ISSN - 1132-6891

ARCHAEOFAUNA

INTERNATIONAL JOURNAL OF ARCHAEOZOOLOGY

VOLUME 25

Junio 2016

ARCHAEOFAUNA

ARCHAEOFAUNA es una revista anual que publica trabajos originales relacionados con cualquier aspecto del estudio de restos animales recuperados en yacimientos arqueológicos. Los manuscritos deben enviarse a:

ARCHAEOFAUNA is an annual journal that publishes original papers dealing with all aspects related to the study of animal remains from archaeological sites. Manuscripts should be sent to:

EUFRASIA ROSELLÓ IZQUIERDO
Laboratorio de Arqueozoología. Dpto. Biología. Universidad Autónoma de Madrid
28049 Madrid. España (Spain)

Para la elaboración de manuscritos, que serán evaluados por un mínimo de dos recensores externos, consultar las instrucciones de la contraportada. Todos los manuscritos no conformes con las normas de publicación serán automáticamente devueltos a los autores. Cada autor o grupo de autores recibirán un pdf de su trabajo.

For preparation of manuscripts, that will be evaluated by a minimum of two external referees, please follow the instructions to authors. All manuscripts not conforming to these instructions will be automatically returned to the authors. Each author (or group of authors) will receive a pdf of his/her (their) work.

Director: ARTURO MORALES MUÑIZ
Laboratorio de Arqueozoología. Dpto. Biología. Universidad Autónoma de Madrid.
28049 Madrid. España (Spain)

Revista incluida en las bases de datos ICYT (CINDOC), Catálogo Latindex, Zoological Record, The Arts & Humanities Citation Index y Current Contents / Arts & Humanities (JCR)

ARCHAEOFAUNA
Laboratorio de Arqueozoología. Depto. Biología.
Universidad Autónoma de Madrid
Cantoblanco 28049 Madrid. España

Editor: Eufrasia Roselló

ISSN: 1132 - 6891

UAM
UNIVERSIDAD AUTONOMA
DE MADRID

Depósito Legal: M - 30872 - 1992

Imprime:
LOKE MULTIPLATAFORMA GRÁFICA, S.L.
c. Progreso, 2 – Nave 9
Polígono Industrial Los Olivos
28906 Getafe (Madrid)
loke@multiplataforma-loke.com

FRONTISPIECE: A sampling of Roman artwork representing dogs.

PORTADA: Muestrario de representaciones de perros en el arte romano.

Índices/Contents

Fish consumption at the ancient market of Monterrey (18th-19th centuries), México, based on archaeological remains. *Ana Fabiola Guzmán, Miriam Espino & Araceli Rivera Estrada* 7-14

Scutes for Sturgeon Size Reconstruction: Traditional and Geometric Morphometric Techniques Applied to *Acipenser sturio* and *A. oxyrinchus*. *Els Thieren & Wim Van Neer* 15-32

The size of domestic cattle, sheep, goats and pigs in the Czech Lengyel and Eneolithic Periods: *Temporal* variations and their causes. *René Kyselý* 33-78

The dogs of Roman Vindolanda, Part I: Morphometric techniques useful in differentiating domestic and wild canids. *Deb Bennett, Greg Campbell & Robert M. Timm* 79-106

The dogs of Roman Vindolanda, Part II: Time-stratigraphic occurrence, ethnographic comparisons, and biotype reconstruction. *Deb Bennett & Robert M. Timm* 107-126

A Post-cranial Osteometrical Database for the Spanish ibex (*Capra pyrenaica* Schinz, 1838). *Laura Llorente Rodríguez & Victoria Quiralte* 127-184

Presencia de felinos (*Felis, Lynx* y *Panthera*) en el registro arqueológico de la Península Ibérica durante el Pleistoceno Superior. *Aritza Villaluenga* 185-204

Faunal Remains from an Almohad (Ad XII/XIII) Silo at the Castle of Aljezur (Portugal). *Diogo Mota & J.L. Cardoso* 205-232

Patterns of ancient animal use at El Mirador: evidence for subsistence, ceremony and exchange. *Erin Kennedy Thornton & Kitty F. Emery* 233-264

Erstnachweise des Feldhamsters als Beigabe in Grabbefunden der Thüringerzeit (Thüringer Königreich, 5/6. Jh. n. Chr.) von Thüringen. *Hans-Volker Karl* 265-272

Announcements 273-280

Archaeofauna 25 (2016): 7-14

Fish consumption at the ancient market of Monterrey (18th-19th centuries), México, based on archaeological remains

ANA FABIOLA GUZMÁN[1,2], MIRIAM ESPINO[1] Y ARACELI RIVERA ESTRADA[3]

[1]Subdirección de Laboratorios y Apoyo Académico, Instituto Nacional de Antropología e Historia. Moneda 16, col. Centro, México 06060, D. F., México.

[2]Departamento de Zoología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional. Prolongación de Carpio y Plan de Ayala, México 11340, D. F., México.

[3]Centro INAH Nuevo León. Rafael J. Verger s/n, Col. Obispado, Monterrey 64010, Nuevo León, México.

(Received *28 October 2013*; Revised *20 January 2014*; Accepted *27 January 2014*)

RESUMEN: Durante los trabajos de remozamiento del actual Museo Metropolitano de Monterrey, se rescataron diversos restos de fauna del antiguo mercado de la ciudad de Monterrey, entre ellos material de peces. Poco se sabe del antiguo consumo de peces en el noreste de México y estos materiales brindan la oportunidad de explorar ese aspecto. Se analizó un total de 1204 restos de peces, de los cuales el 27% fue identificado y representa a 8 taxa de peces dulceacuícolas (bagres y mojarras) y marinos/estuarinos (robalos, jureles, pargos y corvinas). Predominan los materiales de origen marino, particularmente de las corvinas (*Sciaenops ocellata:* 65 % de los restos identificados y el 35 % de los individuos). La tercera parte de las especies y de los individuos son bagres dulceacuícolas. Monterrey está ubicado en la cuenca del Río Bravo, a 300 km de distancia del Golfo de México, por lo que la presencia de ambos componentes pesqueros indica la existencia tanto de un comercio semilocal (ríos) como de uno a distancia (costera). La representatividad de las regiones corporales sugiere que los peces dulceacuícolas se transportaban completos, y posiblemente sea el mismo caso en los peces marinos.

PALABRAS CLAVE: MONTERREY, MÉXICO, PECES DULCEACUÍCOLAS, PECES MARINOS, HUESO, COMERCIO

ABSTRACT: During renovation works in 2008 at the Metropolitan Museum of Monterrey, faunal remains from the ancient market of Monterrey city, including fish, were collected. Little is known on the consumption of fishes in northeastern México during former times thus this material offered an opportunity to explore the issue. A total of 1,204 fish remains were studied, of which 27% were identifiable. These represent eight taxa of freshwater (i.e. catfishes and mojarras) and marine/estuarine fishes including the snook, crevalle jack, snapper, and red drum. Marine taxa, in particular red drum (*Sciaenops ocellata:* 65% of the identifiable remains and 35 % of the individuals) dominated the sample and fully one third of the specimens and taxa were freshwater catfishes. Monterrey City is located in the Rio Grande basin and lies 300 km away from the Gulf of Mexico. For such reason, the presence of these two fish groups revealed the coexistence of semi-local (fluvial) and long-distance (coastal) trade. The representation of body-fish parts suggests that freshwater fishes were transported whole and it is possible that the same applied in the case of those of marine origin.

KEYWORDS: MONTERREY, MÉXICO, FRESHWATER FISH, MARINE FISH, BONE, COMMERCE

INTRODUCTION

Lately, particular attention has been paid in México to interventions that will affect historic sites, due to the opportunity to recover valuable archaeological materials. One of these occasions were the renovation works carried out in 2008 in the current Metropolitan Museum of Monterrey, and led to the discovery of architectural elements of the ancient market and City Hall, as well as faunal remains and other types of cultural material.

Monterrey (27.67° N, 100.31° W) is the capital of Nuevo León State, and is the third city in importance in México after México City and Guadalajara. Monterrey is located approximately 150 km south of the Rio Bravo o Río Grande, the U. S. natural border, and is separated from the coast for nearly 300 km of plain (Figure 1); it is in a semi-arid area nourished by several springs, crossed by the seasonal Santa Catarina River and 30 km away from the Pesquería River, both tributaries to the Rio Bravo; it is also surrounded by mountains, which allow access to various forestry resources.

History of the government house and adjoining stores

Monterrey was finally founded in AD 1596 by 12 Spanish families. It was planned as the capital of the New Kingdom of León, and required a place to set the royal house of government, jail included, building known in Spanish as "Casas Reales", locating it by AD 1626 in the land now occupied by the Metropolitan Museum of Monterrey (Mota y Escobar, 1940; Cavazos Garza, 1980).

The government building had different destruction and rebuilding periods, driven by flood events that seasonally hit the region. The final construction began in AD 1831 and had several extensions completed all in AD 1887. After the independence of Mexico from Spain, the building housed government offices, tribunals, and more recently, museums (Tovar Esquivel & Santa Cruz Vargas, 2009).

Prior to AD 1655, several independent rooms adjoining the north wall of Casas Reales functioned as stores, and whose rent paid religious services. These rooms were purchased in AD 1824 by the council to expand the government house, by then known as Town Hall and later as City Hall. At about AD 1826, at least one of the ground-floor rooms was used as a kitchen or fonda, and in the next western block, there was a square where edible products such as meat were sold and the whole area was rather unhealthy. The rooms survived until AD 1851, when they were added to the City Hall structure, but the new areas kept their function as fondas and groceries until AD 1936, when the market was taken out of this building (Tovar Esquivel & Santa Cruz Vargas, 2009).

Recent archaeological findings

The 2008 excavations were carried out on the patio and corridors of the ground floor, using a 2x2 m-grid and following stratigraphic levels (Rivera Estrada, 2009). The excavation in the northern side also allowed access to the area of the former food stores.

Explored contexts included hearths, walls, and a block of stone grooved suggesting it was used to slaughter and bleed out animals. Among the recovered materials were lithic artifacts, tiles, mosaics, led plates, metal ornaments, fragments of pottery, glass beads, wood, charcoal and bone artifacts.

Faunal remains belong mostly to European domestic species (such as goat, sheep, cow and chicken): some had cut marks (Cruz, 2008), while others were found inside pots and likely were used for broth (Rivera Estrada, 2009). Elements belonging to rodents and other micromammals were found, and also and unexpectedly, fish remains.

The set of materials was consistent with other findings from dumps of the Colonial period, located in old houses and convents from the sixteenth to the eighteenth centuries in the City of Mexico (*e.g.* Guzmán & Polaco, 2003; Jiménez Badillo, 2003; Valentín Maldonado, 2003). At first glance, it was thought that those materials were from Colonial times (Rivera Estrada, 2009), maybe from the eighteenth century, but the radiocarbon dates reveal that part of the deposit could be even more modern, from the nineteenth to the twentieth centuries (AD 1800-1950).

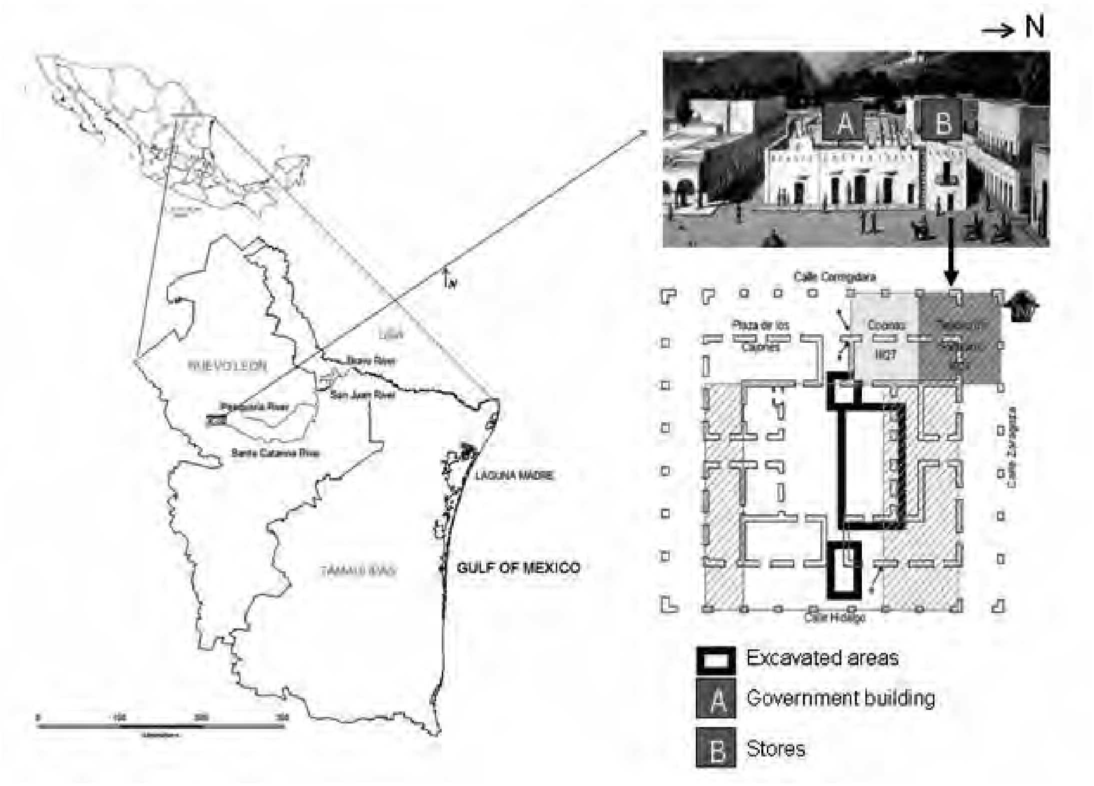

FIGURE 1

Location of the city of Monterrey, Nuevo León, in northern México. Painting taken from Tovar Esquivel & Santa Cruz Vargas (2009). Building plan modified from Tovar Esquivel & Santa Cruz Vargas (2009).

MATERIALS AND METHODS

The study of more than one thousand fish remains, separated from the other faunal elements, followed up the conventional rules relevant to these materials (e.g. Liseau von Lettow-Vorbeck, 1998; Guzmán & Polaco, 2000 and references included there; Reitz & Wing, 2000): (1) cleaning, consolidation and, when necessary, restoration; (2) taxonomic and anatomic classification based on visual examination and verification of preliminary and trouble identifications using specialized literature and the osteological collection of Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano"; (3) quantification of remains (NISP) and individuals (MNI), this last calculated in two ways: MNI_1, based only on anatomical and size criteria, and MNI_2, adding the stratigraphic information; (4) microscopical inspection to analyze and classify taphonomic marks and, (5) analysis of the spatial and vertical distribution of the remains within the site.

RESULTS

Fish resources and their relative importance

One-third of the remains (27.4%) could be taxonomically identifiable, the other part includes elements anatomically identified (but not taxonomically: 44.0%) and non-identifiable in either way (28.6%).

There were eight taxa of bony fish, although only three of them could be identified to species level and happened to be the first evidence of its consumption in the past (Table 1: *Pylodictis olivaris, Sciaenops ocellata*, and "*Cichlasoma*" cf. "*C.*" *cyanoguttatum*); the assemblage comprise two ecological types: marine and freshwater fishes.

Freshwater forms are represented by two types of catfish and one mojarra, with 15 individuals (or 29 when separated by unit and level of excavation), being catfishes more numerous than mojarras (Table 1: 6% remains and 30-31% individuals vs. 0.2% remains and 2-3% individuals). One type of catfish corresponds to genus *Ictalurus*, of which three species are naturally distributed in Nuevo León (Contreras-Balderas *et al*., 1995): *I. furcatus, I. lupus* and *I. punctatus*. The other catfish is named piltonte or piltontle (*Pylodictis olivaris*). These species of catfish are distributed in north-northeast of Mexico and are associated to the rivers that drain into the northern Gulf of Mexico, and except for *Ictalurus lupus*, which is a small size catfish (Page & Burr, 1991: 48 cm total length (TL)), adults of the other three species reach over one meter in length and even get a little larger than 1.5 m TL (Page & Burr, 1991; Miller *et al*., 2005).

As for the mojarra, the species *"Cichlasoma" cyanoguttatum* is widely distributed in the rivers of Nuevo León (Contreras-Balderas *et al*., 1995), making quite possible that the remains correspond to this form. Other species of cichlids are distributed in nearby basins, especially in the coastal slope of neighboring basins with sea outlets (Miller *et al*., 2005).

In general, identified marine fishes have a wide tolerance to changes in salinity (euryhaline), especially in juvenile and pre-adult stages. To this group belong snooks (*Centropomus* sp.), crevalle jacks (*Caranx hippos*), red drums (*Sciaenops ocellata*), and snappers (*Lutjanus* sp.), and recorded 30 individuals (up to 58), being red drums the most represented one (Table 1: 18% remains and 36-49% individuals vs. 3% remains and 24-31% individuals).

There are six species of snooks recorded on the Mexican Atlantic coast, but only the common snook (*Centropomus undecimalis*) and the chucumite or fat snook (*C. parallelus*) reach northeastern Mexico (Rivas, 1986; Robins & Ray, 1986; Castro-Aguirre *et al*., 1999); the first species reaches 1.4 m TL and its wide tolerance to low salinity levels allows it to travel rivers over long distances from the coast; the chucumites are smaller, just over 60 cm TL and are recorded mainly in coastal areas and lagoons (Chavez, 1963; Rivas, 1986; Robins & Ray, 1986; Hoese & Moore, 1998; Castro-Aguirre *et al*., 1999). The crevalle jack grows up to 1 m TL and is distributed throughout the Gulf of Mexico (Castro-Aguirre *et al*., 1999; Secretaría de Pesca, 1989). The red drum, which reaches up to 1.5 m TL, is probably the sciaenid with the greatest tolerance to extreme salinity levels and which has been found in fluvial environments away from the coast (Castro-Aguirre, Espinosa Pérez, and Schmitter-Soto 1999); fisheries on red drum are more common in the northeastern coast of Mexico, since this species is rather unusually south of Lake Tamiahua (21.63° N, 99.55° W) in northern Veracruz (Hildebrand 1958, pers. obs.). The snappers recorded in northeastern Mexico are *L. campechanus* (which normally does not penetrate estuarine areas), *L. cyanopterus*, *L. synagris* and *L. griseus* (Allen, 1985; Castro-Aguirre *et al*., 1999).

Finally, there were one unidentified catfish remain that could belong to a freshwater species (family Ictaluridae) or a marine one (family Ariidae); both kinds of catfishes are known in this area of México (e. g. Miller *et al*., 2005).

The ecological characteristics and geographic distribution of marine fishes, especially the red drum, suggest that fishing was carried out on the northwestern coast of the Gulf of Mexico, most likely in the extensive hypersaline Laguna Madre, in its associated coastal bar, as well as in the mouth of the Río Bravo (Figure 1). The freshwater taxa indicate also the existence of a semi-local fishery, probably from the already mentioned Pesquería River, or from the San Juan River, 45 km southeast of Monterrey (Figure 1).

These conclusions, based on biological information, are reinforced by the quantity of remains and individuals recorded by environment and species (Figure 2). The most consumed fishes were red drums and catfish. This would mean that freshwater fishing, which was a bit less diverse, had a minor role, but not less important, than coastal fishing.

Handling of the fish resource

The skeletal representativeness shows little quantity of cephalic elements, but not its total absence; trunk, fin and skin remains prevail (Table 1). Cephalic elements are more numerous for catfishes, perhaps because the hardness of their cranial bones allows a better preservation, but could also indicate a major closeness from the fishing area to the place of consumption, situation that would make unnecessary to undergo a process of evisceration, cut up and preservation.

For saltwater fish, evidence of transportation of relatively entire specimens is less, due to the limited number of species identified cranial remains, although among the unidentified remains are many

Identification	NISP	NMI$_1$	NMI$_2$	body region																Total
				Head					Trunk				Fins						Skin	
				Neurocranium	Jaws and suspensorium	Hyoid arch	Branchial skeleton	Opercular series	Ribs	Precaudal vertebrae	Caudal vertebrae	Non classified vertebrae	Pectoral girdle and fin	Pelvic girdle and fin	Dorsal and anal fins	Caudal fins	Rays and spines	Not identified remains	Scales	
Ictalurus sp. (freshwater catfish)[1]	60	12	25		1				4	1	2				1					9
* *Pylodictus olivaris* (freshwater catfish)[1]	9	2	2	4	7	8			5	4	1	2	11		1		17			60
Unidentified Siluriformes (catfish)	1												1							1
Centropomus sp. (snook)[3]	6	4	4							2	2		1				1			6
Caranx hippos (crevalle jack)[3]	3	2	3						1		2									3
Lutjanus sp. (snapper)[4]	32	8	14						12				2	2	13	1	2			32
* *Sciaenops ocellata* (red drum)[3]	216	16	37	1					21	36	33	1	21		32	6	62		3	216
** *Cichlasoma*" cf. "C". cyanoguttatum (mojarra)[2]	3	1	3		1			2												3
Unidentified fish remains	530			34	4	9		9	82	6	10	8	21	7	39	10	166	47	78	530
Unidentifable fish remains	344			33				1	15		1	2	3		10	2	81	14	182	344
TOTAL	1204	45	88	72	13	17	0	12	140	49	51	13	60	9	96	19	329	61	263	1204

* = new records for Mexican archaeological contexts. Ecological classification taken from Castro-Aguirre et al. (1999): 1 = primary freshwater fish, 2 = secondary freshwater fish, 3 = estenohaline marine fish, 4 = estenohaline/eurihaline marine fish

TABLE 1

Taxa list, NISP, MNI, ecological classification, and discarded body parts of fishes from the ancient market Monterrey, Nuevo León, México..

cephalic elements (Table 1). So, it is assumed that, just as it happened in other Pre-hispanic, Colonial and Modern inland archaeological sites of México, marine fish were marketed, as a general rule, without removing their head (e.g. Guzmán, 2002, 2005; Guzmán & Polaco, 2003, 2008; Guzmán *et al.*, 2008; Guzmán & Hernández Luna, 2011), a situation which did not restrain the fact that they could had been somehow preserved before its trade (either smoked, salted, dried, etc.).

The presence of burned remains as well as cutmarks (Figure 3), involving different bones of several identified and unidentified taxa, is a further evidence of handling the fishes, that could have been made either by the preservation method or during the cooking phase. Environmental and biological marks were more numerous, though, suggesting remains were, at some point, in a superficial deposit.

Distribution of the remains within the site

Fish remains come from trenches L to P (Figures 1 and 4), which are associated to the courtyard and the northern corridor of the current building. Most remains were concentrated towards the northern half of the patio, particularly in three excavated units (L16, M12 and M15). In accordance with the reconstruction of the limits of the Casas Reales and the stores (Tovar Estrada & Santa Cruz Vargas, 2009), the area of waste would be outside but contiguous to the kitchens, and probably become dispersed into the courtyard of Casas Reales by a process of filling and leveling of the floors (Figure 4).

The stratigraphic distribution of the fish remains within two of the excavation units above mentioned (Figure 5) shows a higher concentration of bones and species from layers III to V. These layers are located at about half a meter deep, suggesting that those are the levels of the original dump.

DISCUSSION AND FINAL COMMENTS

According to the database on archaeoichthyology in Mexico (Polaco & Guzmán, 1997; Guzmán & Polaco, 2005; Guzmán, 2007), this finding is the first record of ancient fish consumption in northern

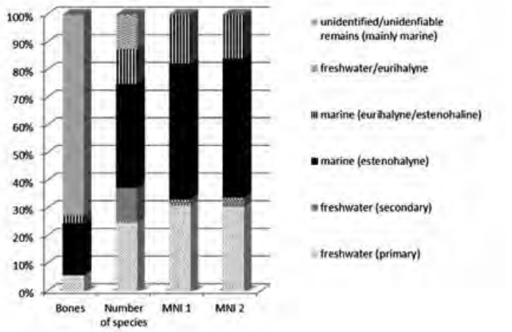

FIGURE 2

Proportion of species, bones and individuals per ecological category of fish.

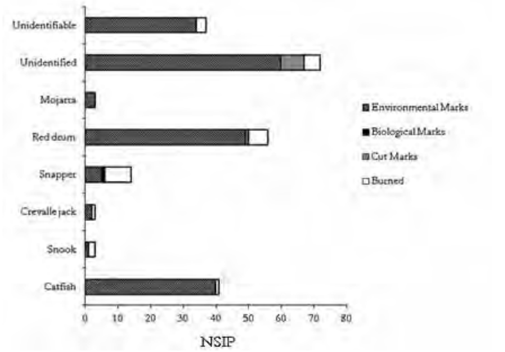

FIGURE 3

Observed taphonomic marks in the fish remains.

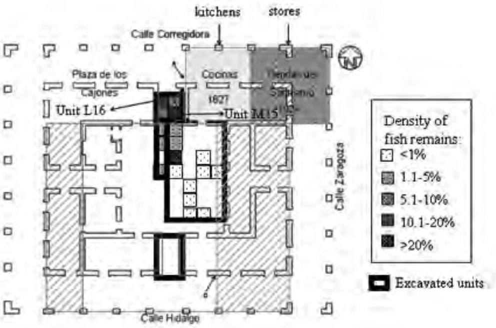

FIGURE 4

Horizontal distribution of fish remains within the ancient kitchen installations (modified from Tovar Esquivel & Santa Cruz Vargas, 2009). Location of units L16 and M15 is marked.

Nuevo León, with three species also first recorded for the country; thus, the continued study of more remains and sites keeps broading the range of species consumed in the past and changing the vision of economic dynamics of ancient Mexican societies. The only other known state record is based in a cleithrum of *Ictalurus*, which was recovered in a native settlement in southern Nuevo León (Álvarez Solórzano & Ocaña Marín, 2000).

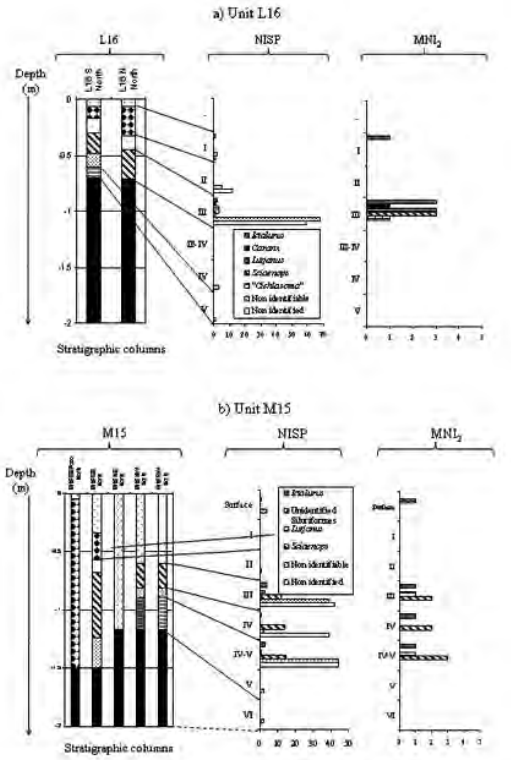

FIGURE 5

Vertical distribution of fish remains in the units with higher concentrations of these bones.

Finding fish remains in Monterrey is somewhat unusual, as economy of northern Mexico, since colonial times to present day, has relied on livestock in such a way that, for example, regional cuisine in Nuevo Leon is based on goat (*Capra aegagrus hircus*).

Unfortunately, the few historical documents for the area do not mention fish consumption among the city dwellers, only referring that it was done by indigenous peoples, many of whom, such as the "Comepescado" or "Fish-eater" people of southern Nuevo León, disappeared or were absorbed almost immediately after the arrival of Spaniards (Orozco y Berra, 1864; Mota y Escobar, 1940). Snook, catfish, mojarra, trout and bream were among the freshwater fishes known at the beginning of the twentieth century (León & Sánchez de Zamora, 1909), corresponding, respectively, to *Micropterus salmoides* (commonly known in México as lobina), ictalurids, cichlids, *Agonostomus monticula* (also known as tepemichin) and *Aplodinotus grunniens*.

Carrying sea fish to Monterrey should not pose major difficulties, as the 300 km in distance to the coast is made of flat land. Written sources from the eighteenth century failed to mention Monterrey as a trade destination city for the products from traditional fishing grounds (*e.g.* Ximénez, 1967). No fish was mentioned by early twentieth century chroniclers of Monterrey, who instead described live chickens and goats in the marketplace waiting to be slaughtered (Saldaña, 1943, in Tovar Esquivel & Santa Cruz Vargas, 2009). It is during the mid-twentieth century when it is known that part of the fish catches of the Laguna Madre was sent to Monterrey, specifically crevalle jacks, exporting red drum catches to the Texas market (Hildebrand, 1958).

Although the exact reason for the fish consumption at the Market remains unsolved (regular or sporadic consumption? Holy Week rite?), the archaeological record is once more an essential tool to provide information which would be impossible to ascertain by other means, broading the range of species consumed in the past and changing the vision of economy dynamics of societies.

REFERENCES

ALLEN, G.R. 1985: *FAO species catalogue. Vol. 6. Snappers of the world: an annotated and illustrated catalogue of lutjanid species known to date*. FAO Fisheries Synopsis 125(6): 1-208.

ÁLVAREZ SOLÓRZANO, T. & OCAÑA MARÍN, A. 2000: *Análisis de los restos óseos procedentes del abrigo del Cañón de Alardín, Nuevo León, México*. Informe del Laboratorio de Arqueozoología. Subdirección de Laboratorios y Apoyo Académico, INAH, México.

CASTRO-AGUIRRE, J. L.; ESPINOSA PÉREZ, H. S. & SCHMITTER-SOTO, J. J. 1999: *Ictiofauna estuarino-lagunar y vicaria de M*éxico. Limusa and Instituto Politécnico Nacional, México.

CAVAZOS GARZA, I. 1980: *El muy ilustre Ayuntamiento de Monterrey desde 1596*. Editorial Ricardo Covarrubias, Monterrey.

CHÁVEZ, H. 1963: Contribución al conocimiento de la biología de los robalos, chucumite y constantino (*Centropomus* spp.) del estado de Veracruz. *Ciencia* 22(5): 141-162.

CONTRERAS-BALDERAS, S.; LOZANO-VILANO, M. L. & GARCÍA-RAMÍREZ, M. E. 1995: Tercera lista anotada y revisada de los peces de Nuevo León. In: Contreras-Balderas, S.; González-Saldívar, F.; Lazcano-Villareal, D. & Contreras-Arquieta, A. (eds.): *Listado preliminar de la fauna silvestre del estado de Nuevo León, México*: 73-78. Consejo Consultivo Estatal para la Preservación, y Fomento de la Flora y Fauna Silvestre de Nuevo León, Monterrey.

CRUZ, J. A. 2008: *Análisis del material óseo del Proyecto de Salvamento Arqueológico "Museo Metropolitano de Monterrey", primer informe*. Centro INAH Nuevo León, Monterrey.

GUZMÁN, A. F. 2002: *Los peces del sitio arqueológico El Coroco, Ciudad de México, Distrito Federal*. Informe del Laboratorio de Arqueozoología. Subdirección de Laboratorios y Apoyo Académico, INAH, México.

— 2005: Restos de peces del sitio Toluquilla, Querétaro. *Arqueo·Ciencias* 1: 15-22.

— 2007: Los peces de las ofrendas del Complejo A del Templo Mayor: una aproximación biológica y arqueozoológica. Tesis Doctoral. Universidad Autónoma de Madrid, Madrid.

GUZMÁN, A. F. & HERNÁNDEZ LUNA, C. A. 2011: *Restos de peces recuperados en las excavaciones del Palacio de la Autonomía Universitaria, Distrito Federal*. Informe del Laboratorio de Arqueozoología. Subdirección de Laboratorios y Apoyo Académico, INAH, México.

GUZMÁN, A. F. & POLACO, O. J. 2000: *Los peces arqueológicos de la Ofrenda 23 del Templo Mayor de Tenochtitlan*. México. Instituto Nacional de Antropología e Historia, México.

— 2003: El consumo de peces en una casa del siglo XVI en la ciudad de México. In: Matos Moctezuma, E. (coord.): *Excavaciones del Programa de Arqueología Urbana*: 39-73. Instituto Nacional de Antropología e Historia, México.

— 2005: La arqueoictiología en México. *Revista Digital Universitaria* 6(8). http://www.revista.UNAM.mx/vol.6/num8/art85/int85.htm.

— 2008: *La arqueofauna del sitio Xalasco*. Informe del Laboratorio de Arqueozoología. Subdirección de Laboratorios y Apoyo Académico, INAH, México.

GUZMÁN, A. F.; GUILLIEM, S. & POLACO, O. J. 2008: The fishes in a 16th century water box in Tlatelolco, Central México. In: Béarez, P.; Grouard, S. &

Clavel, B. (coords.): *Archeologie du poisson. 30 ans d'archéo-ichtyologie au CNRS* (*Hommage aux travaux de Jean Desse et Nathalie Desse-Berset*): 397-407. Éditions APDCA, Antibes.

Hildebrand, H. H. 1958: Estudios biológicos preliminares sobre la Laguna Madre de Tamaulipas. *Ciencia* 17: 51-173.

Hoese, H.d. & Moore, R. H. 1998: *Fishes of the Gulf of Mexico*. 2nd edition. A&M University Press, Texas.

Jiménez Badillo, D. 2003: El rescate arqueológico [de Palacio Nacional]. In: Matos Moctezuma, E. (coord.): *Excavaciones del Programa de Arqueología Urbana*: 87-107. Instituto Nacional de Antropología e Historia, México.

León, A. de, [Juan Bautista Chapa] & Sánchez de Zamora, F. 1909: Historia de Nuevo León, con noticias sobre Coahuila, Tamaulipas, Texas y Nuevo México. In *Documentos inéditos o muy raros para la historia de México* (published by G. García), vol. XXV. Librería de la Vda. De Ch. Douret, México.

Liseau Von Lettow-Vorbeck, C. 1998: El Soto de Medinilla: faunas de mamíferos de la Edad del Hierro en el Valle del Duero (Valladolid, España). *Archaeofauna* 7: 1-215.

Miller, R. R.; Minckley, W. L. & Norris, S. M. 2005: *Freshwater fishes of México*. The University of Chicago Press, Chicago.

Mota y Escobar, A. De La 1940: *Descripción geográfica de los reinos de Nueva Galicia, Nueva Vizcaya y Nuevo León*. 2ª ed. Editorial Pedro Robredo, México.

Orozco y Berra, M. 1864: *Geografía de las lenguas y carta etnográfica de México: precedidas de un ensayo de clasificación de las mismas lenguas y de apuntes para las inmigraciones de las tribus*. J.M. Andrade & F. Escalante, México.

Page, L. M. & Burr, B. M. 1991: *A field guide to freshwater fishes of North America north of Mexico*. Houghton Mifflin Company, Boston.

Polaco, O. J. & Guzmán, A. F. 1997: *Arqueoictiofauna Mexicana*. Instituto Nacional de Antropología e Historia, México.

Reitz, E. J. & Wing, E. S. 2000: *Zooarchaeology*. Cambridge University Press, Cambridge.

Rivas, L. R. 1986: Systematic review of the perciform fishes of the genus *Centropomus*. *Copeia* 1986(3): 579-611.

Rivera Estrada, A. 2009: *Proyecto de Salvamento Arqueológico "Museo Metropolitano de Monterrey"*. Informe técnico. Instituto Nacional de Antropología e Historia, Monterrey.

Robins, C. R. & Ray, G. C. 1986: *A field guide to the Atlantic coast fishes*. Houghton Mifflin Company, Boston.

Saldaña, J. P. 1943: *Historia y tradiciones de Monterrey*. Impresora Monterrey, Monterrey.

Secretaría de pesca, 1989: *Pescados y mariscos de las aguas mexicanas: catálogo*. Secretaría de Pesca, México.

Tovar Esquivel, E. & Santa Cruz Vargas, J. 2009: *Monterrey, origen y destino: el Antiguo Palacio Municipal, de la Colonia a los tiempos revolucionarios*. Municipio de Monterrey e Instituto Nacional de Antropología e Historia-Nuevo León, Monterrey.

Valentín Maldonado, N. 2003: Análisis de material zoológico. In: Matos Moctezuma, E. (coord.): *Excavaciones del Programa de Arqueología Urbana*: 27-37. Instituto Nacional de Antropología e Historia, México.

Ximénez, F. 1967: *Historia natural del Reino de Guatemala*. Publicación Especial de la Sociedad de Geografía e Historia de Guatemala, and Editorial "José de Pineda Ibarra", Guatemala.

Archaeofauna 25 (2016): 15-32

Scutes for Sturgeon Size Reconstruction: Traditional and Geometric Morphometric Techniques Applied to *Acipenser sturio* and *A. oxyrinchus*

ELS THIEREN & WIM VAN NEER*

Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium; Laboratory of Biodiversity and Evolutionary Genomics, KU Leuven, Ch. Debériotstraat 32, B-3000 Leuven, Belgium.

* Corresponding author: Wim Van Neer: [wvanneer@naturalsciences.be]

(Received *18 February 2015*; Revised *2 April 2015*; Accepted *4 May 2015*)

RESUMEN: Se exploran alternativas tradicionales y de morfometria geométrica en la inferencia de la talla del esturión europeo *(Acipenser sturio)* y Atlántico *(A. oxyrinchus)* a partir de placas dérmicas. La correlación existente entre la longitud del pez y diferentes medidas de las placas dérmicas fue evaluada a través de regresiones lineales utilizando 58 esturiones en colecciones de museos. Dado que la precisión de tal técnica era limitada se exploró la posibilidad de determinar la posición de placas dérmicas aisladas dentro de la series corporales en función de su forma y dimensiones. Aunque en las filas laterales y dorsales la forma y tamaño de las placas cambia a lo largo del eje antero-posterior, las diferencias son demasiado graduales para poder establecer la posición original de una placa dentro de la serie. También se constataron las diferencias de talla y forma en placas procedentes de esturiones de distinto tamaño, pero estas tampoco eran suficientemente marcadas como para realizar una estimación precisa de la talla corporal. Se concluye por ello que las placas dérmicas aisladas no pueden proporcionar estimaciones precisas de la tallas corporal. No obstante, los modelos de regresión que presentamo permiten verificar si tanto las placas dérmicas laterales como las dorsales pertenecieron a esturiones de más de un metro de longitud. En caso afirmativo, las placas pueden ser identificadas a nivel de la especie a través de su ornamentación al tratarse ésta de un carácter dependiente de la talla.

PALABRAS CLAVE: RECONSTRUCCIÓN DE LA TALLA, MORFOMETRÍA GEOMÉTRICA, MORFOMETRÍA TRADICIONAL, PLACA DÉRMICA, *ACIPENSER STURIO, ACIPENSER OXYRINCHUS*

ABSTRACT: Different traditional and geometric morphometric approaches are explored for the size reconstruction of European *(Acipenser sturio)* and Atlantic sturgeon *(A. oxyrinchus)* on the basis of isolated bony scutes. The relationship between fish length and different scute measurements was tested with linear regressions using 58 modern sturgeons from museum collections. As the accuracy of this approach was limited, we explored the possibility of determining the position of an isolated scute within its row on the basis of its shape or dimension. In the dorsal and lateral rows, the shape and dimension of the scutes change along the antero-posterior axis, but this difference is too gradual to allow establishing the original position of an isolated scute within the row. No consistent changes in the shape or dimensions of ventral scutes were observed according to their place within the row. Differences in scute shape or dimensions between large and small animals have been documented as well, but these differences were not sufficiently pronounced for an accurate estimation of size. We conclude that isolated scutes cannot provide very accurate fish length reconstructions. However, the regression models presented in this study, allow verifying whether individual lateral and dorsal scutes belonged to sturgeons larger than 1 m total length. In that case they can be identified to species level on the basis of their surface ornamentation, which is size dependent.

KEYWORDS:SIZE RECONSTRUCTION, GEOMETRIC MORPHOMETRICS, TRADITIONAL MORPHOMETRICS, SCUTE, *ACIPENSER STURIO, ACIPENSER OXYRINCHUS*

INTRODUCTION

Relationships between fish size and measurements taken on isolated skeletal elements are provided in the literature for numerous fish species (e.g. Leach *et al.*, 1996; Harvey *et al.*, 2000; Thieren *et al.*, 2012). These equations are used for the back-calculation of fish lengths of archaeological remains, which provide information on former fishing methods, exploited fishing grounds, selective consumer behavior and human impact on fish populations through time (Greenspan, 1998; Leach & Davidson, 2001). When dealing with sturgeon remains from Western European sites, it is essential to first reconstruct fish size of the skeletal elements that need to be identified to species. The distinction between archaeological dermal bones of the two European sturgeon species, *Acipenser oxyrinchus* Mitchill 1815 and *A. sturio* Linnaeus 1758, can be made by the difference in the bone's surface structure, with *A. sturio* having a 'tubercular' surface pattern and *A. oxyrinchus* an 'alveolar' pattern (Magnin, 1964; Desse-Berset, 2009). However, this pattern is to some extent size dependent (Wuertz *et al.*, 2011; Thieren *et al.*, in press). Large *A. oxyrinchus* display the alveolar ornamentation type in most cases, but the ornamentation of small *A. oxyrinchus*, less than 1m total length (TL), is similar to that of *A. sturio*, and this on the scutes as well as on the bones of the head and pectoral girdle (Thieren *et al.*, in press). Therefore, it is important to establish the size of archaeological remains with a tubercular ornamentation pattern before assigning them to species. Skeletal elements of the head and the pectoral girdle allow a rather accurate size estimation (Thieren & Van Neer, 2014). These bones are frequently retrieved from archaeological excavations, and often sufficiently preserved to allow size reconstruction. However, since scutes are more numerous in archaeo-ichthyological assemblages it is worth investigating their potential for fish length reconstruction.

Dermal scutes are found in all acipenserids and occur in 5 rows alongside the body (Figure 1). Besides one median dorsal row, there is a lateral and ventral row on each side of the body, with the number of scutes depending on row and species. *A. oxyrinchus* has 7 to 16 dorsal scutes, 24 to 35 lateral and 6 to 14 ventral scutes, while *A. sturio* has 9 to 16 dorsal, 24 to 40 lateral and 8 to 15 ventral scutes (Jordan, 1910; Vladykov & Beaulieu, 1946; Mohr, 1952; Magnin, 1964; Vasil'eva, 1999; Vecsei *et al.*, 2001; Desse-Berset, 2011; Wuertz *et al.*, 2011). The number of scutes varies between individuals, and, in the case of the paired rows, sometimes even between the left and right row of the same individual (Vladykov & Beaulieu, 1946). Both *A. oxyrinchus* and *A. sturio* keep their scutes throughout their lives with size and thickness increasing during growth (Magnin, 1963). Resorption of scutes observed in other sturgeon species, e.g. *A. fulvescens* (Peterson *et al.*, 2007), has not been reported in *A. sturio* and *A. oxyrinchus*.

