Universidad de Valladolid

FACULTAD DE FILOSOFÍA Y LETRAS

PROGRAMA DE DOCTORADO EN PATRIMONIO CULTURAL Y NATURAL. HISTORIA, ARTE Y TERRITORIO

TESIS DOCTORAL

Homínidos y carnívoros.
El debate caza *v/s* carroñeo a la luz de las técnicas tafonómicas.

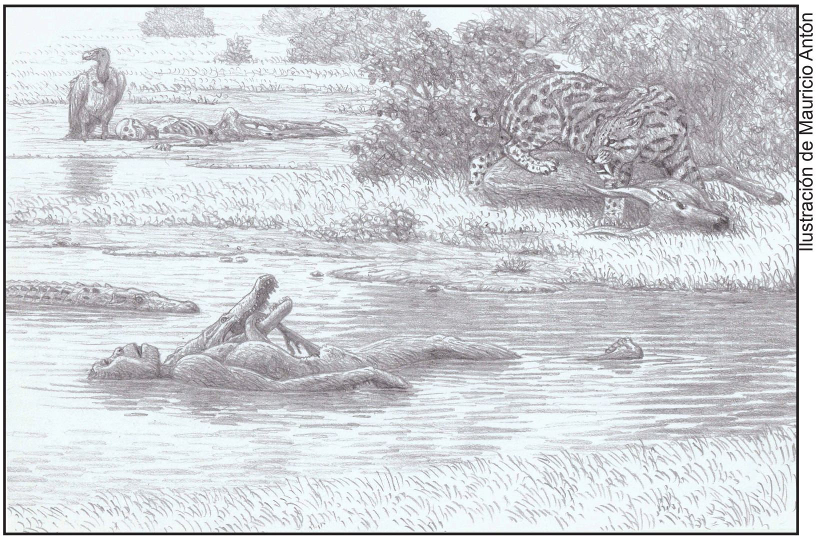

Ilustración de Mauricio Antón

Presentada por Enrique Baquedano Pérez para optar al grado de doctor por la

Universidad de Valladolid.

Dirigida por:

Prof. Dr. Juan Luis Arsuaga Ferreras / Prof. Dr. Manuel Domínguez-Rodrigo

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Valladolid, 2016

Al gran paleontólogo **Emiliano Aguirre,** que *"nací en el año del australopiteco",* por su sabiduría y por su magisterio, pero, sobre todo, por su amistad.

EB.

Ilustración de Dionisio Álvarez y Enrique Baquedano

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Muchos agradecimientos

AGRADECIMIENTOS

Podríamos llenar muchos folios con la relación de los nombres de quienes nos han ayudado en la carrera académica e investigadora hasta hoy, pero no parece razonable abusar de la paciencia del lector.

Agradecemos el esfuerzo y la dedicación fruto de la amistad, de los directores de esta tesis, Juan Luis Arsuaga Ferreras y Manuel Domínguez-Rodrigo, y del tutor, Germán Delibes de Castro.

Del prof. Arsuaga hemos adquirido una visión biologicista de la evolución humana que ha sido esencial para formar nuestra propia concepción global de dicha evolución. Antes de recibir sus enseñanzas, teníamos una visión exclusivamente cultural que se nos hacía incompleta. Además me ha devuelto la costumbre de subirme a las montañas, abandonada desde hace tiempo.

El prof. Domínguez-Rodrigo nos ha abierto las puertas del África subsahariana y de Olduvai Gorge. Con él hemos aprendido la metodología del rigor científico, de la neotafonomía y de la arqueología procesual y experimental. Ambos somos hispano-tanzanos de corazón.

Más de una vez hemos dicho ”Yo de mayor quiero ser como Germán Delibes”. Es nuestro referente como profesor y como persona. Con esto queda dicho todo.

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Perdón por los muchos que omito y que son legión.

A mi familia, Mª José y Amalur, por todo el tiempo que les robo a cuenta de esta obsesión por el conocimiento de la prehistoria.

Por último, *last but not least*, hemos recibido el apoyo administrativo de Enrique Serrano de la UVA, y de Isabel Baquedano Beltrán y Lola Fernández del MAR. También de Danah García y Bárbara Rodríguez en la maquetación final.

Con todo, el único responsable de los errores que aquí se contienen soy yo mismo que no estuve suficientemente atento a las enseñanzas y consejos de mis mayores.

2

Una aclaración previa

UNA ACLARACIÓN PREVIA

La presente tesis doctoral es fruto del compendio de cinco publicaciones editadas en las revistas *Journal of Archaeological Science*, *Quaternary International*, *PLOS ONE*, y *Quaternary Research*, todo ello con un alto nivel de impacto. Así están reconocidas por el *índice Journal Citation Reports* que emite el *Institute for Scientific Information*.

Los cinco artículos contribuyen, en mayor o menor medida, al conocimiento de las relaciones entre homínidos y carnívoros y, en consecuencia, al debate sobre la caza y el carroñeo en la evolución humana, y están basados en técnicas y trabajos propios de la tafonomía arqueológica y de la neotafonomía.

La presentación en esta tesis doctoral se hace desde una perspectiva historiográfica, con especial énfasis en los orígenes de la tafonomía en el África subsahariana y la introducción de los conceptos, los métodos y las técnicas propias de esta disciplina en la arqueología española.

Cómo estas técnicas se han ido implementando desde hace 40 o 35 años (según se proponga 1976 o 1981, alternatívamente, como años fundacionales de esta disciplina) es el hilo conductor de la presentación. La hacemos narrada, a veces, en primera persona y en paralelo a la formación profesional del doctorando. Por ello, tanto el texto como el uso indistintamente del singular o del plural mayestático, se hace con la voluntad de enfatizar unos u otros aspectos de la narración.

3

Introducción

3.1 PRELIMINAR

El comportamiento alimentario de los antiguos homínidos[1] ha sido objeto de interés y discusión casi desde los primeros momentos en que la ciencia europea descubre la existencia "antediluviana" de los seres humanos como fruto de la evolución biológica.

Ya el propio Darwin, no precisamente en su "El origen de las especies" de 1859, donde no menciona a los humanos, si no en "El origen del hombre", de 1871, en el que se centra en este grupo de primates, considera que uno de los motores de la evolución humana ha sido el consumo preferencial de carne, a diferencia del resto de los primates actuales, y ello sin contar con garras, ni afilados colmillos o picos que faciliten la depredación.

El hecho cierto es que los animales carnívoros -cazadores, carroñeros o una mezcla de ambos hábitos- ingieren y digieren un alimento en mucho menos tiempo que los herbívoros, obteniendo sus altas necesidades nutritivas y energéticas de forma más rápida. Liberando tiempo que dedicar a otras actividades vitales.

Hoy sabemos que, en efecto, el consumo cárnico tiene, como predijo Darwin, un papel estelar en la evolución humana, debiendo señalar algunos aspectos esenciales que explican la evolución anatómica en paralelo a la evolución tecnológica y cultural (Zink, K., Lieberman, D. 2016).

También sabemos que las primeras herramientas, fabricadas con unos sencillos cantos tallados muy básicamente, permitieron desventrar y eviscerar las carcasas de los animales, aprovecharlas y machacar sus huesos para acceder a su proteínico y graso contenido.

Con seguridad, la rapidez en la ingesta de proteína animal favoreció el cambio físico de los primeros *Homo*, facilitando su encefalización, incremento de talla, modificación del aparato digestivo y adquisición de mayor fortaleza y destreza.

Sin duda, el manejo del fuego para cocinar la carne debió impulsar notables cambios en la anatomía y, también, en el comportamiento humano (Carbonell, E. 2011 y 2016).

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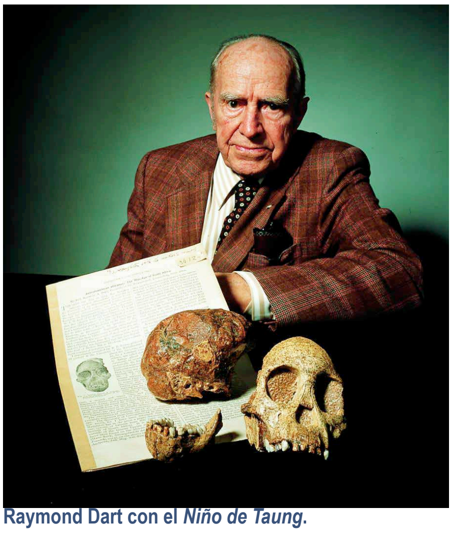
[1] Hemos respetado el título original de la tesis según se inscribió inicialmente, manteniendo el término *homínidos* aunque en puridad debería decir *homininos*. Los estudios genéticos que nos acercan a chimpancés y nos alejan del resto de simios, así lo aconsejan. (Rosas, 2016)

Y, hasta hoy mismo, nuestra relación con el consumo cárnico doméstico o salvaje, tiene una importancia crucial en nuestra alimentación y en nuestras actividades socioeconómicas. Esta aseveración ha sido recientemente enfatizada mediante la hipótesis de la cocina, consistente en que esta preparación artificial de la comida previamente a su ingesta motivó los cambios asociados con la anatomía moderna de los primeros *Homo* (Wrangham, R. 2009).

Nadie, en fin, discute que los primeros representantes del género *Homo* ya fueron importantes consumidores de carne y, sin embargo, la forma en que los humanos han accedido a la carne siempre ha sido, y aún hoy, objeto de acalorados debates científicos.

De eso tratan los trabajos que aquí presentamos compilados.

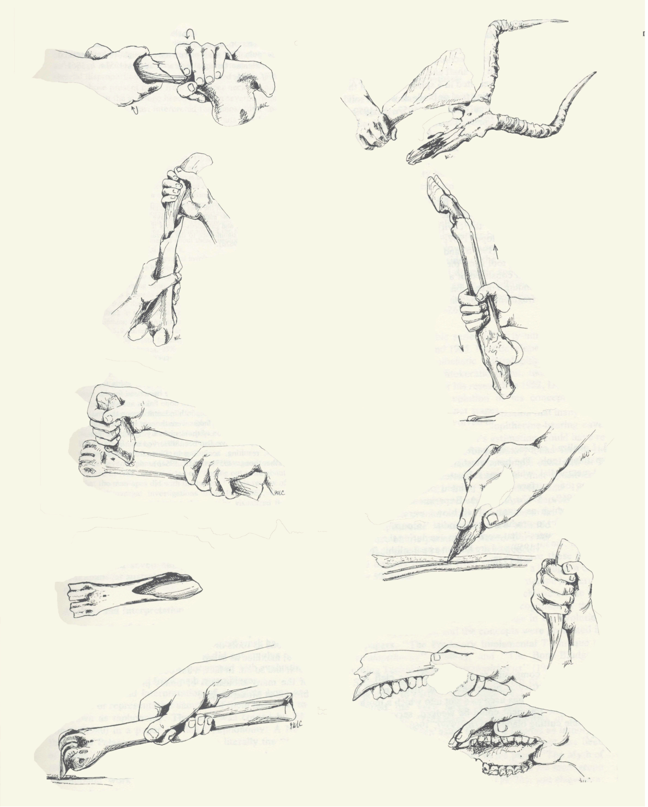


Raymond Dart con el *Niño de Taung*.

Uno de los casos más célebres y que por razones de antigüedad debemos mencionar con especial énfasis, como ejemplo, se refiere a la actividad depredadora de los australopitecinos.

Como es bien sabido, el primer australopiteco se descubrió en 1924, el Niño de Taung, en Sudáfrica y cayó en manos de Raymond Dart quien a principios de 1925 lo publicó en Nature creando la especie *Australopithecus africanus* (Dart, Raymond A.1925).

Los numerosos hallazgos de australopitecinos, y de un nuevo grupo bautizado en 1938 por Robert Broom como parantropos, principalmente en la región del Transvaal sudafricano, de manera frecuentemente asociada a conjuntos de fósiles, de herbívoros en su mayoría, hizo pensar a Dart que dichas acumulaciones eran fruto de la



Alguna de las técnicas que habrían usado los australopitecinos de Makapansgat para crear herramientas o armas. Según Raymond Dart. Ilustración en: C. K. Brian (1981). *The Hunter or the Hunted. An Introduction to African Cave Taphonomy.*. The University of Chicago Press.

actividad venatoria de los australopitecos. Aún más, Dart consideró que algunos de los fósiles rescatados habían sido utilizados por estos primates en sus carnicerías, y lo consideró como la primera industria de factura homínida, en lo que bautizó como *industria osteodontoquerática*. Varios huesos largos, cuernos y, sobre todo, mandíbulas y escápulas habrían sido seleccionados y preparados por los australopitecos, según Dart, para ser utilizados como verdaderas herramientas en sus actividades cinegéticas y de aprovechamiento cárnico.

Tras la celebración del tercer congreso panafricano, en Livingstone en 1955, en que la industria osteodontoquerática fue muy debatida, el primatólogo estadounidense Sherwood ("Sherry") L. Washburn[2] discípulo de Wilfred Le Gros Clark, se internó en la Reserva de Wankie Game (Zimbabue) para estudiar a los papiones. Observando los restos del consumo de carcasas por parte de las hienas llegó a la conclusión de que los australopitecinos, como había apuntado Kennet P. Oakley en 1954, no eran los cazadores sino los cazados y carroñeados por las hienas, publicando un muy importante artículo *Australopithecines: The Hunters or The Hunted?* (Washburn, S.L.1957).

A Washburn, gran conocedor del comportamiento primate no le encajaba la tesis de Dart en su visión de la hominización, y este fue el motivo de su búsqueda.

Algo parecido le sucedió a Charles Kimberly "Bob" Brain, quien en 1965 analizó las colecciones fósiles procedentes de los yacimientos de Sterkfontein, Swartkrans y Kromdraai, al objeto de conformar su propia hipótesis al respecto. Para ello, Bob Brain revisó 19.487 fósiles procedentes de depósitos "breccificados", y en consecuencia muy difíciles de limpiar y preparar como paso previo a su determinación faunística y análisis tafonómico.

Dart había publicado hasta 39 artículos, entre 1949 y 1965, defendiendo su tesis y rebatiendo las acumulaciones por acción de las hienas que se consideraba un origen habitual para las acumulaciones óseas, desde los trabajos de William Buckland (1822) en la cueva de Kirkdale, junto a Yorkshire, y así lo sostenían tanto Washburn como Oakley.

Caricatura de William Buckland entrando en la cueva de Kirkdale. Ilustración: William Daniel Conybeare (1822).

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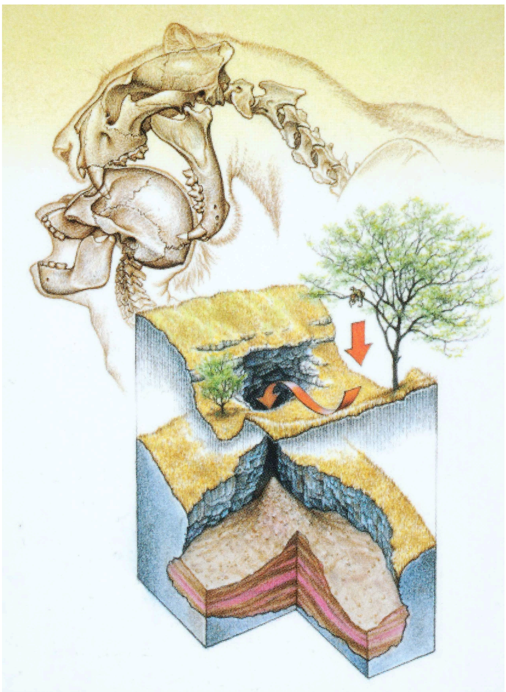
[2] La lectura de la biografía de Washburn, publicada por F. Clark Howell en 2004 (Vol. 84 de Memorias biográficas de la The National Academies Press), es una excepcional lección de historiografía sobre primatología y evolución humana. (Howell, F. Clark. 2004).

Pero Brain concluyó que dichas acumulaciones no eran originadas por los australopitecos ni tampoco por las hienas, sino por los félidos que se subían a los árboles, los leopardos, para escapar del robo de presas por parte de las hienas manchadas. Algunas de estas acacias estarían situadas en dolinas por las que se produciría el transporte hasta su acumulación gravitacional.



Interpretación de Bob Brian sobre la acumulación en Stwartkrans, Sudáfrica. Ilustración: Jay. H. Matternes.

En estos primeros estudios de Brain, que culminarán con la publicación de su célebre “The Hunter or the Hunted. An introduction to African cave Taphonomy” (1981), podemos encontrar los primeros momentos de la tafonomía africana sobre la evolución humana.

El propio Brain (2007) señala que, en realidad, la emergencia de esta disciplina en las cuevas africanas se remonta a 1976 en que, bajo el patrocinio de la WennerGren Foundation, Anna “Kay” Behrensmeyer, Andrew Hill, Alan Walker y el propio Brain, convocan una reunión de 17 científicos especializados en diferentes disciplinas. La reunión se produjo en el castillo de Burg Wartenstein (Alpes austriacos) y las actas se recogieron en “Fossils in the Making-Vertebrate Taphonomy and Paleoecology”, compilado por Kay Behrensmeyer y Andrew Hill (1980).

Al año siguiente, 1981, ve la luz el libro de Pat Shipman “Life History of a Fossil. An introduction to taphonomy and Paleoecology”, el libro de Lewis Binford “Bones: Ancient Man and Modern Myths” y el ya referido de Brain.

Delegados del simposio sobre Tafonomía y Paleocología de Vertebrados, en el castillo Burg Wartenstein en 1976.

Pat Shipman y C. K. "Bob" Brain trabajando con la industria osea de Swartkrans (1987). Cortesía personal de Pat Shipman.

Muchos investigadores consideran 1981 como el año de la fundación de la tafonomía africana moderna. En abril de 2004, el workshop "African Taphonomy: a Tribute to the Career of C. K." (Bob) Brain, en el Stone Age Institute de Bloomington, publicado por dicho instituto en 2007, da buena cuenta de los más de 20 años de estudios tafonómicos que tuvieron lugar en África desde ese año.

Desde luego nada de esto hubiera podido producirse sin el caldo de cultivo que representa la creación, en los años 60, de la llamada *Nueva arqueología*. El desarrollo de la *etnoarqueología* y de la *arqueología experimental*, tan querida por los arqueólogos procesuales, implica una concepción básica similar a la requerida por los tafónomos desde que el ruso Isaac Efremov definiera la nueva disciplina, en 1940, como una faceta más de la paleontología.

Desde 1981 hasta hoy, transcurridos treinta y cinco años, la imagen de la evolución humana ha cambiado exponencialmente y podemos afirmar con rotundidad que la tafonomía ha sido esencial en su devenir.

Participantes en la conferencia sobre tafonomía realizada en Stone *Age Institute*. De izq a dcha: Kathy Schick, Nick Toth, Rob Blumenschine, Curtis Marean, Tim White, Herny Bunn, Gary Haynes, Mohamed Sahnouni, Martha Tappen, Kathy Kuman, Francis Thackeray, Bob Brain, Travis Pickering, Manuel Domínguez-Rodrigo, Sileshi Semaw, Kay Behrensmeyer, Rick Potts y Ron Clarke.

3.2 LA TAFONOMÍA ARQUEOLÓGICA EN ESPAÑA

Pero también en nuestro país estaba ya sembrada la semilla de la discordia tafonómica.

La presencia del modelo interdisciplinar que los estadounidenses trajeron a Ambrona, a Cueva Morín, a la Cueva del Juyo, con la presencia de algunos tafónomos como Richard Klein en aquellos equipos, tuvo una función dinamizadora.

En todo ello el papel de Emiliano Aguirre fue proverbial, pues desde sus primeros trabajos con Biberson en 1962, y sus visitas y contactos con los Leakey y con Dart y Broom en 1968, tuvo un gran interés por lo que entonces se llamaba industria ósea poco elaborada (Villaescusa Fernández, L. 2011).

En los Coloquios Internacionales de Prehistoria de Morella en 1974, 1975 y 1976, la tafonomía y la arqueología tuvieron un papel destacado. Algunos jóvenes investigadores de entonces como Jordi Estévez y Eudald Carbonell, nos han hablado de la gran influencia teórica de Miquel de Renzi, hoy catedrático en Valencia (y gran poeta), y su papel primordial en aquel encuentro, en el que también estuvo Aguirre.

De Renzi nos ha referido (comunicación personal) que a Morella llegó invitado por la arqueóloga Anna Mir, a través del paleontólogo Ramón Salas.

Es Aguirre quien convoca en el Museo Nacional de Ciencias Naturales, en 1979, la *1ª reunión sobre industria ósea poco elaborada o problemática*, aunque nunca llegó a editarse.

En la teoría tafonómica hemos contado con verdaderos maestros como Sixto Fernández, desde la Universidad Complutense. Pero el verdadero impulsor de la tafonomía aplicada a la arqueología en España es Emiliano Aguirre que tenía, como hemos dicho, inquietudes en este sentido desde sus trabajos en Ambrona en los primeros 60. A partir de 1978 en que comienzan sus estudios en la Sierra de Atapuerca, promueve que algunos de sus discípulos como Carlos Díez Fernández-Lomana y Yolanda Fernández-Jalvo, comiencen a trabajar en esta disciplina y algunos otros como Luis Alcalá, también abrazarían otros campos del saber como la paleontología terciaria o los reptiles mesozoicos.

Las excavaciones, en Arganda del Rey, de los yacimientos de Áridos I y II, especialmente en 1976, verán la luz en 1980 de la mano de sus excavadores y estudiosos, Manuel Santonja, Nieves López y Alfredo Pérez-González. Esta monografía es, en nuestra opinión, el primer trabajo verdaderamente interdisciplinar liderado en España por españoles y marca un hito extraordinario en los estudios del paleolítico hispano. Pues bien, en dicho volumen sólo una página escrita por la gran paleontóloga Nieves López, especialista en lagomorfos, se dedica a la tafonomía (Santonja, M., López Martínez, N., Pérez-González, A. 1980).

Sirva el ejemplo de la monografía sobre Áridos para ilustrar cómo en aquel momento, finales de los setenta, la tafonomía en España apenas era utilizada en los estudios arqueológicos.

En el campo de la arqueozoología sí destacaban algunas figuras como Jesús Altuna, (impulsado por José Miguel Barandiarán y Emiliano Aguirre, una vez más) que, en la segunda parte de la década de los setenta, era el referente absoluto en paleontología del Pleistoceno ibérico, y surgirán continuadores como Arturo Morales, especializado en yacimientos holocenos, o Pedro Castaños que se centrará en la cornisa cantábrica, como hiciese el propio Altuna.

A la vista de los datos cruzados en distintas entrevistas (www.museoarqueologicoregional.org) podemos considerar que en España, Emiliano Aguirre en Madrid y Miquel de Renzi en Barcelona y Valencia, son los introductores del interés por la tafonomía arqueológica. De su voluntad y apoyo se deriva la introducción de la tafonomía en la arqueología española.

Tanto Eudald Carbonell como Jordi Estévez y Assumpció Vilá, habían comenzado en Francia con George Laplace, Henry de Lumley y Eugéne Bonifay. Pero con el apoyo de Aguirre y Renzi crearán grupos propios de investigación en esta disciplina. Jordi Estévez inicia la creación en Barcelona el primer equipo de estudio especializado en tafonomía y zooarqueología.

Por otra parte, el impulso de Aguirre y Carbonell propicia que España, gracias a las investigaciones sobre todo en Atapuerca, se una, así, al debate internacional basado en la tafonomía.

La reunión convocada por Sixto Fernández en 1990, sobre “Tafonomía y fosilización”, en la Universidad Complutense, fue la confirmación de este aserto (Fernández-López, S. 1990, Fernández-López, S. 1999).

Como ejemplo, comentaremos los casos de los dos primeros tafónomos, ya mencionados, del equipo de Atapuerca.

Por una parte, Carlos Díez Fernández-Lomana comenzó su colaboración con Aguirre en 1978, ya en la primera campaña de excavación en Atapuerca, a través de un anuncio de Aguirre en la prensa burgalesa.

Más tarde se formó con Camps Fabré, Pathou Matis, Francesco D’Errico o Jean-Philip Brugal. Y desde luego con Jordi Estévez, pero también las lecturas de Shipman, Binford y Behrensmeyer (Diez Fernández-Lomana, C. 2005; Diez Fernández-Lomana, Pérez López y Martínez Moreno. 2010; Diez Fernández-Lomana, J. C. *et alii.* 1999; Cáceres Cuello del Oro *et alii.* 2010; Rosell, J. *et alii* 2010; por citar algunos ejemplos de su producción científica).

Por otra parte, Yolanda Fernández-Jalvo, se formó con Emiliano Aguirre y Sixto Fernández para saltar posteriormente a trabajar con Tim Bromage, Peter Andrews, Francesco D’Errico, Kay Behrensmeyer, y Christian Denys. Estableció contacto con Mary Leakey en el año de su fallecimiento en 1996 (Fernández-Jalvo, Y. 2003; Fernández-Jalvo, Y., y Andrews, P. 2001; 2003 y 2012; Fernández-Jalvo, Y., Diéz, J. C., Bermudez, J. M., Carbonell, E. y Arsuaga, J. L. 1996; Fernández-Jalvo, Y., Diez, J. C., Cáceres, I. y Rosell, J. 1999, entre otros títulos).

A partir de los años noventa, surge toda una pléyade de jóvenes investigadores como los citados y muchos otros.

Hoy podemos decir que nuestro país tiene un plantel de investigadores que, en el campo de la tafonomía arqueológica, trabajan en el mayor nivel de excelencia posible. Como ejemplo citaremos, por ser muy reciente y muy influyente, el artículo de Manuel Domínguez-Rodrigo y Luis Alcalá (2016) sobre las marcas cuestionables de corte en los fósiles de Dikika, de hace 3,3 millones de años. Lo que ha sido considerado el testimonio más antiguo de consumo cárnico en relación con la industria tallada de Lomekwi, tal vez reelaborada.

Sin duda este es un asunto de la máxima relevancia sobre los orígenes del comportamiento humano. Los investigadores españoles están presentes en este debate internacional.

3.3 EL ORIGEN DE UNA INQUIETUD PERSONAL

En los artículos que compendiados se presentan como Tesis Doctoral, y en varios otros, se ha pretendido dar respuesta a una inquietud intelectual y científica que ha rondado mi cabeza desde los primeros momentos de mi interés por la evolución humana[3].

La llegada de Jose Luis Argente como director del Museo Numantino, a finales de 1974, hizo que mis visitas esporádicas al museo se volvieran cotidianas. Todos los días frecuentaba el museo y muchas veces salía de visita con Argente a los yacimientos sorianos.

En una de estas visitas, a Ambrona con Argente, me llamó la atención que en una señal de carreteras, oficial, ponía “Al cementerio de Elefantes, 2’4 km”. Argente me explicó que no se trataba de un cementerio de elefantes, sino de un cazadero donde, precisamente según Howell, los *Homo erectus* espantaban con fuego a los elefantes hasta empantanarlos y darles caza. ¡¡Nada que ver con un cementerio natural!! Por eso aparecían todas esas herramientas líticas junto a los restos de los grandes esqueletos.

En el curso de 1975-76 comencé mis estudios de Geografía e Historia en el Colegio Universitario de Soria y recibí unas buenas clases de Prehistoria a cargo de Jorge Juan Eiroa. Lo que recuerdo con especial interés de aquel curso es el debate sobre la industria osteodontoquerática que Raymond Dart atribuía a los *Australopithecus africanus* y que aún estaba en discusión.

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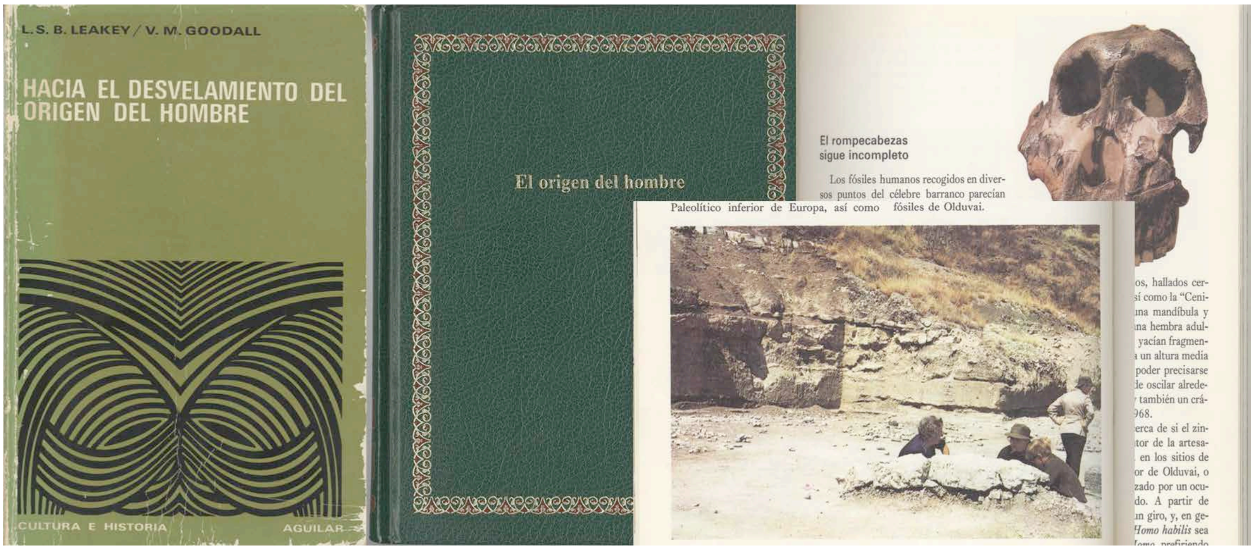
[3].Aún cuando mi vinculación con la arqueología data de mi más tierna infancia, no sería hasta sexto de bachiller (1973-74), cuando mi profesor de filosofía, Juan José Ruiz Cuevas, me inoculará el interés por el origen de la humanidad. Las vías tomistas para explicar el porqué de la existencia humana, no resultaban convincentes sino que, más bien, provocaban hilaridad en cualquier mente inquieta. Debía buscar una explicación racional y científica para un asunto tan apasionante.

No creo que hubiera influido mucho en esta inquietud el que, de niño, me escapara con frecuencia de casa para recoger fósiles de ammonites en las rocas junto a la ermita de “El Mirón”, a las afueras de Soria. Ni que recordara con admiración haber saludado al Padre Aguirre, que vino al Museo Numantino, acompañado de un señor americano con el que, más tarde, establecería gran amistad. Se trataba nada menos que de Francis Clark Howell. Los dos me causaron una profunda impresión, (aunque Howell no hablaba español) y además ¡¡buscaban fósiles humanos en la provincia de Soria!! En Torralba y en Ambrona.

Aunque lo primero que leí sobre evolución humana son los capítulos de Emiliano Aguirre en “La Evolución” de Miguel Crusafont, Bermudo Meléndez y Emiliano Aguirre[4], que Juan Zozaya había comprado para el Museo Numantino, cayeron en mis manos un par de libros que han marcado mi vida. De una parte, “El origen del hombre” de Emiliano Aguirre que fue en 1973 un bestseller de Salvat, y “Hacia el desvelamiento del origen del hombre. Diez decenios de investigación sobre evolución humana” de Louis S. B. Leakey y Vanne Morris Goodall, que editado originalmente en 1969, en inglés, fue puesto en castellano por Aguilar en 1973.

Estos libros que leí entre 1975 y 1976, y los nombres de Emiliano Aguirre y L. S. B. Leakey serán determinantes y van a marcar, en buena medida, mis inquietudes científicas e intelectuales respecto de la evolución humana, en general, y de los fósiles, en particular.



Portadas de los libros *Hacia el desvelamiento del origen del hombre*. L. S. B. Leakey y V. M, Goodall (1973). Aguilar; *El origen del hombre*. E. Aguirre. (1973). Salvat Editores. Colección “Biblioteca Salvat de Grandes Temas”.

El libro de Aguirre incluía una larga entrevista con el paleontólogo francés Pierre Biberson que, conocido sobre todo por sus trabajos en el norte de África, había excavado en Torralba y Ambrona junto a F. Clark Howell y al propio Aguirre, y estaba bastante actualizado sobre los últimos descubrimientos paleoantropológicos.

Biberson habla de “*industrias muy primitivas en las grutas de Australopithecus de África del Sur*”, mientras que Aguirre ya se hacía eco del debate sobre el comportamiento de los australopitecinos y la industria osteodontoquerática (pag. 37 a 40). Si bien Aguirre señala (pag. 98) que en Torralba y Ambrona aparecía industria ósea poco elaborada que obligaba a revisar la industria “creada*”* por Dart en Sudáfrica.

Todo aquello me resultaba de lo más fascinante.

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[4] En la Biblioteca de Autores Cristianos, 1966 (ahora se cumplen 50 años de su publicación). (Crusafont, M., Meléndez, B. y Aguirre, E. (Eds) 1966).

El libro de Leakey y Morris Goodall me causó aún una mayor impresión. Recuerdo especialmente lo relativo al descubrimiento del *Zinjanthropus boisei*, en 1959, y de *Homo habilis* a primeros de 1960 (aunque se anunció el 4 de abril de 1964). Bauticé para mis adentros a *Zinj* como "el príncipe destronado". Su mandato como primer fabricante de utensilios sólo duró unos meses. Desde entonces, siempre he tenido un gran interés (y simpatía) por el grupo de los parantropos y la reconstrucción de su imagen.

También recuerdo a Jane van Lawick–Goodall, discípula de Leakey, y su trabajo sobre etología de los chimpancés. Resulta que, entonces, la gran Jane Goodall se apellidaba así al incorporar el apellido de su entonces esposo, Hugo van Lawick, un Barón holandés de enorme prestigio por sus documentales sobre la fauna del Este de África. El Barón van Lawick fue fuente de inspiración para Félix Rodríguez de la Fuente, que tanto tuvo que ver en la concienciación medioambiental de la sociedad española entre los años 65 y 80 del siglo pasado.

Van Lawick y Rodríguez de la Fuente se encontraron en agosto de 1969, cuando se tomó la célebre fotografía (obra del ilustrador Alfonso Gutiérrez) según la otra persona que posa en la foto, Jesús Mosterín, según comunicación personal del propio filósofo que sería director editorial de la enciclopedia *Salvat de la Fauna* entre 1970 y 1973[5].

Otras lecturas que me influyeron muy sustancialmente, aunque no tanto como los libros citados, a mediados de los setenta fue la "Prehistoria", en la Historia Universal siglo XXI, que recopilada por Alimen y Steve (1976), incluían un capitulo de paleolítico africano escrito por Louis Leakey.

Félix Rodríguez de la Fuente, Jesús Mosterín y Hugo van Lawick en África (1969).

Algo más tarde pude leer la "Historia del hombre" de G.H.R. von Koenigswald en Alianza Editorial (1971), y "El Testimonio fósil de la evolución humana" de W. E. Le Gros Clark, en Fondo de Cultura Económica (1976).

Huelga decir que en aquellos años compatibilicé estas lecturas con las propias del enfoque arqueológico de la evolución humana, más centradas en los aspectos culturales y tecnológicos y en el mal llamado *Viejo mundo*.

Entre 1977 y 1980 trabajé en el campo en varios proyectos arqueológicos paleolíticos a las ordenes de Alfonso Moure, Manuel Santonja, Ángeles Querol, Leslie G. Free-

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[5] También supe, años más tarde, que Vanne Morris Goodal era la madre de Jane Goodall, que firmaba con este pseudónimo aunque su nombre real era Margaret Myfanwe Joseph y era escritora.

man y Joaquín González Echegaray, Pilar López y Rodrigo Balbín, y además recibí excelentes clases de Federico Bernaldo de Quirós en la especialidad de Prehistoria de la Universidad Complutense.

Y en el curso 80-81 asistí al curso de doctorado de Paleontología de Vertebrados que impartían Bermudo Meléndez y Francisco Alférez, también en la UCM.

En el año 82 leí “Lucy: el primer antepasado del hombre” de Donald Johanson y Maitland Edey, en edición de Planeta, que tres años antes se había publicado en inglés. Hice una recensión para “Revista de Arqueología”.

Este libro me emocionó, me recordó los sueños y las inquietudes juveniles y pensé “Esto es lo que yo hubiera querido hacer con mi vida”.

4

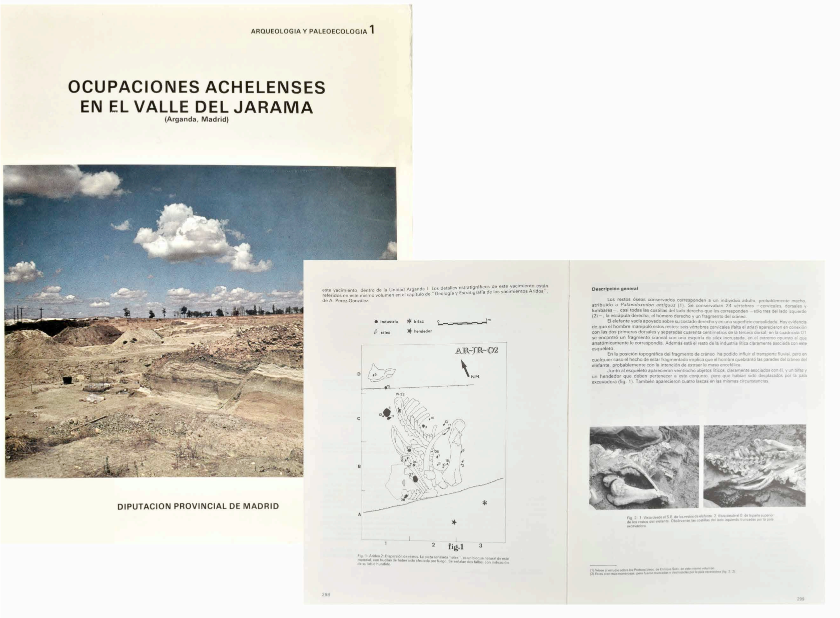
2001, una odisea por el Paleolítico

En 2001, con motivo de los preparativos iniciales de la exposición *Bifaces y elefantes. Los primeros pobladores de Madrid* (VV.AA. 2002), revisamos lo poco que se había publicado sobre el paleolítico en la región madrileña durante los últimos veinte años.

Justo desde la publicación de la memoria de excavación sobre los yacimientos de Áridos al cuidado de M. Santonja, N. López Martínez y A. Pérez-González (1980)[6]. En efecto, eran muy pocos los trabajos sobre el paleolítico madrileño realizados desde entonces, principalmente por I. Rus, y casi todos debidos a la llamada arqueología preventiva, tan poco dada a las interpretaciones de conjunto.

Comenzamos a releer y leer todo lo relativo al Paleolítico antiguo (inferior y medio), con verdadera voracidad e interés.

La conclusión respecto de esos veinte años transcurridos fue que, en el Paleolítico Ibérico, se habían producido avances espectaculares fruto de unos pocos grandes descubrimientos y un sinfín de pequeños hallazgos. Como suele suceder cuando se hace un puzzle. También es así como se reconstruye la prehistoria.


ARQUEOLOGIA Y PALEOECOLOGIA 1

OCUPACIONES ACHELENSES
EN EL VALLE DEL JARAMA
(Arganda, Madrid)

DIPUTACION PROVINCIAL DE MADRID

***Ocupaciones achelenses en el valle del Jarama* (Arganda-Madrid). Publicado por M. Santonja, N. López Martínez y A. Pérez-González. (1980).**

En el campo de la paleontología humana se habían obtenido fósiles muy relevantes que aclaraban y complicaban, a la vez, los árboles filogenéticos que cada autor presentaba. La Sierra de Atapuerca era, en este sentido, una fuente inagotable de información[7].

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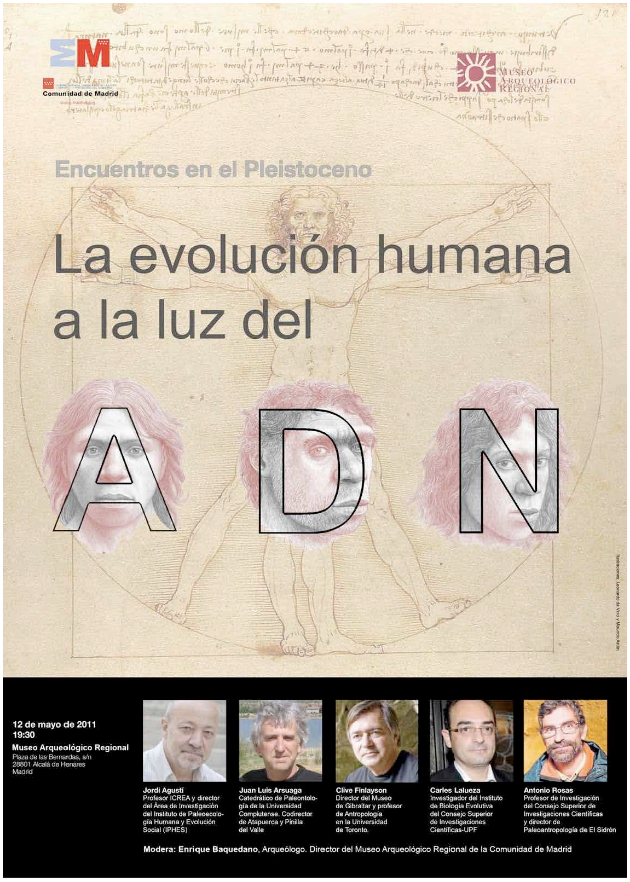
[6] Monografía que el propio Santonja nos obsequió aquel mismo año.

[7] Seguramente la lectura de *La Especie elegida* (1998), y *El collar del neandertal* (1999), de Juan Luis Arsuaga, hicieron renacer nuestra pasión por la evolución humana.



Encuentros en el Pleistoceno

La evolución humana a la luz del ADN

12 de mayo de 2011
19:30
Museo Arqueológico Regional
Plaza de las Bernardas, s/n
28801 Alcalá de Henares
Madrid

Jordi Agustí
Profesor ICREA y director del Área de Investigación del Instituto de Paleoecología Humana y Evolución Social (IPHES)

Juan Luis Arsuaga
Catedrático de Paleontología de la Universidad Complutense. Codirector de Atapuerca y Pinilla del Valle

Clive Finlayson
Director del Museo de Gibraltar y profesor de Antropología en la Universidad de Toronto.

Carles Lalueza
Investigador del Instituto de Biología Evolutiva del Consejo Superior de Investigaciones Científicas-UPF

Antonio Rosas
Profesor de Investigación del Consejo Superior de Investigaciones Científicas y director de Paleoantropología de El Sidrón

Modera: Enrique Baquedano, Arqueólogo. Director del Museo Arqueológico Regional de la Comunidad de Madrid

Cartel de la mesa redonda *Encuentros en el Pleistoceno: La evolución humana a la luz del ADN,* celebrada en el Museo Arqueológico Regional de la Comunidad de Madrid en mayo de 2011.

El estudio de la industria lítica, tan centrado tradicionalmente en el establecimiento de determinaciones tipológicas y culturales, se había volcado de lleno en el análisis de huellas de uso, para determinar la función, y en la tecnología entendida como el estudio de los procesos de talla, y de selección y transporte de materias primas.

Los sistemas de datación habían sido muy perfeccionados y las atribuciones cronológicas por contexto biológico habían afinado exponencialmente en una práctica arqueológica aún más marcada por la geomorfología y por la microestratigrafía.

La metodología arqueológica ha incorporado sistemas de registro mucho más rápidos y precisos como la estación total o el GPS de alta resolución y sobre todo se ha generalizado el uso de la informática avanzada y se han desarrollado los Sistemas de Información Geográfica, los SIG.

Pero, con todo, lo que personalmente consideramos el mayor de los cambios producidos es la introducción y desarrollo de los estudios tafonómicos aplicados a la Evolución Humana.

Desde luego, las investigaciones de los equipos de la Sierra de Atapuerca han sido cruciales para el desarrollo de esta disciplina, especialmente en España y en Europa.

Pues bien, como decíamos más arriba, en 2001 tomamos la decisión de regresar a los estudios paleolíticos para dedicarles el resto de nuestra vida profesional.

5

Metodología

Desde el punto de vista metodológico esta tesis doctoral no es especialmente novedosa y, sin embargo, creemos que en esta cuestión radica la clave de las contribuciones científicas que se aportan, algunas de ellas de indudable interés, a la comunidad académica y social.

En efecto, tres principios han movido metodológicamente estos trabajos:

1. Trabajar de forma trasdisciplinar e integradora, superando antiguas visiones interdisciplinares o incluso multidisciplinares. En nuestra opinión, lo relevante de un equipo o de un investigador no radica en su formación científica de base, si no en lo que se descubre, cómo se estudia y dónde y cómo se publica.

2. Crear equipos contando siempre con los mejores científicos, superando cuestiones de absurda vanidad y egolatría. Esto aunque pueda parecer anecdótico es, en la practica, de gran importancia.

3. Por último, la obsesión por el rigor científico. En efecto, mi generación tiene toda ella un gran compromiso con la conservación del Patrimonio Arqueológico y, puesto que toda excavación implica una destrucción, somos obsesivos con el rigor mas completo en el registro arqueológico.

Nosotros valoramos tanto el rigor científico en el registro arqueológico como la capacidad para hacer propuestas interpretativas novedosas, sugerentes, atractivas o transformadoras[8].

Dicho esto, cabe reconocer que además de los medios humanos de nuestros equipos, hemos contado con todos los medios técnicos e infraestructuras del Museo Arqueológico Regional de la Comunidad de Madrid y del Instituto de Evolución en África, de la Universidad de Alcalá, así como muchos recursos públicos y empresariales. Es casi imposible relatar todos ellos.

La revisión tafonómica del *Elephas Antiquus* de Áridos 2 se hizo en las salas del M.A.R, tras su restauración. Una verdadera preparación del fósil, en la terminología paleontológica[9].

Metodológicamente, implicó revisar todas las superficies corticales del fósil hasta dar con las marcas de corte que las mejores lupas y microscopios nos confirmaron como indudables.

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[8] Sin duda aquí está presente el buen hacer de nuestros maestros y especialmente la mano de Manuel Santonja.

[9] Que tras 25 años durmiendo el sueño de los justos en los almacenes del M.A.N, permanecía en la momia de poliuretano de dos componentes, preparada por la gran restauradora María Sanz, dentro de un cajón que no había sido abierto durante un cuarto de siglo. Contamos con toda la colaboración de la Jefa del Dpto. del museo Dña. Carmen Cacho.

En los yacimientos de Pinilla del Valle, la metodología de prospección y excavación, si ha tenido un papel estelar.

Las prospecciones, no sistemáticas, se han hecho en superficie de forma visual directa y aérea. También se ha usado el Georradar y la Tomografía Computerizada. El hecho cierto es que hemos localizado, al menos, otros seis yacimientos además del inicialmente conocido.

La excavación arqueológica en cada uno de los yacimientos se ha adaptado a la especificidad del mismo.

Todos ellos están posicionados en un mapa general reverenciado según coordenadas totales, pero en el caso de la Cueva del Camino, se respetó la cuadriculación de Alférez y equipo para poder superponer sus plantas con las nuestras. Por ello utilizamos el Sistema Meroc-Laplace, con tallas adaptadas a los estratos geológicos, pero midiendo de forma tradicional como se hizo también en los años ochenta.

En el Abrigo de Navalmaíllo, la cantidad de restos es tal, debido a la gran antropización, que se buscó un sistema, ideado por el Equipo de Atapuerca con la tecnología IBM, para optimizar el tiempo de excavación garantizando la inexistencia de errores en el volcado de los datos.

En la Cueva de la Buena Pinta y en la Cueva Des-Cubierta los datos, mucho menos numerosos, se introducen directamente en la Estación Total y luego se pasan al ordenador tras su contrastación con las medidas obtenidas en campo manualmente.

Todos los sedimentos se lavan y tamizan con dos tamaños de luz diferentes y se trían en los laboratorios de investigación del M.A.R.

Todas las plantas y alzados son tratados con SIG, lo que nos permite mover miles de datos con gran rapidez para facilitar la interpretación arqueológica de los diferentes niveles, que de otra forma sería casi imposible.

Proceso del lavado de sedimentos en los yacimientos del Calvero de la Higuera. Pinilla del Valle. Foto: E.I.P.V - MAR

Asimismo, todos los materiales son limpiados y consolidados antes de su preparación para su debido almacenamiento en condiciones.

Los trabajos de campo en Olduvai Gorge, aunque se hacen en condiciones de supervivencia mejoradas en parte por la creación de la Estación de Investigación “Emiliano Aguirre”, son totalmente rigurosos. La imposibilidad de utilizar maquinaria pesada, obliga a hacer grandes movimientos de tierra para desenterrar primero, y enterrar al final de cada campaña (tarea en la que nos ayudan los asistentes tanzanos).

La estación total lleva el peso del registro y la visión tafonómica de las excavaciones en los yacimientos, todos ellos, al aire libre y en extensión, lo que obliga a tomar todas las inclinaciones de las piezas para poder determinar el proceso de acumulación, deposición y transporte de las mismas.

Agness Gidna, Manuel Domínguez-Rodrigo y Enrique Baquedano revisando restos de carcasas trabajadas por félidos. Foto: Luis Alcalá.

Desgraciadamente, en Olduvai Gorge es imposible lavar todos los sedimentos por la ausencia de agua (escasa incluso para el consumo e higiene personal del equipo de investigación). Pero se muestrea por niveles al objeto de obtener información sobre la microfauna y los restos de talla menores, siempre muy escasos, como puede esperarse en yacimientos al aire libre.

Por último, el trabajo de tafonomía experimental con cocodrilos del Nilo actuales y su comparación con los restos fósiles de FLK, en el Lecho I de Olduvai Gorge, ha implicado un trabajo de varios meses alimentando a los cocodrilos de FAUNIA[10], y rescatando con posterioridad los huesos mordisqueados por los reptiles. Siempre lo hicimos entrando en el recinto de los cocodrilos, hasta que las autoridades nos obligaron a hacerlo protegidos tras unas barras metálicas para asumir menos riesgo.

Con todo, lo mas duro fue limpiar de restos de carne los huesos recuperados. Tarea que se realizó en los laboratorios de la Universidad de Alcalá de Henares (U.A.H.)[11], para posteriormente poder ser estudiados en los laboratorios de tafonomía de la Universidad Complutense de Madrid (U.C.M.).

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[10] Parque zoológico situado a las afueras de la ciudad de Madrid. A cuyos directivos y personal agradecemos todas las facilidades y colaboración recibidas.

[11] Nunca podremos agradecer suficientemente la colaboración de los colegas que nos ayudaron durante meses en estas odiosas tareas.

6

Trabajando en la Cuna de la Humanidad

6.1 OLDUVAI GORGE

Como es bien sabido, incluso todavía a primeros de los ochenta Olduvai Gorge era la dovela clave de la evolución humana. La serie de monografías editadas por Louis y Mary Leakey sobre los trabajos de su equipo en aquellos barrancos siguen siendo hoy una documentación imprescindible para aproximarnos a la evolución humana, en general, y a los orígenes del comportamiento humano, en particular.Todos los paradigmas importantes sobre hominización siguen pasando por Olduvai.

Pero el fallecimiento primero de Louis y luego de Mary Leakey hizo que Olduvai cayera en un relativo olvido durante bastantes años, con algunas incursiones esporádicas de paleoantropólogos tan importantes como Donald Johanson y más tarde Robert Blumenschine y su equipo Olduvai Landscape Paleoanthropology Project (OLAPP). La bibliografía al respecto es de uso habitual y sobradamente conocida.

En 2006, Manuel Domínguez-Rodrigo creó The Olduvai Paleonthropology and Paleoecology Project (TOPPP), e inició sus trabajos en Olduvai. Y en 2008, nos invitó a visitar sus excavaciones en esa misma campaña de junio.

Aquella primera visita a la que acudimos con el paleontólogo Luis Alcalá, avezado africanista con varias campañas en los yacimientos de Peninj, junto al lago Natron, nos permitió excavar en FLK, junto al *Zinj site*, y recorrer todos los yacimientos clásicos de la garganta.

Ese mismo año de 2008, tras una visita de Manuel Domínguez-Rodrigo y Luis Alcalá a las excavaciones en Pinilla del Valle, Domínguez-Rodrigo nos ofreció incorporarnos al proyecto para codirigirlo junto a él, Audax Mabulla y Henry Bunn.

Desde entonces, el equipo español ha trabajado en varios yacimientos en la garganta, si bien nosotros sólo hemos podido excavar en los yacimientos tradicionalmente conocidos como FLK, FLK North, FLK North-north, BK, AMK, PTK y DS.

FLK es uno de los yacimientos más importantes y célebres de la evolución humana. El yacimiento que Louis Leakey bautizó en homenaje a su primera esposa, Frida Leakey, es el lugar donde se descubrió, en el 59, el *Zinjathropus boisei*, bautizado así como homenaje al cuerno de África y a Charles Boise, amigo y patrocinador de los Leakey.

También allí, en los primeros meses de 1960 y 1961 se descubren y describen tanto la industria olduvayense como el primer *Homo habilis*, publicado por Leakey, Tobias y Napier (1964).

Los restos descubiertos por Louis y Mary Leakey en FLK, en el nivel 22 en que aparece el Zinj, son clave en la primera hipótesis y consiguientes debates sobre el comportamiento de los primeros homínidos y, especialmente, sobre su dieta. ¿Fueron cazadores como pensaban los Leakey, ya los primeros habilinos, o fueron carroñeros como se ha sostenido posteriormente por muchos otros investigadores? En la excavación de FLK lo primero que llamó nuestra atención es que el nivel 22 era, en realidad, dos niveles fértiles claramente separados por otro nivel estéril. Al menos había dos niveles de ocupación diferentes y habían sido excavados como un palimpsesto artificial en que se mezclan dos conjuntos diferentes.

Los Leakey excavando en Zinj site (1960). Foto: © Getty Images.

También llamaba la atención que, en una zona los fósiles estaban claramente antropizados y, en otra, habían sido aportados por los félidos. Tanto las marcas, como las especies y las partes esqueletales representadas eran muy diferentes.

Se confirmaba la tesis de Domínguez-Rodrigo, Rebeca Barba y Charles Egeland en “Deconstructing Olduvai”, de 2007, en su debate con Robert Bluemenschine. Todo apunta a que en FLK los homínidos tuvieron un acceso primario a sus presas y no derivado de las presas aportadas por los félidos.

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First Partial Skeleton of a 1.34-Million-Year-Old *Paranthropus boisei* from Bed II, Olduvai Gorge, Tanzania

Manuel Domínguez-Rodrigo[1,2]*, Travis Rayne Pickering[3,4,5], Enrique Baquedano[1,6], Audax Mabulla[7], Darren F. Mark[8], Charles Musiba[9], Henry T. Bunn[3], David Uribelarrea[10], Victoria Smith[11], Fernando Diez-Martin[12], Alfredo Pérez-González[13], Policarpo Sánchez[12], Manuel Santonja[13], Doris Barboni[14], Agness Gidna[1,15], Gail Ashley[16], José Yravedra[2], Jason L. Heaton[5,17], Maria Carmen Arriaza[2]

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Abstract

Recent excavations in Level 4 at BK (Bed II, Olduvai Gorge, Tanzania) have yielded nine hominin teeth, a distal humerus fragment, a proximal radius with much of its shaft, a femur shaft, and a tibia shaft fragment (cataloged collectively as OH 80). Those elements identified more specifically than to simply Hominidae gen. et sp. indet are attributed to *Paranthropus boisei*. Before this study, incontrovertible *P. boisei* partial skeletons, for which postcranial remains occurred in association with taxonomically diagnostic craniodental remains, were unknown. Thus, OH 80 stands as the first unambiguous, dentally associated *Paranthropus* partial skeleton from East Africa. The morphology and size of its constituent parts suggest that the fossils derived from an extremely robust individual who, at 1.338±0.024 Ma (1 sigma), represents one of the most recent occurrences of *Paranthropus* before its extinction in East Africa.

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Introduction

Apart from the occurrence of articulating bones from the same skeleton, the close intrasite vertical (i.e., stratigraphic) and horizontal (i.e., lateral) spatial association of isolated hominin postcranial bone specimens and taxonomically diagnostic craniodental remains is the most secure (but not definitive) way that paleoanthropologists can begin to describe and contrast inter-generic and inter-specific adaptations of the hominin postcranium. Currently, there are secure or fairly secure craniodental-postcranial associations (thus, they meet at least one of the criteria above) for six early Neogene hominin species: *Ardipithecus ramidus* [1]; *Australopithecus afarensis* [2]; *Au.* sp. [3]; *Au. sediba* [4]; *Homo habilis* [5] and *H. ergaster* [6]. The status of *Paranthropus boisei*, a craniodentally highly derived Pleistocene species, is less clear because we know, based on fossil evidence from various stratigraphic intervals and sites in East Africa, that it co-existed with early *Homo* for a significant interval [7]. For instance, KNM-ER 1500, a fragmentary hominin postcranium from Koobi Fora (Kenya), was assigned to *P. boisei* based on its surficial spatial association with a mandible fragment that has a thick corpus and marginal crest [8]. Wood [9] noted, however, that some penecontemporaneous, dentally-identified mandibles of early *Homo* show the very same traits, calling into question the taxonomic attribution of KNM-ER 1500 to *P. boisei*. Wood and Constantino [7] went further, reviewing all claims of *P. boisei* postcranial remains, and deeming each dubious for a variety of enumerated reasons.

