comprensión de la relación entre los agentes. Este artículo introduce el proyecto tafonómico que se explicará y se ampliará después y representa el primer paso hacia el programa de investigación de la presente Tesis Doctoral.

En este sentido, debemos subrayar que la Tesis ha sido construida linealmente, y pese a que el principal objetivo ha sido el de analizar todas las formas de interacción entre homininos y carnívoros, los resultados de un artículo han estimulado nuevas preguntas que han sido tratadas en el siguiente. De este modo, si el Artículo 6 demuestra que los carnívoros son capaces de modificar los espacios antrópicos en un contexto de alternancia por las cavidades que elimina las evidencias de comportamiento moderno y complejo, el Artículo 8 analiza cómo estos animales pueden actuar como agente de destrucción de inhumaciones. Al mismo tiempo, esta idea motiva la pregunta de cómo los carnívoros modifican los fósiles de homininos (Artículo 10), y si este escenario de carroñeo puede ser diferenciado de las evidencias de la depredación (Artículo 9 y 10).

Todos los artículos contribuyen al desarrollo de nuevos métodos para el estudio del comportamiento de los homininos, sin embargo se ha añadido una sección que podemos definir como metodológica. Esta es la sección 4.2 *Methods and techniques.*

En este sentido, los Artículos 3 y 4 (4.2.1 y 4.2.2 respectivamente) están destinados a la discusión de los métodos empleados en los otros artículos. Las técnicas descritas están presentadas aquí como nuevos avances en el campo de la tafonomía para el estudio de las superficies óseas y las modificaciones del espacio por parte de los carnívoros. Así pues, el Artículo 3 describe en detalle la técnica de la realización de moldes y réplica de las superficies óseas para estudiar las modificaciones tafonómicas. Aquí se explica cómo una técnica ya disponible para el análisis del microdesgaste dentario y las trazas de uso, se adapta para poder estudiar las superficies óseas. El artículo subraya la importancia del uso de los moldes y réplicas para un análisis esteromicroscópico de las modificaciones tafonómicas. Asimismo, también se pone de manifiesto los beneficios que esta técnica adaptada tiene para el muestreo, el trabajo de campo o la docencia a través de las réplicas transparentes de alta resolución. Con respecto a la Tesis, el método ha sido aplicado en el Artículo 7 (4.4.1).

Dentro de la misma sección, el Artículo 4 describe la metodología utilizada para desarrollar los experimentos tafonómicos con carnívoros en el *Parque de la Naturaleza de Cabárceno* (Cantabria, España). Aquí, se discuten los resultados de un experimento con la especie de oso pardo (*Ursus arctos*) sobre cómo modifican estos animales un escenario experimental. El objetivo de este artículo es debatir en profundidad el protocolo llevado a cabo en este primer experimento con carnívoros. Los resultados positivos de la experiencia son los que motivan el desarrollo de los experimentos presentados posteriormente al Artículo 6.

En este sentido, un aspecto fundamental de esta Tesis es la sección 4.3, *Experimental approach to hominin-carnivore interaction*, donde los experimentos que se describen buscan la construcción de un marco de trabajo metodológico de referencia para aproximarnos a la interacción desde una nueva perspectiva.

En la misma sección, el Artículo 5 (4.3.1) resume los experimentos tafonómicos llevados a cabo en el marco de la Tesis Doctoral, así como también se especifican las preguntas y los problemas que se quieren responder y tratar con dichos experimentos. Así pues, este trabajo profundiza en la discusión de los experimentos descritos en el Artículo 6 o aplicados a los casos arqueológicos del Artículo 8. También se proporcionan resultados preliminares de algunos experimentos que aún no se han podido publicar de manera extensa y en detalle. En esta línea se introduce el tema de cómo abordamos el estudio de las superposiciones de marcas de carnívoros y de homininos. Este tipo de solapamiento es común en los contextos arqueofaunísticos. El objetivo de este experimento es generar una metodología que permita entender el orden de la superposición para determinar qué agente es el responsable del acceso primario y cuál del secundario, con importantes inferencias sobre el tipo de estrategia de adquisición los recursos practicada en el pasado (por ejemplo, caza *vs*. carroñeo).

La cuestión de cómo los carnívoros modifican superficies líticas también se trata en esta sección, presentada a modo de material complementario no publicado (4.3.1.1). Aquí demostramos como los carnívoros son capaces de modificar la industria lítica, caracterizamos esas modificaciones y resaltamos la importancia de esta investigación a la hora de no confundirlas con trazas de uso debido a su semejanza.

A continuación, el Artículo 6 (4.3.2) se centra en cómo diferentes carnívoros modifican hogares y el conjunto asociado. El experimento se presenta en detalle y se discuten sus implicaciones arqueológicas. En primera instancia, este trabajo apunta a los carnívoros (úrsidos, félidos, cánidos y hiénidos) como importantes agentes post-depositacionales de modificación espacial. El experimento demuestra que los carnívoros son capaces de la destrucción de asociaciones de ciertos elementos en el espacio, que arqueológicamente per-

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miten inferir el comportamiento moderno y complejo, así como de otros marcadores de procesos cognitivos. Finalmente, esta investigación proporciona datos para la caracterización de la modificación tafonómica del espacio por parte de los carnívoros, que en un futuro tendrá que ser modelizada para localizar estos mismos patrones en el registro arqueológico.