Scutes vary considerably in shape and size between rows and also within each row. However, determining the row from which an isolated scute is derived, is straightforward if the element is sufficiently well preserved. Dorsal scutes are symmetrical and dihedral, and they have a distinctive median crest (Magnin, 1963). An unornamented articulation area can be seen in their anterior part (Figure 1c). The dorsal scute row starts from the median nuchal plate which is fully incorporated in the skull roof and ends with the last large scute before the dorsal fin basal fulcrum. Although the fulcrum has a different shape compared to the dorsal scutes, some authors (e.g. Brinkhuizen, 1986; Desse-Berset, 2011) consider this element as the last dorsal scute. Sometimes one or two pairs of smaller bony plates are situated between the last

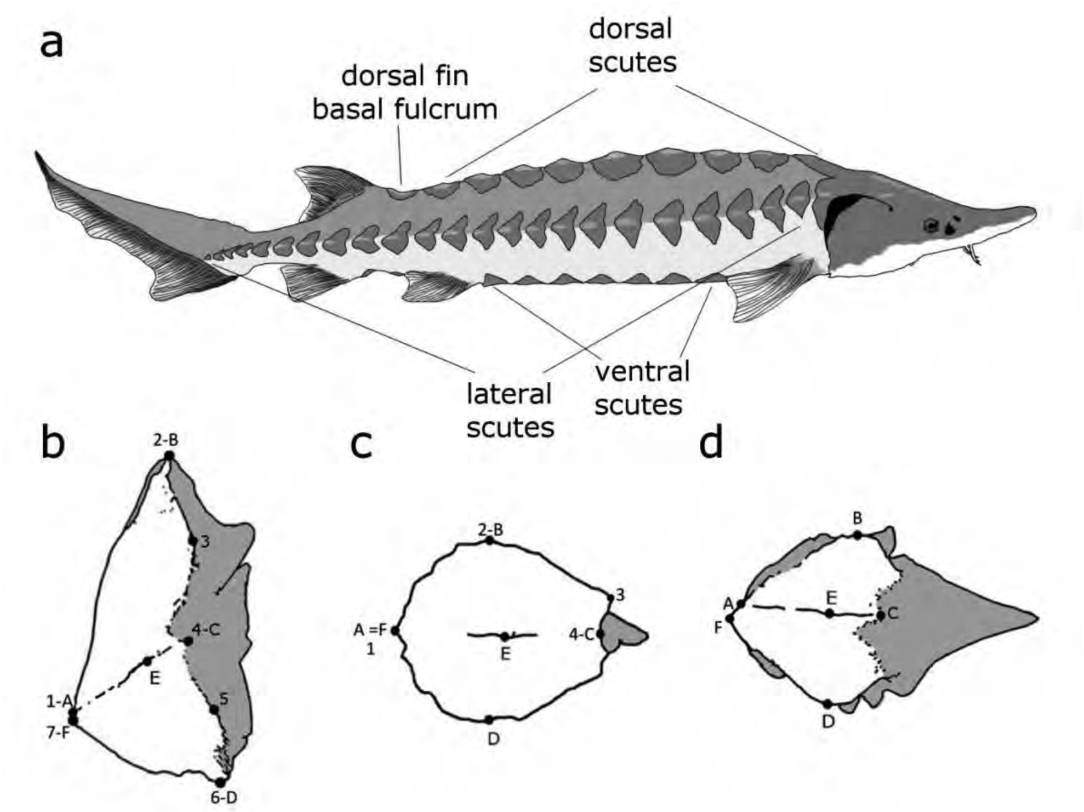

FIGURE 1

Overview of the scutes. a. Complete individual with the dorsal, lateral and ventral scutes; b. Isolated right lateral scute; c. Isolated dorsal scute; d. Isolated right ventral scute. The unornamented articulation area is indicated in grey. Following measurements were defined: M1: B-D; M2: A-C; M3: F-E; M4: B-E; M5: B-C; M6: B-F; M7: D-E; M8: D-C; M9: D-F. Landmarks on lateral scutes (b) are labelled 1 to 7: 1. The point where the keel ends caudally; 2. The dorsal point of the scute 3. Curve point in the upper scute wing, 4. The anteriormost point of the keel in the ornamented part of the scute; 5. The curve point in the lower scute wing; 6. The ventral point of the scute; 7. The posterior point of the scute. Landmarks on the dorsal scute (c) are labelled 1 to 4: 1. The posterior point of the scute; 2. The left lateral point of the scute; 3. Curve point; 4. The anteriormost point of the keel in the ornamented part of the scute.

'regular' dorsal scute and the dorsal fin fulcrum, but these are not considered dorsal scutes. These additional scutes are rounded, they are without the longitudinal crest and do not have the characteristic anterior articulation area.

The lateral scutes are situated on the right and left side of the body at the level of the lateral line. The shape of the lateral scutes is more or less rhomboid, with the crest of the scute usually coinciding with the short diagonal of the rhomboid (Sewertzoff, 1926; Brinkhuizen, 1986) (Figure 1b). Magnin (1963) describes the shape of lateral scutes as triangular, wider than their length and pointing backwards, with the articulation area situated at the base of the scutes. This area does not display any surface structure and lies underneath the previous scute in small animals. The lateral row starts directly behind the supracleithrum, although some authors (e.g. Vladykov & Beaulieu, 1946) consider that bone as the first lateral scute. The last scute with a ridge or crest along its short axis is considered as the last scute.

The ventral scutes occur medio-caudally of the clavicles between the pectoral and pelvic fins. They are also paired and resemble the dorsal scutes but are asymmetrically shaped (Figure 1d). The last scute, and sometimes also the first one, have an aberrant shape, with the last one being more rounded and the first one irregularly shaped.

In addition to the aforementioned scutes, smaller bony plates are situated between the pelvic and anal fin (pre-anal scutes), next to the anal fin base and behind the anal fin (post-anal scutes). These scutes are not further considered in this study. Their shape is very similar to that of the dorsal pairs of smaller scutes mentioned above: they are rounded and without the distinctive crest and characteristic unornamented articulation area.

Attempts have been made before to reconstruct the length of sturgeons from their scutes. For example, van Maren (1971) back-calculated the total length of sturgeon remains from the Neolithic site of Vlaardingen (the Netherlands) by comparing the archaeological scutes with a single modern museum specimen of known size. However, it is unclear how the original position of an archaeological scute within the row was determined in that study. Since the dimensions of scutes vary considerably within one row, this method may have been somewhat inaccurate and the results of van Maren (1971) should therefore be interpreted with caution. Brennan & Cailliet (1989) described a linear relationship between the TL of white sturgeon (*A. transmontanus*) and the width of the median nuchal plate, and between TL and dorsal scute length. It is not mentioned explicitly which dorsal scutes were considered for these relationships. Benecke (1986) calculated total lengths of up to 5 m for archaeological sturgeons from Ralswiek (Germany) by comparing the dorso-ventral and postero-anterior lengths of archaeological scutes to those of the scutes from one recent specimen of known size. Debus (1999) recalculated the total lengths of the same remains, using a linear regression of TL on the dorso-ventral length of the largest lateral scute from 33 Baltic sturgeons (then assumed to be *A. sturio*) and obtained a maximum length of 2.75 m. This method will result to some extent in an underestimation of the TL since it is based on the dimensions of the largest lateral scute of modern sturgeons, and because evidently not all archaeological scutes used for size reconstruction will have been the largest of the sturgeon from which it is derived.

Brinkhuizen (1989: 254-255) used an alternative approach and took into account the size variation along the lateral scute row by providing a minimum and maximum TL estimation for each measurable archaeological scute (assumed to be *A. sturio*). Using 4 museum specimens as a reference, he calculated two least square regressions between the greatest height of the lateral scute and TL of the sturgeon, namely one for the smallest and one for the largest scute of each modern individual. These two regression equations were then used to establish the minimum and maximum length corresponding to 6 lateral archaeological scutes from the Roman site of Velsen (the Netherlands), all assumed to come from the same animal. The size reconstruction ranged between 96 cm - based on the largest archaeological scute assumed to be the largest within the original scute row - and 126 cm, based on the smallest archaeological scute assumed to be the smallest scute within the row.

Finally, using 9 reference specimens, Desse-Berset (2011) constructed a regression model to calculate the TL of *A. oxyrinchus* from the width of the dorsal scute. The model was based on the mean of the widths of the dorsal scutes, excluding both the first scute (the so-called nuchal plate) and the dorsal fin basal fulcrum. The author stipulates that the estimation of the TL would be more precise if the place of the scute within the row could be determined more precisely.

In the present paper, we further explore the possible value of scutes for size reconstruction using three different approaches. The first one is a direct back-calculation of TL based on the regression of TL on different scute measurements. Secondly, we tried to improve the former approach by estimating the position of an individual scute within its row through measurements or through its shape. As a third approach, measurements and shape of individual scutes were used to define size classes.

MATERIAL & METHODS

In this study, 58 dry mounted or liquid preserved *A. sturio* and *A. oxyrinchus* specimens from different European museum collections were used as reference material (Table 1). These include 19 *A. sturio*, 27 *A. oxyrinchus*, 5 hybrids and 7 *A. oxyrinchus*/*A. sturio* (indet.) (for species identifications, see Thieren *et al.*, in press) with sizes ranging between 17.7 and 276 cm TL. For 32 of these specimens, the morphological species identification was confirmed through genetic analysis, either through our own analysis (Thieren *et al.*, in press) or published data (Ludwig *et al.*, 2002; Chassaing *et al.*, 2013). Sixteen of them were identified as *A. oxyrinchus*, 11 as *A. sturio* and 5 as hybrid. The examined specimens were more or less complete, with the scutes still embedded in the animal, for this reason only the visible part of the scute, the part with surface structure, could be examined.

Nr	Specimen	Species
1	AML 8797	*A. oxyrinchus*
2	BAI 1884	*A. sturio*
3	DCB 721	*A. sturio*
4	KUL MD N/A	*A. oxyrinchus*
5	MHNN Z19398	*A. sturio**
6	MHNN Z19558	*A. oxyrinchus**
7	MHNN Z58274	*A. sturio**
8	MHNN Z58275	*A. sturio**
9	MNHN-IC-0000-3108	*A. oxyrinchus**
10	MNHN-IC-0000-3110	*A. oxyrinchus**
11	MNHN-IC-0000-3113	*A. oxyrinchus**
12	MNHN-IC-0000-3115	Hybrid*
13	MNHN-IC-0000-3119	*A. sturio**
14	MNHN-IC-0000-3574	Indet.
15	MNHN-IC-0000-4843	*A. oxyrinchus*
16	MNHN-IC-0000-9114	*A. oxyrinchus*
17	MNHN-IC-1969-0172	*A. oxyrinchus**
18	MNHN-IC-B-2598	*A. oxyrinchus**
19	MRSN N/A	*A. oxyrinchus*
20	NHM 1859.3.51.1	*A. oxyrinchus*
21	NHM 1865.5.23.3	*A. oxyrinchus*
22	NHM 1886.8.24.1	Indet.
23	NHM 1931.12.7.1	*A. sturio*
24	NHM 1986.5.21.1	Indet.
25	NHM 2005.6.22.6	*A. oxyrinchus*
26	NHM 2015.2.18.1	*A. sturio*
27	NRM 94	Indet.
28	NRM 1709	*A. oxyrinchus**
29	NRM 8948	*A. sturio*
30	NRM 13336	*A. sturio**
31	NRM 18265	*A. sturio*
32	NRM 21705	*A. oxyrinchus*
33	NRM 21707	*A. oxyrinchus**
34	NRM 21708	*A. sturio**
35	NRM 21710	*A. sturio**
36	NRM 21712 (Large)	Hybrid*
37	NRM 21712 (Middle)	Hybrid*
38	NRM 21712 (Small)	Hybrid*
39	NRM 35435	*A. sturio**
40	NRM 35438	*A. oxyrinchus**
41	NRM 35439	*A. sturio**
42	NRM 35442	*A. sturio*
43	NRM 36002	Indet.
44	NRM 36074	*A. oxyrinchus*
45	NRM 49317	*A. oxyrinchus**
46	NRM 55538	*A. oxyrinchus*
47	NRM 60292	*A. oxyrinchus**
48	NRM 60821	*A. oxyrinchus*
49	NRM 61784	*A. oxyrinchus*
50	RBINS 1528	*A. oxyrinchus**
51	RBINS 24792	*A. oxyrinchus**
52	RBINS 4449	*A. sturio*
53	RBINS N/A (1)	*A. sturio**
54	RBINS N/A (2)	Hybrid*
55	RBINS N/A (5)	*A. sturio*
56	SML N/A	*A. oxyrinchus**
57	UUZM UPSZTY 170	Indet.
58	UUZM UPSZTY N/A	Indet.

TABLE 1

List of the examined specimens. Genetic identifications are indicated with *

Traditional morphometrics

Traditional morphometry often uses distances between landmarks, angles and ratios to study the shape of objects. For our study we measured the TL of the sturgeons and took nine measurements on dorsal, lateral and ventral scutes (Figure 1b-d). These nine measurements (M1 to M9) were made on scutes with an uneven rank. Only measurements M1 and M2 were recorded for scutes with an even rank due to time constraints. Measurements were made only on the right side of the specimen for the paired scutes of the lateral and ventral row. When this proved to be impossible due to the preservation state or accessibility of the animal, left-sided scutes were measured. Measurements on bones were taken with digital callipers to the nearest 0.1mm.

Landmark-based geometric morphometrics

In order to explore the differences in scute shape in relation to their place within the scute row or to the TL of the animal, landmark-based geometric morphometric techniques were used, in which shape is described by landmark configurations on biological forms or images.

Using tpsDig v.2.16 (Rohlf, 2010a), landmarks were digitized on images of dorsal and lateral scutes only. Ventral scutes are unsuitable for 2D geometric morphometrics because they are strongly angulated, with one half on the scute faced sideways and the other half downwards. Therefore, no coplanar landmarks can be defined. The images of the scutes were taken in an as standardized way as possible, which was not always easy because the reference sturgeon specimens are often large and difficult to access. Only the lateral scutes on the right side of the animal were considered, except when this was impossible due to the preservation state or accessibility of the specimen. In that case, landmarks were digitised on mirrored images of the scutes on the left side of the body. In total, 7 landmarks were digitised on the lateral scutes; on the left part of the dorsal scute 4 landmarks were digitized (Figure 1b-c).

Statistical analysis

Shape analysis

To remove effects of translation, scale and rotation, landmark coordinates were submitted to a General Procrustes Analysis (GPA) in tpsRelw v.1.49 (Rohlf, 2010b). The centroid size, i.e. the square root of the summed squared distances of each landmark to the centroid of the landmark configuration, and the weight matrix (W matrix), containing partial warps and uniform components, were generated for further statistical analysis. TpsSmall v. 1.20 (Rohlf, 2003) was used to test whether the tangent space approximation is sufficient to use the landmark coordinates for statistical analysis. Procrustes distances between specimens in Procrustes alignment were plotted against the Euclidean distances in the tangent space. If slope and correlation were more or less equal to one, the approximation was sufficient and statistical analysis could thus proceed.

General statistical analysis

Scute measurements as ratios to TL and W matrices were subjected to Principal Component Analysis (PCA) to explore the pattern of variation among the different specimens and the different positions within the scute rows. To test for potential species-specific differences in scute dimensions and shape, Analysis of Variance (ANOVA) was used. Pearson correlation coefficients (r) and coefficients of determination (R^2) were determined to evaluate the potential of scute measurements for the estimation of TL. The relationships between TL and the different measurements were modelled using simple linear regression.

Canonical Variates Analysis (CVA) was performed to assess whether the original place within the dorsal, lateral or ventral row of an isolated scute can be estimated with scute measurements or the W matrix and to assess whether an isolated scute can be assigned to a certain size class. CVA on data which is not independent leads to the overestimation of the potential to discriminate between the different classes and to an increased probability of erroneously rejecting the null hypothesis, i.e. that there is no discrimination between groups (type I error). Therefore, in case the percentage of classification was deemed significantly high, results were cross validated by subsequently repeating the CVA with all scutes from one individual used as test-dataset.

Since the number of variables exceeded the number of observations in some groups, which can lead to increased chances of overfitting, CVA was conducted on the original dataset and repeated after the reduction of dimensionality with PCA.

Statistical analysis was performed with STATISTICA (StatSoft Inc., 2013) and R (R Core Team, 2014).

RESULTS AND DISCUSSION

Differences in scute size between species

Differences in scute size between *A. sturio* and *A. oxyrinchus* have been reported in the literature, with scutes of *A. oxyrinchus* being larger than those of *A. sturio* (Magnin, 1964; Desse-Berset, 2011; Wuertz *et al.*, 2011). Our own morphometric analysis on dorsal and lateral scutes from the 32 genetically identified sturgeon specimens confirmed this. Statistically significant differences between species were found for measurements M1/TL and M2/TL on the lateral scutes (ANOVA, M1: $F_{(2,941)}$=3.48, p<0.05; M2: $F_{(1,796)}$=21.56, p<0.001) and dorsal scutes (ANOVA, M1: $F_{(2,341)}$=27.02, p<0.001; M2: $F_{(2,339)}$=22.59, p<0.001). For the ventral scutes, only a statistically significant difference for M1/TL was observed (ANOVA, $F_{(2,267)}$=2.802, p<0.05).

Similar species specific differences were found with geometric morphometric analysis of the scutes. As mentioned above, 2D geometric morphometrics techniques cannot be applied on ventral scutes since they are strongly angulated and no coplanar landmarks could be defined. Seven landmarks were digitized on a total of 605 lateral scutes and 4 landmarks were digitized on a total of 239 dorsal scutes from 10 *A. sturio*, 13 *A. oxyrinchus* and 5 hybrids (for species identification, see Thieren *et al.*, in press). Landmarks were superimposed twice: once for all scutes from the same rank and once for all ranks pooled together. In both cases, the tangent space approximation was considered sufficient for further statistical analysis (slope and correlation coefficient almost equal to 1). Although no species-specific differences in centroid size per rank were detected (ANOVA, p>0.05), when data from all scute ranks were pooled, the centroid size of lateral and dorsal scutes differed significantly between species (ANOVA, lateral: $F_{(2,602)}$=37.3, p<0.00001; dorsal: $F_{(2.236)}$=5.6, p<0.005), with the scutes of *A. oxyrinchus* and hybrids being larger than those of *A. sturio*. This difference in scute size between *A. sturio* and *A. oxyrinchus* is most likely related to the larger number of scutes in *A. sturio*. Because this species has a larger number of scutes, they are smaller compared to those of *A. oxyrinchus* of the same length.

This means that size reconstruction would be more accurate if separate models would be constructed for each species. However, this is not possible because the reconstructed length is needed before a species identification can be carried out (Thieren *et al.*, in press). Archaeological remains from small *A. oxyrinchus* have a tubercular surface pattern similar to that of *A. sturio*, which makes species identification of remains with the tubercular ornamentation difficult when the size of the animal is not known (Thieren *et al.*, in press).

Differences in scute shape and dimensions between different individuals

Another limiting factor for the modelling of the length based on scute dimensions or scute shape is the resemblance of scutes within the individual rows of one specimen. Scute dimensions and shapes of scutes within the rows from one individual are not independent, and it is likely that scutes from the same individual show some resemblance. The difference in scute dimensions between individual specimens was assessed with a PCA on the measurements/TL of all genetically identified specimens. The plot of the first two PC's, which explained in total 94.54% of the observed variation, indicates some clustering per specimen for the lateral scutes (Figure 2). Some clustering is also evident for the dorsal and ventral scute rows (Figure 3 and Figure 4). The interindividual difference in lateral and dorsal scute shape was assessed with PCA of the W matrix. The plot of the first two

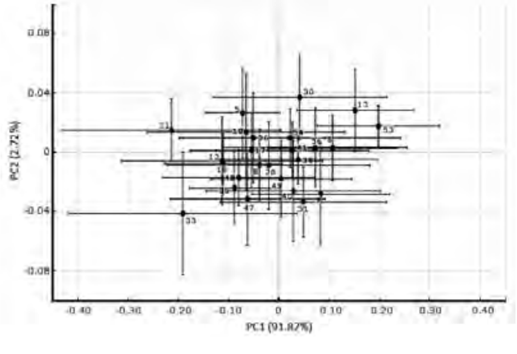

FIGURE 2

Scatterplot of PC2 against PC1, based on lateral scute measurements/TL on genetically identified A. *sturio* and A. *oxyrinchus* museum specimens. Mean ± standard deviation of the PC scores are shown per individual, with specimens numbered as in Table 1.

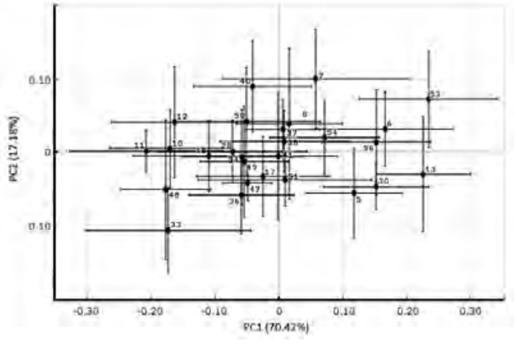

FIGURE 3

Scatterplot of PC2 against PC1, based on dorsal scute measurements/TL on genetically identified A. *sturio* and A. *oxyrinchus* museum specimens. Mean ± standard deviation of the PC scores are shown per individual, with specimens numbered as in Table 1.

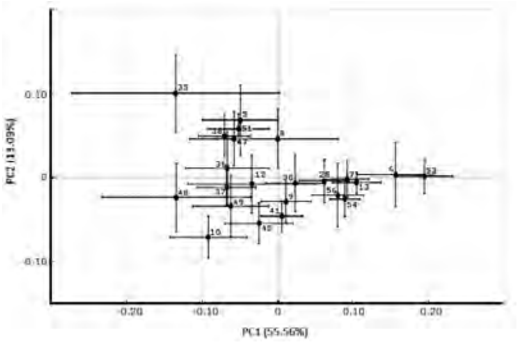

FIGURE 4

Scatterplot of PC2 against PC1, based on ventral scute measurements/TL on genetically identified A. *sturio* and A. *oxyrinchus* museum specimens. Mean ± standard deviation of the PC scores shown per individual, with specimens numbered as in Table 1.

PC's of the PCA on the W matrix of the lateral and dorsal scute rows of all morphologically and genetically identified sturgeons revealed some clustering per specimen, comparable to the traditional morphometric data (Figure 5a and Figure 6a). This confirms that the data is pseudoreplicated, i.e. not independent, which might influence results. As said earlier, dependent data leads to an increased probability of erroneously rejecting the null hypothesis during CVA.

Scute dimensions as indicator of total length

A positive correlation between TL and the different scute measurements for dorsal, lateral and ventral scutes (all ranks pooled together) is observed. Correlation coefficients are all significant (Tables 2-4), indicating some potential for size estimation.

Lateral scutes

Positive correlations between M1 of the largest ($M1_{max}$) and/or smallest ($M1_{min}$) lateral scute of sturgeon specimens and TL have been described by Brinkhuizen (1989) (TL_{min}=-0.16+2.18 $M1_{max}$, R^2=0.99 and TL_{max}= 12.59+4.89 $M1_{min}$, R^2=0.98) and Debus (1999) (TL_{min}=-0.70+2.34 $M1_{max}$, R^2=0.93). These models were applied with M1 of the lateral scutes from the 58 museum specimens. In addition, new regression models were fitted with TL on $M1_{max}$ (TL_{min}=7.82+2.10 $M1_{max}$, R^2=0.91) and TL on $M1_{min}$ (TL_{max}= 58.69+6.65 $M1_{min}$, R^2=0.29) of those museum specimens (Figure 7). The models of Brinkhuizen (1989) were based on 4 specimens (with total lengths of 39, 94, 140 and 225 cm) and Debus (1999) only used specimens from the Baltic Sea, which might influence the accuracy of those models. Our data indicate that, although there is a strong positive correlation between $M1_{max}$ and TL (r=0.95, p<0.0001) this is not the case for $M1_{min}$ and TL (r=0.55, p<0.0001).

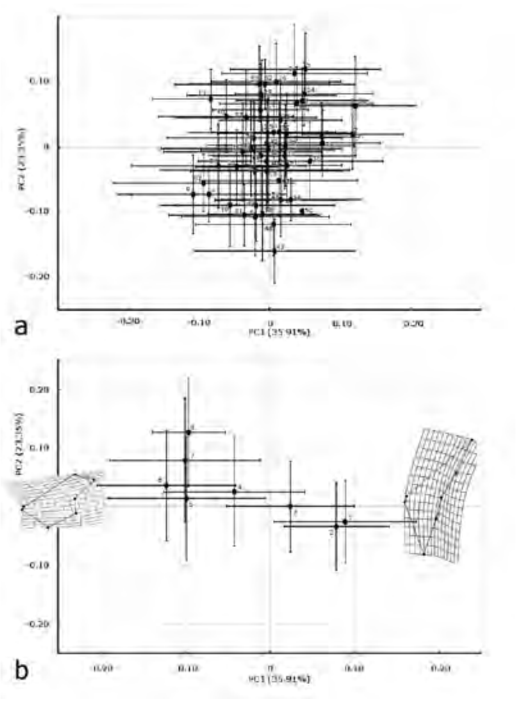

FIGURE 5

Scatterplot of PC2 against PC1, based on the lateral scutes from morphologically and genetically identified museum specimens' W matrix. Mean ± standard deviation of the PC scores shown (a) per individual, with specimens numbered as in Table 1; and (b) per rank. 1: Scutes 1-5; 2: Scutes 6-10; 3: Scutes 11-15; 4: Scutes 16-20; 5: Scutes 21-25; 6: Scutes 26-30; 7: Scutes 31-35; 8: Scutes > 35. Deformations of the reference configurations corresponding to the extremes of PC1 are shown (generated with tpsRelw v. 1.49 (Rohlf, 2010b)).

The models of Brinkhuizen (1989), Debus (1999) and our own model based on $M1_{max}$ were very similar. Consequently, the Standard Errors of Estimate (SEE) for these three models are comparable, between 56.6 and 60.4 cm. Our equation based on $M1_{min}$ and the one from Brinkhuizen (1989) differed considerably, which is reflected in a large difference in SEE of 106 cm. This is probably due to the fact that Brinkhuizen's model was based

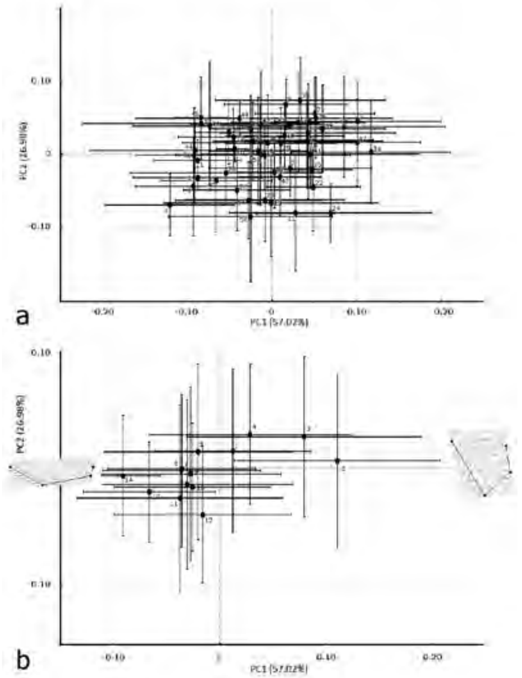

FIGURE 6

Scatterplot of PC2 against PC1, based on the dorsal scutes from morphologically and genetically identified museum specimens' W matrix. Mean ± standard deviation of the PC scores are shown (a) per individual, with specimens numbered as in Table 1; and (b) per rank. Numbers indicate the scute rank. Deformations of the reference configurations corresponding to the extremes of PC1 are shown (generated with tpsRelw v. 1.49 (Rohlf, 2010b)).

on only 4 specimens, which might underestimate the actual existing variation in smallest scute sizes. The size range calculated through the combined use of $M1_{min}$ and $M1_{max}$ is quite large, especially for the larger scutes (Figure 7). However, to identify *A. sturio* and *A. oxyrinchus* to species based on the dermal bone surface morphology, the exact TL does not have to be known. It is sufficient to determine if a sturgeon with a tubercular bone surface morphology is larger or smaller than ~ 1m TL (Thieren *et al.*, in press). Therefore, the maximal possible TL, calculated with $M1_{min}$, is not relevant for species identification. Only the minimum size (TL_{min}) has to be determined, which should be possible with the models with $M1_{max}$. To evaluate the accuracy of the $M1_{max}$-based models in indicating whether individual scutes belong to specimens smaller or larger than 1m TL, they were applied with M1 of each individual scute of each museum specimen. The percentage of scutes from sturgeon < 1m TL with a back-calculated TL_{min} > 1m is small, varying from 0.1% for Brinkhuizen (1989), 2.4% for Debus (1999) and 2% for our own calculation (Table 6). The percentage of scutes from sturgeons > 1m TL which gave a back-calculated TL_{min} < 1m is considerably higher, ranging between 35 and 51%. Since the other measurements (M2 to M9) also showed potential for size reconstruction, with high correlation coefficients (Table 2), the relationship between these $measurements_{max}$ and TL were also modelled. Table 5 gives an overview of the retained models. These models gave similar results as the model with $M1_{max}$ (Table 6).

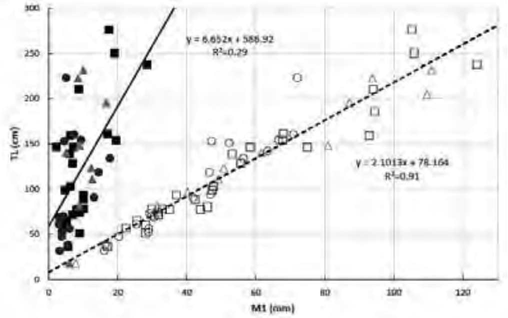

FIGURE 7

Plot of TL on the M1 from the smallest (filled markers) and largest (white markers) lateral scute of A. sturio and A. oxyrinchus museum specimens, with linear regression lines. Square: A. oxyrinchus; Circle: A. sturio; Triangle: hybrids or A. oxyrinchus/A. sturio.

However, since the scutes of *A. sturio* are smaller than those of *A. oxyrinchus*, regression models based on both species will systematically underestimate TL when applied on *A. sturio* scutes, and overestimate TL when applied on *A. oxyrinchus* scutes. When calculated for each species seperately, the percentages of specimens < 1 m TL with a back-calculated length > 1 m TL is quite similar for both species, and vary between 0 and 4.5%, depending on which measurement is used. However, the percentages of *A. oxyrinchus* > 1 m TL with a back-calculated length < 1 m TL vary between 25 and 47%, while those of *A. sturio* vary between 48 and 76%.

The tubercular scute ornamentation of sturgeons smaller than 1 m cannot be confidently used as an identification criterion because it can occur in both *A. sturio* and small *A. oxyrinchus*. As shown above, scutes from sturgeons less than 1m TL will rarely have a back-calculated size larger than 1 m. Hence, when scutes with a tubercular surface pattern with

Scute Rank	M1		M2		M3		M4		M5		M6		M7		M8		M9	
	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2
All	**0.72**	0.52	**0.79**	0.62	**0.75**	0.56	**0.74**	0.55	**0.69**	0.48	**0.76**	0.58	**0.70**	0.49	**0.74**	0.55	**0.71**	0.50
1	**0.90**	0.81	**0.93**	0.87	**0.79**	0.62	**0.87**	0.75	**0.87**	0.75	**0.90**	0.81	**0.87**	0.76	**0.88**	0.77	**0.87**	0.79
2	**0.93**	0.86	**0.91**	0.84	**0.86**	0.74	**0.86**	0.74	**0.87**	0.75	**0.92**	0.85	**0.86**	0.85	**0.85**	0.73	**0.90**	0.83
3	**0.94**	0.89	**0.86**	0.75	**0.78**	0.60	**0.93**	0.86	**0.91**	0.82	**0.93**	0.86	**0.89**	0.79	**0.92**	0.84	**0.92**	0.84
4	**0.95**	0.91	**0.93**	0.86	**0.91**	0.83	**0.92**	0.84	**0.91**	0.83	**0.93**	0.86	**0.92**	0.84	**0.92**	0.85	**0.90**	0.81
5	**0.95**	0.90	**0.90**	0.81	**0.84**	0.70	**0.94**	0.88	**0.91**	0.84	**0.94**	0.88	**0.94**	0.89	**0.95**	0.91	**0.92**	0.84
6	**0.95**	0.91	**0.88**	0.77	**0.82**	0.67	**0.92**	0.86	**0.91**	0.83	**0.94**	0.88	**0.92**	0.85	**0.93**	0.87	**0.89**	0.80
7	**0.95**	0.89	**0.89**	0.80	**0.89**	0.80	**0.94**	0.88	**0.91**	0.83	**0.94**	0.88	**0.93**	0.87	**0.94**	0.89	**0.92**	0.85
8	**0.94**	0.89	**0.91**	0.83	**0.91**	0.83	**0.91**	0.83	**0.88**	0.77	**0.94**	0.88	**0.92**	0.85	**0.94**	0.87	**0.91**	0.83
9	**0.94**	0.89	**0.88**	0.77	**0.81**	0.66	**0.94**	0.88	**0.91**	0.82	**0.93**	0.86	**0.91**	0.82	**0.90**	0.81	**0.91**	0.83
10	**0.93**	0.87	**0.90**	0.81	**0.91**	0.83	**0.91**	0.83	**0.88**	0.77	**0.91**	0.83	**0.87**	0.76	**0.87**	0.76	**0.86**	0.75
11	**0.94**	0.88	**0.93**	0.86	**0.88**	0.77	**0.92**	0.85	**0.87**	0.76	**0.94**	0.88	**0.92**	0.85	**0.92**	0.86	**0.92**	0.85
12	**0.92**	0.85	**0.93**	0.87	**0.88**	0.78	**0.92**	0.84	**0.86**	0.75	**0.92**	0.85	**0.88**	0.78	**0.90**	0.81	**0.89**	0.80
13	**0.92**	0.85	**0.92**	0.85	**0.87**	0.75	**0.91**	0.83	**0.90**	0.81	**0.93**	0.86	**0.89**	0.79	**0.90**	0.81	**0.91**	0.82
14	**0.92**	0.85	**0.92**	0.84	**0.85**	0.72	**0.90**	0.81	**0.88**	0.78	**0.92**	0.84	**0.85**	0.72	**0.88**	0.78	**0.87**	0.76
15	**0.91**	0.82	**0.91**	0.83	**0.85**	0.72	**0.92**	0.84	**0.85**	0.73	**0.92**	0.84	**0.86**	0.75	**0.88**	0.77	**0.90**	0.82
16	**0.92**	0.85	**0.87**	0.76	**0.82**	0.67	**0.90**	0.81	**0.90**	0.81	**0.93**	0.86	**0.84**	0.70	**0.87**	0.76	**0.83**	0.69
17	**0.92**	0.85	**0.89**	0.79	**0.82**	0.67	**0.91**	0.84	**0.87**	0.77	**0.94**	0.88	**0.85**	0.73	**0.87**	0.75	**0.90**	0.80
18	**0.93**	0.86	**0.90**	0.81	**0.83**	0.69	**0.92**	0.86	**0.86**	0.74	**0.86**	0.75	**0.87**	0.76	**0.88**	0.78	**0.86**	0.74
19	**0.90**	0.81	**0.91**	0.83	**0.79**	0.63	**0.88**	0.78	**0.82**	0.67	**0.90**	0.80	**0.85**	0.72	**0.86**	0.74	**0.87**	0.75
20	**0.91**	0.82	**0.91**	0.83	**0.82**	0.67	**0.89**	0.81	**0.87**	0.75	**0.94**	0.89	**0.82**	0.68	**0.87**	0.76	**0.87**	0.75
21	**0.88**	0.78	**0.89**	0.79	**0.77**	0.59	**0.87**	0.76	**0.81**	0.66	**0.89**	0.79	**0.83**	0.68	**0.87**	0.75	**0.86**	0.75
22	**0.87**	0.75	**0.89**	0.80	**0.72**	0.51	**0.77**	0.59	**0.70**	0.50	**0.82**	0.68	**0.77**	0.59	**0.79**	0.62	**0.81**	0.65
23	**0.84**	0.70	**0.84**	0.70	**0.81**	0.65	**0.82**	0.67	**0.76**	0.57	**0.84**	0.70	**0.79**	0.62	**0.79**	0.62	**0.84**	0.70
24	**0.82**	0.68	**0.88**	0.77	**0.80**	0.63	**0.75**	0.56	**0.68**	0.47	**0.80**	0.65	**0.63**	0.40	**0.69**	0.47	**0.78**	0.62
25	**0.82**	0.68	**0.86**	0.73	**0.78**	0.61	**0.86**	0.74	**0.74**	0.55	**0.85**	0.73	**0.66**	0.44	**0.68**	0.47	**0.76**	0.58
26	**0.74**	0.55	**0.86**	0.75	**0.62**	0.39	**0.71**	0.50	**0.66**	0.43	**0.73**	0.53	**0.49**	0.24	**0.61**	0.37	**0.61**	0.37
27	**0.66**	0.45	**0.81**	0.65	**0.75**	0.57	**0.78**	0.61	**0.70**	0.49	**0.76**	0.58	**0.52**	0.27	**0.62**	0.39	**0.60**	0.36
28	**0.86**	0.74	**0.90**	0.82	**0.81**	0.66	**0.83**	0.69	**0.75**	0.56	**0.83**	0.69	**0.60**	0.36	**0.63**	0.39	**0.70**	0.48
29	**0.86**	0.75	**0.87**	0.76	**0.75**	0.56	**0.87**	0.77	**0.83**	0.69	**0.89**	0.80	**0.73**	0.54	**0.75**	0.56	**0.79**	0.64
30	**0.71**	0.51	**0.88**	0.78	**0.61**	0.37	**0.83**	0.69	**0.35**	0.12	**0.86**	0.74	**0.31**	0.10	**0.56**	0.31	**0.64**	0.41

TABLE 2

Pearson correlation coefficient (r) and R^2 values between TL and different lateral scute measurements (M1-M9) per rank and pooled for all ranks, based on measurements on all morphologically identified A. *sturio* and A. *oxyrinchus*. Significant values are in bold ($p<0.05$) or bold underlined ($p<0.002$).

back-calculated lengths of less than 1m are excluded, chances are reduced that small *A. oxyrinchus* would be erroneously identified as *A. sturio*. This means that despite these seemingly disappointing results regarding accurate size reconstruction on the basis of lateral scutes, these bones can be confidently used for species identification when back-calculated total lengths are larger than 1 m. The application of the regression models to sturgeons over 1m TL erroneously yields back-calculated lengths smaller than 1m in about 50% of the cases and hence significantly reduces the number

Scute Rank	M1		M2		M3		M4		M5		M6		M7		M8		M9	
	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2
All	**0.87**	0.77	**0.90**	0.80	**0.88**	0.77	**0.80**	0.64	**0.85**	0.73	**0.87**	0.76	**0.79**	0.62	**0.87**	0.75	**0.88**	0.77
1	**0.95**	0.91	**0.83**	0.66	**0.87**	0.75	**0.92**	0.85	**0.88**	0.78	**0.91**	0.83	**0.87**	0.75	**0.89**	0.79	**0.92**	0.86
2	**0.93**	0.86	**0.89**	0.80	**0.91**	0.83	**0.90**	0.80	**0.86**	0.73	**0.91**	0.83	**0.88**	0.78	**0.90**	0.82	**0.88**	0.77
3	**0.93**	0.86	**0.88**	0.78	**0.86**	0.75	**0.88**	0.77	**0.85**	0.73	**0.90**	0.82	**0.87**	0.76	**0.81**	0.66	**0.92**	0.84
4	**0.93**	0.86	**0.89**	0.78	**0.92**	0.84	**0.88**	0.77	**0.86**	0.85	**0.90**	0.81	**0.87**	0.75	**0.89**	0.79	**0.91**	0.83
5	**0.93**	0.87	**0.88**	0.78	**0.91**	0.83	**0.88**	0.77	**0.89**	0.80	**0.92**	0.84	**0.86**	0.74	**0.91**	0.84	**0.91**	0.83
6	**0.92**	0.84	**0.96**	0.92	**0.92**	0.85	**0.88**	0.78	**0.94**	0.88	**0.91**	0.82	**0.86**	0.74	**0.93**	0.87	**0.93**	0.86
7	**0.91**	0.83	**0.96**	0.93	**0.90**	0.80	**0.88**	0.78	**0.89**	0.79	**0.93**	0.87	**0.83**	0.69	**0.94**	0.88	**0.92**	0.86
8	**0.89**	0.79	**0.94**	0.88	**0.93**	0.87	**0.83**	0.69	**0.92**	0.84	**0.90**	0.81	**0.85**	0.72	**0.92**	0.85	**0.93**	0.87
9	**0.87**	0.76	**0.94**	0.88	**0.90**	0.81	**0.81**	0.65	**0.88**	0.77	**0.86**	0.74	**0.82**	0.68	**0.89**	0.79	**0.89**	0.80
10	**0.85**	0.72	**0.88**	0.78	**0.90**	0.80	**0.79**	0.62	**0.87**	0.76	**0.83**	0.68	**0.78**	0.61	**0.88**	0.78	**0.84**	0.71
11	**0.89**	0.80	**0.94**	0.88	**0.90**	0.82	**0.76**	0.58	**0.92**	0.85	**0.92**	0.84	**0.79**	0.62	**0.91**	0.83	**0.90**	0.81
12	**0.84**	0.71	**0.84**	0.71	**0.87**	0.75	**0.68**	0.46	**0.87**	0.76	**0.75**	0.57	**0.77**	0.59	**0.86**	0.73	**0.79**	0.62
13	**0.86**	0.74	**0.91**	0.83	**0.83**	0.69	**0.46**	0.21	**0.86**	0.75	**0.92**	0.86	**0.54**	0.29	**0.88**	0.77	**0.81**	0.66
14	**0.92**	0.85	**0.88**	0.78	**0.97**	0.95	**0.85**	0.72	**0.85**	0.97	**0.97**	0.94	**0.59**	0.35	**0.89**	0.79	**0.98**	0.96

TABLE 3

Pearson correlation coefficient (r) and R^2 values between TL and different dorsal scute measurements (M1-M9) per rank and pooled for all ranks, based on measurements on all morphologically identified A. *sturio* and A. *oxyrinchus*. Significant values are in bold (p<0.05) or bold underlined (p<0.002).