Here we describe hominin dental and postcranial remains (cataloged collectively as OH 80) that were recovered *in situ* in close spatiotemporal proximity through excavations in Level 4 of the BK (Bell's Korongo) site, in Upper Bed II, Olduvai Gorge (Tanzania). Based on diagnostic morphological criteria, the most complete BK tooth fragments are allocated confidently to *P. boisei*. There are no replicated skeletal elements in the BK Level 4 hominin sample, the state of preservation all of hominin fossils is consistent and they all derive from a circumscribed horizontal area (see SI Appendix). In addition, the BK faunal assemblages, overall, show limited evidence, in the form of bone breakage patterns and tooth mark damage, of significant carnivore involvement in their formations [10]. However, all four of the Level 4 hominin postcranial fossils are broken in patterns consistent with static loading of green bone, such as is accomplished by carnivore chewing (e.g., [11]). Based on taphonomic parsimony, these lines of evidence support the hypothesis that all of the Level 4 hominin fossils derive from a single individual, and, based on taxonomically diagnostic characteristics of the teeth, that that individual represents the species *P. boisei.*

Results and Discussion

Site age and summary

The BK site is situated in Bed II of Olduvai Gorge, directly above tuff IID, which was previously dated at c. 1.2 Ma [12,13]. We have determined a new ^{40}Ar/^{39}Ar age for tuff IID at BK of 1.353±0.035 Ma (1 sigma, full external precision, Renne et al. [14], see Appendix S1). Tuff IID has also been identified as a primary tuff at RHC (Richard Hay Cliff) [13], and we have confirmed this correlation with an age of 1.321±0.032 Ma (1 sigma, full external precision, Renne et al. [14], see Figures S10 and S11 and Table S6 in Appendix S1). Taking an average of these two age constraints, we report the age for tuff IID of Olduvai Gorge as 1.338±0.024 Ma. This age is discussed throughout the remainder of this contribution. Hay [13] also suggested a correlation of tuff IID at BK and RHC with exposed tuffs at JK (Juma Korongo) and MCK (Margaret Cropper Korongo). New ^{40}Ar/^{39}Ar age data (see Appendix S1) show these two tuffs to be 1.992±0.009 and 1.975±0.029 Ma (1 sigma, full external precision, Renne et al. [14], see Appendix S1), respectively, showing such a correlation to be inaccurate. We also attempted to correlate between all sites using glass chemistry but data were equivocal (see Appendix S1).

The hominin-bearing site consists of fluvial deposits eroding into tuff IID and its overlying clay and tufa. To date, a sequence of eight discrete archaeological levels are recognized within a fluvial alluvial deposit (see Appendix S1). The OH 80 hominin fossils were excavated from Level 4, which is characterized by a large assemblage of Mode I stone tools that are associated functionally with abundant vertebrate fossils. Butchery marks link the tools and fossils causally, and a preponderance of the butchery damage occurs on fossils of ungulates of medium, large and very large body sizes [10]. The BK zooarchaeological assemblages [10,15–17], along with those from FLK 22 *Zinjanthropus* (Bed I, Olduvai) and Peninj (Tanzania), constitute the best evidence of hominin butchery and meat-eating in the early Pleistocene.

Dental fossils (Figure 1; Table 1)

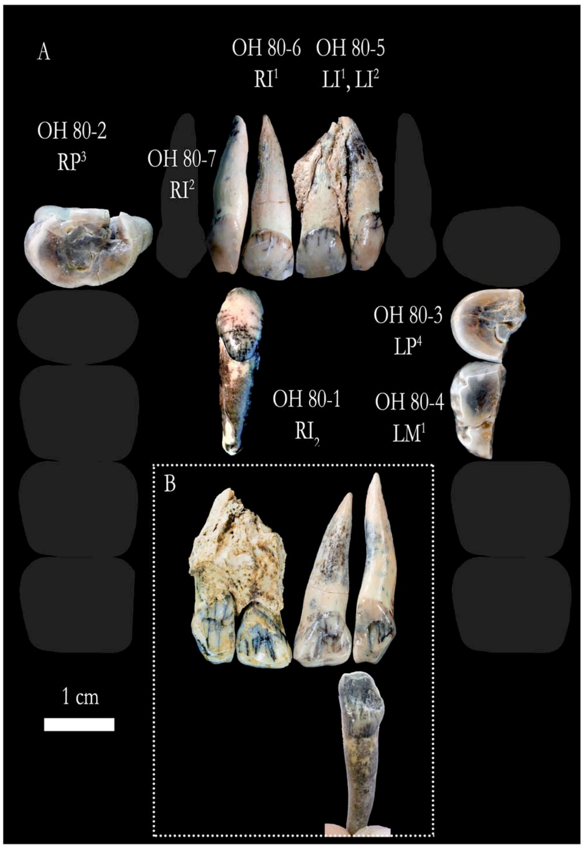

Figure 1. Hominin dental remains from Level 4 at the BK site. Teeth are shown in approximate anatomical position on a schematic dental arcade; anterior teeth are shown in labial view, postcanine teeth in occlusal view (A). Labial views of the anterior teeth are shown in (B). Photographs of individual teeth by J Trueba and MJ Ortega; composition by JL Heaton.
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OH 80-1 is a nearly complete RI$_2$, with just a small chip from the apex on the labial surface of its root. The lingual surface of the crown possesses two prominent marginal ridges converging onto its gingival eminence, which projects strongly distally and shows a bulging tubercle crossed by deep mesial and distal grooves, with other secondary grooves converging on it. The marginal ridges demarcate a lingual fossa, which is most prominent distally. The crown's incisal surface shows flat wear, which extends onto its distal edge sloping cervico-distally, giving the crown strong asymmetry in labial and lingual outline. The enamel bulges just superior to the clearly demarcated cervicoenamel junction (CEJ). The root expands just inferior to the crown and tapers very gently to a deflected tip. Measurements of the mesiodistal (MD) diameters for this tooth and the upper lateral incisors (see below) have been corrected for interstitial wear. Overall, the tooth is very canine-like in form, but its exceedingly small size (MD = 6.2 mm; LL = 6.6 mm) and good occlusion with OH 80-7, a RI^2 described below, are the bases of its allocation as a lower lateral incisor. The mean MD and LL diameters for *P. boisei* I$_2$s are, respectively, 6.4 mm (sd = 0.22; n = 6) and 6.9 mm (sd = 0.79; n = 4), versus C$_1$ mean values of 7.7 mm (sd = 0.92; n = 10) (MD) and 8.7 mm (sd = 0.84; n = 11) (LL) (calculated from data in ref. [9]). Together, the morphology and diminutiveness of OH 80-1 justify its allocation to *P. boisei.*

OH 80-2 is a fragmentary RP^3 attached to a small fragment of maxilla. The maxilla segment is well preserved, showing three partial alveoli, but is otherwise uninformative. The tooth is

Table 1. Comparative metric analysis of the OH80 dentition and the *Paranthropus boisei* available sample (obtained from the reference 9 and the Human Origins Data Base: http://humanoriginsdatabase.org), including OH5.

tooth	specimen	BL	MD
upper I1	OH80-5	6.8	7.8
upper I1	OH80-6	6.8	7.8
upper I1	OH5	8	>10
upper I1	Pb* mean (range)	7(6.1–8)	8.8(8–>10)
upper I2	OH805	7.8	6.1
upper I2	OH80-7	7.9	6.1
upper I2	OH5	7.5	6.9
upper I2	Pb* mean (range)	6.4(5.6–7.5)	6.5(6.2–6.9)
upper P3	OH80-2	16.2	10.4
upper P3	OH5	17	10.9
upper P3	Pb* mean (range)	15.2(14.2–17)	10.8(10.2–12)
upper P4	OH80-3	-	10.5
upper P4	OH5	(17.6–18)	12
upper P4	Pb* mean (range)	15.8(12.2–18)	11.4(9.1–12.5)
upper M1	OH80-4	-	14.2
upper M1	OH5	17.7	15.2
upper M1	Pb* mean (range)	16.2(14.9–17.7)	14.8(13.5–15.7)
lower I2	OH80-1	6.6	6.2
lower I2	Pb* mean (range)	6.9(6.4–8.1)	6.4(6.1–6.6)

*Paranthropus boisei.
Data for *Paranthropus boisei* include mean values plus range (minimum and maximum). Measurements are in mm.
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composed of a nearly complete crown, two buccal roots and one lingual root, which are all clearly separated. Mesially, the crown is missing a portion of its lingual cusp as part of a complicated postmortem fracture that assumes the form of a narrow channel occlusally (45 mm in MD length), and then carries onto the mesial face, where it expands buccolingually at the approximate location of the CEJ. Where undamaged, the CEJ on the lingual face is roughly horizontal superior to a prominent cingulum bulge, typical of *Paranthropus* premolars. On the buccal face of OH 80-2, the enamel bulges inferior to its well-rounded CEJ. There is an oval interproximal wear facet (1.7 mm buccolingually) on the distal side of the crown due to contact with the P^4. The occlusal surface of the crown is moderately worn in a flat pattern, but a mesio-distal groove, separating the buccal and lingual cusps, is still present; the enamel of the crown's distal shoulder shows a slight inflection at the distal terminus of the mesial-distal groove. Remnants of the mesial and distal fossae are also apparent. In occlusal outline, the crown is oval and possesses two low shoulders mesio- and distobuccally, giving OH 80-2 a molariform shape, typical of *P. boisei* [18,19]. The crown of OH 80-2 (BL = 16.2 mm; MD = 10.4 mm) is slightly smaller than are the crowns of the P^{3}s of the *P. boisei* cranium OH 5 (BL = 17.0 mm; MD = 10.9 mm) [18].

OH 80-3 is LP^4 fragment that preserves the lingual portion of its crown and the lingual root, save its apex. The superior portion(s) of the buccal root(s) was/were broken postmortem and is/are missing, but its/their inferior portion(s) connect(s) to the lingual root at slightly less than one third of the lingual root's full length. The preserved crown portion of OH 80-3 (MD = 10.5 mm) is composed mostly of the lingual cusp and well-worn remnants of the mesial-distal groove and distal fossa; the specimen is truncated by a postmortem fracture edge just buccal to these occlusal features. The occlusal surface is worn flat and to the same degree as is OH 80-2, but still maintains a thick enamel cap. Enamel thickness along the natural mesiodistal section ranges from 1.6 to 1.7 mm. Collectively, these observations prompt our assignment of OH 80-3 to *P. boisei* and to the same individual from which OH 80-1 and OH 80-2 are inferred to have derived.

OH80-4 is the partial protocone and hypocone of a LM^1, with an attached lingual root fragment. Because the specimen was naturally fractured postmortem along a mesiodistal plane, it allows measurement of the enamel cap thickness, which is 2.5 mm at the protocone and 2.9 mm at the hypocone. The crown's occlusal surface is moderately worn (slightly less than are those of the OH 80 premolars) but retains evidence of moderate crenulation and a prominent lingual groove, which continues strongly onto the crown's lingual face. The lingual face of the tooth's protocone is traversed by a series of superoinferior trending grooves, representing a complex Carabelli's formation, comparable in intensity to those on the maxillary molars of OH 5. The lingual enamel bulges just inferior to the horizontally running CEJ. The 14.2 mm MD diameter of OH 80-4 is 1 mm shorter than are the MD diameters of the M^{1}s of OH 5 [18]. The preserved lingual root is short (17.4 mm superoinferiorly). Together, these metric and morphological observations (in addition to spatial proximity) prompt the assignment of OH 80-4 to *P. boisei* and to the same individual as represented by OH 80-1, 2 and 3.

OH 80-5 is a 5 cm mesiodistally wide fragment of left maxilla with its implanted I^1 and I^2. The incisors' alveoli are nearly complete lingually but largely broken away labially. Part of the mesial wall of the alveolus for the RI^1 is preserved, in which OH 80-6 (described below) fits perfectly. The crown of the OH 80-5 I^1 is altered diagenetically, with several vertical cracks emanating from the CEJ and with geochemically induced staining (in the form of white circular patches and lines) on its labial face, near the incisal margin. Fine striations, which might be the result of *in vivo* wear and/or postmortem movement of the specimen in abrasive sediments, are also observed on both faces of the tooth's crown. The crown is moderately worn, with the incisal margin curving gently onto the distal corner and, showing a height of 8.4 mm, measured lingually. The crown is also smaller (MD = 7.8 mm; BL = 6.8 mm) than the measurable I^1 of OH 5 (MD>10 mm; BL = 8.0 mm) [18], but accords with the I^1 mean values for the *P. boisei* hypodigm (MD = 8.8 mm [sd = 0.93; n = 4]; BL = 7.0 mm [sd = 0.77; n = 5]) (calculated from data in ref. [9]). The lingual surface is slightly shoveled, showing two well-developed marginal ridges that converge on the moderately developed cingulum bulge. This LI^1 is the antimere of OH 80-6, which, like the OH 80-5 LI^1 is diagenetically discolored in patches and shows nearly identical morphology and dimensions (MD = 7.8 mm; BL = 6.8 mm).

The OH 80-5 LI^2 is the antimere of OH 80-7. OH 80-7 occludes with OH 80-1, the RI$_2$ described above. Like OH 80-1, each of the upper lateral incisors shows distinct, canine-like morphology, evincing strong asymmetry in labial and lingual view and has marked incisal wear that tapers distally, reaching nearly the incisal extent of the cingulum bulge. Fortunately, even though the mesial face of the RP^3 OH 80-2 is damaged (see above), enough of that tooth's mesial interproximal wear facet is preserved to demonstrate that OH 80-7 does not match it, as should be the case if both teeth derived from the same individual and if OH 80-7 was a RC^1 and not a RI^2. The MD diameters of the OH 80-5 I^2 and OH 80-7 are both 6.1 mm; their LL diameters are, respectively, 7.8 mm and 7.9 mm. These values match more closely the mean values of *P. boisei* I^2s (MD = 6.5 mm [sd = 0.35; n = 5]; BL = 6.6 mm [sd = 0.91; n = 6]) than the mean values of *P. boisei* C^1s (MD = 8.8 mm [sd = 0.80; n = 8]; BL = 9.0 mm [sd = 0.86; n = 7]) (calculated from data in ref. [9]). The crowns of both upper lateral incisors are slightly shoveled, with moderately developed marginal ridges and gingival eminences. We note that the morphology of the OH 80 upper lateral incisors is significantly different than that of the upper lateral incisors of OH 5, the latter of which are more similar to typical central incisors in shape and apical wear. OH 80-5 and OH 80-7, in contrast, show interstitial wear, as a result of their more canine-like morphology. Given the similarities between the other teeth of OH 80 and those of the *P. boisei* hypodigm, the most parsimonious approach is to consider the differences in lateral incisor morphology as simply demonstrating a large range of variation in *P. boisei*, It is also worth noting that the OH 5 *P. boisei* holotype is half a million years older than OH 80, so diachronic variation in the two fossils should not be unexpected. However, if new fossil discoveries from OH 80's interval prove to show even more differences with the *P. boisei* hypodigm, then the taxonomic status of OH 80 might, at that time, need to be re-evaluated.

OH 80-8 (MD = 8.6 mm; superoinferior = 13 mm) and OH 80-9 (MD = 8.9 mm; superorinferior = 15.7 mm) (not figured) are two extremely robust molar roots missing their crowns and deriving from teeth other than those previously described. There is, however, no reason to infer that they represent a species other than *P. boisei* or an individual other than that inferred to have provided the previously described dental fossils.

The OH 80 dental fossils are permanent teeth, representing a single adult *P. boisei* (with small anterior teeth and large postcanine teeth that are worn flat, and includes a molariform premolar—a character suite typical of the species [18,19]), and differentiated from the juvenile *P. boisei* represented by OH 3, a deciduous canine and molar set, discovered previously at BK [20]. Based on our new $^{40}Ar/^{39}Ar$ ages for tuff IID, the presence of OH 3 and OH 80 at the site provides a new last appearance datum for *P. boisei*, shifting that datum from c. 1.4 Ma (Konso Formation, Ethiopia; ref. [21]) to younger than 1.338±0.024 Ma.

Humerus

OH 80-10 is a distal portion of a left humerus diaphysis, measuring 88.0 mm in maximum length. The specimen terminates at both ends in green bone fractures and, although no tooth marks are preserved on its periosteal surface, this type of fracture pattern is consistent with damage imparted on long bones by feeding carnivores (e.g., [11]). Its surface is well preserved, with no subaerial weathering (0 in Behrensmeyer's [22] bone weathering stage system) but some manganese dioxide staining on its anterior aspect. Additionally, part of the medial supracondylar crest was removed by diagenetic chemical alteration. The spiral fracture that terminates the specimen proximally is inferior to the nutrient foramen and medial crest. Cortical bone, as measured perio-endosteally, at the proximal fracture is 7.0 mm, considerably thicker than in modern *H. sapiens* [23] (Figures S1 and S2 in Appendix S1). This remarkable cortical robusticity is consistent with the hypothesis that OH 80-10 derives from the same large individual as is represented by the radius specimen, OH 80-11, described below. The distal fracture edge of OH 80-10 is through the superior portion of the supracondylar ridges, with the dorsal periosteal surface in that position presenting a shallow concavity that is the superior-most portion of the otherwise missing olecranon fossa. The distal fracture edge of OH 80-10 is close enough anatomically to the transverse line at which Susman et al. [24] made CT-scan sections on four fossil hominin humeri from Swartkrans Cave (South Africa) that comparisons are possible. The shape of the distal portion of OH 80-10 is broad in ML dimension and flat in AP dimension. This is a similar configuration as that of the inferred Swartkrans *P. robustus* humeral specimens SKX 19495, SK 24600 and SK 2598 [24]. Additionally, like other inferred *Paranthropus* humerus specimens, the distal diaphyseal section of OH 80-10 is, overall, more rounded than the triangular humerus diaphyseal sections of *Homo* [23]. Mediolateral shaft thicknesses taken at the superior margins of the olecranon fossae in SKX 19495, SK 24600 and SK 2598 (range = 28.7–31.6 mm) also accord with that of OH 80-10 (30 mm, a probable underestimate due to the incompleteness of the supracondylar ridges). In contrast, AP thickness in this region is greater for OH 80-10 (15.6 mm) than are those of the Swartkrans specimens (range = 11.1–12.5 mm). The inter-specimen discrepancy in AP thickness might be due to any number of factors, including the possibility that SKX 19495 and SK 24600 are derived from small (female?) individuals [24] and that OH 80-10 is derived from a large (male?) individual. Morphologically, the shaft section shape of OH 80-10 is very similar to SK 24600, with both specimens displaying elongated ML planes and slight concavities anteriorly (remembering, though, that the OH 80-10 section is situated superior to the bicondylar line). In sum, the preserved morphology of OH 80-10 contrasts with that known for definitive early *Homo* humeri and comports with that of inferred *Paranthropus* humeri from Swartkrans. The possibility exists that the Swartkrans specimens in question do not actually represent *Paranthropus*, but currently their allocation, and that of OH 80-10, to that genus is the most parsimonious hypothesis.

Radius

OH 80-11 is a partial right radius, 194 mm in maximum length, with a head, proximal metaphysis and partial diaphysis (Figure 2). The specimen was recovered from a hard concretion matrix. After removal of the encasing matrix, several dry cracks are observable on the bone's cortex; otherwise, its overall surface preservation is fairly good. It lacks subaerial weathering (stage = 0). Although the specimen does not preserve tooth marks, carnivore(s) may have removed its distal end, as its shaft terminates in a green bone fracture. Compared to anatomically relevant *Australopithecus* (KNM-ER 20419, AL-288-1p, StW 431, StW 139) and presumed *Paranthropus* (KNM-ER 1500, SKX 3699, SK 24601) radius specimens, OH 80-11 is extremely robust, absolutely larger than any other known hominin radius fossil from the Pliocene or early Pleistocene (Figures S3 and S4 in Appendix S1). Its ML head diameter is 25.3 mm; its AP head diameter is 26.3 mm. Its articular fovea occupies an eccentric position on the head, with a large beveled margin along the anterior and medial rim of the articular surface, between its proximal and distal portions. This morphology indicates functional stability in the humeroradial and proximal radioulnar joints, as is typical of extant African apes and Asian hylobatids, as well as of all inferred non-*Homo* hominin radii currently known [25] (Figures 3 and S4 in Appendix S1). Comparatively, the Swartkrans proximal radius specimen SK 18b, inferred to represent early Pleistocene *H. erectus* [26,27], shows a straighter angle between the proximal and distal portions of its articular surface and lacks a marked bevel on its anterior and medial sides [24,25], as seen in OH 80-11. In addition, the articular fovea of SK 18b is more centrally positioned, as in modern *Homo*, and in contrast with *Australopithecus* and presumed *Paranthropus* radii [25,28], including OH 80-11.

The neck of OH 80-11 is long (24.4 mm from the distal articular surface to the superior margin of the bicipital tuberosity), as is typical of several inferred non-*Homo* hominin radii [28,29].

Figure 2. The right femur (OH 80-12; left side of image) and right radius (OH 80-11; right side of image) of the OH 80 hominin from Level 4 at the BK site. Both fossils are shown in posterior view; superior is at the top of the image; the bar scale = 1 cm.
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The neck is also relatively constricted mediolaterally (14.8 mm), but quite robust anteroposteriorly (19.1 mm). The dimensions of the neck, as well as those of the bicipital tuberosity (maximum superoinferior length = 33.9 mm; maximum transverse width = 19.0 mm), are absolutely and relatively larger than those documented for any other Pliocene and Pleistocene hominin radius specimen [24,25,28,29]. The overall massiveness of OH 80-11, and specifically that of its bicipital tuberosity, suggests that the individual from which the specimen derived possessed large biceps brachii muscles and the ability for application of great strength in forearm flexion. In contrast to the more anteriorly positioned bicipital tuberosities of definitive *Homo* radii, OH 80-11 shows a more medially placed tuberosity. However, the longitudinal axis of OH 80-11's bicipital tuberosity does not intersect the axis of its interosseous crest, as is common in nonhuman apes and in some Pliocene and Pleistocene hominin radial specimens [30,31]. The longitudinal axis of the interosseous crest of OH 80-11 is posterior to its bicipital tuberosity. Thus, if we are correct in our assignment of OH 80-11 to *P. boisei* (see below), then, necessarily, the posterior position of this axis in *H. sapiens* is not an autapomorphy.

The interosseous crest of OH 80-11 is strongly marked and curved medially, as in other early hominin radius specimens inferred to derive from taxa other than *Homo* [24,28]. Its inferior trajectory also curves posteriorly, possibly positioning the crest axis as well as the tuberosity anteriorly to the ML axis of the articular surface of the distal epiphysis, as in modern humans and in contrast with apes and various species of Pleistocene *Homo* [32]. The proximal portion of the crest shows a medially projecting, superoinferior line of enthesophytic growth. A prominent posterior oblique line opposite the interosseous crest suggests a well-developed pronator teres muscle.

On balance (and continuing to recognize the tenuousness of the taxonomic status of some other early hominin comparative radius specimens), most of the characteristics of OH 80-11 described above suggest that it derives from a non-*Homo* species. Further, because *Australopithecus* is not known from OH 80-11's temporogeographic context, its most parsimonious taxonomic assignment is to *P. boisei* (Figure 3). The only differences between OH 80-11 and other inferred *Paranthropus* and *Australopithecus* radius specimens are simply dimensional. The configuration of the anteromedial rim of the head's articular surface explains most of the differences between OH 80-11 and other Pliocene and Pleistocene hominin proximal radius specimens (Figures 2 and 3). Small, posterolaterally displaced articular foveae are a plesiomorphic feature in African apes, in inferred non-*Homo* fossil hominins [25] and in OH 80-11. In contrast, *H. sapiens* and inferred early *Homo*, such as SK 18b, possess relatively large and centrally-positioned articular foveae with very obtuse angles at the anteromedial section of the articular surface (Figure S3 in Appendix S1). Radial head diameter has been used to derive body weight estimates [33], but we are unconvinced by the efficacy of this approach for bipedal primates and thus do not present relevant data here.

Femur

OH 80-12 is a diaphyseal segment of a right femur (Figure 2). The specimen was recovered in three refitting pieces that join to form a maximum length of 167.0 mm. As with the other OH 80 postcranial specimens, OH 80-12 is not weathered (stage 0), but is covered by a few deposits of manganese dioxide. The reconstructed specimen retains its complete diaphyseal circumference and is truncated by two green bone fracture edges. As distinctive carnivore tooth marks scar the cortex of OH 80-12, we infer that the fracture edges were also created by carnivores. This inference is supported by crenulation, a common taphonomic result of carnivore chewing, on the specimen's proximal fracture edge. Proximally, the specimen ends just inferior to the missing lesser trochanter. The proximodorsal surface of the specimen preserves the gluteal, pectineal and spiral lines (the first two strongly marked and the latter less defined). These lines converge into a prominent *linea aspera* distally, which carries on to the specimen's distal termination, superior to the popliteal surface. The diaphyseal cortex of OH 80-12 is extremely thick (range = 8.3–11.0 mm mid-diaphysis), and the specimen displays a very constricted medullary cavity. Periosteally, OH 80-12 shows some flattening at its proximal end (ML = 30.5 mm; AP = 23.0 mm), with a platymeric index of 0.75.

Day [34] and Walker and Leakey [35] suggest that a thick, platymeric femur shaft is a taxonomically diagnostic feature of early *Homo*. However, given that hominin femur specimens have been assigned to *Paranthropus* based mainly on the morphology of their proximal epiphyses and metaphyses (i.e., it is argued that *Paranthropus* [and *Australopithecus*] femora have small heads and long, anteroposteriorly constricted necks) [7,34], and that no complete or nearly complete femur fossils (i.e., specimens with sizeable lengths of their diaphysis preserved) were previously associated exclusively with *P. boisei* craniodental remains [33], the femur shaft morphology of *Paranthropus* is actually poorly known. Further, some *H. habilis* femur specimens (e.g., OH 62) have morphology similar to that described for *Paranthropus* [7,33,36].

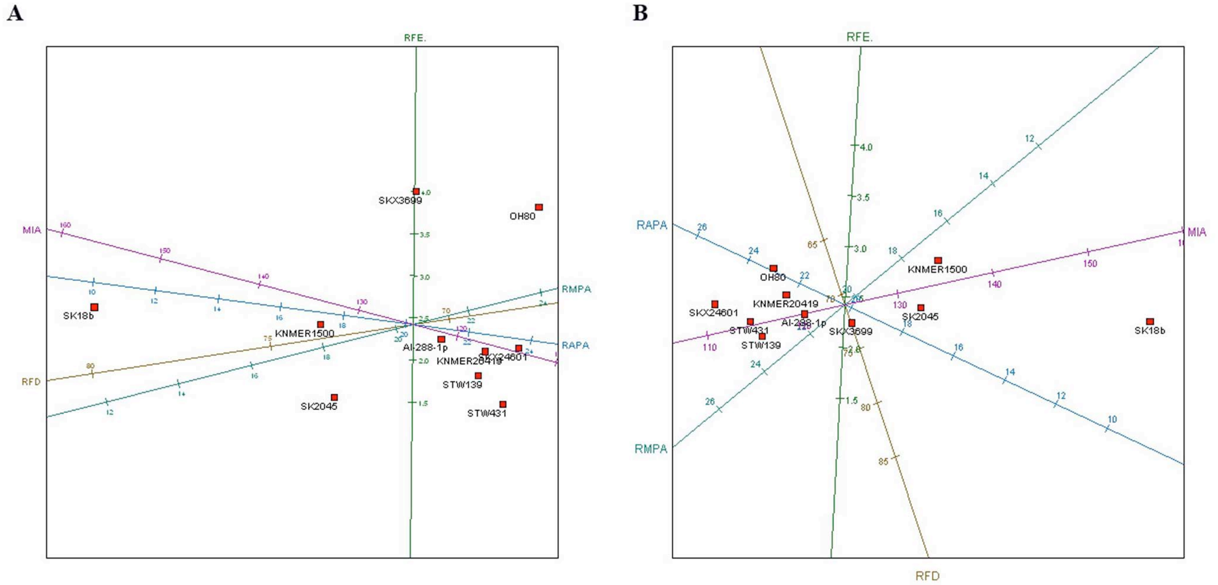

Figure 3. PCA showing the OH80 radius compared to other australopithecine and Homo fossils. A, confirmatory PCA of the variables analyzed for several fossil hominin proximal radial specimens (excluding the variable AP ratio, since predictive diagrams suggested that it was not diagnostic and that it had three times more predictive error margin than the variable with the smallest error and 50% more error than the other variables). The PCA yielded a two-component solution, which accounted for 91.9% of the sample variance. Dimension 1 accounted for 70% of the sample variance; dimension 2 explained the remaining 21.9% of variance. The variables showing the highest scores in factor 1 were MIA (.51), RAPA (−.50), RMPA (−.48) and RFD (−.47). In the second factor, RFE yielded the highest score (.97). B, A similar distribution of the sample can be observed in a MDS analysis, which reached a solution after 77 iterations, consisting of a two-dimensional solution explaining 89.2% of sample variance. The first dimension (71% of inertia) showed the same variables selected as in the PCA but with different scores: MIA (.89), RAPA (.28), RMPA (−.23), RFD(.24). The second dimension is defined by RFD (−.73). Abbreviations: medial proximal-distal intersecting angle (MIA); relative fovea diameter (RFD); relative fovea eccentricity (RFE); relative anterior proximal articular surface width (RAPA); relative medial proximal articular surface width (RMPA) [25]. Horizontal axes display the first dimension and vertical axes show the second dimension of data. Fossils (catalog number, species): KNM-ER 20419, *Australopithecus anamensis*; AL-288-1p, *Australopithecus afarensis*; StW 431, *Australopithecus africanus*; StW 139, *Australopithecus africanus*; SKX 3699, *Paranthropus robustus*; SKX 24601, *Paranthropus robustus*; KNM-ER 1500, *Paranthropus boisei*; SK18b; *Homo erectus*; SK 2045, (?) *Homo erectus*.
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Swartkrans fossils SK 82 and SK 97, two femoral specimens preserving segments of proximal diaphyses and that are attributed to *P. robustus*, show impressive cortical thickness (comprising 77% to 85% of their respective total sections) [37]. SK 82 and SK 97 are also fairly platymeric, with respective platymeric indices of 0.77 and 0.80. Assuming that SK 82 and SK 97 are, in fact, *P. robustus* fossils, then these observations suggest that neither platymeria nor diaphysis cortical thickness is a useful trait for separating early *Homo* from (at least some) non-*Homo* hominin femora [37]. OH 80-12 shares with SK 82 and SK 97 a diaphysis morphology that places the group apart from *H. erectus* [38] (Table 2 and Figures S5, S6, S7 in Appendix S1). The distribution of cortical bone inferior to the lesser trochanter of OH 80-12 represents 85.7% of its shaft section, far from the mean and outside the range for six early *H. erectus* infratrochanteric femoral sections measured at 80% of femoral length [37]. Values for OH 80-12's ML bending rigidity and polar second moment of area are also more similar to those of SK 82 and SK 97 than to those of *H. erectus*. Compared to the only adult early *H. erectus* femur specimen for which measurements at 50% shaft section are available [37], OH 80-12 has a thicker mid-diaphysis cortical section (>90% of total section area), maintaining the inter-taxonomic differences in ML bending rigidity and polar second moment of area as observed with comparisons of infratrochanteric sections (Table 3). In sum, OH 80-12 possesses the thickest femoral diaphysis of all currently known hominins from contexts >1.0 Ma.

Tibia

OH 80-13, a hominin tibia midshaft fragment (retaining <50% of its original circumference), is described in the Appendix S1(Figure S8). Based its close spatial association, comparable anatomical ruggedness and similar state of preservation to the other OH 80 postcranial fossils, described above, we hypothesize that OH 80-13 derived from the same hominin skeleton as did the rest of those fossils.

Table 2. Section properties of proximal femora (at 80% length[1 cm inferior to the lesser trochanter]) of two *Paranthropus robustus* specimens [37] and OH80.

Specimen	CA	MA	TA	%CA	I_X	I_Y	J
SK 82	490	87	577	84.9	21.637	31.261	52.899
SK 97	457	135	593	77.1	21.228	33.779	55.007
OH 80-12*	524	87	611	85.7	26.234	32.458	58.691

CA, cortical area; MA, medullary area; TA, total periosteal area; %CA, [(CA/TA) · 100); Ix, second moment of area about X (ML) axis (AP bending rigidity); Iy, second moment of area about y (AP) axis (ML bending rigidity); J, polar second moment of area. Areas in mm^2, second moments of area in mm^4.
*Measurements from the proximal shaft were obtained near the top of the preserved section, slightly at the same undertrochanteric section as suggested by Ruff et al. [37].
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Table 3. Cross-sectional properties of femoral 50% sections of OH80 and KNM-ER 1808 (*Homo erectus*).

Specimen	CA	MA	TA	%CA	I_X	I_Y	J
OH 80-12*	492	35	526	93.5	21.763	22.161	43.924
KNMER 1808	478	73	551	86.8	20.813	27.251	48.064

CA, cortical area; MA, medullary area; TA, total periosteal area; %CA, [(CA/TA) · 100); Ix, second moment of area about X (ML) axis (AP bending rigidity); Iy, second moment of area about y (AP) axis (ML bending rigidity); J, polar second moment of area. Areas in mm^2, second moments of area in mm^4.
*Measurements taken directly on the proximal break of the shaft at the mid-section.
doi:10.1371/journal.pone.0080347.t003

Conclusions

Wood and Constantino [7] provide a sustained and compelling deconstruction of previous claims of postcranial fossils of *P. boisei*. The demonstrated lack of confidently assigned *P. boisei* postcranials severely limited our understanding of this extinct taxon's biology. Here, we argue that OH 80, the partial hominin skeleton from Level 4, BK, Olduvai Gorge, is very likely that of *P. boisei*. We base these propositions—i.e., that the collective remains sample one adult individual and that that individual is represents the species *P. boisei*—on the principle of taphonomic parsimony. All hominin specimens were recovered *in situ* from the same depositional stratum, the same paleosurface and in close horizontal proximity (Figure S9 in Appendix S1). The remains display an identical state of preservation and the postcranial fossils, which are all inferred to have been modified by carnivores, derive from a larger fossil assemblage and larger site in which carnivore modification of fossils is overall not very conspicuous [10]. Allocation to *P. boisei* of the best preserved dental remains is based on long-tested and well-accepted diagnostic morphological criteria (discussed above in the descriptions). In addition to the close vertical and horizontal spatial linking of these teeth with the postcranial fossils, the postcranials, themselves, show many morphological characteristics that ally them most closely to homologous fossils inferred to derive from non-*Homo* taxa, and that distinguish them from known early *Homo* homologs.

If our taxonomic hypothesis is correct, then the analysis of OH 80 provides new insights to *P. boisei* biology as follows. First, using a minimum dimension of the linea aspera (83.60 mm) as defined in [39], an estimate of 400 mm for the complete OH 80 femur was obtained using the regression formulae from [39]. Based on this reconstructed femoral length, the hominin's minimum stature is estimated to have been 156±3.91 cm. We stress, however, that this estimate was derived from regression formulae based on the dimensions of modern human *linea asperae* [39], and that modern human body proportions are probably not adequate proxies for those of *Paranthropus*. We also recognize that because the OH 80 femur lacks epiphyses (among the best postcranial proxies of body mass), its relevance for further elucidating *P. boisei* body size dimorphism (and its sociobehavioral implications) is limited. With that caveat, application of McHenry's [33] femoral shaft module regressions (using least square formulae) to OH 80-12 yielded the value 701.5, which corresponds to a 50.0 kg human (or 40.0 kg after application of the 0.74 correction of estimate, recommended by McHenry) or to a 61.7 kg non-human hominoid—significantly heavier than estimates for KNM-ER 1500, a presumed female *P. boisei*. This tenuous contrast between the larger, presumed male (OH 80) and smaller, presumed female KNM-ER 1500 postcranium [8], agrees with other postcranial- and skull-based inferences that *P. boisei* was substantially sexually dimorphic in body size [40–44].

Second, comparative analyses of OH 80-12 also demonstrate dimensional overlap in the femora of *P. boisei* and *H. erectus* [45]. In addition, the OH 80-12 femur shares with *H. erectus* femora (e.g., OH 28; [46]) the following features: significant cortical thickness; a platymeric proximal diaphysis; similar arrangement of the gluteal, pectineal and spiral lines. While these findings urge caution for taxonomic allocation of isolated hominin postcranial specimens in geographies where *P. boisei* and *H. erectus* overlapped temporally, other distinguishing features of the two species' femora are apparent. For instance, the spiral line is significantly more marked in OH 80-12 than in known *H. erectus* femora [46]. Further, the gluteal tuberosity of OH 80-12 is more medially oriented than are those of most *H. erectus* femora, which frequently possess well-developed hypertrochanteric fossae and lateral expansions of their gluteal tuberosities, forming convexities that contrast with the concave outlines of their femoral mid-diaphyses [46]. In contrast, the lateral outline of the mid-diaphysis of OH80-12 is straighter (Figure S6 in Appendix S1). These morphological differences probably reflect variance in the biomechanics of the lower limbs of *P. boisei* and *H. erectus*.

Third, morphological analyses of the OH 80-11 radius support the claim that *P. boisei* "had relatively large and powerfully built forelimbs" (ref. [33] p. 427), larger than expected based on lower limb size [41]. The OH 80-11 radius is the most robust forearm bone currently known in the Pliocene and early Pleistocene hominin fossil record. The OH 36 ulna, which was previously tentatively attributed to *P. boisei*, is also powerfully built, with extensive buttressing posterior to its trochlear notch, substantial height and width (beyond the articular surface) of its olecranon, marked curvature of its shaft and a rugged brachial tuberosity [47] (Figure 4).

In addition, the morphology of OH 80-11's proximal articular surface, with lateral eccentricity of its articular fovea, is similar to those of climbing pongids and hylobatids [25]. The morphology of hand bones attributed to South African *P. robustus* is not indicative of regular suspensory activities [29]. Thus, if *P. robustus* and *P. boisei* are monophyletic (a proposition that we do not necessarily accept), then possible regular climbing *P. boisei* climbing is a potential explanation for presumed plesiomorphic, but actually apomorphic, climbing features of the OH 80-11 radius.

No hand bones are securely attributed to *P. boisei*, but the radial morphology of OH 80 is not incompatible with that hominin having possessed similar grasping capabilities as did/does *Homo*, employed for both power and precision grips that are associated with intricate manual manipulations. For context, Susman [29] argued, based analyses of hominin hand bones from Swartkrans, that *P. robustus* was also a tool-maker and -user [29]. (Some of the current authors believe, though, that *H. erectus* was the most likely manufacturer, user and depositor of stone tools at BK.)

In sum, the OH 80 *P. boisei* teeth, from Level 4 at the BK site, establish a new last appearance datum of 1.338±0.024 Ma for that species. Based on taphonomic parsimony, three long limb bone fossils are derived from the same *P. boisei* skeleton as are the OH 80 teeth. These skeletal remains indicate that *P. boisei*—a craniodentally highly specialized species, cofamilial and sympatric with the genus *Homo*—had a robust postcranium, and probably combined terrestrial bipedalism with at least occasional bouts of arboreality.

Figure 4. Ulna (OH36) found in upper Bed II and attributed to Paranthropus (upper) compared to the OH80-11 radius (lower) (Photo: Mario Torquemada).
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Methods

Ethics statement

The analysis was carried out on the following fossils: dentition (from OH 80-1 to OH 80-9), humerus (OH 80-10), radius (OH 80-11), femur (OH 80-12) and tibia (OH 80-13). These fossils are stored at the National Museum of Tanzania at Dar es Salaam. All necessary permits were obtained for the described study, which complied with all relevant regulations. Research was conducted with permits from the Tanzania Commission for Science and Technology (COSTECH) (n° 2013-181-ER-2006-115) and The Antiquities Department of the Ministry of Natural Resources and Tourism (Dar es Salaam, Tanzania) (n° 03/2006-2013).

Methodology

Each dental specimen was examined using a low-power (10x–50x) binocular microscope and, when possible, measurements were taken with a PaleoTech Concepts^{TM} Hillson-Fitzgerald digital dental caliper. Standard gross tooth crown measurements were taken to the nearest tenth of a millimeter (e.g., [18,48,49]). Taxonomic determinations of teeth were based on various features used previously to differentiate *Australopithecus*, *Paranthropus* and early *Homo* dentition, including, but not limited to: number of cusps; relative cusp proportions and occlusal wear pattern (e.g., [18,48–55]). The postcranial fossils were examined macro- and microscopically and measurements were taken on them using a Mitutoyo^{TM} digital caliper.

Several variables related to radius head morphology were selected for the study of OH 80-11, the radius specimen, including: anteroposterior (AP) ratio; medial proximodistal intersecting angle (MIA); relative articular fovea diameter (RFD); relative articular fovea eccentricity (RFE); relative anteroproximal articular surface width (RAPA); relative medioproximal articular surface width (RMPA). All variables but AP ratio were proposed and defined by Patel [25]. Metric measurements of the head and neck followed Senut [56].

A principal component analysis (PCA) was conducted to document relationships among the components of the sample. PCA produce factors that result from the reduction of dimensionality caused by multiple variables. PCA are used in exploratory and confirmatory ways. Exploratory PCA aims to improve prediction and variance accountability by detecting those variables that do not contribute significantly to sample variance. Confirmatory PCA uses selected variables to maximize sample variability and sample component relationship. Given the use of continuous numerical variables, the heterogeneity of these values may bias PCA solutions by overemphasizing the weight of variables displaying high numerical values. For this reason, all variables were centered and scaled prior to their statistical analysis.

As opposed to dimension reduction by orthogonal projection as performed in PCA, in multidimensional scaling (MDS) the points are chosen so that stress (the sum of the squared differences between the inter-sample disparities and the inter-point distances) is minimized [57]. The MDS option we selected for our analyses is the identity transformation, which consists of taking the inter-sample disparities to be the inter-sample dissimilarities themselves. This metric MDS approach uses a Pythagorean metric analysis of inter-point distances, which includes an iterative majorization algorithm to find the MDS solution [57]. This algorithm was considered to have converged as soon as the relative decrease in stress was less than 10^{-6}. The algorithm was also stopped once greater than 5,000 iterations were performed. In MDS, points are related in a low-dimensional Euclidean space [57], with data spatially projected by regression methods admitting non-linearity. The use of MDS in the present study, thus, complements the PCA test.

A canonical variate analysis (CVA) was also used (see Appendix S1). CVA focuses on data grouped into K classes by transforming original variables into canonical variables defined by square distances between the means of the groups obtained by Mahalanobis's D^2. This is scale invariant. CVA produces a higher degree of separation between the group means than either PCA or

MDS [58]. In CVA, biplot axes are determined by the group means.

Analyses were performed in R. Graphic display of PCA and MDS tests were carried out with biplots using the R library "BiplotGUI". Bivariate display of AP and ML measurements was produced with the "ggplot2" R library. Graphic display of multiple correspondence analysis biplot with categorical variables for femora was conducted with the UBbipl R library [59].

For the analysis of the OH 80-12 femur specimen, measurements were taken directly on the proximal shaft, which exhibits a section slightly inferior to the missing lesser trochanter, and on the mid-diaphysis thanks to the natural breaks exposing these sections. In addition, after restoration of the bone, CT scanned sections were taken at the mid-diaphysis section. Average estimates after six repeated measurements were taken in each case, first with digital calipers and then with image software (IQ View Pro 2.6.0). Geometric section properties were obtained from biplanar external and cortical breadths using an Eccentric Ellipse Model [60]. Measurements were processed using the EEM_Macro (http://www.hopkinsmedicine.org/fae/CBR.htm).

Supporting Information

Appendix S1 Supporting information. Figure S1. CT-scan image of AP section of the hominin distal humerus diaphysis (OH 80-10). Although the strong density limits the quality of the image, it clearly shows that the specimen's cortex is thick and its medullary cavity is narrow and full of trabecular bone. Figure S2. Differences between distal humeri attributed to *Homo* and to *Paranthropus* from Swartkrans (1) (upper half) and OH 80-10 (lower half). Note the elongated section distally in OH 80-10, above the biepicondylar line, which extends to the red line. Figure S3. Canonical Variable Analysis (CVA) of australopithecine (Australopithecus+Paranthopus) and Homo proximal radial specimens. CVA increases the inter-group sample differences compared to PCA and MDS. A, CVA including SK2045, which is tentatively identified as Homo sp by morphology, in contrast with SK8b (which is associated with dental remains and, thus, more securely identified). However, SK2045 is spatially placed closer to other australopithecine specimens (see main text, Figure 2), indicating that the morphology of its articular surface is ambiguous. B, CVA of the same hominin radial sample removing SK2045. Differences between Homo and australopithecines are increased. OH80-11 seems thus even closer to the latter. The average amount of predictive error in each variable is reduced from 14% in A to 10% in B. Figure S4. Dimensions (AP = anterior-posterior; ML = medial-lateral) of the proximal articular head of hominin radii of different hominins. Measurements for modern humans are from Senut [3] and for Neanderthal and Atapuerca specimens are from Carretero [4]. Abbreviations: Krp, Krapina; Ferr, Ferrasie; SKX, Swartkrans; STW, Sterkfontein; AT, Atapuerca. Bars for modern humans and Neanderthals show maxima and minima. Figure S5. Multiple correspondence analysis (MCA) of OH 80-12 and the femora of *Homo erectus*. Abbreviations: HTF = hyper-trochanteric fossa; LEGT+lateral extension of the gluteal tuberosity; LAP = *linea aspera* position. *Homo erectus* data from [5]. Figure S6. Comparison of OH 80-12 (right) and three representative femora of *Homo erectus* [5], illustrating different expressions of taxonomically diagnostic criteria. Note OH 80-12's lack of a hypertrochanteric fossa and its more medially placed *linea aspera*, which is also more robust than those of *H. erectus*. Figure S7. CT-scan image of the AP section of OH 80-12 (left) and of diaphysis section (center, right), illustrating the robust thickness of the diaphysis and thickness distribution (second moment of area) according to orientation: A = anterior; P = posterior; L = lateral; M = medial. The femur section is oriented distally (upper) to proximally (lower). The diaphysis section (center,right) is taken at the mid-diaphysis, coinciding with the natural fracture as seen on the left scan. A diaphysis section of a the KNM- ER 1808 *Homo erectus* femur is overlaid (lower right) to show differences. Note the proportionally smaller medullary cavity and more thicker cortex of OH 80-12. Figure S8. OH 80-13 (tibial shaft) compared to a modern human tibia. Image by E. Organista and JL Heaton. Figure S9. Stratigraphic sequence of Upper Bed II, Olduvai Gorge, and location of the BK site (right), with isometric reconstruction showing level 4 and a map with the distribution of materials and location of each of the excavated hominin fossils. Figure S10. Map of Olduvai Gorge showing the localities where the tuff IID samples were collected. Figure S11. Photographs of Tuff IID in each of the localities and stratigraphic position of the tuff at each of them. Figure S11. Photographs of Tuff IID in each of the localities and stratigraphic position of the tuff at each of them. Figure S12. Ar/Ar results for the BK sample. Figure S13. Ar/Ar results for the RHC sample. Figure S14. Ar/Ar results for the MCK sample. Figure S15. Ar/Ar results for the JK sample. Figure S16. Compositions of mineral phases in the Olduvai tuff samples. (a) Ab-rich anorthoclase and plagioclase feldspar compositions. (b) Augite and sodic augite compositions. (c) Spinel and rhombohedral (Ti-rich) Fe-Ti oxide compositions. (d) Hornblende compositions. Loading scores (Table S1). Loading scores (Table S2). Loading scores (Table S3). Loading scores (Table S4). Loading scores (Table S5). Table S6. Ar/Ar results are summarised in the table below and ages are calculated using two different sets of standard ages and decay constants. Table S7. Mineralogy and composition of some phases in the Olduvai Gorge (Tanzania) samples.
(PDF)

Acknowledgments

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Author Contributions

Conceived and designed the experiments: MDR TRP. Performed the experiments: MDR TRP. Analyzed the data: MDR TRP CM DM VS JLH. Contributed reagents/materials/analysis tools: DM VS. Wrote the paper: MDR TRP DM VS. Field work: EB AM HTB DU FDM APG PS MS DB AG GA JY MCA.

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6.2 COCODRILOS EN OLDUVAI

Tras la publicación de los resultados de las nuevas excavaciones en FLK (Domínguez *et alii*, 2010), iniciamos un proyecto que culminó en la correspondiente publicación aquí compilada (Baquedano *et alii*, 2012).

Desde las hipótesis de Potts en los ochenta, y Solomón (1990), solo Jackson Njau y Robert Bluemenschine (2011) habían estudiado neotafonómicamente el trabajo de los cocodrilos en los restos óseos.

En 2010 y 2011, hicimos un experimento neotafonómico, propuesto por Domínguez-Rodrigo, recuperando los huesos largos de grandes herbívoros que suministramos a ocho ejemplares de cocodrilos hembra, recluidos en el parque de Faunia (Madrid).

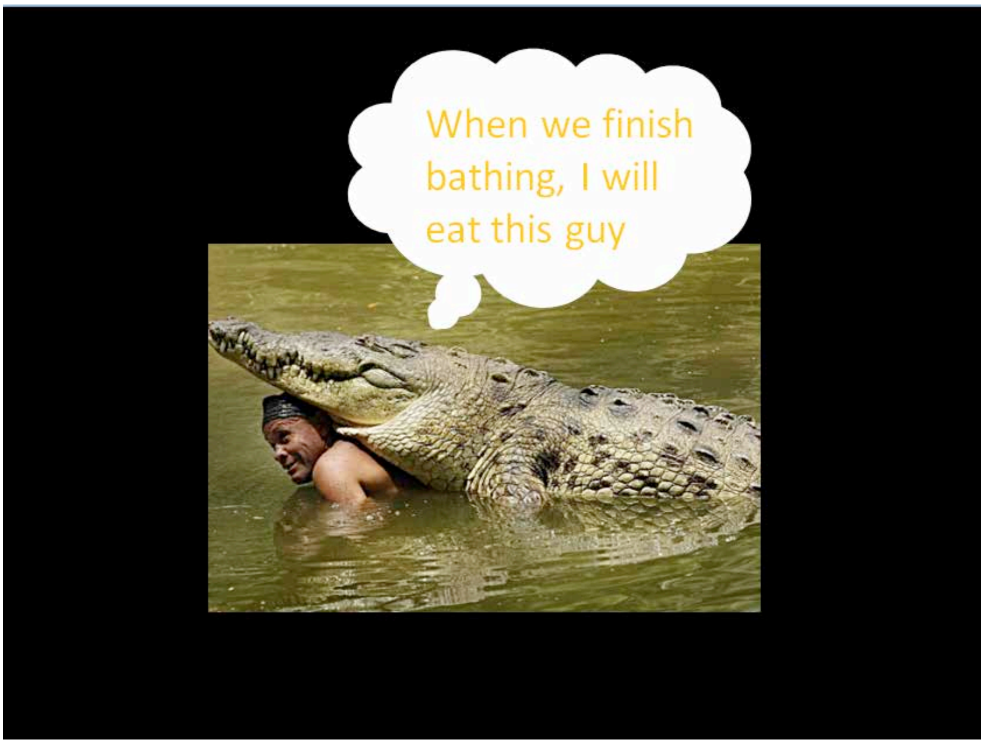
El estudio nos hizo conocer aún mejor el trabajo de los cocodrilos, sus señales, y concluir que las marcas en los fósiles de *Homo habilis* de FLK, más concretamente, en la mano, eran de cocodrilo.

Dando de comer a los cocodrilos de Faunia como parte del estudio experimental.

La presentación de los resultados en el congreso de *Hominide-Carnivore interactions* en Salou, Tarragona (2011), que una vez más organizamos junto a Jordi Rosell, antes de su publicación, sirvió para contar con el respaldo de algunos grandes tafónomos como Gary Haynes, Mary Stiner o Marta Tappen, por citar algunos de los que nos felicitaron.

La comunicación presentada por Baquedano y Domínguez-Rodrigo, provocadora a no poder ser más, consiguió su efecto, y un simple ejercicio de tafonomía experimental tuvo una gran repercusión académica[12].

Personalmente, nos sirvió para convencernos de que la dentición de los cocodrilos no había variado en millones de años, y las marcas de sus dientes en las superficies óseas, como resultado de su masticación, nos permitieron concluir que las señales en la mano de OH7, eran de cocodrilo del Nilo.



Última diapositiva de la comunicación de Enrique Baquedano y Manuel Domínguez-Rodrigo en el Congreso *Hominid-Carnivore Interactions,* celebrado en Salou en octubre de 2011.

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[12] La última diapositiva era una fotografía del costarricense Chito, bañándose con su cocodrilo Pocho, de 445 kilos y cuatro y cuatro metros. Una relación de 20 años. En la fotografía puse un bocadillo saliendo del cocodrilo que decía “Cuando termine el baño me como a este tío”. Era un sarcasmo sobre la incompatibilidad, según algunos autores, de la coexistencia entre humanos y cocodrilos..

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An experimental study of large mammal bone modification by crocodiles and its bearing on the interpretation of crocodile predation at FLK Zinj and FLK NN3

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ABSTRACT

The taphonomic signature of crocodiles as agents of bone modification has been previously identified by specific tooth mark types (e.g., bisected pits) and by a conspicuous presence of these marks: more than 75% of bones modified by crocodiles bear at least one of these distinctive marks. Therefore, crocodile tooth-marking would be notably prevalent in bone assemblages resulting from crocodile predation and active scavenging. The present study contributes to refine this diagnosis by showing greater variability of these types of marks, a different degree of tooth-marking intensity, and a somewhat different distribution of tooth-marked elements according to skeletal parts from previous experiments with crocodiles. Some of these differences are due to different experimental variables and conditions and this highlights the need to understand behavioral variability in crocodile ecological settings. This variability in crocodile tooth-marking probably results from several as-yet-inadequately measured behavioral and ecological factors, such as intensity of feeding competition and differences between male and female crocodile feeding behaviors, among others. Furthermore, this study also contributes to a better definition of the microscopic criteria that can be used to distinguish crocodile-inflicted marks from other types of bone surface modifications. In light of these and previous experimental frameworks, we reevaluate the application of these analogs to modifications documented in hominin fossils from Olduvai Gorge (OH8 and OH35) and the resulting inferences about the hazard posed by crocodiles on the paleolandscape where FLK North North and FLK Zinj (Bed I) were formed. The taphonomic analysis also shows that Olduvai OH8 and OH35 were probably not preyed upon by crocodiles. It is concluded that no tangible evidence can be used to support the interpretation that OH35 was modified by crocodiles and that the overall presence of crocodiles in FLK North North and FLK Zinj was rather marginal, based on the virtual absence of crocodile-modified bones in both archaeofaunal assemblages.

1. Introduction

Human and crocodile interactions have been variously interpreted in the past two centuries (Huxley, 1863; Dubois, 1927). The issue of who is the predator and who is the prey is still debated. Some argue that crocodiles were a serious hazard to hominins, who were frequently eaten by them (Njau and Blumenschine, in press), whereas others find evidence of the opposite in the archaeological record (Braun et al., 2010).

Neo-taphonomic research is crucial when addressing this issue. Pioneering taphonomic studies of reptiles, and more specifically crocodiles, were carried out by Davidson and Solomon (1990) and West (1995). West (1995) suggested that in this relationship, hominins were predatory. By contrast, previous work by Davidson and Solomon (1990) supported predation of hominins by crocodiles at FLK NN, (Bed I, Olduvai Gorge). This has recently been supported and expanded by actualistic work with controlled experiments on crocodiles (Njau, 2006; Njau and Blumenschine, 2006, in press). These authors have provided a valuable experimentally-derived framework for understanding how bones are modified by crocodiles in captive settings. They have documented the frequencies of damage per skeletal part and the macro- and microscopic morphology of tooth marks, and have diagnosed new tooth mark types specifically made by these reptiles. Njau (2006) expanded

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this work to include a study of crocodile-damaged bone in modern habitats of the Serengeti. He demonstrated that in places where crocodiles are most active as predators, bones with crocodile damage could be identified in as much as 75% of the bone assemblage scattered around those places.

Experiments with mammalian carnivores indicate that their bone modification patterns are subject to variability according to a set of ecological and ethological variables (Haynes, 1983; Pobiner, 2007; Domínguez-Rodrigo and Pickering, 2010; Yravedra et al., 2011). Therefore, analogical interpretation is only epistemically supported when this variability is properly assessed. In the case of modern crocodile bone damage, only one systematic study exists (Njau, 2006; Njau and Blumenschine, 2006). The present study intends to broaden the known variability of crocodile bone-modifying behavior (Njau, 2006) by enlarging the sample of actualistic studies and providing different experimental conditions. The results show some important differences with the previous referential study. The behavioral variability documented is of utmost relevance, since a very common pattern of feeding behavior of crocodiles is not collective feeding through competition of dozens of individuals, but either solitary feeding or collective feeding with competition involving only a few individuals (Welman and Worthington, 1943; Guggisberg, 1972; Pooley, 1989; Coffron, 1993; Smet, 1999; Dinets, 2011). Even feeding cooperative behavior seems to be frequent in crocodiles and alligators (King, 1972; Schaller and Crawshaw, 1982). These results urge caution in the interpretation of hominin–crocodile interaction at the Olduvai Bed I sites when using the previous modern analog (Njau, 2006).