La última sección es la 4.4, *Case studies of hominin-carnivore interaction during the Pleistoceno*, dedicado al análisis de casos concretos. Los ejemplos tratados son casos de estudio que proceden de diferentes contextos geográficos y con una adscripción cronológica variada.

En primer lugar, el Artículo 9 (4.4.1) analiza la evolución de la interacción entre homininos y carnívoros del Paleolítico Medio (PM) al Paleolítico Superior (PS). El ejemplo utilizado es el caso arqueológico del Jura de Suabia (Alemania). Esta área es idónea para desarrollar el estudio ya que preserva un registro excepcional en yacimientos como Hohle Fels, Geißenklösterle, Vogelherd o Hohlenstein Stadel. Nuestra aproximación se ha realizado a partir de un enfoque multidisciplinar que parte del estudio estrictamente de los restos y marcas dentarias conservadas en los yacimientos citados. Esta investigación ha sido publicada en un volumen especial de la revista *Journal of Archaeological Science: Reports*, editado por R. Rivales, E. Camarós y C. Sánchez-Hernández. El estudio permite entender aspectos comportamentales en relación a la interacción homininos-carnívoros como las estrategias de caza, actividades de reciclaje, el rol de los ornamentos confeccionados en piezas dentarias o el proceso de la domesticación por parte de los grupos humanos paleolíticos. A partir del análisis se concluye que la explotación de carnívoros evoluciona hacia una complejidad y una intensificación durante el periodo tratado (PM-PS), que genera en la región presiones mutuas y competición por los mismos recursos que llevará incluso a la extinción de algunas especies de carnívoros.

Otro trabajo de esta sección, el Artículo 8 (4.4.2) está focalizado en el estudio de la acción de los úrsidos en las cavidades y las implicaciones que esto tiene a la hora de estudiar el comportamiento Neanderthal. Esta investigación multidisciplinar está basada en estudios actualísticos, experimentales, paleontológicos y etológicos. Los resultados demuestran que los úrsidos son capaces de eliminar las evidencias arqueológicas que permiten inferir comportamiento moderno y complejo. Además, la investigación también apunta hacia los osos como agentes responsables de emular con su actividad lo que puede ser inferido como evidencias comportamentales Neanderthales. En este sentido, se han obtenido interpretaciones novedosas para aproximarnos al estudio del espacio estructurado, los contextos de inhumación (p.e., La Chapelle-aux-Saints) y hasta la expresión gráfica (p.e., Gorham s cave).

En el Artículo 9 (4.4.3) se trata un tema controvertido, los hominінos como presa, estudiado a partir de los ataques de carnívoros. Se ha utilizado una perspectiva forense para afrontar este tema, analizando casos actuales de ataques de carnívoros sobre humanos en todo el mundo para intentar a la vez encontrar este mismo escenario en el registro fósil. En este sentido, los casos forenses modernos se emplean para desarrollar un marco de referencia válido para explicar las evidencias del pasado. Presentamos el caso Neanderthal a modo de prueba del concepto. Nuestros resultados demuestran que los carnívoros pueden haber sido los responsables de las paleopatologías reflejadas en el patrón traumatológico Neandertal. Estos resultados plantean una explicación alternativa a la hipótesis de los *"rodeo riders"* plateada por Berger y Trinkaus en 1995. Además, el patrón traumatológico de los Humanos Anatómicamente Modernos también se discute para mostrar que el ataque de carnívoros sobre homininos es un hecho común a lo largo de la evolución humana.

El artículo 10 (4.4.4) es el último trabajo presentado en la Tesis y consta del análisis tafonómico de diferentes fósiles Neandertales europeos (Cova Negra, Valdegoba, Jarama VI, Moros de Gabasa en España; Spy y Fonds de Fôret en Bélgica; Hohlenstein Stadel en Alemania; y Kalamaki en Grecia). Esta aproximación tafonómica es original y rara vez se ha llevado a cabo. A partir del conjunto paleoantropológico se obtienen conclusiones con importantes implicaciones comportamentales. Nuestra investigación apunta hacia diferentes escenarios que quedan reflejados en los fósiles humanos. Por una lado se distingue entre pequeños y grandes carnívoros como los responsables de las diferentes modificaciones de los fósiles. Por otro lado se identifican actividades animales estrictamente de carroñeo (esta situación se puede poner en relación con nuestras investigaciones experimentales sobre la modificación de inhumaciones por parte de los carnívoros), pero también ataques depredatorios. Este artículo apunta también hacia la necesidad de desarrollar este tipo estudios tafonómicos, aunque en esta Tesis la identificación del origen de la modificación de los carnívoros no obtiene respuesta. En este sentido la Tesis cierra con una pregunta abierta y define las perspectivas futuras en relación con el estudio de la depredación en evolución humana.