Scute Rank	M1		M2		M3		M4		M5		M6		M7		M8		M9	
	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2
All	**0.88**	0.77	**0.84**	0.71	**0.80**	0.64	**0.73**	0.54	**0.72**	0.51	**0.80**	0.65	**0.73**	0.53	**0.72**	0.51	**0.83**	0.69
1	**0.88**	0.78	**0.88**	0.78	**0.91**	0.82	**0.89**	0.79	**0.87**	0.76	**0.88**	0.78	**0.82**	0.67	**0.85**	0.74	**0.89**	0.79
2	**0.86**	0.74	**0.84**	0.70	**0.83**	0.68	**0.80**	0.63	**0.73**	0.53	**0.76**	0.58	**0.79**	0.62	**0.69**	0.48	**0.84**	0.70
3	**0.87**	0.77	**0.86**	0.74	**0.86**	0.74	**0.78**	0.60	**0.87**	0.76	**0.83**	0.69	**0.82**	0.68	**0.76**	0.58	**0.87**	0.76
4	**0.90**	0.81	**0.85**	0.79	**0.82**	0.75	**0.81**	0.62	**0.58**	0.34	**0.81**	0.66	**0.79**	0.62	**0.68**	0.46	**0.84**	0.70
5	**0.90**	0.80	**0.85**	0.73	**0.83**	0.68	**0.81**	0.66	**0.80**	0.64	**0.84**	0.71	**0.83**	0.69	**0.78**	0.61	**0.87**	0.76
6	**0.91**	0.83	**0.83**	0.69	**0.81**	0.65	**0.79**	0.62	**0.53**	0.28	**0.85**	0.72	**0.84**	0.71	**0.71**	0.60	**0.87**	0.76
7	**0.90**	0.82	**0.80**	0.64	**0.79**	0.62	**0.81**	0.66	**0.76**	0.57	**0.88**	0.78	**0.79**	0.62	**0.77**	0.60	**0.80**	0.64
8	**0.88**	0.78	**0.81**	0.65	**0.78**	0.60	**0.78**	0.60	**0.65**	0.42	**0.88**	0.78	**0.63**	0.40	**0.67**	0.44	**0.88**	0.77
9	**0.86**	0.73	**0.84**	0.71	**0.68**	0.46	**0.66**	0.43	**0.74**	0.54	**0.75**	0.56	**0.70**	0.49	**0.78**	0.62	**0.84**	0.70
10	**0.86**	0.73	**0.88**	0.77	**0.90**	0.80	**0.64**	0.41	**0.62**	0.39	**0.89**	0.79	**0.53**	0.28	**0.59**	0.35	**0.83**	0.69
11	**0.81**	0.66	**0.89**	0.78	**0.79**	0.63	**0.56**	0.32	**0.54**	0.29	**0.72**	0.52	**0.57**	0.32	**0.63**	0.40	**0.60**	0.36
12	**0.95**	0.91	**0.92**	0.84	**0.77**	0.59	**0.44**	0.19	**0.84**	0.71	**0.81**	0.65	**0.84**	0.71	**0.70**	0.48	**0.97**	0.94

TABLE 4

Pearson correlation coefficient (r) and R^2 values between TL and different ventral scute measurements (M1-M9) per rank and pooled for all ranks, based on measurements on all morphologically identified A. *sturio* and A. *oxyrinchus*. Significant values are in bold (p<0.05) or bold underlined (p<0.002).

of larger specimens for which a species identification can be obtained. Nevertheless, the remaining specimens that yield size reconstructions above 1m will allow accurate species identification. Table 5

	Lateral			Dorsal						Ventral	
	All scutes			**Excluding first scute**			**All scutes**			**Exluding last scute**	
	Equation	**R^2**	**Min**	**Equation**	**R^2**	**Min**	**Equation**	**R^2**	**Min**	**Equation**	**R^2**
M1	7.816+2.10 M1max	0.91	43.9	4.593+2.54 M1MaxExclD1	0.86	37.6	1.937+2.45 M1max	0.91	40.0	-8.939+4.21 M1MaxEcxlVlast	0.82
M2	0.935+4.78 M2max	0.89	20.7	6.722+2.09 M2MaxExclD1	0.92	44.6	10.324+1.97 M2max	0.90	45.5	-1.797+3.74 M2MaxEcxlVlast	0.86
M3	7.865+8.51 M3max	0.87	10.8	11.241+3.86 M3MaxExclD1	0.89	23.0	10.006+3.89 M3max	0.90	23.1	19.252+5.77 M3MaxEcxlVlast	0.81
M4	5.182+3.47 M4max	0.88	27.3	-1.325+3.88 M4MaxExclD1	0.82	26.1	-5.935+3.95 M4max	0.81	26.8	11.906+5.74 M4MaxEcxlVlast	0.62
M5	14.847+3.70 M5max	0.83	23.0	8.031+2.82 M5MaxExclD1	0.81	32.6	11.756+2.64 M5max	0.81	33.4	14.316+4.73 M5MaxEcxlVlast	0.75
M6	6.181+2.82 M6max	0.91	33.3	7.584+3.01 M6MaxExclD1	0.85	30.7	5.759+2.99 M6max	0.88	31.5	-12.104+4.86 M6MaxEcxlVlast	0.83
M7	8.459+4.08 M7max	0.87	22.4	0.852+3.84 M7MaxExclD1	0.73	25.8	-2.421+3.89 M7max	0.77	26.3	-35.184+8.06 M7MaxEcxlVlast	0.74
M8	6.404+4.00 M8max	0.90	23.4	-3.978+3.12 M8MaxExclD1	0.87	33.3	3.688+ 2.84 M8max	0.84	33.9	-10.607+5.76 M8MaxEcxlVlast	0.78
M9	14.325+3.66 M9max	0.86	23.4	2.877+3.12 M9MaxExclD1	0.86	31.1	0.949+3.11 M9max	0.88	31.8	-4.427+4.77 M9MaxEcxlVlast	0.81

TABLE 5

Equations and R^2 for the equation of TL (cm) based on the maximum value of different scute measurements (mm). The minimum value for each measurement (Min) to attain a back-calculated length of > 1 m TL is also given for the lateral and dorsal scutes

includes the minimum values needed for each measurement to attain back-calculated lengths larger than 1 m TL. Scutes with measurements equal to or larger than this minimum value can be identified to species on the basis of their ornamentation pattern. However, it should be kept in mind that lengths of *A. sturio* are systematically underestimated using these models, while those of *A. oxyrinchus* will be overestimated. This means that the ratio *A. sturio/A. oxyrinchus* in an archaeological assemblage cannot be determined with this method.

Dorsal scutes

Desse-Berset (2011) constructed a model (TL =2.52 $M1_{\text{mean excl. D1}}$-15.54, R^2=0.96) for dorsal scutes, based on the mean width of the dorsal scutes from 9 *A.oxyrinchus* specimens, excluding the first scute and the basal dorsal fin fulcrum.

According to Desse-Berset (2011), M1 does not vary considerably within the dorsal row and is therefore the best measure for TL reconstitutions. Our own measurements on museum specimens indicate that M1 (excluding the first dorsal scute) can vary up to 2.3% of the TL of an individual. We tested Desse-Berset's (2011) model on the museum specimens, also without taking into account the basal dorsal fin fulcrum. Using this model, about 3.5% of the back-calculated TL from sturgeons < 1m TL was larger than 1m, and 40% of the back-calculated TL from sturgeons > 1m TL was smaller than 1m (Table 6). This means that, similar to the lateral scutes, the dorsal scutes with a back-calculated length larger than 1m can be confidently used for species identification. It also appears that a large percentage of scutes from sturgeons larger than 1m would mistakenly be excluded for species identification.

Similar to the lateral scutes, least squares linear regression models were developed for the dorsal scutes, based on TL and on the maximal measurements ($M1_{max}$– $M9_{max}$), both with and without the first dorsal scute (Table 5). With these, the percentages of back-calculated TL_{min} > 1m based on scutes from sturgeons < 1m TL (ranging from 0.9 to 8.4% vs 3.5%, Table 6) were comparable to the results with Desse-Berset's (2011) equation. The percentage of back-calculated TL_{min} < 1m based on scutes from sturgeons > 1m TL ranges from 19.6% to 30.0% for the model without the first dorsal scute and from 22.5% to 31.6% for the model including that scute. In both cases, this is a slight decrease compared to the 39.7% attained with Desse-Berset's (2011) model. As with the lateral scutes, these regression models would wrongfully indicate that many scutes from sturgeons > 1m TL came from sturgeons <1m, but only few scutes from sturgeons < 1m TL would be back-calculated as >1m, which is important for correct species assignment, as explained above for the lateral scutes. As for the later-

	Dorsal scutes			**Ventral scutes**			**Lateral scutes**		
	25 cm	**50 cm**	**1m**	**25 cm**	**50 cm**	**1 m**	**25 cm**	**50 cm**	**1 m**
W matrix + CS	48.4	59.9	78.7				51.8	59.7	80.0
PC1&PC2 (W matrix) + CS	46.3	58.4	78.5				33.7	43.9	68.0
Measurements	61.7	68.3	81.3	55.7	53.2	73.7	42.7	56.2	71.4
PC1&PC2 (measurements)	54.8	59.6	79.0	44.3	50.4	71.7	38.6	45.9	67.4

TABLE 6

Percentage of correct classification based on measurements, the weight matrix (and centroid size (CS)) and the first two principle components (and CS) from a PCA on W matrix or the measurements in a specific size class.

al scutes, the minimum value of each measurement needed to attain a back-calculated total length of 1 m is given in Table 5. However, as is the case with back-calculations based on lateral scutes, the TL of *A. sturio* will systematically be underestimated using the models in Table 5, while that of *A. oxyrinchus* will be overestimated. The percentages of *A. oxyrinchus'* back-calculated TL_{min} < 1 m based on scutes from sturgeons > 1 m TL vary between 6.5 to 22%, while those of *A. sturio* vary between 37 and 71%. The percentages of *A. oxyrinchus'* back-calculated TL_{min} > 1 m based on scutes from sturgeons < 1 m TL varies between 0 to 15%, while those of *A. sturio* varies between 0 and 1%. Again, a larger proportion of *A. sturio* will be excluded for species analysis, meaning that also for the dorsal scutes the ratio *A. sturio*/*A. oxyrinchus* in an archaeological assemblage cannot be inferred with this method.

Ventral scutes

For ventral scutes, models were constructed for the back-calculation of TL_{min} similar to those for the lateral and dorsal scutes, based on the 9 scute measurements (M1-M9) on the largest ventral scute from each specimen (Table 5). The last ventral scute was excluded for analysis since it has a distinctive and aberrant shape. With these models, with R^2 values varying between 0.62 and 0.86, between 7.6 and 22.6% of the total lengths based on scutes from sturgeons < 1m TL were back-calculated larger than 1m, and between 14.6 and 27.3% of the lengths based on scutes from sturgeon > 1m TL were back-calculated smaller than 1 m. Similar to the back-calculations based on lateral and dorsal scutes, the TL of *A. sturio* will systematically be underestimated, while that of *A. oxyrinchus* will be overestimated. The percentages of *A. oxyrinchus*' back-calculated TL_{min} < 1 m based on scutes from sturgeons > 1 m TL varies between 5 to 39%, while that of *A. sturio* varies between 2.5 and 11.5%. The percentages of *A. oxyrinchus*' back-calculated TL_{min} > 1 m based on scutes from sturgeons < 1 m TL varies between 7 to 24%, while those of *A. sturio* varies between 21 and 51%. Although the percentages of scutes from sturgeons >1m TL that are back-calculated < 1m TL is smaller compared to the dorsal and lateral scutes, the percentage of scutes from sturgeons < 1m TL with back-calculated lengths > 1m TL is larger. It thus appears that ventral scutes are less reliable for size reconstruction than dorsal and lateral scutes, and therefore more difficult to identify to species. Ventral scutes with a tubercular ornamentation pattern should only be included for species identification when direct comparison with specimens of known length indicate that they are clearly from animals much larger than 1m.

Estimation of scute rank based on traditional and geometric morphometrics

Desse-Berset (2011) suggested that the accuracy of size reconstruction could increase if the exact place of the scute within the dorsal row could be established. This should also be the case for lateral and ventral scutes. Therefore, the correlation coefficients between the 9 measurements and TL and R^2 values were calculated separately for each scute rank for the lateral (Table 2), dorsal (Table 3) and ventral scutes (Table 4). Most correlations were significant at the 0.05 significance level. For the lateral scutes an increase in both r and R^2 values could be observed for all ranks, which was not always the case for the dorsal and ventral scutes. This suggests that especially for lateral scutes, knowing the original rank of the scute will pro-

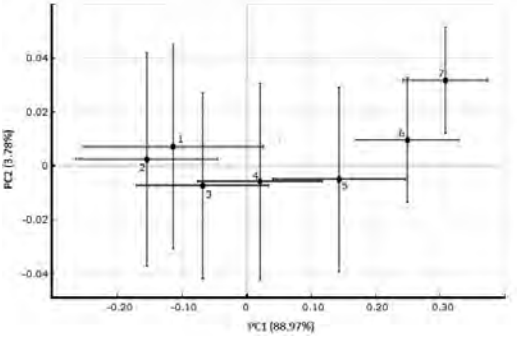

FIGURE 8

Scatterplot of PC2 against PC1, based on lateral scute measurements/TL on morphologically and genetically identified A. *sturio* and A. *oxyrinchus* museum specimens. Mean ± standard deviation of the PC scores are shown per rank. 1: scutes 1-5; 2: Scutes 6-10; 3: Scutes 11-15; 4: Scutes 16-20; 5: Scutes 21-25; 6: Scutes 26-30; 7: Scute >30.

vide more accurate size reconstructions. For dorsal or ventral scutes, the effect of knowing the scute rank is less pronounced, but may also lead to an improvement of the size prediction accuracy. However, establishing the original scute rank of an isolated scute is not straightforward. In the following part, we explore different possibilities (traditional and geometric morphometrics) to determine the original place of an isolated scute within the row.

A PCA was performed on the measurements/TL on all specimens for the different scute rows. For the lateral scutes, the ordination plots categorized by ranks grouped per five (scute 1 to 5, 6 to 10, and so on) do not delineate any distinct groups, although there seems to be a gradual change in scute dimensions from the anterior part of the row, located more to the negative end of PC1, towards scutes at the posterior end of the row, located more to the positive end of PC1 (Figure 8). This explains the improvement mentioned above in r and R^2 values when scutes are considered per rank for estimating TL (Table 2). Lateral scutes seem to cluster somewhat per individual (Figure 2), but scutes within the same group of ranks from different individuals also seem to group together. This might allow a rough estimation of the original rank of the scute based on traditional morphometric data. A CVA was performed on all morphologically identified animals with scutes grouped rank 1 to 5, rank 6 to 10 and so on. The analysis classified 31.8% of the cases correctly, versus 12.6% classified correctly with ungrouped ranks. Although an improvement in percentage of correct classification is observed with the ranks grouped per five, this improvement does not allow an accurate estimate of the rank of an isolated scute. Therefore, the possibilities of geometric morphometric techniques to establish the provenance of an individual isolated scute within the row have been explored. The data points in the ordination plot of the PCA on the W matrix of the lateral scutes were categorized by rank (Figure 5b) instead of by individual (Figure 5a). A gradual change from scutes at the beginning of the row (at the positive end of PC1) towards scutes at the end of the row (at the negative end of PC1) can be observed, similar to the ordination plot of the PCA on scute dimensions (Figure 8). Landmark configurations on the two extreme ends of PC1 are shown (Figure 5b) to give an indication of the change in scute shape from the first to the last scute. A MANOVA on the W matrix of the scutes grouped per 5 indicated a significant overall difference between the different groups (l=0.27, $F_{(70,6601)}=23.40$, p<0.0001). However, only 43.6% of the cases was classified correctly. When the CVA was repeated on the first two PC’s, only 20.9% was classified correctly (l=0.95, $F_{(10,2282)}=6.24$, p<0.0001).

For the dorsal and ventral scutes, no consistent improvement in r and R^2 was observed (Table 3 and 4), which is reflected in the ordination plots. For the dorsal scutes, there seems to be a gradual change in scute dimensions from scutes at the beginning of the row (more located to the negative end of PC1 and the positive end of PC2, Figure 9) to scutes towards the caudal end of the row (more to the positive end of PC1 and negative end of PC2, Figure 9). However, this trend is much less

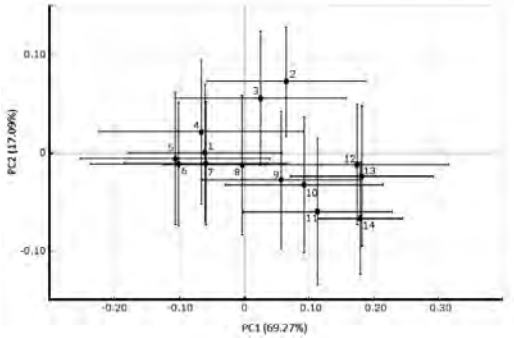

FIGURE 9

Scatterplot of PC2 against PC1, based on dorsal scute measurements/TL on morphologically and genetically identified A. *sturio* and A. *oxyrinchus* museum specimens. Mean ± standard deviation of the PC scores are shown per rank. Numbers indicate the scute rank.

pronounced than in the lateral rows. Since traditional morphometry did not prove satisfactory for the estimation of lateral scute ranks, only geometric morphometric techniques are applied on dorsal scutes. When the data points from the PCA on the dorsal scutes' W matrix are categorized per rank (Figure 6b) instead of individual (Figure 6a), a gradual shape change from scutes at the anterior end of the row (at the positive end of PC1 and PC2) to scutes at the posterior end of the row (at the negative end of PC1 and PC2) can be observed, similar but more pronounced compared to the change in scute dimensions (Figure 9). A CVA on the W matrix and the dataset consisting of the first two PC's indicated a significant difference between the different ranks ($p<0.0001$), but also here the percentage of correct classification was low (18.76% for the W matrix, 12.58% for the dataset consisting of the first two PC's).

For the ventral scutes, the ordination plot of the first two PC's of a PCA on the measurements/TL did not show any clustering per rank or gradient change in scute dimensions (Figure 10). Therefore, no further attempts were made to classify the scutes according to their rank.

We can conclude that the percentage of correct classification for dorsal and lateral scutes is too low to allow a reliable estimate of the original rank of an individual scute. For ventral scutes, it was not tested if scutes could be classified to rank based on scute measurements, since - unlike the dorsal and lateral scutes - a first exploration of the data did not give any indications this would be possible.

Scute dimensions or shape as an indication for wider size classes

Since the scutes offer limited possibilities for an accurate estimation of TL, it was evaluated whether the shape or dimensions of individual scutes allow attributing them to a particular size range.

Different arbitrary chosen bin sizes were tested (25cm, 50cm and 1m). In Table 6 we present the percentages of correct classification from a CVA on the traditional measurements, on the W matrix and centroid size, and on the reduced datasets consisting of the first two PC's of a PCA on the measurements or the first two PC's of a PCA on the W matrix and centroid size. The percentages of correct classification of the CVA on the reduced datasets are, as expected, smaller than the ones based on the complete datasets. The difference between both is small for the dorsal scutes; only for the measurements in the 25 cm and 50 cm size class it is larger than 5%. For the ventral scutes, this difference is larger than 5% for the CVA in the 25 cm size class. For the lateral scutes, the difference was larger than 5% in all cases. This possibly indicates some overfitting when performing CVA on the complete datasets.

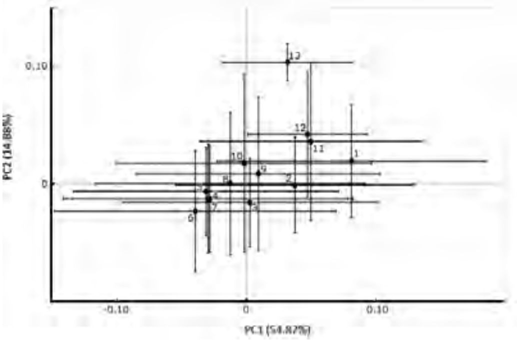

FIGURE 10

Scatterplot of PC2 against PC1, based on ventral scute measurements/TL on morphologically and genetically identified A. *sturio* and A. *oxyrinchus* museum specimens. Mean ± standard deviation of the PC scores are shown per rank. Numbers indicate the scute rank.

For the dorsal scutes, percentages of correct classification were highest with a CVA performed on the measurements; for the lateral scutes with a CVA on the W matrix. For all three scute types (except for the measurements on the ventral scutes), the percentage of correct classification increased when bin size increased. However, all percentages were quite low, with the best attained results around 80% of the dorsal scutes, around 70% of the ventral scutes and around 80% of the lateral scutes classified correctly in the 1m size class. In the 25 and 50 cm bin sizes, correct classifications are obtained in only 34% to 70% of the cases. These percentages might still be an overestimation since intra-individual scute similarity is not taken into account. However, because of the low percentages of correct classification, the models were not cross validated.

Next to the disappointing low accuracy of the models, this method is quite labor-intensive, requiring all nine measurements on the scutes, for only a rough estimation of size. Moreover, it is not always possible to take all measurements on archaeological scutes, which are often fragmented.

CONCLUSION

In this study, different methods for size reconstruction based on sturgeon scutes were explored using traditional and geometric morphometric techniques. It appears that the back-calculation of TL or the estimation of size classes based on the scute shape or scute dimensions are not very accurate due to the wide variation among scutes within one row. A positive correlation between different scute measurements and TL does exist, but this correlation is not strong enough to allow a precise size reconstruction. This is partly due to the fact that the exact position of an isolated scute within a scute row cannot be accurately determined. Although a difference was observed in scute dimensions and shape from the anterior towards the posterior end of the dorsal and lateral row, this difference is not pronounced enough to accurately establish the rank of a scute within these rows. A size-related difference in scute shape and scute dimensions was also observed, but likewise, this difference is not marked enough to allow an adequate classification into size classes.

The regression equations based on scute measurements can be used to estimate whether an individual dorsal or lateral scute belonged to a sturgeon larger or smaller than 1m. Although the back-calculated length of many scutes from sturgeons > 1m TL will be smaller than 1m, the percentage of small sturgeon (< 1m TL) back-calculated as larger than 1m is small. The latter finding is of relevance for the adequate use of scutes for the discrimination between the *A. sturio* and *A. oxyrinchus* which is based on the ornamentation pattern of the external surface (Desse-Berset, 2009). The surface pattern is species-specific in most fish larger than 1m, but smaller individuals of *A. oxyrinchus* can show a more *A. sturio*-like pattern (Thieren *et al*., in press). Scutes with a back-calculated TL over 1m, calculated with the regression equations mentioned above, can thus be safely used for species identification. However, it must be kept in mind that more *A. sturio* scutes than *A. oxyrinchus* scutes will be excluded for species identification. The length of *A. oxyrinchus* is systematically overestimated, while the length of *A. sturio* is underestimated using the proposed regression models: scutes of *A. sturio* are smaller than *A. oxyrinchus*, and the regression equations are based on the combined measurements of *A. sturio* and *A. oxyrinchus*. Therefore, scutes cannot be used to determine proportions of *A. oxyrinchus* and *A. sturio* in a given archaeological assemblage. However, they can be used to indicate the presence or absence of the species. Preference for size reconstruction should be given to head elements, for which no difference in the regressions between the two species was observed (Thieren & Van Neer, 2014). Consequently, species identifications based on these elements can be used to determine the *A. sturio*/*A. oxyrinchus* ratio in an archaeological assemblage.

Given the difference in scute size and scute number between *A. sturio* and *A. oxyrinchus*, species-specific equations for size back-calculation might produce somewhat larger accuracy. However, this would require more modern reference specimens than presently available. Even with such equations, scutes will probably never allow precise length estimation because the number of scutes also tends to vary within species and because the size of scutes varies within one row.

ACKNOWLEDGEMENTS

This paper presents research results of the Interuniversity Attraction Poles Programme - Belgian Science Policy. For the permission to study sturgeons under their care we thank the curators of the natural history collections in the following institutes: Aquarium-Muséum de Liège (Belgium); Groningen Institute of Archaeology (the Netherlands); KU Leuven Museum voor Dierkunde (Belgium); Muséum d'histoire naturelle de Nantes, France; Muséum national d'Histoire naturelle (France); Muséum régional des sciences naturelles de Mons (Belgium); Natural History Museum (UK); Natuurmuseum Bruinenberg (the Netherlands), Naturhistoriska riksmuseet (Sweden); Royal Belgian Institute of Natural Sciences (Belgium); Stadsmuseum Lokeren (Belgium); Evolutionsmuseet (Sweden). D.C. Brinkhuizen (Groningen, the Netherlands) provided a sample from his personal collection. We would also like to thank N. Boon for her helpful input for the statistical analysis and A. Ervynck for his useful comments.

REFERENCES

Benecke, N. 1986: Some remarks on sturgeon fishing in the southern Baltic region in medieval times. In:

Brinkhuizen, D.C. & Clason, A.T. (eds.): *Fish and Archaeology. Studies in osteometry, taphonomy, seasonality and fishing methods*: 9-17. B.A.R. (International Series) 294. Oxford.

BRENNAN, J. S. & CAILLIET, G. M. 1989: Comparative Age-Determination Techniques for White Sturgeon in California. *Transactions of the American Fisheries Society* 118: 296-310.

BRINKHUIZEN, D. C. 1986: Features observed on the skeletons of some recent European Acipenseridae: Their importance for the study of excavated remains of sturgeons. In: Brinkhuizen, D.C. & Clason, A.T. (eds.): *Fish and Archaeology. Studies in osteometry, taphonomy, seasonality and fishing methods*: 18-33. B.A.R. (International Series) 294. Oxford.

— 1989: *Ichthyo-archeologisch onderzoek: Methoden en toepassing aan de hand van Romeins vismateriaal uit Velsen (Nederland)*. Proefschrift ter verkrijging van het doctoraat in de Wiskunde en Wetenschappen. Rijksuniversiteit Groningen, Groningen.

CASTELNAUD, G. 2011: Sturgeon Fishing, Landings, and Caviar Production During the Twentieth Century in the Garonne Basin and the Coastal Sea. In: Williot, P.; Rochard, E.; Desse-Berset, N.; Kirschbaum, F. & Gessner, J. (eds.): *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758. The Reunion of the European and Atlantic Sturgeons*: 177-194. Springer-Verlag, Berlin.

CHASSAING, O.; DESSE-BERSET, N.; DUFFRAISSE, M.; HUGHES, S.; HÄNNI, C. & BERREBI, P. 2013: Palaeogenetics of western French sturgeons spotlights the relationships between *Acipenser sturio* and *Acipenser oxyrinchus*. *Journal of Biogeography* 40(2): 382-393.

DEBUS, L. 1999: Meristic and morphological features of the Baltic sturgeon (*Acipenser sturio* L.). *Journal of Applied Ichthyology* 15(4-5): 38-45.

DESSE-BERSET, N. 2009: First archaeozoological identification of Atlantic sturgeon (*Acipenser oxyrinchus* Mitchill 1815) in France. *Comptes Rendus Palevol* 8(8): 717-724.

— 2011: Discrimination of *Acipenser sturio, Acipenser oxyrinchus* and *Acipenser naccarii* by Morphology of Bones and Osteometry. In: Williot, P.; Rochard, E.; Desse-Berset, N.; Kirschbaum, F. & Gessner, J. (eds.): *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758. The Reunion of the European and Atlantic Sturgeons*: 23-52. Springer-Verlag, Berlin.

GESSNER, J.; SPRATTE, S. & KIRSCHBAUM, F. 2011: Historic Overview on the Status of the European Sturgeon (*Acipenser sturio*) and Its Fishery in the North Sea and Its Tributaries with a Focus on German Waters. In: Williot, P.; Rochard, E.; Desse-Berset, N.; Kirschbaum, F. & Gessner, J. (eds.): *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758. The Reunion of the European and Atlantic Sturgeons* 195-219. Springer-Verlag, Berlin.

GREENSPAN, R. L. 1998: Gear Selectivity Models, Mortality Profiles and the Interpretation of Archaeological Fish Remains: A Case Study from the Harney Basin, Oregon. *Journal of Archaeological Science* 25(10): 973-984.

HARVEY, J. T.; LOUGHLIN, T. R.; PÉREZ, M. A. & OXMAN, D. S. 2000: *Relationship between Fish Size and Otolith Length for 63 Species of Fishes from the Eastern North Pacific Ocean*. NOAA Technical Report NMFS 150. U.S. Department of Commerce Seattle, Washington.

JORDAN, D. S. 1910: *A Manual of the Vertebrate Animals of the Northern United States*. Tenth Edition. A.C. McClurg and Company, Chicago.

LEACH, B. F.; DAVIDSON, J. M.; HORWOOD, L. M. & ANDERSON, A. J. 1996: The estimation of live fish size from archaeological cranial bones of the New Zealand barracouta *Thyrsites atun*. *Tuhinga, Records of the Museum of New Zealand* 6: 1-25.

LEACH, F. & DAVIDSON, J. 2001: The use of size–frequency diagrams to characterize prehistoric fish catches and to assess human impact on inshore fisheries. *International Journal of Osteoarchaeology* 11(1-2): 150-162.

LUDWIG, A.; DEBUS, L.; LIECKFELDT, D.; WIRGIN, I.; BENECKE, N.; JENNECKENS, I.; WILLIOT, P.; WALDMAN, J. R. & PITRA, C. 2002: Fish populations: When the American sea sturgeon swam east. *Nature* 419(6906): 447-448.

MAGNIN, É. 1963: *Recherches sur la systématique et la biologie des Acipenséridés Acipenser sturio L., Acipenser oxyrhynchus Mitchill, Acipenser fulvescens Raf.* Thèses présentées à la Faculté des Sciences de l'Université de Paris pour obtenir le Grade de Docteur ès Sciences Naturelles. Université de Paris, Paris.

— 1964: Validité d'une distinction spécifique entre les deux acipensérides: *Acipenser sturio* L. d'Europe et *Acipenser oxyrhynchus* d'Amérique du Nord. *Le Naturaliste Canadien* XCI(1): 5-20.

MOHR, E. 1952: *Der Stör.* Die Neue Brehm-Bücherei 84. Akademische Verlagsgesellschaft Geest & Portig K.G., Leipzig.

PETERSON, D. L.; VECSEI, P. & JENNINGS, C. A. 2007: Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. *Reviews in Fish Biology and Fisheries* 17: 59-76.

R CORE TEAM 2014: *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

ROHLF, F. J. 2003: *tpsSmall* v. 1.20. Departement of Ecology and Evolution. State University of New York, Stony Brook, NY. http://life.bio.sunysb.edu/morph/softdataacq.html.

— 2010a: *tpsDig* v. 2.16. Departement of Ecology and Evolution. State University of New York, Stony Brook, NY. http://life.bio.sunysb.edu/morph/softdataacq.html.

— 2010b: *tpsRelw* v. 1.49. Departement of Ecology and Evolution. State University of New York, Stony Brook, NY. http://life.bio.sunysb.edu/morph/softdataacq.html.

SEWERTZOFF, A. N. 1926: The development of the scales of *Acipenser ruthenus*. *Journal of Morphology* 42(2): 523-560.

STATSOFT INC. 2013: *STATISTICA (data analysis software system)* v. 12. www.statsoft.com.

THIEREN, E.; OTTONI, C.; POPOVIC, D. & VAN NEER, W. in press: Inter- and intraspecific variation in the surface pattern of the dermal bones of two sturgeon species; *Journal of Applied Ichthyology.*

THIEREN, E. & VAN NEER, W. 2014: New Equations for the Size Reconstruction of Sturgeon from Isolated Cranial and Pectoral Girdle Bones. *International Journal of Osteoarchaeology*: first published on August 12, 2014 as doi: 10.1002/oa.2407.

THIEREN, E.; WOUTERS, W.; VAN NEER, W. & ERVYNCK, A. 2012: Body length estimation of the European eel *Anguilla anguilla* on the basis of isolated skeletal elements. *Cybium* 36: 551-562.

VAN MAREN, M. 1971: *Steurresten uit de Vlaardingen-cultuurnederzettingen te Vlaardingen en Voorschoten*. Scriptie Instituut voor Prae- en Protohistorie. Universiteit Amsterdam, Amsterdam.

VASIL'EVA, E. D. 1999: Some morphological characteristics of Acipenserid fishes: considerations of their variability and utility in taxonomy. *Journal of Applied Ichthyology* 15(4-5): 32-34.

VECSEI, P.; CHARETTE, R.; TRUKSHIN, I.; MALIEPAARD, T.; HOCHLEITHNER, M. & LAFLEUR, Y. 2001: *CITES identification guide - sturgeons and paddlefish : guide to the identification of sturgeon and paddlefish species controlled under the Convention on International Trade in Endangered Species of Wild Fauna and Flora.* Environment Canada, Ottawa.

VERHEY, C. J. 1963: Het voorkomen van de Steur (*Acipenser sturio* L.) in Nederland na 1931. *De Levende Natuur* 66(1): 15-16.

VLADYKOV, V. D. & BEAULIEU, G. 1946: Etudes sur l'esturgeon (*Acipenser*) de la province de Québec. *Le Naturaliste Canadien* LXXIII: 141-204.

WUERTZ, S.; REISER, S.; GESSNER, J. & KIRSCHBAUM, F. 2011: Morphological Distinction Between Juvenile Stages of the European Sturgeon *Acipenser sturio* and the Atlantic Sturgeon *Acipenser oxyrinchus*. In: Williot, P.; Rochard, E.; Desse-Berset, N.; Kirschbaum, F. & Gessner, J. (eds.): *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758. The Reunion of the European and Atlantic Sturgeons*: 53-64. Springer-Verlag, Berlin.

Archaeofauna 25 (2016): 33-78

The size of domestic cattle, sheep, goats and pigs in the Czech Neolithic and Eneolithic Periods: Temporal variations and their causes

RENÉ KYSELÝ
Institute of Archaeology of the Czech Academy of Sciences, Prague, v.v.i.
Letenská 4, CZ-118 01 Praha.
kysely@arup.cas.cz

(Received *8 September 2015*; Revised *20 October 2015*; Accepted *30 October 2015*)

ABSTRACT: Osteometric data were analysed from the main domestic animals existing in central Europe during the Neolithic and Eneolithic (Chalcolithic) periods, specifically cattle (*Bos taurus*), sheep (*Ovis aries*), goats (*Capra hircus*), and pigs (*Sus domesticus*). The results are based on a combined evaluation of selected dental and postcranial measurements (in total nearly 1100 measured values) obtained from archaeological material from the Bohemian and Moravian (Czech Republic) Lengyel and Eneolithic periods (4700-2200 BC, including Moravian Painted Ware, Funnelbeaker, Baden-Řivnáč, and Bell-Beaker Cultures for example) and adjacent Neolithic and Early Bronze Age cultures (Linear and Stroked Pottery, Únětice). Results on the animals´ body size and their variation over time are presented, and possible interpretations of the secular changes in size are discussed in detail. Apart from the general, well known trend showing a reduction in cattle size over time, some anomalies were found. Based on osteometric comparisons, there are indications of cross-breeding between wild and domestic forms and/or the local domestication of cattle in the Bohemian Řivnáč Culture (3200-2800 BC), and of pigs in the Proto-Eneolithic to Funnelbeaker Cultures (4300-3350 BC). The observed body-size increase in sheep in the territory of the Czech Republic during the Early-Middle Eneolithic corresponds to the previously hypothesised importation of a new breed throughout Europe during the second half of the 4th millennium BC.

KEYWORDS: OSTEOMETRY, BODY MASS, DOMESTICATION, CROSS-BREEDING, CHALCOLITHIC, *Bos taurus*, *Ovis aries*, *Capra hircus*, *Sus domesticus*, AUROCHS, WILD BOAR

RESUMEN: Este trabajo analiza datos osteométricos de los principales animales domésticos centroeuropeos durante el Neolítico y Eneolítico (Calcolítico) como la vaca (*Bos taurus*), la oveja (*Ovis aries*), la cabra (*Capra hircus*) y el cerdo (*Sus domesticus*). Los resultados se basan en cerca de 1.100 medidas dentarias y postcraneales obtenidos a partir de materiales arqueológicos de Bohemia y Moravia (República Checa) en culturas como la de Lengyel y otras calcolíticas en un rango de entre 4700-2200 a. C. En ellas están presentes horizontes de las cerámicas pintadas de Moravia, cultura de los vasos de embudo (TBK), cultura de Baden, así como el Campaniforme, además de otras culturas adyacentes como la de Cerámica a Bandas (LBK), la de Cerámicas impresas (Stichbandkeramik, STK) y la de Únětice. Se presentan datos sobre tallas corporales y su variación diacrónica valorando pormenorizadamente las posibles causas de los cambios seculares detectados. Además de una bien constatada tendencia referida a la progresiva reducción de la talla del vacuno con el tiempo, se detectan una serie de anomalías. De este modo, se especula sobre posibles cruces habidos entre el vacuno doméstico y salvaje o una posible domesticación local del uro en la cultura Bohemia de Řivnáč (3200-2800 a.C.), así como del cerdo en las culturas Proto-Eneolíticas y de cerámica de embudo (4300-3350 a.C.). El incremento de talla del ovino en el territorio de la república Checa durante el Eneolítico Antiguo y Medio, en cambio, refuerza la postulada importación de una nueva raza de oveja en Europa durante la segunda mitad del cuarto milenio a.C.

PALABRAS CLAVE: OSTEOMETRÍA, MASA CORPORAL, DOMESTICACIÓN, CRUZAMIENTO, CALCOLÍTICO, *Bos taurus, Ovis aries, Capra hircus, Sus domesticus*, URO, JABALÍ

INTRODUCTION

There is a relatively large amount of archaeozoological data, analyses and results available from the area of central Europe, but very little is known internationally about the Bohemian and Moravian regions. For instance, a synthesis by Bökönyi (1974) does not include any locality from the Czech Eneolithic, a synthesis by Benecke (1994) includes only four localities, and a survey by Glass (1991) only two localities. A short overview including the selective evaluation of the size of domestic animals was written by Peške (1994). Detailed synthetic studies analysing breeding and hunting in the Czech Republic during the early agricultural period have appeared only recently (Roblíčková, 2003a, b; Kyselý, 2010a, 2012; Kovačiková *et al.*, 2012). The work presented here tries to partly fill this gap using selection of so far unpublished osteometric analyses of the author (Kyselý, 2010a), based on a synthetic study of 140 archaeozoological collections originating from 104 Lengyel and Eneolithic settlements, about half of which provided measurement data for the analyses presented below. Thus, this work expands on the knowledge of animal breeding in the Czech lands outlined in the previous study analysing the paleoeconomic situation in the Lengyel and Eneolithic periods (Kyselý, 2012).

This study is based on the measurements of bones and subsequent analyses of the obtained osteometric data. Morphological signs and other characteristics are only marginally taken into account. However, the results can be applied on a broader scale, because the size of animals is related to their genetic background, breed origin, zootechnical interventions, economic utilization and their role in the life of people.

AIMS

The basic aims of the study are

(1) to provide a large set of metric data documenting a variety of skeletal dimensions, body size and variability in body size of domestic cattle, sheep/goats and pigs from the Czech territory during the Lengyel and Eneolithic periods;

(2) to detect the changes in the size of these animals over time;

(3) to provide interpretations of found secular changes.

MATERIAL AND METHODS

Terms and acronyms

Taxonomic nomenclature of domestic mammals follows Gentry *et al.* (2004). Archaeological cultures and periods and their absolute dating follow local, Bohemian and Moravian chronology and terminology (Podborský, 1993; Jiráň & Venclová, 2013-2014; see Figure 2). Acronyms of measurements are after Driesch (1976).

B = breadth

BBC = Bell-Beaker C.

BC = before Christ calib.

Bd = distal breadth

BO = Bohemia

Bos indet. = undetermined form of cattle (*Bos taurus* / *Bos primigenius*)

Bp = proximal breadth

BP = *Bos primigenius*

BT = *Bos taurus*
C. = (archaeological) culture
CA = *calcaneus*
CH = *Capra hircus*
CR = the Czech Republic
CWC = Corded Ware C.
En./ Eneolithic = Chalcolithic or Copper Age (*sensu* Bohemian and Moravian chronology)
GAC = Globular Amphora C.
GB = greatest breadth
GL = greatest length
H_2 = heritability
inf. = inferior
KHD = Kutná Hora-Denemark site (east Bohemia)
L = length
LBK = Linear Pottery C. (Linearbandkeramik)
LGK = Lengyel C.
M1, M3 = *molar 1, molar 3*
MMK = Moravian Painted Ware C.
MO = Moravia
MTC = *metacarpus*
mtDNA = mitochondrial DNA
MTT = *metatarsus*
NISP = number of identified specimens
OA = *Ovis aries*
O/C = *Ovis* / *Capra*
P1 = *premolar 1*
prox. = proximal
Řivnáč C. = local Bohemian Middle Eneolithic culture (derived from Baden C.)
SS = *Sus scrofa*
SSD = *Sus domesticus*
STK = Stroked Pottery C. (Stichbandkeramik)
Sus indet. = undetermined form of pig (*Sus domesticus* / *Sus scrofa*)
TRB = Funnelbeaker C. (Trichterbecherkultur)
WH = the withers height

Thematic and temporo-spatial definition

The study is limited to typical farm mammals; cattle, sheep, goats and pigs, that played a substantial role in European prehistoric husbandry and were interrelated. Dogs and horses have been analysed morphometrically elsewhere (Kyselý, 2010a; Kyselý & Peške, 2016). In the Czech lands, domestic fowl has not been reliably documented in the studied period (Kyselý, 2010b). In the studied region some of the domestic mammals had, and still have, wild ancestors with which they could potentially have been cross-bred. Some of the comparisons also include osteometric data from bones of these wild forms. These concern aurochs, which were still quite common in the region in the Neolithic and Eneolithic periods (Kyselý, 2005, 2008 a, b, 2012), and wild boar, which were common in all Holocene periods (Kyselý, 2005).

The work compares osteometric data obtained as part of the study of archaeozoological finds from the Czech Republic (CR). The majority of the data used here comes from the localities of Bohemia (the western part of CR), especially its central and northern parts. This region is mostly surrounded by medium-sized mountains, which result in its partial isolation (Figure 1). A smaller dataset comes from southern Moravia (the eastern part of CR), which is open to the relatively warmer Pannonia lowland and which is part of a north-south migration corridor. However, the distance between the two regions and their geographical and climatic differences are not great. Relatively stable temperatures, a climate without dramatic changes and similar vegetation are assumed within the studied period. The evaluated time span includes the Holocene climatic optimum, with a temperature probably slightly higher than nowadays (Ložek, 1973; Dreslerová *et al.*, 2007). All the localities included come from the lowland regions, the altitudinal span being only c. 160-300 m above sea level (Figure 1).