2. Method

Eight female crocodiles were used in the present experiment; one small (1.3 m in length from nose to end of tail), two medium-sized (1.8 m) and five large (2.3 m–3.10 m). They were fed in an enclosure in a zoo (Faunia, Madrid, Spain), where they are exposed to the public (Fig. 1). Crocodiles were fed once a week over a period of four months with a total of 19 partial carcasses. Carcass portions, comprising mostly articulated limbs of suids (pig and boar) and bovids (sheep and cow) were prepared by butchers, which resulted in the removal of most feet bones. Only in two instances in which suid limbs were used were feet attached to them. More specifically, the carcasses included four suid forelimbs and five suid hindlimbs, six sheep forelimbs and three cow hindlimbs. In all cases, sheep limbs were articulated to their respective scapulae. For the suid carcass sample, only in one case was the scapula attached to the limb. Four pelves were articulated to some of the suid hindlimbs and two pelves were articulated to two cow hindlimbs. Most feeding episodes were carried out by single individuals without undergoing competition from other crocodiles. Carcasses were retrieved after 15 h of exposure to crocodiles, although most of the feeding took place in the first hour. Feeding was monitored by us for the first 1.5 h, in order to attribute carcass modification to specific individuals. Monitoring by us stopped after carcass remains were abandoned by crocodiles. Zookeepers were afterwards monitoring crocodiles at regular intervals to document if carcass remains were further accessed by crocodiles. Every feeding episode was photographed and videotaped. A total of 198 elements were retrieved for analysis (Table 1). The end and shaft of each unfused bone from juvenile carcasses was counted as one element. Bones were frequently retrieved with flesh scraps adhering to them. These were mostly removed by an enzyme (Neutrase .8 L) in the laboratory. Only in a few cases, bones were disarticulated with the aid of surgical scalpels, in a controlled manner so as not to inflict marks on bone surfaces. Despite special care put into this operation, five marks were created, but they were easily identified because of the controlled cleaning protocol and also because the morphology of these marks (extremely thin grooves) cannot be mistaken with any mark created by carnivore teeth. After the removal of the scraps, bones were cleaned with enzymes and then were submerged in a solution of water and hydrogen peroxide (H_2O_2) for one hour prior to drying.

Fig. 1. Crocodile from FAUNIA eating a juvenile cow limb.

Bone surfaces were analyzed using a 60W light and 15× hand lenses. Each mark was then microscopically analyzed using a binocular microscope (Motic) with magnifications of 20×–40× and an incorporated digital camera (MC V3), which transfers high-resolution images to a computer. Marks were also observed under a handheld digital microscope (Dinolite AM413FVT) with magnifications of 10×–200× and analyzed using the microscope's (Dino Capture 2.0) software.

For the study of mark frequency and morphology, tooth marks were analyzed using the following variables:

1. Mark type. Marks were identified using similar criteria to Njau and Blumenschine (2006). They were initially divided into four types: pits (with and without bisections), scores, punctures and hooks (Fig. 2). Bisected marks were particularly abundant (Fig. 3). Pits and scores showed two types of morphologies: some displayed similar characteristics to mammalian carnivore tooth pits and scores (U-sections with polished or crushed inner surfaces) (Fig. 4), while others showed a V-shaped section with a linear depression caused by the carinae of individual teeth (Fig. 5). Although Njau and Blumenschine (2006) only describe bisected pits, it would be accurate to

Table 1
Number of tooth-marked remains retrieved after carcass consumption by crocodiles. Numerator is for the number of tooth-marked specimens. Denominator is for the total number of specimens of each skeletal part. Percentages are in parenthesis.

	Ovine	Suid	Bovine
humerus	3/6(50)	3/4(75)	–
radius	0/6(0)	0/4(0)	–
ulna	1/6(16.6)	3/4(75)	–
femur	–	4/5(80)	2/3(66.6)
tibia	–	3/5(60)	1/4(25)
metapodials	–	1/11(9)	–
scapula	3/6(50)	1/1(100)	–
pelvis	–	1/4(25)	1/2(50)
vertebra	0/16(0)	–	1/4(25)
compact[a]	0/30(0)	1/67(1.4)	1/10(10)
total	7/70(10)	16/105(15.2)	5/23(21.7)

[a] Carpals, tarsals, phalanges.

Fig. 2. One of the more heavily tooth-marked specimens in the experimental sample (juvenile suid femur) with several bisected marks.

also mention the presence of bisected scores (as opposed to those scores with same internal morphology as tooth scores made by mammalian carnivores, showing only crushing or polishing) (Figs. 4 and 5). These bisected scores can have the same type of linear depression dividing the score into two sides (Fig. 5A) and can occasionally be accompanied by microstriations (see below) (Fig. 5B). In tooth pits and punctures occurring on cancellous bone, frequently a single or a small double thin score (bisection) could be detected longitudinally on the rim of the mark as a by-product of the impact of the carinae as well as the tooth cusp on bone surface. The presence of the bisection in these marks has been argued to be distinctive of crocodiles (Njau and Blumenschine, 2006) (Fig. 3). Given the diversity of all these marks, they can be collectively referred to as carinated. In the present work, the term "carinated mark" will be applied to both bisected pits and scores as well as punctures with bisections emanating from them.

2. Presence/absence of internal microstriations and their morphology (continuous, discontinuous). This was carried out with the aid of 15× hand lenses and confimed under the microscope (at <50×).
3. Number of microstriations inside the groove. Although microstriations could be easily identified with 15× lenses, marks were observed under a digital microscope at 20×–50× and microstriations were counted under this magnification.
4. Trajectory of the microstriations (straight or curved) when present.
5. Element type and element portion where marks were documented.

Data were first used in raw format when comparing mark frequencies anatomically. Then, when comparing marks made on dense versus cancellous bone, they were modified using bootstrapping procedures. Randomized bootstrap methods were preferred over permutation approaches (e.g., Monte Carlo) because it was assumed, after examining the raw data, that differences of tooth mark types on cancellous and dense bone could be representative of different populations. Therefore, a non-parametric bootstrapping approach using an alternative model was carried out. Data were randomly resampled 1000 times because given the characteristics of the data, that number of replicates maximized accuracy in prediction of mean differences, standard error of mean difference and power (Pattengale et al., 2010). Mean values were established within adjusted bootstrap intervals using a bias-corrected-and-accelerated (BC_a) method (Efron, 1987). BC_a tends to produce good interval limits, more adjusted than typical studentized interval estimates (Zieffler et al., 2011). For the significance of the differences, both bootstrapped *T* tests were carried out and Cohen's δ values were obtained. Cohen's δ provides a value from 0 to 1 in which the mean difference is considered of small effect ($\delta = \sim.2$), medium effect ($\delta = \sim.5–7$), and large effect ($\delta = \sim.8$). All computations were made with the bootstrap functions of the "boot" R library.

3. Results

3.1. Anatomical distribution of tooth marks

The assemblage collected contained 28 tooth-marked bones (14.1%) (Tables 1 and 2). All bones but two were complete. The total number of tooth marks documented was 133, which averages 4.7 marks per each tooth-marked specimen; the minimum number of marks per tooth-marked specimen is 1 and the maximum is 20. This is less than one tenth of the maximum number of marks for each tooth-marked specimen reported by Njau and Blumenschine in their experimental assemblage (which shows an average of 50 marks per tooth-marked specimen). Our assemblage, despite comprising a few more elements than theirs, is substantially less tooth-marked, according to both NISP and number of marks in each tooth-marked specimen.

Pelvis and scapulae are the most tooth-marked elements in this experiment (Table 2). Tooth marks on the pelvis occurs mostly on the ilium. Marks on the scapula were documented on the proximal blade, along the blade and even on the neck. After the girdle, long bones were the second most tooth-marked elements, although substantially less than reported by Njau and Blumenschine (2006). Most marks on long bones were observed on shafts, with fewer marks occurring on ends. The mode is one mark per specimen and the median is two marks per specimen. Upper limb bones (humerus and femur) are more highly tooth-marked than

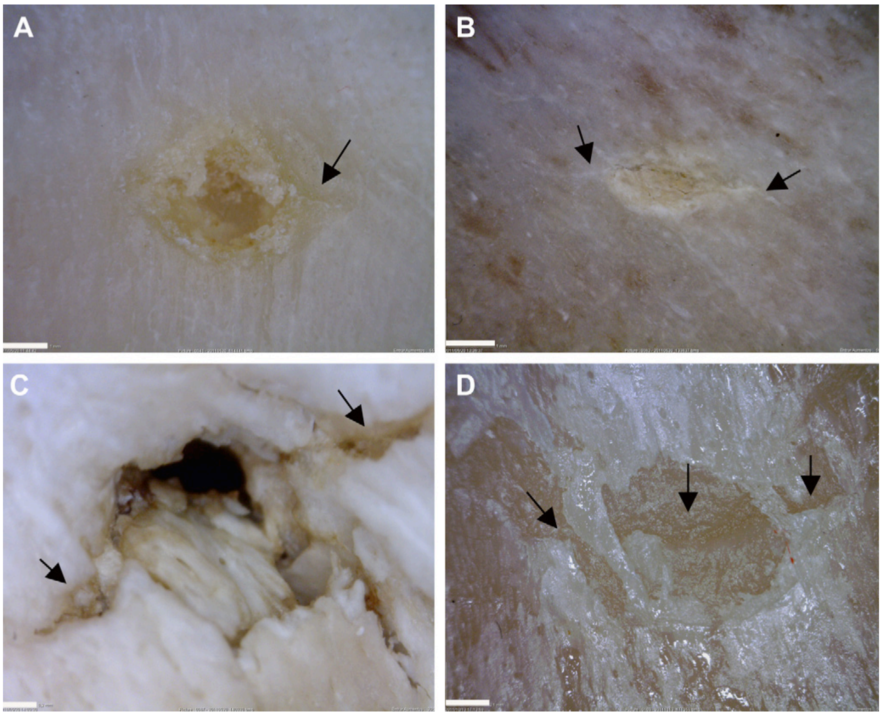

Fig. 3. Tooth pits (A, B, D) and puncture (C) with bisections made by crocodiles. In some cases, the bisection occurs on one side of the pit (A) and in other cases, on opposite sides (B, C, D). Scale for A, B, D = 1 mm. Scale for C = .2 mm.

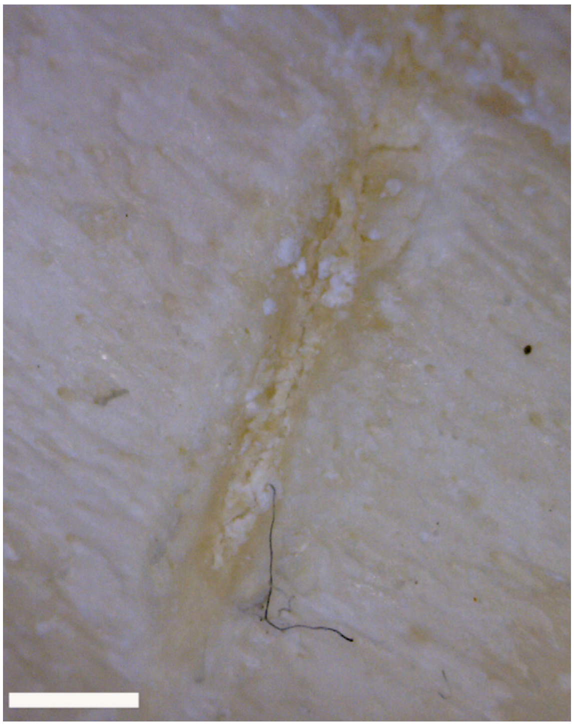

Fig. 4. Tooth score lacking microstriations, showing internal crushing and shoulder flaking made by crocodiles. Scale = 1 mm.

intermediate limb bones (radius-ulna and tibia). The radius is unmarked in our collection. In contrast, the olecranon of the ulna is more highly tooth-marked. Axial bones, namely vertebrae, were more tooth-marked than reported by Njau and Blumenschine (2006). In contrast, compact bones were substantially less tooth-marked than reported by these authors. The few examples documented in our assemblage occurred mainly on calcanea.

3.2. Tooth mark types and their frequencies

The 133 tooth marks documented include pits ($n = 56$), scores ($n = 65$) and punctures ($n = 11$) (Tables 3 and 4). Out of these, 57 marks bear a bisection: 33 bisected pits (24.8% of total tooth marks) and 24 bisected scores (18% of total tooth marks). Given that the presence of the bisection, imprinted on bone surface by the carinae of teeth, is the most diagnostic feature of crocodile bone damage (Njau and Blumenschine, 2006), 43% of the tooth marks in the experimental assemblage can be confidently identified as caused by crocodiles. This diagnosis contrasts with the other experimental analog available, in which it was claimed that "the majority of crocodile tooth marks (ca. 90%) cannot be distinguished from mammalian carnivore marks" (Njau, 2006: 114). The confidence in the identification of agent is even more solid when looking at the number of tooth-marked bones with the presence of at least one bisected pit or score. A total of 23 bones (82.1% of the tooth-marked specimen sample) bear at least one carinated mark. This overwhelming crocodile signal suggests that a crocodile-modified assemblage should be highly conspicuous and relatively easy to identify when analyzing bone surface modifications.

Most of these carinated marks occur on dense cortical bones (namely, long bone shafts) ($n = 51$; 89%) in contrast with cancellous and trabecular bone ($n = 6$; 11%) (Tables 3 and 4). Some marks bearing

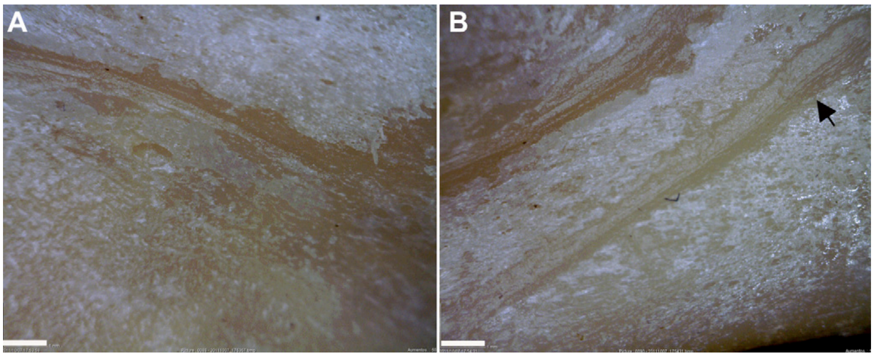

Fig. 5. Tooth scores made by crocodiles, showing three discontinuous microstriations (A) and more continuous microstriations (B). In both images it can be seen that scores are either curvy or, if they are generally straight, they have sections with a curved trajectory (arrow). Scale = 1 mm.

bisections also show internal microstriations. A total of 18 marks (13.5% of total mark sample; 31.5% of carinated marks) show microstriations. They occur more frequently on bisected scores ($n = 13$) than on bisected pits ($n = 5$). All these marks are located on dense cortical surfaces of long bone shafts. In addition, 30 marks lacking bisection bear microstriations. All of them also occur on long bone shafts. These microstriated marks are also more frequent on scores ($n = 22$) than on pits ($n = 8$). This shows that up to 36% of all tooth marks caused by crocodiles have internal microstriations, which is a trace that has the potential to be mistaken with those caused by either stone tool use or trampling (Domínguez-Rodrigo et al., 2009).

Some criteria can be used to aid in differentiating these marks from those inflicted with stone tools. A microscopic analysis of these microstriations shows that most of them occur in small numbers (mean = 3.6; median = 3 microstriations per mark). In contrast, microstriations are commonly more abundant in trampling and cut marks. It is very common that some microstriations in tooth marks made by crocodiles do not run the entire length of the score, but rather are interrupted. Frequently, they are sinuous trajectories, instead of straight ones as is typical of stone tool microstriations (Fig. 5). An additional diagnostic trait is that the bulk of scores with microstriations (76.6%) show curved or sinuous (but not straight) trajectories (Fig. 5). This feature has also been documented in two striae fields caused by crocodiles, which (in contrast with isolated striae fields made by hammerstone percussion) show curved trajectories instead of straight ones. However, two marks in our collection show a closer resemblance to marks traditionally interpreted as trampling marks (Fig. 6)(Domínguez-Rodrigo et al., 2009).

The differences in the distribution of marks according to structural bone type (dense cortical shafts *versus* cancellous/trabecular ends) have also been shown to be statistically significant. A bootstrapped group comparison of carinated marks on cancellous/trabecular and on dense cortical bone showed that there is a mean difference of 34.3% (adjusted bootstrap interval +/−2.1%) more carinated marks on the latter type of bone. This difference is of medium effect (Cohen's $\delta = .56$). This difference was also supported by a bootstrapped *T* test ($t = 71.59$; $p = .000$). The same type of bootstrapped analysis for mark type (pits *versus* scores) showed that there is a mean difference of 28.3% (adjusted bootstrap interval +/−1.8%) more scores on dense bone compared to cancellous/trabecular bone. This difference is of great effect (Cohen's $\delta = .82$). This difference was also supported by a bootstrapped *T* test ($t = 59.55$; $p =< .000$). Accordingly, this suggests that when analyzing assemblages with different proportions of marks distributed on cancellous/trabecular bone versus dense cortical bone, interpreting estimates of mark frequencies and distribution based on general analogical frameworks that do not differentiate structural bone types can be misleading. It also indicates that since microstriations (which occur more frequently on scores) and carinated marks (bisected pits and scores) are the landmark signatures of crocodile bone modification and they occur more frequently on dense cortical bone, there is a great potential to identify crocodile-modified assemblages given the better preservation of long bone shafts in paleontological and archaeological assemblages.

Table 2
Distribution of the number of specimens for four postcranial anatomical regions and the frequency of tooth-marked specimens in raw numbers and percentages.

	Njau and Blumenschine (2006)			This study		
	NISP	TM-NISP	%	NISP	TM-NISP	%
axial	66	2	3	20	2	10
girdle	14	6	42.9	13	6	46.1
long bone	32	22	68.8	58	20	34.4
compact bone	74	10	13.5	107	2	1.8
total	191	40	20.9	198	28	14.1

4. Discussion

This work intends to build upon the solid experimental work on crocodile modification of large mammal bones carried out by Njau and Blumenschine (2006). In their work, these authors stressed that crocodiles could be differentiated from mammal carnivores by the following factors:

1. Crocodile-created assemblages are composed of primarily complete elements, with minimal fragmentation.
2. These elements exhibit absence of gross gnawing.
3. Crocodile-made bone assemblages lack disarticulation of complete skeletal units, with the potential of abandoning a large portion of articulated specimens.
4. A proportion of the marks (bisected pits and punctures and hook scores) have a distinctive morphology not documented in tooth marks produced by mammalian carnivores.
5. Tooth-marked specimens usually bear dozens of marks.

Table 3
Distribution of tooth mark types (pits, scores and punctures) according to bone type (cancellous/trabecular and dense cortical).

	Cancellous bone	Dense bone
pits	10	45
scores	9	56
punctures	11	2
total	30	103

Table 4
Frequencies of carinated marks without microstriations, with microstriations and of marls lacking bisection but showing microstriations, according to tooth mark type (pits, score) and bone type (cancellous/trabecular versus dense cortical bone).

	n	Pits	Scores	Cancellous bone	Dense bone
carinated marks	57	33	24	6	51
carinated marks with microstriations	18	5	13	0	18
marks with microstriations	30	8	22	0	30

Our study confirms point 1. With the exception of a proximal tibia, a phalanx and a metatarsal of a suid, the remainder of bones were abandoned unbroken by crocodiles. NISP ($n = 198$) values are very close to MNE ($n = 196$) values. In our experimental sample, bones also lack gross gnawing, which confirms point 2. A few tooth pits were observed on some long bone ends, but gnawing and furrowing were not documented. Point 3 is also supported by our study. Crocodiles did not disarticulate most of the skeletal units that were fed to them. Only in one case, did crocodiles separate the femur from the tibia. Njau and Blumenschine (2006) also reported no disarticulation of humerus-radius and only one case of disarticulation of the femur-tibia joint.

Regarding point 4, not a single hook mark was observed in our sample, despite having documented a few instances of "death rolls" (Njau, 2006). This is not exceptional, since in their collection, Njau and Blumenschine only report 11 hook marks (out of more than 2000 tooth marks). Given the smaller number of tooth marks in our sample, the absence of hook marks is not surprising. The presence of carinated marks is indicative of crocodile bone modification only when they occur in certain frequencies. However, we believe that the categorical statement of bisected marks being caused *only* by crocodiles is unsupported. Galán et al. (2009: Fig. 6) reported bisected pits caused by modified hammerstones which were indistinguishable from those made by crocodiles. Furthermore, occasional bisected pits can also be observed on some bones modified by mammal carnivores. We have documented them on bones modified by lions and wolves (see Fig. 7). Some lion canines also have carinae (Fig. 8A), which can cause V-shaped marks with a bisection (Fig. 8B). Therefore, taphonomists have to be extremely cautious in attributing isolated bisected marks to specific agents. According to our experimentation with crocodiles, only when bisected marks occur in certain frequencies and in combination with marks bearing microstriations can a safer attribution to crocodiles be made. Rather than seeing this as a drawback, it should be contemplated as an advantage, since the proportion of bisected marks in crocodile-modified assemblages can be as high as >40% of the whole tooth-marked assemblage; even higher when considering the number of specimens bearing at least one bisected mark (>80% in both Njau and Blumenschine's study and ours). This makes crocodile bone modification potentially highly conspicuous on the landscape (Njau, 2006).

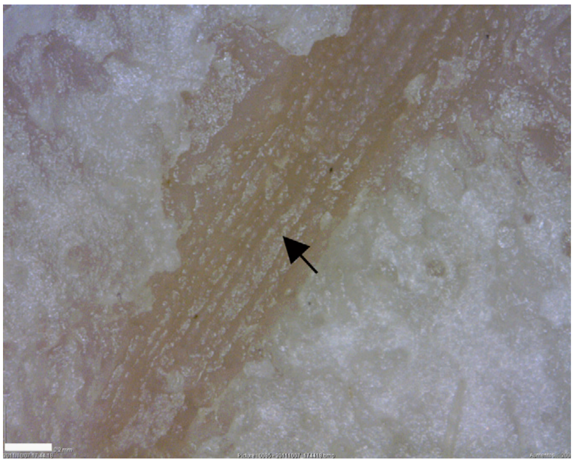

Fig. 6. Crocodile tooth score showing straight trajectory and internal microstriations. Notice the uneven separation in between microstriations and the discontinuous (arrow) and curvy or sinuous nature of some of them. Scale = .2 mm.

The most marked difference between our study and Njau and Blumenschine's can be observed in the proportion of tooth-marked elements and in the intensity of tooth marking. Our sample shows overall a smaller frequency of tooth-marked specimens and their distribution is slightly different from that reported by Njau and Blumenschine (2006). This is especially relevant when comparing tooth marks on compact and axial bone. Long bones are tooth-marked at a frequency that is almost half of that reported by the other authors. This contrast is also documented in the frequencies of tooth marks per tooth-marked specimen. Njau and Blumenschine's sample shows an average of tooth marks per tooth-marked specimen that is >10 times those documented in our study. This can be explained in part by the different number of crocodiles feeding on carcass parts in both experiments. In our experiment, we never documented the eight crocodiles feeding on the same carcass. Only one of the larger crocodiles (usually the one higher up in the hierarchy) would feed on a carcass at a time. Smaller crocodiles would also feed independently when the larger ones were distracted feeding on a different carcass or skeletal unit. In contrast, Njau (2006) reports that several of his experiments involved 20 (in some cases even up to 30) medium-sized crocodiles subjected to competition when consuming carcasses. This extreme competitive situation does not model what commonly occurs in crocodile carcass feeding in modern savannas (personal observations), but rather on locations exhibiting exceptional feeding bonanzas, such as river-crossing areas for migratory animals, where crocodiles congregate and can compete for carcasses (e.g., the Maasai Mara river crossing during the wildebeest and zebra migration).

We argue that the situations in the captive settings where crocodile experimentations have been carried out, which enabled a controlled collection of data, are highly influential on some of the results reported by Njau and Blumenschine (2006) and by ourselves. We question that either of them faithfully reproduce most of (or even the most common) crocodile behavior in natural savanna settings. For this reason, we present results on tooth mark frequencies and anatomical locations only to show variability within the spectrum of degrees of carcass modification reported in captivity and potentially documented in the wild. Neither Njau and Blumenschine's study nor ours should be uncritically used to identify crocodile bone damage in natural settings when using frequency of tooth marks and intensity (number of tooth marks per tooth-marked specimen) of tooth marking.

In contrast, both studies can be analogically useful to document distribution of mark types, since these are mechanically produced and depend on the effector's morphology instead of the conditions of the captive enclosure where experimentation was carried out. Our study further confirms the morphological diagnosis of crocodile tooth marks initially described by Njau and Blumenschine (2006) and expands it by including new microscopic criteria. Njau and Blumenschine (2006) did not elaborate on microscopic characteristics (>10×) beyond commenting that some marks had internal striae. In the present study, we have quantified such marks, which constitute a non-negligible portion of the tooth mark sample. We have shown that they usually display few internal microstriations, and interrupted microstriations with non-straight trajectories are not uncommon. However, we have also reported

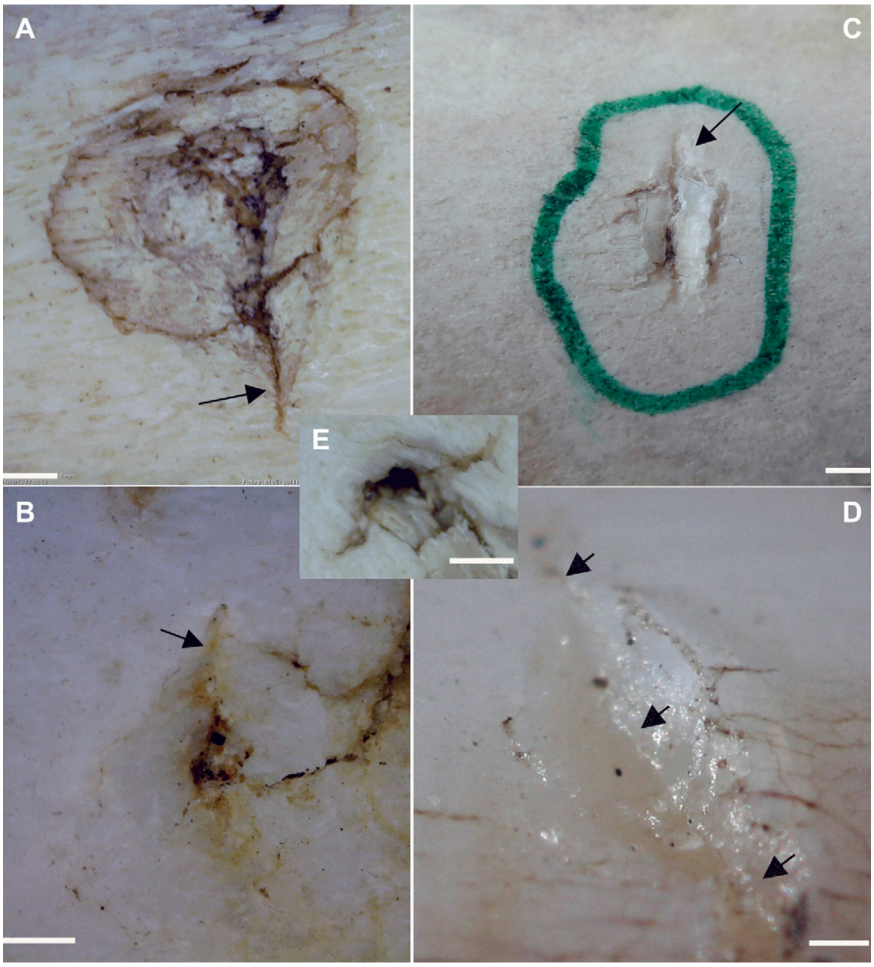

Fig. 7. Bisected pits documented on bones modified by wolves (A), lions (B), modified hammerstones (C, D) (Galán et al., 2009) and crocodiles (E). Arrows show the bisection made by dental carinae. Notice the resemblance between the pit with the bisection crossing the internal surface of D and a similar mark made by crocodiles. Scale = 1 mm.

a couple of cases in which it was more difficult to distinguish the marks from those created by trampling.

How does this new study contribute to the interpretation of hominin–crocodile interaction in the past? Recently, Njau and Blumenschine (in press) have argued that two separate hominins at FLK NN3 and FLK Zinj (Bed I, Olduvai Gorge) were preyed on by crocodiles, showing that the places were high-risk and not apt for behaviors typical of living floors (prolonged stay and food-sharing behaviors). The only empirical evidence for this interpretation is the presence of crocodile marks on the OH8 foot bones and on the OH35 tibia. We argue that empirical evidence supporting the following arguments is necessary to increase the heuristics of this interpretation:

1. A connection between the taxa to which these hominin fossils belong and the taxon responsible for the FLK Zinj and FLK NN3 archeological sites is necessary. At the time these sites were created (ca 1.85 Ma), there were a minimum of four hominin taxa in East Africa (*Homo habilis, Homo rudolfensis, Homo erectus* and *Paranthropus boisei*). There is no evidence that the species to which OH8 and OH35 belonged were the agents responsible for these sites. It is commonly argued that one species of *Homo* could be responsible for these sites. Some researchers even argue that OH8 may belong to a Paranthropus (Gebo and Schwartz, 2006). A predation hazard for one hominin type does not necessarily imply the same hazard for a different hominin species, so determining what OH8 and OH35 represent taxonomically and whether they were responsible for the archaeological records of FLK Zinj and FLK NN3 is crucial before asserting that the locations were dangerous for stone-tool-using hominins. Current evidence does not contradict that OH8 might have died naturally on the landscape (irrespective of whether or not it participated in the formation of the archaeological assemblage at FLK NN3) and a crocodile could have scavenged its remains. This could receive some support from a similar interpretation made by Njau and Blumenschine (in press) on OH35. The theorical interaction of a leopard and a crocodile on the tibia and fibula suggests to Njau and Blumenschine (in press) that OH35 was probably preyed upon by a felid and then scavenged by a crocodile, since no example is known of a leopard scavenging from a crocodile. In this scenario crocodiles could not have been a major hazard agent to hominins.
2. If the setting where these archaeological sites formed were hazardous because of crocodile presence, a strong taphonomic

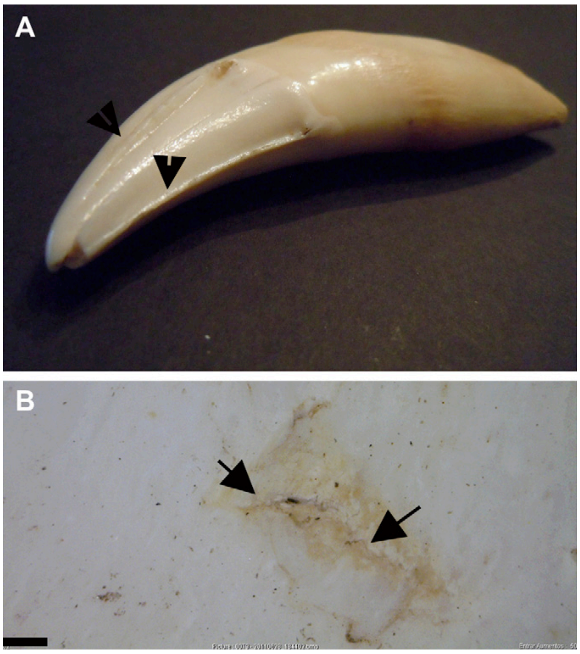

Fig. 8. A, canine of a lion showing dental carinae (arrows). B, V-shaped score made by a lion with presence of bisection, probably caused by a dental carina (arrows). Scale = 1 mm. The observation of more than one carina on some mammal carnivores invalidates Njau and Blumenschine's (2006: 149) assertion that " a lack of bicarinated teeth in any mammalian carnivore indicates that they cannot produce bisected pits".

signature of crocodile presence and activities would be expected on the bones accumulated at the sites and their surrounding landscape. The present study shows that bisected marks could represent >40% of marks inflicted by crocodiles. In a crocodile-infested environment, one would expect a high number of carcass remains accumulated and consumed by crocodiles, with more than 80% of their tooth-marked bones bearing at least one bisected mark. This is supported by actualistic studies of carcasses accumulated at ponds and riverine settings where crocodiles may have actively preyed them and modified them, with as many as 75% of bones showing carinated marks (Njau, 2006). In contrast, Njau (2006) argued that only 2 bones from FLK Zinj (1.1%) and 2 (4.6%) bones from FLK NN3 bore bisected marks. This is strongly supportive of a rather marginal presence of crocodiles in the paleolandscape and, thus, a low hazard risk scenario. The specimen numbers of the bones with bisected marks as identified by Njau (2006) were not reported, and cannot be contrasted by other researchers, but in another taphonomic study of these assemblages, no clear bisected mark attributed to crocodiles was identified (Domínguez-Rodrigo et al., 2007). In addition, in a recent landscape study of the FLK 22 paleolandscape, randomly testing more of 3000 m^2 of such a paleoenvironment, not a single bone was retrieved showing any trace of crocodile-inflicted modifications (Domínguez-Rodrigo et al., 2010). This argues against the location being hazardous because of crocodile presence.

3. We concur with Njau and Blumenschine (in press) that OH8 bears clear traces of modifications inflicted by a small reptile (probably a crocodile). The abundance of bisected pits on the talus is the best argument support to this interpretation (Fig. 9). However, we argue that attribution of the OH35 modifications to crocodiles is not well supported. The main argument used by our colleagues to interpret modifications on the distal end of OH35 as crocodile-made is the presence of one half bisected pit. In our analysis, we have not clearly identified any bisected mark on the specimen. Even if our identification were not accurate, the presence of a single bisected mark is not a definitive proof of crocodile intervention (see above). The sporadic presence of bisected marks made by mammalian carnivores means that we cannot rule out their involvement in the modification of OH35. Njau and Blumenschine (in press) argued that OH35 proximal end shows typical damage inflicted by leopards. Leopards usually deflesh their tree-stored carcasses before they fall to the ground (Cavallo, 1998). A defleshed bone would have been of no interest to any crocodile. The damage reported on the distal end of OH35 is similar to that inflicted by some mammalian carnivores which do not destroy dense epiphyses (e.g., foxes on ovicaprid remains) (Yravedra, 2006: 240). Similarly-sized carnivores, such as jackals, could have equally have been responsible for the type of damage documented on the distal end of the OH35 tibia. Therefore, if damage on OH35 cannot be definitely attributed to crocodiles, given that FLK NN3 and FLK Zinj were formed in different stratigraphic moments (Leakey, 1971), there is no empirical basis to the support the argument that during the formation of FLK Zinj, the place was a hazardous spot. It has been taphonomically shown that FLK NN3 was not a living floor but a natural palimpsest (Domínguez-Rodrigo et al., 2007). However, FLK Zinj is an anthropogenic assemblage that shows that hominins repeatedly butchered carcasses on the spot, more than 200 m away from the only place where a spring has been identified and where crocodiles could have potentially lived (FLK NN1) (Domínguez-Rodrigo et al., 2007, 2010). However, the surrounding landscape lacks crocodile-modified bones, indicating that if crocodiles were present, their impact on local mammals was rather marginal. This suggests that the place was not hazardous at the time FLK Zinj was being formed.
4. Njau and Blumenschine (in press, Fig. 4) also attribute the modification of OH35 to crocodiles based on corresponding tooth marks on the distal articular surface of the tibia and the throclea of the talus. After having examined the original specimens, we can say that the corresponding mark on the talus shows a deep elongated pit, which can only have been produced by the apex of the effector perpendicular to the articular surface; that is, in the same direction as the axis of the tibia in the reconstructed image. In contrast, the "corresponding" mark on the articular edge of the tibia can only have been produced by an effector acting parallel or obliquely to the

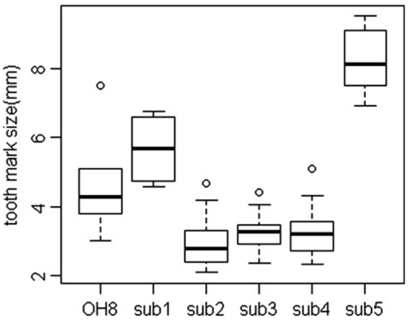

Fig. 9. Boxplot showing the sample distribution of tooth mark length documented in five subadult crocodiles (sub) and OH8. Sub 1 is 150 m long; sub 3 is 110 cm long; sub 4 is 104 cm long; sub 5 is 170 cm long. Sub 2 is incomplete but by the measurements of the head it is smaller than 1 m when compared to the other individuals.

horizontal plane of the articular surface of the talus (See animation in Supplementary online information). This suggests that although there is apparent size correspondence between both marks, there is no functional correspondence. It also would explain why tooth marks on the distal tibia of OH35 are bigger than on the OH8 talus and, in contrast to these, they are round-shaped and lack bisections. These marks on the distal tibia are effectively indistinguishable from those inflicted by a small mammal carnivore Furthermore, the remaining marks on the posterior proximal articular surface of the talus show that the effectors must have been oriented with their axes perpendicular to the surface, which implies that in the moment the tooth marks were imprinted on this surface, the talus must have been already disarticulated from the tibia. This could support the alternative interpretation that when the crocodile had access to OH8, the foot could have been already disarticulated from the leg, given that crocodiles rarely dismember limb skeletal units, as discussed above.

5. Tooth pit size of the marks documented on the OH8 talus suggest that a small reptile (crocodile) modified this element. Tooth mark casts taken from crocodiles of different ages and sizes, stored at the Museum of Comparative Anatomy of the Complutense University, support this interpretation (work in progress). Casts were made by making teeth penetrate the resin sufficiently for the carinae to create a bisected mark. This was done with several teeth from different sized individuals. Marks of the same morphology and size as documented on the OH8 talus were only obtained on crocodiles smaller than 1.5 m (Fig. 9). It could be argued to what extent such a small crocodile could constitute a predation hazard, but this shows that no hominin predation by a large or medium-sized crocodile is documented at FLK NN3. The only taphonomically-supported interpretation that can be made is that OH8 was modified by a small reptile, probably representing a small subadult crocodile, although whether this happened pre- or post-mortem is not known. Without knowing this, hazard risks at the site, based exclusively on crocodile bone damage, cannot be confidently evaluated.

5. Conclusions

Huxley (1863: 39) provided the first reference to the prey-predator relationship between primates and crocodiles: *"The only animal the Orang measures his strength with is the crocodile, who occasionally seizes him on his visits to the water side. But they say that the Orang is more than a match for his enemy, and beats him to death, or rips up his throat by pulling the jaws asunder!"*. Huxley's (1863) description, irrespective of its veracity, stresses that apes have substantially more strength in their arms than modern humans. It is known that the upper limbs of Plio-Pleistocene hominins were more similarly built to them than to us in terms of strength. Therefore, they may have posited a bigger threat to crocodiles than inferred if considering only hominins' overall smaller body size than modern humans. Fortunately, the available taphonomic studies allow identifying the potential traces of hominin–crocodile interactions.

The present experimental study supports previous assessments of the degree of bone damage inflicted by crocodiles while consuming carcasses. More than 80% of elements bear at least one diagnostic, easily identifiable crocodile-made mark. This is further supported by actualistic studies of bone damage in riverine settings where crocodiles feed, where a minimum of 75% of tooth-marked bones also bear specific crocodile-inflicted traces (Njau, 2006). This makes crocodile carcass-consumption activities potentially conspicuous on the landscape. Environments with an abundance of crocodiles should be reflected in a high presence of crocodile-modified bones. In contrast, these are marginally represented in some Olduvai Bed I sites (FLK Zinj, FLK N and FLK NN) and their surrounding landscapes (Domínguez-Rodrigo et al., 2010), thus suggesting a low predation hazard for hominins and granting more support to the alternative interpretation of the crocodile-modified hominin OH8 remains as post-mortem access to the carcass by crocodiles.

The intensity of tooth-marking varies between both experimental sets (Njau & Blumenschine's and ours) suggesting that this is highly affected by the experimental conditions of the captive crocodiles used. The larger sample used by Njau and Blumenschine, probably containing a higher number of males, which are highly competitive, contrasts with the much smaller sample used by us. Our sample also contains only females, which may explain minimal competition over carcasses; most feeding episodes were carried out by single individuals without interference from others. This impacts the intensity of bone damage and the presence or absence of hook-shaped tooth marks.

Our study has expanded the interpretation of crocodile tooth marks by showing different proportions of mark types according to long bone portion. It has also elaborated on the microscopic definition of crocodile-inflicted marks by analyzing the proportion of traces of carinae, including microstriations. The results contribute to a diagnosis of these microscopic features in crocodile tooth marks, which can help differentiate them from other biostratinomic processes, although in a couple of instances, similarities with trampling marks were strong.

Future studies on crocodiles are encouraged by these results. Given that bone modifications by some mammalian carnivores vary according to whether they are carried out in captivity or in the wild, the next logical step would be to experiment with crocodiles in their natural environments. Until that is made, both experimental scenarios have a limited applicability to the past.

Acknowledgments

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Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jas.2012.01.010.

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6.3 BELL´S KORONGO

La excavación en BK (Bell´s Korongo) fue excepcionalmente interesante, comenzando por su localización en un paraje bellísimo dentro de la garganta secundaria, poblado de bosque de ribera estacional y jirafas, papiones, gacelas, hienas y alguna presencia de leopardos. También nos acompañaban los masáis menos occidentalizados[13].

En este yacimiento del Lecho II, ya excavaron los Leakey y se hizo célebre por la aparición de grandes herbívoros antropizados como sivaterios y un NMI de 25 *Paelorovis*. En un contexto tecnológico achelense que Mary Leakey (1971) denominaba "olduvayense evolucionado" por el escaso porcentaje de bifaces.

Nosotros también rescatamos la carcasa de un elefante con marcas de corte, en 1'36Ka. El elefante más antiguo consumido por homínidos.

Excavando la carcasa de un proboscideo en Bell's Korongo (BK). Foto: Manuel Domínguez-Rodrigo.

Pero con todo, lo más interesante fue el hallazgo de un esqueleto parcial asociado de un *Paranthropus boisei.*

Así es, la asociación inédita entre varios elementos dentales nos permitió, no sin mucho trabajo, atribuir a los boisei varios fósiles apendiculares muy mal conocidos y, sobre todo, un radio de proporciones espectaculares que nos habla de las costumbres locomotoras de esta especie. La publicación en 2013 (Manuel Domínguez-Rodrigo *et alii*) tuvo un gran impacto y hemos recibido muchas peticiones de moldes de estas piezas.

7.3.1 PHILIP TOBIAS KORONGO

Pero volviendo al Lecho I, en 2011, dimos en prospección con un yacimiento inédito en el nivel 22, el mismo del Zinj, a menos de un kilómetro de FLK aunque separado por un promontorio que corta la línea visual.

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[13] Los paseos por la garganta secundaria entre BK y SHK (Sam Howard Korongo) no los olvidaré mientras viva.

Este yacimiento se descubrió a los pocos días del fallecimiento de Philip Tobías[14] y lo bautizamos en su honor: Philip Tobias Korongo (PTK).

PTK tiene un gran interés por su posición estratigráfica y topográfica, así como por conservarse en buen estado, pero ha dado un hallazgo que lo convierte en yacimiento estrella. Me refiero a la falange proximal de un meñique izquierdo de homínido (Domínguez-Rodrigo, M. *et alii.* 2015).

En efecto, se trata de una falange correspondiente a una mano anatómicamente moderna en casi 1,9 millones de años y en un contexto cultural olduvayense.

Es la mano de un individuo que ya apenas sube a los árboles en un mundo en el que sólo deberían existir parantropos y habilinos. Todo un misterio en el que pueden estar muchas claves para comprender algunas de las dudas que aún albergamos sobre el origen del comportamiento humano.

El yacimiento, también inédito, de AMK (bautizado en homenaje al arqueólogo tanzano Amin Mturi) se localizó en prospección. Parece que no hay actividad antrópica, pero descubrimos un cráneo parcial, con sus maxilares, de *Therapithecus*, muy espectacular.

El yacimiento de Philip Tobias Korongo (PTK). Foto: Enrique Baquedano.

El descubrimiento reciente de un yacimiento, también directamente situado sobre los basaltos en que se inicia la secuencia estratigráfica del barranco, bautizado como DS, David site[15], actualmente en proceso de excavación, nos está deparando hallazgos sorprendentes que aún se encuentran en estudio.

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[14] Tobías, no sólo fue el descubridor del "Zinj" y uno de los creadores de *Homo hábilis,* fue además un luchador contra el apartheid en Sudáfrica y buen amigo de los paleoantropólogos españoles, especialmente de Aguirre, con quien compartía año de nacimiento (1925). Como dice Aguirre el año en que se publicó *Australopithecus africanus* en Nature.

[15] Por el geólogo del equipo David Uribelarrea que es quien lo encontró.

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New excavations at the FLK *Zinjanthropus* site and its surrounding landscape and their behavioral implications

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ABSTRACT

Renewed excavations at FLK Zinj and its surrounding landscape have yielded valuable information regarding its paleoecological situation and the prehistoric behavioral function of the site. The density of materials at the main cluster of the site excavated by Leakey contrasts with the bone and lithic scatters surrounding the site. The location of FLK Zinj, situated a few hundred meters away from a freshwater spring, would have enabled hominins access to water, plants and game. The appeal of the spot for hominins (also explained by the presence of a wooded habitat) is confirmed by inferences of its redundant use prior and during the formation of the FLK Zinj paleosol, as witnessed by materials accumulated both under and on the waxy clay deposit that constitutes the FLK Zinj stratum. The single-cluster nature of the site indicates central-place behavior and evidence is provided that hominins occupied the site at a time of very low predation hazards in the area.

Introduction

The FLK 22 *Zinjanthropus* (FLK Zinj) site (1.84 Ma) in Bed I, Olduvai Gorge (Tanzania), has played a pivotal role in the reconstructions of early Pleistocene hominin behavior for the past three decades. Paleoanthropological data from the site have been used to infer "home base", "central place foraging" and "food sharing" behaviors by early hominins (Isaac, 1978, 1981, 1983; Bunn, 1982, 1983; Bunn and Kroll, 1986, 1988; Rose and Marshall, 1996; Domínguez-Rodrigo, 2002), where ungulate carcasses were transported to the site after having been obtained through hunting and/or confrontational scavenging (see review in Domínguez-Rodrigo et al., 2007). FLK Zinj has also been used to support passive scavenging models based on the interpretation of the site as a time-averaged carnivore kill site (Binford, 1981), a hominin refuge (Blumenschine, 1991; Blumenschine et al., 1994) and a carcass processing spot with stone caching (Potts, 1988) resulting as an epiphenomenon of hominin stone raw material transport and discard behavior (Potts, 1991). Under the latter group of models, FLK Zinj was considered as an unremarkable area in a barren lacustrine floodplain (Blumenschine and Masao, 1991), based on Hay's (1976) original interpretation of its geological context as a "near-lake" location. It was also claimed that the site, as well as others from Olduvai Beds I and II, are not necessarily paleoanthropologically high-density anomalies on the landscape—since, in the specific case of FLK Zinj, it was initially conceived as a patch (localized concentration of bones and lithics) in contrast to the surrounding, low-density scatters of materials—but similar to other unremarkable patches in the nearby paleoenvironments (Blumenschine and Masao, 1991). If this is true, it means that the biotic agents who accumulated the bones at FLK Zinj did not intentionally select the spot over others to carry out their taphonomically documented activities.

FLK Zinj and all other Bed I sites (except DK) are clustered in a very small area of Olduvai Gorge. There are at least two possible reasons that this is the case. First, it could be mere coincidence. Second, it could be a reflection of specific landscape and/or habitat feature(s) that attracted prehistoric hominins and carnivores to preferentially carry-out some of their subsistence activities in this discrete area. The ecotones in modern savannas where carnivore predation occurs most frequently and where

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subsequent hominin scavenging is theoretically feasible are obviously not favorable for "central place foraging" behaviors by hominins. Instead, paleoanthropological indications of hominin central places are predicted in reconstructed paleohabitats that are inferred to have had low carnivore competition and risk (Domínguez-Rodrigo, 2001), or where such risk was reduced by the presence of natural features like climbable trees. Determining whether FLK Zinj was created in such a habitat or ecotone is of utmost relevance, given that the use of such ecotones by hominins does not seem to have been unusual (e.g., FxJj50 at Koobi Fora, Kenya (Bunn et al., 1980)). However, other than the rather ambiguous "near-lake" location of FLK Zinj provided by Hay (1976), no more detailed paleoecological reconstruction of the locale has been elaborated in the half-century since it was excavated.

That type of fine-scale paleoecological reconstruction is essential for a fuller picture of the site's prehistoric function for early hominins and other animals. The taphonomic indicators suggesting primary access to complete ungulate carcasses by hominins, presumably through hunting and/or confrontational scavenging (Bunn and Kroll, 1986; Domínguez-Rodrigo et al., 2007) has elicited alternative scenarios that hominins may have acquired large amounts of carcass flesh from herd ungulates who died in mass drownings (Capaldo and Peters, 1995) or in droughts (Lam, 2008). These alternatives to hominin hunting/confrontational scavenging obviously required opposing ecological conditions: mass drownings occur in wet conditions (wet season) and droughts occur in very arid and dry circumstances (prolonged dry season). Again, prior to the current work discussed here, there was little information to test these alternative hypotheses or any other proposed climatic scenarios involving ancient FLK Zinj.

Fifty years after Mary Leakey excavated FLK Zinj, the advance of the analytical techniques currently available (soil isotope signatures, bone and teeth isotopic components, study of phytoliths, soil mineral composition) allows us to now test these alternative hypotheses about the paleoecology and behavioral dynamics of FLK Zinj. In order that TOPPP (The Olduvai Paleoanthropology and Paleoecology Project) could apply some of these techniques to FLK Zinj, we necessarily had to expose and sample from a larger surface of the FLK Zinj paleoanthropological level both on- and offsite. The offsite work provides the clues about the vital, wider paleoecological context and the conditions that led to the formation of FLK Zinj in its precise locale and not somewhere else. This expansive field approach allowed us to thoroughly test the various hominin behavioral reconstructions for FLK Zinj discussed above.

Our results support the hypothesis that the FLK Zinj locality functioned as a spot consciously selected by hominins to carry out specific activities, as a result of which anthropogenic materials and hominin feeding refuse accumulated there in a much higher density than observed in the immediate area surrounding the site. The significance of these results are amplified because FLK Zinj is one of only two (the other being BK, upper Bed II, (Domínguez-Rodrigo et al., 2009)) primarily anthropogenically derived sites >1.0 Ma from Olduvai Gorge (Domínguez-Rodrigo et al., 2007). The site is truly a rare gem among paleoanthropological localities.

Sample and methods of data recovery and analysis

Excavating the FLK Zinj area

The FLK Zinj site occupies the southernmost gully of the area comprised by the FLK sites (FLK, FLK N and FLK NN) (Leakey, 1971). It was hypothesized that the FLK NN 1 site was contemporaneous with FLK Zinj (Leakey, 1971). Since FLK NN 1 occupies the northernmost part of the area covered by the three sites, we decided to sample all the area between FLK Zinj and FLK NN by excavating large test trenches between them in outcrops that contain the waxy clay sediments overlain by Tuff IC, which enclose the FLK Zinj archaeological level time period.

In addition, to test both the FLK Zinj level around Leakey's main excavation at FLK and the areas away from the site toward the north (Fig. 1), three trenches were opened to the east and south of the main excavation (FLK T1, FLK T5, and FLK T6), and two more were opened across from the gully into the sedimentary wall that transitions between FLK and FLK N (FLK T4 and FLK T7). Two other elongated trenches along a profile exposed by Leakey's excavation of the site were opened at FLK NN (FLK NNT1 and FLK NNT2). These two latter trenches were excavated strictly for geological purposes, and given that they were not archaeological trenches and that no archaeological materials were found in them, they will not be counted when adding the total area of the FLK Zinj level exposed in analyses discussed here. Between FLK N and FLK NN, two trenches were opened following an outcrop that is exposed to the west of both sites (FLK NWT1 and FLK NWT2). In all these trenches described, the FLK Zinj paleosurface was exposed and excavated. In total, seven trenches were excavated exposing 57 m^2 of FLK Zinj paleosurface. In other words, our excavations increased the area of FLK Zinj paleosol previously exposed (that corresponding to the main excavation by Leakey) by ~20%. The total area sampled by these trenches in the FLK Zinj gully alone extends over 3000 m^2 (Fig. 2).

Excavations of these trenches involved the use of large tools (picks and shovels) to remove the overburden of sterile sediment across thick stratigraphic sequences, and small tools (trowels, brushes, screwdrivers and, small wooden and metal digging sticks) when reaching any fossiliferous level. Dry sieving with 2-mm mesh was systematically carried out. Only selected sediment for microfaunal research was wet-sieved with a finer mesh (1 mm). Trenches were not divided into smaller one-meter squares (except for FLKT1) since our use of total stations guaranteed extreme accuracy in plotting the spatial distribution of stone artifacts and fossil bones. Due to its larger size compared to other trenches, FLK T1 was excavated in a 1-m^2 grid upon reaching the FLK Zinj level. The lithological criterion (excavation followed natural layers) was hierarchically superior to the artificial spit criterion in deciding the way the excavation proceeded. Excavations through the sedimentary sequence at each trench was by 10-cm spits within each of the geological layers.

Trenches

A description of the trenches targeting the FLK Zinj stratum follows, but does not repeat previously published information on the geological sequence of Olduvai Bed I (for those details, see Hay (1976) and Ashley et al. (2010)) (Fig. 1).

FLK T1 is a 4×3 m trench, excavated from just above the Nge'ju Tuff, down to the tuffaceous clay underlying the waxy clay, which comprises the FLK Zinj level (Fig. 1). FLK T1 is situated on the east wall of Leakey's main excavation. The FLK Zinj geological layer in FLK T1 averages 20 cm in thickness and consists of green waxy clay, with a minor silt component.

FLK T5 is a 2×2 m trench placed ~20 m to the southeast of the main excavation. Vertically, it extends from the top of Tuff ID to the base of the FLK Zinj level waxy clay. Thickness of the clay is 18–21 cm.

FLK T6 is a 2×2 m trench located 18 m to the east of the main excavation, extending from the top of Tuff IC to the top of Tuff IB. The Tuff IC and the FLK Zinj clay levels are disturbed in the east side of the trench. The undisturbed waxy clay has an average thickness of 23 cm.

FLK T4 is a 2×2 m trench that occupies the bottom of a geological step-trench, which exposes the stratigraphy from the base of Tuff IF to the FLK Zinj level. The trench is located on the north side of the main Leakey excavation and about 30 m north from FLK T1. The mean thickness of the FLK Zinj waxy clay is 20–22 cm.