Todos los resultados son valorados y discutidos en un contexto y debate más amplio en la sección 5, *Discussion and Conclusions.*

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Corrigendum

In Paper 2 (Camarós and Cueto, 2013), it should say methods instead of methodologies in the title and text.

In Paper 9 (Camarós et al., 2015), the carnivore damage on the Cova Negra specimen (CN42174b) was described and published as punctures. It should say tooth pits according to the most common and actual scientific bibliography.

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The present doctoral thesis is a compendium of scientific publications presented by Edgard Camarós.

Papers that compose the dissertation are:

Rosell, J., Baquedano, E., Blasco, R., **Camarós, E**. (2012). New insights on Hominid-Carnivore interactions during the Pleistocene. *Journal of Taphonomy*, 3-4 (10): 125-128.

Camarós, E., Cueto, M. (2013). New methodologies for the recovery of human behaviour through the evolution of hominid-carnivore interaction during the Pleistocene. *Antiquity* (Project Gallery), 87 (335).

Camarós, E., Sánchez-Hernández, C., Rivals, F. (accepted). Make it clear: Molds, transparent casts, and lightning techniques for stereomicroscopic analysis of taphonomic modifications on bone surfaces. *Journal of Anthropological Sciences*

Camarós E., Cueto M., Teira L.C., Tapia J., Cubas M., Rivals F., (2013). Aproximación experimental a la modificación de hogares por parte de carnívoros durante el Pleistoceno. Metodología y primeros resultados. *Sèrie Monogràfica del MAC*, 25.2: 417-424.

Camarós, E., Cueto, M., Teira, L.C., Ollé, A., Rivals, F. (in press). Walking with carnivores: Experimental approach to hominin-carnivore interaction. R. Alonso, D. Canales and J. Baena (Eds.), *Playing with the time. Experimental Archaeology and the study of the past*, Servicio de Publicaciones de la Universidad Autónoma de Madrid.

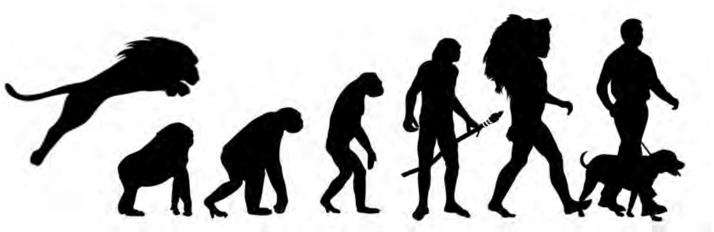
Camarós, E., Cueto, M., Teira, L.C., Tapia, J., Cubas, M., Blasco, R., Rosell, J., Rivals, F. (2013). Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications. *Journal of Archaeological Science*, 40: 1361-1368.

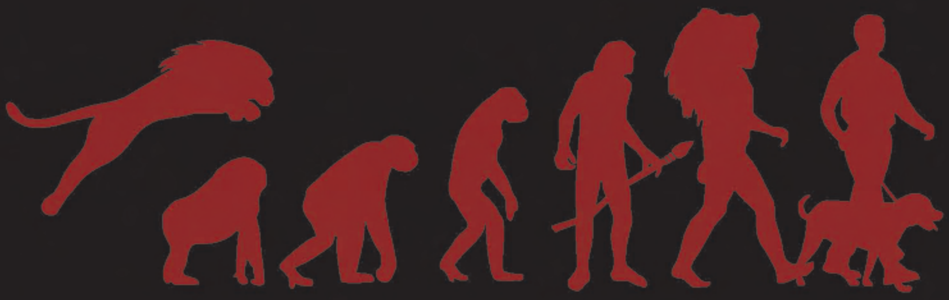
Camarós, E., Münzel, S.C., Cueto, M., Rivals, F., Conard, N.J. (accepted). The evolution of Paleolithic hominin-carnivore interaction written in teeth: Stories from the Swabian Jura (Germany). *Journal of Archaeological Science: Reports*

Camarós, E., Cueto, M., Teira, L.C., Münzel, S.C., Plassard, F., Arias, P., Rivals, F. (accepted). Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behaviour. *Quaternary International*

Camarós, E., Cueto, M., Lorenzo, C., Villaverde, V., Rivals, F. (2015). Large carnivore attacks on hominins during the Pleistocene: A forensic approach with a Neanderthal example. *Archaeological and Anthropological Sciences*, doi: 10.1007/s12520-015-0248-1

Camarós, E., Cueto, M., Rosell, J., Blasco, R., Duhig, C., Darlas, A., Díez, C., Harvati, K., Jordá, J.F., Montes, L., Villavarde, V., Rivals, F. (submitted). Neanderthal fossils with carnivore damage: Taphonomic approach and behavioral implications. Journal of Human Evolution





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Institut Català de Paleoecologia
Humana i Evolució Social

ISBN: 978-84-608-3696-4