As in Kyselý (2010a, 2012), the study is focused on the Lengyel and Eneolithic periods, i.e. c. 4700-2200 BC. Nevertheless, to detect broader tendencies, available data representing the preceding Neolithic cultures (LBK, STK) and the immediately following Early Bronze Age culture (Únětice C.) are also included - thus the work comprises nearly 4000 years of history (c. 5600-1700 BC). The Lengyel and Eneolithic periods in the given region include 11 archaeological cultures or their subphases (for the cultures represented in CR see Table 1 and Figure 2). In terms of the number of settlement localities as well as the amount of osteometric data, the TRB and Řivnáč Cultures are the best-represented (i.e. the Early and Middle Eneolithic, c. 3800-2800 BC). Other archaeological cultures present in the Czech Republic are, in terms of the quantity of

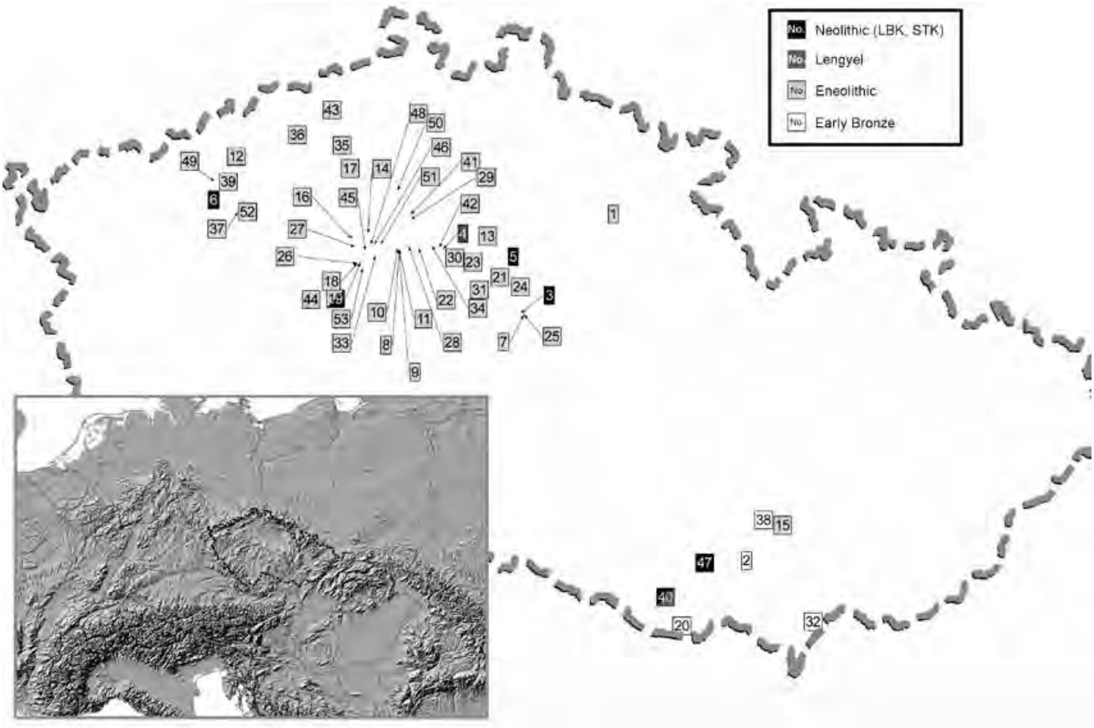

FIGURE 1

Map of the Czech Republic with localities which provided osteometric data for the study. Localities are sorted according to main archaeological periods. Locality codes correspond to those used in Table 1. The position of the Czech Republic in the Central European geomorphological situation is shown in Figure inset. Broken lines = state border of CR. Image by R. Kyselý with using geographical map from http://www.eea.europa.eu/.

osteometric data, represented less or only rarely, or are not represented at all (e.g. Corded Ware C.).

Localities, data and taphonomy

The localities that provided the data for the analyses presented here (Figures 3-29) are given in Table 1 and Figure 1. Most of them are part of the synthesis by Kyselý (2010a), which includes osteometric data representing the majority of the processed Lengyel and Eneolithic material thus far obtained through archaeological excavations in the territory of the Czech Republic. Methodological uniformity is largely ensured by the fact that the data were mostly obtained, or at least were methodologically treated, by the author himself. The primary osteometric data, the survey on fauna, quantifications and other data related to the material and localities are included in Kyselý (2010a) and other source studies cited in Table 1. Unlike in the source works, small corrections have been made including the re-interpretation of the status (domestic / wild / indet.) of some finds. Newly obtained data from the well-known Neolithic locality Bylany are also included.

Only selected measurements were analysed. Of the total amount of collected osteometric data nearly 1100 data (measuring) representing c. 900 finds from 53 localities (Table 1) have been used. The amount of data in individual animal species and single dimensions differ: a total of c. 730 metric values for cattle have been analysed, c. 110 for sheep/goats and c. 230 for pigs. In the graphs, the material is mostly presented in the form of primary osteometric values (points). These primary data could also be tested statistically. However, in the case of the relatively extensive material from sites at Makotřasy, Chotěbudice and Hostivice-Sadová (Clason, 1985; Kovačiková *et al.*, 2012) the primary data were not published, and therefore only the available histograms or boxplots are used here.

site code	site name	region	period / phase	culture (stage)	source of primary osteometric data	source of further information	osteometric data used **		
correspond to Figure 1		*	see Figure 2	see Figure 2 *			*Bos*	O/C	*Sus*
1	Benátky	BO	Eneolithic early	TRB-Baalberge	Kyselý, 2010a	Kyselý, 2012	X		
2	Blučina-Cezavy	MO	Bronze	Únětice C.	Roblíčková, 2003b, 2004	Roblíčková, 2003a	X	X	
3	Bylany	BO	Neolithic (pre-Lengyel)	LBK	R. Kyselý, unpublished	Peške et al., 1998	X		X
4	Čelákovice	BO	Lengyel	LGK (late phase)	Kyselý, 2010a	Kyselý, 2012	X		X
5	Choťánky	BO	Neolithic (pre-Lengyel)	STK	R. Kyselý, unpublished		X	X	X
6	Chotěbudice	BO	Neolithic (pre-Lengyel)	LBK	Kovačiková et al., 2012		x***		
7	Cimburk	BO	Eneolithic early	TRB-Baalberge	Kyselý, 2010a	Peške, 2000; Kyselý, 2012	X		X
7	Cimburk	BO	Eneolithic early/middle	TRB-Baalberge + Boleráz phase	Kyselý, 2010a	Peške, 2000; Kyselý, 2012	X		X
8	Ďáblice-K Letňanům	BO	Proto-Eneolithic	Jordanów C. (late phase)	Kyselý, 2010a	Kyselý, 2007a, 2012	X	X	X
9	Ďáblice-K lomu	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2007b, 2012	X		X
10	Ďáblice-křižovníci	BO	Eneolithic early	TRB-Siřem	Kyselý, 2010a	Kyselý, 2012	X		
11	Ďáblice-Legionářů	BO	Proto-Eneolithic	Jordanów C. (late phase)	Kyselý, 2010a	Kyselý, 2009, 2012	X		X
11	Ďáblice-Legionářů	BO	Eneolithic Proto-/early	Jordanów C. (late phase) / TRB	Kyselý, 2010a	Kyselý, 2009, 2012	X	X	
12	Droužkovice	BO	Proto-Eneolithic	Jordanów C. (Schussenried)	Kyselý, 2010a	Kyselý, 2012	X		
13	Dvory-Liduška	BO	Eneolithic early	TRB	Kyselý, 2010a	Kyselý, 2012	X		
14	Holubice	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X		X
15	Holubice II	MO	Eneolithic late	BBC	Peške, 1985a		X	X	
16	Homolka	BO	Eneolithic middle	Řivnáč C. (middle phase)	Ambros, 1968; Bogucki, 1979		X	X	X
17	Hostěnice	BO	Eneolithic early	TRB-Salzmünde	Kyselý, 2010a	Kyselý, 2012, 2013	X	X	X
18	Hostivice-Litovice	BO	Eneolithic early	TRB-Baalberge	Kyselý, 2002a	Kyselý, 2012	X		
19	Hostivice-Sadová	BO	Neolithic (pre-Lengyel)	LBK	Kovačiková et al., 2012		x***		
19	Hostivice-Sadová	BO	Eneolithic early	TRB	Kyselý, 2010a	Kyselý, 2012	X		X
20	Hrádek	MO	Bronze	Únětice C.	Roblíčková, 2003b, 2004	Roblíčková, 2003a	X		
21	Hradenín	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X	X	
22	Jenštejn	BO	Proto-Eneolithic	Jordanów C. (phase Jenštejn)	Beech, 1995		X		X
23	Klučov	BO	Eneolithic middle	GAC	Kyselý, 2010a	Kyselý, 2008d, 2012	X		X
23	Klučov	BO	Eneolithic middle	Řivnáč C. (early phase)	Kyselý, 2010a	Kyselý, 2008d, 2012	X		X
24	Kolín (bypass)	BO	Eneolithic middle	řivnáč starší	Dobeš et al., 2013		X		
25	Kutná Hora-Denemark	BO	Eneolithic middle	Řivnáč C. (middle-late phase)	Kyselý, 2008b	Kyselý, 2008a, 2012	X	X	X
26	Litovice	BO	Eneolithic early	TRB	Kyselý, 2010a	Kyselý, 2012	X	X	X
26	Litovice	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X		X
27	Makotřasy	BO	Eneolithic early	TRB-Siřem	Clason, 1985		x***		
28	Miškovice	BO	Eneolithic middle	Řivnáč C. (early phase)	Kyselý, 2010a	Kyselý, 2012, Ernée et al. 2007	X	X	X
29	Mlékojedy	BO	Eneolithic early	TRB-Baalberge	Kyselý, 2010a	Kyselý, 2012	X		
29	Mlékojedy	BO	Eneolithic middle	Baden C. (phase II)	Kyselý, 2010a	Kyselý, 2012			X
30	Mochov	BO	Eneolithic early	TRB-Salzmünde	Kyselý, 2010a	Kyselý, 2012	X	X	X
31	Molitorov	BO	Eneolithic early	TRB	Kyselý, 2010a	Kyselý, 2012			X
32	Moravská Nová Ves	MO	Bronze	Únětice C.	Roblíčková, 2003b, 2004	Roblíčková, 2003a	X	X	
33	Nebušice	BO	Proto-Eneolithic	Jordanów C. (Schussenried)	Kyselý, 2010a	Kyselý, 2012	X		X
34	Ostrov-Zápy	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X	X	X
35	Prosmyky	BO	Eneolithic early	TRB	Kyselý, 2010a	Kyselý, 2012	X		X
36	Radovesice	BO	Eneolithic late	BBC	Beech, 1993		X		
37	Siřem	BO	Eneolithic early	TRB-Siřem	Kyselý, 2010a	Kyselý, 2012; Likovský & Kyselý, 2008			X
38	Šlapanice	MO	Bronze	Únětice C.	Roblíčková, 2003b, 2004	Roblíčková, 2003a	X	X	X
39	Soběsuky	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X	X	X
40	Těšetice-Kyjovice	MO	Neolithic (pre-Lengyel)	LBK	Dreslerová, 2006		X	X	X
40	Těšetice-Kyjovice	MO	Lengyel	LGK (MMK-Ia)	Dreslerová, 2006		X	X	X
41	Tišice	BO	Eneolithic middle	Baden C. / Řivnáč C. (late phase)	Kyselý, 2010a	Kyselý, 2012			X
42	Toušeň-Hradišťko	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X	X	X
43	Trmice	BO	Proto-Eneolithic	Jordanów C. (Schussenried)	Kyselý, 2010a	Kyselý, 2012	X	X	X
44	Trubín	BO	Proto-Eneolithic	Jordanów C. (Schussenried)	Kyselý, 2010a	Kyselý, 2012	X		X
45	Tuchoměřice	BO	Proto-Eneolithic	Jordanów C. (early phase)	Kyselý, 2010a	Kyselý, 2012	X	X	
45	Tuchoměřice	BO	Eneolithic middle	Řivnáč C. (early phase)	Kyselý, 2010a	Kyselý, 2012	X		
45	Tuchoměřice	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X		X
46	Úholičky	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2008c, 2012		X	X
46	Úholičky	BO	Eneolithic late (+middle?)	BBC (+ Řivnáč C.?)	Kyselý, 2010a	Kyselý, 2008c, 2012			X
47	Vedrovice	MO	Neolithic (pre-Lengyel)	LBK	Nývltová-Fišáková, 2004		X	X	
48	Velké Přílepy-Skalka	BO	Eneolithic early	TRB	Kyselý, 2010a	Kyselý, 2012	X	X	
48	Velké Přílepy-Skalka	BO	Eneolithic early	TRB-Salzmünde	Kyselý, 2010a	Kyselý, 2012	X		X
48	Velké Přílepy-Skalka	BO	Eneolithic early	TRB-Siřem	Kyselý, 2010a	Kyselý, 2012	X		
48	Velké Přílepy-Skalka	BO	Eneolithic early/middle	TRB-Siřem, Salzmünde, Baden, GAC	Kyselý, 2010a	Kyselý, 2012	X	X	X
48	Velké Přílepy-Skalka	BO	Eneolithic early/middle	Baden C. (/ TRB + Boleráz)	Kyselý, 2010a	Kyselý, 2012			X
49	Vikletice	BO	Eneolithic early	TRB-Siřem	Kyselý, 2010a	Kyselý, 2002b, 2012	X	X	X
50	Vlíněves	BO	Eneolithic middle	Řivnáč C.	R. Kyselý, unpublished	Dobeš et al., 2011	X		X
51	Žalov	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012	X		X
52	Želeč	BO	Proto-Eneolithic	Jordanów C. (Schussenried)	Kyselý, 2010a	Kyselý, 2012	X		
53	Zličín	BO	Eneolithic middle	Řivnáč C.	Kyselý, 2010a	Kyselý, 2012			X

TABLE 1

List of the Czech localities used in this study, arranged alphabetically. Locality codes correspond to those used in the map in Figure 1. *For acronyms see text; **Data available and used for particular taxon marked by ×, O/C = *Ovis / Capra*; ***Raw data not given, only histograms available.

There are geographic differences in the representation of cultures, since in Bohemia osteometric data from the Lengyel, Late Eneolithic (BBC) and Early Bronze (Únětice C.) are almost absent, while in Moravia osteometric data from the Early and Middle Eneolithic (TRB, Řivnáč, Jevišovice C.) are missing (cf. Table 1 and Figure 2). Nevertheless, all the analysed assemblages come from

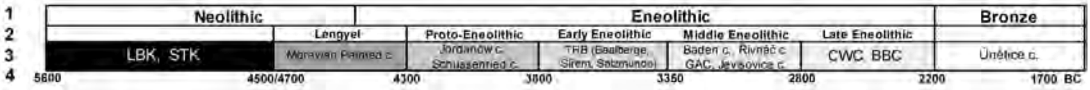

FIGURE 2

Chronology and dating of the Czech archaeological cultures and periods (after Pavlů & Zápotocká *et al.*, 2013; Neustupný *et al.*, 2013; Jiráň *et al.*, 2013). 1 = main periods, 2 = period sub phases, 3 = archaeological cultures, 4 = dating (BC calibrated). All presented cultures except CWC and Jevišovice C. yielded osteometric data.

localities representing lowland agricultural settlements (either in flat land or on mounds or promontories). All of the material comes from sunken archaeological features; material from caves, tells, peat or underwater sites, and material from the settlement layers is not represented. Therefore, considering their similar origins, the individual samples are in the right condition to conduct taphonomic processes with comparable impacts. In general, the material is heavily fragmented as reflected in the very low number of complete long bones for example. Thus, the work has to rely on dimensions other than the lengths of long bones. With regard to strong taphonomic disintegration and reduction of skeletons and spatial distribution of the material (in many archaeological contexts, features and sites), the author expects that in most cases one individual is represented only by one bone/fragment.

As the evidence of one locality can potentially be anomalous, it is preferable for the evaluation that the results from the most analysed cultures are based on more than one locality (cf. Table 1). A particularly large number of localities are available in the case of the dominant Funnelbeaker (TRB) and Řivnáč Cultures. Nevertheless, the really numerous osteological samples are available for only a small number of localities. As one locality (sample) usually provided only a small amount of osteometric data, this study operates with units formed by the grouping (merging) of several samples (localities). The method of fusion and categorization, as well as the quantity of the data used for the analysis is obvious from individual graphic comparisons.

General remarks on the size and metric variability

The work takes into consideration the following facts, assumptions and studies:

(1) Genetically-based variability of body size and bone dimensions in conspecific populations living at the same place and time consists of several components which were for the purposes of archaeozoology clearly defined by Payne & Bull (1988). The main components are: (a) individual age, (b) sex (including castration), (c) breed/form/taxon and (d) residual individual variability. It is necessary to also take into consideration the effect of pathologies (Albarella, 1997; Bartosiewicz, 2013). The fact that sexual dimorphism in size (and dimensions of bones) is reduced in domesticated forms compared with wild forms is also taken into account (Bökönyi, 1962; Benecke, 1994; Hannah *et al.*, 2005; Zeder *et al.*, 2006).

(2) As well as genetic influences, the size of the body, size of bones and variability in the size is also influenced by the physical condition, diet, milking and other external conditions, and therefore are also affected by the method of feeding, human care and general management of the animals. The fact that these factors influence the growth leads from observations within zootechnology and anthropology as well as zoology. It is also well known in archaeozoology (Higham, 1969). Of course, the influence of external factors is limited. For example heritability (H^2) of the wither height in domestic ungulates is said to be high; in artiodactyls H^2 is usually between 0.5 and 0.8 depending on various factors (for cattle see Nephawe *et al.*, 2004; Riley *et al.*, 2007). There is only a small amount of data available on bone size heritability. On the length of cattle metacarpus and metatarsus Wilson *et al.* (1977) found that h^2 are 0.48 and 0.59. H^2 for the breadth and depth of metapodials are, based on the same study, between 0.29 and 0.65.

(3) Animals crossbred between breeds of a different body size have, on average, a body size somewhere between those of the parents. This fact is also generally valid for

farm animals. Nevertheless, it is necessary to take into consideration the possibility of the specific influence of heterosis or, on the contrary, of outbreeding depression (e.g. Johnson, 1981; Frisch, 1987). The well-known phenomenon of ‘regression to the mean’ (Galton, 1886) is also of general validity.

(4) The body size is reflected in the sizes of postcranial bones. The lengths of long bones of domestic animals correlate relatively well with the withers height (WH), and are used for WH estimation[1]. It is obvious that the average body weight representing the given breed/taxon is also reflected in the sizes of the bones, especially cross-sectional measurements of limb bones, as they bear the animal’s weight (Uerpmann & Uerpmann, 1994; Meadow, 1999; Mendoza *et al.*, 2006; Kyselý, 2008a). According to Scott (1985, 1990) and Gingerich (1990) in particular the breadths of long bones and lengths of the humerus and femur have, on the supra-specific level, a rather high correlation with an average body mass. On an intra-specific level, the correlation of dimensions of the postcranial bones with the body mass is not very high, but it is positive and in many cases statistically significant (see for example studies concerning domestic cattle: Higham, 1969; Noddle, 1973; Dikeman *et al.*, 1976; Wilson *et al.*, 1977; Bergström & Wijngaarden-Bakker, 1983). In palaeontology the craniodental measurements are also used for the assessment of the body size, but they are under other selection pressures and therefore their correlation with the dimensions of extremity bones and with WH is lower (Damuth, 1990; Uerpmann & Uerpmann, 1994; Mendoza *et al.*, 2006). However, even the estimation of the height from extremity bones is accompanied by problems and inaccuracies, which are particularly reported in estimations based on short bones such as the talus and calcaneus and, in the case of pigs, also the metapodials (see methodical papers cited[1]). Despite these inaccuracies, selected estimations are provided in this paper as an alternative to the raw osteometric data, which helps to image the ancient breeds (Table 2).

(5) In a broader geographic frame, it is necessary to take into consideration the general clinial variability and eco-geographic principles such as Bergmann´s rule (Bergmann, 1847) or Allen´s rule (Allen, 1877). However, within the relatively small Czech territory, it did not play a significant role, and therefore it is not taken into account for the intra-regional frame.

(6) In the broader time frame it is necessary to consider domestication trends. The general tendency of body-size reduction during the course of domestication in a number of species, including cattle, sheep, goats and pigs, is widely known (e.g. Zeuner, 1963; Bökönyi, 1974; Davis, 1981; Clutton-Brock, 1999; Zeder *et al.*, 2006; see also note[13]). Sophisticated and systematic breeding, based on artificial selection such as grading up and resulting in large breeds was, in the Czech lands, only applied in the 20th century AD, although occasional imports of animals of foreign breeds are recorded from the 17th century AD (Petrášek, 1972). The actual forms of the temporal trends and evolution of the animal size in the studied region are analysed in the results section.

(7) Climate models for the Czech territory reveal temperature fluctuations of a mere 1ºC and 100 mm of precipitation in the period ranging from the Neolithic to the Bronze Age (Dreslerová, 2012. Dreslerová *et al.*, 2007). Natural selection could affect domestic animals but rapid changes in body size would be unlikely under such circumstances. For such reason the impact of climate, and the other natural agents has not been considered important for our study (see Kyselý & Peške, 2016).

(8) The proportions of the body and osseous dimensions also depend on various factors. The above-mentioned factors, for example sex and age, can thus result in distinctive allometries and significant morphological variability; strikingly in the case of the size of horns of domestic bovids, but pronounced allometries also occur between the pairs of dimensions, such as the length vs. breadth of extremity bones and the sizes of teeth vs.

---

[1] Methods in Driesch & Boessneck, 1974; May *et al.*, 1996; May & Teichert, 2001; Teichert, 2005; Rehazek & Nussbaumer, 2012.

long bones. The individual skeletal dimensions react to the above-mentioned factors differently, as described for domestic cattle, sheep and pigs in papers by Higham (1969), Bartosiewicz (1984, 1985, 1987, 2013), Payne & Bull (1988), Berteaux & Guintard (1995) and Davis (2000). For example, the higher load of the forelimbs than hind limbs may lead to size-determined allometries (Bartosiewicz, 1987, 2013). The result of the disproportional load is the fact that the breadths of the fore limb bones display more sexual dimorphism than do equivalent bones in the hind limb, which is especially apparent and well known in metacapals (described in cattle by Calkin, 1960, 1962; Higham, 1969; Bartosiewicz, 1987; Thomas, 1988; Berteaux & Guintard, 1995). The allometries, often reflecting geographical or chronological position, commonly develop during the process of domestication of animals, including European cattle, sheep/goats

A - *Bos*					**measurements (mm)**				**indices (metapodials only)**			**withers height (cm)**								
												after Fock (1966)		after Calkin (1960)			after Matolcsi (1970)			
site (see Table 1 and Figure 1)	culture (see Figure 2)*	zoological determination*	anatomy*	sex, age (C = castrate)	GL	Bp	SD	Bd	Bp/GL*100	SD/GL*100	Bd/GL*100	indices for females used	indices for males used	indices for females used	indices for castrates used	indices for males used	indices for females used	indices for castrates used	indices for males used	sexually undifferentiated index used
Vedrovice	LBK	BT	MTC	not given	not given												145.1 (index not given)***			
Prosmyky	TRB	BT	MTT		200.3	46.2	26.6	54.2	23.1	13.3	27.1	107.2	111.2	107	110	111.8	105.8	114.4	112.6	
Cimburk	Baalberge	BT	MTC		(210)			70			(33.3)	(126)	(131.3)	(125.6)	(128.7)	(131)	(127.1)	(142.2)	(132.9)	
Hostivice-Litovice	Baalberge	BT	Femur	♀ **	367	115.5	38.3	100.5												118.5
Hostivice-Litovice	Baalberge	BT	Humerus	♀ **	290	104.4	39.6	82												120.1
Hostivice-Litovice	Baalberge	BT	Radius	♀ **	267.5	83.7	41.8	74.6												115
Hostivice-Litovice	Baalberge	BT	Tibia	♀ **	329.5	99.3	40.4	64.4												113.7
Hostivice-Litovice	Baalberge	BT	MTC	♀ **	191.8	60.8	31.3	62.3	31.7	16.3	32.5	115.1	119.9	114.7	117.6	119.7	116	129.8	121.4	
Hostivice-Litovice	Baalberge	BT	MTC	♀ **	192.2	60.1	32.1	62.3	31.3	16.7	32.4	115.3	120.1	114.9	117.8	119.9	116.3	130.1	121.7	
Hostivice-Litovice	Baalberge	BT	MTT	♀ **	218.5	51	27	56.7	23.3	12.4	25.9	116.9	121.3	116.7	120	121.9	115.4	124.8	122.8	
Makotřasy	TRB-Siřem	BT	MTC	not given	two estimations of WH from Clason (1985): 123 cm and 124 cm by two MTC (after Boessneck 1956)*** which are smaller than most of other MTC found in Makotřasy															
Hostěnice	Salzmünde	BT	MTC	♀?, subad.	192.5	57	32.1	62.2	29.6	16.7	32.3	115.5	120.3	115.1	118	120.1	116.5	130.3	121.9	
Hostěnice	Salzmünde	BT	MTT		228		27.3	61.8		12	27.1	122	126.5	121.8	125.2	127.2	120.4	130.2	128.1	
Vikletice	TRB (Siřem)	BT	MTC	♂?	188.4	61.2	33.9	64.7	32.5	18	34.3	113	117.7	112.7	115.5	117.6	114	127.5	119.3	
Homolka	Řivnáč C.	BT	Tibia		329		37	60												113.5
Holubice	Řivnáč C.	BT	MTC	C?, subad?	224.2	64	35	62	28.5	15.6	27.7	134.5	140.1	134.1	137.4	139.9	135.6	151.8	141.9	
Homolka	Řivnáč C.	BT	MTT		226.5	46	28	56	20.3	12.4	24.7	121.2	125.7	121	124.3	126.4	119.6	129.3	127.2	
Homolka	Řivnáč C.	BT	MTT		226	46	26	51	20.4	11.5	22.6	120.9	125.4	120.7	124.1	126.1	119.3	129	126.9	
Toušeň-Hradišťko	Řivnáč C.	BP	MTC		230.8	74.8	38.2	72.5	32.4	16.6	31.4	138.48	144.25	138		144	139.6		146.1	
Tuchoměřice	Řivnáč C.	BT	MTC	♀	190.2	51.7		53.9	27.2		28.3	114.1	118.9	113.7	116.6	118.7	115.1	128.8	120.4	
Tuchoměřice	Řivnáč C.	BT	MTC	♀	190.6	51	27	54.2	26.8	14.2	28.4	114.4	119.1	114	116.8	118.9	115.3	129	120.6	
Tuchoměřice	Řivnáč C.	BT	MTT		(221)	42.4	24.3	51	(19.2)	(11)	(23.1)	(118.2)	(122.7)	(118)	(121.3)	(123.3)	(116.7)	(126.2)	(124.2)	
Kutná Hora-Denemark	Řivnáč C.	BP	MTT		279.5	65.5	40	74.9	23.4	14.3	26.8	149.5	155.1	149.3		156	147.6		157.1	
Klučov	Řivnáč C.	BT	Femur		(405)	124.1	38.7													(130.8)
Klučov	Řivnáč C.	BT	Humerus		328.2		38.3	90.5												135.9
Klučov	Řivnáč C.	BP	Tibia		441	117.4		76.8												152.1
Klučov	Řivnáč C.	BT	MTC	C?	219.5	62.4	36.5	63.3	28.4	16.7	28.8	131.7	137.2	131.3	134.6	137	132.8	148.6	138.9	
Klučov	Řivnáč C.	BT	MTC	C?	(219.5)		(36.7)	62.1			(28.3)	(131.7)	(137.2)	(131.3)	(134.6)	(137)	(132.8)	(148.6)	(138.9)	
Klučov	Řivnáč C.	BP	MTT		283.1	60.1	31.5	70.7	21.2	11.1	25	151.5	157.1	151.2		158	149.5		159.1	
Tuchoměřice	Řivnáč C.	BT	Humerus		311		42.6	87.1												128.8
Šlapanice	Únětice C.	BT	MTT	not given	244	51.2	30.6	64.1	21	12.5	26.3	130.5	135.4	130.3	134	136.1	128.8	139.5	137.1	
Blučina-Cezavy	Únětice C.	BT	MTC	not given, ♀?	189.1	50.7	30.2		26.8	16		113.5	118.2	113.1	115.9	118	114.4	128	119.7	
Blučina-Cezavy	Únětice C.	BT	MTT	not given	222.6	42.6	25.2	53	19.1	11.3	23.8	119.1	123.5	118.9	122.2	124.2	117.5	127.2	125.1	
Blučina-Cezavy	Únětice C.	BT	MTT	not given	213.1	46.7	29	59.1	21.9	13.6	27.7	114	118.3	113.8	117	118.9	112.5	121.8	119.8	
Blučina-Cezavy	Únětice C.	BT	MTT	not given	222.5			50.3			22.6	119	123.5	118.8	122.2	124.2	117.5	127.2	125	
Blučina-Cezavy	Únětice C.	BT	MTT	not given	214.2	43			20.1			114.6	118.9	114.4	117.6	119.5	113.1	122.4	120.4	

B - *Ovis/Capra*				**measurements (in mm)**					**withers height (cm)**			
site (see Table 1 and Figure 1)	culture (see Figure 2)*	zoological determination*	anatomy*	GL (HS)	GLl	Bp	SD	Bd	indices for *Capra* used (after Schramm, 1967)	indices for *Ovis* used (after Teichert, 1975; Tab. 4)	calculated after May & Teichert (2001; Tab. 2a), using indices for males	calculated after May & Teichert (2001; Tab. 2b), using indices for females
Vedrovice	LBK	OA	MTC	not given						82.4***		
Těšetice-Kyjovice	LBK	OA	CA	53						60.4	59.3	
Těšetice-Kyjovice	LBK	OA	CA	58						66.1	62.6	
Těšetice-Kyjovice	LBK	OA	Talus		26					59	64.1	
Choťánky	STK	OA	CA	54.6						62.2	60.4	
Těšetice-Kyjovice	MMK	CH	MTC	97		24	17	27	55.8			
Těšetice-Kyjovice	MMK	CH	MTT	104		21			55.5			
Těšetice-Kyjovice	MMK	OA	Talus		23					52.2	62.3	
Těšetice-Kyjovice	MMK	OA	Talus		24					54.4	62.9	
Těšetice-Kyjovice	MMK	OA	Talus		28					63.5	65.3	
Těšetice-Kyjovice	MMK	OA	Talus		29					65.8	65.8	
Těšetice-Kyjovice	MMK	OA	Talus		31					70.3	66.9	
Těšetice-Kyjovice	MMK	OA	Talus		32					72.6	67.4	
Jenštejn	Jordanów	OA	CA	57.6						65.7	62.4	
Velké Přílepy-Skalka	TRB	OA	Femur	181.7		45.2	17	38.3		64.1	67.7	65.8
Hostěnice	Salzmünde	OA	MTT	130.3		18.8	10.3	22.2		59.2	63	64.4
Velké Přílepy-Skalka	Siřem to GAC	O/C	Talus		31.2			20.2		70.8	67	
Toušeň-Hradišťko	Řivnáč C.	CH	MTC	129.1		28.9	19.7	32.8	74.2			
Toušeň-Hradišťko	Řivnáč C.	OA	CA	64.8						73.9	67	
Toušeň-Hradišťko	Řivnáč C.	OA	MTT	124.5		20	10.3	22.9		56.5	61.4	63.5
Toušeň-Hradišťko	Řivnáč C.	OA	Talus		33.9			22.5		76.9	68.4	
Toušeň-Hradišťko	Řivnáč C.	OA	Talus		30.9			19.6		70.1	66.9	
Homolka	Řivnáč C.	O/C	CA	65						74.1	67.1	
Homolka	Řivnáč C.	O/C	Talus		32					72.6	67.4	
Homolka	Řivnáč C.	O/C	Talus		30.5					69.2	66.7	
Homolka	Řivnáč C.	O/C	Talus		30					68	66.4	
Homolka	Řivnáč C.	O/C	Talus		28					63.5	65.3	
Homolka	Řivnáč C.	O/C	Talus		27					61.2	64.7	
Hradenín	Řivnáč C.	O/C	Talus		32.4					73.5	67.6	
Toušeň-Hradišťko	Řivnáč C.	O/C	Talus		33.8			21.9		76.7	68.3	
Úholičky	Řivnáč C.	O/C	Talus		35.3			22.1		80.1	69.1	
Holubice II	BBC	O/C	Talus		27					61.2	64.7	
Moravská Nová Ves	Únětice C.	OA	MTC	131.9						64.5	65.4	66.6
Šlapanice	Únětice C.	OA	talus		29.9					67.8	66.3	
Blučina-Cezavy	Únětice C.	OA	talus		28.1					63.7	65.3	
Blučina-Cezavy	Únětice C.	OA	talus		27.7					62.8	65.1	
Blučina-Cezavy	Únětice C.	OA	talus		27					61.2	64.7	
Blučina-Cezavy	Únětice C.	OA	talus		25.9					58.7	64.1	
Šlapanice	Únětice C.	OA	MTC	(123)		21	12			(60.1)	(62.6)	(65.2)
Šlapanice	Únětice C.	OA	MTC	(122)		21.7	13.4			(59.7)	(62.3)	(65.1)
Šlapanice	Únětice C.	OA	MTC	(121)		22.6	13.7			(59.2)	(62)	(64.9)
Šlapanice	Únětice C.	OA	MTC	(130)		(21.8)				(63.6)	(64.8)	(66.3)
Blučina-Cezavy	Únětice C.	CH	MTC	112		(24.3)	16	27.9	64.4			

C - *Sus*				**measurements (mm)**	**withers height (cm)**	
site (see Table 1 and Figure 1)	culture (see Figure 2)*	zoological determination*	anatomy*	GL or GLl	calculated after Teichert (1969)	calculated after May et al. (1996; Tab. 2b)
Těšetice-Kyjovice	LBK	SSD	Talus	36	64.4	77.7
Těšetice-Kyjovice	LBK	SSD	Talus	39	69.8	80.3
Těšetice-Kyjovice	LBK	SSD	Talus	40	71.6	81.1
Těšetice-Kyjovice	MMK	SSD	CA	75	70.1	78.3
Těšetice-Kyjovice	MMK	SS	CA	110	102.7	95
Těšetice-Kyjovice	MMK	SS	Talus	54	96.7	91.3
Těšetice-Kyjovice	MMK	SS	Talus	51	91.3	89.2
Ďáblice-K Letňanům	Jordanów (late)	SSD	Talus	42.4	75.9	83
Litovice	TRB	SS	MTC 3	(97.5)	104.5	99.4
Litovice	TRB	SSD	MTC 4	(80.7)	85	88.3
Hostivice-Sadová	TRB	SSD	Talus	40	71.6	81.1
Cimburk	Baalberge	SS	CA	109.5	102.3	94.8
Makotřasy	TRB-Siřem	SSD	not given	not given	60-78.2***	
Hostěnice	Salzmünde	SS	MTC 4	(100.4)	105.7	100.7
Hostěnice	Salzmünde	SS	MTC 3	100.6	107.8	101.3
Hostěnice	Salzmünde	SS	MTT 3	108.5	101.3	100.4
Hostěnice	Salzmünde	SS	MTT 4	120.1	106.2	101.3
Hostěnice	Salzmünde	SS	Talus	56.2	100.6	92.7
Mochov3	Salzmünde	SSD	MTC 3	75.3	80.7	85.4
Velké Přílepy-Skalka	Salzmünde	SSD	MTC 3	72.9	78.1	83.8
Velké Přílepy-Skalka	Salzmünde	SSD	MTC 3	73.4	78.7	84.1
Velké Přílepy-Skalka	Salzmünde	SSD	MTT 4	92	81.3	87.5
Velké Přílepy-Skalka	Baden (/TRB+Boleráz)	SSD	Talus	(43)	(77)	(83.4)
Tišice	Baden/Řivnáč	SSD	Talus	43.4	77.7	83.7
Miškovice	Řivnáč (early)	SSD	Talus	40.8	73	81.7
Holubice	Řivnáč C.	SSD	Talus	42.9	76.8	83.3
Homolka	Řivnáč C.	SSD	CA	81	75.7	81.4
Homolka	Řivnáč C.	SS	CA	104.5	97.6	92.6
Homolka	Řivnáč C.	SSD	Talus	44.5	79.7	84.6
Homolka	Řivnáč C.	SSD	Talus	42.5	76.1	83
Homolka	Řivnáč C.	SS	Talus	50	89.5	88.5
Homolka, hut B	Řivnáč C.	SSD	MTC 4	79.4	83.6	87.4
Homolka, hut B	Řivnáč C.	SSD	CA	83.4	77.9	82.6
Homolka, hut B	Řivnáč C.	SS	Talus	52	93.1	89.9
Ostrov-Zápy	Řivnáč C.	SSD	MTC 3	74	79.3	84.5
Ostrov-Zápy	Řivnáč C.	SSD	Talus	40.9	73.2	81.8
Soběsuky	Řivnáč C.	SSD	MTC 3	76	81.5	85.8
Soběsuky	Řivnáč C.	SSD	MTC 3	76.3	81.8	86
Toušeň-Hradišťko	Řivnáč C.	SSD	MTC 3	75	80.4	85.2
Toušeň-Hradišťko	Řivnáč C.	SSD	CA	78	72.9	79.9
Toušeň-Hradišťko	Řivnáč C.	SSD	CA	80.3	75	81.1
Toušeň-Hradišťko	Řivnáč C.	SSD	MTT 3	83.7	78.2	86.4
Toušeň-Hradišťko	Řivnáč C.	SSD	MTT 3	86.4	80.7	88
Toušeň-Hradišťko	Řivnáč C.	SSD	MTT 4	93.5	82.7	88.3
Toušeň-Hradišťko	Řivnáč C.	SS	CA	97.5	91.1	89.4
Toušeň-Hradišťko	Řivnáč C.	SS/SSD	Talus	50.7	90.8	89
Tuchoměřice	Řivnáč C.	SS	Talus	53.8	96.3	91.2
Kutná Hora-Denemark	Řivnáč C. (late)	SSD	CA	80.1	74.8	81
Kutná Hora-Denemark	Řivnáč C. (late)	SSD	CA	80.5	75.2	81.2
Kutná Hora-Denemark	Řivnáč C. (late)	SS	CA	98.2	91.7	89.7
Kutná Hora-Denemark	Řivnáč C. (late)	SS	CA	102.2	95.5	91.6
Kutná Hora-Denemark	Řivnáč C. (late)	SS	CA	111.7	104.3	95.8
Kutná Hora-Denemark	Řivnáč C. (late)	SSD	Talus	42.4	75.9	83
Kutná Hora-Denemark	Řivnáč C. (late)	SSD	Talus	47.1	84.3	86.5
Kutná Hora-Denemark	Řivnáč C. (late)	SS	Talus	53.6	95.9	91
Kutná Hora-Denemark	Řivnáč C. (late)	SS	Talus	52.8	94.5	90.5
Kutná Hora-Denemark	Řivnáč C. (late)	SS	Talus	55.3	99	92.2
Kutná Hora-Denemark	Řivnáč C. (late)	SS	Talus	55.2	98.8	92.1
Kutná Hora-Denemark	Řivnáč C. (late)	SS	Talus	55.8	99.9	92.5
Šlapanice	Únětice C.	SSD	Talus	40.3	72.1	81.3

TABLE 2

Estimations of the withers height of the Czech Neolithic, Eneolithic and Early Bronze Age cattle (sub-table A), sheep/goats (sub-table B) and pigs (sub-table C). Selected bone measurements and indices included. Grey – estimations by indices in concordance with the sex of an individual. Numbers in parentheses indicate approximate values. *For acronyms see text; **One individual (cattle no. 1 from pit 3, after Kyselý 2002a); ***Exact indices or values not given in original sources, therefore heights are not used in Figure 3, 17 and 21.

and pigs (e.g. Lasota-Moskalewska, 1980; Lasota-Moskalewska *et al.*, 1987).

Methods

Those samples with questionable archaeological dating, and finds suspected of intrusion were excluded from the analyses. The dimensions were measured according to Driesch (1976).

In the graphical presentation the measured values as well as the calculated withers heights are grouped according to archaeological age and provenance, which leads to segmentation of the studied period. This segmentation (i.e. merging of the samples/localities) is individual in each graphical analysis; it was necessary because the distribution of the available metric data between the individual comparisons is sometimes highly uneven. Segmentation of the studied period (Lengyel + Eneolithic) in the graphs is numbered starting from 1, the preceding Neolithic (LBK + STK) is labelled as 0. Even though time scale is categorized linear regression was applied. In comparisons with the distinctive decreasing or increasing time trend the linear regression is calculated and displayed in graphs. The non-parametric Mann-Whitney *U* test was used for the testing differences between means of size in particular periods, applied with respect to the amount of available data.

The bones of non-adult individuals and pathological bones have been excluded. The individual age has been assessed not only on the basis of the epiphyseal fusion, but also based on the character of the bone surface and muscle insertions; especially in the case of the elements with an early fusion of the epiphysis or the elements without the epiphysis (talus). In the case of molars dimensions the effect of age or the degree of eruption and abrasion has been taken into consideration (cf. Payne & Bull, 1988). The metric values obviously influenced by age have been excluded. After this methodical treatment, the variability within one time horizon and one region consists mainly of the following genetically-based components:

- (*a*) the sex (sexual dimorphism);
- (*b*) the form or breed (particularly domestic/wild form in the given case).

The dimensions that display lower sexual dimorphism and lower variability, and that do not display marked allometric differences are preferred in the analyses that follow. In general, those measurements having the best potential to characterize the body size have been selected for the identification of size changes in time. For example, it was taken into account that the dimensions of bones of hind limbs in the artiodactyls are usually less sexually dimorphous than the size of bones of forelimbs as described above. It was also taken into account that many dental dimensions (cheek teeth) show relatively little sexual dimorphism - probably as a result of the rule described by Carranza & Pérez-Barbería (2007). Logically, in the process of selection, in addition to the value of the information provided by the measurement, the amount of available data has also been taken into account. Therefore, the dimensions of the phalanges and molars have also been used and the greatest level of attention was paid to cattle, as they are the most abundant. One of the reasons for carrying out parallel analysis of several dissimilar dimensions is to avoid the risk of making an interpretation based on a single source, which could potentially be erroneous due to random distortion or due to methodological, allometric, demographic or taphonomic reasons. The details concerning the selection of dimensions and of the procedures and methods are given in single species analyses in the results section. Further details concerning particular assemblages and methods are included in Kyselý (2010a).