FLK T7 is a 2×2 m trench that is positioned 10 m east of FLK T4, following the front of the same outcrop across from the gully where the main excavation lies. The sedimentary sequence started on the clays overlying Tuff IC and continued down to the tuffaceous clays

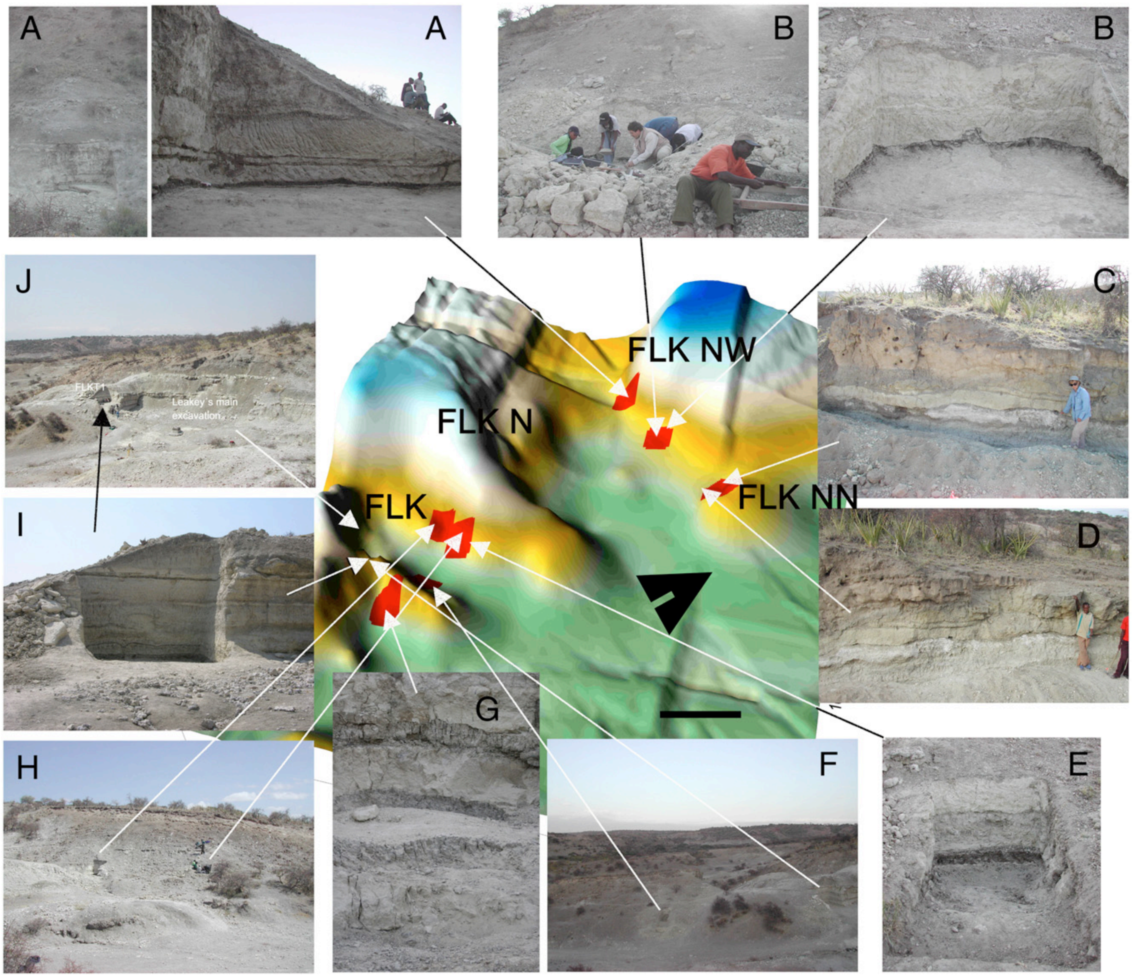

Figure 1. Distribution of all the test trenches carried out in the FLK, FLK NW and FLK NN gullies. Photos show images of trenches. A, FLK NWT1; B, FLK NWT2; C, FLK NN (east side); D, FLK NN (west side); E, FLK T7; F, location of FLK T1 (right) and FLK T6 (left); G, FLK T5; H, location of FLK T4 (left) and FLK T7 (right); I, FLK T1; J, location of FLK T1 by Mary Leakey's main excavation. See Fig. 2 for a scale of the area. Scale bar in the reconstructed topography = 50 m. Black arrow points north.

underlying the FLK Zinj waxy clay. The waxy clay is homogeneous in texture and its thickness varies from 18 to 22 cm.

FLK NWT1 is a 4 × 4 m trench situated between FLK N and FLK NN. When combined with FLK T1, these two trenches comprise the largest area we excavated. FLK NWT1, located on a corner of the outcrop where the western and northeastern walls meet, extends from just above the Nge'ju Tuff to the bottom of the FLK Zinj waxy clay. The average thickness of the FLK Zinj waxy clay on the two exposed walls is slightly thinner than at the FLK trenches: 12 cm in the north wall and 17 cm in the west wall.

FLK NWT2 is a 3 × 3 m trench that is set 25 m north of FLK NWT1, following the same outcrop. Excavation of FLK NWT2 started at the top of Tuff IC, which reaches a considerable thickness in this trench and is harder here than at any other trench, making excavation more difficult. The underlying FLK Zinj level was also slightly thinner in FLK NWT2 than in the FLK area, with an average thickness of 16 cm. The trench showed a small fault in the middle of the excavation, which occurred prior to depositions of Tuff IC.

The FLK Zinj waxy clay in the FLK NW trenches is different than in the FLK area. Whereas in the latter, the geological layer is almost pure waxy clay from top to bottom, in the FLK NW trenches the clay shows white laminated bands (Fig. 3) reminiscent of what in the geotrenches, a few meters away at FLK NN, is a carbonate deposit of tufa, resulting from the diagenesis of soil due to the presence of fresh water (Fig. 4) (Ashley et al., 2010). When acid was applied to the clay in the FLK NW trenches, it was revealed as diatomite lenses, indicating the ancient presence of water. This interpretation is supported by the abundant aquatic fauna, including fish, turtle and waterfowl bones, recovered from FLKNWT1.

The analytical sample

The samples used for analysis consists of the stone artifacts and the fossils retrieved in each trench (Table 1). Analyses were carried out measuring the density of remains contained in the FLK Zinj waxy clay layer in each trench and comparing them to detect meaningful differences in material density across the landscape. The statistical tests applied in the analysis are described below. Fossil bones, identified to skeletal part, carcass size and taxon (when possible), were also carefully inspected for bone surface modifications. In addition to fossil and stone tool densities, a comparison of the FLK Zinj bovid diversity to bovid diversity in several modern African ecosystems was conducted to provide a more accurate reconstruction of the FLK Zinj paleoecology.

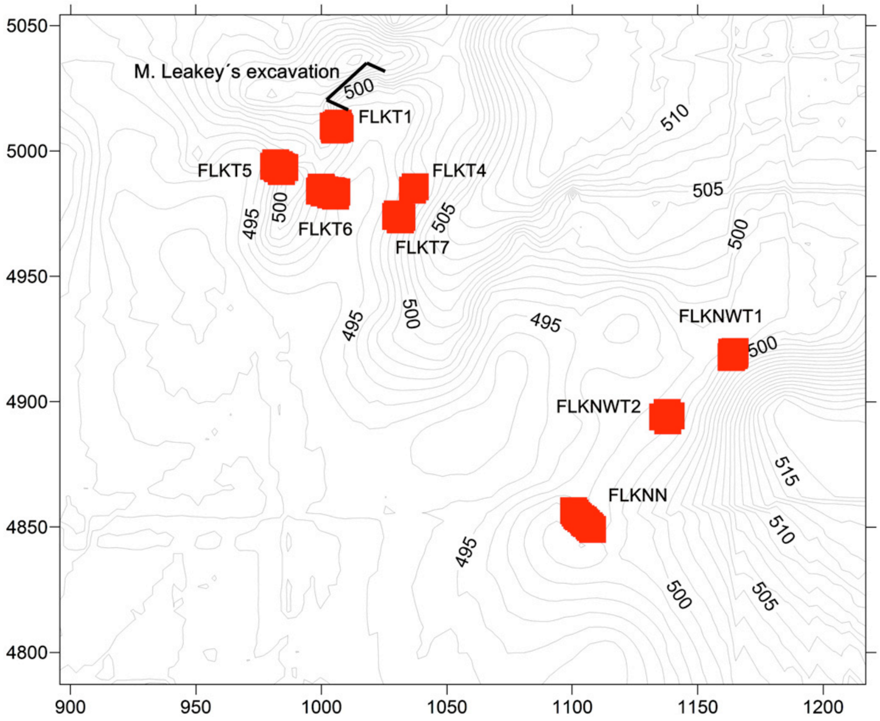

Figure 2. Topographic distribution of all the trenches excavated. Symbols do not show the actual trench sizes.

Statistical treatment of data

Samples from the densities of stone tools and fossils from each trench were inspected for normality using Shapiro–Wilks tests, which are more adequate for small samples than are Kormogorov–Smirnov tests. The non-normal distribution of the samples required the use of non-parametric tests. For the purpose of comparing densities of materials across the Zinj landscape, Kruskal–Wallis H test was used. This test is a nonparametric alternative to one-way analysis of variance. It tests the null hypothesis that samples do not differ in mean rank for the criterion variable. By taking rank, instead of median, it is very powerful in situations of skewed distribution of data and reveals differences among multiple groups. For pairwise comparisons between trenches, the Mann–Whitney U test was used. Although less powerful when the basic assumptions are not met, one-way ANOVA post-hoc statistical tests such as Bonferroni test (for unequal group sizes) were used for pairwise comparisons, so that Type I errors could be avoided. This will be shown as a contrast to the nonparametric tests.

Comparisons between the FLK Zinj bovid diversity and the bovid tribe representation of a large array of ecosystems were made in order to provide ecological proxies for the site. For this purpose, a hierarchical agglomerative cluster analysis of several African national parks representing wooded biomes and more open savanna landscapes was made. The proximity matrix was obtained using the square Euclidean distance and the dendrogram was constructed using the method of average linkage between groups. This was a preferred method over Ward's, because the latter's algorithm is biased towards producing clusters with the same number of members and requires a normal distribution of the sample. To strengthen the conclusions of the cluster analysis, a ternary graph was programmed in R, using all the data from each bovid group and bootstrapped 10,000 times with replacement.

Measuring the density of remains at FLK Zinj

All the trenches, except FLK T6, yielded lithic artifacts and/or fossils in the FLK Zinj paleosol, implying that hominins did not concentrate *all* their material-discard activities just in Leakey's main excavation area. Unexpectedly, the revealed archaeological materials occurred both at the top of the waxy clay, at the contact with the base of Tuff IC and in the top 10 cm of the clay (as documented by M. Leakey, 1971), *and* at the base of the waxy clay, in contact with the underlying tuffaceous clay; this was, again, the case for every trench but FLK T6, which was likely disturbed (Fig. 5). In Leakey's excavated collection, some archaeological specimens are so heavily encrusted in consolidated sediment, that they were preserved with the adhering sedimentary matrix. In our newly excavated sample from Leakey's main site, we have only observed this phenomenon on bones recovered from the lower level of the FLK Zinj clay. The only other newly excavated sample in which we have documented this consolidated sediment is in the upper level of the FLK Zinj waxy clay at FLK NWT1 (see Fig. 5A). This indicates that there were at least two distinct intervals during which hominins used the area and discarded materials on the ground during the formation of the FLK Zinj waxy clay. How these new details impact previous interpretations of FLK Zinj remains to be seen. Leakey (1971) clearly described that her assemblage from FLK Zinj was excavated from the upper 10 cm of clay, most specifically in contact with the overlying Tuff IC. In fact, Leakey comments that she had to wet the tuff the evening before each excavation in order to detach the underlying bones from the base of the tuff surface. Thus, we have no reason to believe that the contents of the FLK Zinj paleosol have a different provenience. However, it is necessary to emphasize that several of the specimens Leakey retrieved were very possibly located at or near the base of the waxy clay, as we have documented in FLK T1, FLK T4, FLK T5, FLK NWT1, and FLK NWT2.

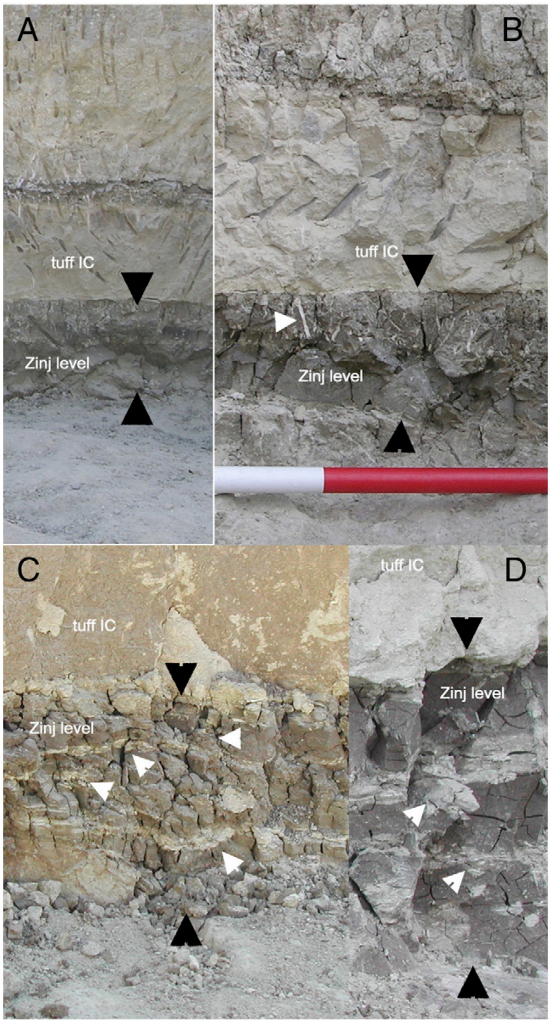

Figure 3. Aspect (at different scales) of the waxy clay level containing the FLK Zinj archaeological horizon: A, FLK T1; B, FLK T4; C, FLK NW1; D, FLK NW2. A and B show the typical clay texture found in trenches made in the FLK gully, with carbonated bioturbations (white arrows) on top of the sequence and waxy clay on the remaining part of the sequence. C and D show the structure of the same geological level at FLK NW, where the waxy clay is interbedded with carbonate levels and concretion nodules (white arrows), showing a greater presence of humidity in the paleoenvironment. Black arrows show the upper and lower boundaries of the FLK Zinj waxy clay level.

Given the impossibility of separating the materials from the upper FLK Zinj level (first 10 cm of the waxy clay) from the few retrieved from the lower FLK Zinj level (the surface of the underlying tuffaceous clay and the overlying 5 cm of the waxy clay separated by an archaeologically sterile mid-section of the waxy clay) in Leakey's collection, we analyze their density by combining trench data for that from the top and bottom of the FLK Zinj waxy clay level in each trench. Unfortunately, the best way to compare the background density of fossils and artifacts to that excavated by Leakey from FLK Zinj began by counting the number of fossil specimens and lithics per square meter plotted on her original site map. We overlaid a grid composed of 1 m^2 units on Leakey's (1971) site distribution map to accomplish these counts per square meter: only remains from complete squares were counted and, because they do not include materials recovered during sieving, our counts underestimate the actual totals from Leakey's original excavations (Fig. 6). As a result of these counts, Leakey's map was divided into three areas: one containing a dense cluster of materials and surrounding areas to its south and west containing scatters of materials (Fig. 6).

The archaeological materials that we excavated from the new trenches were also tallied per square meter. Statistical analysis of the density of materials between the areas at the main excavation and each of the new trenches was carried out by using non-parametric tests since the samples are not normally distributed and heterocedastic despite logarithmic and square-rooted transformations (see above Sample and methods of data recovery and analysis).

There is a sharp contrast between the FLK Zinj cluster and all other areas in density of recovered materials (Table 1; Fig. 7). The scatter south of the main cluster at FLK Zinj is also materially denser than the rest of the sampled surrounding landscape. The trenches in the FLK gully show a higher density of lithics than those from FLK NW. Based on mean material density values, the cluster area and the south scatter at FLK Zinj seem to contrast with the density of materials across the sampled surrounding landscape. Interestingly, FLK T4 shows a higher fossil density value than does the west scatter at FLK Zinj, suggesting that early hominin activities (assuming the bones in FLK T4 are of anthropogenic derivation) were not restricted just to the vicinity of the main cluster area.

A Kruskall–Wallis test (Table 2) shows that there are significant differences ($H(\chi^2) = 55.3$; $p = .000$) in bone density values across the landscape sampled, with the highest concentrations in the FLK Zinj main cluster area, in the south scatter, in FLK T4 and in the west scatter. This is also the case for lithic densities ($H(\chi^2) = 48.6$; $p = .000$) (Table 3), but with a more defined contrast between the FLK Zinj main cluster and the south scatter compared to the other trenches, and a marked decrease in density according to distance from the main cluster. This suggests that most stone tool-discarding activities were spatially concentrated around the FLK Zinj main cluster and south scatter areas. It also shows that lithic and bone densities are independent phenomena, given the significantly higher presence of bones at FLK NWT1 due to natural non-anthropogenic processes (see below).

A pairwise comparison (Mann–Whitney tests) of fossil densities from all the excavated areas demonstrates important differences between the west and the south FLK Zinj bone scatter areas and the fossil densities in the newly excavated trenches, but these differences are not statistically significant. However, all the pairwise comparisons between the main FLK Zinj cluster and the other trenches (areas) reveal that there are important and significant differences in densities of bones distributed across the landscape (Table 4). Even the west and south scatter areas show significant contrasts in bone concentration values.

When the Mann–Whitney test is applied to the lithic density data, the FLK Zinj main cluster is also significantly denser in artifact concentration than is the rest of the sampled surrounding landscape, as are the south and the west FLK Zinj scatters in several comparisons (Table 5). The greater number of significant values in Table 4 for lithics when compared to bones (Table 4) indicates a greater contrast in lithic densities, which suggests that stone tools are more spatially concentrated at FLK Zinj than bones and that their occurrence along the paleolandscape is less diffuse. This indicates that hominin butchery activities were focused at the site; an inference corroborated by the lack of hominin modified bones in any of the newly excavated trenches and their concentration at the FLK Zinj main cluster and south and west scatter areas.

Because of the heterocedastic nature of our sample, one predicts that Bonferroni tests of our data should not yield powerful results, but these results, nonetheless, lead to similar interpretations as our Mann–Whitney results (Table 6). Applying Bonferroni tests only to the materials showing the smallest number of significant density values (in this case, bones) the results from the nonparametric tests are validated. In all cases, the FLK Zinj main cluster shows a significant

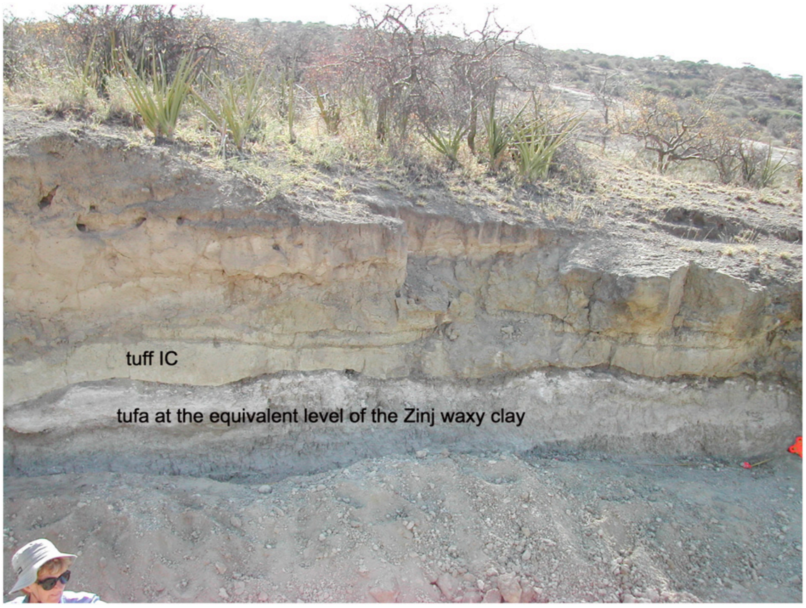

Figure 4. Tufa exposed at FLK NN, resulting from an underground spring system under tuff IC, contemporaneous with the FLK Zinj paleosurface.

contrast in material density with all the compared areas (trenches), with mean values up to ten times higher.

The higher density of fossils excavated from FLK T4 than recovered from the scatter west of the FLK main excavation area may be circumstantial, since FLK T4 has a much smaller sampled area (4 m^2) than does the FLK Zinj west scatter (124 m^2). The smaller size of FLK T4 would not allow any room for spatial variation in density. In fact, the FLK T4 values compare very well with any of the denser parts of the west scatter. This is suggestive of a similarly diffuse scatter around a large area of the periphery of the main cluster, much larger than previously assumed by the extent of Leakey's excavation.

Likewise, the high-density of fossils from FLKNWT1 is due to the presence of the partial carcass of a subadult suid, which was buried undisturbed by carnivores and hominins. This also indicates that natural processes, and not just hominin butchery behaviors, can also account for important accumulations of bone remains in these same places.

In sum, our new excavations and statistical analyses corroborate the earlier anecdotal suspicion that FLK Zinj is a materially dense anomaly on the Olduvai landscape. Bones are more densely concentrated at the site than in any other of the sampled areas. Stone tools are even more concentrated there than are bones when compared to the rest of the sampled landscape. These results prompt the following questions: (1) What did that ancient site have to offer to hominins so that it was selected during a minimum of two independent depositional events? (2) More specifically, what exactly did the site hold of attraction to hominins' second depositional interval, which is the only one when hominins apparently created a clearly defined cluster of materials significantly denser than in the remaining landscape? Geologically, this latter interval is represented by 10 cm of a clay deposit containing mostly unweathered bones and overlain by an airfall ash layer.

Table 1
Number of bone and lithic specimens found at the new trenches excavated in the Zinj waxy clay stratum.

	Lithic		Bone	
	Upper Zinj	Lower Zinj	Upper Zinj	Lower Zinj
FLK NWT1	1	3	20	31
FLK NWT2	0	0	7	0
FLK T5	2	0	1	2
FLK T4	2	0	13	2
FLK T7	1	0	0	0
FLK T6	0	0	0	0
FLK T1	5	2	14	7

Paleoenvironmental setting of FLK Zinj

One feature that is striking about the FLK, FLK N, FLK NW and FLK NN gullies beyond their clustering in a very small area is that each shows a recurrent presence of hominins and carnivores throughout most of their geological sequences. At FLK, Leakey (1971) uncovered various multiple artifact- and fossil-bearing levels; from top to bottom they are levels 7, 10, 11, 12, 13, 15, 16, 17, 21 and 22 (Zinj level). This is illustrated in Fig. 8, where most of the sequence exposed at FLK T1 is shown with the distribution of archaeological materials spanning an important part of the sequence and some preliminary correlations of the levels we uncovered with those reported by Leakey (1971). The same levels were detected in FLK NWT1, where even level 20 has a higher density of archaeological materials than does Level 22.

At FLK North, FLK N 1–2 occur directly under Tuff IF. Our on-going excavations at the site have expanded the number of archaeological levels discovered there by Leakey, meaning that if the records at FLK and FLK N are combined, there is a fairly continuous sequence of stone tools and fossils from the bottom of middle Bed I to the top of Bed I. Most of the low-density assemblages throughout the Bed I sequence are interpreted as the result of natural abiotic processes, but with an important input from carnivores (Domínguez-Rodrigo and Organista, 2007). In all events, the repeated use of the space around these three localities over such a vast time span suggests that there was something extraordinary about the paleoecological situation of the area.

In FLK NWT1, our excavation unearthed a wealth of microfaunal fossils (Fig. 9), a partial carcass of a juvenile suid (*Kolpochoerus limnetes*) and some ribs and vertebrae of a medium-sized bovid. The suid bones (including both scapulae, humeri, radii, femora, tibiae, one ulna, one innominate, both hemimandibles, some loose teeth, three rib fragments, and several isolated skull specimens) are very fragile and show multiple

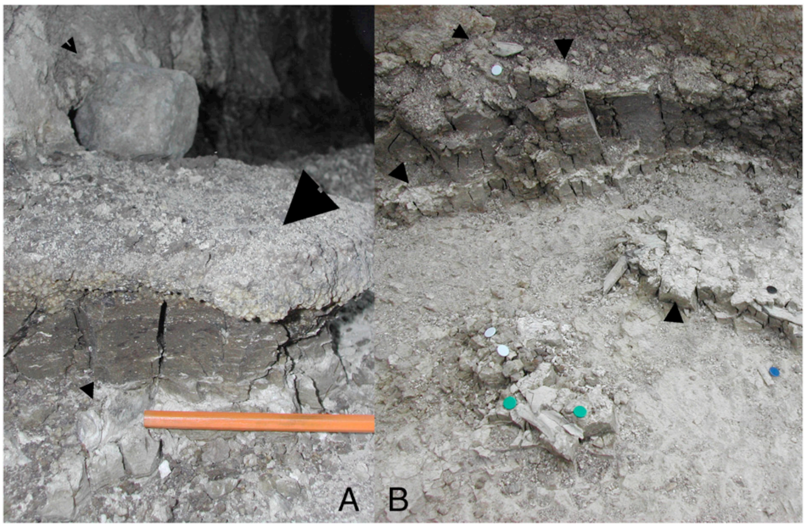

Figure 5. Vertical distribution of archaeological materials at FLKNWT1. A, small arrows show the location of a stone tool and a fossil bone at the top and the bottom of the Zinj waxy clay stratum respectively. Big arrow shows a clay patch with intense cemented sediment similar to some specimens documented in Leakey´s collection. B, small arrows show the carbonated layers interbedded with the Zinj waxy clay. Color pins show the presence of fossil bones on top and bottom of the sequence. Those at the bottom in the foreground belong to a partial carcass of a juvenile suid (see Fig. 10).

diagenetic cracks but have good cortical preservation and show no sign of subaerial weathering. The distribution of the macrofaunal remains and a couple of lithic artifacts might initially suggest some functional association between these classes of evidence at the site (Fig. 10). However, the lack of butchery marks on the bones, which show excellent cortical preservation, argues against that association. The skeleton also lacks carnivore-inflicted damage, so, our current best inference based on the skeleton's taphonomy is that a suid carcass was deposited at the site without hominin or carnivore intervention. Corroborating this inference, the distribution of fossils and lithics occupies a different vertical position than the suid in the FLK Zinj waxy clay stratum (Fig. 5). The lithics and bovid ribs were excavated from the upper FLK Zinj paleosol and the suid skeletal remains were found in the lower FLK Zinj paleosurface. Bones belonging to a snake, a turtle, and several fishes were also retrieved from the upper part of the FLK Zinj stratum. However, the most abundant microfaunal remains are those of birds, and they are important for the paleoecological information they provide.

FLK NWT1: paleoenvironmental interpretation of avian remains

There are very few studies of late Pliocene and early Pleistocene avian paleontology in East Africa (see though, Brodkorb and Mourer-Chauviré, 1982, 1984a,b). The FLK outcrops at Olduvai house the localities with the highest density of avian fossils and broadest taxonomic diversity of birds known from any African fossil site. And, FLK NWT1 is probably the densest spot among all the FLK outcrops surveyed and excavated so far: abundant bird fossils were recovered from both its upper and lower FLK Zinj levels. In fact, the bird remains are so abundant in FLK NWT1 that they covered significant areas of the FLK Zinj paleosurfaces as our excavations progressed (Fig. 9). Table 7 shows preliminary estimates, based on a sample of 479 individual fossils, of the occurrence of avian taxa from this trench. Twenty-two of the fossils (4.6% of the total bird fossil sample) could not be identified any more specifically than Aves. Among the remaining, identified remains, most are exclusively African taxa. There is a high representation of migratory species: charadriiforms (85.4%), followed by anseriforms (5.2%) constitute the bulk of the sample. In fact, taxa that are ecologically reliant on bodies of water like lakes, rivers, pools, swamps, etc.—i.e. anseriforms, charadriiforms, podicipediforms and rallids—amount to 445 fossil bones, representing 92.9% of the total sample.

More specifically, we identified abundant remains of birds that move on floating vegetation. Taxa linked to more open habitats (galliforms and columbiforms) make up only 1.0% of the sample. Passeriforms, which show preference for wooded and bushy environments constitute 1.2%. It is extremely unlikely that the remarkably large proportion of aquatic bird species is attributable to simply stochastic events or taphonomic bias. Instead, it is probably a fairly accurate reflection of the actual taxonomic structure of the local bird paleocommunities.

The paleoecological implication of these results is that major bodies of non-moving or slowly moving water must have existed in the vicinity of the FLK NWT1 when its upper and lower FLK Zinj paleosurfaces were forming. The prominent presence of charadriiforms indicates that part of the body of water contained a somewhat shallow silty bottom, which was accessible to limnicole birds. In addition, the presence of podicipediforms, and rallids and the abundance of birds adapted to floating vegetation all suggest that there were deeper areas with ample floating vegetation covers, as can be found in modern ponds created by springs.

FLK NWT1: paleoecological information provided by fish remains

Very few fish remains were recovered from FLKNWT1 (total number of identified specimens [NISP] = 153, minimum number of individuals [MNI] = 10). A high recovery rate is indicated by the very small size of some specimens, such as vertebrae measuring just 2 mm in diameter. In addition, the presence of some very fragile cichlid cranial bones indicates excellent preservation. Therefore, the paucity of fish remains likely reflects their scarcity at the site, rather than inadequate recovery or poor preservation.

Only two taxa were identified: *Clarias* sp. (catfish) and Cichlidae (tilapia). *Clarias* dominates both levels, with 54 fragments belonging to a minimum of four individuals in the upper level, and 79 specimens attributable to another four individuals in the lower level. Cichlids are rare, with just six remains attributable to one individual in level 22 upper, and 14 remains attributable to another individual in level 22 lower (Table 8). Based on measurements of the first vertebra

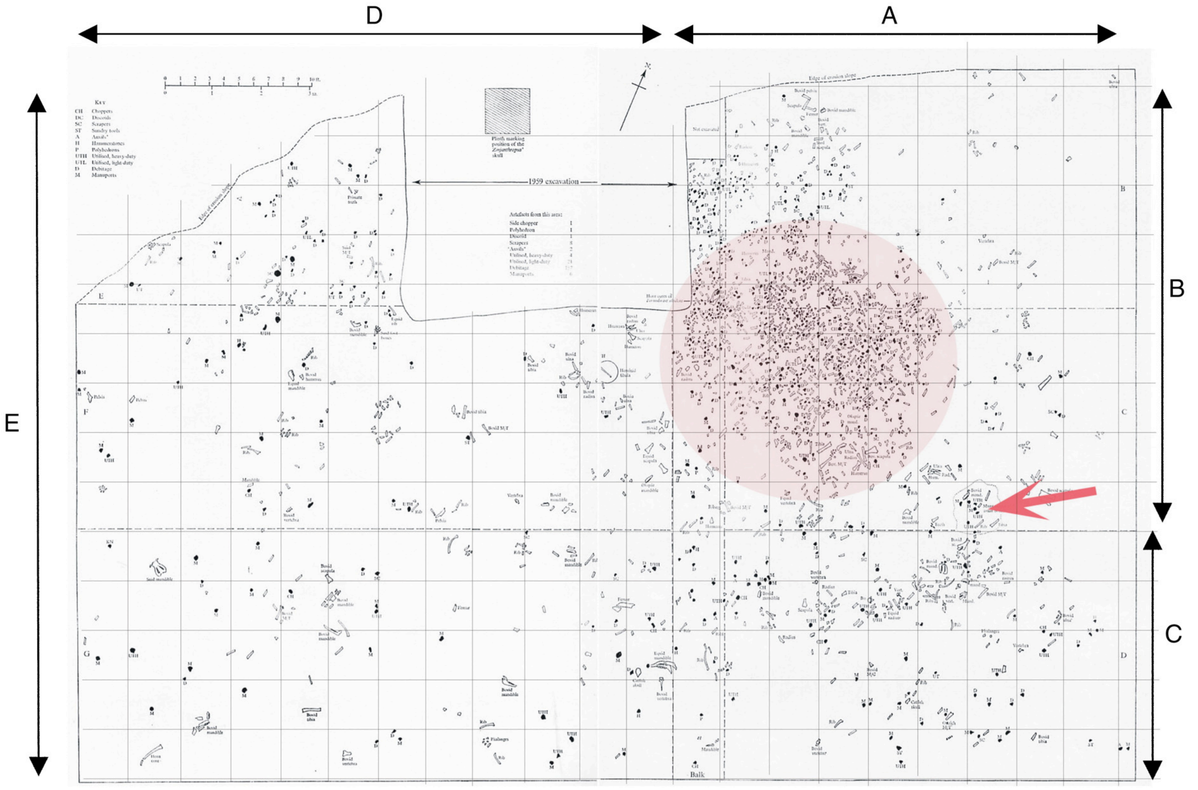

Figure 6. Map of the FLK Zinj main excavation by M. Leakey (1971) overlaid by a 1-m^2 grid. The areas defined are: FLK Zinj West (comprised by the grid DxE), FLK Zinj South (comprised by the grid AxC), and FLK Zinj Cluster (comprised by the grid AxB). The shaded circle shows the densest part of the cluster. Arrow points at microfaunal accumulation including bird bones, which could also indirectly indicate the presence of trees used by raptors as roosting places.

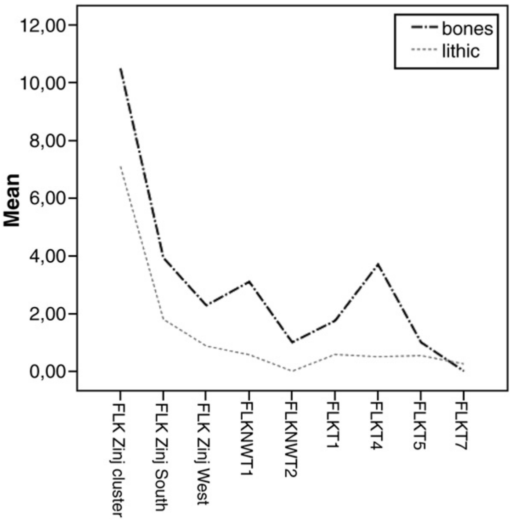

Figure 7. Mean values per square meter of fossil bones and lithic artifacts in each of the excavated trenches.

(following Van Neer and Lesur, 2004), a single tilapia was estimated to be 16 cm in total length, and it was certainly a juvenile since tilapia mature at ca. 25 cm. Based on measurements of the pectoral spine and articular, 14 specimens of *Clarias* have estimated total reconstructed live lengths averaging 25–35 cm; these are also quite small and young individuals, since *Clarias* mature at ca. 50 cm.

Clarias and Cichlidae were also identified as the only two taxa present at 11 Olduvai Gorge sites by Greenwood and Todd (1970) and Stewart (1994). At these sites, Stewart saw little to no evidence of hominin modification on the fish bones, with the possible exception of BK, and she interpreted most sites as the result of natural deposition. At FLKNWT1, we also interpret the fish remains to be the result of natural deposition in shallow, fresh water. *Clarias* can survive in very poor water conditions and are usually found in muddy-bottomed, shallow waters at the edges of lakes and swamps (Witte and de Winter, 1995). The dominance of *Clarias* at FLK NWT1 fits well with our interpretation of the trench's location as a spring (see Ashley et al., 2010). It is also consistent with Stewart's (1994) observation that *Clarias* dominated lake-margin sites in lower and middle Bed I, while cichlids were more abundant in upper Bed I and Bed II times. Cichlids thrive in a number of habitats but prefer shorelines or other shallow waters, and juveniles, in particular, are found in papyrus stands at the edges of lakes or ponds, where nesting takes place (Witte and de Winter, 1995). Although our sample size is far too small to make a strong argument, it is worth noting that the two individuals documented at FLK NW are certainly juveniles based on their small size. Considering these habitat data together, it seems likely that the fish recovered at FLK NW died *in situ* in a shallow-water setting, perhaps being stranded as the spring dried up. Similar stranding of fish in receding waters at several Olduvai sites was suggested by Leakey (1971) and again by Stewart (1994).

Table 2
Mean rank values (Kruskal–Wallis test) of bone densities at each excavated trench.

Ranks	Trenches	N	Mean rank
Bone	FLK NWT1	16	120.22
	FLK NWT2	7	90.71
	FLK T5	5	95.80
	FLK T7	4	40.00
	FLK T4	4	166.12
	FLK Zinj West	127	129.29
	FLK Zinj South	45	149.97
	FLK Zinj Cluster	78	205.05
	FLK T1	12	127.21
	Total	298	

Table 3
Mean rank values (Kruskal–Wallis test) of stone artefact densities at each excavated trench.

Ranks	trenches	N	Mean rank
Lithic	FLKNWT1	16	91.44
	FLKNWT2	7	69.00
	FLKT5	5	110.20
	FLKT7	4	94.75
	FLKT4	4	120.50
	FLK Zinj West	127	133.17
	FLK Zinj South	45	182.16
	FLK Zinj Cluster	78	187.02
	FLKT1	12	124.67
	Total	298	

The spring at FLK NN

Two north–south oriented exposures (~35 m long and at least 10 m wide) at FLK NN were scraped, dug, measured and sampled to determine the depositional environment during Middle Bed I time. The exposure located 200 m to the north of the main FLK Zinj excavation, is stratigraphically equivalent to Level 22 and reveals a large carbonate (tufa) mound draped with Tuff IC (Fig. 4). The stratigraphy and vertical and lateral changes in sediment composition suggest that the tufa was deposited at the same time as the FLK Zinj fossil and artifact horizon. The sequence of sediments starts with a tuff (0.35 m thick) overlain with a thin waxy clay which grades into the carbonate bed which, in turn, is overlain with a thin waxy clay (3 cm) and capped with Tuff IC. The tufa and waxy clay sandwich are equivalent to the ~20 cm thick waxy clay at FLK Zinj. At its thickest point (~0.5 m), the tufa bed is white to light beige in color and relatively pure (i.e., homogeneous). On the margins of the tufa mound the carbonate thins and pinches out and is noticeably mixed with waxy clay. The two lithologies are admixed creating sedimentary structures that are similar to the trampling and general bioturbation by ungulates observed at modern watering holes (LaPorte and Behrensmeyer, 1980; Ashley and Liutkus, 2002).

Stable isotope analyses of the tufa mound documents that the carbonate was deposited from a freshwater source, i.e., a spring fed by groundwater (Ashley et al., 2010). The reported δ^{18}O values of −4.0 to −1.0 are robust evidence for a meteoric-fed surface water source located in the midst of rich fossil sites in the environs of FLK.

The FLK Zinj site and its vegetational context

The prehistoric location of FLK Zinj, just a few meters from a permanent source of potable water means it probably was surrounded by abundant tree and bush cover. Indeed, this reconstruction agrees with Sikes's (1994) earlier soil isotope data, which indicate a, riverine or ground water forest in a 1-km^2 area covered by Blumenschine and Masao's (1991) initial landscape study area in lowermost Bed II in 1989. The isotopic signal detected in middle Bed I (FLK Zinj level) was similar to that documented in lower Bed II (Sikes, 1994). Although Sikes (1994, Fig. 1), demonstrated that carbon isotope values for wetland soils and sediments can be similar to those of non-wetland soils, she, for two reasons (personal communication), settled on a non-wetland soil interpretation for the FLK Zinj paleosol carbon isotope values. First,

Table 4
Mann–Whitney U values for pairwise comparisons of bone density values (number of specimens per square meter) between newly excavated trenches and areas at FLK Zinj. Numbers in bold and with * indicate a significant value ($p<.05$).

Bones									
	FLK NWT1	FLK NWT2	FLKT5	FLKT7	FLK T4	FLK ZINJ WEST	FLK ZINJ SOUTH	FLK ZINJ CLUSTER	FLK T1
FLK NWT1									
FLK NWT2	48.5								
FLK T5	36.5	15.5							
FLK T7	14	6	4						
FLK T4	24	6.5	5	**2***					
FLK ZINJ WEST	930	313	238	**78***	181				
FLK ZINJ SOUTH	282	89	67	**20***	79	2440			
FLK ZINJ CLUSTER	**309***	**85***	**62.5***	**20***	**19***	**2395.5***	**1065.5***		
FLK T1	85	26.5	19.5	**6***	16	753.5	226.5	**205.5***	

Cerling et al. (1989) showed that there is a systematic difference of 14–7‰ between the carbon values for coexisting soil carbonate and soil organic matter (SOM). The bottom of her Table 2 shows that there is a 14.1‰ difference between the FLK Zinj SOM and $CaCO_3$, so this fits with theoretical expectations. Second, as also argued in Sikes' (1994) paper on the basal Bed II paleosols, the existence of the pedogenic carbonate and its oxygen isotope values supports a non-wetland terrestrial interpretation. However, whether one argues on the basis of organic carbon, inorganic carbon or both, the isotopic data show that there is still a significant woody C_3 component present in Olduvai Bed I. Cerling and Hay (1986) presented carbonate istope data for Bed I, specifically. Carbon values for seven reported pedogenic carbonates (three just above the basal lava in the western lake margin; four in the eastern lake margin—the Zinj carbonate between Tuffs IB and IC, one from FLK N about a meter below Tuff IF, and two more just below IF) range from 5.8 to 3.7‰. This indicates the presence of 45 to 60% C_4 plants. Four data points represent grassy woodland; three fall into an interpretational overlap zone of grassy woodland or wooded grassland. Because of isotopic effects during carbonate precipitation, there is an overlap of up to 2‰ between physiognomic categories. The FLK Zinj carbonate—referenced in Sikes's (1994) Table 2 with a value of 5.7‰—falls into the grassy woodland category. Recent results on middle and upper Bed I soil sediments support this previous interpretation and show that the landscape at that time was a mosaic of grassy woodland and wooded grassland (Sikes and Ashley, 2007). In other words, the basin was significantly wetter and contained many more C_3 plants than it does today.

Plummer and Bishop's (1994) ecomorphological analysis of the Olduvai bovids, contrary to a taxon-based approach of paleohabitat reconstruction, reconstructed middle Bed I as more closed and intermediate than inferred from species count, even when the representation of alcelaphines and antilopines is taken into account. FLK NN 1 shows a "high representation of bovids with the closed habitata morphology" and "FLK I is dominated by intermediate and closed-habitat morphologies" (Plummer and Bishop, 1994: 66). A recent study of bovid representation in some Oldowan sites (Plummer et al., 2008), using the frequencies of the triple bovid group suggested by Shipman and Harris (1988)—Alcelaphini and Antilopini, Reduncini and Bovini, Tragelaphini and Aepycerotini—shows that FLK Zinj, when compared with modern African biomes is similar to Fina National Park (Mali) and close to Kainji (Nigeria), which was the closest affinity to the site in Shipman and Harris's (1988) analysis. Both modern parks, each defined as 100% Sudanian woodland, are well-wooded. FLK NN 1 plots with even more modern wooded ecosystems than does FLK Zinj. Fig. 11b shows that where FLK Zinj shares the same cluster as Fina and Kainji, FLKNN 1 shares an independent cluster with Hluhluwe (94% woodland and 6% forest) and Bicuar (89% woodland and 11% forest). Therefore, the bovid groups from both Olduvai sites are represented in the same proportions as those observed densely wooded modern African biomes. This relationship is even more realized with the analytical inclusion of *all* large-sized bovids, instead of excluding hippotragines, as in the original analyses (Fig. 11a). Including this bovid tribe, whose representation in several national parks is highly variable, places FLK Zinj in a cluster with a group of parks that are 100% wooded or wooded and forested and FLK NN1 now shares a cluster with Cuelei (*Brachystegia* woodland with riverine ecosystems) and Bicuar, even more forested.

One could argue that the relationship revealed by these cluster analyses is also influenced by analytical artifacts (clustering method, proximity matrix method) as much as by the high variation of the analogical samples used. Review of Shipman and Harris's (1988) and Vrba's (1980) lists of parks with their respective census shows that some parks had extremely large faunal counts (e.g., Serengeti = >700,000 individuals) whereas others were extremely small (e.g., Bicuar = 2500 individuals). In order to avoid this bias that could result from this variation inter-park sample sizes, we performed a statistical analysis aimed at homogenizing sample sizes and correcting for small samples sizes. We did so by bootstrapping 10,000 times all the data from each national park and plotting them in two separate groups: one corresponding to wooded ecosystems and the other one corresponding to open savanna biomes (Fig. 12). When plotting the areas corresponding to the 95% confidence intervals of each group and that of the FLK Zinj and FLK NN 1 sites, a greater variability in bovid

Table 5
Mann–Whitney U values for pairwise comparisons of lithic artefact density values (number of specimens per square meter) between newly excavated trenches and areas at FLK Zinj. Numbers in bold and with * indicate a significant value ($p<.05$).

				LITHICS					
	FLK NWT1	FLK NWT2	FLK T5	FLK T7	FLK T4	FLK ZINJ WEST	FLK ZINJ SOUTH	FLK ZINJ CLUSTER	FLK T1
FLK NWT1									
FLK NWT2	45.5								
FLK T5	32.5	10.5							
FLK T7	30.5	10.5	8.5						
FLK T4	23	**7***	9	6					
FLK ZINJ WEST	**694***	**227.5***	261.5	179.5	229				
FLK ZINJ SOUTH	**127.6***	**35***	**50***	**32.5***	45	**1801***			
FLK ZINJ CLUSTER	**285.5***	**98***	**18***	**27***	**12***	**3191***	1523		
FLK T1	67.5	**21***	26	17.5	23	712.5	**145***	**283.5***	

Table 6
Bonferroni test values for pairwise comparisons of bone density values (number of specimens per square meter) between newly excavated trenches and areas at FLK Zinj.

Multiple comparisons

Bone

(I) trenches	(J) trenches	Mean difference (I–J)	Std. error	Sig.	95% Confidence interval	
					Lower bound	Upper bound
FLK NWT1	FLK NWT2	2.18750	2.85729	1.000	−7.0366	11.4116
	FLK T5	2.18750	3.23046	1.000	−8.2413	12.6163
	FLK T7	3.18750	3.52472	1.000	−8.1912	14.5662
	FLK T4	−.56250	3.52472	1.000	−11.9412	10.8162
	FLK Zinj West	.90404	1.67265	1.000	−4.4957	6.3038
	FLK Zinj South	−.74583	1.83526	1.000	−6.6705	5.1789
	FLK Zinj Cluster	**−7.27404***	1.73044	.001	−12.8603	−1.6877
	FLK T1	1.43750	2.40784	1.000	−6.3356	9.2106
FLK NWT2	FLK NWT1	−2.18750	2.85729	1.000	−11.4116	7.0366
	FLK T5	.00000	3.69196	1.000	−11.9186	11.9186
	FLK T7	1.00000	3.95200	1.000	−11.7581	13.7581
	FLK T4	−2.75000	3.95200	1.000	−15.5081	10.0081
	FLK Zinj West	−1.28346	2.44794	1.000	−9.1861	6.6191
	FLK Zinj South	−2.93333	2.56181	1.000	−11.2035	5.3368
	FLK Zinj Cluster	**−9.46154***	2.48779	.006	−17.4928	−1.4303
	FLK T1	−.75000	2.99873	1.000	−10.4307	8.9307
FLK T5	FLK NWT1	−2.18750	3.23046	1.000	−12.6163	8.2413
	FLK NWT2	.00000	3.69196	1.000	−11.9186	11.9186
	FLK T7	1.00000	4.22967	1.000	−12.6545	14.6545
	FLK T4	−2.75000	4.22967	1.000	−16.4045	10.9045
	FLK Zinj West	−1.28346	2.87475	1.000	−10.5639	7.9970
	FLK Zinj South	−2.93333	2.97231	1.000	−12.5287	6.6620
	FLK Zinj Cluster	**−9.46154***	2.90875	.046	−18.8517	−.0713
	FLK T1	−.75000	3.35621	1.000	−11.5847	10.0847
FLK T7	FLK NWT1	−3.18750	3.52472	1.000	−14.5662	8.1912
	FLK NWT2	−1.00000	3.95200	1.000	−13.7581	11.7581
	FLK T5	−1.00000	4.22967	1.000	−14.6545	12.6545
	FLK T4	−3.75000	4.45846	1.000	−18.1431	10.6431
	FLK Zinj West	−2.28346	3.20187	1.000	−12.6199	8.0530
	FLK Zinj South	−3.93333	3.28974	1.000	−14.5535	6.6868
	FLK Zinj Cluster	**−10.46154***	3.23243	.049	−20.8967	−.0264
	FLK T1	−1.75000	3.64032	1.000	−13.5019	10.0019
FLK T4	FLK NWT1	.56250	3.52472	1.000	−10.8162	11.9412
	FLK NWT2	2.75000	3.95200	1.000	−10.0081	15.5081
	FLK T5	2.75000	4.22967	1.000	−10.9045	16.4045
	FLK T7	3.75000	4.45846	1.000	−10.6431	18.1431
	FLK Zinj West	1.46654	3.20187	1.000	−8.8699	11.8030
	FLK Zinj South	−.18333	3.28974	1.000	−10.8035	10.4368
	FLK Zinj Cluster	**−6.71154***	3.23243	.049	−17.1467	3.7236
	FLK T1	2.00000	3.64032	1.000	−9.7519	13.7519
FLK Zinj West	FLK NWT1	−.90404	1.67265	1.000	−6.3038	4.4957
	FLK NWT2	1.28346	2.44794	1.000	−6.6191	9.1861
	FLK T5	1.28346	2.87475	1.000	−7.9970	10.5639
	FLK T7	2.28346	3.20187	1.000	−8.0530	12.6199
	FLK T4	−1.46654	3.20187	1.000	−11.8030	8.8699
	FLK Zinj South	−1.64987	1.09385	1.000	−5.1811	1.8813
	FLK Zinj Cluster	**−8.17807***	.90704	.000	−11.1062	−5.2499
	FLK T1	.53346	1.90421	1.000	−5.6138	6.6807
FLK Zinj South	FLK NWT1	.74583	1.83526	1.000	−5.1789	6.6705
	FLK NWT2	2.93333	2.56181	1.000	−5.3368	11.2035
	FLK T5	2.93333	2.97231	1.000	−6.6620	12.5287
	FLK T7	3.93333	3.28974	1.000	−6.6868	14.5535
	FLK T4	.18333	3.28974	1.000	−10.4368	10.8035
	FLK Zinj West	1.64987	1.09385	1.000	−1.8813	5.1811
	FLK Zinj Cluster	**−6.52821***	1.18032	.000	−10.3386	−2.7178
	FLK T1	2.18333	2.04852	1.000	−4.4298	8.7965
FLK Zinj Cluster	FLK NWT1	**7.27404***	1.73044	.001	1.6877	12.8603
	FLK NWT2	**9.46154***	2.48779	.006	1.4303	17.4928
	FLK T5	**9.46154***	2.90875	.046	.0713	18.8517
	FLK T7	**10.46154***	3.23243	.049	.0264	20.8967
	FLK T4	**6.71154***	3.23243	.049	−3.7236	17.1467
	FLK Zinj West	**8.17807***	.90704	.000	5.2499	11.1062
	FLK Zinj South	**6.52821***	1.18032	.000	2.7178	10.3386
	FLK T1	**8.71154***	1.95516	.000	2.3998	15.0233
FLK T1	FLK NWT1	−1.43750	2.40784	1.000	−9.2106	6.3356
	FLK NWT2	.75000	2.99873	1.000	−8.9307	10.4307
	FLK T5	.75000	3.35621	1.000	−10.0847	11.5847
	FLK T7	1.75000	3.64032	1.000	−10.0019	13.5019
	FLK T4	−2.00000	3.64032	1.000	−13.7519	9.7519
	FLK Zinj West	−.53346	1.90421	1.000	−6.6807	5.6138

(continued on next page)

Table 6 (*continued*)

Multiple comparisons

Bone

(I) trenches	(J) trenches	Mean difference (I–J)	Std. error	Sig.	95% Confidence interval	
					Lower bound	Upper bound
FLK T1	FLK Zinj South	−2.18333	2.04852	1.000	−8.7965	4.4298
	FLK Zinj Cluster	**−8.71154***	1.95516	.000	−15.0233	−2.3998

Data in bold are significant at a sigma level of .05.
*The mean difference is significant at the 0.05 level.

group representation can be documented among wooded biomes, which accounts for their widespread distribution in the whole area covered by the triangle. Open ecosystems are restricted to a large variability of Alcelaphini and Antilopini and Tragelaphini and Aepycerotini but a fairly small proportion of Reduncini and Bovini. The area occupied by FLK Zinj and FLK NN1 is outside the range documented for open ecosystems and well within the core of wooded biomes. The location of FLK Zinj close to the outermost boundary of the open ecosystems suggests a slightly more open woodland situation than the mere taxonomic comparisons with unbootstrapped samples.

Thus, the presence of woodland in the vicinity of the lacustrine plain, in relation to archaeological sites, seems to be indicated by the independent but converging studies of microfauna (Jaeger, 1976; Fernández-Jalvo et al., 1998), macrofauna (Shipman and Harris, 1988; Plummer and Bishop, 1994; Plummer et al., 2008), fossil pollen (Bonnefille, 1984) and carbonate isotopic analyses (Sikes, 1994). Ecomorphological analyses also suggest the same. The analyses of metapodials from bovids indicates that the most widely represented antilopini taxon (*Antidorcas recki*) during middle Bed I shows morphologies indicative of mixed habitats instead of open habitats as they do nowadays (Plummer and Bishop, 1994). This is supported by the ecomorphological analysis of cranial remains, where the morphology of the jaws is indicative of a mixed diet of grazing and browsing (Spencer, 1997). Therefore, the presence of antilopini is not indicative of open habitats as they are in modern savannas. When considering all the available evidence, it is thus fair to assume that the actual location of FLK Zinj was in a wooded setting.

One interesting feature that we documented while excavating the FLK Zinj paleosol was the profuse distribution of thick carbonated root casts, which could belong to various bush/tree plants (Fig. 13). This certainly supports the interpretation that the setting where the site occurred was not just grassy.

The presence of trees at FLK Zinj is also suggested by the recovery of abundant remains belonging to the Acacia rat, *Thallomys* (Jaeger, 1976). In addition, several fossils of bush baby (*Galago* cf. *senegalensis*), quite similar to the modern species found at the site (Leakey, 1965) suggest the presence of thicker tree cover, given that bush-baby primates are confined to woodland and forest (Kingdon, 1997).

The presence of woody plants, trees or shrubs is also attested by the recent discovery of abundant micro-botanical remains in the form of globular silica bodies (phytoliths) in the archaeological level 22 (Ashley et al., 2010). In current soils, the abundance of globular granulate phytoliths typical for woody dicots (mainly trees and

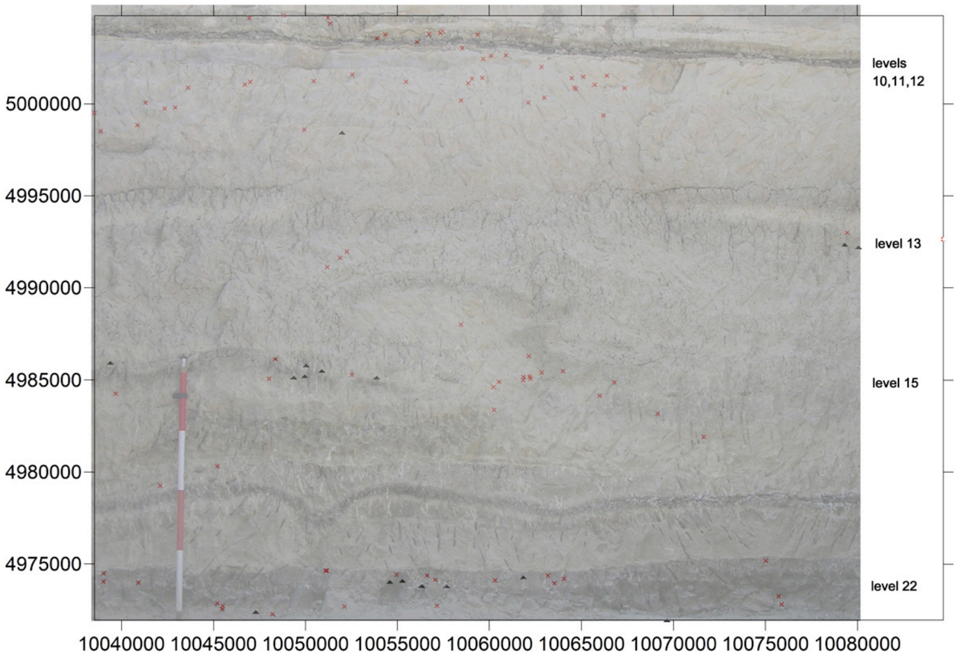

Figure 8. Main wall of FLK T1 exposed by excavation showing the geological strata (from under the Ngeju tuff to the bottom of the Zinj waxy clay underlying Tuff IC) and showing the vertical distribution of fossils and artifacts in various archaeological levels which tentatively correspond to those described by M. Leakey in the main excavation. Notice the distribution of archaeological materials on top and bottom of the Zinj waxy clay (lower part of the sequence) without materials distributed in the middle part of the sequence of the clay stratum. Light crosses are fossil bones; black triangles are stone tools.

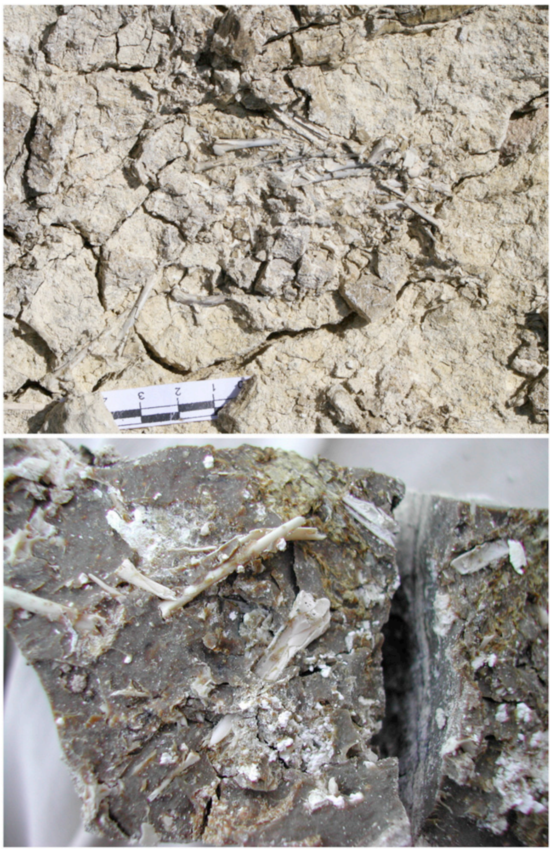

Figure 9. Example of concentration of microfaunal remains (dominated by bird bones) at FLK NWT1 (upper) and a close-up example thereof (bottom).

shrubs) and globular echinate phytoliths typical for palms (Piperno, 1988) reflects the density of the tree cover (Barboni et al., 2007) and may be used to reconstruct past vegetation types at paleoanthropological sites (WoldeGabriel et al., 2009). In the Zinj context, globular (arboreal) phytolith may account for up to 95% in some samples. Such high percentages, however, are difficult to interpret in terms of density of the tree cover because of the overall poor preservation of the phytoliths, which suggests that preferential dissolution may have occurred and biased the fossil assemblage.

A recent analysis of limb strength and locomotion in *Homo habilis*, through cross-sectional bone strength measurements of OH62 shows many affinities with chimpanzees, which indicates that even if fully bipedal when moving terrestrially, it engaged in frequent arboreal behavior (Ruff, 2008). This suggests that the presence of *Homo habilis* remains should be linked to the presence of arboreal cover. In Bed I, *H. habilis* fossils are conspicuously more abundant on the intersection of FLK NN–FLK than anywhere else in the gorge, maybe because trees were more abundant there than in other parts of the gorge.

Carnivores and hominins at the spring

Domínguez-Rodrigo et al.'s (2007) taphonomic re-evaluation of the Olduvai Bed I sites suggested that all the sites but FLK Zinj (the only anthropogenic site identified) were palimpsests in which carnivores had been responsible for the accumulation of most faunal remains. Their taphonomic results also suggested that the area where most of the Bed I sites cluster must have possessed some specific ecological conditions that prompted carnivores and hominins to overlap in the use of the same places. The presence of carnivores, such as lions, leopards, jackals, hyenas, and saber-toothed felids (*Megantereon*, *Dinofelis*), whose remains were found in the same area (Lewis, 1997), suggests that part of the area's prehistoric herbivore biomass must have used the floodplain edaphic grasslands on at least a seasonal basis, encouraging a high degree of carnivore activity in the area. Competition among carnivores could have prompted carcass transportation by solitary hunters (*i.e.*, medium-sized felids) and in some cases by larger felids to safe spots where bone remains were repeatedly accumulated.

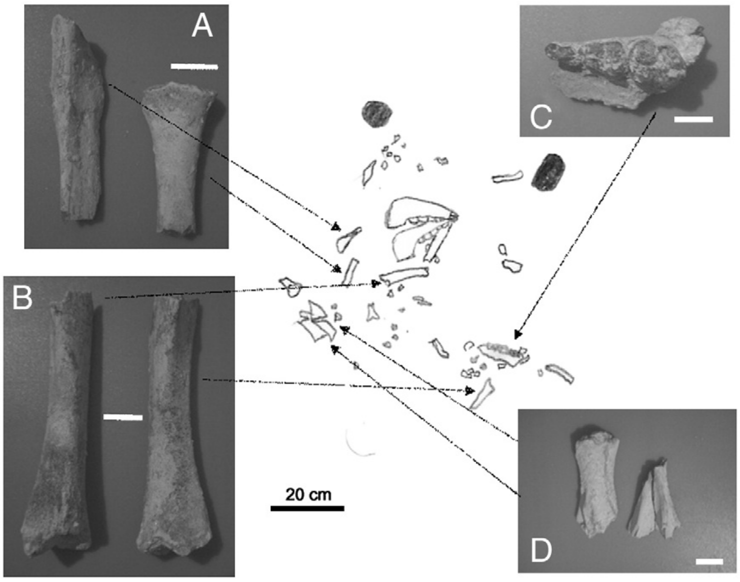

Figure 10. Map showing the suid remains clustered in the central part of the FLK NWT1 trench at the bottom of the Zinj clay stratum, with two stone tools (on the upper Zinj paleosol). A, ulna and radius; B, both tibiae; C, part of a fragmented maxillar bone with upper dentition; D, part of the scapular blades with the beginning of the spine. Scale in photos = 2 cm.

Table 7
Distribution of avian remains into major taxonomical groups in FLK NWT1. Numbers are for NISP and MNI (in parentheses).

	Podicipediforms	Anseriforms	Charadriiforms	Rallids	Galliforms	Columbiforms	Passeriforms	Accipitriforms	Others
Habitat preferences	Inland bodies of water	Inland bodies of water	Shorelines marsh, springs	Shorelines	Open country/woodland	Open country/parkland	Scrubland/parkland	Wide range	
NW 20			7 (2)	1 (1)				1 (1)	1 (1)
NW 22 A	1 (1)	19 (7)	274 (38)	8 (4)	1 (MNI: 1)	3 (1)	5 (2)		21 (3)
NW 22 B		4 (2)	126 (15)		1 (1)		1 (1)		
NW 22		2	2	1					
Total: 479	1	25	409	10	2	3	6	1	22
Percentages	0.2	5.2	85.4	2.1	0.4	0.6	1.2	0.2	4.6

It was suggested that lions, leopards and *Dinofelis* were likely candidates for the carnivore-generated accumulations discovered in sites that were previously believed to have been made by hominins (Domínguez-Rodrigo et al., 2007). According to Leakey (1971), FLK NN, which lies about 200 m away from FLK Zinj (Fig. 2), occupied a contemporaneous stratigraphic position as FLK Zinj during its upper level (FLK NN 1). This site, excavated by Leakey (1971), revealed three levels with fossil and/or stone artifacts. FLK NN 1 (the upper level) and FLK NN 3 (the lower level), previously considered anthropogenic, are clearly carnivore-made accumulations. Tooth mark frequencies, a very low degree of bone fragmentation and an abundance of complete elements seem to support a non-bone crunching carnivore as the main agent responsible for the accumulation of bones in both assemblages (Barba and Domínguez-Rodrigo, 2007; Domínguez-Rodrigo and Barba, 2007a).

FLK NN 2 was previously interpreted as a carnivore-created bone accumulation (Bunn, 1986; Potts, 1988). Egeland's (2007) taphonomic re-evaluation of the assemblage indicated that a medium- to large-sized felid could have been responsible for the accumulation, with hyenas acting as intermittent scavengers. Given that analyses of the materials from the under- and overlying levels provide sustained support for this hypothesis, the FLK NN site could, in fact, have resulted from repeated use of the same space primarily by felids as a hunting and feeding site, with the resulting bone residues subsequently scavenged by hyenas. The only indication of hominin involvement with the FLK NN faunas is in the form of just two cut-marked bone specimens from FLK NN 2, and the level lacks stone tools (Bunn, 1986). The few stone flakes recovered from FLK NN 1 and FLK NN 3 can be explained by hominins visiting the sites briefly, at times during which no activity related to carcass-processing took place, or at least left durable bone residues *in situ*. Most of the purported artifacts in both levels (Leakey, 1971; Potts, 1988) are instead likely natural ecofacts rather than "manuports," (personal observations) as was previously argued by Torre and Mora (2005).

Thus, for a long span, which is represented by the three excavated levels at FLK NN, carnivores used the same spot for predation and carcass consumption. The appeal of the locus is now apparent in its prehistoric proximity to a permanent water source. Based on observations in modern savannas, permanent water sources often become the focus of serial predation by carnivores during the dry season (Domínguez-Rodrigo, 1993, 1996). During the formation of the FLK NN tufa, by the action of a freshwater spring, the Olduvai paleolakeshore was quite a distance from the area where the sites are clustered. It is likely that the spot where the site was formed was the one of the few freshwater sources nearby during the dry season causing herd animals to congregate in the area during that season. That, in turn, would have drawn carnivores to the area, ultimately generating the bone accumulations around the spring as they hunted and fed.

Table 8
Summary of fish remains from FLKNWT1.

Level	Taxon	NISP	MNI
22 upper	*Clarias* sp. (catfish)	54	4
	Cichlidae (tilapia)	6	1
	Total	60	5
22 lower	*Clarias* sp. (catfish)	79	4
	Cichlidae (tilapia)	14	1
	Total	93	5

By the time the FLK Zinj floor was forming, it seems that carnivore activity around the spring was quite reduced. For example, the FLK NN 1 fauna is composed of just a few bones fragments (NISP = 257), compared to the underlying levels, where carnivore activity at the site was at its apogee. Remains from a total of 14 carcasses have been identified in the FLK NN 1 assemblage, including a partial skeleton (mostly teeth and some axial elements) of a *Tragelaphus strepsiceros*. Very few elements per skeleton survived in the assemblage, which indicates a high degree of carcass destruction and/or time-averaging. The lack of hominin butchery marks and the presence of tooth marks on bone specimens suggest a carnivore origin for the assemblage. The identification of specimens showing Behrensmeyer's (1978) weathering stages from 0 to 4, especially on the larger component of the assemblage indicates the assemblage accumulated over a longer time than did the FLK Zinj fauna (Barba and Domínguez-Rodrigo, 2007; Domínguez-Rodrigo and Barba, 2007b). By extension, one can argue that when hominins created the cluster at FLK Zinj, carnivores were not as active around the spring as in earlier times. Further, these data suggest that when hominins created FLK Zinj, they did so by choosing a spot where carnivore activity was minimal, away from the spring area where carnivore risk may have been higher, at a time when carnivores were relatively inactive around the spring. This inference of minimal carnivore presence when hominins were using FLK Zinj is reinforced by the paucity of carnivore-modified bone in the sampled landscape surrounding the site. Only two recovered specimens (3.9% of the total NISP) bear tooth marks. Encephalized hominins were evidently up to the task of a level of complex decision-making, of developing a foraging strategy that capitalized on an evident availability of prey nearby in a setting that did not expose them to too much risk of becoming prey themselves.

The hominin-created ungulate skeletal part patterning at FLK Zinj, dominated by long limb bone and mandible specimens, has been explained in two different ways. Either hominins transported fleshed long limb bones from acquisition sites to FLK Zinj for butchery (Bunn and Kroll, 1986, 1988; Bunn, 1991) or axial elements were eventually deleted by feeding carnivores from whole or near-whole ungulate carcasses deposited at the site (Marean et al., 1992; Capaldo, 1995, 1997; Domínguez-Rodrigo et al., 2007). The latter idea is sustained by the fact that ungulate axial remains comprise nearly one third of all the bone MNE counts at the FLK Zinj site (Bunn, 1982; Domínguez-Rodrigo et al., 2007), although their percentage minimum animal unit (%MAU) values are substantially lower than those for long limb bones. Hominin transport of complete carcasses to FLK Zinj would mean a wider range of edible carcass parts and higher overall nutritional yield available to those hominins. Recently, Bunn (2007) argued that complete carcass transport by modern foragers is best explained by the fact that boiling technology allows them to extract grease from cancellous bone tissue, so the relatively nutritionally low-yielding axial elements are worth carrying

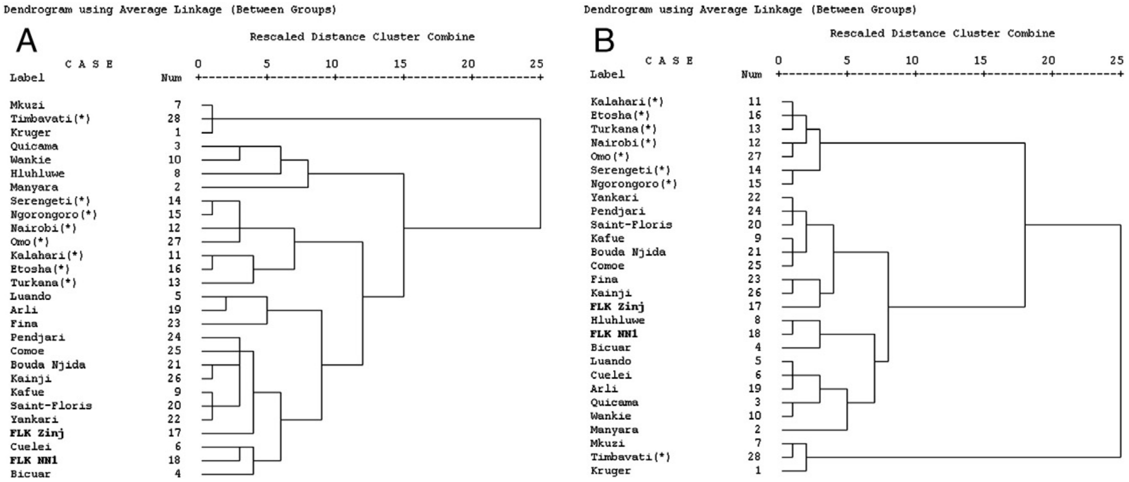

Figure 11. Hierarchical agglomerative cluster analyses of several African national parks representing wooded biomes and open savanna landscapes (with asterisks). Data on bovid tribe census for each park are from Shipman and Harris (1988) and Vrba (1980). The proximity matrix was obtained using the square Euclidean distance and the dendrogram was made using the method of average linkage between groups (UPGMA). A, cluster dendogram obtained using all major bovid tribes, including alcelaphini, antilopini, reduncini, bovini, tragelaphini, aepycerotini and hippotragini. B, cluster dendogram derived using Shipman and Harris (1988) three bovid groups: alcelaphini and antilopini, reduncini and bovini, and tragelaphini and aepycerotini.

over distance to camp. For example, modern Hadza foragers from Lake Eyasi (Tanzania) deflesh ungulate skeletons and transport the flesh separately from the vertebrae, which are carried to the camp only because they are boiled for grease extraction. Bunn (2007) argues that in the absence of a boiling technology in the early Pleistocene, the incentive for the transport of axial bones by modern humans was not present.

We harness current experimental taphonomic models and our new paleoecological data to assess if one of these two explanations better models the prehistoric reality of the formation of the FLK Zinj fauna. If, as we contend, carnivore activity on the landscape surrounding the FLK Zinj site was limited during the depositional phases of that archaeological level, how was it that they (carnivores) seemingly deleted the hundreds of missing axial bones that are necessary to account for the estimated number of carcasses that contributed to the FLK Zinj fauna? To answer this question, it is necessary to understand the impact of carnivore ravaging on human-accumulated bone assemblages and how that relates to the frequencies of the resulting bone deletion, comparing different anatomical parts of the same skeleton. Modern actualistic studies on carnivore ravaging can provide a useful insight into this process. Capaldo's (1995) large experimental sample provides a test of the interpretation that the missing skeletal portions in the FLK Zinj fauna were deleted by carnivores. His “hammerstone-to-carnivore” experiments modeled, in different African savanna settings, the destructive taphonomic behavior of hyenas on bone assemblages first modified by

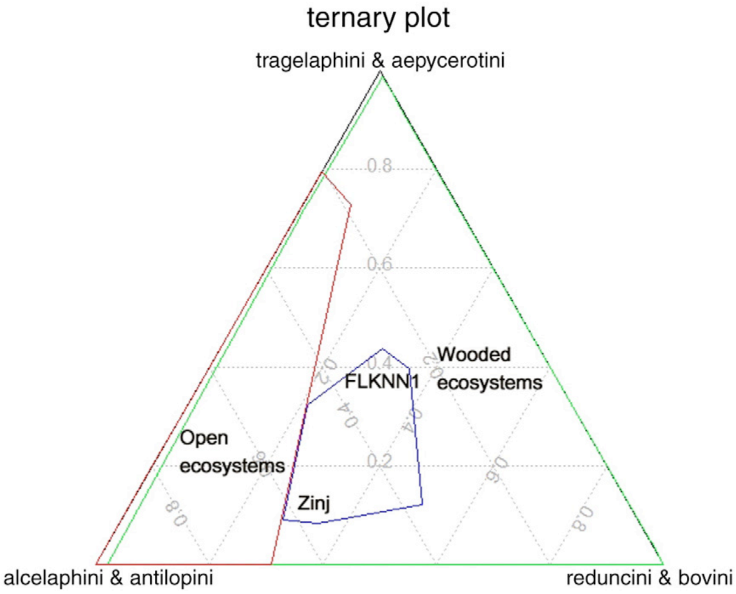

Figure 12. Ternary graph programmed in R, using all the data from each bovid group (alcelaphini and antilopini, reduncini and bovini, and tragelaphini and aepycerotini) from Fig. 13 and bootstrapped 10,000 times. Large variability of data from wooded biomes accounts for the widespread overlap of this sample.

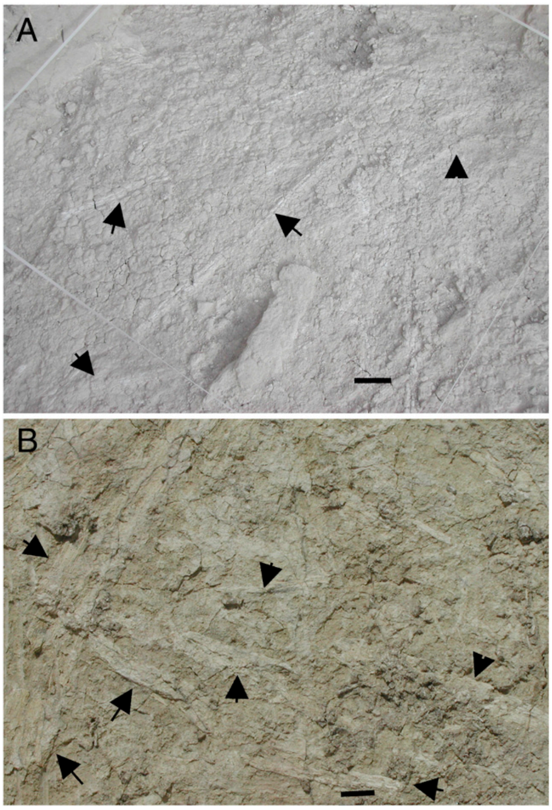

Figure 13. Arrows show some of the fossil root casts on the FLK Zinj paleosol (A) and FLK NWT1 (B). Scale = 5 cm.

humans defleshing and demarrowing ungulate carcasses. Capaldo (1995) reports that 93% of axial bones (vertebrae and ribs) were deleted by carnivore ravaging in this experimental sample, as well as 81% of long limb bone ends, when comparing element count before and after carnivore intervention. In addition, 53% of the surviving limb bone epiphyseal specimens were tooth-marked. It could be argued that the tooth-mark percentage of the surviving epiphyses is related to the survival of these portions and these, in turn, can be related to the survival of axial elements, since carnivores target axial elements before consuming long bone ends (Capaldo, 1995). Thus, with this assumption, a relationship is established among three variables: the more intense carnivore impact on a deposited fauna, the greater the deletion of axial elements from carcasses, the greater the deletion and frequency of tooth marks on long limb bone ends.

There are only 65 axial bone specimens from small animals (Bunn's (1982) size 1 and 2) and 90 from medium-sized animals (Bunn's (1982) size 3) in the FLK Zinj fauna (Domínguez-Rodrigo et al., 2007). Long limb bone end specimens (50 for small animals and 60 for medium-sized ones) represent, respectively, 45% and 42%, of the total minimal number inferred by the long bone MNE reconstruction (110 for small animals and 142 for medium-sized animals). That means that there is a loss of epiphyseal bone portions of 55% in small animals and 58% in medium-sized carcasses, according to the minimal number of complete bones inferred. A total of 24% of epiphyseal fragments from small carcasses and 28.3% of epiphyseal specimens from medium-sized carcasses are tooth-marked (Domínguez-Rodrigo et al., 2007). Using Capaldo's (1995) experimental dataset for comparison the tooth-marked frequencies of epiphyseal portions at FLK Zinj would indicate an epiphyseal loss of 36.7% for small animals and 43% for medium-sized animals. The mismatch between the actual documented loss in the FLK Zinj fauna and the expected loss according to tooth-marked epiphyseal frequencies is simply a product of employing a theoretical model. We utilize the documented loss and the expected loss of epiphyseal portions as the maximum and minimal estimates to interpret the loss of axial bones from the FLK Zinj assemblage in a broad perspective. For small animals a range of 41% to 62% of axial bones is estimated to have been deleted by carnivore ravaging, and between 49% and 66% of medium-sized animal axial bones.

Using teeth, Bunn (1982) and Bunn and Kroll (1986) estimated that 48 ungulate carcasses are represented at FLK Zinj. Using ungulate long limb bones, a more conservative estimate of a minimum of 21 carcasses potentially having been represented by some portions of the postcranial skeleton is inferred (Domínguez-Rodrigo et al., 2007). Reasoning from the most conservative estimate to minimize errors, a minimum of 1113 axial bones from 21 carcasses should have been once been present in at FLK Zinj if whole carcasses were originally transported to the site. Thus, the identification of just 155 ungulate axial bones in the FLK Zinj fauna implies that 86% of the axial skeletons of those carcasses were lost. This

Table 9
Theoretical estimates of axial and long bone end deletion using Capaldo's (1995) experimental data on bone placement and recovery after carnivore ravaging in savanna environments. Ratios of axial, and long bone end loss, and of long bone end loss:percentage of tooth-marked long bone specimens. Theoretical bone loss estimate for the Zinj faunal assemblage is shown. See the text for comparison with estimates based on MNI and MNE.

Capaldo (1995), Appendix 4. Part 1 and Part 3.				
Hammerstone-carnivore				
		Placement	Recovery	Percentage loss
Axial bones (ribs and vertebrae		1054	77	92.7
Long bone ends		460	88	81
				Percentage
TOOTH-marked long bone ends			47/88	53.4
Ratio %loss long bone end: %TM long bone end	1.53			
Ratio %loss axial bone: %loss long bone end	1.14			
				Estimated
FLK Zinj		Small carcasses	Large carcasses	Percentage loss according to Capaldo's data
Axial bones		65	90	
Long bone ends		50	60	
TM% long bone ends		24	28.3	
Ratio %loss long bone end: %TM long bone end		24 × 1.53	28.3 × 1.53	36.7 for small 42.8 for large
Ratio %loss axial bone: %loss long bone end		36.7 × 1.14	42.8 × 1.14	41.8 for small 49 for large

is a loss 30%–45% higher than the range estimated from the application of Capaldo's (1995) experimental data (Table 9). Together, these observations indicate to us that the early Pleistocene hominids who created the FLK Zinj fauna practiced a mixed carcass transport strategy: (1) The extreme paucity of ungulate axial elements at the site is probably not related to post-hominid, carnivore destruction of select parts of whole skeletons, but rather to selective transport of long limb bones from carcasses by hominids. (2) The presence, though, of *some* axial elements in the assemblage indicates that hominids did transport some carcasses to the site in a complete or nearly complete state, which carnivores may have subsequently ravaged. The predominant role of hominids and minimal role of carnivores in forming the FLK Zinj fauna is also supported by the paucity long limb bone epiphyseal specimens that are tooth-marked, especially those that are preserved as complete ends.

It has been argued (Domínguez-Rodrigo and Barba, 2006) that studies which suggested a high degree of tooth-marking on the FLK Zinj bones (Blumenschine, 1995; Capaldo, 1997) are flawed because those original estimates are inflated by the mistaken inclusion of natural biochemical marks in counts of carnivore tooth marks (and subsequent defenses of those original claims of high tooth mark frequencies (Blumenschine et al., 2007) have also been proved fatally flawed (Domínguez-Rodrigo and Barba, 2007c)).

In sum, then, the limited evidence of significant carnivore ravaging (and biasing) of the FLK Zinj bone assemblage means that the fauna is much more indicative of hominin subsistence behavior than of non-anthropogenic taphonomic processes. Taking this into account, hominin behavior at FLK Zinj can now be better understood from the taphonomic study of the archaeofaunal assemblage and the analysis of carcass obtainment strategies that it reflects; hominins at FLK Zinj may have used the wooded/bushy character of the FLK Zinj paleolandscape to actively engage in ambushing ungulates (see Bunn and Pickering, 2010). As a result, hominins might have been able to choose which resources to transport to FLK Zinj to be processed and consumed.

Conclusions

The FLK, FLK N and FLK NN sites span most of the Bed I stratigraphic sequence, from lower Bed I (FLK NN 4) to uppermost Bed I (FLK N 1–2). Each of these sites shows evidence of hominin and carnivore use of the same spaces over a vast amount of time (thousands of years) when considering all sites collectively. The reason for site clustering could be ecological: a freshwater spring system would have fed the lake floodplain at that specific point, drawing herbivores to the plant resources, which are extremely diverse and abundant near springs (Copeland, 2004). Carnivores and hominins would have followed herbivores. Hominins would also have felt drawn to the area by the available plant resources (Copeland, 2004, 2007). The carbonate record of freshwater sources on the landscape migrated across the landscape through time likely due to rift-related tectonics. Carbonate spring deposits occur at FLK NN in middle Bed I time, at FLK in upper Bed I time and in VEK, HWK-E and MCK during the lowermost Bed II time (Ashley et al., 2009).

The recent paleoecological information discovered by TOPPP's on-going research also falsifies Capaldo and Peters (1995) and Lam's (2008) suggestions that the carcasses accumulated by hominins at FLK Zinj could have been passively obtained from either mass drowning or from carcass gluts caused by intensive droughts. Had any of these events occurred at the time the site was formed, this should be reflected by a high number of carcasses occurring at or near the spring. Given the paucity of carcass remains found at the spring (FLK NN 1 and on-going work around it) it is evident that animals were not drawn *en masse* to the spring due to a drought. No mass deaths are documented there either. Therefore, carcasses, obtained through more aggressive strategies, must have been those transported to the FLK Zinj locality.

Our work reinforces the hypothesis that FLK Zinj is a “central-place” (hominins selected the spot and repeatedly transported carcasses and raw materials to it), in a low-competition setting (wooded place), in an ecological context ~200 m away from a permanent source of potable water (spring). Hominin butchery activities are documented only at the site; no cut-marked or percussion-marked bone specimens were found anywhere else on the sampled landscape. This area seems to have been appealing for hominins and carnivores for thousands of years since there is almost continuous occupation from the FLK Zinj times until Bed II times. The FLK Zinj bone assemblage was formed at the time when the taphonomy of the landscape and the underlying and overlying sites indicates that carnivore presence was most marginal. This is probably not a coincidence. The single-cluster nature of the FLK Zinj site does not seem to be a consequence of site exposure and also suggests that the socio-economic organization of the hominin group(s) responsible for its formation was different from modern humans (characterized by multi-cluster home bases (Yellen, 1977)) and/or that site functionality was different from modern foragers' “central places”.

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6.4 DIFUSIÓN CIENTÍFICA Y SOCIAL

Las labores del equipo de investigación en Olduvai Gorge, dirigido actualmente por Manuel Domínguez-Rodrigo, Audax Mabulla y Enrique Baquedano, inició los trabajos de campo en los yacimientos de la Garganta en 2006. Nosotros nos incorporamos en 2008.

Desde entonces y hasta ahora, se han publicado casi un centenar de publicaciones, todas ellas de impacto, entre las que destacan dos números monográficos de las revistas Journal Archaeological Science (Pickering, T.R, *et alii* 2012) y Quaternary International (Domínguez-Rodrigo, M., *et alii* 2014).

El equipo TOPPP ha dictado numerosas conferencias, ponencias y comunicaciones tanto en universidades como en congresos internacionales.

Personalmente he dictado conferencias especificas sobre nuestros trabajos en Olduvai en las universidad Autónoma de Madrid y de Burgos. He presentado comunicaciones en el Congreso de Salou sobre homínidos y carnívoros, ya mencionado, y en la reunión de la Sociedad Europea para el Estudio de la Evolución Humana (ESHE), que tuvo lugar en Leipzig.

Ademas, Olduvai Gorge forma parte recurrentemente de nuestras conferencias, académicas y públicas, sobre evolución humana.

TOPPP también se ha ocupado de la difusión social entre el gran público, como acreditan las numerosas apariciones y reportajes en medios de comunicación masivos. Con todo, lo mas importante de nuestra actividad difusora es la celebración de la exposición *La Cuna de la Humanidad*, que se ha presentado en el Museo Arqueológico Regional de la Comunidad de Madrid en Alcalá de Henares, en el Museo de la Evolución Humana en Burgos y, actualmente, está en CosmoCaixa de Barcelona y en el Museo Nacional de Tanzania en Dar es Salam.

Exposición *La Cuna de la humanidad* . Muestra itinerante sobre evolución humana en África celebrada primeramente en el Museo Arqueológico Regional de la Comunidad de Madrid entre febrero-julio de 2014; en el Museo de Evolución Humana de Burgos entre julio de 2014-enero de 2015 y en CosmoCaixa de Barcelona entre marzo 2016-marzo 2017. Fotos: Mario Torquemada/MAR; M.E.H., Burgos, Junta de Castilla y León., Obra Social “la Caixa”.

Esta exposición, que ha sido visitada por cientos de miles de personas se convertirá en exposición estable en el museo de Dar es Salam y, una versión ligeramente distinta, será la base museológica del nuevo museo que actualmente se construye en Olduvai.

El catalogo de la misma es ya un referente habitual en las citas bibliográficas sobre Arqueología de los Orígenes humanos.

Los comisarios fuimos Manuel Domínguez-Rodrigo y Enrique Baquedano, y comisarios adjuntos, Fernando Diez y Audax Mabulla.

En los propios yacimientos se han hecho acciones de difusión como elementos previos de un futuro geoparque liderado por el paleontólogo Luis Alcalá. El cartel explicativo situado en FLK, con ilustración de Manuel López Herrera, según fuentes de Baquedano, Domínguez-Rodrigo, Bunn y Mabulla, es hoy el mayor reclamo para el gran público en el fondo de la garganta. Dicha ilustración también sirvió de cartel oficial del congreso de Arusha con motivo de 50 aniversario del descubrimiento del Zinj.

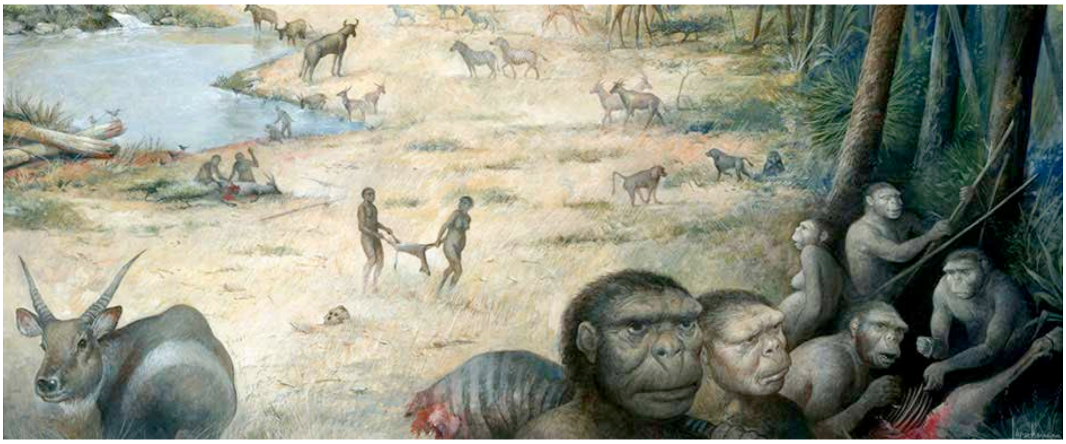
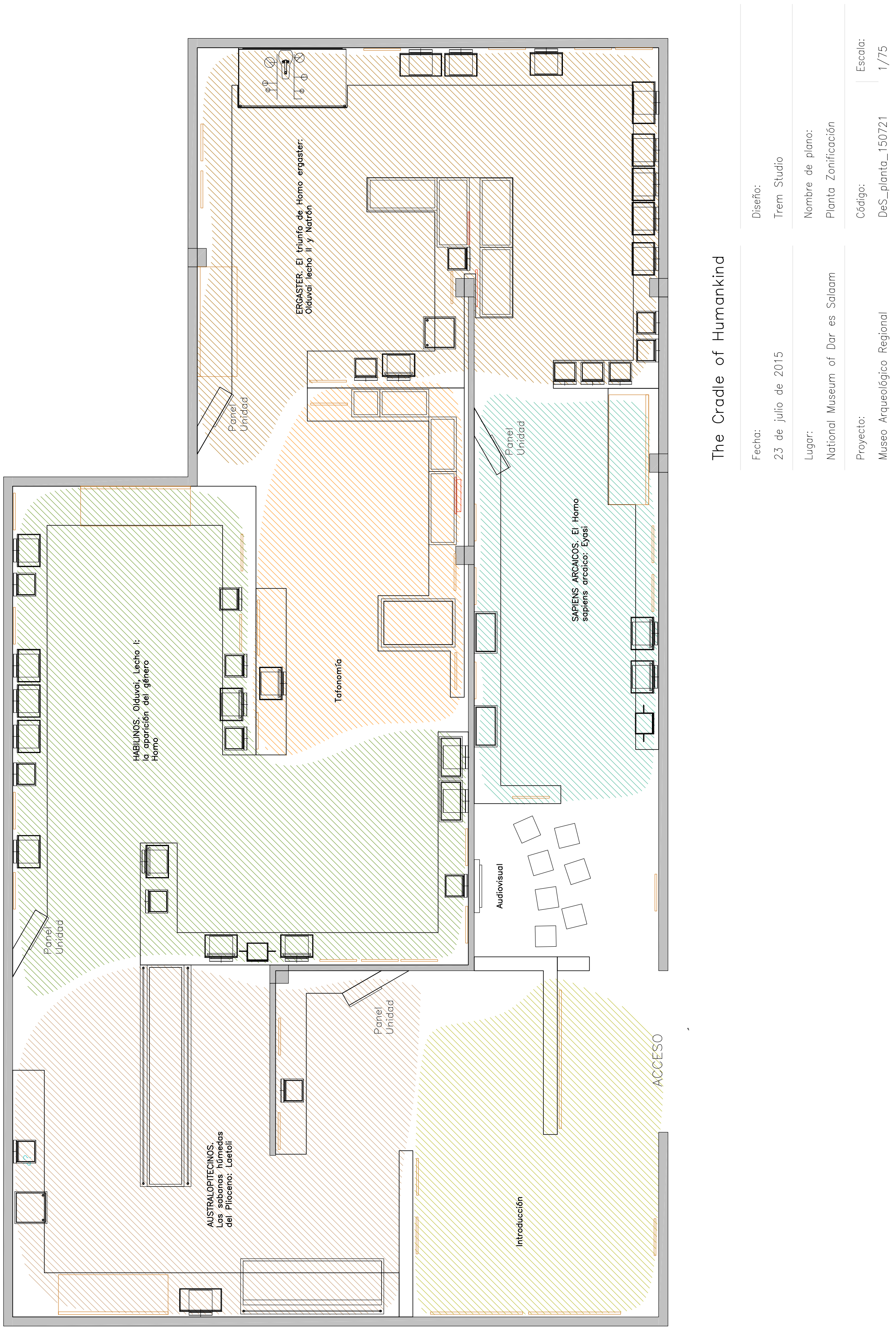


Ilustración del cartel oficial del Congreso de Arusa. Autor: Manuel López Herrera, según fuentes de Baquedano, Domínguez-Rodrigo, Bunn y Mabulla.

También de cara al público infantil y juvenil se ha editado, en 2016, un libro con textos de Rafael Mendoza Gaspar e ilustraciones de Margarita Lliso,bajo nuestra dirección científica,que explica nuestra actividad arqueológica en los yacimientos tanzanos y las conclusiones sobre la vida en la prehistoria de los primeros homínidos.

“Viviendo en la Cuna de la Humanidad”.Un libro para el público infantil y juvenil.



Plano de la instalación museográfica de la Cuna de la Humanidad como parte de la exposición permanente del Museo Nacional de Dar es Salaam.

7

El Elefante de Áridos 2

7.1 ÁRIDOS 2

Muestra *Bifaces y elefantes* celebrada en el Museo Arqueológico Regional de la Comunidad de Madrid entre septiembre de 2002-enero 2003. Foto: Mario Torquemada/MAR.

Uno de los mayores retos de la exposición “Bifaces y elefantes” (VV.AA. 2002) fue el rescate, limpieza y restauración del *Elephas antiquus* de Áridos 2 que sus excavadores habían bautizado cariñosamente como “Miguelito” [16] (Santonja, M., López, N., Pérez-González, A. Eds. 1980).

La limpieza y restauración del fósil la encomendamos a la restauradora Pía Rodríguez Frade, quien hizo un excelente trabajo. El reto era complejo pues consistía en recuperar los restos de la carcasa proboscídea, preparándolos para su exhibición con una limpieza profunda que, a la vez, no afectara a una posterior relectura de las superficies corticales conservadas.

A sugerencia de Joaquín Panera y Susana Rubio, la revisión inicial fue realizada por José Yravedra, quien vio marcas de corte inequívocas que fueron confirmadas por Manuel Domínguez Rodrigo (Yravedra, J., Domínguez-Rodrigo, M., Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., Baquedano, E., 2010).

Restauración: el antes y el después del tratamiento de limpieza y consolidación del *Elephas antiquus* procedente del yacimiento Áridos II en 2002. Trabajo y fotos: Pia Rodríguez Frade.

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[16] En homenaje a Mijail Bakunin. El pensador libertario que nada más morir el dictador Franco estaba muy en boga en España.

Este descubrimiento tiene un gran interés puesto que aunque junto a esta carcasa aparecía asociada industria lítica en el mismo nivel arqueológico, ni ésta presentaba remontajes claros ni el esqueleto manifestaba intervención humana de manera rotunda, como sí sucedía en Áridos 1.

7.2 TORRALBA Y AMBRONA

Sin duda este estudio nos devolvía a la problemática de los yacimientos de Ambrona y Torralba.

En Torralba del Moral y en Ambrona, el Marqués de Cerralbo, Enrique Aguilera y Gamboa, ya había concluido a partir de sus excavaciones arqueológicas, iniciadas en 1909 en Torralba y en 1914 en Ambrona, que los humanos primitivos eran cazadores de grandes animales, al asociar las osamentas de grandes herbívoros con la industria lítica del entorno (Cerralbo, Marqués de. 1913).

Las escenas recreadas por Cerralbo sobre la vida de estos humanos primitivos no dejaban de aproximarse a una visión bucólica del campesinado soriano, según Santonja, Pérez González y Flores (2005).

Los trabajos ya mencionados de un equipo internacional liderado por F. C. Howell en aquellos yacimientos juegan un papel excepcional en la historiografía de la evolución humana en la Península Ibérica.

Francis Clark Howell tuvo noticia de la existencia de estos yacimientos, a través de Luis Pericot, en el III congreso Panafricano celebrado en Leopoldville, en 1959, que dirigía John Desmond Clark.

Y al año siguiente solicitó permiso de prospección y financiación a la Wenner - Gren Foundation, con lo que pudo hacer, junto con K. Butzer, un primer trabajo de análisis del terreno en 1960.

Excavó entre 1961 y 1963 (Aguirre, 2005) siempre acompañado de Biberson, Aguirre, Butzer, Freeman, Klein y otros entre lo más granado de la paleoantropología mundial en aquellos momentos.

Recuérdese que en los años sesenta, la arqueología francesa del paleolítico comienza a encontrar un serio competidor entre los investigadores norteamericanos, especialmente en África, y en las épocas más antiguas. Durante muchos años Desmond Clark, en Berkeley, y Clark Howell, en Chicago[17], de punta a punta del continente americano, crearán sendas escuelas universitarias con proyectos muy ambiciosos apoyados económicamente por las instituciones de la sociedad civil.

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[17] Con el tiempo, Howell pasará a Berkeley y Freeman liderará Chicago.

Pues bien, con un equipo extraordinario para los primeros años, las conclusiones de Howell serían, con muchísimas pequeñas aportaciones, similares a las de Cerralbo. Torralba y Ambrona, se tratarían de *kill site*, unos cazaderos, de grandes animales, preferentemente de proboscideos (Howell F. C., Butzer K. W., Freeman L. G., Klein R. G., 1995).

Como quiera que, en 1963, Aguirre había conseguido que se creara el museo *in situ* de Ambrona, cubriendo varios restos dejados al aire libre, adrede por Howell, existían varias señales indicativas de la dirección y los kilómetros así como del rótulo “Al cementerio de elefantes”, según se ha comentado más arriba.

El 8 de octubre de 1979, publiqué mi primer artículo (una contraportada de *Soria Semanal*) titulado “Sobre el yacimiento de Ambrona”, con una fotografía del museo[18], aclarando que aquel lugar no era un cementerio sino un cazadero de elefantes.

Los trabajos de Glynn Isaac[19] en Olorgesaille, Peninj o Koobi Fora y su colaboración con Richard Leakey, en los que nos introdujo Manuel Santonja, así como nuestras conversaciones, muy posteriores, con Henry Bunn, discípulo directo y amigo de Isaac, no han hecho sino incrementar nuestro interés por sus líneas de investigación.

Por otra parte, y aunque Isaac sostendrá postulados completamente distintos a los que más tarde defenderá Lewis Binford (es decir, la caza frente al carroñeo), los análisis arqueológicos de Isaac son muy novedosos. Se interesa por la forma en que se han creado los yacimientos y, en consecuencia mantiene una visión muy tafonómica de la arqueología, *sensu lato*.

Haber excavado con Leslie Gordon Freeman y Joaquín González Echegaray en la Cueva del Juyo,durante la campaña de 1979[20], nos facilitó visitar varios días las excavaciones que, de nuevo en Ambrona entre 1980 y 1983, realizaron bajo la dirección de Howell y Freeman un equipo internacional e interdisciplinar.

crónicas provinciales

Sobre el yacimiento de Ambrona

Podemos afirmar, sin temor a equivocarnos, que el yacimiento de Ambrona es uno de los más importantes de Europa de cara al estudio del Pleistoceno, en sus más variados aspectos: geológico, palinológico, paleontológico y sobre todo arqueológico.

Somos conscientes de que una gran parte del público soriano ignora que en su provincia existe un museo paleontológico o no sabe lo que representa. Así pues, en nuestro afán de difusión de los conocimientos científicos, haremos una descripción de los consecutivos descubrimientos y de las conclusiones a las que se han llegado.

Haciendo historia de los diferentes hallazgos, habrá que hacer alusión a la vecina localidad de Torralba del Moral, donde al colocar la conducción de aguas para la antigua estación de ferrocarril, aparecieron los primeros restos de grandes animales. Esto era hacia el año 1888, sin que apenas fueran conocidos hasta que el Marqués de Cerralbo realizara entre los años 1909 y 1911 una serie de excavaciones que le llevaron a calificar el hallazgo como la estación prehistórica más antigua de Europa.

En pocos años, el yacimiento fue visitado por los más famosos especialistas del mundo, en Arqueología: Breuil, Obermaier, Wernert, Cartailhac, Harlé, etc. y los españoles Alcalde del Rio, Cabré, Hernández Pacheco, etc.

En 1961 y bajo la dirección del parleoantropólogo, profesor F. Clark Howell, comienza una serie de campañas con carácter internacional e interdisciplinar. Entre los años 1961y 1963 se llevaron a cabo excavaciones, tanto en Torralba como en Ambrona, en las que participaron los norteamericanos F.C. Howell, K.W. Butzer, L.G. Freeman, T.F. Lynch, etc., el francés P. Biberson, el inglés, D. Collins y los españoles E. Aguirre, J, Menéndez-Amor y estudiantes de las Universidades de Madrid y Zaragoza.

Vamos con lo auténticamente importante, si en pocas palabras tenemos que definir que es lo que encontró, diríamos que es “un cazadero de elefantes de hace 400.000 años”, bueno en realidad, lo que se ha encontrado son los restos de esas grandes cacerías.

A pesar de que no están publicadas las memorias definitivas de las excavaciones ni los resultados últimos de los diferentes laboratorios, parece ser que han aparecido restos de elefante, de caballo, de buey, de ciervo, de león y de rinoceronte, sobre todo de elefante, esto en cuanto a los restos paleontológicos.

Con los estudios de polen y de las formas estratigráficas de los suelos se ha determinado que el clima en que se produjeron las matanzas de animales fue un clima glaciar (tal vez la glaciación Mindel) con lo que (ante la imposibilidad de obtener fechas absolutas) tendríamos fechas entre el 300.000 y el 400.000. Ahora bien, el hecho de que estos restos son fruto de la actividad humana lo demuestra una serie de hallazgos, entre los que se encuentra sobre todo los útiles de piedra, comunmente llamados hachas de piedra tallada (bifaces), hendidores y raspadores (correspondientes al Achelense medio, bastante primitivo todavía). Así mismo, nuestro “cazador de elefantes” trabajaba el hueso y la madera. El hueso lo tallaba o lo afilaba, la madera era endurecida al fuego del que quedan algunos restos.

El cuadro de descubrimientos hubiese quedado completo al encontrarse algún resto del “cazador de elefantes”. Comparando los vestigios de la cultura encontrados con los de otras similares, se ha establecido que nuestro cazador no era otro que el “hombre erectus”, hipótesis que habrá de confirmar en sucesivas excavaciones.

En realidad todos los estudios a los que hemos hecho referencia no tienen otro sentido que el conocimiento del hombre y sus actividades, y como conclusiones, F. Clark Howell ha reconstruido los hechos que se llevaron a cabo en el sitio de Ambrona.

Los cazadores de varias hordas se reúnen como cada año para preparar una gran cacería aprovechando el paso obligatorio que supone el valle de Ambrona. Las únicas armas son lanzas de madera con la punta endurecida al fuego, cuchillos de hueso y hachas de piedra, y sobre todo el fuego que les servirá para ahuyentar a los animales hacia los pantanos, donde al quedar enfangados son presa fácil. Les quitan la piel y les despedazan con los raspadores de sílex. La carne la llevan, los huesos los rompen para extraer la médula.

En una excavación llevada a cabo con bases científicas se aprovecha al máximo el mínimo detalle. Por ejemplo, por la distribución de los huesos sobre el terreno se puede obtener la forma de descuartizar al animal. En el Museo Arqueológico Nacional de Madrid, existe una reconstrucción sobre maqueta que, aunque peca de efectista, puede ser muy útil para darnos una idea de las diferentes actividades mencionadas. Hoy en día se conservan “in situ” gran parte de los restos óseos encontrados, protegidos por un pequeño edificio (al que se accede por carretera completamente asfaltada, por la carretera de Ambrona a Torralba, a un kilometro y medio hay un desvio indicado y a unos 400 metros está el museo paleontológico), y que merece la pena visitar aunque sólamente sea por contemplar los colmillos, algunos de más de 3 metros, de elefantes cazados por las gentes sorianas de hace casi 400.000 años.

Es de suponer que el yacimiento se extienda por todo el valle y por tanto se debe conservar intacto, hecho que no sucede, pues a unos 25 metros del Museo comienzan tierras de labranza y a no más de 50 metros han aparecido algunos restos óseos destrozados por el arado.

Cuando la excavación de Ambrona se convirtió en empresa internacional (1961) hubo algunos intentos de que la administración comprase las tierras del valle, y desde entonces el problema parece ser que ha estado olvidado. Pero el olvido y la desidia es un fenómento que afecta a la casi totalidad de los complejos arqueológicos provinciales; problemas que desde estas páginas de Soria Semanal daremos a la luz.

Enrique Baquedano Peréz

Breve

CONATO DE MOTIN
EN LA PRISION DE SORIA

Un conato de motín ha tenido lugar en la cárcel de Soria, días pasados, por parte de un grupo de presos políticos, entre ellos algunos de los acusados del secuestro de que fue objeto el teniente general Villaescusa. Al parecer, la revuelta fracasó ante la negativa de los reclusos comunes a unirse a la actitud de rebeldía del mencionado grupo que optó, ante la situación, abandonar su intento tras dialogar con representantes del cuerpo de prisiones.

NUEVO MAGISTRADO
DE TRABAJO

Por primera vez en muchos años Soria va a contar con un Magistrado de Trabajo con residencia en nuestra ciudad, ante el nombramiento de que ha sido objeto para el puesto don Domingo Bosque. Don Francisco Gisbert que ocupaba provisionalmente la Magistratura ha sido destinado al Juzgado número 17 de Madrid. El señor Bosque había ejercido años atrás en el Juzgado de Almazán.

DINERO PARA LA CRUZ ROJA

A 280.000 pesetas ha ascendido la cuestación de la Cruz Roja que tuvo lugar el pasado día 2, festividad de San Saturio. Los sorianos han respondido en esta ocasión con cuarenta mil pesetas más que el año anterior. La cantidad es todavía insuficiente para hacer frente a los gastos de la institución en la provincia cuyo presupuesto asciende a un millón doscientas mil pesetas.

HALLAZGO DE PINTURAS
GOTICAS EN SAN NICOLAS

Los únicos restos de pintura gótica conocidos hasta hoy en esta provincia han sido hallados en las ruínas de la iglesia de San Nicolás en nuestra ciudad. A pesar de la importancia de estas pinturas el Consejero de Bellas Artes no ha conseguido interesar a entidad alguna para rescatarlas de su enclave actual, ya que de seguir en el mismo podrían sufrir graves deterioros ante el estado en que se encuentran las ruínas de la calle Real. Se espera que en la próxima semana el Instituto de Restauraciones de Madrid pueda iniciar finalmente la recuperación de estos fragmentos que serán depositados en el Museo Provincial.

Acaba
de morir
un niño.
UNICEF
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soria semanal
Suscripción anual: 750 pesetas

Artículo de prensa: “Sobre el yacimiento de Ambrona”. *Soria Semanal,* 1977. Enrique Baquedano .

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[18] Que cuidaba el bueno de Pedro Puerta.

[19] Fallecido muy prematuramente en 1985 con 47 años de edad.

[20] La participación de Richard Klein y varias de sus alumnas en este proyecto, fue nuestro primer contacto con la tafonomía arqueológica.

También tuvimos la oportunidad de visitar, en varias ocasiones, las excavaciones que Santonja y Pérez-González iniciaron en Ambrona en 1990, así como sus trabajos en el yacimiento de la Cuesta de la Bajada, Teruel, también del Pleistoceno medio.

Es muy importante destacar que en esta ocasión, Santonja y Pérez González, contarán con la participación de los tafónomos Paola Villa y Francesco D´Errico, en Ambrona, y de Manuel Domínguez-Rodrigo, en Cuesta de la Bajada, y con los paleontólogos Carmen Sesé y Enrique Soto en los estudios de determinación anatómica.

Los tres yacimientos: Áridos, Ambrona y Cuesta de la Bajada, tienen cronología mesopleistocena y su función es, en todo caso, el aprovechamiento de carcasas de grandes herbívoros. Pero la propuesta tecnológica de los homínidos será achelense en Áridos y Ambrona, en el miembro inferior, y musteriense en el miembro superior de Ambrona y Cuesta de la Bajada.

La coexistencia de achelense y musteriense y, finalmente, su sustitución es una de las preguntas más atractivas sobre la prehistoria europea. Probablemente tenga que ver con la presencia de diferentes especies de homínidos o, al menos, con diferentes poblaciones de una misma especie humana.

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Cut marks on the Middle Pleistocene elephant carcass of Áridos 2 (Madrid, Spain)

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ABSTRACT

Áridos 1 and Áridos 2 (Madrid, Spain) are two Middle Pleistocene sites belonging to the isotopic stages 9–11. Both places contain partial carcasses of *Elephas* (*Paleoxodon*) *antiquus* associated to Acheulian stone tools. In this work, the taphonomic study of the elephant remains of Áridos 2 is presented. This study has documented several cut marks on different bones, which indicate bulk flesh and viscerae extraction by Middle Pleistocene hominins. Several arguments are provided to support that at least some of the cut marks were made with handaxes, further suggesting that some of these artifacts were butchering tools in this stage of human evolution. Although cut marks on elephant carcasses have been documented at some Middle Pleistocene sites, very few have been published in detail to allow consideration of their status as hominin-imparted marks. By doing so, the present study provides more evidence of large carcass exploitation by hominins during this period.

1. Introduction

One of the recurrent phenomena in Paleolithic archaeology is the spatial association of stone tools and elephant bones in various sites both in Europe and Africa (Villa et al., 2005; Domínguez-Rodrigo, 2008). From the earliest discoveries during the nineteenth century until the present, several interpretations have been produced to account for this association. Some researchers argued that they were the result of some sites having acted as hunting grounds where hominins were actively engaged in preying on proboscideae (Cerralbo, 1913; Howell, 1966; Butzer, 1972; Freeman, 1994; Howell et al., 1995; Radmilli and Boschian, 1996), butchery places where carcass obtainment strategies were not identifiable (Leakey, 1971), scavenging spots (Shipman, 1986; Binford, 1987; Martos, 1998; Fosse, 1998; Mussi, 2005), or natural traps (Anconetani et al., 1996). Others, more marginally, have argued that several of these spatial associations of stone tools and elephant bones were accidental in nature and not functionally related (Mussi, 2005; Villa et al., 2005; Domínguez-Rodrigo et al., 2007).

A hypothesis that has been gaining credibility in the past few years is that regular exploitation of resources from elephant carcasses cannot be documented prior to the European Upper Paleolithic (Frison and Todd, 1986; Frison, 1989; Martos, 1998; Fosse, 1998; Villa et al., 2005; Gaudzinski et al., 2005; Surovell and Waguespack, 2008). Only, exceptionally, at some earlier sites can this activity be documented, probably corresponding to a marginal strategy in hominin subsistence. Middle Pleistocene sites such as La Cotte de Saint Brelade (Channel Island of Jersey) or Lehringen (Germany) are defended by some as places where elephant hunting may have taken place (Scott, 1986; Thieme and Veil, 1985). It has also been argued that if the exploitation of elephant meat were a marginal activity, the exploitation of elephant bones might still have been more frequent for the purpose of manufacturing tools (Gaudzinski et al., 2005; Mussi and Villa, 2008).

This diversity of interpretations is due to the scarcity of taphonomic evidence and absence of arguments that could be used to interpret the association of stone tools and elephant bones properly. Only exceptionally have cut marks and percussion marks on prehistoric elephant bones been documented (e.g., Shipman and Rose, 1983; Villa et al., 2005). Several authors argue that finding this type of evidence is highly unlikely for various reasons. Bone preservation in a large portion of sites is too poor, weathering also deletes part of these traces, the periostium on several bones is too thick to allow stone tools modify bone surfaces, and cartilage,

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tendons, ligaments and the large muscle masses also do not enable frequent contact between stone tool edges and bone surfaces (Villa, 1990; Martos, 1998; Fosse, 1998; Mussi, 2005; Villa et al., 2005; Gaudzinski et al., 2005; Schreve, 2006; Mussi and Villa, 2008). Actualistic butchery observations also show that elephant butchery can be performed leaving very few traces on bones (Crader, 1983; Haynes, 1991). In sum, cut marks on elephant bones are a very uncommon type of taphonomic evidence. For this reason, several researchers have turned their attention to indirect types of evidence such as isotopic analyses, use wear analyses of associated stone tools or the taphonomic study of the context where the elephant bones are found to discuss the possibility of elephant consumption by hominins (Weber, 2000; Schreve, 2006; Mussi and Villa, 2008).

However, the presence of cut marks still remains the most straightforward evidence in support of hominin exploitation of carcasses. This is why the identification of cut marks has to be carried out with utmost care. For instance, the earliest evidence reported for cut-marked elephant bones comes from FLK North 6 (Olduvai Gorge, Tanzania), which was interpreted as a butchery spot (Leakey, 1971; Bunn, 1982). However, the taphonomic reanalysis of the remains has shown these marks to be the result of trampling. No taphonomic arguments can be provided to defend that hominins exploited the elephant remains at the site (Domínguez-Rodrigo et al., 2007). This cautions against the reporting of cut-marked elephant bones without publishing enough information (e.g., detailed magnified binocular or S.E.M. photographs) to show the features necessary to identify such marks as hominin-imparted.

The oldest examples of elephant bones bearing cut marks have been documented in Middle Pleistocene sites such as Ambrona (Spain), La Polledrara and Castel di Guido (Italy), Bilzingsleben (Germany) and La Cotte de Saint Brelade (Channel Island of Jersey). At Ambrona, very few cut-marked bones have been discovered despite the number of elephants, suggesting a marginal but repeated role for hominins sporadically exploiting carcass remains (Shipman and Rose, 1983; Villa et al., 2005). Polledrara and Castel di Guido are known for the artifacts made on elephant bone (Pitti and Radmilli, 1984; Anzidei and Cerilli, 2001), but some of them also bear cut marks suggesting some exploitation of carcasses (Mussi, 2005). La Cotte de Saint Brelade also includes several elephant bones with cut marks (Scott, 1986). Bilzingsleben has yielded several cut-marked elephant bones, among which a foot bone bearing some cut marks on its articular surface is probably the most widely known (Mania, 1990). At Gesher Benot Ya'akov an elephant skull was discovered lying on an anvil, surrounded by stone artifacts, and with some marks above the nasal bone and the occipital suggestive of human exploitation (Goren-Imbar et al., 1994).

Use wear analyses on artifacts from sites where stone tools appear spatially associated to elephant bones have also produced several artifacts suggesting the processing of meat at Gröbern (Germany) and Áridos 2 (Spain), which enables conjecture about the exploitation of elephant meat by hominins (Weber, 2000; Ollé Canellas, 2005).

In favor of the argument that a scarcity of cut-marked elephant bones does not necessarily imply marginal use of elephant carcass resources, it should be stressed that cut-marked elephant bones are also scarce during the Upper Pleistocene (Nývltová Fišáková, 2005). At Mousterian sites such as Kulna (Moravia) or Santo Antao do Tojal (Portugal), there is taphonomic evidence supporting hominin exploitation of elephant carcasses. At Kulna, some possible cut marks were identified (Moncel, 2001) and at Santo Antao do Tojal, two small flint flakes were located embedded in one of the femur fragments (Zbyszewski, 1943), although they could be located in such a position by post-depositional sedimentary processes, given the fluvial context of the site (Sousa and Figueiredo, 2001). In the Gravettian sites of Krakow Spadzista Street b and Milovice G (Poland), a few cut-marked bones were found (Svoboda et al., 2005). Late Pleistocene sites such as Algar de Joao Ramos (Portugal), Gontsy (Ucraine) and Lugovkaye (Russia) have also yielded few cut-marked bones (Zbyszewski, 1943; Sousa and Figueiredo, 2001; Maschenko et al., 2003; Zenin et al., 2003; Iakovlevaa and Djindjian, 2005).