RESULTS

Cattle **(***Bos taurus***)**

A classification of the cattle (*Bos*) as domestic cattle (*Bos taurus*) or aurochs (*Bos primigenius*) by using metric limits can be problematic and uncertain. With regard to the existence of overlap in most dimensions (Grigson, 1969; Lasota-Moskalewska & Kobryń, 1989; Kyselý 2008a), some of the finds remained unclassified (labelled as '*Bos* indet.'). Specimens which are clearly outside the overlap were interpreted as domestic or wild according to morphometrics, with the help of measurements and suggestions given in Degerbøl & Fredskild (1970), which is based mostly on Danish material, and Bökönyi (1995), based mostly on material from the Carpathian Basin.

The appropriateness of using these two sources comes from their geographical proximity to the studied area and from the position of the studied area between both regions, with respect to the fact that aurochs body size changed only very little during the Holocene (Lasota-Moskalewska & Kobryń, 1990). The determination was in only one case confirmed by the molecular-genetic method (Kyselý & Hájek, 2012).

Absolute size

A combination of the indices from the work of Driesch & Boessneck (1974) and Matolsci (1970) has been used for the calculation of withers height, of which the indices according to Matolcsi are preferred (Table 2, Figure 3). Only in the case of potential castrates is the index by Calkin preferred, as it was created on the basis of a more representative number of neutered individuals. The method of assessment of body mass based on the withers height was proposed by Vigne (1991; the mass is marked as LWa), however, his calculation states weights roughly 10-15% higher than the figures of the combined data (height vs. mass) for various primitive tauroid breeds, according to the examples in Petrášek (1972) and Vohradský (1999). Therefore, the weight data in the following text are given after LWa correction (the calculated LWa is systematically reduced by 13%).

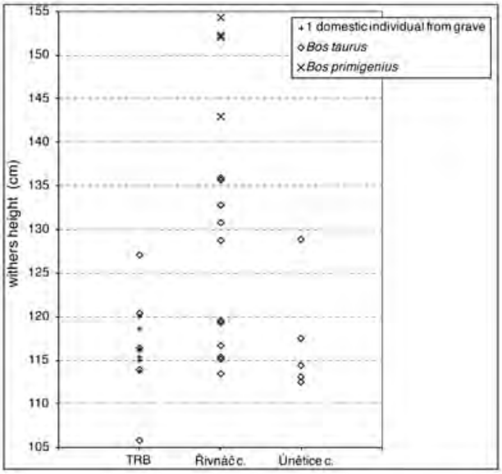

FIGURE 3

Withers heights of cattle (*Bos*) from the two best-represented Eneolithic cultures in the Czech Republic. Based on heights in Table 2 calculated using Matolcsi´s indices. Since a strong predominance of females is observed or expected, indices for females were used in the case of metapodia.

According to finds of long bones from the best-represented periods, i.e. TRB and Řivnáč Culture, withers height (WH) in domestic cows from the Bohemian region was calculated at c. 114-117 cm (n = 17; Table 2). It corresponds with the average body mass c. 350-390 kg. Males could have been c. 5-10 cm higher. Identification of castrates according to isolated bones is mostly very difficult or impossible. However, based on breadth-length index and absolute length, three metapodials from the analysed collection may be castrates (Table 2, 6). The height of these potential castrates was c. 134-138 cm (using the index according to Calkin, 1960), which corresponds to c. 540-590 kg. All these values are considerably lower than the size of aurochs, which during the period of Řivnáč C. attained WH between c. 140 and 160 cm, which corresponds to c. 700-1020 kg (n = 4; Figure 3, Table 2). The values of the WH (if males and females are considered together) suggest that domestic cattle from the TRB period may have been about 5 cm lower (~ 50 kg) than those in the following Řivnáč C. In the Bronze Age WH is somewhat smaller (Roblíčková, 2004), which seems to be true also for the earliest Bronze Age culture, Únětice C. (Figure 3).

The metacarpus and metatarsus lengths are less dependent on sex than the length of other long bones, and according to some calculations are even statistically independent of the sex (Calkin, 1962; Higham, 1969; Wilson *et al.*, 1977; Grigson, 1982; Bartosiewicz, 1984, 1985; Thomas, 1988; Berteaux & Guintard, 1995). Therefore, these dimensions are especially suitable for comparison of the body height even in the case where the metapodials are not sexed (Figure 4). From this point of view, however, castrates are problematic since they can have elongated metapodial bones[2]. However, we can assume that the number of castrates in the herd was probably very low (cf. share of males and possible castrates in Table 2, 6), so that they do not influence statistics too much. The comparison of Czech Eneolithic cattle with cattle in neighbouring regions shows that the Czech finds fall into the

---

[2] A castration causes the delayed fusion of the epiphyses and consequently the prolongation of the bone lengths (Boessneck, 1956; Calkin, 1960, 1962; Matolcsi, 1970; Grigson, 1982; Thomas, 1988).

		n	arithmetic mean (mm)	median (mm)	min.-max. (mm)
metacarpus - length	Bohemia	9	203.2	194	188.4-224.2
	neighbouring regions	50	196.6	195.9	182-223
metatarsus - length	Bohemia	6	220.1	223.5	200.3-228
	neighbouring regions	41	226	225	180-257

TABLE 3

Statistics of metapodial lengths of Czech Eneolithic cattle (data from this study) compared with those taken from Eneolithic cattle burials/depositions from neighbouring central European states (data from localities after Kyselý, 2002a) - the same data as in Figure 4. Domestic cattle is here defined using the following criteria: MTC length maximally 230 mm and MTT length maximally 260 mm (with respect to Degerbøl & Fredskild, 1970; Kobryń & Lasota-Moskalewska, 1989; Bökönyi, 1995).

size variation of central European cattle (Figure 4). The mean values of the metapodial lengths in both groups, i.e. Bohemia vs. surrounding areas, do not substantially differ (Table 3).

Changes over time

In the majority of the graphic analyses (Figures 5, 7, 8, 10, 12, 13 & 15) there are presented only the finds determined as domestic cattle (*Bos taurus*) and finds classified as *Bos* indet. Aurochs could be excluded from these comparisons, since a distinctive change in aurochs size is not presumed (cf. Lasota-Moskalewska & Kobryń, 1990). This procedure can assist better visibility of temporal trends in domestic cattle. The dental measurements analysed are the length of the third molar and length of the molar row (Figures 5-7), which in *Bos* are probably only slightly and statistically insignificantly sexually dimorphous, as Grigson (1974, 1982) states and as metric data on aurochs from Degerbøl & Fredskild (1970) suggest. Of the postcranial measurements, the bones of a hind limb have been preferred (tibia and talus; Figures 10, 11, 12) as their breadths are less sexually dimorphous than the breadths of bones of a forelimb (see above). In the literature the distal breadth of the metacarpus is frequently used for comparison. This dimension has therefore also been included (Figures 8, 9), although it displays relatively strong

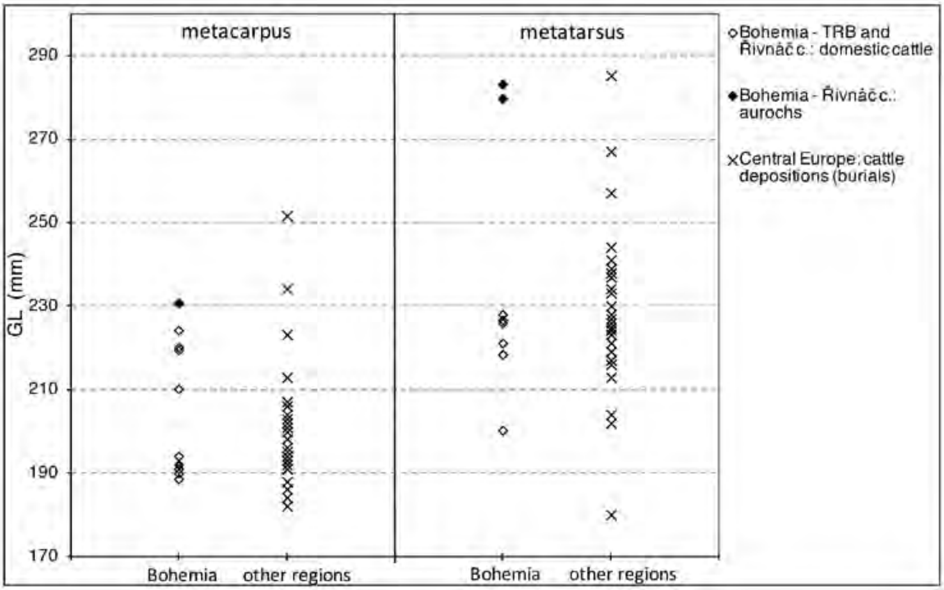

FIGURE 4

Lengths of metapodials (GL) of Czech Eneolithic cattle (data from this study) compared with those taken from Eneolithic cattle burials/depositions from neighbouring central European countries (data from localities included in Kyselý, 2002a) - the same data as in Table 3.

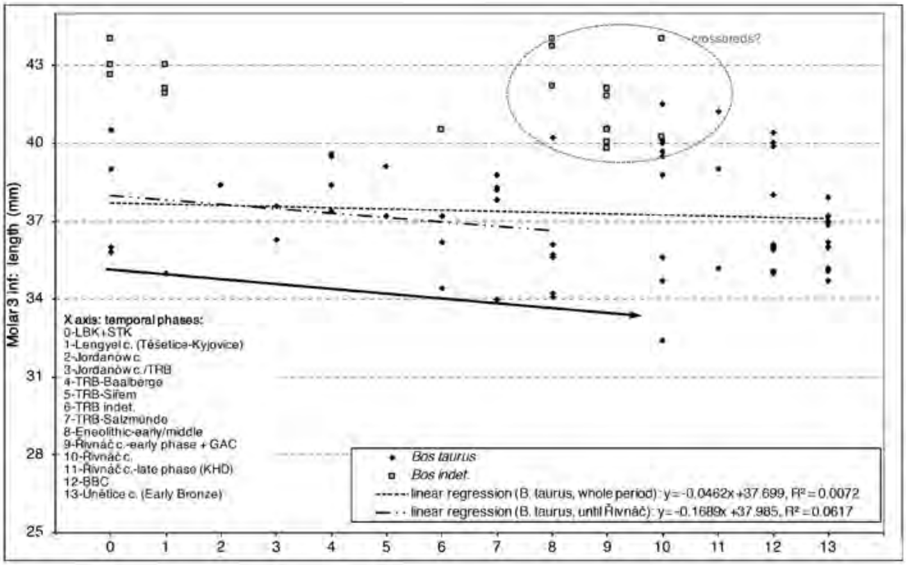

FIGURE 5

Variation over time (X axis) of the *Molar 3 inferior* greatest length (on Y axis, identical to measurement no. 10 in Driesch, 1976) of Czech Eneolithic cattle (*Bos*). *Bos taurus* and *Bos* indet. are included, aurochs is not included. Categories on the X axis are ordered chronologically (pre-Lengyel period labelled as 0). Full lines with arrows indicate roughly min. and max. limits for all or most of the *Bos taurus* cases. Broken lines show linear regressions. Circle indicates the position of potential crossbreds. For sources of data and sites see Table 1and text. For acronyms, terms, methods, definitions and dating of cultures see text and Figure 2.

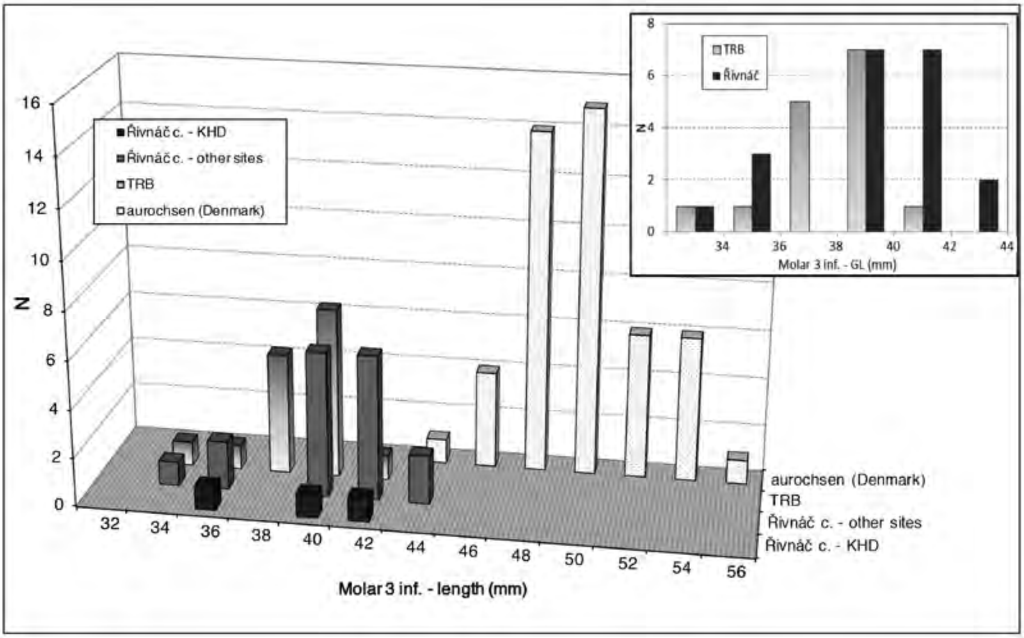

FIGURE 6

Histograms representing the distributions of *Molar 3 inferior* greatest lengths of Czech Eneolithic cattle (*Bos*) from the two osteologically best-represented cultures (TRB and Řivnáč C.) and from Kutná Hora-Denemark site (KHD) compared with Danish aurochs. Figure inset presents simplified comparison of the two cultures (incl. KHD). For sources of data and sites see Table 1 and text. Measurements of Danish aurochs according to Degerbøl & Fredskild (1970). For acronyms, terms, methods, definitions and dating of cultures see text and Figure 2. Compare results in Figure 5.

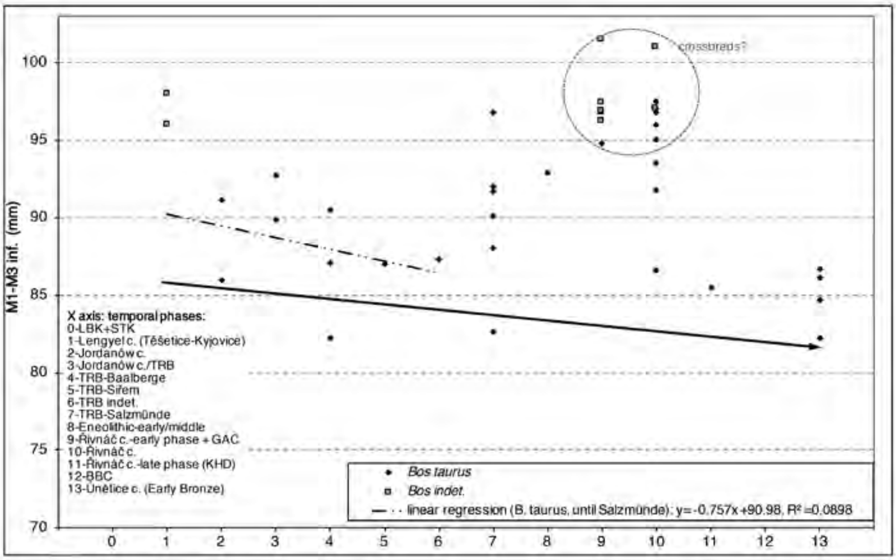

FIGURE 7

Variation over time (X axis) of the *Molar inferior* row alveolar length (on Y axis, identical to measurement no. 8 in Driesch, 1976) of Czech prehistoric cattle (*Bos*). See Figure 5 for further explanatory notes.

sexual dimorphism and a strong overlapping between the domestic and wild forms. The distal tibia (see Bd in Figures 10 & 11) and distal metapodial epiphysis (Bd in Figures 8, 9) fuse at the age of 2-3 years (Silver, 1969; Schmid, 1972), the time when body growth is almost finished or has substantially slowed down. Using fully fused distal ends of these elements eliminates the bones of non-final size. Furthermore, the *phalanges proximales* are compared, which are abundantly represented in the material (Figures 13-15). Their distal breadth is not considerably influenced by the position of the element within the body (according to Bartosiewicz, 1993), thus, at least in the case of distal breadth (Figure 15), all the *phalanges proximales* can be seamlessly evaluated together regardless of whether they originate from fore or hind limb.

Based on the osteometric comparisons, the following facts have been found:

(1) During the studied time interval there is an observed reduction in body size of domestic cattle. It was repeatedly observed in both studied dental (Figures 5, 7) and all studied postcranial (Figures 8, 10, 12, 13, 15) measurements, which is apparent from the inclination of the regression lines. The continuous decreasing trend is visible particularly from the Neolithic up to the turn of TRB and Řivnáč Culture. Subsumption into the category domestic or wild can be partly subjective. Therefore, since the minimum undoubtedly represents domestic animals, it is important that this trend is also displayed by minimal values of partial distributions (see arrows in the graphs).

(2) An interruption of the above described trend was observed, resulting in the shift of distribution towards a bigger body size in the period of the Řivnáč Culture. The difference between the cattle sizes in the Řivnáč C. and previous TRB culture is statistically significant in three of the four evaluated measurements (Table 7). It includes the shift of the mean and sometimes also the shift of the minimum (Figures 12-15). This leads to the accumulation of the values in the transitional (overlapping) zone between the sizes of domestic cattle and aurochs. This shift and the increased frequency of individuals of a ‘transitional size’ are displayed in the period of Řivnáč C. by all postcranial as well as dental measurements, perhaps with the exception of the metacarpus distal breadth (see circles in Figures 5, 7, 8, 10, 12, 13, 15). The shift between Řivnáč C. and the previous TRB is specially demonstrated by histograms (Figures 6, 9, 11, 14).

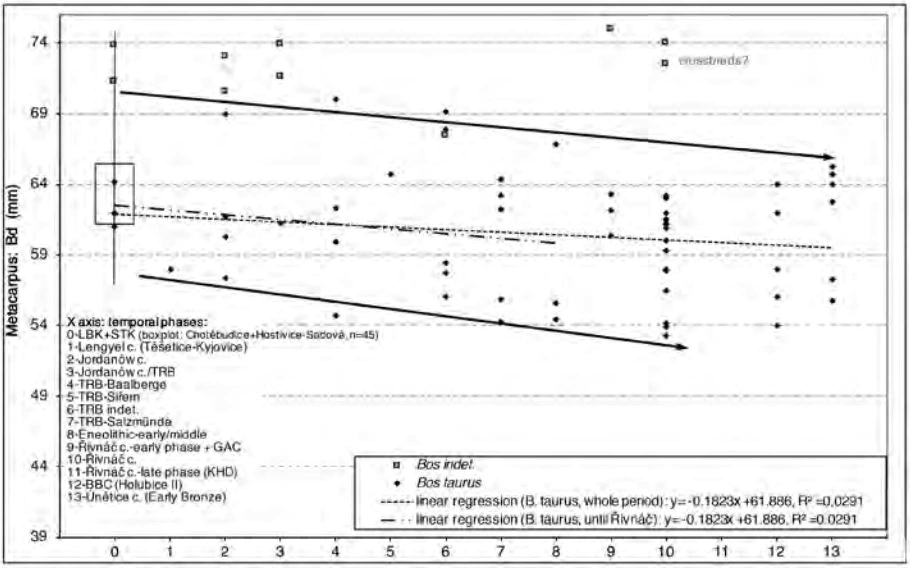

FIGURE 8

Variation over time (X axis) of the *Metacarpus* distal breadth (Bd on Y axis) of Czech prehistoric cattle (*Bos*). Boxplot (based on the histogram by Kovačiková *et al.*, 2012) shows min.-max. (line) and 25%-75% quantiles (box) of *Bos taurus* + *Bos* indet. The boxplot is not included into the calculation of regression. See Figure 5 for further explanatory notes.

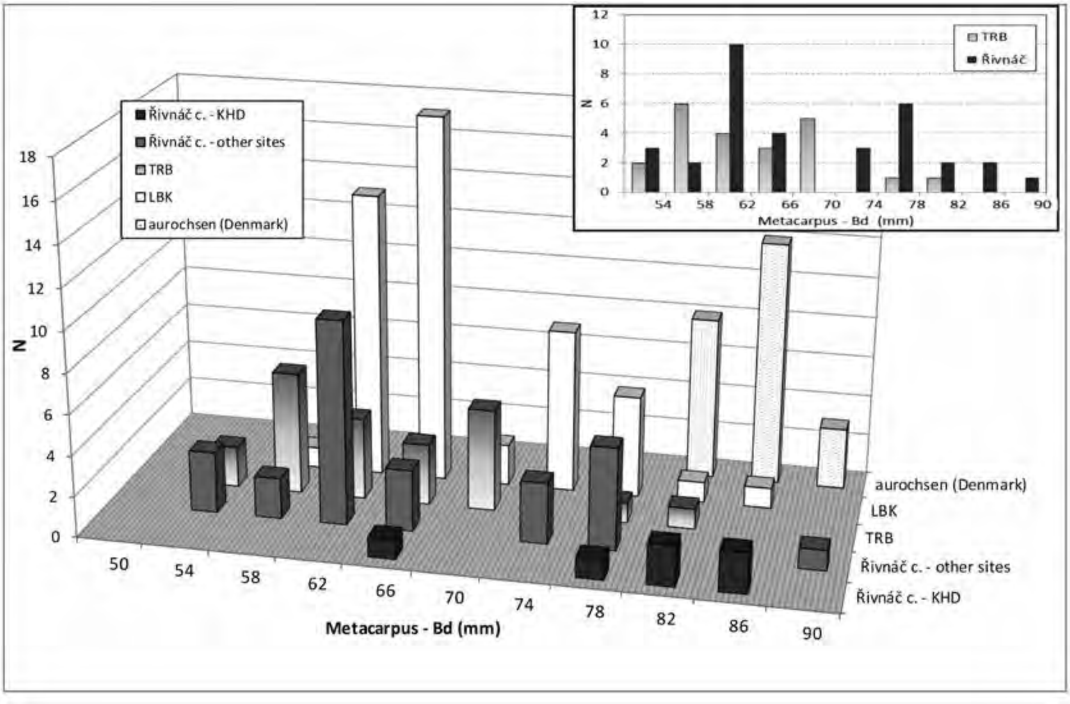

FIGURE 9

Histograms representing the distributions of *Metacarpus* distal breadths of Czech Neolithic and Eneolithic cattle (*Bos*). See Figure 6 for further explanatory notes. Compare results in Figure 8 obtained by using the corresponding data (data from Chotěbudice and Hostivice-Sadová included).

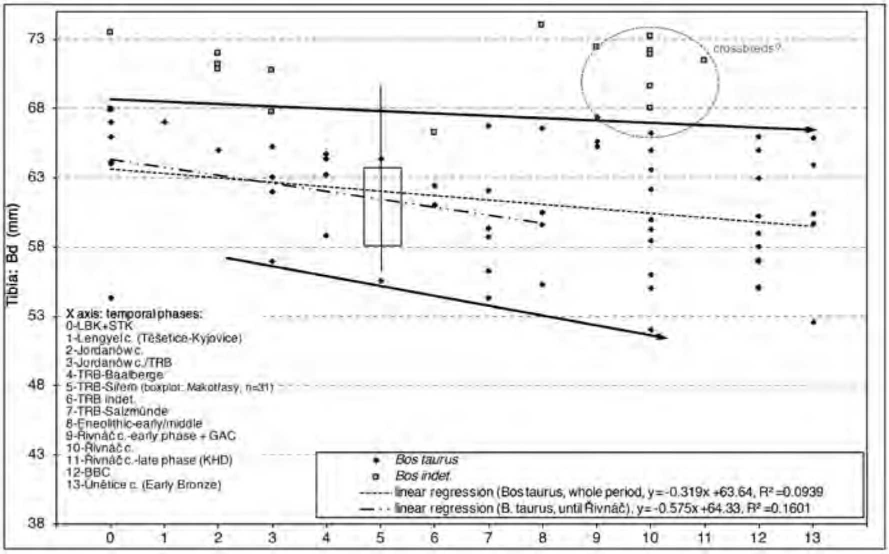

FIGURE 10

Variation over time (X axis) of the *Tibia* distal breadth (Bd on Y axis) of Czech prehistoric cattle (*Bos*). Boxplot (see notes in Figure 8) is based on the histogram by Clason (1985). See Figure 5 for further explanatory notes.

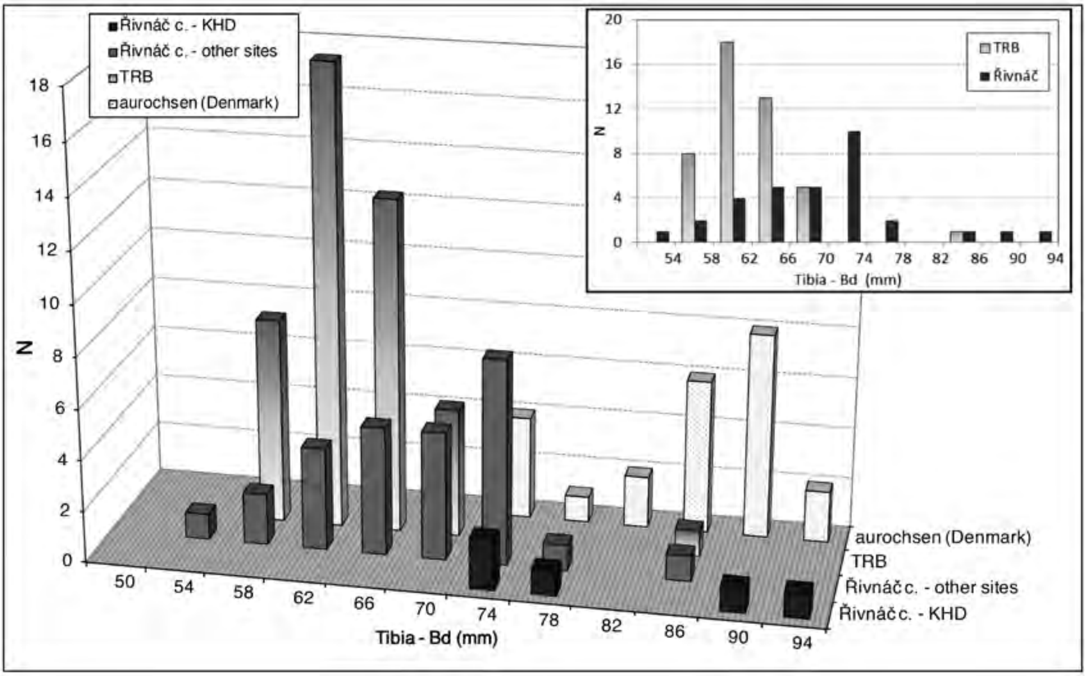

FIGURE 11

Histograms representing the distributions of *Tibia* distal breadths (Bd) of Czech Eneolithic cattle (*Bos*). See Figure 6 for further explanatory notes. Compare results in Figure 10 obtained by using the corresponding data (data from Makotřasy included).

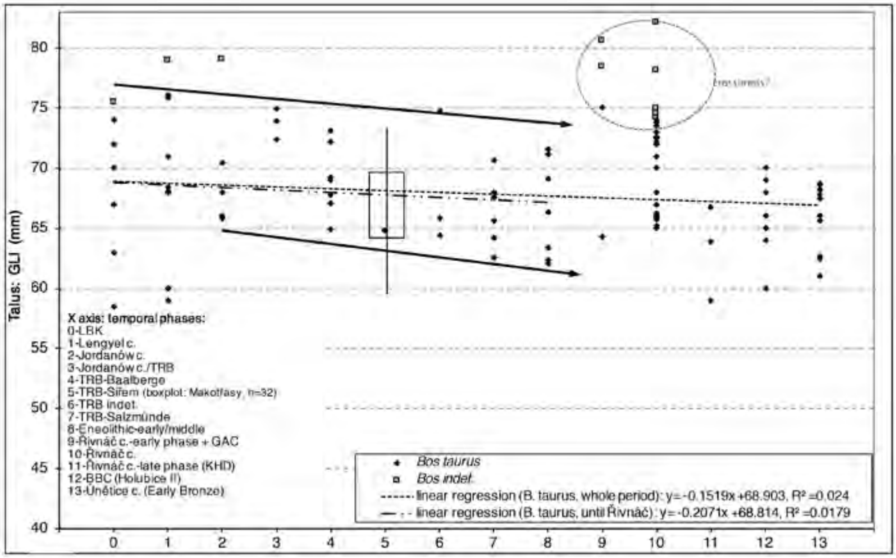

FIGURE 12

Variation over time (X axis) of the *Talus* lateral length (GLl on Y axis) of Czech prehistoric cattle (*Bos*). Boxplot (see notes in Figure 8) based on the histogram by Clason (1985). See Figure 5 for further explanatory notes.

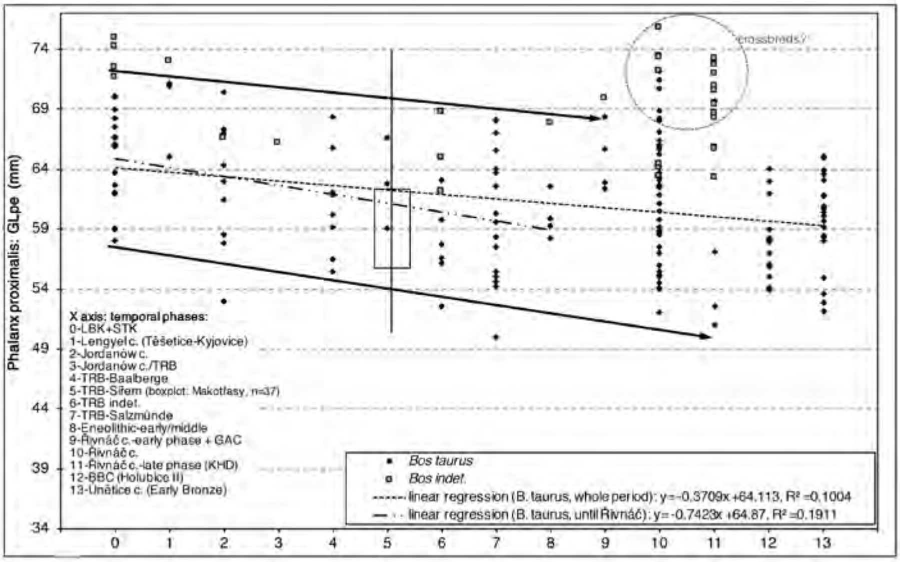

FIGURE 13

Variation over time (X axis) of the *Phalanx proximalis* peripheral length (GLpe on Y axis) of Czech prehistoric cattle (*Bos*). All phalanges included, regardless of position in the body. Boxplot (see notes in Figure 8) based on the histogram by Clason (1985). See Figure 5 for further explanatory notes.

(3) Disproportion between the resulting distributions of dental dimensions and distributions of postcranial dimensions have been observed: almost no teeth attain the size of aurochs, not even in Řivnáč C. (Figure 6), while postcranial dimensions correspond in a number of cases to aurochs (Figures 9, 11 & 14).

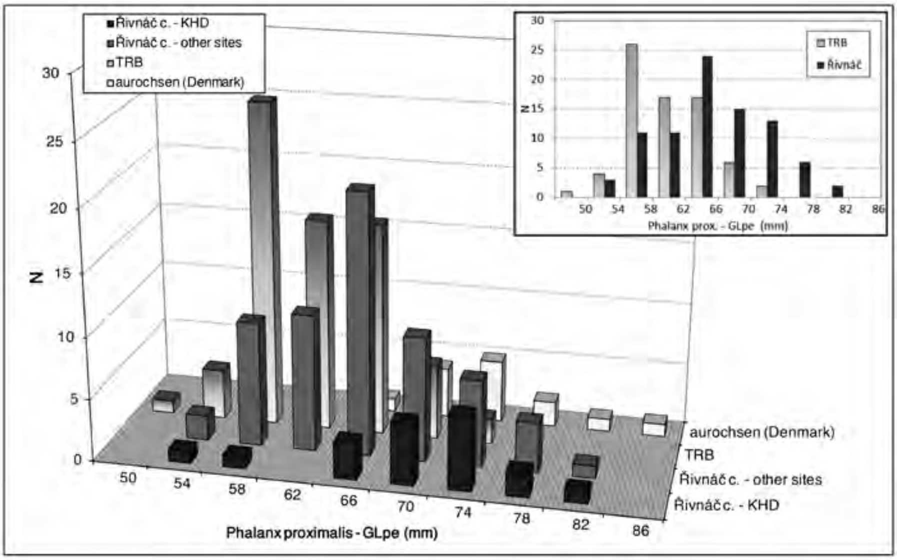

FIGURE 14

Histograms representing the distributions of *Phalanx proximalis* peripheral lengths (Glpe) of Czech Eneolithic cattle (*Bos*). See Figure 6 for further explanatory notes. Compare results in Figure 13 obtained by using the corresponding data (data from Makotřasy included).

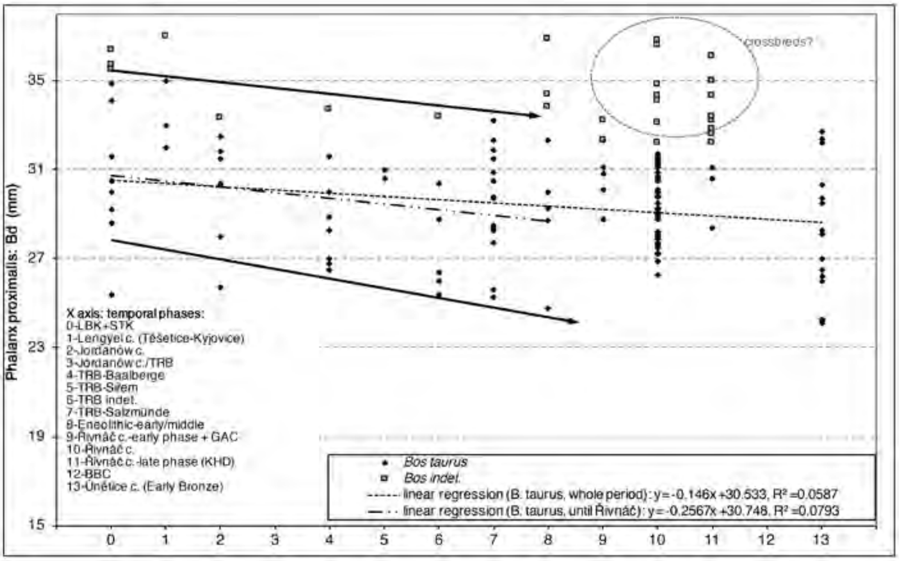

FIGURE 15

Variation over time (X axis) of the *Phalanx proximalis* distal breadth (Bd on Y axis) of Czech prehistoric cattle (*Bos*). All phalanges included, regardless of position in the body. See Figure 5 for further explanatory notes.

Interpretations

Wide metric variabilities found within most of the time horizons (Figures 9, 11, 14) clearly show that the given collection does not represent a single, genetically closed population. This is obvious from comparison with variability in the single homogenous cattle population (e.g. in Higham, 1969; Berteaux & Guintard, 1995). On the basis of metric values, the presence of aurochs as well

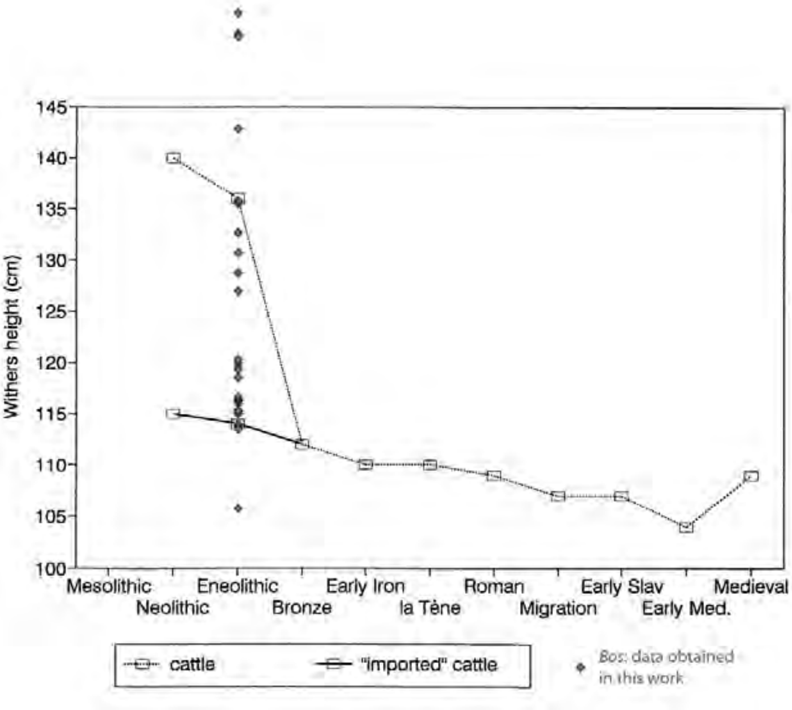

FIGURE 16

Changes in the cattle withers height in Bohemia from the Neolithic to the Middle Ages according to Peške (1994). Data from this study both domestic and wild, presented by grey diamonds are projected onto the original graph constructed by Peške (black squares and lines). Bifid line given for Neolithic-Eneolithic cattle represents the coexistence of domestic and wild forms.

as domestic cattle is also apparent. This proves the coexistence of domestic and wild forms. Also, the occurrence of two or more domestic breeds in the region is not excluded entirely. One could conclude this from the presence of hornless and loose horn cattle beside horned cattle (Ambros, 1988; Kyselý, 2010c), but this observation could also be just the effect of a specific combination of alleles in individuals from a single population. However, in the Neolithic-Eneolithic period a long-term coexistence of genetically non-fused domestic breeds of different body sizes is not expected in such a small region as Bohemia. Several observed outliers, for example particularly small cattle in LBK+LGK according to talus and tibia, can be extremes of real size variability; but unrecognized intrusion from the later period is also not fully excluded. The size of domestic cattle found within the present study does not contradict earlier results from Bohemia (cf. Ambros, 1968; Clason, 1985; Peške, 1994) or results from neighbouring central European regions[3]. The presence of domestic cattle of a very small size, typical for western and south-western European regions was also observed in southern Germany (Glass, 1991; Benecke, 1994). This smaller ('western') breed is presently presumed as far as the northern Pre-Alps (Austria, Mondsee C.; Pucher, 2004, 2006, 2010), but it has not been found further eastwards or in the North (i.e. in Hungary and Poland; Bökönyi & Kubasiewicz, 1961). Also, within Bohemia and Moravia, the influence of a smaller 'western' breed has not been described and is neither expected nor observed.

The general trend of reduction in cattle body size from the Neolithic up to the Middle Ages –with a temporary increase in size in the Roman period in the regions that were not outside the Limes Romanus–

---

[3] Poland, Slovakia, Hungary, Austria, Germany; according to data in Matolcsi, 1970; Bökönyi, 1974; Lasota-Moskalewska, 1980, 1989; Glass, 1991; Benecke, 1994; Makowiecki & Makowiecka, 2000; Pucher, 2004, 2006; Bogucki, 2008; Makowiecki, 2009; see also Figure 4.

was observed in all central European countries[4], so the Czech territory is not an exception. Some results suggest that an especially rapid reduction in size occurred during the course of the Bronze Age or between the Eneolithic and Bronze Age[5]. The results from the East Alpine area even suggest a rather sudden change in cattle size, detected before the beginning of the Late Bronze Age (Pucher, 2013). In the central European region this trend gradually resulted in small medieval cattle of a WH in cows of only c. 100-110 cm with individuals smaller than 100 cm not exceptional[6] (cf. Figure 16); and an individual estimated to be 89 cm high was even detected in Bohemia (Peške, 1985b). Some dimensions evaluated in this study suggest a relatively rapid body-size reduction in the pre-Řivnáč period as well: an extrapolation of respective regressions three thousand years later (i.e. in the Middle Ages) would result, on an assumption of the linear trend, in much smaller cattle than were actually observed in reality[7]. The comparisons usually show repeated reduction in size after the Řivnáč anomaly; some dimensions seem to also reveal reduction between BBC and Únětice C. (i.e. between the Eneolithic and Bronze Age; Figures 3, 5).

To explain the body-size increase in domestic cattle in the Řivnáč C. (see point *2*), the below mentioned possible reasons have been taken into consideration:

(*a*) the cross-breeding between domestic and wild forms;

(*b*) independent local domestication of European aurochs;

(*c*) the adoption or increased frequency of castration of bulls, or change to management preferring males;

(*d*) the importation of a bigger breed into the studied region;

(*e*) an increased degree of hunting of aurochs (possibly females classified as *Bos* indet. or misinterpreted as domestic);

(*f*) better care, especially higher quality feed.

In support of and against these interpretations, the following arguments are taken into consideration:

Arguments against model (*c*): The castrates are larger and have prolonged long bones when compared to uncastrated bulls[2], nevertheless, the body-size increase in the Řivnáč C. has also been detected in the dentition measurements and the breadths of limb bones which are not as greatly influenced by castration (see above and Pöllath & Peters, 2005; Bartosiewicz, 2013, 82-83). Additionally, the use of non-dimorphous or slightly dimorphous dimensions, as in the case of this study (see above), minimizes the influence of sex ratio on the distribution. Arguments against (*d*): From central Europe or adjacent areas very large domestic breeds are not reported in the Eneolithic; finds of domestic cattle from regions neighbouring the Czech territory more or less match the breeds with withers height on average 115-125 cm (Matolcsi, 1970; Bökönyi, 1974; Benecke, 1994; Makowiecki & Makowiecka, 2000; Kyselý, 2002a). This is also valid for the Baden Culture in Hungary and eastern Austria (where WH is about 115-120 cm; Matolcsi, 1970; Bökönyi, 1974; Pucher, 2006), which is the assumed source region for the Řivnáč Culture. Moreover, in the case of imports, one would expect mixing with local breeds; but for the cross-breeding to cause such a strong anomaly, the imported breed would have reached considerable body size (similar to the size of aurochs), which is hardly probable.

A similar disproportion to that described in point (*3*) has already been observed for the region in earlier works (Kyselý, 2008a,b, 2010a), where a very low proportion of teeth and cranial fragments falling into the size range of *Bos primigenius* also suggests a very small percentage of pureblood aurochs, which is in contrast to the results from extremity bones. This disproportion may be explained (A) by allometries or (B) by means of taphonomy, in case aurochs heads had been left on kill-site, i.e. outside

---

[4] It follows from a number of studies based on the material from Bohemia (Peške, 1994; Roblíčková, 2004), the Netherlands (Clason, 1967), Poland (Lasota-Moskalewska, 1980, 1989; Makowiecki, 2009), Austria (Pucher, 2006, 2010, 2013), Switzerland (Schibler & Schlumbaum, 2007), Hungary (Matolcsi, 1970; Bökönyi, 1974), Germany (Nobis, 1954; Boessneck, 1958; Teichert, 1984) and central Europe in general (Glass, 1991; Teichert, 1993; Benecke, 1994), similar situation is also in Britain (Jewell, 1962)

[5] For various regions see: Lasota-Moskalewska, 1980, 1989; Benecke, 1994; Peške, 1994; Roblíčková, 2004; Makowiecki, 2009; Pucher, 2013.

[6] For various regions see Peške, 1985b, 1994; Kratochvíl, 1988; Lasota-Moskalewska, 1989; Teichert, 1993; Kyselý, 2000, 2003; Makowiecki, 2009.

[7] The extrapolated data for c. AD 1000: only c. 43 mm in the case of the tibia distal breadth and c. 42 mm in the case of the phalanx proximalis length (cf. Figures 10, 13), which would correspond to females smaller than 85 cm.

the settlement, and thus cannot be represented in the graphs. Allometries are typical for an unsettled phenotype, as would be a phenotype originated through cross-breeding or domestication. For example, a crossbred animal usually does not display an accurately mean phenotype, rather it is a mosaic of the features of both parents. So, if the first explanation (A) is true this disproportion can be an argument for hypothesis (*a*). On the other hand the observation does not support hypothesis (*b*), since during domestication cheek teeth are much more stable than bones (~ postcranial dimensions, body size), thus reacting with delay (e.g. Clutton-Brock, 1999).

The incorporation of indigenous wild cattle into introduced domestic stocks (i.e. genetic contributions from the aurochs gene pool) could happen via the cross-breeding of domestic and wild forms or via independent local domestication of European aurochs (hypotheses *a* and *b*). However, the new domestication of aurochs, when not combined with cross-breeding with domestic cattle, is difficult to imagine in a situation where domestic cattle were abundant (the most frequent species in Czech Neolithic and Eneolithic assemblages; Kyselý, 2012; Kovačiková *et al.*, 2012) and when was no reason for the total disappearance of existing domestic cattle. Therefore, independent local domestication is considered inprobable; although these two phenomena can be related to one another and they are not (or are hardly) distinguishable solely on the basis of osteomorphometry. The significant evidence for cross-breeding of domestic and wild forms is the shift of total distribution towards the bigger sizes including the shift of the average and the minimum. A simple contribution in the form of the hunting of aurochs would probably not shift the distribution of domestic cattle and respective statistics (mainly the minimum) in the observed way. The influence of a heterosis effect on the size of crossbreeds of first generations, which may lead to their clearer visibility and emphasis in the graphic comparisons, should also be considered. On the other hand, outbreeding depression is improbable in the case of the combination of the primitive Neolithic breeds and genetically similar aurochs. Based on the discussion given above, the author of the paper inclines to the 'cross-breeding' model (*a*). A relatively strong representation of aurochs in the Czech Eneolithic (Kyselý, 2005, 2008a,b, 2012) makes conditions suitable for that.

Although it is not possible to exclude better feeding and care for domestic cattle in the Řivnáč C., an argument against that hypothesis (*f*) is the evidence which points to the regressive husbandry development only in the Řivnáč C. (for example the increased proportion of hunting and meat-oriented sheep/goat utilisation; Kyselý, 2012).

Sheep/goats **(***Ovis*/*Capra***)**

Only some finds could have been more closely determined as sheep (*Ovis aries*) or as goats (*Capra hircus*). Within more closely determined Lengyel and Eneolithic finds in the CR sheep dominate over goats and in the Middle Eneolithic the absence of goats has even been detected (Kyselý, 2012: Graph 38). Therefore, the results based on the material determined only as sheep/goats mainly concern sheep.

Absolute size

Finds suitable for the calculation of withers height of goats are quite rare and for sheep more copious data are available only in the material from the Lengyel period and the Řivnáč Culture. The majority of estimations were calculated on the basis of short bones (calcaneus and talus), although these give less reliable results than long bones. Nevertheless, the advantage is that the talus and calcaneus lengths are only slightly sexually dimorphous (c. 2-5%, according to Davis, 2000). The determined average WH in sheep is 63.1 cm in the Lengyel period and 69.5 cm in the Řivnáč C. (Table 2 and Figure 17). These withers heights were estimated with the help of indices provided by Teichert (1975) and Schramm (1967) (for alternative exponential calculations of WH according to May & Teichert, 2001, see Table 2). This could correspond with the average body mass of about 40-45 kg and 50-55 kg respectively[8]. Sheep from neighbouring central European regions reported in a comparable period by Bökönyi (1974), Benecke

---

[8] The rough estimation of body mass is based on the data for various primitive breeds according to Vohradský (1999) and Sambraus (1999).

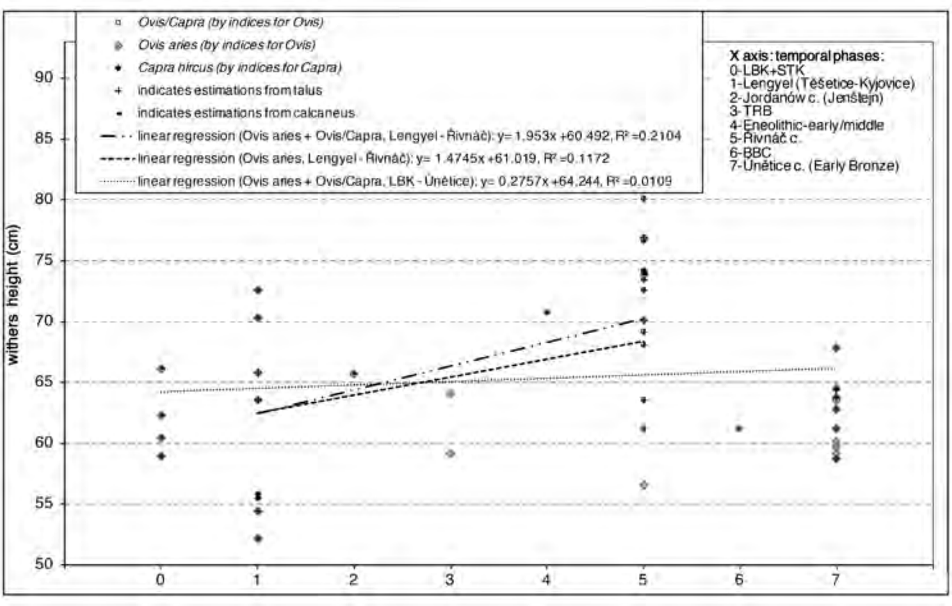

FIGURE 17

Variation over time (X axis) of the withers height (Y axis) of Czech prehistoric sheep and goats (*Ovis / Capra*). Based on heights in Table 2 estimated by indices for sheep (after Teichert, 1975) and indices for goats (after Schramm, 1967). For further explanatory notes and methods see text and Figure 5.

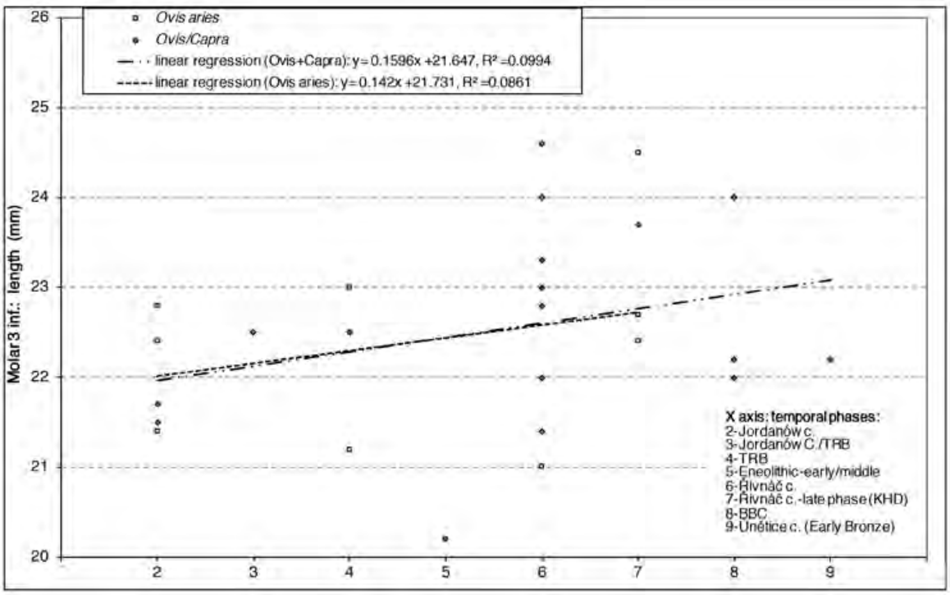

FIGURE 18

Variation over time (X axis) of the *Molar 3 inferior* greatest length (on Y axis, identical to measurement no. 10 in Driesch, 1976) of Czech prehistoric sheep and goats (*Ovis / Capra*). For further explanatory notes and methods see text and Figure 5.

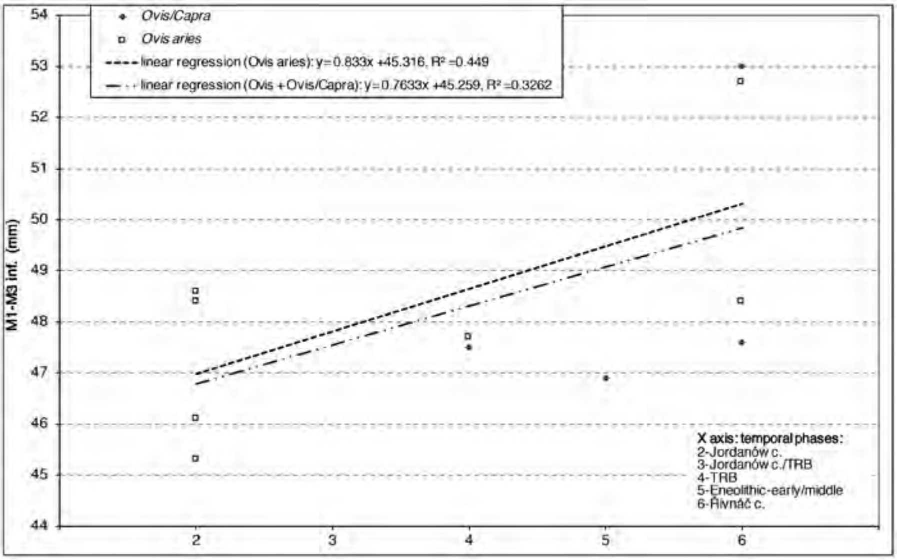

FIGURE 19

Variation over time (X axis) of the *Molar inferior* row alveolar length* (on Y axis identical to measurement no. 10 in Driesch, 1976) of Czech prehistoric sheep and goats (*Ovis / Capra*). For further explanatory notes and methods see text and Figure 5.

(1994) and Makowiecki & Makowiecka (2000) had similar heights.

Changes over time

The body size and many skeletal dimensions are dependent on sex. However, it can be presumed that the dental dimensions used for the comparisons (Figures 18, 19) are not particularly sexually dimorphous (as follows from c. 5-6% inter-sex difference in P2-M3 in wild goats; Fandos & Vigal, 1993). In addition to the dental dimensions, the moderately dimorphous distal humerus (dimorphism c. 7% inter-sex difference; Davis, 2000) and the weakly dimorphous calcaneus and talus (see above, in Figure 17 talus and calcaneus are distinctly indicated) have also been used. An almost identical shape for the regression of sheep and the regression of small domestic ruminants, considered as a whole, was found (see regression lines in Figures 18-20). Therefore, the results based on whole (sheep-goats) material are acceptable for sheep. Analyses of mutually diverse dental (Figures, 18, 19) and postcranial (Figures 17, 20) dimensions suggest an increase in body size which occurred in the period between the Lengyel C. and the Middle Eneolithic. Some comparisons correspond to a change during the course of the Jordanów and Řivnáč Cultures or even a leap between TRB and the Řivnáč C. (Figures 17-19). The differences between the sizes in the earlier and later periods are, according to some tests, statistically significant (Table 7).

Interpretations

To explain the body-size increase, the following potential causes have been taken into account:

(*a*) the adoption or increased frequency of castration of rams, or change to management preferring males;

(*b*) the importation of a bigger breed into the studied region;

(*c*) better care, especially higher quality feed.

The increase in body size of sheep in the Eneolithic was not observed only in the studied region, but also in the surrounding areas of the Czech Republic (e.g. Benecke, 1994; Döhle, 1994). The influx of bigger sheep has been already described by Bökönyi, who placed this event, based on Hungarian finds, somewhere at the end of the Eneolithic or on the cusp between the Eneolithic and Bronze Age (Bökönyi, 1974, 1987). This phe-

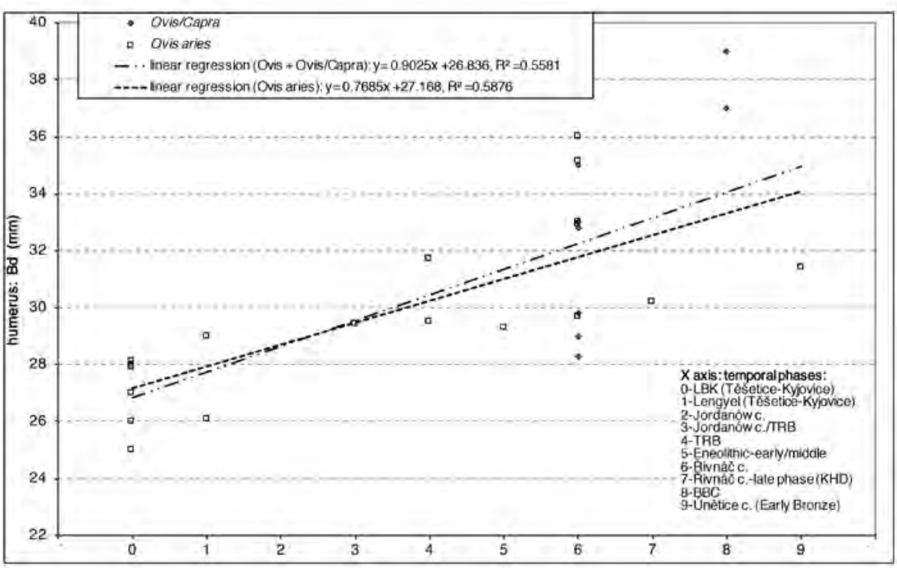

FIGURE 20

Variation over time (X axis) of the *Humerus* distal breadth (Bd on Y axis) of Czech prehistoric sheep and goats (*Ovis / Capra*). For further explanatory notes and methods see text and Figure 5.

nomenon seems to be extended to a large part of Europe, although some comparisons suggest that the body enlargement happened earlier (comparable to the Czech Early Eneolithic; Döhle, 1994) while others suggest a later date (Bökönyi, 1974, 1987; Benecke, 1994).[9] This fact is often explained by the importation of a new bigger breed (see discussion section). The appearance of this new breed in central Europe is dated to the second half of the fourth millennium BC (perhaps with the Baden Culture) which roughly corresponds to the Middle Eneolithic in the Czech concept of archaeological periodization. With regard to the limited amount of available data from the CR it is difficult to identify details of size development, nevertheless, most of the results also fit the idea of the importation of a larger breed during the period mentioned above, that is, either during the Middle Eneolithic represented by the Baden-Řivnáč cultural complex (c. 3350-2800 BC), or on the cusp between the TRB and Řivnáč C. (Figures 17-19), although the evaluation of the distal humerus (Figure 20) does allow an earlier body enlargement. As the increase is also observed in the sexually slightly dimorphous dimensions, it is highly improbable that the sheep size increase was the result of a change management influencing the proportion of the sex, or castration, cf. hypothesis (*b*). Hypothesis (*c*) is analogical to the situation in cattle. In the following Bronze Age no further increase in size was observed within the Czech territory; the sheep were on the contrary rather smaller than in the Řivnáč Culture. The WH in the Bronze Age is usually between 60 and 70 cm (*x* = 64, n = 43), specifically in the first Bronze Age culture (Únětice C.) it is mostly 60-64 cm (according to Roblíčková, 2004, b; see also Table 2 and Figure 17).

Pigs (*Sus domesticus*)

In the classification of the pig (*Sus*), distinguishing between domestic pigs (*Sus domesticus*) and wild boar (*Sus scrofa*) by using metric limits can be problematic and uncertain. With regard to the existence of an overlap in most dimensions, part of the finds remained unclassified (labelled as ‘*Sus* indet.’). Specimens which are clearly outside the overlap were interpreted as domestic or

---

[9] Bökönyi put BBC and CWC to the Early Bronze Age. There could therefore be a degree of artificial bias due to the existence of the various regional chronology categorizations.

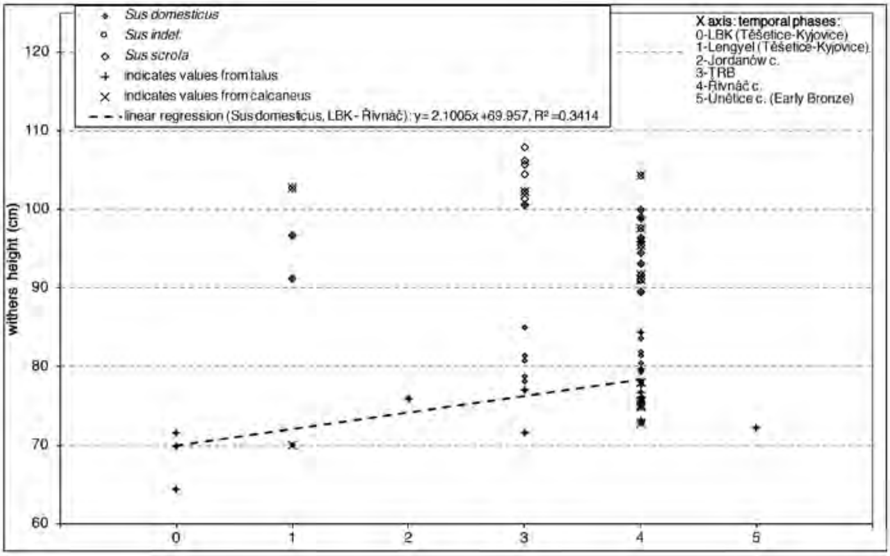

FIGURE 21

Variation over time (X axis) of the withers height (Y axis) of Czech prehistoric pigs (*Sus*). Based on heights in Table 2 calculated using Teichert´s indices. For further explanatory notes and methods see text and Figure 5.

wild according to metric and morphology with the help of measurements and suggestions given in Lasota-Moskalewska *et al.* (1987), Bökönyi (1995), Mayer *et al.* (1998) and Albarella *et al.* (2009).

Absolute size

Teichert's indices (1969) were preferentially used to calculate WH, while calculations of WH based on May *et al.* (1996) were used as an alternative (Tables 2, 4; Figure 21). Due to a lack of complete stylopodium and zeugopodium bones WH was calculated from short bones (talus and calcaneus) and metapodials. A larger amount of data for withers height estimates is available only from the Řivnáč Culture. When calculated using Teichert´s indices, an average WH of 76.2 cm was estimated for Řivnáč C. pigs using the talus and calcaneus bones, while an average value of 81 cm was estimated using the metapodials (for detailed statistics see Table 4). Corresponding to these height figures is an average body weight of approximately 60-80 kg - estimated on the basis of combined data for height × weight in today's wild boar (according to Herre, 1986). Compared to later phases (TRB, Řivnáč), the body size of domestic pigs could have been considerably less in the earlier (LBK + LGK) period (cf. Tables 4, 5). Lengyel and Eneolithic pigs identified as wild boar are substantially larger than pigs determined as domestic.

Changes over time

Comparisons were made using dimensions for which a particularly low sexual dimorphism was determined or is assumed, and which are recommended and commonly used (according to Payne & Bull, 1988; Albarella & Payne, 2005; Albarella *et al.*, 2009). Specifically analysed are the breadth of the distal tibia (Figure 27), the length of the talus and calcaneus (included in Figure 21, labelled separately) and selected dental dimensions (Figures 22-26). In the case of the dimensions of molars used in the comparisons, the influence of individual age can be almost entirely ruled out. Although the average size and the size range were both greater for males than for females, the differences between the sexes were not found to be statistically significant in all ten measurements of individual molars evaluated by Mayer *et al.* (1998). Dimorphism in the breadth of molars is only 0-4% according to Payne &

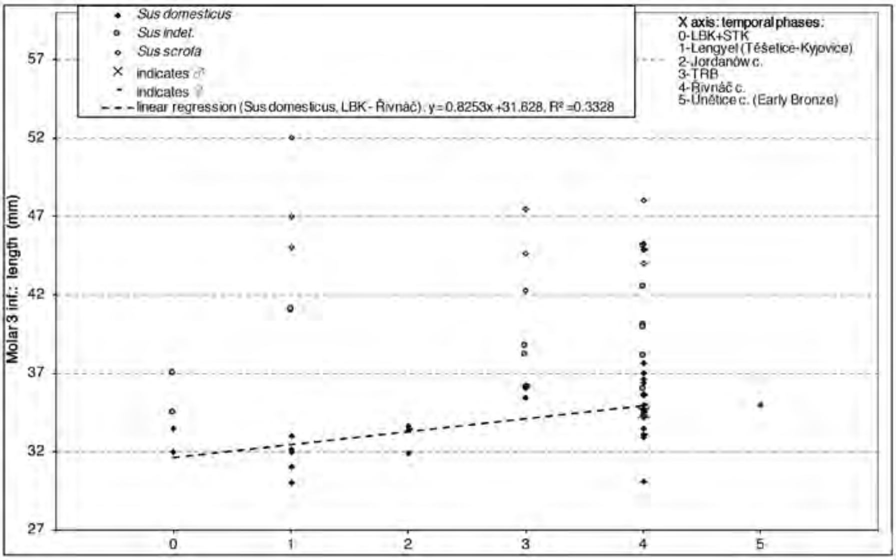

FIGURE 22

Variation over time (X axis) of the *Molar 3 inferior* greatest length (on Y axis identical to measurement no. 10 in Driesch, 1976) of Czech prehistoric pigs (*Sus*). For further explanatory notes and methods see text and Figure 5.

Bull (1988), the degree of dimorphism in the length of rows of molars is probably also low (cf. Herre, 1986). Also included is the frequently used M_3 length, despite the fact that it is highly variable and exhibits more pronounced dimorphism (cf. Kratochvíl, 1981; Herre, 1986; Payne & Bull, 1988) (Figure 22, 23).

Comparisons identified the following changes in time:

(1) All of the analysed dimensions, such as dental (Figure 22-26), postcranial (Figures 21, 27), lengths (Figure 21-23) and breadths (Figures 24-27), indicate a body-

	Sus domesticus						
	n	calculated after Teichert (1969)			calculated after May *et al*. (1996)		
		arithmetic mean (mm)	median (mm)	min.-max. (mm)	arithmetic mean (mm)	median (mm)	min.-max. (mm)
LBK + Lengyel	4	69	70	64.4-71.6	62.9	62.8	61.9-64.1
TRB	8	78.9	78.7	71.6-85	68.4	68.6	64.1-71.8
Řivnáč C.	20	77.6	77.2	72.9-84.3	66.7	65.7	63.6-71.0
	Sus scrofa						
	n	calculated after Teichert (1969)			calculated after May *et al*. (1996)		
		arithmetic mean (mm)	median (mm)	min.-max. (mm)	arithmetic mean (mm)	median (mm)	min.-max. (mm)
LBK + Lengyel	3	96.9	96.7	91.3-102.7	72.9	70.7	69.4-78.7
TRB	7	104.1	104.5	100.6-107.8	79.9	81	71.7-82.5
Řivnáč C.	13	95.9	95.9	89.5-104.3	72.4	71.3	69-79.4

TABLE 4

Statistics of WH of Czech Neolithic and Eneolithic pigs based on data from Table 2. See text for acronyms.

dimension	Eneolithic		LBK+LGK		Middle Ages
	arithmetic mean (mm)	n	arithmetic mean (mm)	n	arithmetic mean (mm)
Molar 3 inf. - L	35	18	31.9	6	30.3
Molar 3 inf. - B	16.1	18	15.1	6	14.8
M1-M3 inf.	70.2	14	67	1	63.5
Tibia - Bd	30.1	21	26.8	6	28-29
Talus - GLl	42.8	10	38.3	3	40.2
Calcaneus - GL	80.6	6	75	1	78.4

TABLE 5

Comparison of selected dimensions of pigs determined as domestic (*Sus domesticus*) between the Eneolithic (from Proto-Eneolithic to Late Eneolithic; this study), the Neolithic-Lengyel period (LBK, LGK; this study) and the Middle Ages (Mikulčice site; Kratochvíl, 1981). See text for acronyms.

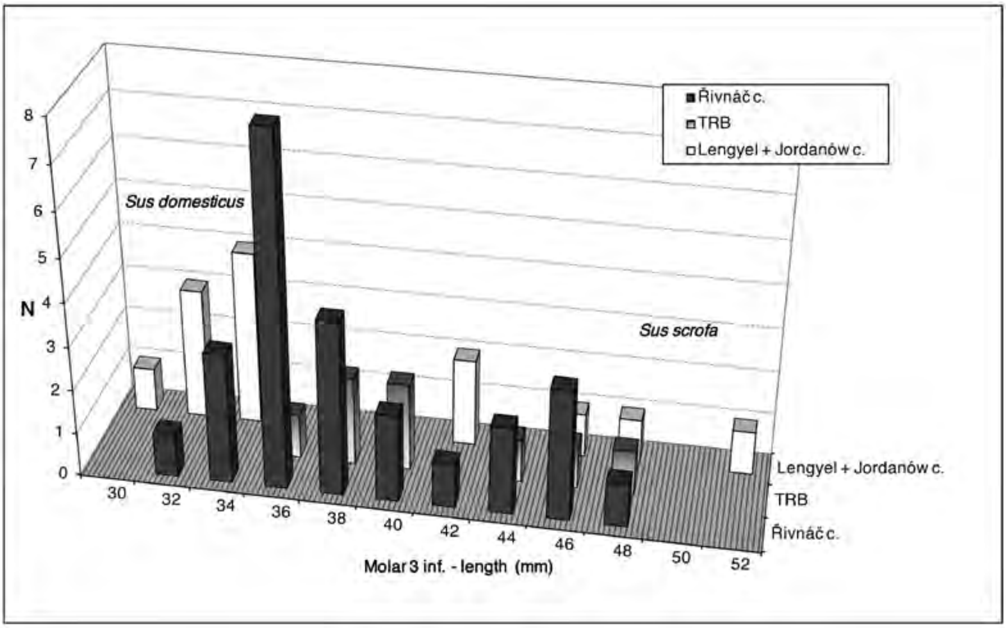

FIGURE 23

Histograms representing the distributions of the *Molar 3 inferior* greatest lengths of Czech prehistoric pigs (*Sus*) in the three cultural phases (LGK+Jordanów, TRB and Řivnáč C.). For further explanatory notes and methods see text and Figure 6. Compare results in Figure 22 obtained by using the corresponding data.

size increase in domestic pigs during the course of the Neolithic and Eneolithic (see the slope of regression lines). Some dimensions narrow the change down to the Proto-Eneolithic and TRB periods, since the most graphically visible jump occurs specifically between these two cultures. Median values grow significantly between the early and late phases of the studied period (Table 7). Absence of data from Baalberge doesn't allow us to reconstruct the development of the size more precisely, but relatively low values from Makotřasy, dated to the middle of TRB (Table 2), suggest the possibility that domestic pigs were not affected by a growth in body size until the Salzmünde phase of TRB. Some dental dimensions indicate a repeated body-size reduction in the Řivnáč Culture. These trends are apparent in cases where only 'reliably' identified domestic pigs are evaluated, as well as when finds of *Sus domesticus* are put together with finds of *Sus* indet.

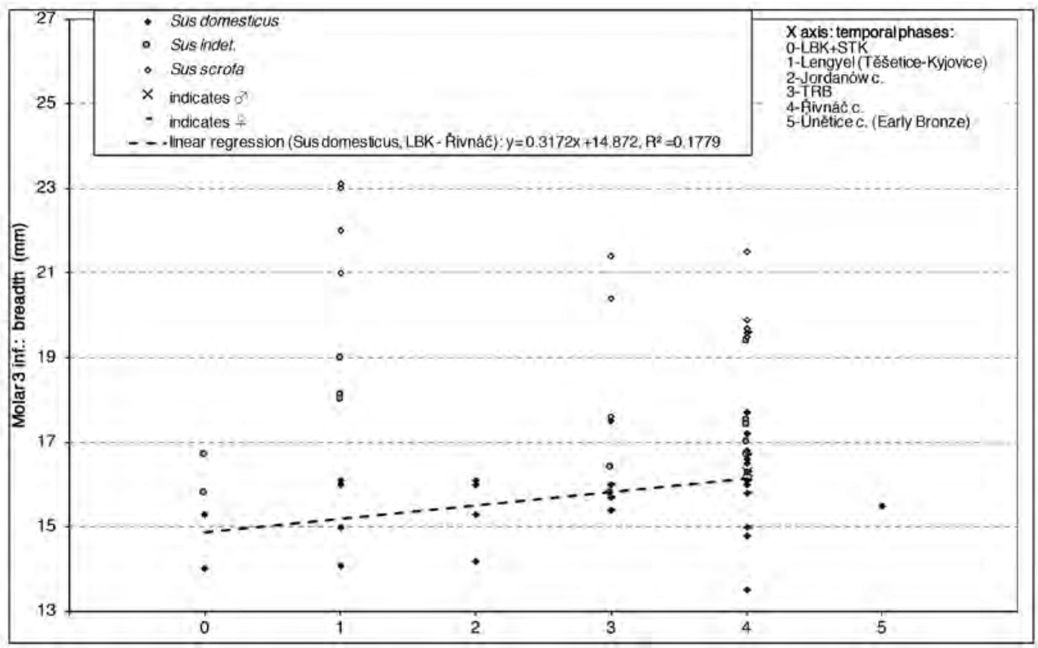

FIGURE 24

Variation over time (X axis) of the *Molar 3 inferior* greatest breadth (on Y axis, identical to measurement M3WA according to Albarella *et al*., 2009) of Czech prehistoric pigs (*Sus*). For further explanatory notes and methods see text and Figure 5

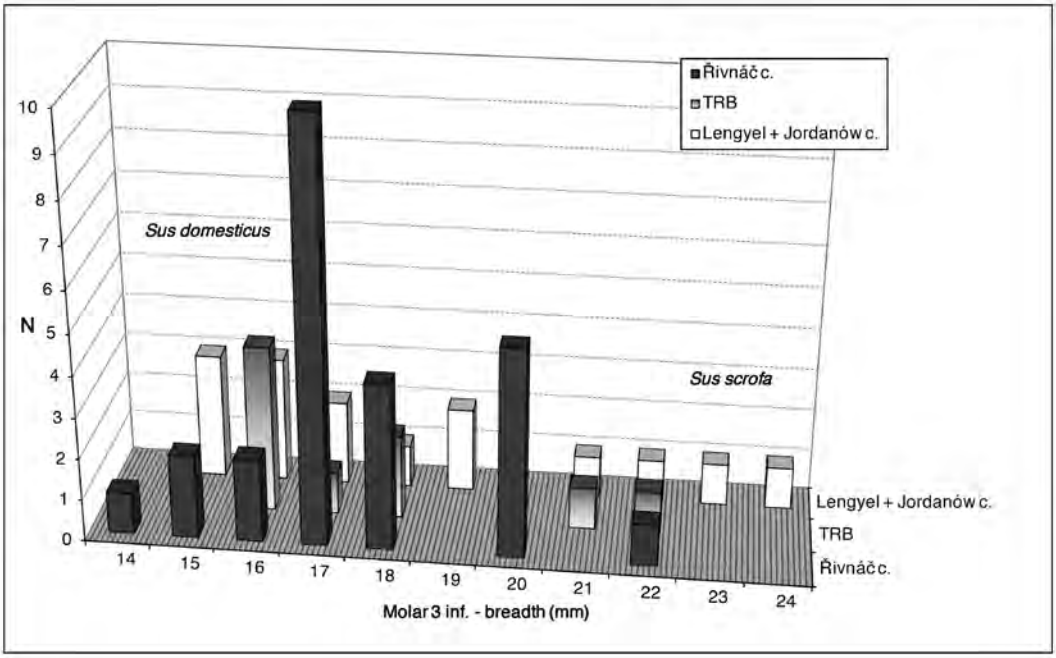

FIGURE 25

Histograms representing the distributions of the *Molar 3 inferior* greatest breadths of Czech prehistoric pigs (*Sus*). See Figure 23 for further explanatory notes. Compare results in Figure 24 obtained by using the corresponding data.

(2) Domestic pigs in the TRB and Řivnáč Cultures are on average larger than domestic pigs from the Early Middle Ages in the studied area. The difference is greater in dental dimensions than in postcranial dimensions. This is seen in a comparison with the size of domestic pigs from the early medieval Great Moravian site of Mikulčice[10] (Table 5). Nevertheless, domestic pigs from the earlier period (LBK + LGK) were smaller than TRB and Řivnáč C. pigs and could be identical in size or even smaller than the pigs from early medieval Mikulčice (cf. Table 5; Figure 21, 27).

(3) Even if a small amount of applicative primary data is available, the frequency of domestication traits, particularly the absence of premolar 1 (Figure 29) and the shortening of M_3 (Figure 28), seems to decrease in the Middle Eneolithic in comparison with previous periods.

Interpretations

The wide metric variabilities found within most of the time horizons clearly show that the given collection is not made up of a single, genetically closed, population[11]; smaller individuals apparently represent domestic pigs (*Sus domesticus*) and larger individuals wild boar (*Sus scrofa*). Thus, the evidence suggests the coexistence of domestic and wild forms, an interpretation that is also supported by the bimodal nature of distributions (Figures 23, 25). The markedly smaller size of domestic pigs compared to the size of wild boars is a common phenomenon in the earliest stages of agricultural history. In central Europe, including the Czech Republic, noticeably small pigs (sometimes referred to as 'turbary pigs' or *Sus scrofa palustris*[12]) are typical for the Early Neolithic (Rütimayer, 1861; Bökönyi, 1974; Lasota-Moskalewska *et al.*, 1987; Benecke, 1994; L. Peške *pers. com.*).

The increase in the physical dimensions of pigs observed in the studied period is in contrast to the general domestication trend. This general trend is not as strong as that observed during prehistory and early history in domestic cattle, but a tendency toward a reduction in body size has been observed for at least the pre-Roman period (Teichert, 1970, 1993; Lasota-Moskalewska *et al.*, 1987).

Attention has been paid in particular to the following potential causes for the body-size increase:

(*a*) cross-breeding between domestic and wild forms;

(*b*) independent local domestication of European wild boar;

(*c*) the importation of a larger breed to the studied region;

(*d*) the hunting of wild boar;

(*e)* a change in the sex ratio or castration;

(*f*) better care, especially higher quality feed.

In similarity with the situation for cattle and sheep/goats, the differences between the time phases described in point (*1*) are clearly not the result of inter-site, or inter-culture differences in the management having potential influences on the sex ratio (*e*). This follows for several reasons: The dimensions used usually exhibit a low degree of sexual dimorphism and their consequent distributions are therefore weakly dependent on the sex ratio. The low influence of sex on the resulting trends is also evident from the position of the sexually determined finds in the overall distribution, since many of the relatively big domestic pigs are females, even in the later phases (Figures 22, 24, 26). Moreover, registered differences in the sex ratio between the individual phases of the studied period are not great (Table 6), which again does not suggest a strong influence of the sex ratio.

Earlier comparisons suggest some regional differences. For example, somewhat larger pigs have been recorded in the period 3500-1500 BC in Hungary and eastern Europe and smaller pigs in southern and western Europe (Lasota-Moskalewska *et al.*, 1987). Benecke (1994) records especially large pigs in the Lengyel and Baden Cultures in the Danube region and in Slovakia, which is (according to Benecke) probably environmentally conditioned. Nevertheless, a local (i.e. Czech) or

---

[10] The data from Mikulčice (south Moravia, CR) published by Kratochvíl (1981) represent one of the largest collections of osteometric data from a single site in the whole of Europe, and they are thus particularly representative.

[11] Evaluated according to the degree of variability within a single sample (population) given in Payne & Bull (1988), Albarella *et al.* (2009) and Herre (1986).

[12] For an explanation and discussion of the terms 'turbary pig' and *Sus srofa palustris*, compare, for example, Bökönyi (1974) and Rowley-Conwy *et al.* (2012).

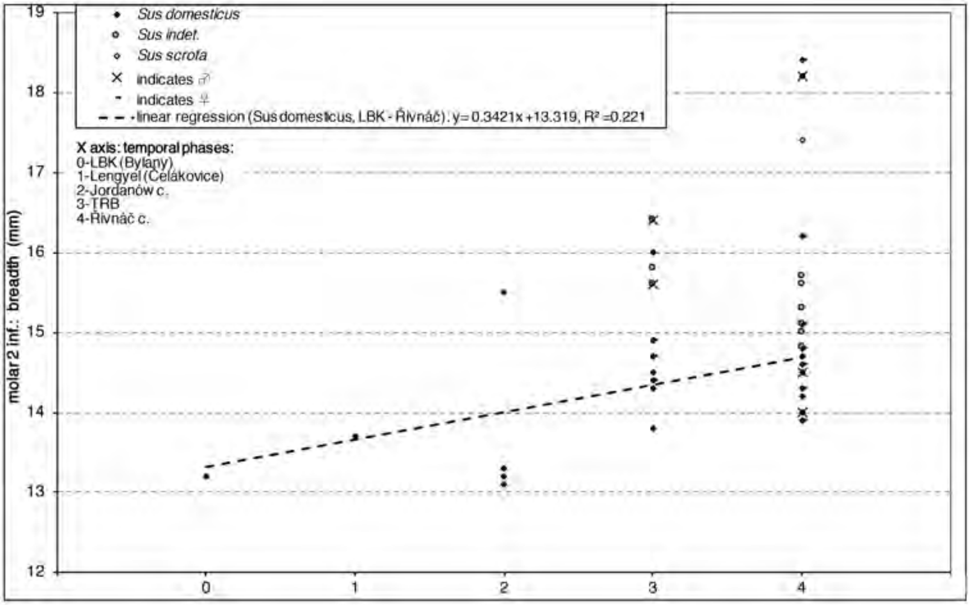

FIGURE 26

Variation over time (X axis) of the *Molar 2 inferior* greatest breadth (on Y axis) of Czech prehistoric pigs (*Sus*). For further explanatory notes and methods see text and Figure 5.

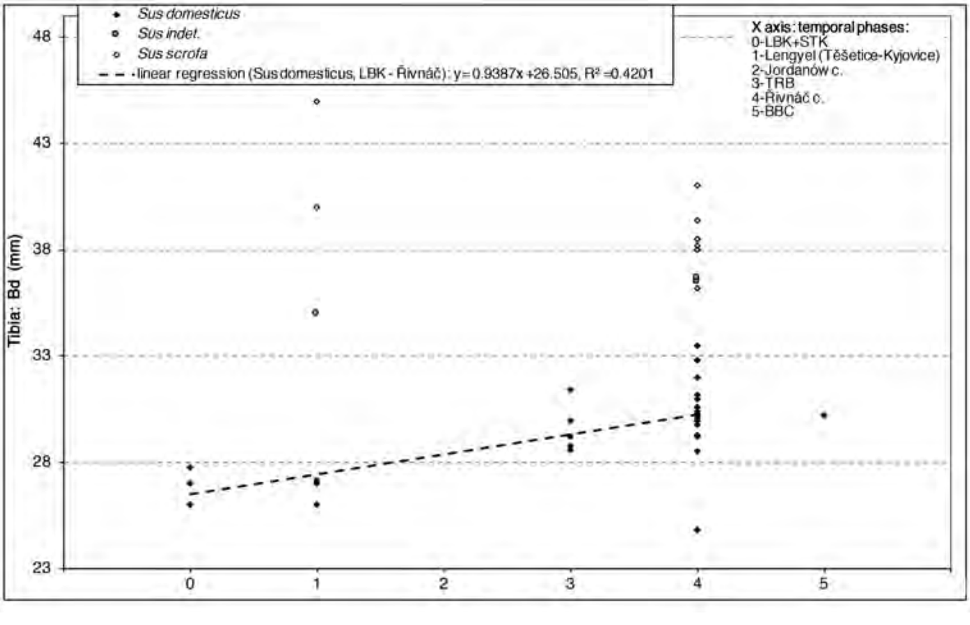

FIGURE 27

Variation over time (X axis) of the *Tibia* distal breadth (Bd on Y axis) of Czech prehistoric pigs (*Sus*). For further explanatory notes and methods see text and Figure 5.

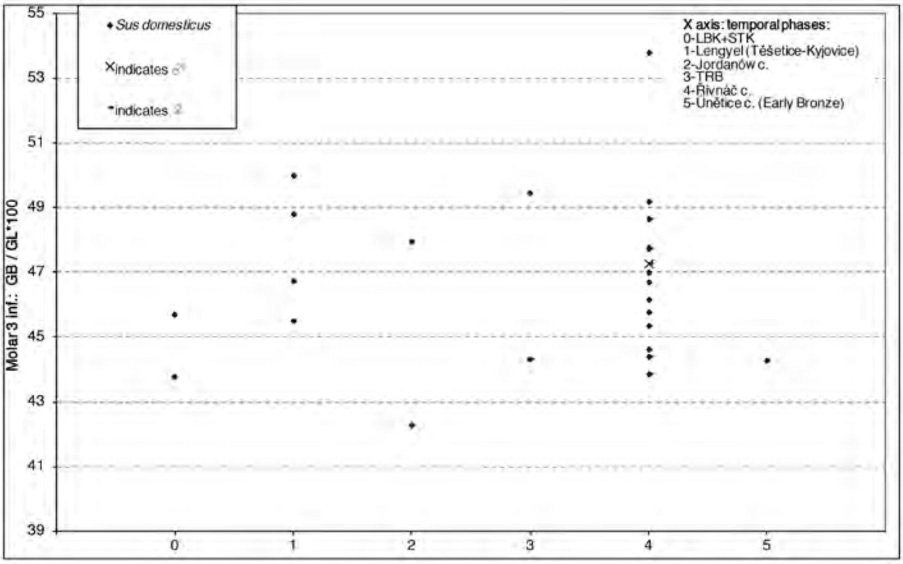

FIGURE 28

Variation over time (X axis) of the *Molar 3 inferior* greatest breadth/length index (GB/GL*100 on Y axis) of Czech prehistoric pigs (*Sus*). For further explanatory notes and methods see text and Figure 5.