This work expands previous evidence of elephant cut-marked bones by reporting newly found cut marks on bones from the Middle Pleistocene site of Áridos 2 (Spain) (Santonja et al., 1980a,b, 2001; Villa, 1990). Our study shows the presence of cut marks on some bones from the articulated partial carcass of an *Elephas antiquus* uncovered at the site. This increases the number of Middle Pleistocene sites where elephant butchery is reported and well documented.

2. Location and characteristics of Áridos (Arganda, Madrid, Spain)

Áridos 1 and 2 are situated to the left margin of the Jarama river to the southeast of Madrid (Fig. 1). The micromammal study suggests that the sites can be placed within the isotopic stages 9–11 (López Martínez, 1980; Santonja et al., 2001; Sesé and Soto, 2002). Both sites are located in a floodplain (overbank facies) (Pérez-González, 1980; Pérez-González and Uribelarrea, 2002) and both bear lithic artifacts spatially associated with partial elephant carcasses.

In Áridos 1 a surface of 112 m^2 was excavated exposing two paleosurfaces (Santonja and Querol, 1980a). The articulated carcass remains of an *E. antiquus* was found on the oldest paleosurface, concentrated in an area of 50 m^2 (Soto, 1980; Santonja and Querol, 1980b). A total of 331 lithic pieces and mandibular fragments of two bovids were also found (Santonja and Querol, 1980a). Bone surfaces are mostly moderately well preserved. The lithic assemblage is characterized by the abundance of flakes and some refitting was successfully carried out (Santonja et al., 1980a,b). The discrete association of stone tools and bones, despite the absence of cut marks, has been interpreted as functional, despite the differences with the overlying paleosurface (e.g., where only two flakes were recovered) (Mourer-Chauviré, 1980; López Martínez, 1980; Díez, 1992).

Áridos 2 was situated about 200 m away from Áridos 1 (Santonja and Querol, 1980c; Santonja and Pérez-González, 2002). The site is located at the top of the stratigraphic unit of Arganda I (Pérez-González, 1980). This unit is the top of a fluvial sequence including the units Arganda II, III and IV, spanning a thickness of 40–50 m in the mid- and lower valley of the Jarama river. These overlying sequences were created by the sinking of the underlying karst system composed of Miocene evaporitic rocks, which are the substrate of the Tertiary basin of Madrid in this region. Dates obtained through AAR (amino acid racemization) (379.7 ± 45 ka) and ESR (electron spin resonance) (384 ± 77 ka) for the Arganda I unit containing the site indicate that Áridos 2 could be assigned to the end of MIS 11 (Moreno et al., in press; Panera et al., in press). Áridos 2 correlates with the units B, C and D of the stratigraphic column documented in Áridos 1 (Fig. 1). These units are muddy overbank deposits and secondary pebble and sandy low-energy channels that existed in the wide alluvial plain of the meandriform Jarama river.

The preserved surface of this site is very small (10 m^2) because erosion caused by two channels destroyed most of the site. In addition, modern human exploitation of the quarry altered an important part of the site (for example, half of the rib cage of the elephant was removed by the bulldozer). A partial elephant skeleton associated with 34 lithic artifacts was found on the paleo-

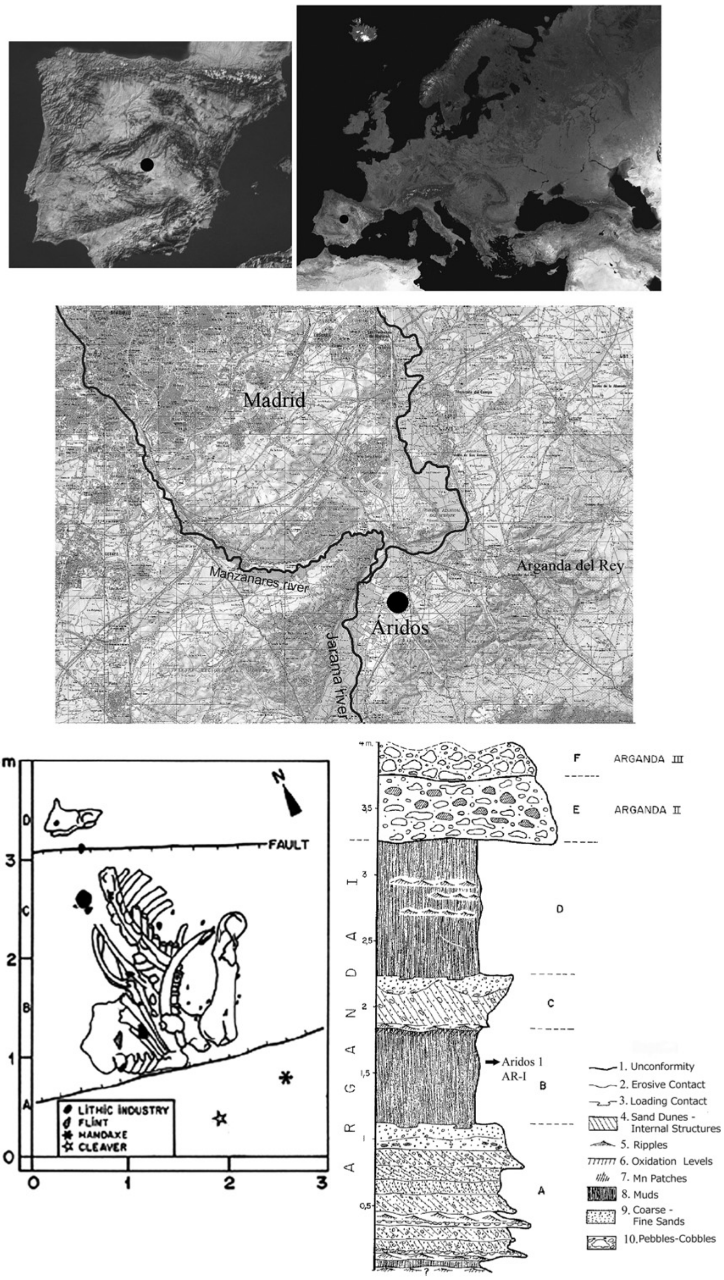

Fig. 1. Geographic situation, stratigraphic position of Áridos 2 and excavated area. The stratigraphic column shows the sequence at Áridos 1, where the Arganda I, II and III units are differentiated. The sandy and muddy facies (A, B, C and D) at the top of Arganda I can also be observed.

floodplain surface and overlain by sands and gravels (Santonja and Querol, 1980c). No significant sedimentary disturbance of the assemblage has been identified due to the small size of the lithic pieces and the lack of abrasion or polishing. Although two small channels were located to the east and north of the assemblage, and they contributed with sands to the local sedimentary matrix, no taphonomic indicator shows that the carcass may have been transported by any hydraulic jumble, although some rearrangement of the smaller components (e.g., lithics) and some *in situ* reorientation or tilting of some bones could be hypothesized. Furthermore, the identification of meat use wear polishing on the edges of several of the artifacts indicates they probably were used to butcher the elephant (Ollé Canellas, 2005). The elephant was an adult male of about 40 years, 4.6 m tall and almost 5000 kg (Soto, 1980). The stone tool assemblage is composed of 26 flakes, four cores, one burin, one backed knive, one handaxe and one cleaver.

At the end of the excavation (October, 1976), the elephant remains were covered in polyurethane to be transported in a block

Fig. 2. Remains of the elephant carcass from Áridos 2 as are currently exhibited.

to the National Museum of Archaeology in Madrid. They were not removed from the polyurethane cast until 2002 when the Regional Archaeological Museum of Madrid restored them and the elephant was exposed at the exhibit “Handaxes and Elephants: the first inhabitants of Madrid” (Panera and Rubio-Jara, 2002a,b) (Fig. 2). This enabled its detailed taphonomic study reported here.

3. Sample characteristics and method of analysis

The elephant carcass is composed of a right scapula and humerus, a cranial fragment, 24 vertebrae and almost all the ribs of the right side and three of the left side. The entire assemblage is almost articulated (Figs. 1–3).

The anatomical articulation of the elephant bones in the block extracted first for transport to the museum and later, for permanent exhibit at the museum, conditioned that bone inspection could only be performed visually, without moving them from the block. Therefore, the analysis of bone surfaces was restricted to those surfaces exposed in their current position (Fig. 2). Bones were screened with hand lenses using a magnification of 10×, 15× and 20×. Then, marks identified were molded using a fluid water-compatible high-resolution silicone (ISP 4823). The negatives were turned into positive casts with high-resolution resin (Esaflex Feropur PR 55 E-01 and Feropur E 55 E+01). The entire process was carried out under the supervision of the museum’s restoration expert, since bone surfaces had been previously consolidated and the consolidating product had to be removed from the identified cut marks prior to molding them with silicone.

Fig. 4. Sets of cut marks on the elephant scapular surface. Arrows indicate the location of the clusters 1 & 3. Cluster 2 location is indicated, although it cannot be seen in this photograph.

The resin molds of cut marks were then analyzed under a binocular microscope and a SEM (Scanning Electron Microscope) at the Complutense University of Madrid.

4. Results

The partial elephant carcass is mainly represented by axial and cranial elements (Fig. 3). The only long bone present is a humerus. The absence of the remaining long bones cannot be explained because of the partial destruction of the site.

Several cut marks were identified on the scapular blade (Figs. 4–7) and one the ventral side of one rib (Fig. 8). Cut marks on the scapula occur in groups in three different places (Fig. 4). The first set of marks shows several deep grooves larger than 30 mm with an open V-shaped section. The clayish matrix of the soil filled part of the grooves (Fig. 5). The second set of marks is comprised of two straight V-shaped long grooves with a substantial amount of flaking on the shoulders (Fig. 6). A gap linked to a crack fracture intersects the cut mark. The third set of marks (Fig. 7a) is somewhat different since these are broader than the previous ones and at least two examples of fork-shaped marks, like those documented experimentally in cut marks created with a retouched edge, can be observed (Domínguez-Rodrigo et al., 2009a). Fig. 7b and c are experimentally-created cut marks made with handaxes (de Juana et al., in press). Fig. 7b shows the bifurcation of the groove causing a “fork-shaped” mark similar to the longest curvy groove located on the elephant scapula (Fig. 7a). Fig. 7c shows another

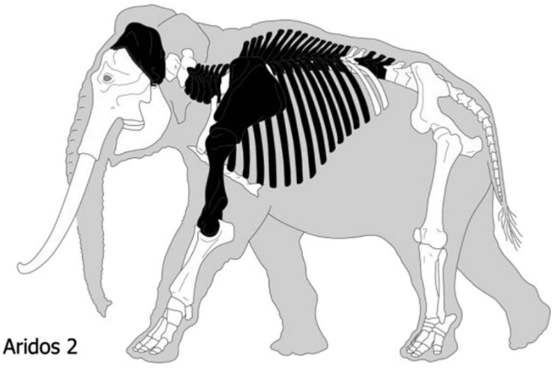

Fig. 3. Skeletal representation of the elephant carcass at Áridos 2.

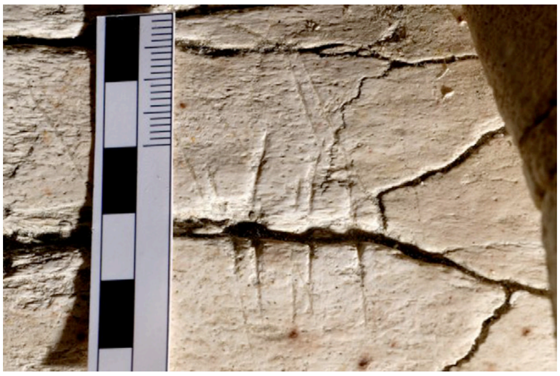

Fig. 5. Cluster 1 of cut marks on the elephant scapula.

Fig. 6. Cluster 2 of cut marks on the elephant scapula.

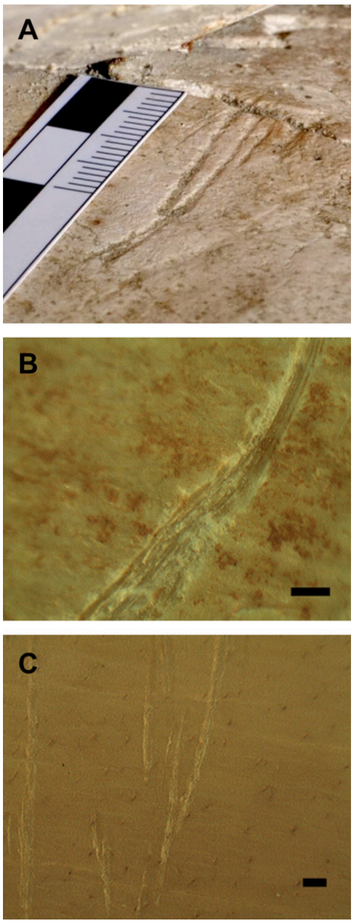

Fig. 7. A, Cluster 3 of cut marks on the Áridos 2 elephant scapula. B, experimental "fork-shaped" cut mark made with a handaxe consisting of a bifurcating groove. C, experimental "fork-shaped" cut mark made with a handaxe consisting of two joining grooves. The pattern is observed on the main long grooves to the right and also on the lower smaller grooves located to the left of the first "fork-shaped" mark. The experimental marks shown in B and C are from a single stroke. Experimental data are from de Juana et al. (in press). Scale for 7b and 7c is 1 mm.

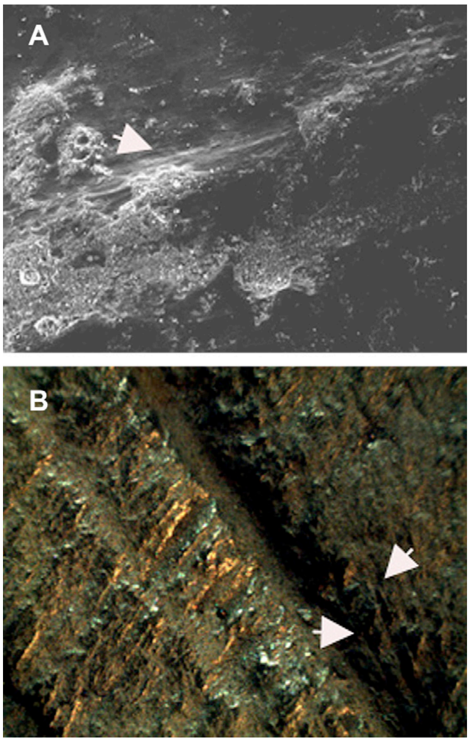

Fig. 8. A, S.E.M. image (100×) showing a portion of one of the cut marks displaying some microstriations (arrow) at the base on the groove, close to the wall of the mark where some hertzian cones can also be documented. B, another cut mark showing a V-shaped section with accompanying shoulder effect (broader shallower groove to the left) where some microstriations (arrows) are documented both on the internal side of the wall and the edge of the mark. This image has been obtained by using a binocular microscope (20×) on the high-resolution positive mold of the mark prepared for S.E.M. inspection.

pattern of "fork-shaped" marks created by the junction of two independent grooves created by a single stroke, as documented in the two longest grooves from the set of marks on the elephant scapula. In addition, the absolute widths of several grooves (see scale in Figs. 4–7) exceed the dimensions of marks made with simple or retouched flakes (Domínguez-Rodrigo et al., 2009a) and are similar to those reported for cut marks made with handaxes (de Juana et al., in press). This interpretation is further supported by the discovery of meat use wear polish on the spatially associated handaxe that was found near the elephant remains (Ollé Canellas, 2005). Mark section shape, the intensity of flaking on the shoulder of some of the marks, and the straight trajectory of the marks are criteria that clearly identify these marks as cut marks instead of trampling marks. This is further supported by the absence of oblique intersecting striations and the micro-abrasion marks which occur in almost 100% of cases where bones are trampled (Domínguez-Rodrigo et al., 2009a). Furthermore, although bone preservation is very poor (Fig. 8) and a lot of microflaking caused by bone modification has removed most of the original microstriations, high magnification is useful to spot some remnants of the original striated groove. Fig. 8 captures some of the microstriations that have survived in only a portion of the main body of the groove, showing that an abrasive agent (e.g., stone tool edge) created the wide mark.

Cut marks on the rib form two sets. The left set is composed of few and widely spaced marks with V-shaped straight trajectories

Fig. 9. Cut marks on the ventral side of the elephant rib.

and the right set has several parallel marks, all of them V-shaped, some with intensive flaking on the edge (Fig. 9). These characteristics as well as the presence of the bulk of the axial skeleton above this rib prevents them from having been caused by trampling. The presence of these cut marks on the ventral side of the ribs suggest that they were caused during evisceration. This is important since evisceration, even in a carcass this size, occurs in the earliest stages of its consumption by carnivores. Therefore, this may be suggestive of hominins having had access to this carcasses either before carnivores did or at the very early stages of carcass consumption (Fig. 10).

Most of the cut marks show all the characteristics of cut marks made with simple flakes or with tools whose edges have not been retouched. Only the third set of marks on the scapula seems to have been made with a retouched tool, given its broad section shape and the intersecting fork-shaped pattern. This feature, together with the absolute width of the grooves, supports the hypothesis that these marks may have been created with handaxes or large retouched tools (Domínguez-Rodrigo et al., 2009a,b). This functional interpretation of the lithic tools and the taphonomic data reported here is also supported by the use—wear analysis of part of the lithic assemblage assemblage (Ollé Canellas, 2005, 419—441).

In addition to the anthropogenic exploitation of the elephant, carnivore intervention has also been detected. Several tooth marks have been identified together with intense furrowing on the distal epiphysis of the humerus (Fig. 11). The size of the tooth pits as well as the degree of furrowing clearly identify hyenids as the carnivores responsible for these modifications. Some chewing on one rib end has also been observed.

Fig. 10. Elephant carcass at the initial stage of being scavenged by lions. Eventration has already taken place at this early stage where meat has not been targeted yet. Obtained at Tarangire National Park (photo: Agness Gidna).

Fig. 11. Distal humerus epiphyseal end and metadiaphysis showing gnawing. Lower image shows a close-up detail of the distal epiphysis.

5. Conclusions

Cut marks have been found on the scapula and one rib of the elephant at Áridos 2, indicative of butchery and involving both defleshing and evisceration. This is suggestive of early access to the carcass by hominins. Haynes (2005) shows that viscerae disappear fast in the consumption of elephant carcasses by carnivores. This is also indicative of large carcass consumption during the Middle Pleistocene by hominins, not solely restricted to the Upper Pleistocene (Gaudzinski et al., 2005; Surovell and Waguespack, 2008). The evidence from Áridos 2 can be added to similarly documented elephant butchery behaviors taphonomically reported in sites such as Ambrona (Villa et al., 2005), Gesher Benot Ya'akov (Goren-Inbar et al., 1994), La Cotte de St Brelade (Scott, 1986) and other sites where, even if cut-marked bone is absent, such as at Lerhingen (Thieme and Veil, 1985) and Gröbern (Weber, 2000), the tight spatial association of elephant carcass remains and stone tools, as well as the presence of a fragment of a wooden spear, are suggestive of exploitation of these carcass remains by hominins. It is obviously difficult to assess whether these resources were acquired through hunting or scavenging (Fosse, 1998; Mussi, 2005). Arguments supporting both options are available (Villa and Lenoir, 2009). The natural deposition of carcasses at Ambrona with their occasional exploitation by hominins has been defended by Villa et al. (2005). The much more spatially discreet accumulation found in La Cotte de St Brelade with better taphonomically-supported evidence of repeated butchery of most of the individuals represented in the accumulation, as well as the location of the site at the foot of a cliff, are better understood as the result of an intentionally active acquisition strategy displayed by hominins (Scott, 1986).

One way or another, what is becoming relevant is that the exploitation of elephant and other large carcasses during the Middle Pleistocene (e.g., woolly rhinoceros at La Cotte de St Brelade (Scott, 1986) and Boxgrove (Parfitt and Roberts, 1998)) was more than a marginal strategy of protein obtainment by hominins. This is documented not only at European sites but also at African sites, such as several Middle Pleistocene sites in Middle Awash, where remains of hippopotamus occur in association with stone tools, several of them bearing cut marks (de Heinzelin et al., 2000). Exploitation of resources from these large animals has also been documented earlier in Africa, during the Lower Pleistocene. For example, several cut-marked hippopotamus bones have been documented at Buia (Fiore et al., 2004) and even earlier at Koobi Fora (Bunn, 1994). However, the evidence of consumption of these animals prior to 1 Ma is so scanty that there are no arguments supporting anything but a marginal and irregular exploitation of these carcasses at that time. Exploitation of animals larger than 1000 kg has also been documented at BK (Upper Bed II, Olduvai Gorge, Tanzania) at around 1.2 Ma (Domínguez-Rodrigo et al., 2009b). Beyond documenting the inclusion of faunal taxa larger than 1000 kg in the diet of hominins, archaeologists are faced now with the need to explain why consuming resources from such large animals becomes more visible after the end of the Lower Pleistocene in the archaeological record.

The discovery of a butchered elephant at Áridos 2 reported in the present work is relevant because it shows one of the earliest pieces of evidence of this type of behavior associated with an Acheulian site and where a convincing case can be made for handaxe use for butchery of a proboscidean carcass.

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8

El Valle de los Neandertales

8.1 LOS YACIMIENTOS DEL CALVERO DE LA HIGUERA EN PINILLA DEL VALLE

Vista aérea. Yacimientos del Calvero de la Higuera. Pinilla del Valle. Foto: E.I.P.V - MAR

En 2001 tomamos la decisión de revisar el entonces conocido como “Yacimiento Paleontológico de Pinilla del Valle”.

El equipo de F. Alférez había abandonado trece años antes su excavación y teníamos varias preguntas que formular a aquel yacimiento que, a primeros de los años 80, fue un lugar muy apreciado en el Pleistoceno Ibérico, especialmente por la aparición de dos dientes de homínido (Alférez, F., Íñigo, C. 1982; Alférez, F., Molero, G. 1982; Alférez, F. *et alii* 1982, 1983 y 1985; Alférez, F., Chacón, B. 1996; Alférez, F., Buitrago, A.M. 1994).

Queríamos saber si el yacimiento estaba casi agotado o no, si estaba en abrigo o en cueva, si era Pleistoceno Medio o Superior y, sobre todo, queríamos saber si el agente causante del nivel fosilífero eran los *anteneandertales,* como sostenían Alférez y equipo, o eran las hienas manchadas como había apuntado Carlos Diez Fernández-Lomana en su Tesis Doctoral[21] (1992).

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[21] Más tarde supimos que también el paleontólogo segoviano Alfonso Arribas, durante el propio proceso de excavación, sostenía lo mismo.

También queríamos ponerlo en valor, adecentarlo y protegerlo física y jurídicamente declarándolo Bien de Interés Cultural.

Para todo ello, creamos un equipo interdisciplinar dirigido por José Mª Bermúdez de Castro, Alfredo Pérez- González y yo mismo. En 2006 se produjo la llegada de Juan Luis Arsuaga en sustitución de Bermúdez de Castro, que se incorporó al CENIEH. La aportación de Arsuaga ha representado un impulso exponencial al proyecto.

Cueva de Camino. Yacimientos del Calvero de la Higuera. Pinilla del Valle. Foto E.I.P.V - MAR

8.2 LA CUEVA DEL CAMINO

Hicimos una primera campaña de quince días, en 2001, en el que hoy conocemos como el yacimiento de la Cueva del Camino y, ese mismo año, comprobamos varias cosas.

El yacimiento no estaba en un abrigo sino en una cueva con sus techos caídos, y además había sido parcialmente desmantelado por la acción de la máquina que abrió un camino en paralelo al embalse de Pinilla, en el río Lozoya.

Por otra parte, las faunas cálidas como *Testudo hermanni, Hystrix* cf. *brachyura,* y *Dama dama*, apuntaban a un momento cálido en el inicio del pleistoceno superior[22] como ya venía apuntando la paleontóloga Nuria García y posteriormente confirmarían los diferentes métodos de datación absoluta.

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[22] Como ya venía apuntando la paleontóloga Nuria García y posteriormente confirmarían los diferentes métodos de datación absoluta. Ella sostenía que, el oso de la Cueva del Camino, era ya una especie propia de comienzos del Pleistoceno Superior.

Pero lo principal era que, frente a lo estimado por el equipo de Alférez (y que nosotros tomábamos inicialmente como hipótesis cierta), el yacimiento se trataba de un cubil de *Crocuta Crocuta.*

Los argumentos eran contundentes:

1. Menos que anecdótica presencia de industria lítica.
2. Ninguna presencia de restos de fuego. Ni carbones, ni huesos quemados, ni hogares, ni industria alterada por la acción del fuego.
3. Indiferencia en la relación de presas tanto en tamaño como en especie, salvo un gran porcentaje de gamo (*Dama dama*).
4. Gran presencia de carnívoros, muy especialmente *Crocuta crocuta*, con individuos inmaduros.
5. El trabajo de los fósiles es, indiscutiblemente, característico de la acción de las hienas que no rompen la diáfisis para obtener el tuétano, pero sí mordisquean y consumen las epífisis de los huesos largos por su contenido en colágeno.

Frente a lo que pudiera aparentar un cierto fracaso arqueológico, el equipo estaba muy satisfecho por la gran información aportada por este yacimiento sobre el entorno (clima, paisaje, flora y fauna) en que vivieron los homínidos en el Valle del Lozoya.

8.3 EL ABRIGO DE NAVALMAÍLLO

Además, en ese mismo verano de 2002, gracias a la sugerencia del paleontólogo Guillermo Molero, localizamos un segundo yacimiento en la ladera del arroyo de Navalmaíllo, distante unos 80 metros del camino, con indudables restos de actividad humana en forma de industria lítica musteriense que terminó siendo un campamento de neandertales. Lo que hoy conocemos como “El Abrigo de Navalmaíllo”.

Quince campañas de excavación mensuales y estivales se han practicado en este lugar que presenta varios niveles de ocupación con industria musteriense entre hace unos 80.000 y 40.000 años.

Las características de este yacimiento son las siguientes:

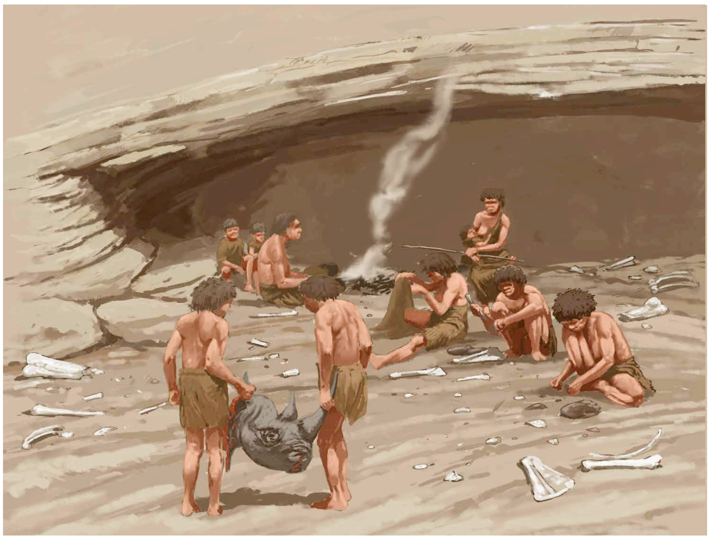
1. Una extensión bajo la cornisa rocosa de unos 350 mts^2.
2. Un excelente estado de conservación salvo por la acción de la escorrentía de las aguas, la caída de grandes bloques de la ceja del abrigo y la construcción de un horno para hacer cal en el siglo XIV.

3. La industria lítica se caracteriza por la gran variedad de materias primas, aunque, muy profusamente, la roca más tallada es el cuarzo. Los utensilios más frecuentes son: denticulados, raederas, puntas y lascas. La técnica *levallois* se utiliza sólo en las materias primas de más calidad y la talla centrípeta lleva al agotamiento de los núcleos que producen objetos de muy pequeño formato. Auténticos microlitos.

4. Los hogares se organizan con bloques de dolomía alrededor, que serán enrojecidos por la acción del fuego, con oxidación, y oscurecidos en condiciones reductoras. Casi todos ellos están muy alterados por la escorrentía de las aguas y en su interior contienen restos de fauna e industria lítica quemados.

5. La fauna, presa de los neandertales, se compone en exclusiva de grandes herbívoros. Los fósiles aparecen muy machacados, con marcas claras de percusión en fresco para la extracción del tuétano y con marcas de corte producidas por el fileteado de la carne.

6. No han aparecido restos fósiles humanos.



Abrigo de Navalmaíllo. Ilustración: Dionisio Álvarez y Enrique Baquedano. 2006

Abrigo de Navalmaíllo. Yacimientos del Calvero de la Higuera. Pinilla del Valle. Foto: E.I.P.V - MAR

8.4 LA CUEVA DE LA BUENA PINTA

Esta cavidad fue descubierta en prospección durante la campaña de excavación de 2003 y de inmediato fuimos conscientes de su gran potencial. Por ello se denominó de esta manera.

Desde entonces, un total de catorce campañas de excavación se han realizado en dicho lugar, localizando, en nivel holoceno, una madriguera con restos de varios carnívoros (y muchos conejos) que han alterado un enterramiento sin ajuar de la Edad del Bronce.

A continuación, aparece un potente nivel del Pleistoceno superior en un momento frío, probablemente un estadio isotópico 3, en torno a hace 45.000 años, con un cubil de hienas y faunas fósiles como la liebre silbadora y la liebre variable. También aparecieron un par de molares con coronas muy agotadas, seguramente neandertales, que se presentarán en la reunión de la ESHE 2016, en el Museo Arqueológico Regional de la Comunidad de Madrid.

Y por último, un nivel antrópico, con industria musteriense que se ocupó en el vestíbulo de esta cueva antes de su desmantelamiento. No contamos con fechas precisas para esta ocupación, si bien todo apunta a un estadio cálido.

Cueva de la Buena Pinta. Yacimientos del Calvero de la Higuera. Pinilla del Valle. Foto: E.I.P.V - MAR

8.5 LA CUEVA DES-CUBIERTA

En 2009, descubrimos una gran cavidad también en prospección, fruto de un análisis y reflexión peculiar.

En efecto, las últimas campañas en la Cueva de la Buena Pinta aportaban restos de topillo Vaufrey (*Microtus vauyfrensis*) y de topillo de las brechas (*Microtus brecciensis*). Nuestro especialista en roedores insistía en que dichos restos estaban reelaborados, procedentes de otros niveles erosionados, y conservaban muestras de sedimento matricial diferente. Sólo podían venir, en opinión del paleontólogo César Laplana, de un nivel del Pleistoceno medio.

Cueva Des-Cubierta. Yacimientos del Calvero de la Higuera. Pinilla del Valle. Foto: Javier Trueba/ Madrid Scientific Films.

Pusimos todo el interés en localizar este yacimiento que sólo podía estar en una zona superior del Calvero, por encima de la Cueva de la Buena Pinta.

En la primavera, abril y mayo, de 2009 con una cuadrilla de tres arqueólogos, un geólogo y varios peones, limpiamos el manto vegetal en una extensión inicial de unos 800 m^2 y ¡dimos, contra todo pronóstico, con una gran cavidad!

Desde entonces, en ocho campañas de excavación, hemos podido recuperar toda la planta de la galería principal que, zigzagueando, tiene varias bocas, además de un conducto que lleva a la Cueva de la Buena Pinta y otro que se interna en el karst del Calvero.

La cueva, destruida en su parte superior, presentaba una erosión diferencial entre las dolomías de la propia caja y los rellenos muy brechificados y cementados en superficie. Los techos estaban completamente erosionados, por ello decidimos llamar a esta caverna como la "Cueva Des-Cubierta", porque la descubrimos yendo a buscarla y porque carece de cubierta.

Los rellenos, aún en excavación, y estudios iniciales son excepcionalmente importantes.

El paquete estratigráfico inferior, muestra niveles del pleistoceno medio que contienen, al menos, un cubil de hienas. Por encima, los niveles del pleistoceno superior, nos ofrecen escenas de enorme interés. La dentición decidual y la mandíbula, sin las ramas, de un individuo infantil apuntan con claridad a una inhumación rodeada de hogares y de lo que los cazadores actuales denominarían "trofeos de caza" (uro, bisonte y ciervo), es decir, las astas y los cuernos con el correspondiente arranque del cráneo. Siempre situados sobre hogares de pequeño y mediano tamaño. Además, un cráneo de rinoceronte de estepa (*Stephanorhinus hemitoechus)*, sin el maxilar superior ni la mandíbula, parece apuntar en la misma dirección, si bien éste no está ubicado encima de ningún hogar.

Esto sucedió hace entre 40 y 42.000 años, según varias dataciones por C14 y, sin duda, fue protagonizado por los neandertales.

La escena funeraria recuerda al enterramiento infantil de Roc de Marsal, si bien en Des-Cubierta parece existir un rito funerario y otro de naturaleza aún indeterminada, de forma recurrente en un grupo de homínidos, que puede corresponderse con la última fase de ocupación del Abrigo de Navalmaíllo o con otros campamentos aun no descubiertos. Nunca nos hemos atrevido a utilizar el término "Santuario" para calificar los restos hallados en Des-Cubierta, pero es indudable el carácter funerario y ritual de este lugar.

La publicación por el equipo de Jacques Jaubert de un posible santuario en la cueva de Bruniquel, junto al río Aveyron en Toulouse, hace 175.000 años, nos anima a decir en público lo que llevamos cinco años diciendo en privado (Jaubert, 2016).

Todo esto es una primera hipótesis de trabajo que se presentará en la reunión de la ESHE 2016 de Alcalá de Henares para su debate y sincera petición de propuestas interpretativas.

8.6 UN PARAÍSO NEANDERTAL

Además de estos cuatro yacimientos comentados, en el propio Calvero, existe otro abrigo con ocupación, probablemente de hienas, al aparecer restos en conexión anatómica. Este sitio lo llamamos el "Abrigo del Ocelado", por la presencia ocasional de este reptil.

El georradar parece estar detectando más galerías junto a Des-Cubierta que aún no hemos tenido tiempo de confirmar.

En otro de los calveros, el Calvero de Toconal, también hemos descubierto otros dos yacimientos, “Toconal” y “Carrión”, con ocupación humana y hiénida, que conocemos muy superficialmente.

Parece que todos los calveros albergan Karst con cavidades donde moraron tanto los neandertales como las hienas manchadas.

Este Valle alto del rio Lozoya debió ser un verdadero paraíso para los neandertales que entre 250.000 y 40.000 años lo convirtieron en su zona de campeo y habitación.

La reconstrucción del paleopaisaje con su correspondiente flora y fauna, en permanente transformación, nos hace soñar con un valle donde se mezclan especies que hoy consideramos endémicas de Euroasia y de África.

Por un lado leones, leopardos, hienas manchadas, y rinocerontes. Y por otro lobos, osos, perros rojos, linces, uros, bisontes, caballos, asnos, cérvidos y rebecos.

Con los neandertales en la cúspide de la pirámide trófica.

8.7 DIFUSIÓN CIENTÍFICA

Hay un principio básico en Arqueología, y en ciencia en general, según el cual aquello que no se discute y se difunde en el seno de la comunidad científica es como si no existiera.

Por ello, el equipo de investigación en Pinilla del Valle ha tenido una política permanente de presentación académica de sus resultados.

La primera actividad en este ámbito científico fue en el XV congreso de la UISPP de 2006, que tuvo lugar en Lisboa bajo el título “Neandertal and carnivore occupations in Pinilla del Valle (Community of Madrid, Spain)” publicado en las series BAR, en 2011[23].

EL PAÍS.com Ciencia

TRIBUNA: ENRIQUE BAQUEDANO

Neandertales en el Valle Alto del Lozoya

ENRIQUE BAQUEDANO 26/10/2009

Al iniciar, en el año 2002, el estudio del poblamiento prehistórico en el Valle Alto del río Lozoya, en la sierra madrileña, no podíamos ni sospechar, aunque éramos muy optimistas, el ritmo que adoptarían los acontecimientos. En efecto, la idea inicial consistía en intervenir en un yacimiento paleontológico de Pinilla del Valle al objeto de conseguir su protección física y jurídica, su limpieza y acondicionamiento para la visita, y, de paso, su revisión científica.

Dicho yacimiento se conocía desde 1979 y en él, hasta 1989, un equipo de paleontólogos de la Universidad Complutense, con Alférez, Maldonado, Molero e Iñigo a su cabeza, descubrió una gran cantidad de restos faunísticos fósiles y, entre ellos, dos molares humanos que colocaron este yacimiento en el escaso listado de lugares con restos humanos anteriores a nuestra especie en la Península Ibérica, y el único en la Comunidad de Madrid.

Pero tanto la cronología como, sobre todo, el origen tafonómico de esta excepcional acumulación de fósiles fueron discutidos desde el primer momento en el seno de la comunidad científica.

Así es, Alférez y su equipo, con mucho voluntarismo y los escasos medios económicos y técnicos de entonces, atribuyeron el yacimiento a un origen antrópico de fines del Pleistoceno Medio, hace unos 200.000 años.

Las nuevas campañas de excavación y prospección en la zona de los Calveros y, singularmente, en el Calvero de la Higuera, nos han permitido determinar que el yacimiento de la Cueva del Camino es un cubil de hienas formado en el último interglaciar, el Eemiense, (durante el estadio isotópico 5), entre 100.000 y 90.000 años. Pero, al tiempo que esta revisión nos producía, a qué negarlo, una gran decepción, comenzó a producirse una serie de hallazgos cada campaña más excepcionales, que nos llevan a un balance provisional verdaderamente espectacular.

Artículo de prensa: “Neandertales en el valle alto del Lozoya”. E. Baquedano. *El País.* 26/10/2009.

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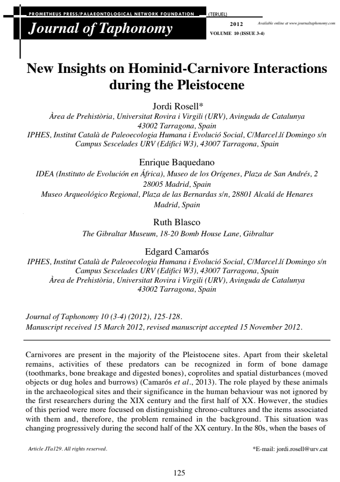
[23] Como anécdota de aquella sesión, comentaré que vino a escucharme con un gran interés el paleontólogo Josep Gibert. Fue la última vez que le vi con vida.

Rosa Huguet durante su intervención en la *1ª Reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica*, celebrada en el Museo Arqueológico Regional de la Comunidad de Madrid en 2009. Foto: Mario Torquemada/MAR.

En 2008, impartíamos la conferencia "La arqueología del Pleistoceno en la cuenca y en la sierra madrileñas" como lección inaugural en las IX Jornadas de Arqueología de la Sociedad de Ciencias Aranzadi, en San Sebastián.

También, ese año dictamos la conferencia "Excavaciones en el yacimiento de Pinilla del Valle" en la Asociación Española de Amigos de la Arqueología.

En 2009, dirigimos con Jordi Rosell, el encuentro científico "Homínidos y carnívoros" en el que se presentaron tres comunicaciones en una sesión exclusiva sobre Pinilla del Valle, y se concluyó con una excursión para visitar aquellos yacimientos.



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New Insights on Hominid-Carnivore Interactions during the Pleistocene

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Journal of Taphonomy 10 (3-4) (2012), 125-128.
Manuscript received 15 March 2012, revised manuscript accepted 15 November 2012.

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

Article JTa129. All rights reserved. *E-mail: jordi.rosell@urv.cat

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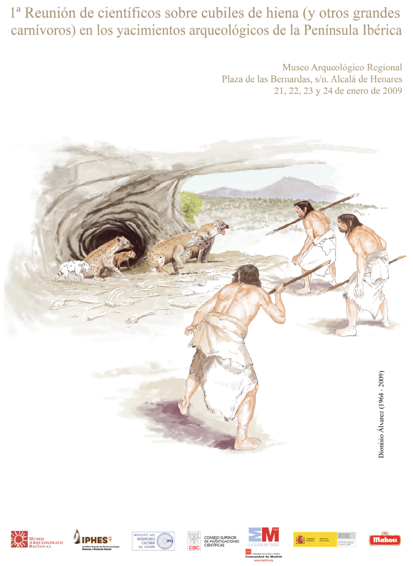
"New insights on Hominid-Carnivore interactions during the Pleistocene". J. Rosell, E. Baquedano, R. Blasco y E. Camarós. (2012). *Journal of Taphonomy*, 10, 3-4 :125-128.

En 2010, impartimos la lección inaugural del "Máster Erasmus Mundus en Arqueología del Cuaternario y Evolución humana" de la Universidad Rovira i Virgili, en Tarragona, con el título "Homínidos y carnívoros: competencia en un mismo nicho ecológico en el Pleistoceno. Los yacimientos del Calvero de la Higuera en Pinilla del Valle".



Cartel de la *1ª Reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica*, celebrada en el Museo Arqueológico Regional de la Comunidad de Madrid en 2009. Ilustración: Dionisio Álvarez y Enrique Baquedano.

En 2011, dictamos la conferencia "El Valle del Lozoya, Valle de los neandertales" en el Museo de la Evolución Humana, en Burgos.

8.8 DIFUSIÓN SOCIAL

Convencidos, como estamos, de que el patrimonio y la investigación arqueológica deben tener como objetivo último y principal su conocimiento y disfrute por el gran público, el Equipo de Investigación en Pinilla del Valle (E.I.P.V) siempre ha tenido un especial cuidado a este aspecto.

Desde la segunda campaña de excavaciones, todos los años, hemos convocado “jornadas de puertas abiertas” que han sido seguidas muy mayoritariamente por el público interesado.

Se han dictado numerosas conferencias divulgativas en colegios, institutos y ayuntamientos, por parte de todo el E.I.P.V.

Se ha editado el libro infantil “Viviendo la prehistoria en el Valle del Lozoya”.

Conferencia TEDxGranVia en 2012 sobre “De homínidos y carnívoros en la evolución humana“.

***Viviendo la Prehistoria en el Valle del Lozoya*. R. Mendoza y M. Lliso. (2011).**

El valle de los *neandertales*

EN LA ÚLTIMA DÉCADA, EN LOS YACIMIENTOS DE PINILLA DEL VALLE (MADRID) HA AFLORADO UN CAMPAMENTO DE LA ESPECIE CASI INTACTO, AHORA VISITABLE. LOS CODIRECTORES DE LA EXCAVACIÓN EXPLICAN SU VALOR

La reciente inauguración del Parque Arqueológico del calvero de la Higuera, en Pinilla del Valle (Madrid), culmina un largo proceso de investigación, conservación y difusión científica acariciado durante largo tiempo. Fue en 2005, tras descubrir la cueva de la Buena Pinta y confirmar que el yacimiento de Navalmaíllo era un importantísimo campamento neandertal al abrigo de una cornisa rocosa, cuando vislumbramos el sueño de crear allí un parque arqueológico dedicado al mundo de los neandertales. Pero el trabajo en la zona había arrancado mucho antes.

Entre 1979 y 1989, un equipo de paleontólogos de la Universidad Complutense de Madrid, dirigido por Francisco Alférez, organizó varias campañas de excavación en el yacimiento de la cueva del Camino, muy cercana al embalse de Pinilla del Valle. Los trabajos sacaron a la luz una excepcional colección de restos fósiles de herbívoros y carnívoros que inicialmente fueron atribuidos, en su acumulación, a la actividad de los “homínidos anteneandertales”.

Las dudas entre los científicos sobre el “agente acumulador” nos llevaron en 2002 a revisar aquel yacimiento, abandonado hacía trece años. Fue entonces cuando iniciamos una nueva etapa de investigación, con un equipo transdisciplinar, que acabó atribuyendo la formación de este yacimiento a la acción de la hiena manchada, *Crocuta crocuta*. Pero al mismo tiempo que nuestros presagios se confirmaban, un escenario nuevo se abrió ante nuestros ojos, con el hallazgo de un sinfín de yacimientos insospechados.

Vaya por delante que un cubil de hienas en el inicio del Pleistoceno Superior, hace unos 100.000 años, es de un gran interés por sí mismo para el conocimiento de la evolución humana. Las hienas son poco selectivas en cuanto a sus presas y nada elegidas para su carroñeo, por lo que transportan y acumulan en sus cubiles, para alimentar a sus crías, restos muy representativos de la fauna existente en el entorno próximo a su madriguera y en un momento determinado.

En el cubil de la cueva del Camino aportaron un par de molares de *Homo neanderthalensis*, junto a restos principalmente de gamo, *Dama dama*, entre los herbívoros, y de hienas, entre los carnívoros.

Ya en 2002 apreciamos indicios de un nuevo yacimiento, esta vez arqueológico, en la ladera del mismo montículo, el calvero de la Higuera, erosionado lateralmente por el arroyo de Navalmaíllo. Las excavaciones realizadas desde entonces nos permitieron descubrir que el yacimiento era un campamento, como ya hemos dicho, de neandertales, que se cobijaron al amparo de un abrigo rocoso con más de 350 metros cuadrados de extensión.

La caída de los bloques de la cornisa saliente en el abrigo ha protegido casi íntegramente los restos que nos dejaron los homínidos, en dos ocupaciones muy lejanas en el tiempo, aunque superpuestas. El nivel F tiene una antigüedad de unos 77.000 años, y el nivel Alfa de unos 45.000.

Solo un pequeño horno para hacer cal, datado en el siglo XIV, ha alterado parcialmente la disposición de los restos tal y como los dejaron los neandertales. Es por ello que nos encontramos una gran cantidad de piedras talladas, industria lítica, correspondiente al tecnocomplejo que conocemos como musteriense, bautizado así por su atribución en el yacimiento del abrigo de Le Moustier, en la Dordoña francesa.

HOGAR, DULCE HOGAR. La industria lítica de Navalmaíllo presenta una gran cantidad de lascas y otros utensilios retocados con filos denticulados y muescas que sirvieron para cortar la carne y trabajar la piel y la madera, como señalan todos los estudios de arqueología experimental. Dicha industria se encuentra en torno a los hogares que los homínidos utilizaron para cocinar, calentarse, alumbrar, secar, ahumar, protegerse, comunicarse... El hogar era el centro de la vida de los neandertales, como es habitual en todo grupo de cazadores-recolectores.

Y naturalmente aparecen también los restos de sus pitanzas: uros (*Bos primigenius*), caballos (*Equus caballus*), rinocerontes de estepa (*Stephanorhinus*

Reconstrucción de escena en el ABRIGO DE NAVALMAÍLLO. Ilustración de Yolanda González y Enrique Baquedano.

“El valle de los Neandertales”. E. Baquedano, J.L. Arsuaga y A. Pérez-González (2016). *La aventura de la historia*. 211 :74-77.

Y, sobre todo, se ha inaugurado el 27 de septiembre de 2015 “El Parque Arqueológico del Calvero de la Higuera” en Pinilla del Valle, Madrid, con visitas guiadas permanentemente, salvo en invierno por razones climatológicas.

En FITUR, en enero 2016, se ha presentado la marca turística “El Valle de los Neandertales”.

Todo ello organizado por el Museo Arqueológico Regional de la Comunidad de Madrid, con la asistencia científica del E.I.P.V.

Quaternary International 275 (2012) 55–75

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Understanding the ancient habitats of the last-interglacial (late MIS 5) Neanderthals of central Iberia: Paleoenvironmental and taphonomic evidence from the Cueva del Camino (Spain) site

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ABSTRACT

The Cueva del Camino site (Pinilla del Valle, Madrid) represents the most complete MIS 5 record from the Iberian Peninsula (away from the Mediterranean margin), including a large accumulation of fossilized remains of small and large vertebrates and two human teeth. The presence of carnivores (mainly hyenas) and humans suggests that the site should be interpreted as a spotted hyena den, a human occupation, or both. During an earlier phase of excavation undertaken during the 1980s, an anthropic origin was suggested for the accumulation at the site. However, research was resumed in 2002, leading to an increase in the number of vertebrate remains recovered, as well as the recognition of new vertebrate species. These have now been incorporated into the site's list of fauna. In addition, new palaeobotanical, geochronological and stratigraphic data have been recorded and analysed, and the human teeth identified as being of Neanderthal origin. Floristic data (pollen and charcoal remains) obtained for the north sector of this site indicate an open landscape with *Pinus sylvestris-nigra* as the main arboreal taxon. The available evidence suggests this accumulation to be the result of spotted hyena activity during a warm phase of Marine Isotope Stage 5 (MIS 5) in an environment in which fallow deer was the most abundant herbivore.

1. Introduction

One of the main interests in the Last Interglacial period (MIS 5) lies in the fact that it is believed to represent the last time when the earth's climate was similar to the present day. However, this period is poorly recorded in inland Iberia, and only a few scattered localities near the Mediterranean rim have been recognized in the Iberian Peninsula for MIS5. This paper presents a study of Cueva del Camino, an archaeo-palaeontological site placed in Central Iberia, which includes a very rich and diversified MIS5 fauna and flora record associated with *Homo neanderthalensis* remains.

The Late Pleistocene site of Cueva del Camino was discovered in 1979. Excavations were performed at the site from 1980 until 1989

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by Alférez et al. (1982), who reported numerous remains of animals and two human molars. These animal remains have been extensively studied (Alférez and Molero, 1982; Alférez et al., 1982, 1983, 1985; Alférez, 1985, 1987; Alférez and Iñigo, 1990; Toni and Molero, 1990; Maldonado Díaz, 1991; Alférez and Roldán, 1992; Buitrago Villaplana, 1992; Alférez and Buitrago, 1994; Alférez and Chacón, 1996; Maldonado, 1996; Bochenski, 2007). The faunal association of the site led Alférez et al. (1982) to provisionally assign it to the Riss-Würm (Eemian) interglacial period or some Riss interstadial period. The two human teeth were claimed to be pre-Neanderthal (Alférez and Roldán, 1992), and the accumulation was originally interpreted as the result of human occupation (Alférez et al., 1982). Díez (1993), however, reinterpreted it as a spotted hyena den.

In 2002 a multidisciplinary research team began new excavations at the small limestone hill known as El Calvero de la Higuera. This comprises several cave deposits, those of Cueva del Camino among them. Excavations at the Cueva del Camino site were undertaken between 2002 and 2009 (one month's summertime excavation period per year) and the data gathered have led to the publishing of new articles (Laplana and Sevilla, 2006; Arsuaga et al., 2010, 2011; Huguet et al., 2010; Pérez-González et al., 2010).

The present work describes a complete study of the Cueva del Camino site using different techniques. The fossil material studied comes from the new excavation period, but includes the human teeth recovered during the earlier excavation work. Geochronometric and biochronological data are taken into account in order to ascertain the age of the deposit. New palaeobotanical (anthracological and pollen analysis) and taxonomic (micro- and macrovertebrate) data allow the environment of the site and its surrounding area to be reconstructed. Taphonomic analyses were made to establish the origin of the accumulation. Using both classic and virtual techniques, the human teeth found at the site were compared to Neanderthals and modern humans.

2. Study area

2.1. Geological context

The Cueva del Camino site is part of the Calvero de la Higuera archaeological complex (Pinilla del Valle, Madrid, Spain). It is located in the upper valley of the Lozoya river in the Sierra de Guadarrama, a mountainous alignment with a NE-SW direction and general pop-up structures that form part of the Sistema Central range (Fig. 1).

The upper valley of the Lozoya River is a tectonic depression (pop-down) which runs in the same direction as the pop-up of the Sistema Central. To the north, the valley is bordered by the Montes Carpetanos (Carpetano Mountains), among which Peñalara is the highest peak (2428 m) of the entire Sierra de Guadarrama. To the south, it borders the Cuerda Larga Mountains, of which the Cabeza de Hierro is the highest point (2380 m).

From a geological point of view, the upper valley of the Lozoya River lies within the *Esquisto-Grauváquico* Complex of the Central Iberian Zone, which is formed by deformed and metamorphosed Proterozoic to Carboniferous rocks with intrusions of different types of granitoids prior to the Permian (Vera, 2004). The main Variscan deformation occurs during the Carboniferous, although it was during the Alpine Orogeny when the pop-down of the Lozoya River formed. The oldest rock outcrops consists of orthogneisses, leucogranites, adamellites, granitoids, migmatites and to a lesser degree schists and quartzites (Arenas et al., 1991; Bellido et al., 1991). Lamprofids, porfids and late quartzite dykes are also present.

The Mesozoic sedimentation, of Late Cretaceous age (Bellido et al., 1991), begins with sands, clays and gravels in the so-called Utrillas facies. Over this formation, sands, lutites and carbonates can be found, as well as sandstones and dolomites, the latter with a thickness of about 35 m. Karst processes have occurred within the dolomites, forming lapiaz and sinkholes at the rock surface, and

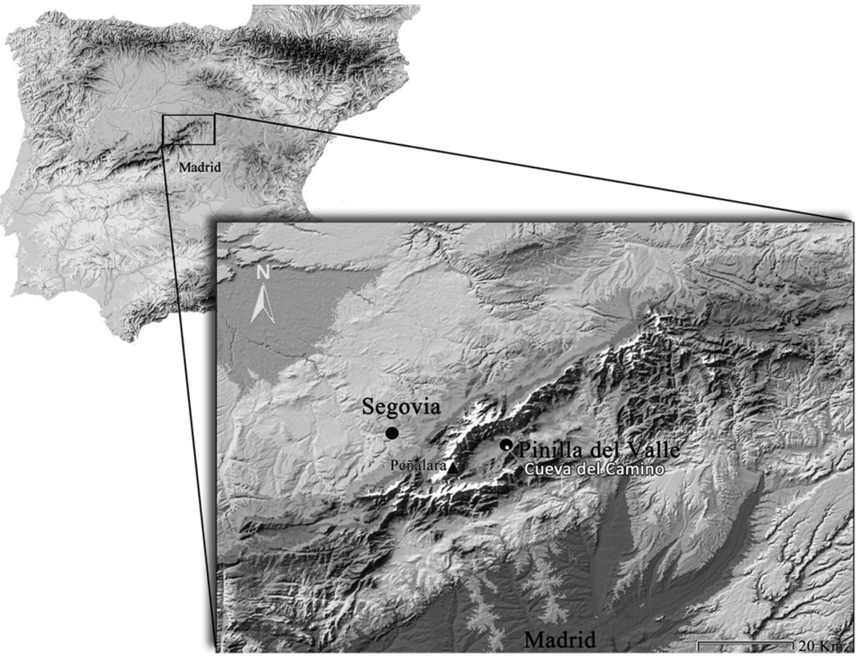


Fig. 1. Location of the Sierra de Guadarrama. Detail of the Lozoya Valley, home to the Cueva del Camino site.

rock shelters within caves. The archaeological sites of Calvero de la Higuera are all associated with these types of processes.

Quaternary deposits in the Lozoya valley area are very well represented. The Calvero de la Higuera archaeological sites (1114 m) are associated with cavities that evolved on a *cuesta* from Late Cretaceous carbonate rocks, with a slight inclination towards the Lozoya River. The Lontanar and Valmaíllo streams are two affluents on the right margin of the Lozoya River that dissect the cuesta relief of Calvero de la Higuera, leaving the three known sites in a hanging geological position.

2.2. *Present day vegetation*

The Mediterranean landscape is divided into a series of microenvironments characterized by bioclimatic heterogeneity depending on altitude, latitude and topographic aspects (Peinado Lorca and Rivas Martínez, 1987). In the Valle de Lozoya vegetation series map (Fernández, 1988), the study area lies within the *Luzulo forsteri-Querceto pyrenaicae* series, corresponding to mesothermophilous woods comprising Pyrenean oak (*Quercus pyrenaica*), which grow on siliceous soils in mainly sub-humid, high continentality supra-Mediterranean bioclimates. This zone reaches the limit of the Mediterranean climate, separated from typical Thermo- and Meso-Mediterranean zones where Neanderthals preferably settled (Fig. 2).

2.3. *Site*

The Cueva del Camino site is made up of four sectors (Fig. 3): the North, Central, Diaclasa Roja and South sectors (Arsuaga et al., 2010). Some 96.70% of the macrofauna remains identified (i.e., the number of identified specimens [NISP]) come from the North (Level 5) and Central sectors. The differences between the macrofauna associations of these two sectors are very small; they were therefore studied together (Arsuaga et al., 2010).

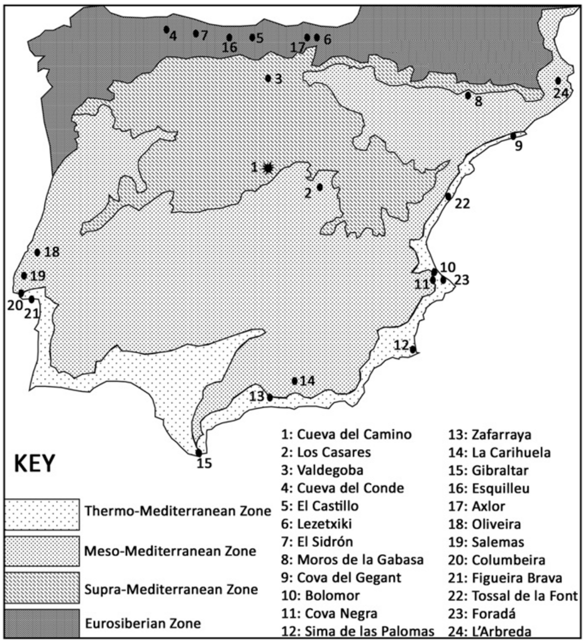


Fig. 2. Climatic zone distribution and main Neanderthal sites of the Iberian Peninsula. Modified from Rivas Martínez (1987).