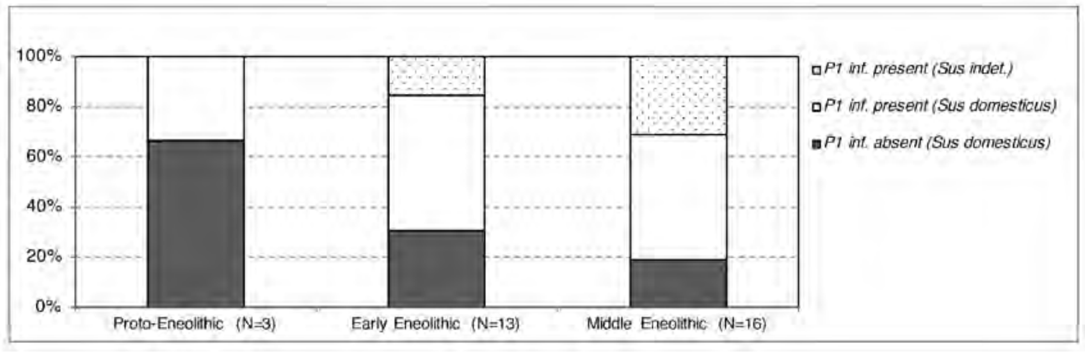

FIGURE 29

Frequency of presence/absence of *Premolar 1* in various temporal phases within Czech Eneolithic pigs (*Sus*). Note: According to Herre (1986) the share of mandibles without P_1 is only 22% among wild boars (N=124). Within the Czech Eneolithic no wild boars without P_1 were observed (this study, n = 8: P_1 and P^1 together)

possibly northern origin is assumed for the key Jordanów and TRB Cultures, which lack distinct and mass ceramic imports from the Danube region and evidence for a broad immigration to the CR (Neustupný *et al*., 2013). Under these circumstances, an osteometrically detectable (i.e. mass) import of a relatively difficult to transport species, such as the pig, from the Danube region or even more remote areas of Eastern Europe is not assumed. Moreover, if the body size of ‘Danube pig’ was environmentally conditioned, their large size would not persist in the new living conditions of central Bohemia.

As with cattle, the shift in the overall distribution of size (average, minimum values) is difficult to explain merely as the result of the hunting of wild boar (or possibly larger feral pigs) involved in interpretation (*d*). However, this pattern corresponds well to a population formed by local domestication or to a population created by cross-breeding as interpretations (*a*) and (*b*) suggest. Shortness of M3 and missing of P1 are traits of advanced domestication that are clearly observed in earlier phases of the studied period. The reduction in the frequency of these signs over time (Figure 28, 29) corresponds to the notion of an influence from the wild boar gene pool, as well as an increase in body size. However, the existence of these signs in Řivnáč C. may be in concordance with the persistence of genetic information from previous domestic breeds. The rapid appearance of such signs would have been unlikely in the case of reoccurring, new domestication.

The repeated body-size reduction in domestic pigs in the period of the Řivnáč Culture indicated by certain comparisons could, with the validity of model (*a*) or (*b*), represent a restart of the general body-size reduction domestication trend. The fact that pigs with a height at the withers of 62-82 cm ($x = 72$ cm, n = 21; Roblíčková, 2004), thus slightly smaller than in the Eneolithic, were reported for the ensuing Bronze Age in the Czech territory also supports this trend.

DISCUSSION

In all animals evaluated, an increase in body size was observed. This contradicts a common trend known from the early (an also later) stages of domestication as described and discussed by many authors[13]. The phenomenon therefore warrants further discussion.

Cattle

Osteometric comparisons have revealed a trend involving the relatively swift reduction in the size of domestic cattle (*Bos taurus*). This is not surprising, since body-size reduction is a common phenomenon in the process of cattle domestication. This trend matched the results obtained in surrounding regions, even though the regionally specific form of WH development can differ somewhat. A distinct anomaly was detected in Bohemia involving a repeated body-size increase in the Middle Eneolithic (Řivnáč Culture, c. 3200-2800 BC). Discussion in the results section led to the conclusion that the most probable interpretation is that the anomaly is the result of cross-breeding between domestic and wild cattle.

The idea, that central European domestic cattle stocks were influenced by the aurochs gene pool either through local domestication or through the cross-breeding of domestic and wild forms, is not new. The possibility of cross-breeding was suggested and discussed by Bökönyi (1962, 1969, 1974) for the Herpály, Tisza and Lengyel Cultures in Hungary and adjacent areas, by Lasota-Moskalewska (1980) for Poland, by Müller (1964) and by Döhle (1990) for the Linear Band Ceramic in central Germany and by Kyselý (2008a) for the Kutná Hora-Denemark settlement (Řivnáč Culture) in Bohemia. A number of genetic studies analysing cattle mtDNA suggest that the cross-breeding of domestic and wild forms could have occurred, but the contribution of European aurochs to the gene pool of domestic breeds was very small (Beja-Pereira *et al.*, 2006; Edwards *et al.*, 2007; Achilli *et al.*, 2009; Bonfiglio *et al.*, 2012; Schibler *et al.*, 2014). Nevertheless, even independent local domestication of aurochs in Italy is suggested (Bonfiglio *et al.*, 2010). However, if breeding did occur between wild males and domestic females (a more probable combination), the contribution of aurochs would not be detectable using mtDNA since mtDNA is not inheritable from males. Therefore, a substantially greater contribution of aurochs to the gene pool of domestic cattle than that suggested by the conclusions of the archaeogenetic studies is not ruled out. The results of our osteometric analyses propose that the Middle Eneolithic in Bohemia could be one of the periods

---

[13] The causation of body-size reduction in domesticates is a difficult question, which requires in-depth analysis and consideration. Here I would like to mention 'the conscious selection' of smaller animals, especially of smaller males, for the purpose of easing human-cattle relationship, the shrinking of territory and altered selection pressure, the emphasis on numbers of animals as opposed to quality, limitation of fodder available in the winter' (Boessneck & Driesch, 1978), impossibility to feed at night due to protection against predators (Clutton-Brock, 1999), early weaning, early mating of heifers, paedomorphism and others (see Zeder *et al.*, 2006), climatic evolution and ecological degradation (Vigne, 1999), or genetic fragmentation and isolation accompanied by the founder effect and inbreeding (Vigne, 1999). Recently supportive evidence for insufficient winter nutrition being the causation is proposed (Hejcman *et al.*, 2014).

taxon	period	male	probably male	indet., castrates?	female	probably female
Bos taurus	Proto-Eneolithic	-	-	-	1	4
	TRB	-	3	-	5	9
	Řivnáč C.	-	1	3	8	6
***Bos taurus* total**		**0**	**4**	**3**	**13**	**15**
Bos indet.	TRB + Řivnáč C.	-	1	-	1	5
Bos primigenius	Řivnáč C.	-	4	-	2	1
Capra hircus (mostly horncores)	Proto-Eneolithic + TRB	2	2	-	3	-
Ovis aries (mostly horncores)	FBC+Řivnáč C.	8	1	-	2	-
Ovis/Capra (mostly pelves)	Proto-Eneolithic + TRB + Řivnáč C.	3	4	-	10	1
***Ovis/Capra* total**		**13**	**7**	**0**	**15**	**1**
Sus domesticus	Proto-Eneolithic	1	-	-	4	-
	TRB	4	-	-	12	1
	Řivnáč C.	13	-	-	21	1
***Sus domesticus* total**		**18**	**0**	**0**	**37**	**2**
Sus indet.	Proto-Eneolithic + TRB	9	-	-	3	-
	Řivnáč C.	9	1	-	1	-
Sus scrofa	Proto-Eneolithic + TRB	5	-	-	-	-
	Řivnáč C.	25	3	-	8	-

TABLE 6

The comprehensive quantification of sex-determinable finds of cattle (*Bos*), sheep/goats (*Ovis/Capra*) and pigs (*Sus*) according to material from Eneolithic settlements in Bohemia (ritual and other anomalous findings excluded). Sex determination obtained by using pelvic and metacarpal bones in the case of cattle, using pelvises and horn cores in the case of sheep/goats, using canine teeth or their alveoli in the case of pigs. Quantified by NISP. From Kyselý (2010a; 2012), updated. For acronyms see text.

and locations where such cross-breeding occurred. If this hypothesis is correct, the degree of the impact on the metric composition of the population eliminates the possibility of an isolated mating event; to the contrary, this must have involved mass cross-breeding activity. Since such hybridization is only manifested in mtDNA to a small extent, the combination of domestic females and aurochs males must have occurred most frequently during the presumed mating. In such a case, intentional and systematic human-controlled cross-breeding can be assumed. Another, more complex, scenario is that feral individuals escaped from captivity were genetically influenced by aurochs and subsequently re-introduced into breeding. A particularly distinct indication of cross-breeding was found at the periphery of the area occupied by the people of the Řivnáč Culture, specifically at the Kutná Hora-Denemark site (Kyselý, 2008a).

Such an anomaly has not been broadly observed in neighbouring central European regions for the corresponding time (cf. Matolcsi, 1970; Bökönyi, 1974; Benecke, 1994). However, it appears that somewhat larger cattle were also detected in the contemporary Cham Culture in southern Germany, in the Jevišovice and Baden Cultures in Austria (cf. results in Pucher, 2004, 2006, 2010) and perhaps even in the Baden Culture in Slovakia (cf. Benecke, 1994: Table 25).

Sheep and goats

An increase in physical size was repeatedly observed amongst sheep, *Ovis aries*, during the course of the Czech Neolithic and Eneolithic in more osteometric comparisons. It is not clear whether the increase was in the form of gradual trend or a sudden change in size, although some comparisons suggest a sudden increase. An increase in the body size of sheep seems to be in contrast to the general trend observed in earlier stages of caprine domestication (Clutton-Brock, 1999; Vigne, 1999), and in the domestication of cattle and pigs. Nevertheless, if we accept the sudden increase during the period of the TRB and Baden-Řivnáč Cultures, then a similar phenomenon was observed in sheep and in cattle, as well as in pigs. However, the same causation for both was not found. We cannot explain the increase in sheep size by cross-breeding with an indigenous wild ancestor, or the fact that it had been hunted, as no such indigenous ancestor existed in the region. On the other hand, it is hardly possible to explain the increase in cattle or pig body size due to the importation of a large breed (see above).

The body enlargement in sheep can be best explained as the result of the importation of a new breed (see results section), whose origin could have been from the south-east (where the Czech Middle Eneolithic Baden-Řivnáč cultural complex also originated; Neustupný *et al.*, 2013). It has been suggested that the new, larger breed could have been a woolly breed (Bökönyi, 1974; Teichert, 1993; Benecke, 1994; Schibler *et al.*, 1997; Schibler, 2004). According to this ‘new breed hypothesis’ the assumed introduction and spread of a new breed would have occurred over a large part of Europe relatively quickly. This was signalled, for example, by body-size increase in sheep in a comparable period in central Europe and in the Balkans, specifically in the Bernburg and Baden horizon of central Europe and at the beginning of the Bronze Age in Macedonia (Benecke, 1994). The theory of the import of a woolly breed in this period is also supported by the nature of the kill-off patterns from the Czech Eneolithic, where supporting evidence for the possible use of sheep wool is the strongest in the Řivnáč Culture, i.e. 3200-2800 BC (Kyselý, 2012). The mass emergence of spindle whorls occurred at the same time. In the studied region, the growth of spindle whorls was observed in the Boleráz horizon at the Cimburk site (east Bohemia, c. 3400-3300 BC; Zápotocký, 2000, Neustupný *et al.*, 2013), and their common occurrence was also determined in the Baden, Cham and Řivnáč

taxon	measurement analysed	phases compared	statistics	significance
Bos taurus	Phalanx prox. GLpe	LBK+LGK X TRB	*U*= 153, p=0.0006, n1=21, n2=31	XX
Bos taurus	Phalanx prox. Bd	LBK+LGK X TRB	*U*= 80, p=0.022, n1=11, n2=28	X
Bos taurus	Phalanx prox. GLpe	LBK+LGK X BBC+Únětice	*U*= 91.5, p=0.000003, n1=21, n2=35	XX
Bos taurus	Phalanx prox. Bd	LBK+LGK X BBC+Únětice	*U*= 73, p=0.0015, n1=16, n2=18	XX
Bos (all *Bos* finds)*	Phalanx prox. GLpe	TRB X Řivnáč	*U*= 1668, p=0.0000006, n1=73, n2=85	XX
Bos (all *Bos* finds)*	Molar 3 inf. GL	TRB X Řivnáč	*U*= 90, p=0.045, n1=15, n2=20	X
Bos (all *Bos* finds)*	Metacarpus Bd	TRB X Řivnáč	*U*= 267, p=0.099, n1=22, n2=3	
Bos (all *Bos* finds)*	Tibia Bd	TRB X Řivnáč	*U*= 331, p=0.00006, n1=32, n2=45	XX
Ovis + Ovis/Capra	humerus Bd	LBK+LGK X TRB+Řivnáč+BBC	*U*= 1.5, p=0.0012, n1=8, n2=17	XX
Ovis + Ovis/Capra	humerus Bd	LBK+LGK X Řivnáč+BBC	*U*= 1.5, p=0.00022, n1=8, n2=14	XX
Ovis + Ovis/Capra	humerus Bd	LBK+LGK+TRB X Řivnáč+BBC	*U*= 10.5, p=0.0003, n1=11, n2=14	XX
Ovis aries	humerus Bd	LBK+LGK X TRB+Řivnáč	*U*= 0, p=0.00063, n1=8, n2=9	XX
Ovis + Ovis/Capra	withers height	LBK+LGK X Řivnáč	*U*= 25, p=0.014, n1=10, n2=13	X
Ovis + Ovis/Capra	withers height	LBK+LGK+TRB X Řivnáč	*U*= 40, p=0.014, n1=13, n2=14	X
Ovis + Ovis/Capra	M3 inf. GL	Jordanów+TRB X Řivná+ BBC	*U*= 40, p=0.107, n1=9, n2=15	
Sus domesticus	withers height	LBK+LGK X TRB+Řivnáč	*U*= 0.5, p=0.0016, n1=4, n2=30	XX
Sus domesticus	Tibia Bd	LBK+LGK X TRB+Řivnáč	*U*= 6, p=0.00098, n1=6, n2=21	XX
Sus domesticus	M3 inf. GL	LBK+LGK+Proto-En. X TRB+Řivnáč	*U*= 17.5, p=0.00055, n1=10, n2=18	XX
Sus domesticus	M3 inf. GB	LBK+LGK+Proto-En. X TRB+Řivnáč	*U*= 43.5, p=0.027, n1=10, n2=18	X
Sus domesticus	M2 inf. GB	LBK+LGK+Proto-En. X TRB+Řivnáč	*U*= 20, p=0.011, n1=6, n2=22	X

TABLE 7

Selected results of the statistical tests evaluating the difference between the medians of metric distributions in two time phases. The Mann-Whitney test (*U*) was used in all the cases. X = statistically significant at the 95% confidence level, XX = statistically significant at the 99% confidence level. See Table 1, Figure 2 and text for more information about the cultures and material. In cases when only histograms were available in the source data the middle values of each metric category span had to be used in the calculation of the *U* statistic. For acronyms see text.

Cultures (Burger, 1988; Zápotocký & Zápotocká, 2008; Neustupný *et al.*, 2013). Within the Switzerland territory, spindle whorls first appeared during the period of the Corded Ware Culture (c. 2800 BC, Schibler, 2004). A change in the composition of weaving artefacts was also observed at the contemporary Bronocice site (southern Poland, TRB-Baden; Milisauskas & Kruk, 2011). Moreover, the increased importance of sheep is also indicated by the almost complete disappearance of goats from Czech material in this period, i.e. 3200-2800 BC (according to Kyselý, 2012). The given indications correspond time-wise to the current opinion that, worldwide, 'no actual woven woollen textiles are firmly dated before about 3000 BC, but they were very widespread by 2800 BC' (Anthony, 2007) and to the earliest European direct finds of spinnable wool from the Clairvaux-les-Lacs site (eastern France, 3000-2900 BC; Hundt, 1986), the Novosvobodnaya site (Russia, Kurgan 2, 2849-2693, BC, *p* =96%; Shishlina *et al.*, 2003; Anthony, 2007; (Shishlina *et al.*, 2008) and others from the middle of the third millennium BC in Switzerland and Germany (Sherratt, 1983). When the situation in Mesopotamia (where wool production may have originated) was studied through kill-off patterns, Pollack (1999) showed that the shift there to a wool-sheep butchering pattern occurred no earlier than the Late Uruk period, after 3350 BC.

Pigs

The introduction of domestic pigs (*Sus domesticus*) into central Europe at the beginning of the Neolithic (as part of the 'Neolithic package'), originally suggested on the basis of the small body size, was later confirmed by a genetic study (Larson *et al.,* 2007). But the study indicated that the mtDNA of Near East pigs (Y1 haplotype) soon disappeared from the historical record, and that only mtDNA from indigenous European wild boar was detected in the bones of domestic pigs from later periods (at least since 3900 BC) and in modern European breeds. Therefore, the cited publication suggests an entirely different scenario than in the case of cattle. Recently, Larson *et al.* (2011) stated that it is not yet known whether 'the replacement of the pig was the result of continual hybridization by the only locally available source of wild boar, thus minimizing and then eliminating the genomic input of Near Eastern wild boar, or a more active selection against those pigs who displayed Near Eastern affinities'. They also stated that 'it is unknown whether the process, concluding that modern European pigs are derived from European wild boar, was independent or was kick-started by the introduction of Near Eastern domestic pigs into Europe, however the second possibility is more probable'. Although the date of the described replacement is not precisely identified in the archaeogenetic study, the authors originally speculated that the main change could have occurred during the first five centuries following the importation of the Neolithic package (Larson *et al.*, 2007, 2011). However, a new study has proven the existence of the Y1 haplotype in the Middle Chalcolithic (Gumelniţa C., c. 4500-3950 BC), based on archaeological material from Romania, and it was suggested that Y1 was replaced during the Bronze Age (2000-1200 BC) (Evin *et al.*, 2014).

The genetic replacement described above is consistent with the increase in the body size of pigs in the Czech territory as described in this study. The presented osteometric analysis potentially narrow the period of this event down to the Proto- to Early Eneolithic (i.e. 4300-3300 BC), during the course of which the change in size was detected most clearly (Figures 21-27). The change approximately 1400 to 2400 years after the importation of the Neolithic to the studied region is somewhat later than the genetic replacement proposed by the authors of earlier archaeogenetic studies (Larson *et al.*, 2007, 2011). If the interpretation of the change in the body size of pigs in the Czech territory as the result of cross-breeding with wild boar, or the independent domestication of local wild boar, is correct it occurred under conditions in which pigs had already been raised for a long time. This is clear from the presence of domestic pigs in the region in the earliest phases of the Neolithic, whose domestic status is evident from the small sizes recorded in LBK and STK (Figures 21-27). In addition, previous determinations from many Czech sites suggest the common presence of domestic pigs in these cultures (Peške, 1994, 1997; Peške *et al.,* 1998; Kovačiková, 2009). A later dating of the event would thus not testify to the entirely independent domestication of wild boar, but, at the least, to a style inspired by methods originating in the Near East. The generally low share of pigs in the LBK and STK periods in central Europe (Bökönyi, 1974; Benecke, 1994; Döhle, 1994; Kovačiková *et al.,* 2012) could represent the primary situation, prior to local domestication or cross-breeding, followed by a rising abundance due to local domestication or cross-breeding leading to a relatively large percentage of domestic pigs in the Eneolithic (as recorded in Kyselý, 2012). The increase in abundance of European domestic pigs is also stated by Larson *et al.* (2007). In the actual conditions of the Eneolithic it seems less probable that the body size of *de novo* domesticated animals reduced as quickly as graphic comparisons suggest. This, together with the existence of domestication traits even in the Řivnáč Culture (Figure 28, 29), correspond better to the possibility of cross-breeding instead of entirely new domestication. However, local domestication and cross-breeding could be combined, which is easy to imagine in the case of easily reproducible and easily manageable animals, such as pigs. Since the feralization of primitive pig breeds is simple, it is also possible to consider the presence of feral pigs even in the Eneolithic, a situation that would be a good basis for the bidirectional flow of genetic information (domestic < > wild).

The small number of analysed mtDNA samples originating from the bones of pigs found at four archaeological sites in the Czech territory points to the presence of haplotypes identical to central European wild boar (Larson *et al.*, 2007; Pavelka, 2007)[14], of which only three finds from the Kutná Hora-Denemark site (Řivnáč C.) and three more from the Dolní Beřkovice site (STK?) were morphometrically ‘reliably’ identified as domestic. If the dating of the Dolní Beřkovice finds is really STK, the archaeogenetic study suggests the incorporation of wild boar genes to domestic stock in the Czech territory quite early; otherwise the archaeogenetic study suggests it at least in the Middle Eneolithic (Řivnáč C.).

The local domestication of European pigs had already been presumed earlier. For example, Bökönyi (1974) presents a number of cases of large domestic pigs, which he interprets as being due to the local domestication or as the result of cross-breeding. According to this author, these activities could have occurred more frequently during the Neolithic, ‘reaching a peak in the period between the end of the Neolithic and the end of the Bronze Age’ (according to the Hungarian chronology[9]). Domestic pigs also increased in body size in Austria around 4000 BC (Pucher, 2006, 2010). Benecke’s comparisons (1994: Abb. 64) do not rule out an increase in body size in the Early Bronze Age. The increase in body size was also described in regions of Europe other than central Europe (Larson *et al.*, 2007), so the phenomenon could be widespread. As in the case of domestic cattle, a combination of the following opposing trends could occur: (1) an increase in body size as the result of the inclusion of a wild ancestor in the domestic breed gene pools and (2) a general domestication trend involving body-size reduction.

Concluding remarks

The author has tried to methodically exclude or reduce the influence of age, sex and pathologies on the results by the selection of measurements. The effect of allometry, taphonomy, other deforming factors and the effect of randomness is minimized by the combined appraisal of more skeletal dimensions of a mutually different nature. Therefore, the observed temporal size changes and tendencies are not highly influenced by sex ratio, castration, slaughtering strategies, allometries, taphonomy or randomness.

The possible influence of external factors, not based on genetics (higher quality feed, lactation period, stabling) is difficult, if not impossible, to filter out. Nevertheless, it seems improbable that differences between studied cultures or between studied settlements, in the way animals were fed or conditions in which they were raised, were so distinct within the Neolithic-Eneolithic that they could cause systematic bias and statistical difference in body size. As for diet, Higham (1969), for example, considers it ‘intrinsically unlikely that only certain animals were raised on a high plane of nutrition in prehistoric settlements’. It seems more reasonable to assume an opportunistic approach to raising and feeding animals that would result in the statistical levelling of possible individual deviations. Moreover, the heritability of physical and osseous dimensions is relatively high. For

---

[14] Sites: Homolka (Řivnáč or Únětice C.; haplotypes ANC--Aside and ANC-Cside according to Larson *et al.*, 2007), Kutná Hora-Denemark (Řivnáč C.; haplotype GL222 according to Pavelka, 2007), Dolní Beřkovice (dating after J. Řídký, 2009 and *pers. com.* STK?; haplotype GL222 according to Pavelka, 2007) and Velké Přílepy-Kamýk (dating after Klementová & Hložek, 2005 and D. Daněček *pers. com.* cf. Late Bronze; haplotype GL222 according to Pavelka, 2007).

these reasons, this (non-genetic) factor is not emphasised in interpretations. As was already argued, environmentally conditioned selection does not seem to be very probable due to the stable climatic conditions of the Middle Holocene in central Europe. Furthermore, sophisticated artificial selection leading to a rapid increase in body size is not assumed due to the level of breeding in the Neolithic and Eneolithic.

In addition to the factors discussed above, it is also possible to contemplate a culturally-conditioned selective influence on the composition of settlement waste and, hence, osteological assemblages. Also unknown for the given period is the level of the social and economic diversification of the occupied area, which could possibly have created the need for selective import/export. Nevertheless, the author of this study assumes that these two factors have a much lower, if any, impact on the osteometric composition than, for example, on the species or age composition of the sample. Therefore, they should not impact the conclusions and interpretations presented here.

The author is aware that despite the relatively large total volume of metric data, some of the presented conclusions are based only on a small amount of available data. Some of the conclusions must therefore be regarded as preliminary. The author is likewise aware of many factors whose influence cannot be distinguished by an osteological study, including the heretofore less considered heterosis effect, the founder effect, the possibility of feralization as early as the Neolithic and Eneolithic, or the handling of animals in a manner that defies economically conditioned pragmatic rules. Collecting additional data, especially from as yet less represented cultures and future studies across Europe could help resolve questions such as: Do the body size changes in farm animals determined in various regions have the same cause? Could it be a result of the inclusion of a wild ancestor in the domestic stock gene pools or a result of independent local domestication? Did it occur in various regions at the same time, or at various times?

CONCLUSIONS

This study presents the available metric data documenting a variety of skeletal dimensions, body size and variability in size of Neolithic, Eneolithic and Bronze Age domestic cattle (*Bos taurus*), sheep/goats (*Ovis*/*Capra*) and pigs (*Sus domesticus*) originating in archaeological sites in the territory of the Czech Republic. In particular, the detection of changes in body size and trends in size development of these animals over time were the focus of the study. As well as presenting the data and its comparisons, detailed discussions and some theoretical ideas are included in the paper. The main results and the most probable interpretations are listed below.

A gradual body-size reduction of domestic cattle was observed from the Neolithic to the Early Bronze Age in the Czech territory, which is the same as or similar to the trend in other European regions. During the Early Eneolithic Funnelbeaker Culture and Middle Eneolithic Řivnáč Culture the withers height of domestic cows was c. 114-117 cm on average, whilst bulls could be 5-10 cm higher.

There was an anomalous increase in domestic cattle body size in Řivnáč C. (c. 3200-2800 BC) in Bohemia. After considering various arguments, this anomaly was interpreted as most probably being the result of the cross-breeding of domestic females and aurochs males. Other interpretations, like a higher frequency of hunting of aurochs or local domestication of aurochs, are considered less likely.

The bodysize increase in sheep corresponds with the hypothesis that larger, probably woolly, sheep were imported into Central Europe. According to the Czech osteometric data, this change could have occurred between or within the TRB and Baden-Řivnáč C. (i.e. in the second half of the 4th millennium BC). In the Lengyel period, sheep were only 62.5 cm high in the withers on average, later in the Middle Eneolithic sheep reached c. 69.5 cm on average.

The withers height of domestic pigs in the Middle Eneolithic was 73-84.5 cm. In earlier periods (Linear Pottery, Lengyel) pigs were markedly smaller. The increase in pig body size occurred during or between the Proto- and Early Eneolithic (c. 4300-3350 BC). This increase is interpreted as being the result of genomic input of indigenous wild boar to the domestic stock gene pool, through cross-breeding between domestic and wild forms or local wild boar domestication. If true, this finding identifies the place and time (or one of the places and times) of the replacement of domestic pigs of Near Eastern ancestry by European wild boar - a genetic event demonstrated by earlier archaeogenetic studies.

ACKNOWLEDGEMENTS

This study was produced with institutional support RVO: 67985912. I thank J. Řídký and D. Daněček for information about dating of features from Dolní Beřkovice and Velké Přílepy-Kamýk.

REFERENCES

Achilli, A.; Bonfiglio, S.; Olivieri, A.; Malusa, A.; Pala, M.; Kashani, B. H.; Perego, U. A.; Ajmone-Marsan, P.; Liotta, L. & Semino, O. 2009: The multifaceted origin of taurine cattle reflected by the mitochondrial genome. *PLoS One* 4(6): e5753.

Albarella, U. 1997: Shape variation of cattle metapodials: age, sex or breed? Some examples from Mediaeval and Postmediaeval sites. *Anthropozoologica* 25-26: 37-47.

Albarella, U. & Payne, S. 2005: Neolithic pigs from Durrington Walls, Wiltshire, England: a biometrical database. *Journal of Archaeological Science* 32: 589-599.

Albarella, U.; Dobney, K. & Rowley-Conwy, P. 2009: Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology* 14(2): 103-36.

Allen, J.A. 1877: The influence of physical conditions in the genesis of species. *Radical Review* 1: 108-140.

Ambros, C. 1968: Remains of fauna found in the Eneolithic settlement on Homolka. In: Ehrich, R.W. & Pleslová-Štiková, E. (eds.): *Homolka: An Eneolithic site in Bohemia*: 440-469. Monumenta archaeologica 16, Praha.

— 1988: Funde hornloser Hauswiederkäuer aus urgeschichtlichen Siedlungen in der Slowakei. *Weimarer Monographien zur Ur- und Frühgeschichte* 22: 18-27.

Anthony, D. W. 2007: *The Horse, the Wheel, and Language*. Princeton University Press, Oxfordshire.

Bartosiewicz, L. 1984: Sexual dimorphism of long bone growth in cattle. *Acta Veterinaria Hungarica* 32(3-4): 135-146.

— 1985: Interrelationships in the formation of cattle long bones. *Zoologischer Anzeiger* 215(3-4): 253-262.

— 1987: Cattle metapodials revisited: a brief review. *ArchaeoZoologia* 1(1): 47-51.

— 1993: The anatomical position and metric traits of phalanges in cattle (*Bos taurus* L., 1758). *Revue de Paléobiologie* 2(12): 325-334.

— 2013: *Shuffling nags, lame ducks: the archaeology of animal disease*. Oxbow Books, Oxford.

Beech, M. 1993: A report on animal bones from some Bell Beaker features at Radovesice, Teplice district, N.W. Bohemia, Czechoslovakia. In: Turek, J.: *Osídlení z období zvoncovitých pohárů v povodí řeky Bíliny v severozápadních Čechách*: 180-190. Diploma thesis. Faculty of Arts, Charles University in Prague, Praha.

— 1995: The animal bones from the Hallstatt settlement of Jenštejn, central Bohemia, Czech Republic. In: Dreslerová, D. (ed.): *A Late Hallstatt Settlement in Bohemia. Excavation at Jenštejn 1984*: 99-140. City of Prague Museum, Institute of Archaeology of the Academy of Sciences of the Czech Republic in Prague, Praha.

Beja-Pereira, A.; Caramelli, D.; Lalueza-Fox, C.; Vernesi, C.; Ferrand, N.; Casoli, A.; Goyache, F.; Royo, L. J.; Conti, S.; Lari, M.; Martini, A.; Ouragh, L.; Magid, A.; Atash, A.; Zsolnai, A.; Boscato, P.; Triantaphylidis, C.; Ploumi, K.; Sineo, L.; Mallegni, F.; Taberlet, P.; Erhardt, G.; Sampietro, L.; Bertranpetit, J.; Barbujani, G.; Luikart, G. & Bertorelle, G. 2006: The origin of European cattle: evidence from modern and ancient DNA. *PNAS* 103: 8113-8118.

Benecke, N. 1994: Archäozoologische Studien zur Entwicklung der Haustierhaltung in Mitteleuropa und Südskandinavien von den Anfängen bis zum ausgehenden Mittelalter. *Schriften für Ur- und Frühgeschichte* 46. Akademie Verlag, Berlin.

Bergmann, C. 1847: Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3(1): 595-708.

Bergström, P. L. & Van Wijngaarden-Bakker, L. H. 1983: De metapodia als voorspellers van formaat en gewicht bij runderen (The metapodia as predictors of size and weight in cattle). *IVO-Rapport* B 206. Instituut voor Veeteeltkundig Onderzoek "Schoonoord", Amsterdam.

Berteaux, D. & Guintard, C. 1995: Osteometric study of the metapodials of Amstertdam Island Feral Cattle. *Acta Theriologica* 40(2): 97-110.

Boessneck, J. 1956: Ein Beitrag zur Errechnung der Widerristhöhe nach Metapodienmaßen bei Rindern. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 68: 75-90.

— 1958: *Zur Entwicklung vor- und frühgeschichtlicher Haus- und Wildtiere Bayerns im Rahmen der gleichzeitigen Tierwelt Mitteleuropas*. Studien an vor- und frühgeschichtlichen Tierresten Bayerns II, München.

Boessneck, J. & Driesch Von Den, A. 1978: The significance of measuring animal bones from archaeological sites. In: Meadow, R. & Zeder, M. (eds): Approaches to Faunal Analysis in the Middle East. *Peabody Museum Bulletin* 2: 25-39.

Bogucki, P. 1979: Mammal remains from hut B at the eneolithic settlement of Homolka. *Archeologické rozhledy* 31(1): 83-92.

— 2008: The Animal Economy of the Brześć Kujawski Group. In: Grygiel, R. (ed.): *Neolit i Poczatki epoki brazu w rejonie Brześcia Kujawskiego i Osłonek Lodz*: 1670-1690. Fundacja Badań Archeologicznych imienia Profesora Konrada Jażdżewskiego, Łódź.

Bökönyi, S. 1962: Zur Naturgeschichte des Ures in Ungarn und das Problem der Domestikation des Hausrindes. *Acta Archaeologica Academiae Scientiarum Hungaricae* 14: 175-214.

— 1969: Archaeological problems and methods of recognizing animal domestication. In: Ucko, P. & Dembleby, G. (eds.): *The domestication and exploitation of plants and animals*: 219-230. Gerald Duckworth & Co. Ltd., London.

— 1974: *History of domestic mammals in central and eastern Europe*. Akadémiai Kiadó, Budapest.

— 1987: Horses and sheep in East Europe in the Copper and Bronze Ages. In: Skomal, S. (ed.): *Proto-Indo-European: The archaeology of a Linguistic Problem*: 136-144. Institute for the Study of Man, Washington.

— 1995: Problems with using osteological materials of wild animals for comparisons in archaeozoology. *Anthropológiai Közlemények* 37: 3-11.

Bökönyi, S. & Kubasiewicz, M. 1961: Neolithische tiere Polens und Ungarns in Ausgrabungen. Tail 1. Das Hausrind. *Wydzial Nauk Przyrodniczo-Rolniczych* 8(1). Budapest - Szczecin.

Bonfiglio, S.; Achilli, A.; Olivieri, A.; Negrini, R.; Colli, L.; Liotta, L.; Ajmone-Marsan, P.; Torroni, A. & Ferretti, L. 2010: The enigmatic origin of bovine mtDNA haplogroup R: sporadic interbreeding or an independent event of *Bos primigenius* domestication in Italy? *PLoS One* 5(12): e15760.

Bonfiglio, S.; Ginja, C.; De Gaetano, A.; Achilli, A.; Olivieri, A.; Colli, L.; Tesfaye, K.; Agha, S.H.; Gama, L.T.; Cattonaro, F; Penedo, M. C. T.; Ajmone-Marsan, P.; Torroni, A. & Ferretti, L. 2012: Origin and spread of *Bos taurus*: new clues from mitochondrial genomes belonging to haplogroup T1. *PLoS One* 7(6): e38601.

Burger, I. 1988: *Die Siedlung der Chamer Gruppe von Dobl, Gemeinde Prutting, Landkreis Rosenheim, und ihre Stellung im Endneolithikum Mitteleuropas*. Materialhefte zur bayerischen Vorgeschichte 56. Furth, Bayern.

Calkin, V. I. 1960: Izmenchivost metapodii i eo znachenie dla izuchenia krupnogo rogatogo skota drevnosti (Metapodalia variation and its significance for the study ancient horned Cattle). *Biulleten Moskovskovo Obshchestva Iszpytatelei Prirodi - Otdel biologicheski* 65: 109-126.

— 1962: Livestock raising and hunting in the woodland strip of Eastern Europe. Materials and studies concerning the archaeology of the Soviet Union 107: 1-140.

Carranza, J. & Pérez-Barbería, F.J. 2007: Sexual selection and senescence: male size-dimorphic ungulates evolved relatively smaller molars than females. *The American Naturalist* 170: 370-380.

Clason, A. T. 1967: Animal and man in Holland's past: an investigation of the animal world surrounding man in prehistoric and early historical times in the provinces of North and South Holland. *Palaeohistoria: Acta et communicationes Instituti Bio-Archaeologici Universitatis Groninganae* 13 A+B. J.B. Wolters, Groningen.

— 1985: The animal bones and implements. In: Pleslová-Štiková, E. (ed.): *Makotřasy: A TRB site in Bohemia*: 137-161. Fontes Archaeologici Pragenses 17. National museum, Praha.

Clutton-Brock, J. 1999: *A natural history of domesticated mammals*. Cambridge University Press, Cambridge.

Damuth, J. 1990: Problems in estimating body masses of archaic ungulates using dental measurements. In: Damuth, J. & Macfadden, B.J. (eds.): *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*: 229-253. Cambridge University Press, Cambridge.

Davis, M. J. S. 1981: The effects of temperature change and domestication on the body size of the late Pleistocene to Holocene mammals of Israel. *Paleobiology* 7(1): 101-114.

— 2000: The effect of castration and age on the development of the Shetland sheep Skeleton and a metric comparison between bones of males, females and castrates. *Journal of Archaeological Science* 27: 373-390.

Degerbøl, M. & Fredskild, B. 1970: The Urus (*Bos primigenius* Bojanus) and neolithic domesticated cattle (*Bos taurus domesticus* Linné) in Denmark. Det Kongelige Danske Videnskabernes Selskab. *Biologiske Skrifter* 17(1).

Dikeman, M. E.; Albrecht, M. D.; Crouse, J. D. & Dayton, A. D. 1976: Visual appraisal of bovine cannon bone size related to performance, carcass traits and actual metacarpus measurements. *Journal of Animal Science* 42(5): 1077-1088.

Dobeš, M.; Limburský, P.; Kyselý, R.; Novák, J. & Šálková T. 2011: Příspěvek k prostorovému uspořádání obytných areálů z konce středního eneolitu. Řivnáčské osídlení ve Vlíněvsi. *Archeologické rozhledy* 63: 375-424.

Dobeš, M.; Šumberová, R. & Kyselý, R. 2013: Bošácká keramika z Kolína - Doklad kontaktu postbadenských kultur v závěru středního eneolitu. *Archeologické rozhledy* 65: 382-400.

Döhle, H. J. 1990: Linearbandkeramische Tierknochen von Eilsleben, Kr. Wanzleben - einige Aspekte der frühen Haustierhaltung. *Jahresschrift für mitteldeutsche Vorgeschichte* 73: 41-48.

— 1994: *Die linienbandkeramischen Tierknochen von Eilsleben, Bördekreis: ein Beitrag zur neolithischen Haustierhaltung und Jagd in Mitteleuropa*. Veröffentlichungen des Landesamtes für Archäologie Sachsen-Anhalt 47. Landesmuseum für Vorgeschichte, Halle.

Dreslerová, G. 2006: Zpracování zvířecích kostí z neolitického sídliště Těšetice - Kyjovice (okr. Znojmo, Česká republika). *Archeologické rozhledy* 58(1): 3-32.

Dreslerová, D. 2012: Human response to potential robust climate change around 5500 cal bp in the territory of Bohemia (the Czech Republic). *IANSA* 3(1): 43-55.

Dreslerová, D.; Horáček, I. & Pokorný, P. 2007: Přírodní prostředí Čech a jeho vývoj. In: Kuna, M. (ed.): *Archeologie pravěkých Čech 1*: 23-50. Institute of Archaeology of the Academy of Sciences of the Czech Republic in Prague, Praha.

Driesch, Von Den A. 1976: *A guide to the measurement of animal bones from archaeological sites*. Peabody Museum Bulletin 1. Harvard University, Harvard.

Driesch, Von Den A. & Boessneck, J. 1974: Kritische Anmerkungen zur Widerristhöhenberechnung aus Längenmassen vor- und frühgeschlichtlicher Tierknochen. *Säugetierkundliche Mitteilungen* 22(4): 325-348.

Edwards, C. J.; Bollongino, R.; Scheu, A.; Chamberlain, A.; Tresset, A.; Vigne, J. D.; Baird, J. F.; Larson, G.; Ho, S. Y. W & Heupink, T. H. *et al.* 2007: Mitochondrial DNA analysis shows a Near Eastern Neolithic origin for domestic cattle and no indication of domestication of European aurochs. P*roceedings of the Royal Society of London* B 274: 1377-1385.

Ernée, M.; Dobeš, M.; Hlaváč, J.; Kočár, P.; Kyselý, R. & Šída, P. 2007: Zahloubená chata ze středního eneolitu v Praze 9 - Miškovicích. Výsledky archeologických a přírodovědných analýz. *Památky archeologické* 98: 31-108.

Evin, A.; Flink, L. G.; Balasescu, A.; Popovici, D.; Andreescu, R.; Bailey, D.; Mirea, P.; Lazar, C.; Boroneant, A.; Bonsall, C.; Strand Vidarsdottir, U.; Brehard, S.; Tresset, A.; Cucchi, T.; Larson, G. & Dobney, K. 2014: Unravelling the complexity of domestication: a case study using morphometrics and ancient DNA analyses of archaeological pigs from Romania. *Philosophical Transactions of the Royal Society* B 370: 2013.0616.

Fandos, P. & Vigal, C. R. 1993: Sexual dimorphism in size of the skull of Spanish ibex *Capra pyrenaica*. *Acta Theriologica* 38(1): 103-111.

Fock, J. 1966: *Metrische Untersuchungen an Metapodien einiger europäischer Rinderrassen*. Dissertation. University München, München.

Frisch, J. E. 1987: Physiological reasons for heterosis in growth of *Bos indicus* × *Bos taurus*. *The Journal of Agricultural Science* 109(2): 213-230.

Galton, F. 1886: Regression towards mediocrity in hereditary stature. *The Journal of the Anthropological Institute of Great Britain and Ireland* 15: 246-263.

Gentry, A.; Clutton-Brock, J. & Groves, C. P. 2004: The naming of wild animal species and their domestic derivatives. *Journal of Archaeological Science* 31: 645-651.

Gingerich, P. D. 1990: Prediction of body mass in mammalian species from long bone lengths and diameters. *Contributions from the Museum of paleontology, University of Michigan* 28(4): 79-92.

Glass, M. 1991: *Animal Production Systems in Neolithic Central Europe*. B.A.R. (International Series) 572. Oxford.

Grigson, C. 1969: The uses and limitations of differences in absolute size in the distinction between the bones of aurochs (*Bos primigenius*) and domestic cattle (*Bos taurus*). In: Ucko, J. & Dimbleby, G.W. (eds.): *The domestication and exploitation of plants and animals*: 277-293. Gerald Duckworth & Co. Ltd., London.

— 1974: The craniology and relationships of four species of Bos. 1. Basic craniology: *Bos taurus* L. and its absolute size. *Journal of Archaeological Science* 1: 353-379.