2.3.1. *North sector*

This sector is the largest in spatial terms. Seven levels (numbered 3–9) have been identified (Arsuaga et al., 2011; Pérez-González et al., 2010) (Fig. 3). Levels 3 and 4 are of allogenic origin and are associated with the changes to the Valmaíllo stream that occurred over time. Levels 5–9 are autochthonous in character, associated with the karst environment. Level 5, dated to 90.961 ± 7881 ka by thermoluminescence (TL) in sediment samples (Pérez-González et al., 2010) (Fig. 3), contains 53.33% of the NISP of macrofauna and the greatest biodiversity. *Felis silvestris, Lynx* cf. *pardinus* and *Mustela putorius,* however, only appear in the upper levels (8–9), although the micromammal association of Levels 6–9 is similar to that of Level 5. Most of the microfaunal remains (>60%) come from this sector. The microvertebrate association from the North sector differs from those of the other sectors by the greater abundance of Cabrera's vole, the field mouse and the rabbit among the small mammals, and the Ladder snake and Herman's tortoise among the reptiles. The greater part of the anthracological samples studied come from this sector, mainly from Level 5.

2.3.2. *Central sector*

This has a particularly high density of macrofauna remains. The accumulation is chaotic but bears no evidence of water transport (Fig. 4). It is interpreted as a gravitational deposit. Some 38.92% of the NISP of macrofauna come from this sector. The micromammal species of this sector are the same as for the North sector, although the abundance of rabbits and field mice is lower. Fewer charcoal remains are seen than in the North sector.

2.3.3. *Diaclasa Roja sector*

This is a thin (20 cm) fossiliferous layer between the level of the stream and the bedrock (Fig. 3). This layer contains the remains of both macro- and microvertebrates (2.11% of the NISP). It lies at the same depth as the remains described for the Central sector, of which it might be a lateral continuation.

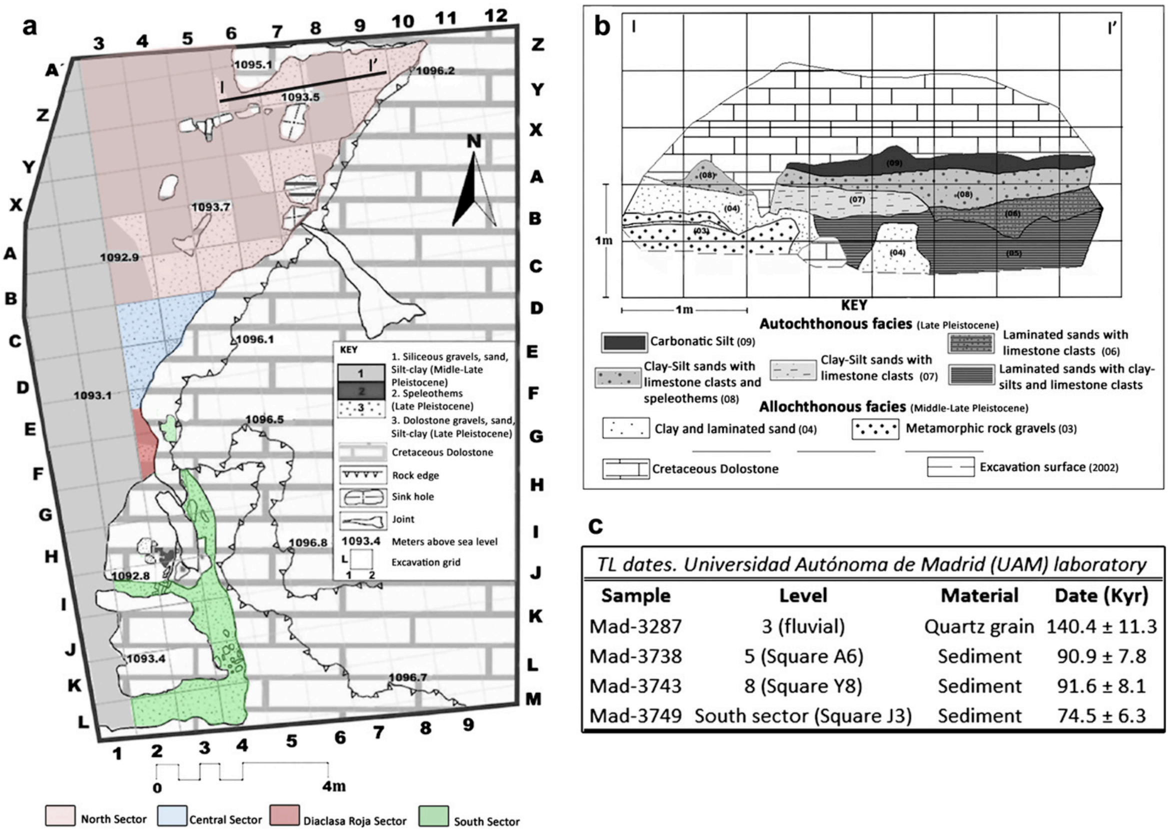
2.3.4. *South sector*

This is represented by the infilling of a fissure running along a flat surface above the Central sector (Fig. 3). Macrofaunal remains are more scarce here (1.25% of the NISP of macrofauna), and the microfauna shows some peculiar characteristics. The association is dominated by *Microtus arvalis*, alongside *Chionomys nivalis* (in small numbers). A small number of anthracological remains were also found.

3. Materials and methods

3.1. *Palynology*

Standard protocols for palynomorph extraction (Coûteaux, 1977) and the determination of the pollen concentration (Girard and Renault-Miskovsky, 1969) were followed. A Nikon Alphaphot-2 YS2 microscope (10 × 40 objective) has been used to examine the pollen remains. The number of grains counted always exceeded 300 per sample. Pollen taxa were quantified via pollen diagrams using TILIA® and TILIA-GRAPH® software (Grimm, 1987). Taxa were gathered and grouped according to their arboreal, shrubby or herbaceous nature. Pollen percentages for all palynomorphs are based on the sum of terrestrial pollen types. The pollen sum excludes aquatic taxa, fern and algal remains. With the aim of determining the biological diversity record, rarefaction analysis was performed (Analytic Rarefaction 1.3) (Birks and Line, 1992; Bronk Ramsey, 2000).



TL dates. Universidad Autónoma de Madrid (UAM) laboratory

Sample	Level	Material	Date (Kyr)
Mad-3287	3 (fluvial)	Quartz grain	140.4 ± 11.3
Mad-3738	5 (Square A6)	Sediment	90.9 ± 7.8
Mad-3743	8 (Square Y8)	Sediment	91.6 ± 8.1
Mad-3749	South sector (Square J3)	Sediment	74.5 ± 6.3

Fig. 3. a) Site map showing the four sectors defined for the excavated areas; b) stratigraphic section (I–I') and c) TL dates for the main levels. Modified from Pérez-González et al. (2010).

3.2. Anthracology

Small charcoal fragments (1–2 mm) were recovered after washing and sieving the sediment, as well as by manual flotation (2007 campaign). Anthracological sampling techniques have been standardized and integrated into the methodology for excavating caves and rock shelters across Iberia (Uzquiano, 1997; Badal et al., 2003). Charcoal fragments were manually fractured to provide transversal, tangential and radial sections, and were observed by reflected light microscopy using an OLYMPUS BX60 microscope with dark/bright field objectives. Botanical determinations made use of the Atlas Keys for Fresh Wood (Greguss, 1955; Jacquiot, 1955; Greguss, 1959; Jacquiot et al., 1973; Schweingruber, 1978, 1990) and the Charcoal Identification Guide (Vernet et al., 2001). The nomenclature employed was that of *Flora Europaea* (Tutin et al., 1964).

The North sector provided 318 charcoal fragments, of which 281 fragments came from Level 5; the Central sector yielded 62 and the South sector 47. The present study was therefore only based on the anthracological information provided by the North sector (Level 5).

Fig. 4. Detail of the large accumulation of long bones (at least 3 equid metapods are represented) characteristic of the Central sector of the site. Photograph taken during the 2009 campaign. Scale in centimetres.

3.3. Microvertebrates

Afer excavations were resumed in 2002, great care was taken to recover all the microvertebrate fossils given their importance as a source of biochronological data and their value as palaeoenvironmental indicators. In the excavated area of the site, 1 m × 1 m squares were opened and the soil was removed by natural levels. For each square and level, samples were divided vertically at intervals of 10 cm in order to detect possible variations in the small vertebrate assemblages within the levels. The sediment thus separated was freed from silt by water hosing the excavated soil in super-imposed 2 mm and 0.5 mm screens. Occasionally 1 cm sieves were added to retain larger-sized sediment particles (gravel or small boulders) and thereby prevent in situ breakage of small vertebrate remains. Water sieving of all the excavated sediment was conducted during the field campaigns. The resulting residues were sun-dried, packed and conveniently labelled.

Sorting of the fossils was done both during the field campaigns and later in the laboratory. For the larger-sized fraction of the residue, retained in the 2 mm sieve, the fossils were picked out directly with the naked eye, whereas the residue between 2 mm and 0.5 mm was sorted using Leica L2 binocular stereomicroscopes at 10× magnification. All the fossil bones and fragments in the samples were sorted, even when unidentifiable. Charcoal fragments, seeds and snail shells were also sorted.

The microvertebrate fossils have been studied using an Olympus SZX12 stereomicroscope provided with a drawing tube and an Olympus DP71 digital camera. For bones and teeth identification osteological keys and handbooks such as Bailon (1999), Blain (2005), Chaline (1972, 1974), Esteban and Sanchiz (1985, 1991), Holman (1998), Felten et al. (1973) and Sevilla (1988), among others, were used. The small vertebrate remains were identified with the aid of comparative material obtained from bird pellets and carnivore droppings collected in the vicinity of the site, as well as with comparative collections loaned by the Museo de Ciencias Naturales of Madrid (CSIC) and the Estación Biológica of Doñana (CSIC, Sevilla).

3.4. Human molar remains

Morphological features were scored according to the criteria defined by the Arizona State University Dental Anthropology System (ASUDAS) (Turner et al., 1991) and also considered some recently-described features which reliably distinguish Neanderthals from *Homo sapiens* (Bailey, 2004, 2006; Gómez-Robles et al., 2007). In addition to the mesiodistal (MD) and buccolingual (BL) crown dimensions, the crown and cusp base areas as well as the occlusal polygon (measured only in the M1) were measured following previously established protocols (Wood and Engleman, 1988; Bailey, 2004). The individual cusp outlines were traced in 2D digital photographs using the PhotoshopTM software program following the main cusp fissures on the occlusal surface of each tooth. The measured crown area (MCA) was calculated as the sum of the individual cusp base areas. The teeth were oriented so that the cervical margin was perpendicular to the axis of the camera lens and a scale was included in each photo for calibration purposes. Location of the cusp tips in the worn M1 (for establishing the occlusal polygon) was estimated at the center of the wear facet on each cusp. Comparative analysis focused on Late Pleistocene European fossils attributed to Neanderthals and *Homo sapiens*. To determine whether these two teeth represent the same individual, their degree of attrition was compared, and a regression analysis of the MD and BL diameters was made with molars of other Neanderthal individuals with both of these teeth preserved.

Both molars were also subjected to computed-tomography (CT) scanning using a YXLON Compact (YXLON International X-Ray GmbH, Hamburg, Germany) industrial multi-slice scanner at Burgos University, Spain to study the topography of the enamel-dentine junction in the M1. Specimens were aligned along the long axis with the occlusal surface upwards and the scans were collected at the maximum resolution obtainable (pixel size = 0.027 mm) which allowed the distinction of the interface between the enamel and dentine for the entirety of the cross-sectional slice data.

3.5. Taphonomical analysis

This study has gathered data from the material found between 2002 and 2009. A Nikon SMZ800 (Stereoscopic zoom microscope) has been used to examine surface modification on all bone fragments (Figs. 5 and 6).

Carnivore damage on the surface of bones is classified into pits, punctures, and scores. Crenulated edges, furrowing and evidences of corrosion of bone caused by stomach acid as carnivore modification (Haynes, 1980; Maguire et al., 1980; Binford, 1981;

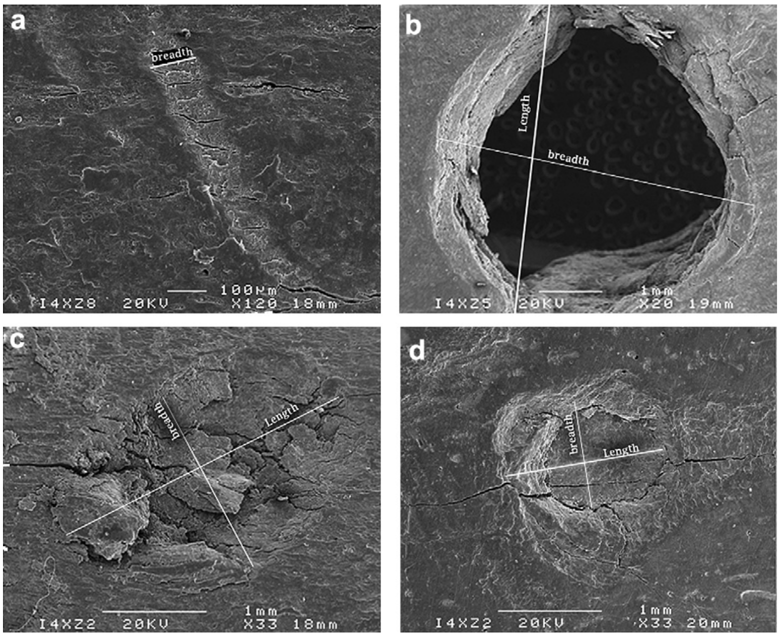


Fig. 5. Examples of SEM images of tooth marks (a: scores; b: punctures and c–d: pits) showing the measurements considered in this study.

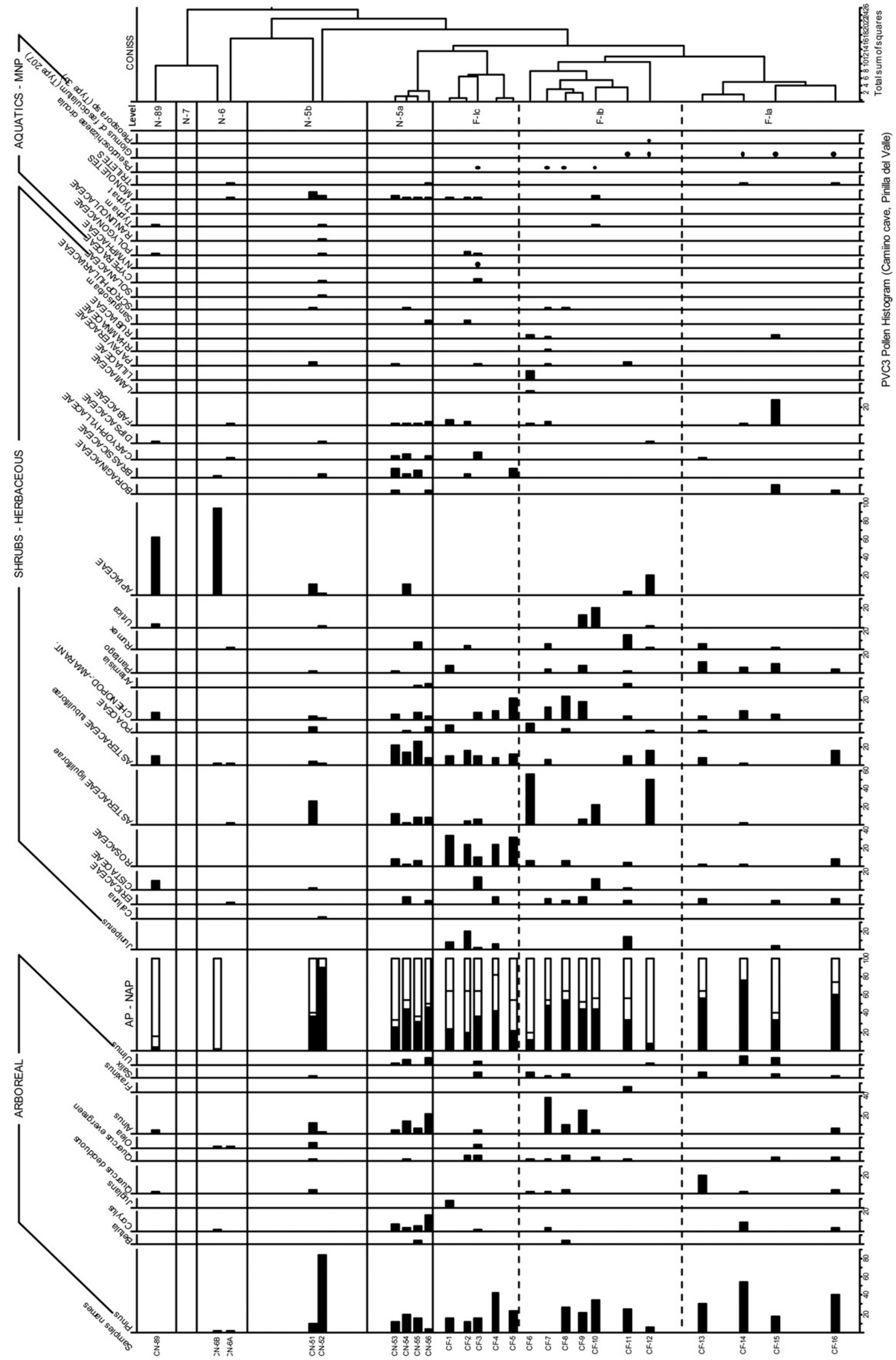


Fig. 6. Pollen histogram.

Table 1
Summary of the anthracological information obtained from the site's stratigraphic record (North sector).

Sector	North sector						Central & Diaclasa Roja sector		South sector
Level	4	5		6	7	8/9			
	N	*N*	%	*N*	*N*	*N*	*N*	%	*N*
Pinus sylvestris	5	226	80.42	8	2	12	35	56.45	
Betula sp.	2	17	6.04			5	3	4.83	
Quercus pyrenaica		1	0.35				11	17.74	26
Fraxinus angustifolia		1	0.35						
Salix-Populus		1	0.35						
Quercus ilex									5
Quercus sp.									2
Maloideae		3	1.06				4	6.45	
Indeterminables		32	11.38	1		2	9	14.51	14
Total	7	281		9	2	19	62		47

Haynes, 1983b) have also been considered. Tooth mark distribution in the bone portions is done following the methods of Selvaggio and Wilder (2001) Domínguez-Rodrigo and Piqueras (2003) and Delaney-Rivera et al. (2009). Conspicuous marks were measured in length and breadth (Fig. 5). Measurements were taken with an electronic caliper. For the identification of the carnivore species that acted on the assemblage, tooth marks have been measured and then compared to data published by Domínguez-Rodrigo and Piqueras (2003), Saladié et al. (2011) and Delaney-Rivera et al. (2009).

With the aim of identifying the process of breakage (green or dry bone fragmentation) all long bone fragments were analyzed following the criteria developed by Villa and Mahieu (1991), Bunn (1983), Haynes (1983a) and Lyman (1993, 1994). This method considers: the fracture location (following Lyman (1993, 1994)); the fracture outline (longitudinal, transverse and V-shaped); the angle formed by the fracture surface and the bone cortical surface (oblique, right or mixed); the characteristics of the fracture edges (jagged or smooth); shaft fragment length (1: shafts that are less than one-fourth the original length; 2: is a length comprised between one-fourth and one-half; 3: is between one-half and three-fourths; 4: is more than three-fourths, essentially a complete or almost complete shaft); and shaft circumference (1: bone circumference is less than half of the original; 2: circumference is more than half in at least a portion of the bone length and 3: complete circumference in at least a portion of the bone length).

To understand the origin of the accumulation of bone remains at the Cueva del Camino site taphonomic criteria proposed by previous authors were followed. Cruz-Uribe (1991) details some criteria for distinguishing bone assemblages accumulated by hominids from those produced by the activity of hyenas. These criteria are discussed by Pickering (2002) and Kuhn et al. (2010). The criteria used in this study are: Carnivore-ungulate ratio (MNI carnivores / MNI carnivores + MNI ungulates), bone modification and damage to bone surfaces, Bone breakage, Representation of small hard bones. Kuhn et al. (2010) suggest that of all the previously established and re-evaluated criteria, the only two that can truly differentiate between accumulations of hominids and hyenas do not form part of the criteria proposed by Cruz-Uribe or Pickering: the abundance of coprolites and/or 2) the presence of juvenile hyena remains.

4. Results

4.1. Cueva del Camino pollen data

The PVC3 pollen sequence from the N profile represents the following levels: Fluvial (F), Level 5 (N-5), Level 6 (N-6), Level 7 (N-7) and Level 8-9 (N-8/9). 38 terrestrial taxa were identified Fig. 6 including 11 trees, 5 shrubs and 22 herbaceous plants, as well as 6 aquatic taxa represented by monolete and trilete spores, and 3 non-pollen microfossils (NPMs). *Pinus* was the main regional element, accompanied in lesser proportions by evergreen and deciduous *Quercus* along with *Corylus* and Oleaceae. *Betula* was detected in certain samples. Riparian taxa (*Alnus*, *Salix* and *Ulmus*) were generally well represented. Ericaceae, *Juniperus*, Rosaceae and Cistaceae made up the company of shrubs, the role of which in the plant landscape was not very important. Asteraceae (Liguliflorae and tubuliflorae) were present, along with Chenopodiaceae and nitrophilous taxa such as *Plantago*, *Rumex* and *Urtica*, together being the most representative of herbaceous plants.

4.2. Anthracological analysis

An anthracological analysis was made of the entire excavated area of this site (i.e., the North, Central and South sectors). The north sector (Level 5) provided detailed information allowing correlations with the palynological and faunal results to be established. The charcoal assemblages showed *Pinus sylvestris-nigra* to be dominant (80%), followed by *Betula* and Maloideae in very small amounts (6% and <1% respectively). Scarce meso-hygrophilous elements were also recorded (*Quercus pyrenaica* type, *Fraxinus angustifolia*, *Salix-Populus*); these must have grown in sheltered conditions bearing in mind the topographic characteristics of the area (Table 1 and Fig. 7).

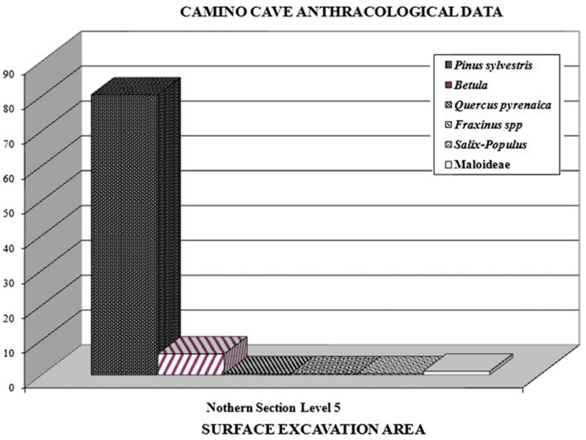


Fig. 7. Anthracological histogram showing the main woody species identified in the North sector (Level 5).

Table 2
Microvertebrates identified at the site. The data listed by Alférez et al. (1982) and Toni and Molero (1990) refer to excavations conducted in the 1980s. The right-hand column shows the species identified in the recent excavations (2002-2005 campaigns).

Alférez et al. (1982)	Toni and Molero (1990)	This paper	
Order Rodentia			
?Allocricetus bursae	*Allocricetus bursae*	*Allocricetus bursae*	Extinct hamster
Apodemus sylvaticus	*Apodemus sylvaticus*	*Apodemus sylvaticus*	Wood mouse
Arvicola aff. *sapidus*	*Arvicola sapidus*	*Arvicola sapidus*	Southern water vole
		Arvicola cf. *terrestris*	Water vole
Castor fiber	*Castor fiber*	*Castor fiber*	European beaver
		Chionomys nivalis	Snow vole
Eliomys quercinus	*Eliomys quercinus*	*Eliomys quercinus*	Garden dormouse
	Hystrix sp.	*Hystrix* cf. *brachyura*	Malayan porcupine
Microtus arvalis-agrestis	*Microtus agrestis*	*Microtus agrestis*	Filed vole
Microtus arvalis-agrestis	*Microtus arvalis*	*Microtus arvalis*	Common vole
Microtus brecciensis	*Microtus brecciensis*	*Microtus cabrerae*	Cabrera's vole
Pitimys cf. *savii* group	*Pitimys* cf *duodecimcost.*	*Microtus* gr. *duodecimcost.*	Mediterranean pine vole
	Microtus cf. *malei*	*Microtus* aff. *malei*	Male's vole
		Microtus cf. *vaufreyi*	Vaufrey's vole
Clethrionom. cf. *glareolus*	*Clethrionomys glareolus*	*Myodes* cf. *glareolus*	Bank vole
	Pliomys lenki	*Pliomys coronensis*	Brasov's vole
	Sciurus vulgaris	*Sciurus vulgaris*	Red squirrel
Order Lagomorpha			
Lepus sp.		*Lepus* sp.	Hare
Oryctolagus sp.		*Oryctolagus cuniculus*	Rabbit
Order Erinaceomorpha			
Erinaceus sp.		*Erinaceus europaeus*	Western hedgehog
		Erinaceus sp.	Hedgehog
Order Soricomorpha			
Crocidura cf. *russula*		*Crocidura russula*	Greater white-toothed shrew
Sorex araneus		*Sorex* gr. *araneus*	Common shrew
		Sorex minutus	Pygmy shrew
		Galemys pyrenaicus	Pyrenean desman
		Neomys fodiens/anomalus	Water shrew
Talpa cf. *caeca*		*Talpa europaea*	Common mole
		Talpa occidentalis	Iberian mole
Order Chiroptera			
Chiroptera indet.		*Rhinol. ferrumequinum*	Greater horseshoe bat
		Rhinolophus hipposideros	Lesser horseshoe bat
		Myotis myotis/oxygnathus	Mouse-eared bat
		Myotis nattereri	Natterer's bat
		Plecotus auritus/austriacus	Long-eared bat
Order Anura			
Discoglossidae indet.		*Alytes* cf. *obstetricans*	Common midwife toad
		Pelobates cultripes	Western spadefoot
Bufo bufo		*Bufo bufo*	Common European toad
Bufo calamita		*Bufo calamita*	Natterjack toad
		Hyla meridionalis	Stripeless treefrog
		Rana cf. *iberica*	Iberian frog
		Pelophylax perezi	Southern marsh frog
Order Chelonia			
Testudo sp.		*Testudo hermanni*	Hermann's tortoise
Emydidae indet.			
Order Squamata			
Lacerta sp.		*Timon lepidus*	Ocellated lizard
		Lacertidae indet.	"Small-sized lizards"
		Anguis fragilis	Slow worm
Order Serpentes			
Colubridae indet.		*Natrix maura*	Viperine snake
		Natrix natrix	Grass snake
		Coronella cf. *austriaca*	Smooth snake
		Coronella cf. *girondica*	Southern smooth snake
		Malpolon monspessulanus	Montpellier snake
		Rhinechis scalaris	Ladder snake
		Vipera latasti	Lataste's viper

These results reflect a flora with montane affinities (the altitude of the site is 1114 m), with pine the most abundant taxon in the surroundings, including the calcareous slopes where the Cueva del Camino cave opens. The appearance of other taxa is related to topographic compartmentalisation of the territory where calcareous southern exposures (with pine) alternate with more humid siliceous slopes (with birch and deciduous oaks) and valleys bottom providing shelter for meso-hygrophilous elements (ash, willow /poplar).

The pollen data for the same section and level also record abundant *Pinus* located at some distance, as revealed by palynomorphological inspection. Nevertheless, the anthracological results confirm the local presence and abundance of *Pinus* on the calcareous southern slope of the El Calvero de la Higuera area.

4.3. *Faunal assemblage*

4.3.1. *Microvertebrate record*

Alférez et al. (1982) and Toni and Molero (1990) provide lists of the small vertebrates (several amphibian and reptile species, together with a wide range of micromammals) collected at the site during the 1980s, as well as a description of the rodent species found. However, no reference to any particular level is given. Among the micromammals, rodent remains stand out in terms of species richness (14 species). Four insectivore species and two lagomorphs were also recognised, as well as some unidentified species of chiroptera. On the basis of certain taxa (e.g., a small-sized porcupine, among others), the association was placed within a warm phase of either the late Riss or the Riss-Würm interglacial period.

At least 51 species of small vertebrates are now recognised (Table 2) including 33 small mammals, 7 amphibians and 11 reptiles (Laplana and Sevilla, 2006; Arsuaga et al., 2010). The reptiles and amphibians show a relatively large increase in the number of recognised species since the earlier lists. Over 90% of the microfaunal remains analysed came from the North and Central sectors. With respect to the north sector, the great majority came from Level 5.

The rodents remain the best represented group of small mammals, with three new species added to the list: *Arvicola* cf. *terrestris*, *Chionomys nivalis* and *Microtus* cf. *vaufreyi*. Other changes with respect to earlier fauna lists include the reassignment of *M. brecciensis* to *Microtus* (*Iberomys*) *cabrerae* since the abundant material obtained in recent campaigns more closely resembles the latter species. Taxonomic revisions since the first lists are also responsible for certain changes. For example, *Pliomys coronensis* has replaced *P. lenki*, and *Clethrionomys* has been changed to *Myodes* following more recent and now generally accepted criteria (Kowalski, 2001; Wilson and Reeder, 2005).

Microvertebrate remains are present in all levels and areas of the site, although richness differs from one area to another. The fluviatile beds at the base contain very few microvertebrate bones (just a few, isolated remains of *Apodemus* sp. and *Microtus* sp.). Most of the microvertebrate material comes from Levels 5 to 9 in the north sector, and from the central and south sectors.

Though the majority of the microvertebrate species are represented in every sector of the site, some important exceptions exist. Thus, Male's vole (*M.* aff. *malei*) is only represented in the north sector, and although the Cabrera vole (*M. cabrerae*) and the hamster (*Allocricetus bursae*) are frequent in the north sector their frequencies fall in the central sector, and reach zero in the south sector. These area-dependent differences in the rodent assemblage are probably related to slight differences in the age of the sediments, an explanation analysed in a forthcoming paper.

Remains previously identified as *M. oeconomus* and included in a faunal list built with the material from the recent excavations at Cueva del Camino (Laplana and Sevilla, 2006) have been reassigned to *M.* aff. *malei*. The molar morphology of these species is very similar, to the extent that some authors refer to the fossil material as *M. oeconomus-malei* (Pemán, 1985; Sesé, 2006). According to the diagnostic criteria of Nadachowski (1990, 1991), in particular the more common development of the T6 triangle and the higher values of the A/L index in *M. malei*, the first lower molars found at Cueva del Camino are closer to those of this species than to those of *M. oeconomus*. However, the "*nivalis*" morphotypes, frequent in typical *M. malei*, are absent in the samples. Thus, the material from Cueva del Camino is referred to as *M.* aff. *malei*. This taxon seems to have had a wider thermal tolerance range than *M. oeconomus*, given that it was a common species at the beginning of the British Late Pleistocene (Nadachowski, 1991), a period characterized by a warmer climate.

4.3.2. Macrovertebrate record

The Cueva del Camino site has provided an important mammal collection including two human finds. In the present work, only the remains found during the 2002–2009 field seasons are included. Among the ungulates, six Artiodactyla species have been identified (*Dama dama*, *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, *Rupicapra rupicapra*, *Sus scrofa*), along with two Perissodactyla species (*Equus ferus* and *Stephanorhinus hemitoechus*). The carnivore assemblage is composed of the following species: *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Mustela putorius*, *Mustela nivalis*, *Crocuta crocuta*, *Lynx* cf. *pardinus*, *Felis silvestris*, *Panthera leo*, Felidae indet. (*Panthera pardus* size). Level 5, from where this assemblage comes, have been dated by TL to 90,961 ± 7881 (MIS 5) (Arsuaga et al., 2010; Pérez-González et al., 2010) (Fig. 8).

The spotted hyena is represented at Cueva del Camino by adult and immature individuals (minimum number of individuals [MNI]: juveniles = 3; MNI adults = 3), (Fig. 9). The remains of the juveniles consist of milk teeth and tooth germs, while the adult group is represented by permanent teeth showing advanced stages of wear. Compared to a modern *Crocuta crocuta* specimen and some specimens of *Crocuta crocuta spelaea* from the Late Pleistocene, the only complete upper carnassial (P^4) found at Cueva del Camino is proportionally broader compared to its length. However it does not differ significantly and no further interpretations can be made.

A few dental and postcranial remains of *U. arctos* have been recovered. The analyses of the dental material suggest a typical arctoid model, the size of which falls among the highest values for modern Iberian brown bears. The dental remains of *Canis lupus* and *Vulpes vulpes* represent one adult specimen each. The dimensions are in both cases comparable to those of modern wolves and foxes. Two adult phalanges (MNI = 1) of *Panthera leo* have also been recovered. Compared to the phalanges of the large Middle Pleistocene lions arriving in Europe (García, 2003), the Cueva del Camino specimens are considerably smaller. However, they are larger than those of modern lions, in agreement with the size reduction seen from the Middle to the Late Pleistocene. A single remain (a phalange) of a medium-sized felid has been attributed to *Panthera* sp, probably a leopard. Based on size, this fossil also could be attributed to a jaguar (*P. gombaszoegensis*), although the chronological range of this species is earlier. In any event, the specimen can at least be assigned to this genus. A very small number of diagnostic remains of *Lynx pardinus*, *Felis silvestris*, *Mustela putorius* and *Mustela nivalis* show that these small felid species and mustelids were present in the Cueva del Camino area.

Fallow deer (MNI = 26) are highly predominant at the site, making up 52.5% of all ungulates. Buitrago Villaplana (1992) classified these fossils as *Dama clactoniana*. However, Made (2001) assigned the remains to *Dama dama geiselana*, based on the size of the teeth. The present data support Made's assignment. *Cervus elaphus* (MNI = 7) is the second most abundant species among the ungulates, accounting for 8.2% of the total remains. Teeth and antler fragments are the most common elements. *Capreolus capreolus* is the rarest among the Cervidae (MNI = 1). *Bos primigenius* (MNI = 4) represents some 5.6% of the ungulates. Teeth, carpal, tarsal and metapodial remains are the most abundant elements. *Rupicapra rupicapra* is represented by an isolated dental element but its presence provides interesting environmental information pointing to the presence of alpine fauna in the surroundings of the cave. *Sus scrofa* (MNI = 2) is also scanty in the assemblage with only 1.9% of the total ungulate remains. *Equus ferus* (MNI = 4) represents 7.4% of the ungulates. Cranial and postcranial dimensions together with dental morphological traits show these remains belong to *Equus ferus*. The rhinoceros (MNI = 2) represents a small percentage (1.4%) of the ungulates. Although the rhinoceros

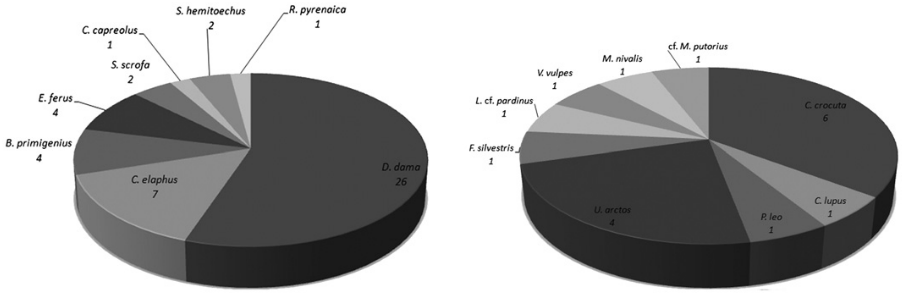


Fig. 8. MNI of ungulates (left) and carnivores (right) of the site.

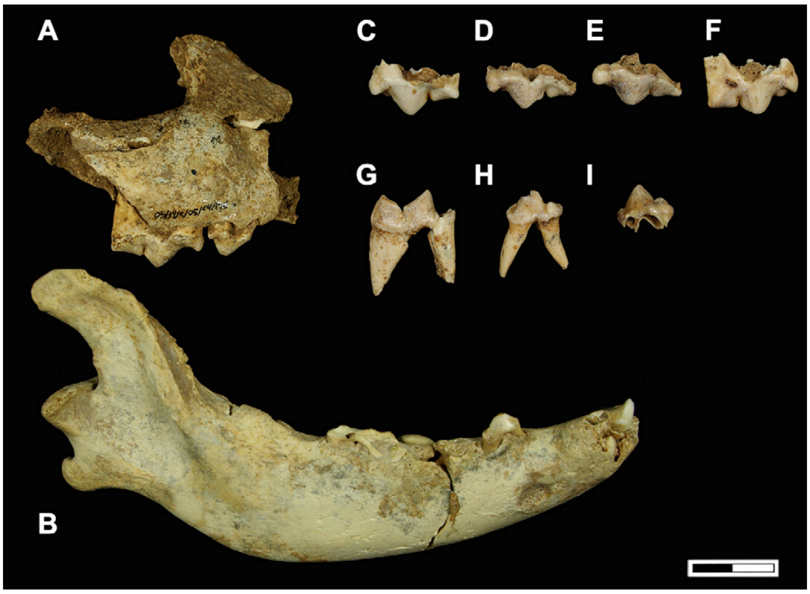


Fig. 9. Cranial remains and dentition of *Crocuta crocuta* juveniles. A) Fragment of a right maxilla with dP^3 and dP^2 (05/34/C/05/C4/146); B) Right hemimandible with dP_4, dP_3 and dC_0 (04/20/C/Z8/5/91); C) left dP^3 (03/35/C/X7/05/41); D) left dP^3 (03/35/C/B5/05/205); E) left dP^3 (03/35/C/A5/06/1); F) right dP^3 (03/35/C/B5/05/103) G) left dP_4 (03/35/B5/05/227); H) right dP_3 (03/35/C/B5/05/236); I) right dP_3 (germ) (03/35/C/X7/05/15). Scale = 2 cm.

fossils are mostly fragmentary teeth, the morphology and dimensions are diagnostic of *Stephanorhinus hemitoechus*.

4.4. *Human remains*

During the 1982 field season, a right M^1 was recovered from square D-3. Subsequently, during the 1984 field season, a right M^3 was recovered from square A-3 at a depth of 124 cm below datum. Human teeth have previously been reported from Cueva del Camino (Alférez et al., 1982; Alférez and Roldán, 1992) and have been examined in several comparative dental morphology studies (Gómez-Robles et al., 2007; Martinón-Torres et al., 2007, 2008; Quam et al., 2009). These teeth are described below and their taxonomic affinities highlighted.

4.4.1. *Right M^1 (Figs 10–12)*

The right M^1 has four main cusps preserved. Slight damage to the crown surface is present along the mesial border, and wear (Grade 4; Smith, 1984) has resulted in exposure of the dentine at all four cusp tips. This wear is greater on the lingual cusps, particularly the protocone (which has essentially been worn flat) than on the buccal cusps. The mesial interproximal facet is wider (5.3 mm) and taller (2.3 mm) than is the distal (2.6 mm in height), which is limited to the upper portion of the distal enamel face, just below the level of the occlusal surface. Root formation is complete (Ac calcification stage), indicating that the tooth is fully formed. Modern human standards suggest a minimum age at death of 9.2–10.1 years (Anderson et al., 1976).

Two small areas on the distal face at the junction of the metacone and hypocone and on the hypocone might be interpreted as mild evidence of hypoplasia; here, the enamel appears thinner than on the surrounding tooth surface. There is evidence of alteration of the enamel surface on the mesial and buccal faces of the paracone as well as the distal and lingual faces of the hypocone. These alterations represent slight erosions in the form of grooves and pockmarks. The grooves, which show no predominant orientation, extend to the roots in some areas and even cross the cervicoenamel junction. This random pattern of distribution suggests they are the result of post depositional taphonomic processes.

The hypocone is well developed (ASUDAS Grade 4), but no metaconule (ASUDAS Grade 0) or Carabelli's structure (ASUDAS

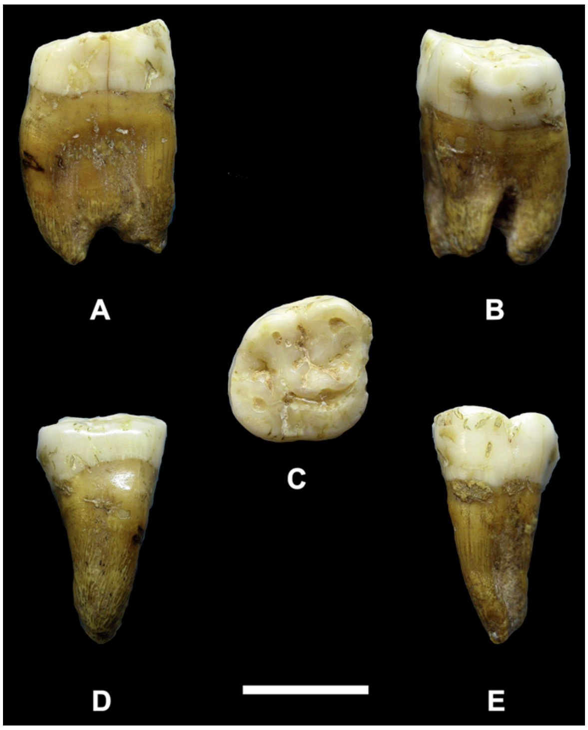


Fig. 10. The Cueva del Camino M^1 in mesial (A), distal (B), occlusal (C), buccal (D) and lingual (E) view. Scale = 1 cm.

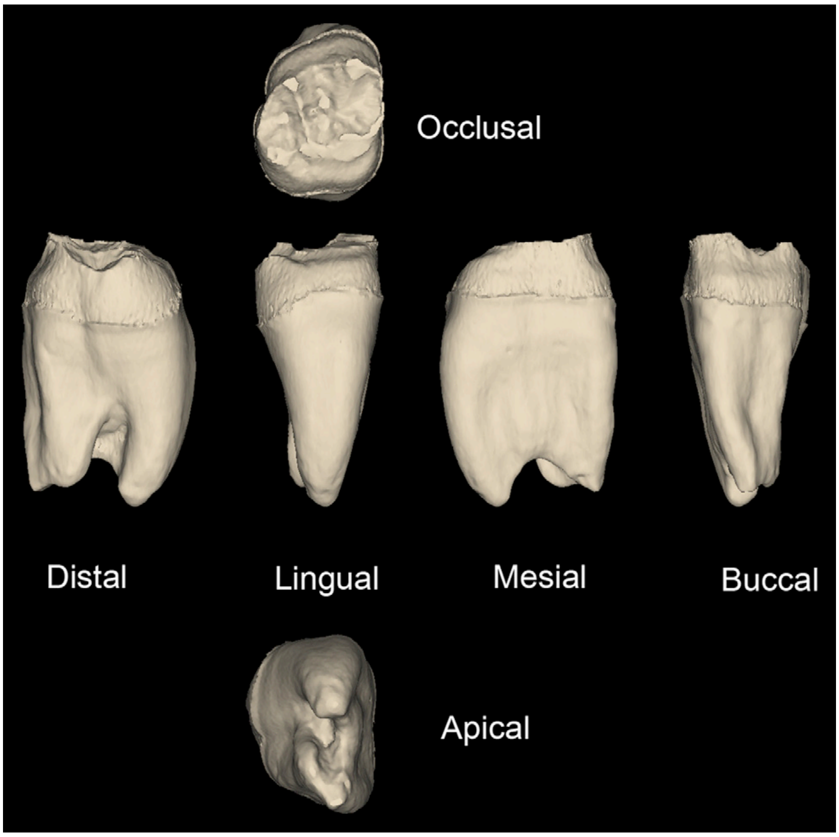


Fig. 11. Virtual reconstruction of the Cueva del Camino M^1 showing the topography of the enamel dentine junction. Note the absence of both a metaconule and any trace of a Carabelli's structure.

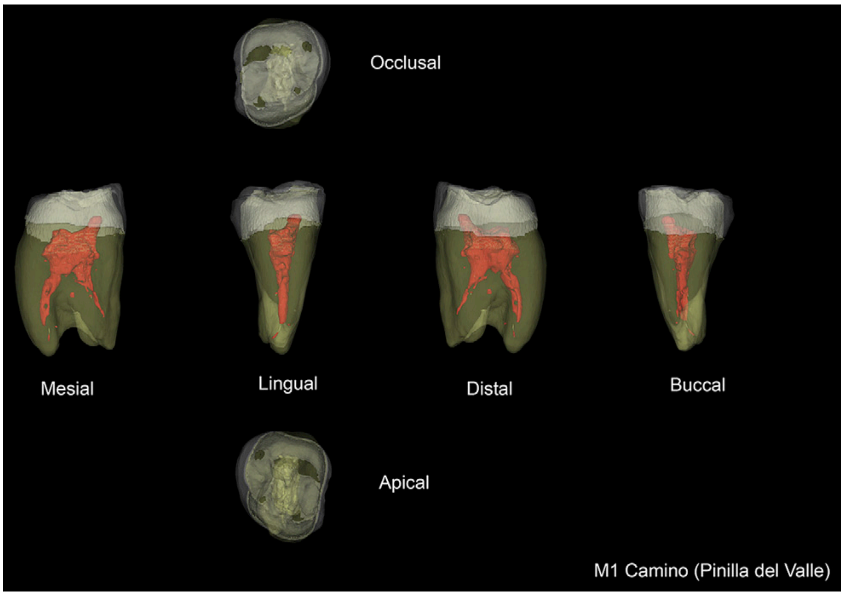


Fig. 12. Virtual reconstruction of M^1 showing the enamel (white), dentine (green) and pulp chamber (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Dimensions of the two human teeth recovered at the site compared with the teeth of Upper Pleistocene and recent humans.

Specimen/sample	Tooth	MD (mm) Mean ± s.d. (*n*) (range)	BL (mm) mean ± s.d. (*n*) (range)	Measured crown area (mm^2) mean ± s.d. (*n*)	Source
Pinilla del Valle	M^1	12.0	12.0	111.1	Present study
Neandertals		11.1 ± 0.8 (22)	11.9 ± 0.4 (22)	112.3 ± 16.6 (21)	Bermúdez de Castro (1993), Quam et al. (2009)
UP *H. sapiens*		10.7 ± 0.8 (24)	12.3 ± 0.7 (24)	99.6 ± 10.2 (15)	Frayer (1977), Quam et al. (2009)
Contemporary *H. sapiens*		9.7 ± 0.9 (57)	10.8 ± 1.1 (64)	96.6 ± 14.0 (59)	Manzi et al. (1997), Quam et al. (2009)
Pinilla del Valle	M^3	8.4	11.5		Present study
Neandertals		9.6 ± 0.7 (16)	12.0 ± 1.0 (16)		Bermúdez de Castro (1993)
UP *H. sapiens*		9.5 ± 1.0 (12)	11.1 ± 1.2 (14)		Frayer (1977)
Contemporary *H. sapiens*		8.2 ± 0.9 (49)	10.3 ± 1.4 (49)		Manzi et al. (1997)

Grade 0) is present either on the crown surface Fig. 10 or the enamel-dentine junction Fig. 11. The roots are short (lingual root length = 15.5 mm) and stout, and there is a considerable fusion of the three original roots. The mesiobuccal and distobuccal roots are fully fused, while the lingual root has a separate apex and is separated from the other roots for at least the last 6.1 mm of its length Fig. 12. Thus, some degree of taurodontism is present.

The large MD dimension (12.0 mm) of the Cueva del Camino M^1 (Table 3) is just over one standard deviation above the Neanderthal mean, while the BL dimension (12.0 mm) is similar to that recorded for both Neanderthals and Upper Palaeolithic *H. sapiens* specimens. The measured crown area (MCA; 111.1 mm^2) is very similar to the Neanderthal mean value.

The relative occlusal polygon area (25.3) falls within one standard deviation below the Neanderthal mean (Table 4), but is clearly outside the range of variation reported in both fossil and contemporary *H. sapiens* samples.

With respect to the relative cusp base areas, the Cueva del Camino M^1 also shows the reduced metacone commonly seen in Neanderthal specimens (Bailey, 2004). Finally, the angles of the occlusal polygon, centred on the main cusp tips, compare most favourably those reported for Neanderthals (Bailey, 2004) particularly in the most diagnostic of these (Angle C) centred on the metacone.

4.4.2. Right M^3 (Figs. 13 and 14)

The right M^3shows little tooth wear and no mesial interproximal contact facet, although the root formation is complete (Ac formation stage). This indicates the tooth had completed its formation and suggests a minimum age at death of 18.2–18.8 years by modern human standards (Anderson et al., 1976). In contrast to the M^1, numerous localized hypoplastic defects can be seen on the buccal and distal faces of the enamel surface (Fig. 13). The crown outline shows two small chips on the paracone, one on the buccal side and one on the mesial side. The paracone and (extremely reduced) metacone are intact, but the crown shows some damage, with most of the protocone and the mesial portion of the hypocone missing. This fracture extends downwards to involve the cervical half of the lingual root, although the root chamber is not exposed. This fracture is argued to be premortem and to represent a localized trauma produced by a hard object travelling at high speed (Alférez and Roldán, 1992).

In distal view, the root appears to show two separate buccal and lingual components, but radiographic analysis suggested the presence of only a single pulp chamber (Alférez and Roldán, 1992). This has been confirmed through CT analysis, and the roots are fully fused (Fig. 14). Thus, like the M^1, the M^3 is also characterized by taurodontism. The root length is 13.6 mm in mesial view. Just below the cervico-enamel junction on the mesial face, there is a shallow groove running in the BL direction consistent with a toothpick groove.

The degree of dental wear in both molars is compatible with their belonging to the same young adult individual. The comparison of the MD and BL dimensions of M^1 and M^3 revealed a modest positive correlation for MD ($r = 0.54$), but a stronger positive correlation ($r = 0.74$) for BL. The Camino teeth fall very close to the BL Neanderthal regression line Fig. 15 and the evidence is consistent with their belonging to the same individual.

4.5. Taphonomy and the origin of accumulation

The present work, mostly examines the material found between 2002 and 2009, from all levels and all sectors of the site. To understand the origin of the accumulation of bone remains at the Cueva del Camino site taphonomic criteria proposed by previous authors were followed. The criteria used in this study are discussed below.

4.5.1. Carnivore-ungulate ratio (MNI carnivores/MNI carnivores + MNI ungulates)

According to Cruz-Uribe (1991), the percentage of carnivore remains in hyena assemblages is always at least 20% of the total,

Table 4
M^1 occlusal polygon, cusp base areas and cusp angles in the recovered teeth and those of contemporary humans.

Specimen/ sample[a]	Relative occlusal polygon mean ± s.d. (*n*) (range)	Relative protocone area mean ± s.d. (*n*) (range)	Relative paracone area mean ± s.d. (*n*) (range)	Relative metacone area mean ± s.d. (*n*) (range)	Relative hypocone area mean ± s.d. (*n*) (range)	Angle A (deg.) mean ± s.d. (*n*) (range)	Angle B (deg.) mean ± s.d. (*n*) (range)	Angle C (deg.) mean ± s.d. (*n*) (range)	Angle D (deg.) mean ± s.d. (*n*) (range)
Pinilla del Valle	25.3	34.6	27.1	17.1	21.2	102.8	68.1	118.7	71.1
Neandertals	26.7 ± 1.8 (17) (23.2–30.5)	29.7 ± 2.4 (18)	25.4 ± 2.1 (18)	21.0 ± 1.5 (18)	23.8 ± 2.2 (18)	106.1 ± 5.2 (17) (98.5–115.7)	66.7 ± 6.7 (17) (53.9–76.8)	118.0 ± 10.0 (17) (98.0–137.5)	69.0 ± 6.1 (17) (53.3–80.8)
Upper Paleolithic *H. sapiens*	32.7 ± 1.9 (5) (28.6–33.5)	31.8 ± 1.7 (12)	25.8 ± 2.7 (12)	23.0 ± 1.6 (18)	19.5 ± 3.1 (12)	106.3 ± 4.4 (5) (100.8–110.6)	71.1 ± 2.7 (5) (67.6–73.3)	110.3 ± 4.9 (5) (100.3–112.9)	73.3 ± 4.8 (5) (68.8–80.8)
Contemporary *H. sapiens*	37.5 ± 5.4 (24) (27.0–50.4)	30.1 ± 2.0 (59)	25.8 ± 2.1 (59)	22.9 ± 1.8 (59)	20.5 ± 2.5 (59)	101.4 ± 10.1 (24) (80.3–128.3)	74.3 ± 4.0 (24) (62.9–79.0)	106.2 ± 5.5 (24) (95.5–115.7)	78.6 ± 7.7 (24) (59.0–90.2)

Relative occlusal polygon area = Absolute occlusal polygon area/MCA.
Relative cusp areas = Absolute cusp areas/MCA.
[a] Comparative data from Bailey et al. (2008).

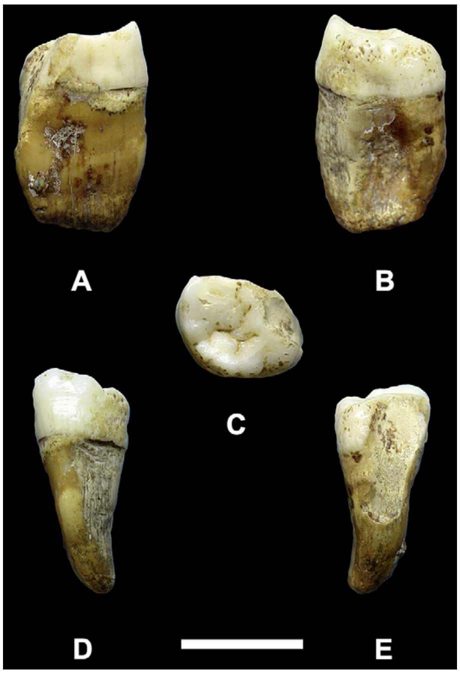


Fig. 13. The Cueva del Camino M^3 in mesial (A), distal (B), occlusal (C), buccal (D) and lingual (E) view. Scale = 1 cm.

whereas in archaeological assemblages carnivores always make up less than 13% of the total carnivore plus ungulate MNI (Klein and Cruz-Uribe, 1984). At the Cueva del Camino site the carnivore-ungulate ratio is 27.7%.

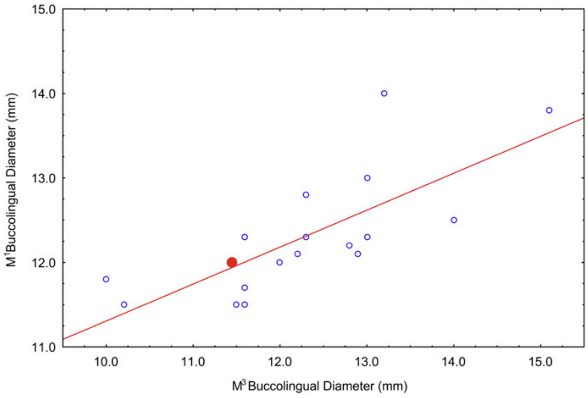


Fig. 15. Relationship between the BL diameters of Neanderthal M^1 and M^3 teeth. Regression line: $y = 6.935 + 0.437(x)$. $r = 0.7449$; $p < 0.001$; $r^2 = 0.5549$. Neanderthal sample: Axlor (Basabe, 1973); La Quina 5 (JMBC pers. Com.); Le Moustier (Bilsborourgh and Thompson, 2005); Saccopastore 2 (Lumley, 1973); Shanidar (Trinkaus, 1983); Spy (Lumley, 1973); Tabun (Lumley, 1973).

4.5.2. *Bone modification and damage to bone surfaces*

After conducting the taphonomic study on the bone collection at the deposit, marks from carnivore activity were estimated to be the most abundant alterations in all sectors and levels of the site (Fig. 16 and Table 5). Thus, 55.9% of the material analysed shows modifications allocated to carnivore activity. As can be seen in Table 5, the most characteristic marks both in the North (level 5) and Central Sectors are scores and pitting. In general, there are very few punctures and furrowing is well represented, particularly in the epiphyses of long and large-sized bones, compact bones and flat bones. Another modification typical of carnivores is the evidence of disintegration due to gastric acids. At the Cueva del Camino site, 4.91% of the total sample analysed have been found with clear evidence that they were digested. According to Cruz-Uribe (1991), damage is seen

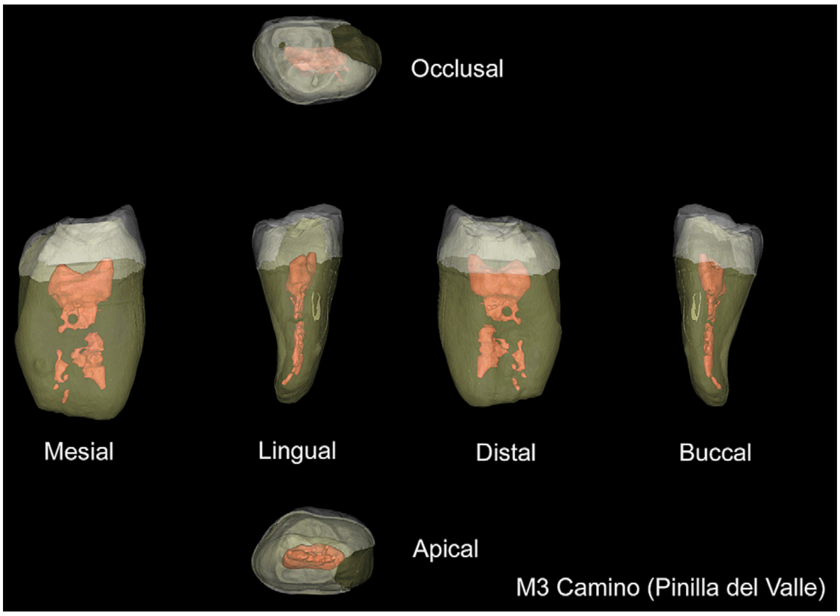


Fig. 14. Virtual reconstruction of M^3 showing the enamel (white), dentine (green) and pulp chamber (red).

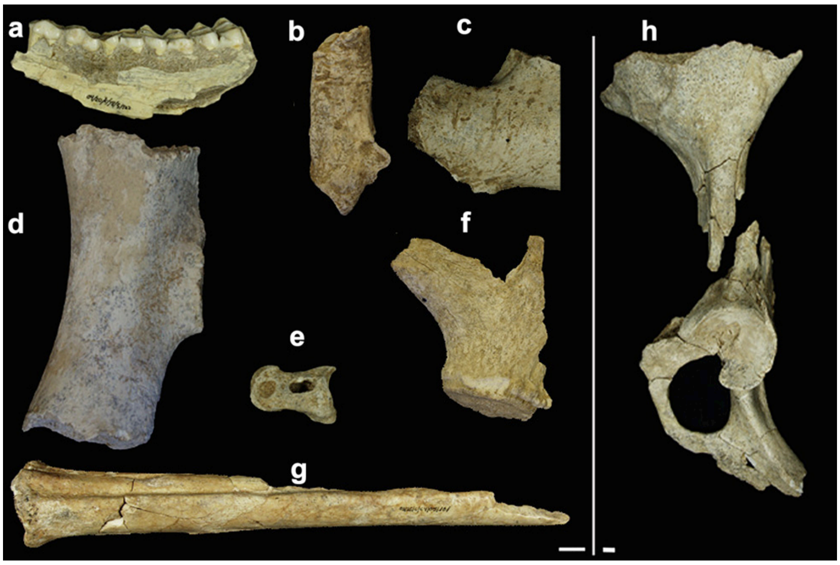


Fig. 16. Carnivore-made marks on some bone remains from the site. a) Left mandible of *Dama dama* (04/20/C/Y8/5/122) showing crenulated edges. b) Right calcaneum of *Dama dama* (06/37/C/05/B3/12): note the pitting and scoring. c) *Equus ferus* innominate fragment (05/34/C/05/C4/49) showing pitting and scoring. d) *Equus ferus* femur (04/20/C/Z8/5/24) with a "cylinder shape" and crenulated edges. e) Medial phalange of *Cervus elaphus* (03/35/CA4/05/29) showing a puncture. f) Left antler of *Dama dama* (05/34/C/05/B4/101) with gnaw marks. g) Right metatarsal of red deer (03/35/C/C4/05/101). h) Left innominate of *Equus ferus* (06/37/C/05/C4/74). Scale = 1 cm.

on at least 50% of bones in modern assemblages, but much less is seen in fossil assemblages. Kuhn et al. (2010) report an average 39.2% of bones to be damaged in the ancient hyena dens they studied. Metric data on the tooth marks are summarised in Table 6.

4.5.3. *Bone breakage*

Of the remains analysed, 6.5% of the sample, were complete bones, with no fractures. Thus, over 93% of the bone samples had fractures. Of the fractured remains, 21.0% corresponded to unidentifiable bone splinter fragments. For bone fragments that could be identified, at least for the size of the ungulate, the fracturing characteristics were established as depicted in Table 7.

As can be seen in Table 7, the oblique orientation of the fractures is dominant in both weight sizes, where longitudinal and transversal fractures are similarly represented. With regard to the fracture angle, there is a predominance of fractures with oblique and mixed angles. The properties of the fracture edges in the majority of cases are characterised by being smooth, with a high percentage of crenulated edges in the sample. When quantifying the fracturing patterns of the long bones for diaphyseal lengths and circumferences (Table 7), the majority of the sample is represented by diaphyses with complete circumferences and incomplete diaphyseal lengths Fig. 17. According to Cruz-Uribe (1991), hyena accumulations are characterised by many bone cylinders, while hominid collections have more broken shafts and complete epiphyses. Broken shafts alone are not diagnostic of hominid or hyena collections. Both Cruz-Uribe (1991) and Pickering (2002) indicate that hyena accumulations show an abundance of cylinder-type fragments. According to Kuhn et al. (2010), the presence of cylinders is indicative of carnivore activity, but not specifically of hyena activity.

Table 5
Tooth mark frequencies of in the Cueva del Camino assemblage according to the distribution in the bone portions, geological unit and ungulate size. PE: Proximal Epiphysis; DE: Distal Epiphysis; DPH: Diaphysis.

	Long bones			Flat bones		Articular bones
	PE	DPH	DE	Cortical	Cancellous	Dense cortical
Central sector						
Big-sized ungulate						
Pits	5.13	53.85	2.56	40.00	20.00	45.45
Scores	10.26	48.72	10.26	40.00	20.00	27.27
Punctures	0.00	2.56	0.00	0.00	0.00	9.09
Furrowing	5.13	5.13	2.56	0.00	50.00	36.36
Middle-sized ungulate						
Pits	0.00	52.00	2.00	0.00	0.00	27.27
Scores	2.00	36.00	2.00	33.33	0.00	36.36
Punctures	0.00	0.00	0.00	11.11	0.00	0.00
Furrowing	0.00	4.00	2.00	0.00	0.00	27.27
North Sector (Level 5)						
Big-sized ungulate						
Pits	3.03	24.24	3.03	54.55	18.18	19.05
Scores	9.09	39.39	3.03	36.36	18.18	9.52
Punctures	3.03	6.06	0.00	9.09	0.00	0.00
Furrowing	9.09	15.15	3.03	9.09	9.09	4.76
Middle-sized ungulate						
Pits	1.20	37.95	4.82	28.85	3.85	4.88
Scores	0.60	32.53	3.01	26.92	1.92	19.51
Punctures	1.20	3.01	1.20	9.62	1.92	9.76
Furrowing	0.00	4.82	0.60	7.69	1.92	2.44

Table 6
Statistical values of pits, punctures and scores analyzed in the sample of the Cueva del Camino assemblage. The data displayed in the table show length and width in dense cortical (*n*: number of cases; Max: maximum value; Min: minimum value; C.I.: Confidence Interval for mean and St. Dev.: Standard Deviation).

		n	Mean	Min	Max	St. Dev.	IC −95%	IC +95%	CV
Pits	Length	14	2.29	1.61	3.21	0.49	2.01	2.58	21.55
	Width	14	1.86	1.13	2.85	0.47	1.60	2.13	24.95
Punctures	Length	11	3.36	2.00	4.50	0.94	2.73	3.99	27.94
	Width	7	2.77	1.72	4.32	0.96	1.88	3.66	34.72
Scores	Width	12	1.75	0.93	3.35	0.78	1.25	2.24	44.39

Table 7
Fracture properties in Cueva del Camino assemblage. *Long bones only.

		Big-sized ungulates	Middle-sized ungulates
Fracture outline	Longitudinal	7.14	6.00
	Transversal	9.52	6.67
	Curved	83.33	87.33
Fracture angle	Oblique	64.71	78.57
	Right	11.76	16.07
	Mixed	23.53	5.36
Edges	Smooth	46.15	60.94
	Jagged	35.90	15.63
	Crenulated	17.95	23.44
Shaft circunference[a]	<1/2	22.58	32.69
	>1/2	12.90	25.00
	Complete	64.52	42.31
Shaft fragment[a]	<1/4	54.84	46.15
	1/4–1/2	6.45	30.77
	1/2–3/4	29.03	21.15
	>3/4	9.68	1.92

[a] Long bones only.

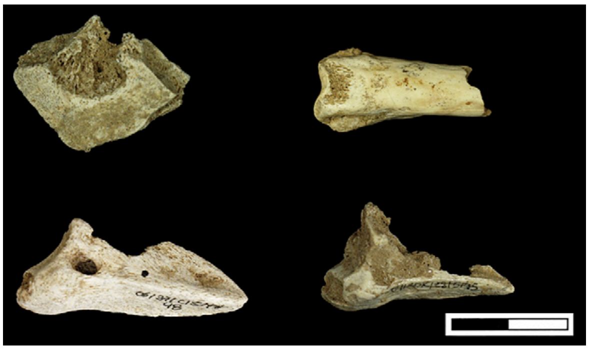


Fig. 18. Small hard bones digested. Scale = 1 cm.

4.5.4. *Representation of small hard bones*

At the Cueva del Camino site there are 139 small, high-density bones, including carpals and tarsals (excluding the astragalus and calcaneum), sesamoids and phalanges – 4.4% of the total. Cruz-Uribe (1991) indicates that elements such as sesamoids, small tarsal bones, carpal bones and phalanges are present only in small numbers in accumulations produced by hyena activity, since these animals tend to eat them. Pickering (2002) supports the idea that these bone elements usually appear, but in a digested form. Fig. 18 shows some small, hard, digested bones from the Cueva del Camino site. For Kuhn et al. (2010) these elements can be present in the range of 0–23% of the total MNI for postcranial remains at hyena dens.

The study by Kuhn et al. (2010) suggests that of all the previously established and re-evaluated criteria, the only two that can truly differentiate between accumulations of hominids and hyenas do not form part of the criteria proposed by Cruz-Uribe or Pickering: the abundance of coprolites and/or 2) the presence of juvenile hyena remains.

4.5.5. *Presence of hyena coprolites*

Coprolites are found both inside and outside hyena dens (Sutcliffe, 1970; Kruuk, 1972). However, at the Cueva del Camino site, only six hyena coprolites – all very fragmentary – have been

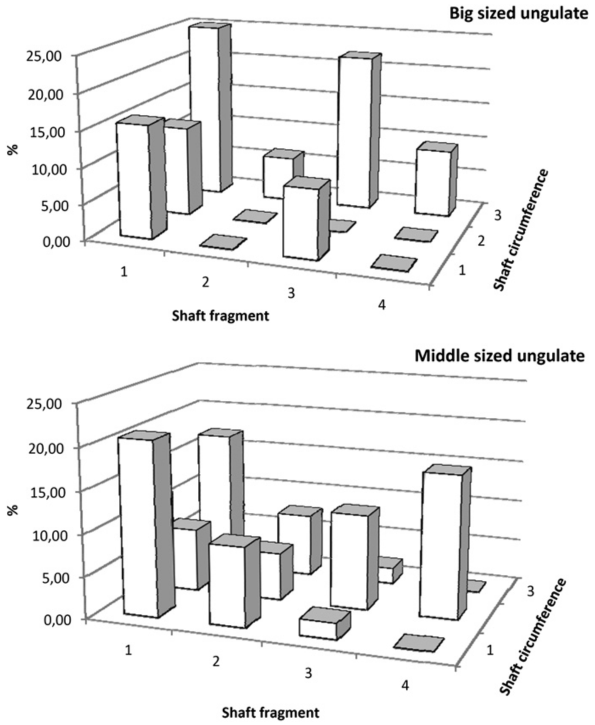


Fig. 17. Three-dimensional bar diagrams showing relative frequencies of shaft fragment by shaft circumference in big sized (superior image) and medium sized ungulates (inferior image). *Shaft length* categories are: 1: <¼ of the original length; 2: ¼ to ½; 3: ½ to $^{3}/_{4}$ and 4: >$^{3}/_{4}$ or complete. *Shaft circumference* categories are: 1: bone circumference is less than half of the original; 2: circumference is more than half, and 3: complete circumference in at least a portion of the bone length.

Table 8
Number of lithic artefacts from the different sectors and levels of the site.

Sector	North sector							Central
Level	3	3–4	4	5	7	8	8–9	5
NR	11	32	6	52	1	1	1	1

recorded. They are insufficient in number to be diagnostic of a hyena den.

4.5.6. *Presence of juvenile hyena*

Deciduous hyena teeth are good indicators of the use of a den by cubs (Villa et al., 2010). The juvenile remains recorded consisted of milk teeth and tooth germs. An MNI of 3 has been estimated for *Crocuta crocuta* among the Cueva del Camino remains.

4.6. *Stone tools*

From 2002 to 2009, 105 lithic remains have been found at Cueva del Camino (Table 8), 52 of them belonging to Level 5. The raw materials for the lithic remains are predominantly quartz. At Camino the lithics size mean are 27 × 20 mm. Cores and retouched elements are scarce ((7.1% ($N = 6$)), while fragments and flakes predominate the assemblage (28.6% ($N = 24$) and 51.2% ($N = 43$) respectively). The operative chains are fragmentary.

5. Discussion

5.1. *Paleobotanical analysis*

The palynological composition reflects a continental Mediterranean climate, with more temperate and humid conditions in the lower half of the sequence (Levels N-F and N-5) compared to drier, colder conditions at the top of the sequence (Levels N-6, N-8/9). A quantitative and qualitative progression can be seen between these sets of conditions in terms of the forest cover Fig. 19 with the appearance of xerophytic over nitrophilous taxa. The presence of NPMs, i.e., *Glomus* cf. *fasciculatum* (type 207), *Pleospora* sp (type 3 b) and *Pseudoschizaea circula*, (Geel, 1978; López Sáez et al., 2000; Riera et al., 2006), is explained by the degradation of the landscape.

The presence of *Betula*, along with deciduous *Quercus, Corylus, Ulmus, Alnus* and *Salix* in the palynological spectrum, confirms the existence of refugia in more sheltered areas such as the bottom of valleys where water availability would be good. The Rosaceae recorded in the pollen diagram might correspond mainly to the Maloideae recorded in the anthracological assemblages.

The charcoal analysis suggests vegetation with a strong pioneering character, clearly reflected in the presence of *Pinus* and, to a lesser extent, *Betula*. These taxa characteristically appear at the beginning of interstadial or interglacial climatic vegetation cycles. The date obtained for Level 5 (90 ka, TL) is contemporaneous with an interstadial event of MIS 5.

5.2. *Biochronology of the faunal association*

The faunal association of the site led Alférez et al. (1982) to provisionally assign it to the Riss-Würm (Eemian) interglacial period or some Riss interstadial period. The new faunal data have clarified the biochronological aspects as follows.

From a chronological standpoint, the rodent association of Cueva del Camino is characteristic of the first half of the Late Pleistocene in the Iberian Peninsula. Some species represented in the North and Central sectors are more common in the Middle Pleistocene, becoming progressively scarcer during the Late Pleistocene until their disappearance from the area. Such is the case of the Malaysian porcupine, which inhabited the Peninsula throughout the Middle Pleistocene and the first half of the Late Pleistocene, its most recent citations coming from the MIS 3 sites of La Mina (in Burgos; (Díez et al., 2008)) and Cueva de A Valiña (in Lugo; Fernández Rodríguez, 2006). Other rodents present in the Cueva del Camino assemblage are first recorded at the start of the Late Pleistocene, such as *M. cabrerae* and *A. terrestris*. The incipient differentiation observed in the enamel pattern of the molars of *A. terrestis* indicates an age within the first half of the Late Pleistocene. In the south sector, the presence of the snow vole (*Chionomys nivalis*) suggests a slightly more modern age than for the remainder of the site. The earliest record of this species in the Iberian Peninsula is from the lower levels of the Cueva de la Carihuela (Ruiz Bustos, 2000), dating from the MIS 5 or the transition to MIS4 (Fernández et al., 2007), and is more common in younger localities.

The ungulates of Cueva del Camino provide a clear example of an interglacial faunal complex. Similar mammal associations are

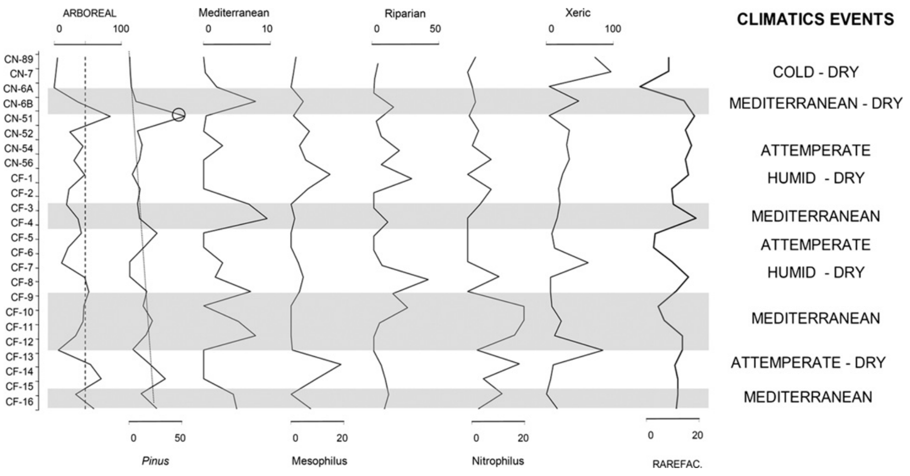


Fig. 19. Change in main plant taxa groups.

documented at a number of Eemian *s.l.* sites, such as Barrington and Trafalgar Square (Great Britain) (Stuart, 1982), Taubach and Burgtonna I (Germany) (Kolfschoten, 2000; Kahlke, 2002). The term Eemian is here used in a broad sense, referring to the warm (interglacial) period preceding the cold episodes of the Late Pleistocene. The Cueva del Camino site is of special interest in the Iberian Peninsula given the high proportion of *Dama dama* remains and because it is one of the most recent known Iberian assemblages of this species.

In the Iberian Peninsula, spotted hyenas first occur in late Early Pleistocene sites (García and Arsuaga, 1999). The most recent occurrence of *Crocuta crocuta* is at Cueva de las Ventanas (Granada), a tardiglacial site about 12,500 cal radiocarbon BP (Carrión et al., 2001). Brown bears (*Ursus arctos*) first occur in Europe during the late Middle Pleistocene at a moment when *U. spelaeus* fully occupied the continent. The latest clear occurrence of *Panthera pardus* in the Iberian Peninsula was between 30 and 22 ka at Cueva Morín (Cantabria; Level 5b: Gravettian-Aurignacian; (Altuna, 1971)) and Amalda VI (Basque Country; Gravettian Level; (Altuna, 1984)).

The carnivore assemblage of Cueva del Camino provide little detail in terms of age range, but points to an interval from the late Middle Pleistocene to around 30–22 ka: thus it is consistent with the radiometric age obtained by TL (90.961 ± 7881 years), corresponding to isotopic stage 5c which was a generally temperate time.

5.3. Environmental reconstruction from faunal remains

The faunal analysis developed by Alférez's team confirms a paleoenvironment characterized by open forest and warm climate. The new data supports this hypothesis.

Regarding the microvertebrate assemblage, the most outstanding feature of the Cueva del Camino is its high species richness. Several factors may be responsible for this, not least the steep valley in which the locality lies. The altitude differs by about 1000 m from the base of the valley to the summits of the surrounding mountains, favouring the development of a variety of biotopes, each with its distinctive species. Another factor favouring a high diversity of small vertebrates might be the nearby Pico de Peñalara (2428 m), which lies at the head of the valley. This mountain determines that the area enjoys more rainfall and more humid conditions than the surrounding regions. A positive correlation has been described between rainfall and mammalian species richness (Moreno-Rueda and Pizarro, 2009). For these same reasons, the Sierra de Guadarrama, and particularly the high part of the Lozoya Valley, is even now one of the areas of Central Spain with the highest vertebrate species richness (Tellería, 1999).

From a paleoenvironmental point of view, several microvertebrates identified in the fossil assemblage at Cueva del Camino can be considered typically thermophilous, e.g., the Cabrera vole or the Malaysian porcupine. Herman's tortoise and the Montpellier snake can be similarly viewed. These taxa, together with the absence of cold climate-adapted species are indicative of warm environmental conditions during the formation of the North and Central sectors of the site. The scarcity or absence of these thermophilous taxa, together with the presence of the snow vole and the abundance of the field vole in the South sector, suggest colder conditions for this part of the site.

Interestingly, typically forest-dwelling rodents such as the squirrel or the bank vole (*Myodes* cf. *glareolus*) were also found in the North and Central sectors, although only in proportions of around 0.1%. These animals are very rare in other micromammal associations of the Iberian Pleistocene. The abundance of field mouse remains (>40% of all rodent remains) is also indicative of forest masses, which must have alternated with more open areas occupied by different types of vole. In the South sector, the absence of forest species, the lesser abundance of the fieldmouse (10%), and the dominance of rodent associations by the common vole (*M. arvalis*) indicate a more open landscape than within the other sectors.

Analysis of the macrofauna allows the reconstruction of the Lozoya Valley's early Late Pleistocene palaeoecology. The ungulate association at Cueva del Camino shows an environmental complex composed of different ecosystems. During the Late Middle and Late Pleistocene interglacial periods, *Bos primigenius* inhabited the forests, although these must have had open patches. A forest environment is also supported by the presence of *Dama dama*, *S. scrofa* and *C. capreolus*. Open areas (grasslands) were inhabited by *E. ferus* and *S. hemitoechus*. A third ecological component related to the altitude of the site is suggested by the presence of *R. rupicapra*, a species characteristic of rocky, high mountain areas. The absence of *U. spelaeus* at Cueva del Camino an abundant species in the nearby site of Reguerillo (Torres, 1974), might be explained by the different preferences of these taxa. Cave bear remains are rarely recovered in sites other than deep caves (as in the case of Reguerillo), while brown bear remains are often found in open air, cave entrance or rock shelter sites. Mild climatic conditions might also explain the predominance of brown bears at Cueva del Camino.

The carnivore species recovered from Cueva del Camino have a wide climatic tolerance range, allowing them to be found associated with both warm and cold faunas. No typically cold taxa such as *Alopex lagopus* or *Gulo gulo* have been recovered. The absence of such species cannot provide much of a clue with respect to the climate, but it is in line with the suggested mild period reflected by Cueva del Camino – a time when browsing ungulates were common on open land, when brown bears would have inhabited the forests, and when lions would have patrolled the steppeland. Lions and hyenas today occupy open areas such as savannas, but during the Pleistocene these species might have occupied a wider range of habitats. Pole cats, wolves and foxes can also inhabit different habitats but are more commonly found in woodlands, i.e., in environments similar to that in the area of Cueva del Camino. Thus a varied, temperate ecosystem can be interpreted, where there were forested areas but also more open spaces attractive to lions and hyenas.

5.4. Human remains

The degree of hypocone development in the M^1 is similar to that commonly found among Neanderthals, which generally show large hypocones. However, a metaconule and some development of a Carabelli structure are seen in about 64% and 68% of Neanderthal specimens respectively (Bailey, 2006). The frequencies of these traits are somewhat lower (53% and 40% respectively) in Upper Palaeolithic modern humans, but their absence in the Cueva del Camino M^1 is not diagnostic with respect to taxonomic affinity. While not as pronounced as in some Neanderthal specimens, the external crown outline of this tooth shows what can be characterized as a bulging hypocone, which seems to conform to the derived shape identified in specimens attributed to the Neanderthal evolutionary lineage (Gómez-Robles et al., 2007). The presence of a taurodont pulp chamber is a variable feature found at low frequency (<5%) in living humans (Hillson, 1996) but at high frequency in Neanderthals (Kallay, 1963). This chamber has also been documented in *Homo erectus* teeth from Zhoukoudian (Weidenreich, 1937).

In its overall crown dimension, the Cueva del Camino M^1 compares most favorably with European Neanderthal specimens. The relative sizes of the occlusal polygon and cusp base areas also provide clear indications of the taxonomic affinities. Low values for the relative occlusal polygon area, as in the Camino M^1, indicate relatively internally placed cusp tips, a feature argued to represent a derived Neanderthal condition (Smith, 1989; Bailey, 2004).

Although the reduction of the metacone is known to occur in earlier *Homo* species (Quam et al., 2009), it reaches its maximum expression in specimens attributed to the Neanderthal evolutionary lineage (Bailey, 2004). The very small metacone in the Cueva del Camino M^1 indicates Neandertal taxonomic affinities. The M^3 is the most variable of the upper molars, and the crown and root morphology are largely undiagnostic as to taxonomic affinities. Nevertheless, this tooth is not inconsistent with a Neandertal classification.

5.5. *Taphonomy and signs of human presence at Cueva del Camino*

The first interpretations of the site indicated that this cave was probably occupied by humans (Alférez et al., 1982). Subsequently, Díez (1993) reinterpreted the origin of the accumulation as a spotted hyena den. The present work tends to corroborate the interpretation of the latter author. The presence of human teeth at the site obliges the possibility that some human activity took place either within the cave or at its mouth. Unfortunately clues on what that activity was have likely been lost through erosion or the building of the road that passes by the site. These teeth may, however, have been transported to the site by hyenas or other carnivores, which are thought to be the main (perhaps only) agents responsible for the accumulation of the large mammal remains.

The proportion of possible cut marks is just 0.4%, and only on the acetabulum of a single innominate that belongs to a specimen of *Cervus elaphus* are cut marks clear. Thus, there is little reason to think that humans commonly processed the bodies of animals at the site. The raw materials for the lithic remains (predominantly quartz) are the same as those documented at the other archaeological sites in the surrounding area (Navalmaíllo Shelter, Descubierta and Buena Pinta caves). However, in contrast to those other archaeological sites, the frequency of lithics compared to faunal remains is minor (it represents 2.8 % of the record).

Because of the infrequency of lithics at Camino, the possibility that their presence at the site was due to taphonomic processes and not of anthropogenic origin must be tested. Different criteria were used for assessment (Villa and Soressi, 2000), including the lithic record composition as well as special features of the faunal record such as the scarcity of cut marks and the lack of evidence for anthropogenic fracturing of bones.

The proximity of Descubierta cave, an earlier locality, with a very rich lithic sample, provides an abundance of stone tools at the surface of the hill, just above Cueva del Camino. It is possible that this material could have entered through different fractures in the rock walls of the cave. Support for this hypothesis is provided by comparing the size of the lithic artifacts found at Cueva del Camino with those of Descubierta cave. At Camino the lithics are typically smaller (mean 27 × 20 mm) while being larger at Descubierta (mean 58 × 44 mm). In this case, this small size would mean selective transport by natural processes. Additionally, cores and retouched elements are scarce, while fragments and flakes predominate in the assemblage. The operative chains are fragmentary, which support this hypothesis.

No burned bones were discovered during the 2002–2009 campaigns; such findings would have been clear evidence of controlled fire being used. The isolated pieces of charcoal recovered might indicate that fires were made close by. Indeed, these charcoal pieces do not seem to have been the product of natural fires for the following reasons: i) the stratigraphy does not include any layer of ash that might represent a bushfire. Further, carbon microparticles on the pollen slides are very scarce and discontinuous; ii) the carbonised remains only correspond to wood; no carbonised fruits, seeds, leaves or bark have been found; iii) many species with different ecological (e.g., sunny or shady) and soil (silicic and calcic) requirements are represented by these charcoal pieces. This might indicate that the original wood was brought from different places.

It is therefore possible that the small charcoal remains found at the site were transported there by geological means from nearby human dwelling areas, probably higher up the slope. None of the evidence above goes against interpreting the Cueva del Camino as a den used by carnivores, particularly hyenas. Furthermore the data suggest the Neanderthals of the area only rarely, if ever, used the cave.

Human remains or traces of human presence have also been recorded in other carnivore dens, such as: Wezmeh cave (Iran) (Trinkaus et al., 2008; Mashkour et al., 2009), Geula cave (Israel) (Monchot, 2005), Les Auzières 2 and Bois Roche (France) (Marchal et al., 2009; Villa et al., 2010) or Zourah cave (Morocco) (Monchot and Aouraghe, 2009).

Fracturing pattern results show that there is a predominance of fractures with bevelled and mixed angles with respect to the fracture angle. The properties of the fracture edges in the majority

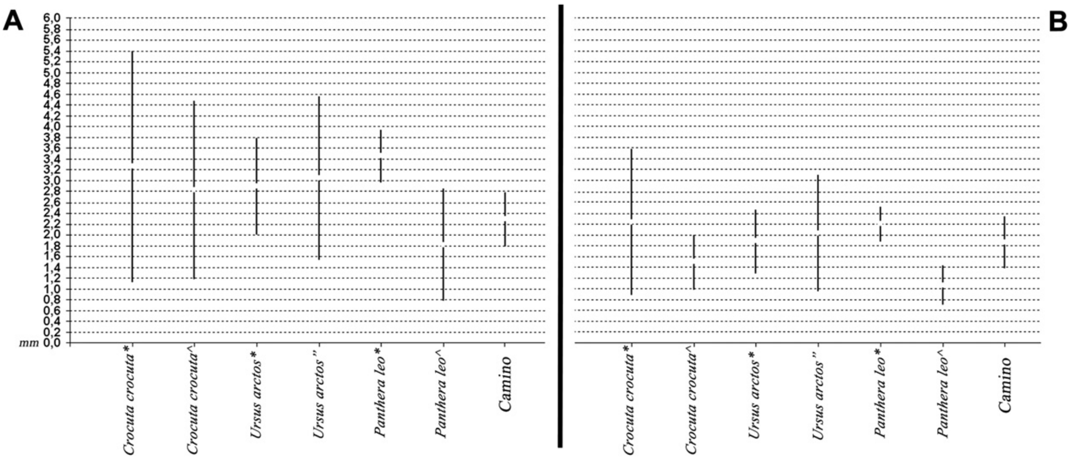


Fig. 20. Mean ± 1 Standard Deviation of carnivore tooth pit sizes according to bone type and length/breadth recovered from Cueva del Camino site. A: Length in dense cortical; B: breadth in dense cortical. Legend data from: *Domínguez-Rodrigo and Piqueras (2003); ^Delaney-Rivera et al. (2009); "Saladié et al. (2011).

of cases are characterised by being smooth, with a high percentage of crenulated edges in the sample. These data suggest that the majority of the sample was fractured during a biostratinomic stage and that carnivores played a role in the fracturing processes. There is abundant evidence of carnivorous activity in the fossiliferous association at this site. However, it is not easy either to assign a taxon responsible for modifying and accruing these bones. Tooth mark metric data from this site have been compared with those published earlier. Fig. 20 shows an important overlapping of the tooth mark values in relation with published data. The high frequency of gnaw marks and digested bones, the carnivore/ungulate ratio, the abundance of juvenile hyena and the patterns of bone breakage suggest that the Cueva del Camino was a hyena den (*Crocuta crocuta*).

6. Conclusions

Iberian Peninsula is rich in Neanderthal occupations dated to Middle-Upper Paleolithic through the entire Mediterranean coast margin, ranging from the French border to the Straits of Gibraltar (Arsuaga et al., 1989, 2005; Daura et al., 2005; Finlayson et al., 2006; Walker et al., 2011). However the Cueva de Camino fossil assemblage, located in a mountain habitat (in the limit of Mediterranean conditions), is of special interest because it constitutes the most complete and ancient inland Iberian record, where the Neanderthals lived.

In general, the pollen composition of the site corresponds to the installation of a continental Mediterranean climate, with more temperate and more humid conditions represented in the lower half of the sequence (Levels N-F and N-5), and drier, colder conditions represented towards the top (Levels N-6, N-8/9). This change was accompanied by a progressive loss (both qualitative and quantitative) of forest cover, the appearance of xerophytic taxa, and the gradual loss of nitrophilous plants.

The results of charcoal analysis suggest a strong pioneering character for the site's vegetation, dominated by *Pinus* and to a lesser extent *Betula*. These taxa are characteristic of the beginning of interstadial and interglacial vegetation cycles. Certainly, the date obtained for Level 5 (90 ka TL) is contemporaneous with one of the interstadial events of MIS 5. This stadial-interstadial cyclicity might have been responsible for this pioneering character of the vegetation.

Several of the microvertebrates identified in the fossil assemblage at Cueva del Camino are typically thermophilous species. From a chronological point of view, the rodent assemblage is characteristic of the first half of the Late Pleistocene in the Iberian Peninsula.

The ungulates of Cueva del Camino provide a clear example of an interglacial faunal complex. The site is of special interest in the Iberian Peninsula given the high proportion of *Dama dama* remains, and because it is one of the most recent known Iberian assemblages for this species. The carnivore species recovered from the site showed a wide climatic tolerance range, and have been reported associated with both warm and cold faunas. Thus, a varied, temperate ecosystem can be interpreted, with forested areas but also more open spaces attractive to lions and hyenas.

The M^1 specimen from Cueva del Camino shows a number of derived features seen at high frequencies in Neanderthals, including the shape of the crown outline, the crown and cusp dimensions, the relative size and internal placement of the individual cusps and the taurodont pulp chamber. While the external morphology of M^3 is largely undiagnostic, it is not inconsistent with a Neanderthal classification, and both teeth likely belonged to the same individual. These results are broadly similar with previous suggestions (Alférez and Roldán, 1992) of Neanderthal affinities for the specimens. However, the present study provides a more detailed analysis based on recent findings, places the human teeth within a clear Upper Pleistocene context and provides comparative data for further studies of Neanderthal dental morphology and evolution.

The high frequency of gnaw marks and digested bones, the carnivore/ungulate ratio, and the patterns of bone breakage suggest that the Cueva del Camino megafaunal assemblage was accumulated by carnivores. The abundance of juvenile hyena suggests that the site was a hyena den (*Crocuta crocuta*) during the Late Pleistocene.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quaint.2012.04.019.

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9

Periodización del debate caza *v/s* carroñeo

En historiografía no siempre es fácil establecer conocimientos absolutos o que no sean, al menos, opinables o discutibles. Sin embargo, a efectos de analizarlos de una forma más comprensible conviene estructurarlos y periodificarlos[24].

En el caso del debate caza *v/s* carroñeo hemos previsto acercarnos a él, además de con nuestras excavaciones, análisis de marcas y experimentos neotafonómicos, así como de numerosas lecturas, mediante varias entrevistas personales con investigadores de referencia[25].

Algunas de estas conversaciones, no grabadas, pues se produjeron en las noches olduvayenses, se han mantenido con Manuel Domínguez-Rodrigo y con José Yravedra, aisladamente con cada uno de ellos, y por tanto la estructura que a continuación proponemos, es de nuestra exclusiva responsabilidad.

1ª Etapa. Los homínidos cazadores. Elaboración del paradigma.

Desde Darwin, todos los investigadores seminales en la Evolución Humana dieron por hecho que el acceso a la carne por parte de los homínidos debió producirse en las etapas más antiguas de dicho proceso, y que este consumo cárnico era fruto de la actividad cinegética, como ocurre con mayor frecuencia en la etología de los carnívoros. Esta visión se implantaría más profusamente a partir de los trabajos de Raymond Dart, cuya industria osteodontoquerática tendría como función principal la caza y aprovechamiento de los animales por parte de los antepasados del linaje humano: los australopitecos.


Louis Leakey y Raymond Dart

Mayor repercusión social tendrán los trabajos de Robert Ardrey, un escritor y guionista cinematográfico de éxito en Hollywood[26], que también obtuvo éxito en el campo de la difusión antropológica. Junto a muy numerosos artículos y entrevistas con investigadores, Ardrey es autor de

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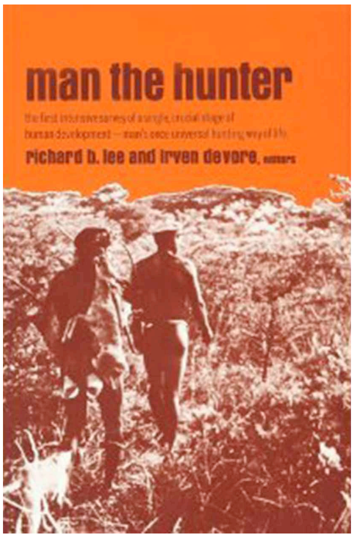
[24] Los momentos iniciales del debate caza *versus* carroñeo se corresponden casi totalmente con los orígenes de la tafonomía africana, puesto que caminan de la mano y se alimentan simbióticamente. Por ello, muchos de los datos se repiten respecto de la historiografía desarrollada en la Introducción de esta Tesis.

[25] En una serie aún inconclusa que puede verse en la página web del Museo Arqueológico Regional de la Comunidad de Madrid.

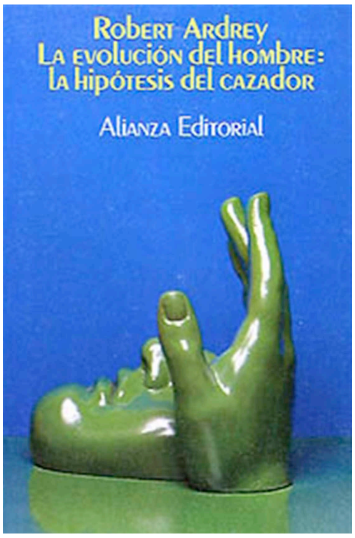
[26] Obtuvo incluso una mención a un Óscar por el guión de la memorable "Khartoum" (1966), protagonizada por Charlton Heston y Laurence Olivier.



Portada del libro *Man the Hunter*. Lee, R. y Devore, I. 1968

cuatro libros recogidos en la selección Nature of Man series. Los cuatro libros son: African Génesis: A Personal Investigation into the Animal Origins and Nature of Man, publicado en 1961; The Territorial Imperative: A Personal Inquiry into the Animal Origins of Project and Nations, de 1966; The Social Contract: A Personal Inquiry into the Evolutionary Sources of Order and Disorder, en 1970; y The Hunting Hypothesis: A Personal Conclusion Concerning the Evolutionary Nature of Man, 1976.

Ardrey tomará principalmente la información inicial de los trabajos de paleoantropólogos como Raymond Dart y Robert Broom, aunque también de algunos sociólogos como Konrad Lorenz, uno de los padres de la etología como disciplina científica, así como muchos otros investigadores africanistas. Entre otros Charles K. Brain y Louis S.B. Leakey, con los que tomó contacto personal directo y continuado.



Portada del libro *La Evolución del Hombre: La Hipótesis del Cazador*. Adrey, R. 1976

Sin duda, Ardrey será el difusor de unas teorías (principalmente la Hipótesis del Cazador), en buena medida construidas y, sobre todo, estructuradas por él, pero que se hacen con trabajos de otros autores. Desde luego el congreso “Man the Hunter” convocado por Richard Lee e Irvin DeVore, en 1966, en la Universidad de Chicago, y su correspondiente publicación, en 1968, tuvieron un papel fundamental.

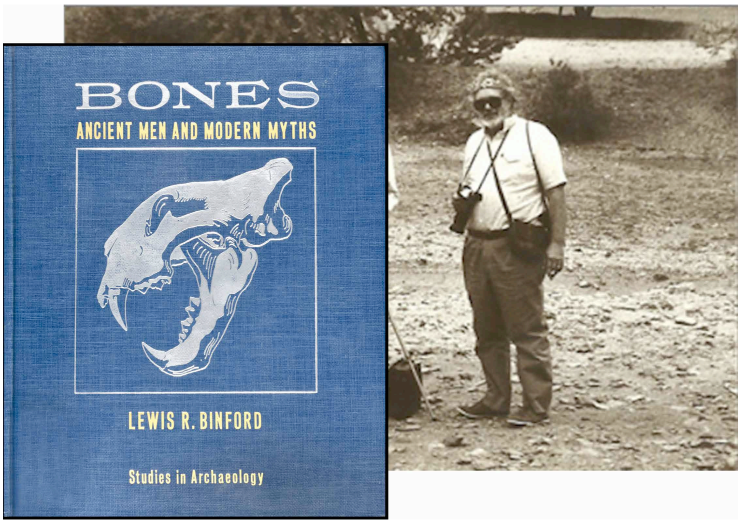
Esta primera gran etapa que historiográficamente hemos denominado *de elaboración del paradigma,* en términos metodológicos está considerada por algunos de nuestros entrevistados como una fase precientífica. Nosotros preferimos denominarla como fase hipotético-deductiva, puesto que incorpora los elementos propios de ambas disciplinas, la arqueología y la paleontología, que aún no han sufrido la gran revisión propia de la llamada Nueva Arqueología, que representará un impulso científico abismal.

Un momento de transición. El quinquenio 1976-1981.

Esta primera etapa inicial del debate culminará, para la mayoría de mis contertulios en 1981 con la aparición de varias publicaciones, en este mismo año, que darán al traste con la esencia del paradigma cazador.

Sin embargo, en nuestra opinión, el quinquenio 1976-1981 tiene un especialísimo interés por la gran cantidad de trabajos que cuestionan el paradigma, como ya había sucedido en la primera etapa (Washburn, Clark, Leakey o Brain, entre ellos), pero sobre todo por el cuestionamiento de la metodología empleada.

Recuérdese el simposio del Castillo de Burg Wartenstein, en 1976, donde el propio Bob Brain sitúa el nacimiento de la tafonomía aplicada a la arqueología de los orígenes humanos. Aunque las actas recopiladas por Behrensmeyer y Hill no verán la luz hasta 1980, un año antes que los ya mencionados libros de Shipman, Brain y Binford. Por eso la mayoría de autores considera 1981 como año fundacional de esta disciplina.



Lewis Binford y la portada de su libro *Bones.*

2ª Etapa. 1981 a 1996. El cambio de paradigma.

La etapa que comienza en 1981 supone la preponderancia de la alternativa al hombre cazador: el hombre carroñero.

En esta segunda etapa la discusión científica se centra en el estudio de los perfiles anatómicos de las presas, teniendo el análisis de las marcas de corte un papel secundario.

Entre 1990 y 1995 se produce un claro liderazgo del profesor Robert Blumenschine y su equipo de la Universidad de Rutgers que trabajan en paralelo con los fósiles de la Garganta de Olduvai, en su Lecho I, y sus experimentaciones con carnívoros en las sabanas de la planicie del Serengetti y de la caldera del Ngorongoro.

El equipo de Blumenschine estudiará con detenimiento los procesos tafonómicos en la sabana relativos a la caza y al carrroñeo, observando la etología de los grandes depredadores como leones, leopardos, guepardos y chacales, y carroñeros como hienas, buitres y córvidos, comparándolos con los de primates como chimpancés y papiones: así, pueden establecer *la ecología del carroñeo*.

Por otra parte, otorgarán menos relevancia al estudio de los perfiles anatómicos de las presas, y prestarán mayor atención al análisis de las marcas de corte y marcas de percusión en fresco.

Despiece Waterbuck. Ilustración de Mauricio Antón. Catálogo de la exposición *La cuna de la Humanidad* (Domínguez-Rodrigo y Baquedano, 2014)

Concluyen que los habilinos debieron tener un acceso secundario (tras los félidos) y no marginal (tras los hiénidos) a las carcasas de los grandes herbívoros.

Esta hipótesis se convierte en el nuevo paradigma que ya es hijo, como las etapas siguientes, de los conceptos propios de la llamada Nueva Arqueología o Arqueología Procesual.

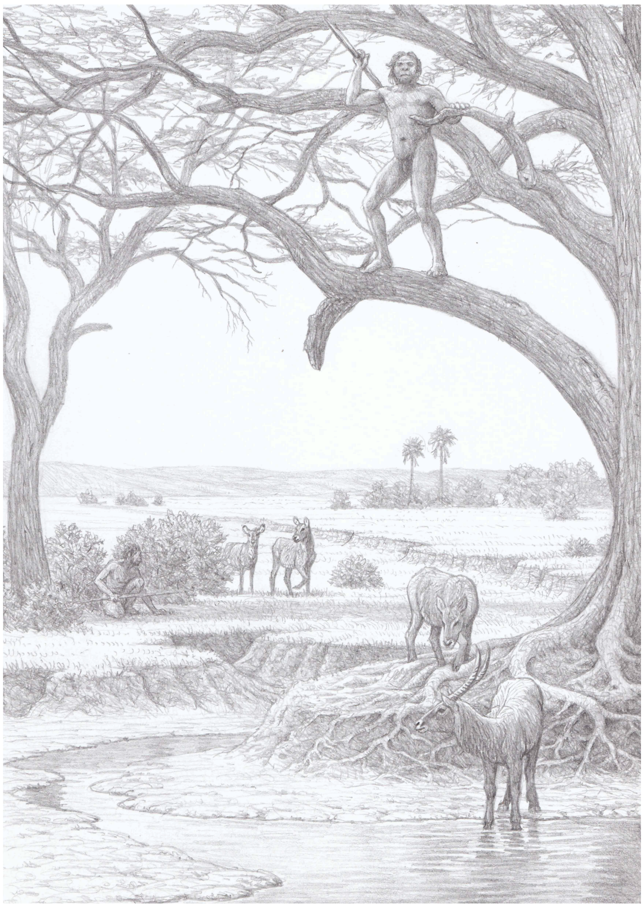
El estudio del medio ambiente, el análisis pormenorizado de hasta los mínimos detalles y la etnoarqueología son elementos determinantes.

3ª etapa de 1997 a la actualidad. Un debate científico sobre evidencias.

En 1997 el debate se posiciona entre los equipos de Blumenschine y Manuel Domínguez-Rodrigo, defensor este último, de un hombre cazador desde las primeras etapas, y en concreto los habilinos de FLK, cuyos fósiles revisa (junto a Rebeca Barba y Charles Egeland) en “Deconstructing Olduvai” (Domínguez-Rodrigo, M.; Barba, R.; Egeland, C. P. 2007).

A partir de este debate entre los equipos de Blumenschine (OLAPP en Olduvai Gorge) y de Domínguez-Rodrigo (TOPPP en Olduvai Gorge) la dialéctica se traduce en marcas de dientes como distintivo de carroñeo y marcas de corte como señales de caza.

Hoy el debate, afortunadamente, se ha reconducido al terreno de lo estrictamente científico, de donde nunca debiera haber salido, se completa con el estudio de los perfiles anatómicos y se proyecta innovando con otra propuesta de la Arqueología Procesual: la estadística, y más concretamente, la metodología estadística multivariante.



Un habilino accede desde el alto de un árbol a un antílope de agua según la hipótesis de Manuel Domínguez-Rodrigo. Ilustración de Mauricio Antón. Catálogo de la exposición *La cuna de la Humanidad* (Domínguez-Rodrigo y Baquedano, 2014)

10

Conclusiones

La visión historiográfica de la arqueología es algo para lo que desde siempre hemos tenido un especial interés, seguramente porque nos fue inculcado por nuestros profesores y maestros desde la etapa universitaria.

En relación con la tafonomía, hemos realizado una serie de entrevistas personales en vídeo, muy visitadas en la página web del Museo Arqueológico Regional (www.museoarqueologicoregional.org). Esta serie está inconclusa y nos proponemos continuarla en los próximos años.

Ver la forma en que la tafonomía está siendo decisiva en el debate caza versus carroñeo, ha sido el objeto de esta Tesis Doctoral. No repetiremos aquí, por manifiestamente innecesario, las conclusiones de cada uno de los artículos compilados.

Cuál es nuestra manera personal de ver este asunto, es lo que expondremos a continuación.

Como ya se ha citado al comienzo de esta presentación, Darwin, en su “Descent of Man”, ya intuyó que los homínidos necesitamos de herramientas en nuestro deseo de acceder a la carne, puesto que carecemos de colmillos, picos y garras para entrar al interior de las presas, como hacen los carnívoros, y eviscerarlos.

Y así es. El registro fósil parece hacer coincidir el inicio del consumo cárnico, con el uso de utensilios líticos y la evolución anatómica de los primates homínidos. Si bien estos conceptos están sometidos a debate y reformulación.

Pero esto no significa que este acceso haya sido ejercido sobre animales cazados por ellos mismos o implique carroñeo sobre animales predados con anterioridad.

En nuestra opinión, el debate ha estado marcado, al menos inicialmente, por un exceso de maximalismo. O sólo se caza o sólo se carroñea. De forma excluyente. Además, el enrocamiento en una u otra posición, ha dificultado que el debate trascurriera por unos cauces razonables.

Diremos que, personalmente, sentimos una gran admiración por los Leakey o Isaac, como la sentimos también por Binford o Brain. Son, sin la menor duda, grandísimos investigadores y la ciencia de la paleoantropología siempre estará en deuda impagable con ellos. Pero seguramente en la evolución humana las cosas han sucedido de una manera mucho más circunstancial.

Creemos que lo que nos dijo Ortega, sobre el hombre y sus circunstancias, sirve para todas las especies que nos han traído hasta aquí.

Sabemos, por ejemplo, que los neandertales son cazadores de herbívoros de gran tamaño, incluyendo rinocerontes, bisontes o uros, y sabemos que, en otros lugares, comen presas tan pequeñas como conejos y tortugas. Parece evidente que esto se debe a la presión del entorno medioambiental -las circunstancias de Ortega- sin menoscabo de razones culturales. En Pinilla del Valle, p. e., los neandertales se centran siempre en grandes animales, pero en yacimientos como Bolomor, más antiguo, la misma especie está comiendo presas pequeñas (Blasco, R. 2008; Blasco, R. y Peris, J. F. 2012).

En Áridos y Ambrona, es muy probable que los heidelbergenses estén carroñeando las partes más suculentas y bien conservadas de los grandes herbívoros, incluyendo a los proboscídeos, y estén cazando presas más fáciles como équidos y cérvidos (Sesé, C., Soto, E., 2005; D´Errico, F. y Vila, P. 2005; Vila, P., Soto, E., Santonja, M., Pérez-González, A., Mora, R., Parcerisas, J., Sesé, C. 2005).

Lo mismo vemos en África. Los habilinos de FLK o PTK están cazando presas medianas y pequeñas como antílopes y gacelas, y vemos como en BK los ergaster están carroñeando Pelorovis y Sivaterio, que son presas de tamaño mucho mayores (Wedelin, L. y Lewis M. E. 8 2014).

Aun cuando el género Homo es muy especial, sin duda, debemos fijarnos en lo que nos dice la arqueología y la tafonomía, pero también las leyes de la naturaleza que operan en nuestro entorno así como la etnología de los grupos de cazadores-recolectores. Hemos visto a los pueblos africanos cazando elefantes con jabalinas a gran distancia y, a veces, haciendo heridas que serán mortales por las infecciones o emponzoñando flechas, como los Hadzabe. Estos mismos que, junto al Lago Eyasi, también carroñean y lanzan sus flechas contra cualquier ser comestible. La capacidad humana para cazar en persecución prolongada lo facilita[27]. Lo hemos visto en directo. Con unos y con otros.

En sentido inverso, hemos visto cómo animales estrictamente carroñeros, como el buitre leonado, pueden atacar presas vivas en circunstancias ambientales de gran escasez y estrés. Manda el hambre.

Nosotros mismos, los humanos que vivimos en nuestras cómodas casas occidentales, tenemos un comportamiento cultural muy marcado por nuestra historia biológica, cazadora y carroñera.

Sin embargo, en ciencia es importante distinguir entre creencias, intuiciones e hipótesis, por una parte, y teorías y leyes, por otro. La construcción de hipótesis de trabajo es imprescindible para conducir la investigación que nos lleve a la elaboración de paradigmas. Los hechos no pueden reconstruirse sólo sobre la base de la aplicación de las leyes naturales, si no sobre datos y evidencias. Por ello es tan importante la experimentación que “demuestre” la concreción de lo que a veces parece obvio. Nuestras concepciones apriorísticas, por muy bien que conozcamos

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[27] Es un sistema parecido al que usan los dragones de Komodo y muchas serpientes.

el funcionamiento de las cosas en la sabana, debe estudiarse a fondo y establecer un corpus de información que, acumulando datos rigurosos procedentes de multitud de situaciones y escenas diferentes, nos lleven a elaborar verdaderas teorías científicas.

No es suficiente, con suponer que las cosas funcionan de una determinada manera en virtud de las leyes biológicas, necesitamos “demostrarlo” para que sea aceptado por la comunidad científica. Y por ello el estudio de la evolución humana es tan tributario de la tafonomía, con sus conceptos, métodos y técnicas.

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Líneas de investigación futuras

Tras la defensa de esta Tesis doctoral, nuestra línea de trabajo continuará, sobre todo, en torno a los yacimientos de Olduvai Gorge y Pinilla del Valle.

En Pinilla del Valle nos proponemos:

- Centrarnos en la excavación de la Cueva Des-Cubierta.
- Continuar la prospección de nuevos yacimientos.
- Investigar en relación con el mundo funerario y ritual de los neandertales.
- Preparar una gran exposición sobre Pinilla del Valle.

Inauguración del Parque Arqueológico en el Valle de los Neandertales en septiembre de 2015. Fotos: Mario Torquemada/MAR.

Todo ello en Colaboración con Juan Luis Arsuaga, Alfredo Pérez González y todo el E.I.P.V.

Abrigo de Navalmaíllo. Ilustración: Yolanda González y Enrique Baquedano.

Organizar, con Juan Luis Arsuaga, la 6ª reunión de la ESHE (Sociedad Europea para el estudio de la Evolución Humana), en el Museo Arqueológico Regional, en Alcalá de Henares, y presentar allí los resultados provisionales de las excavaciones en Pinilla del Valle.

En Olduvai Gorge nos proponemos:

- Culminar la excavación de DS.
- Dirigir el curso "Descubriendo la Cuna de la Humanidad", que se celebrará en CosmoCaixa en octubre, 2016.
- Instalar la exposición "La Cuna de la Humanidad", como exposición permanente, en el Museo Nacional de Tanzania, en Dar es Salaam.
- Hacer la museografía del nuevo Museo de Olduvai Gorge.
- Culminar la creación de la Estación científica "Emiliano Aguirre" a pie de la garganta.
- Culminar la creación a pleno rendimiento del I.D.E.A (Instituto de Evolución en África) en una nueva sede (calle Covarrubias, 36. Madrid).
- Elaborar un libro sobre "Los homínidos de Olduvai Gorge"

Todo ello en colaboración con Manuel Domínguez-Rodrigo y el equipo T.O.P.P.P.

Con Manuel Domínguez-Rodrigo y con Mauricio Antón nos proponemos escribir un artículo sobre la evolución de la imagen de los parantropos en las reconstrucciones ilustradas.

La estación "Emiliano Aguirre" en Olduvai Gorge. Foto: Javier Trueba/ Madrid Scientific Films.

Manuel Domínguez-Rodrigo, Charles Musiba y Enrique Baquedano, observan con atención el cráneo de OH5, holotipo de *Paranthropus boisei*. Museo Nacional de Dar es Salaam Foto: Mario Torquemada/MAR.

Con Juan Luis Arsuaga y Belén Márquez nos proponemos escribir un trabajo sobre la evolución de la imagen de los neandertales a partir de los últimos descubrimientos científicos.

Por último, organizar con Jordi Rosell, un encuentro, en 2017, sobre el poblamiento, o no, de Europa por el estrecho de Gibraltar.

12

Una aclaración final

Nací en 1958 y, consiguientemente, tengo 58 años. Cuando algunas personas leen sus Tesis doctorales a edad provecta es, con frecuencia, porque esas personas realizaron tardíamente sus estudios.

No es mi caso. Al contrario. Mi vocación arqueológica nace en mi más tierna infancia, y mi inquietud por la arqueología prehistórica y la evolución humana surge antes de terminar el bachiller superior en mi Soria natal.

Terminé mi licenciatura en el curso 1979-80 y, en junio de 1980, leí mi "Memoria de licenciatura", dirigida por D. Martín Almagro Basch sobre "El Arte cuaternario en la Cuenca del Cares-Deva".

En el curso 80-81, hice mis cursos de doctorado y matriculé mi Tesis Doctoral sobre "La industria ósea de los pueblos celtibéricos". También bajo la dirección de Almagro Basch.

Hubiera querido continuar trabajando en la Cueva de Llonín (Asturias), pero circunstancias que prefiero no relatar me lo imposibilitaron. Fue José Luis Argente Olivar, director del Museo Numantino entonces, quien, conociendo mi interés por la industria ósea, me sugirió el tema señalado.

La muerte de D. Martín en 1984 y mi dedicación a oficios no estrictamente arqueológicos, hizo que hasta el año 2000 no retomara el asunto, matriculando la Tesis Doctoral en la Universidad de Valladolid, bajo la dirección del Prof. Germán Delibes de Castro y centrada en "La industria ósea de Numancia".

Aunque este trabajo estaba muy avanzado, el inicio de excavaciones arqueológicas en Pinilla del Valle, Madrid, en 2002, y en Olduvai Gorge, Tanzania, en 2008, hizo que propusiera una Tesis centrada en el objeto de mi interés científico principal. Las relaciones entre los homínidos y los carnívoros en la evolución humana.

No sé si esto que digo sirve de disculpa por mi tardanza, pero confío en que al menos sirva de explicación.

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