— 1982: Sex and age determination of some bones and teeth of domestic cattle: a review of the literature. In: Wilson, B.; Grigson, C. & Payne, S. (eds.): *Ageing and sexing animal bones from archaeological sites*: 7-23. B.A.R. (British series) I09. Oxford.

Hannah, J.; O'regan, A. & Kitchener, C. 2005: The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review* 35(3-4): 215-230.

Herre, W. 1986: *Sus scrofa* Linnaeus, 1758 - Wildschwein. In: Niethammer, J. & Krapp, F. (eds.): *Handbuch der Säugetiere Europas. Band 2/II: Paarhufer - Artiodactyla (Suidae, Cervidae, Bovidae)*: 36-66. AULA-Verlag GmbH, Wiesbaden.

Higham, C. F. V. 1969: The metrical attributes of two samples of bovine limb bones. *Journal of the Zoological Society of London* 157: 63-74.

Hejcman, M.; Hejcmanová, P.; Stejskalová, M. & Pavlů, V. 2014: Nutritive value of winter-collected annual twigs of main European woody species, mistletoe and ivy and its possible consequences for winter foddering of livestock in prehistory. *The Holocene* 24(6): 659-667.

Hundt, H. J. 1986: Tissue et sparteries neolithiques. In: Petrequin, P. (ed.): *Les sites littoraux neolithiques de Clairvaux-les-Lacs (Jura), Tome I: Problematique generale, l'exemple de la station III*: 233-242. Editions de la Maison des sciences de l'homme, Paris.

Jewell, P. A. 1962: Changes in size and type of cattle from Prehistoric to Medieval times in Britain. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 77: 159-167.

Jiráň, L. (ed.) *et al.* 2013: *The Prehistory of Bohemia 4. The Bronze Age*. Institute of Archaeology of the Czech Academy of Sciences in Prague, Praha.

Jiráň, L. & Venclová, N. (eds.) *et al.* 2013-2014: *The Prehistory of Bohemia 1-7*. Institute of Archaeology of the Czech Academy of Sciences in Prague, Praha.

Johnson, R. K. 1981: Crossbreeding in swine: experimental results. *Journal of Animal Science* 52: 906-923.

Klementová, J. & Hložek, J. 2005: Velké Přílepy, k. ú. Kamýk, nálezová zpráva, záchranný archeologický výzkum, Roztoky u Prahy. Unpublished report, no. 2471/08. Archiv of the Institute of Archaeology of the Czech Academy of Sciences in Prague, Praha.

Kobryń, H. & Lasota-Moskalewska, A. 1989: Certain osteometric differences between the aurochs and domestic cattle. *Acta Theriologica* 34: 67-82.

Kovačiková, L. 2009: Příspěvek k poznání výživy a hospodářského zázemí neolitického sídliště v Černém Volu, okr. Praha-západ. *Archeologické rozhledy* 61: 254-264.

Kovačiková, L.; Bréhard, S.; Šumberová, R.; Balasse, M. & Tresset, A. 2012: New insights into the subsistence and early farming from Neolithic settlements in Central Europe: archaeozoological evidence from the Czech Republic. *Archaeofauna* 21: 71-97.

Kratochvíl, Z. 1981: Tierknochenfunde aus der grossmährischen Siedlung Mikulčice. 1: Das Hausschwein. *Acta Scientiarum Naturalium Academiae scientiarum bohemoslovacae, Brno* 9(3).

— 1988: Das Hausrind aus Mikulčice und seine Bedeutung [4]. *Acta Scientiarum Naturalium Academiae scientiarum bohemoslovacae, Brno* 22(9).

Kyselý, R. 2000: Archeozoologický rozbor materiálu z lokality Rubín a celkový pohled na zvířata doby hradištní. *Památky archeologické* 91: 155-200.

— 2002a: Osteological analysis of animals buried in Hostivice (Prague-West district) - Funnel Beaker culture (TRB) and a comparison of animal remains from Hostivice with other contemporary finds from the Czech Republic and Central Europe. *Památky archeologické* 93(1): 29-87.

— 2002b: Zvířecí kosti ze sídliště kultury nálevkovitých pohárů ve Vikleticích (okr. Chomutov). In: Čech, P. & Smrž, Z. (eds.): *Sborník Drahomíru Kouteckému*: 315-322. Ústav archeologické památkové péče severozápadních Čech, Most.

— 2003: Savci (Mammalia) z raně středověkého hradu Stará Boleslav (střední Čechy). In: Boháčová, I. (ed.): *Stará Boleslav. Přemyslovský hrad v raném středověku*: 311-334. Mediaevalia archaeologica 5. Institute of Archaeology of the Academy of Sciences of the Czech Republic in Prague, Praha.

— 2005: Archeologické doklady divokých savců na území ČR v období od neolitu po novověk (Archaeological evidence of wild mammals in the Czech Republic from the Neolithic to the Modern times). *Lynx* 36: 55-101.

— 2007a: Zvířecí kosti z archeologických objektů jordanovské kultury v Praze-Ďáblicích. *Archeologie ve středních Čechách* 11(1): 125-130.

— 2007b: Zvířecí kosti z objektů řivnáčské kultury z výzkumu v Praze-Ďáblicích v letech 2002 a 2004. *Archeologie ve středních Čechách* 11(1): 167-170.

— 2008a: Aurochs and potential crossbreeding with domestic cattle in Central Europe in the Eneolithic period. A metric analysis of bones from the archaeological site of Kutná Hora-Denemark (Czech Republic). *Anthropozoologica* 43(2): 7-37.

— 2008b: Animal bone analysis from a Řivnáč culture horizon at the Kutná Hora-Denemark site (Kutná Hora district, Czech Republic). In: Zápotocký, M. & Zápotocká, M. (eds.): *Kutná Hora - Denemark: hradiště řivnáčské kultury (ca 3000-2800 př. Kr.)*: 341-418. Památky archeologické - supplementum 18.

— 2008c: Nálezy obratlovců z eneolitických objektů v Úholičkách (okr. Praha-západ) z r. 1994 a 1998. *Archeologické rozhledy* 60: 305-308.

— 2008d: Zvířecí kosti z Klučova - pískovny „Na vrchu“. *Památky archeologické* 99: 85-87.

— 2009: Zvířecí kosti z eneolitických objektů v Praze-Ďáblicích, ul. Legionářů. *Archeologie ve středních Čechách* 13(1): 169-172.

— 2010a: *Archeozoologická problematika eneolitu* Čech (Archaeozoology of the Czech Eneolithic). Dissertation. Faculty of Science, Charles University in Prague, Praha.

— 2010b: Review of the oldest evidence of domestic fowl (*Gallus gallus* f. *domestica*) from the Czech Republic in its European context. *Acta Zoologica Cracoviensia* 53A(1-2): 9-34.

— 2010c: Breed character or pathology? Loose cattle horns from the Eneolithic site of Hostivice-Litovice (Czech Republic). *Journal of Archaeological Science* 37(6): 1241-1246.

— 2012: Paleoekonomika lengyelského období a eneolitu Čech a Moravy z pohledu archeozoologie. *Památky archeologické* 103: 5-70.

— 2013: An analysis of osteological material from the late Funnel Beaker culture settlement in Brozany, northwestern Bohemia. *Archeologické rozhledy* 65(3): 504-534.

Kyselý, R. & Hájek, M. 2012: MtDNA haplotype identification of aurochs remains originating from the Czech Republic (Central Europe). *Environmental Archaeology* 17(2): 118-125.

Kyselý, R. & Peške, L. 2016: Horse size and domestication: Early equid bones from the Czech Republic in the European context. *Anthropozoologica* 51(1): 15-39.

Larson, G.; Albarella, U.; Dobney, K.; Rowley-Conwy, P.; Schibler, J.; Tresset, A.; Vigne, J. D.; Edwards, C. J.; Schlumbaum, A. & Dinu, A. 2007: Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *PNAS* 104 (39): 15276-15281.

Larson, G.; Cucchi, T. & Dobney, K. 2011: Genetic aspects of pig domestication. In: Ruvinksy, A. & Rothschild, M. (eds.): *The Genetics of the Pigs*: 14-37. CAB International, Oxford. 2nd edition.

Lasota-Moskalewska, A. 1980: Morphotic changes of domestic cattle skeleton from the Neolithic Age to the beginning of the Iron Age. *Wiadomości Archeologiczne* 45(2): 119-163.

— 1989: Differences in the body size of cattle in the archaeozoological materials in the polish territories. *Przaglad Archeologiczny* 36: 89-95.

Lasota-Moskalewska, A. & Kobryń, H. 1989: Description of intermediate forms in the evolution of *Bos primigenius* f. *taurus* on the basis of osteometric characteristics. *Acta Theriologica* 34: 625-642.

— 1990: The size of aurochs skeletons from Europe and Asia in the period from the Neolithic to the Middle Ages. *Acta Theriologica* 35: 89-109.

Lasota-Moskalewska, A.; Kobryń, H. & Swiezynski, K. 1987: Changes in the size of domestic and wild pig in the territory of Poland from the Neolithic to the Middle Ages. *Acta Theriologica* 32: 51-81.

Likovský, J. & Kyselý, R. 2008: Lidské a zvířecí kosterní pozůstatky z objektů kultury nálevkovitých pohárů ze Siřemi (okr. Louny). *Archeologie ve středních Čechách* 12(1): 131-134.

Ložek, V. 1973: *Příroda ve čtvrtohorách*. Academia, Praha.

Makowiecki, D. 2009: Animals in the landscape of the medieval country side and urban agglomeration of the Baltic Sea countries. In: *Atti Delle Settimane LVI, Tomo primo, Cittá e campagna nei secoli altomedievali, Spoleto, 27 marzo - 1 aprile 2008. Spoleto (Settimane di Studio Della Fundazione Centro Italiano di Studi Sull'Alto Medioevo, 56)*: 427-444.

Makowiecki, D. & Makowiecka, M. 2000: Gospodarka zwierzętami społeczności kultury pucharów lejkowatych (grupy: wschodnia i radziejowska) oraz kultury amfor kulistych. In: Kośko, A. (ed.): *Archeologiczne badania ratownicze wzdłuż gazociągu tranzytowego. Tom III Kujawy, cz. 4. Osadnictwo kultur późnoneolitycznych oraz interstadium epok neolitu i brązu: 3900 - 1400/1300 przed Chr.*: 347-378. Wydawnictwo Poznańskie, Poznań.

Matolcsi, J. 1970: Historische Erforschung der Körpergröße des Rindes auf Grund von ungarischem Knochenmaterial. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 87: 89-137.

May, E.; Reichert, M. & Hannemann, K. 1996: Allometric aspects to the determination of the withers height in pigs on the basis of the data of M. Teichert. *ArchaeoZoologia* 8(1-2): 125-139.

May, E. & Teichert, U. M. 2001: Berechnung der Widerristhöhe bei Schafen aus Extremitätenmaßen mit Hilfe von Regressionsgleichungen oder Faktoren? In: Buitenhuis, H. & Prummel, W. (eds.): *Animals and Man in the Past*: 33-37. ARC-Publicatie, Groningen.

Mayer, J. J.; Novak, J. M. & Brisbin, I. L. 1998: Evaluation of molar size as a basis for distinguishing wild boar from domestic swine: Employing the present to decipher the past. In: Nelson, S. M. (ed.): Ancestors for the pigs: Pigs in prehistory. *Research papers in science and archaeology* 15: 39-54. MASCA, Philadelphia.

Meadow, R. H. 1999: The use of size index scaling techniques for research on archaeozooogical collections from the Middle East. In: Becker, C.; Manhart, H.; Peters, J. & Schibler, J. (eds.): *Historia Animalium Ex Ossibus. Studia honoraria 8: Beiträge zur Paläoanatomie, Archäologie, Ägyptologie, Ethnologie und Geschichte der Tiermedizin*: 285-301. Verlag Marie Leidorf, Rahden/Westf.

MENDOZA, M.; JANIS, C. M. & PALMQVIST, P. 2006: Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *Journal of Zoology* 270(1): 90-101.

MILISAUSKAS, S. & KRUK, J. 2011: Late Neolithic/Late Copper Age 3500-2200 BC. In: Milisauskas, S. (ed.): *European Prehistory: A Survey*: 293-325. Springer, New York. 2nd edition.

MÜLLER, H. H. 1964: Die Haustiere der Mittleldeutschen Bandkeramiker. *Naturwissenschaftliche Beiträge zur Vor- und Frühgeschichte* 17: 6-181.

NEPHAWE, K. A.; CUNDIFF, L. V.; DIKEMAN, M. E.; CROUSE, J. D. & VAN VLECK, L. D. 2004: Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score, height and body condition score measurement of cows and carcass traits of their steer relatives. *Journal of Animal Science* 82: 647-653.

NEUSTUPNÝ, E.; DOBEŠ, M.; TUREK, J. & ZÁPOTOCKÝ, M. 2013: *The Prehistory of Bohemia 3. The Eneolithic*. Institute of Archaeology of the Czech Academy of Sciences in Prague, Praha.

NOBIS, G. 1954: Zur Kenntnis der ur- und frühgeschichtlichen Rinder Nord- und Mitteldeutschlands. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 63: 155-194.

NODDLE, B. A. 1973: Determination of the body weight of cattle from bone measurements. In: Matolcsi, J. (ed.): *Domestikations-forschung und Geschichte der Haustiere*: 377-389. Akadémiai Kiadó, Budapest.

NÝVLTOVÁ-FIŠÁKOVÁ, M. 2004: Fauna z lokality Vedrovice. In: Lutovský, M. (ed.): *Otázky neolitu a eneolitu 2003*: 63-68. Ústav archeologické památkové péče středních Čech, Praha.

PAVELKA, J. 2007: Území České republiky ve vztahu k předpokládaným vícenásobným centrům domestikace prasat. In: *Opomíjená archeologie 2005 - 2006 (Neglected archaeology 2005 - 2006)*: 219-232. Faculty of Philosophy and Arts, University of West Bohemia in Pilsen, Plzeň.

PAVLŮ, I. & ZÁPOTOCKÁ, M. (eds.) *et al.* 2013: *The Prehistory of Bohemia 2. The Neolithic*. Institute of Archaeology of the Czech Academy of Sciences in Prague, Praha.

PAYNE, S. & BULL, G. 1988: Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *ArchaeoZoologia* 2(1, 2): 27-66.

PEŠKE, L. 1985a: Osteologické nálezy kultury zvoncovitých pohárů z Holubic a poznámky k zápřahu skotu v eneolitu. *Archeologické rozhledy* 37(4): 428-440.

— 1985b: Domácí a lovná zvířata podle nálezů na slovanských lokalitách v Čechách. *Sborník Národního muzea / Journal of the National Museum (Prague) - řada historická / series historica* 39: 209-216.

— 1994: The History of Natural Scientific Methods in the Archaeological Institute and Their Present Objectives. In: Fridrich, J. (ed.): *25 Years of Archaeological Research in Bohemia*: 259-278. Památky archeologické - supplementum 1.

— 1997: The oldest LnK evidence from Nové Dvory (Czech Republic). *Archeologické rozhledy* 49(3): 546.

— 2000: Die osteologischen Funde von Cimburk. In. Zápotocký M. (ed.): *Cimburk und die Höhensiedlungen des frühen und älteren Äneolithikums in Böhmen*: 89-92. Památky archeologické - supplementum 12.

PEŠKE, L.; RULF, J. & SLAVÍKOVÁ, J. 1998: Bylany-ekodata. Specifikace nálezů kostí a rostlinných makrozbytků. In: Pavlů, I. (ed.): *Bylany Varia 1*: 83-118. Institute of Archaeology of the Academy of Sciences of the Czech Republic in Prague, Praha.

PETRÁŠEK, F. 1972: *Geneze chovu skotu v Českých zemích*. Academia, Praha.

PODBORSKÝ, V. (ed.) 1993: *Pravěké dějiny Moravy*. Vlastivěda moravská. Země a lid, nová řada, sv. 3, Brno.

POLLACK, S. 1999: *Ancient Mesopotamia*. Cambridge University Press, Cambridge.

PÖLLATH, N. & PETERS, J. 2005: On the possible use of the LSI scaling technique for stature analysis in cattle. *Revue de Paléobiologie*, vol. spéc. 10: 225-235.

PUCHER, E. 2004: Der mittelneolithische Tierknochenkomplex von Melk-Winden (Niederösterreich). *Ann. Naturhist. Mus. Wien* 105A: 363-403.

— 2006: Ein neuer Tierknochenfundkomplex aus einer Siedlung der Badener Kultur in Ossarn bei Herzogenburg in Niederosterreich. *Archäologie Österreichs* 17(2): 104-116.

— 2010: Sechs Jahrtausende alpine Viehwirtschaft. Online publication, available from: www.anisa.at/Pucher%20Viehwirtschaft%20ANISA%20Internet%202010.pdf [letzter Zugriff: 10.01.2011].

— 2013: Die spätbronzezeitlichen Tierknochen aus der Grabung 1993/94 auf dem Hallstätter Salzberg. In: Pucher, E.; Barth, F.E.; Seemann, R. & Brandstätter, F. (eds.): *Bronzezeitliche Fleischverarbeitung im Salzbergtal bei Hallstatt*: 11-51. Mitteilungen der Prähistorischen Kommission, Band 80. Verlag der Österreichischen Akademie der Wissenschaften, Wien.

REHAZEK, A. & NUSSBAUMER, M. 2012: Sex, Breed or Rearing Conditions? A Multivariate Approach to Assessing Shape Variations in Mediaeval Cattle Metapodials from Bern, Switzerland. In: Lefèvre, Ch.

(ed.): *Proceedings of the General Session of the 11th International Council for Archaeozoology Conference (Paris, 23-28 August 2010)*: 41-54. B.A.R. (International Series) 2354. Oxford.

ŘÍDKÝ, J. 2009: Zpráva o záchranném archeologickém výzkumu v Dolních Beřkovicích (okr. Mělník). Unpublished report, no. 13769/09. Archiv of the Institute of Archaeology of the Czech Academy of Sciences in Prague, Praha.

RILEY, D. G.; COLEMAN, S. W.; CHASE JR. C. C.; OLSON, T. A. & HAMMOND, A. C. 2007: Genetic parameters for body weight, hip height, and the ratio of weight to hip height from random regression analyses of Brahman feedlot cattle. *Journal of Animal Science* 85(1): 42-52.

ROBLÍČKOVÁ, M. 2003a: Domesticated animal husbandry in the Bronze Age on the basis of osteological remains. *Archeologické rozhledy* 55(3): 458-499.

— 2003b: *Hospodářská a divoká zvířata doby bronzové na základě osteologických pozůstatků*. Dissertation. Faculty of Science, Masaryk University, Brno.

— 2004: Zvířecí osteologické pozůstatky ve vybraných lokalitách doby bronzové. In: Hašek, V.; Nekuda, R. & Ruttkay, M. (eds.): *Ve službách archeologie 5*: 180-192. Muzejní a vlastivědná společnost, Brno.

ROWLEY-CONWY, P.; ALBARELLA, U. & DOBNEY, K. 2012: Distinguishing Wild Boar from Domestic Pigs in Prehistory: A Review of Approaches and Recent Results. *Journal of World Prehistory* 25(1): 1-44.

RÜTIMAYER, L. 1861: *Die Fauna der Pfahlbauten der Schweiz*. Neue Denkschr. d. Allg. Schweiz. Ges. d. gesamt. Nahirw. Bd. 19. Schweighauser, Basel.

SAMBRAUS, H. H. 1999: *A colour atlas of livestock breeds*. Wolfe Publishing Ltd., London.

SCHIBLER, J. 2004: Bones as a key for reconstructing the environment, nutrition and economy of the lake-dwelling societies. In: Menotti, F. (ed.): *Living on the lake in prehistoric Europe. 150 years of lake-dwelling research*: 144-161. Routledge, London.

SCHIBLER, J.; HÜSTER-PLOGMANN, H; JACOMET, S; BROMBACHER, C.; GROSS-KLEE, E. & RAST-EICHER, A. 1997: *Ökonomie und Ökologie neolithischer und bronzezeitlicher Ufersiedlungen am Zürichsee*. Monographien der Kantonsarchäologie Zürich 20. Zürich.

SCHIBLER, J. & SCHLUMBAUM, A. 2007: History and economic importance of cattle (*Bos taurus* L.) in Switzerland from Neolithic to Early Middle Ages. *Schweizer Archiv für Tierheilkunde* 149: 23-29.

SCHIBLER, J.; ELSNER, J. & SCHLUMBAUM, A. 2014: Incorporation of aurochs into a cattle herd in Neolithic Europe: single event or breeding? *Scientific Reports* 4: 5798. DOI: 10.1038/srep05798.

SCHMID, E. 1972: *Atlas of Animal Bones*. Elsevier Pub. Company, Amsterdam.

SCHRAMM, Z. 1967: Kości długie a wysokość w kłebie u kozy. *Roczniki wyźszei szkoły rolniczej w Poznaniu* 36: 89-105.

SCOTT, K. M. 1985: Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the American museum of Natural History* 19: 197-288.

— 1990: Postcranial dimensions of ungulates as predictors of body mass. In: Damuth, J. & MacFadden, B.J. (eds.): B*ody Size in Mammalian Paleobiology: Estimation and Biological implications*: 301-335. Cambridge University Press, Cambridge.

SHERRATT, A. 1983: The secondary exploitation of animals in the old world. *World Archaeology* 15(1): 90-104.

SHISHLINA, N. I.; ORFINSKAYA, O. & GOLIKOV, V. 2003: Bronze Age Textiles from the North Caucasus: New Evidence of Fourth Millennium BC Fibres and Fabrics. *Oxford Journal of Archaeology* 22: 331-344.

SHISLINA, N. I.; ZAZOVSKAYA, E. P.; PLICHT, J.; HEDGES, R. E. M.; SEVASTYANOV, V. S. & CHICHAGOVA, O. A. 2009: Paleoecology, subsistence, and 14C chronology of the Eurasian Caspian Steppe Bronze Age. *Radiocarbon* 51(2): 481-499.

SILVER, I. A. 1969: The ageing of domestic animals. In: Brothwell, D. & Higgs, E. (eds.): *Science in Archaeology - Survey of Progress and Research*: 283-302. Thames and Hudson, London.

TEICHERT, M. 1969: Osteometrische Untersuchungen zur Berechnung der Widerristhöhe bei vor- und frühgeschichtlichen Schweinen. *Kühn-Archiv* 83: 237-292.

— 1970: Größenveränderungen der Schweine vom Neolithikum bis zum Mittelalter. *Archiv für Tierzucht* 13: 229-240.

— 1975: Osteologische Untersuchungen zur Berechnung der Widerristhöhe bei Schafen. In: Clason, A.T. (ed.): *Archaeozoological studies*: 51-69. North Holland and American Elsevier, Amsterdam.

— 1984: Size variation in cattle from Germania Romana and Germania Libera. In: Grigson, C. & Clutton-Brock, J. (eds.): *Animals and Archaeology: 4. Husbandry in Europe*: 93-103. B.A.R. (International Series) 227. Oxford.

— 1993: Size and utilisation of the most important domesticated animals in Central Europe from the beginning of domestication until the late Middle Ages. In: Clason, A.T.; Payne, S. & Uerpmann, H.-P. (eds.): *Skeletons in her Cupboard - Festschrift for Juliet Clutton-Brock*: 235-238. Oxbow Monograph 34, Oxford.

— 2005: Vergleich zwischen gemessener und berechneter Widerristhöhe bei einem Deutschen Schwarzbunten (Holstein) Milchrind. *MUNIBE (Antropologia – Arkeologia)* 57: 483-486.

THOMAS, R. N. W. 1988: A statistical evaluation of criteria used in sexing cattle metapodials. *ArchaeoZoologia* 2(1-2): 83-92.

UERPMANN, H. P. & UERPMANN, M. 1994: Animal bone finds from excavation 520 at Qala´at al-Bahrain. In: Højlund, F. & Andersen, H. H. (eds.): *Qala´at al-Bahrain - The northern city wall and the Islamic fortress*: 417-444. Jutland Archaeological Society Publications 30(1). Moesgaard, Aarhus.

VIGNE, J. D. 1991: The meat and offal weight (MOW) method and the relative proportion of ovicaprines in some ancient meat diets of the north-western Mediterranean. *Rivista di Studi Liguri* 57(2): 21-47.

— 1999: The skeletal size of caprines as an indicator for the early diffusion of husbandry in the north-western Mediterranean basin, especially southern France (6th-5th millennia cal B.C.). In: Becker, C.; Manhart, H.; Peters, J. & Schibler, J. (eds.): *Historia animalium ex ossibus*: 469-486. Verlag Marie Leidorf GmbH, Rahden.

VOHRADSKÝ, F. 1999: *Místní plemena domácích zvířat tropů a subtropů*. Academia, Praha.

WILSON, L. L.; ROTH, H. B.; ZIEGLER, J. H. & SINK, J. D. 1977: Bovine metacarpal and metatarsal dimension: sex effects, heritability estimates and relation to growth and carcass characteristics. *Journal of Animal Sciences* 44: 932-938.

ZÁPOTOCKÝ, M. 2000: *Cimburk und die Höhensiedlungen des frühen und älteren Äneolithikums in Böhmen*. Památky archeologické - supplementum 12.

ZÁPOTOCKÝ, M. & ZÁPOTOCKÁ, M. 2008: *Kutná Hora - Denemark: hradiště řivnáčské kultury (ca 3000-2800 př. Kr.)*. Památky archeologické - supplementum 18.

ZEDER, M. A.; BRADLEY, D. G.; EMSHWILLER, E. & SMITH, B. D. 2006: *Documenting Domestication: New Genetic and Archaeological Paradigms*. University of California Press, Berkeley.

ZEUNER, F. E. 1963: *A History of Domesticated Animals*. Hutchinson of London, London.

Archaeofauna 25 (2016): 79-106

The dogs of Roman Vindolanda, Part I: Morphometric techniques useful in differentiating domestic and wild canids

DEB BENNETT[1*], GREG CAMPBELL[2] & ROBERT M. TIMM[3]
[1]Equine Studies Institute, P.O. Box 411, Livingston, CA, USA
[2]The Naïve Chemist, 150 Essex Rd., Southsea, Hants, UK
[3]Department of Ecology and Evolutionary Biology & Natural History Museum, University of Kansas, Lawrence, KS, USA
[*]Corresponding author: office@equinestudies.org; Equine Studies Institute, P.O. Box 411, Livingston, CA 95334 USA

(Received *8 September 2015*; Revised *29 November 2015*; Accepted *11 December 2015*)

ABSTRACT: The Roman-era fort-village complex at Vindolanda in northern England, occupied from about A.D. 50 to A.D. 415, has yielded extensive well-preserved remains of the domestic dog, *Canis familiaris*. Herein, utilizing a novel combination of biostatistical techniques to identify parameters that best differentiate canids, we test the hypothesis that the inhabitants of Vindolanda selectively bred dogs. We also differentiate dog remains from wolves and foxes, similarly-sized canids that occur throughout Eurasia. The Vindolanda dogs are less morphologically diverse than modern dogs but much more diverse than dogs of the British Neolithic and Iron Age. They are as morphologically diverse as dogs excavated from other Romano–British sites, and only slightly less diverse than the whole known population of Roman-era dogs sampled from across Europe and North Africa. Vindolanda dogs thus underwent greater directional selection than expected from natural environmental forces, suggesting that selective breeding rather than random panmixis maintained diversity. The Vindolanda dog sample will make an ideal subject for DNA analysis, since it contains dogs undergoing incipient diversification from dingo-like ancestors.

KEYWORDS: *CANIS FAMILIARIS*, CRANIOMETRICS, DE GROSSI MAZZORIN-TAGLIACOZZO ANALYSIS, DOMESTIC DOG, MULTIVARIATE ANALYSIS, PRINCIPAL COMPONENT ANALYSIS, ROMANO–BRITISH, VINDOLANDA

RESUMEN: El fuerte-poblado romano de Vindolanda en el norte de Inglaterra fue ocupado desde el 50 al 415 A.D. y ha proporcionado una importante colección de restos bien conservados de perro, *Canis familiaris*. En este trabajo, utilizando una combinación inédita de técnicas bioestadísticas para determinar los parámetros que mejor diferencian cánidos, verificamos la hipótesis referida a una cría selectiva de perros por parte de los habitantes de Vindolanda. Al tiempo, discriminamos los restos de perros de los de lobo y zorro común, dos especies de cánidos de talla semejante al perro distribuidos por toda Eurasia. Los perros de Vindolanda se encuentran morfológicamente menos diferenciados que sus parientes actuales pero mucho más que sus parientes británicos del Neolítico y Edad del Hierro. Su diferenciación morfológica es igual de amplia que la de los perros procedentes de otros yacimientos romano-británicos y solo ligeramente inferior a la documentada para todos los perros de época romana procedentes de Europa y el Norte de Africa. Por ello, parece que los perros de Vindolanda sufrieron una selección direccional superior a la esperada cuando se asume sólo la existencia de presiones ambientales lo cual sugiere que fue una cría selectiva, y no tanto una panmixis aleatoria de individuos, lo que mantuvo tal grado de diversificación. Los perros de Vindolanda constituyen un grupo ideal para realizar análisis de

ADN toda vez que parece incorporan individuos que manifiestan una diversificación incipiente a partir de antecesores con aspecto de dingo.

PALABRAS CLAVE: *CANIS FAMILIARIS*, CRANIOMETRÍA, ANÁLISIS DE GROSSI MAZZORIN-TAGLIACOZZO, PERRO DOMÉSTICO, ANÁLISIS MULTIVARIANTE, ANÁLISIS DE COMPONENTES PRINCIPALES, ROMANO-BRITÁNICO, VINDOLANDA

INTRODUCTION

The oldest undisputed dog remains go back about 15,000 years (Nobis, 1979; Crockford, 2000b; Morey, 2010), although the origin of dogs remains a contested topic. It now seems probable that there is no single source population for domestication but rather people from various areas independently brought wolf pups into captivity and began the domestication process.

Canid remains are frequently found at archaeological sites. Often these are attributed to dogs, but few researchers have rigorously tested how to tell dog remains from wolves or foxes, similarly-sized canids that occur throughout Eurasia (see Davis & Valla, 1978). Herein, we present criteria for differentiating dog, wolf, and fox remains and document the range of morphological variation in the dogs of Vindolanda, a nearly 2,000 year old site near Hadrian's Wall in north–central England which lay at the northwestern fringe of the Roman Empire. The canid remains constitute the largest and best-preserved sample of dog bones from any single site of Roman date in Britain.

With the current recognition of nearly 350 breeds of dogs by the World Canine Organization (Fédération Cynologique Internationale, FCI), it is clear that intense selection by humans has had a great effect on the morphology of this animal. Another major goal of this study is thus to characterize the initial differentiation of distinctive dog phenotypes from a generalized "primitive" morphology. We develop a comparative database of more than 500 recent specimens including red fox (*Vulpes vulpes*) and two samples of wolf (recent North American *Canis lupus* and late Pleistocene *Canis* from Natural Trap Cave, Wyoming; Martin & Gilbert, 1978). Feral *Canis familiaris* (Australian dingoes, Carolina dogs from the southeastern U.S., and New Guinea singing dogs) are included in some comparisons. Our sample of modern domestic dogs comprises 179 individuals belonging to 83 breeds.

We extend the groundbreaking work of Harcourt (1974) and Baxter and colleagues (Baxter, 2002, 2010a, 2010b; Baxter & Nussbaumer, 2009; Phillips *et al*., 2009) and introduce a novel procedure for morphometric analysis which combines principal components analysis (PCA) with the ratio comparison technique of De Grossi Mazzorin & Tagliacozzo (2000).

SITE LOCATION AND EXCAVATION HISTORY

Vindolanda is a fort–village complex situated 3 km south of Hadrian's Wall in northern England (Figure 1). It was occupied almost continuously from about A.D. 50 to the fall of the Roman Empire

FIGURE 1

Vindolanda's location, 3 km (2 mi) south of Hadrian's Wall, within the United Kingdom and the county of Northumberland.

in A.D. 415 and beyond (Birley, 2003). Systematic excavation begun in the 1960s has yielded a collection of over 20,000 bones of birds and mammals. Fifty years of excavation at Vindolanda has demonstrated a complex succession of nine forts built one on top of the other over the whole period of its occupation (see Birley, 2003 and Blake, 2014 for summary). Bones, including those of dogs, have been recovered from every Vindolanda context and time period (Hodgson, 1977; Hambleton, 2003; Bennett, 2005, 2014; Bennett & Timm, 2013). Of these, some 520 or about 2.6% pertain to the domestic dog, *Canis familiaris*. We review and interpret the time-stratigraphic and specific context associations of Vindolanda dog bones in Part II of this series on the dogs of Roman Vindolanda (Bennett & Timm, 2016).

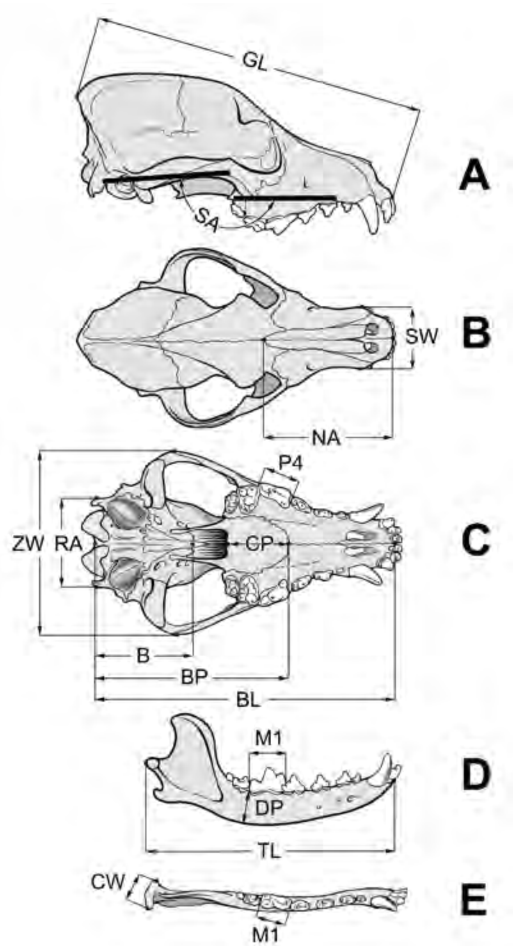

FIGURE 2

Measurements on skull and jaws. Heavy bars in (A) delineate the orientation of the basicranium and palate; the parameter SA (skull angle, called "β" by Nussbaumer, 1982; Baxter & Nussbaumer, 2009) represents the angular difference between them. (D, E) Measurements on jaw rami.

MATERIALS AND METHODS

Recovery, Comparison, Measurement and Analytical Techniques

Most Vindolanda bones were recovered by standard hand troweling methods, except those from below the East Granary (Bennett & Timm, 2013) which were recovered by 0.5-mm wet and dry sieving. Measurements were taken with electronic calipers and recorded to the hundredth mm. Parameters are a combination of those recommended by Lüps (1974), Driesch (1976), Nussbaumer (1978, 1982), and Baxter & Nussbaumer (2009) (Figures 3, 4). The relative downbending (klinorhynchy) or upbending (airorhynchy) of the snout was assessed using a six-inch fine-toothed contour gauge.

We employ a total of 26 variables in order to maximize sample size while ensuring a robust set of measurements for each skeletal element. Numerous literature reports on dogs of the Roman era reference collections unearthed and reported after Harcourt (1974); these are summarized in our dataset as "post-1974". In analyses utilizing previously published data, we ignore the small error

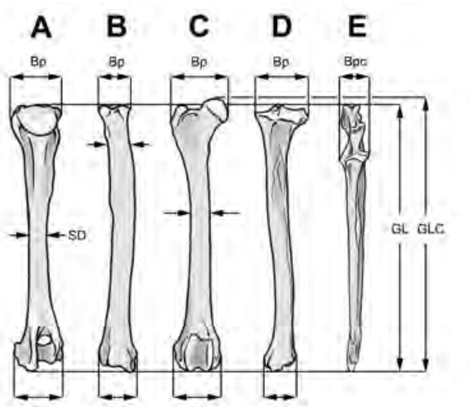

FIGURE 3

Measurements on limb bones. Letter abbreviations after Driesch (1976). (A), humerus; (B), radius; (C) femur; (D) tibia; (E) ulna.

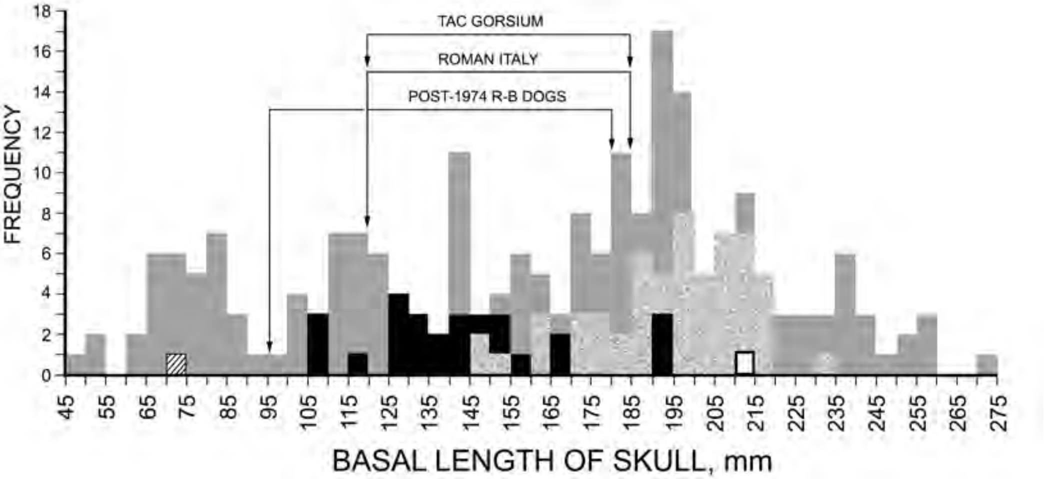

FIGURE 4

Raw size of skulls. Tac Gorsium data from Bökönyi (1984); Roman Italy from DeGrossi-Mazzorin & Tagliacozzo (2000); Classe from Farello (1995); Heidelberg–Neuenheim from Luttschwager (1965); Yasmina from MacKinnon & Belanger (2002).

that arises from different researchers performing the measurements (99% of measurements utilized in this study were taken by the senior author). We also ignore the small difference between minimum shaft diameter and mid-shaft diameter (we label this “composite” factor MSD). Statistical analysis was performed with Version 1.91 of the PAST freeware (Hammer *et al*., 2001).

Measurements and abbreviations for skulls and jaws are given in Figure 2 (A–E) and for limb bones in Figure 3 (A–E).

Procedure for Multivariate Analysis

The simplest analytical technique we employed consists of selected ratios, called indexes (Harcourt, 1974) (Figure 9). We utilized Principal Component Analyses (PCA’s; Figures 10, 11) primarily to predict parameters that best differentiate canid skulls and jaws, and then constructed De Grossi Mazzorin–Tagliacozzo Analyses (MTA’s, see discussion below; Figures 12–20) which effectively display them.

MTA (De Grossi Mazzorin & Tagliacozzo Analysis): Building upon Harcourt’s (1974) work, De Grossi Mazzorin & Tagliacozzo (2000) hit upon the very useful idea of plotting limb stoutness index against projected withers height. MTA graphically compares a linear measurement with a ratio. Ideally the linear measurement is representative of other measures of size, and the ratio represents a readily-interpretable aspect of body shape or conformation. The MTA technique can thus be generalized, for example to produce easily-interpreted graphical representations of selected skull parameters (Figures 12–15).

Limb-bone MTAs (Figures 16–20) efficiently separate dogs of different conformation and are especially useful because archaeological dog limb bones often survive in large numbers (for example Ayton, 2011). We use Harcourt’s (1974) stoutness index (with MSD as numerator) for humerus, radius, and femur, but not for tibias or ulnas because the point selected for measurement of MSD on a bone with a continuously tapering shaft seems rather arbitrary. Therefore, for tibias we use a “stoutness index” (calculated as width across the proximal articular surface, Bp × 100) / bone length) (Figure 17), while for ulnas we use the breadth across the base of the humeral articulation (Bpc × 100/ bone length) (Figure 20). Utilizing a different numerator in calculating the tibia and ulna ratios yields different vertical scales, but the overall picture as shown by the MTA’s is consistent with results for humerus, radius, and femur (Figures 16–20).

Because the number of parameters measured on postcranial bones was small and were known beforehand to be diagnostic, MTA’s were constructed without the use of PCA in the analyses of limb bones (Figures 16–20 and see visual key, Figure 21). The very large dataset of modern domestic dogs not included in PCA's has, however, been included in our MTA's whenever it was useful in providing an overall sense of morphometric range.

PCA (Principal Component Analysis): All measurements were converted to their base-10 logarithms prior to analysis, to make the allometric relationships between dimensions linear (Gould, 1966), to make all dimensions of approximately equal statistical weight (their means and ranges are of the same order of magnitude), and to reduce some biases common in biological data (positive skew, and small dimensions being inherently less variable than large) (Jolicouer, 1963; Jolliffe, 2002: 24). Modern domestic dogs were omitted from PCA to give the remaining wild-type canid samples comparable statistical weight.

Herein, we significantly extend the multivariate analysis of canid bone measurements pioneered by Morey (1992, 2010) and Baxter and colleagues. For reasons outlined below, we prefer PCA to the DFA (discriminant function) or CVA (canonical variate) techniques used by some previous authors. PCA is not a technique for discriminating groups, but for visualising trends and clusters in multivariate data (Jolliffe, 2002: 1). A series of mutually orthogonal axes (the principal components, or PCs), with their origins at the data's multivariate mean, are fitted sequentially to account for as much as possible of the variability left unexplained by all previously-defined PCs (Jolliffe, 2002). The contribution of each of the original variables (here, the log-transformed dimensions) to each PC is calculated using "loadings" (Table 1) determined by the axis-fitting calculations (see Jolliffe, 2002 for an explanation of the mathematics employed). Geometrically, PCA can be thought of as re-centering the origin of the original variable axes (x, y, z, ...) to the center of the "cloud" of data-points (at its multivariate mean), and then rotating the Cartesian axes to the axes of the ellipsoid which best approximates the "data-cloud" (PC1, PC2, PC3, ...) (Hammer & Harper, 2006: 83). When the first two or three PC's account for most of the variation, the data-cloud can be usefully displayed in one or two two-dimensional plots using PC's as axes (see figure 4.5 of Hammer & Harper, 2006).

The 95% confidence ellipses included on our plots help to visualize any contrast in overall trend between the samples; their long axes are the line of best correlation between the two PC-scores for a sample, and their widths are a measure of the poorness of fit to that correlation (Jolliffe, 2002). The plots are biplots because they include "rays" for each variable defined by the PC loadings for that variable (Jolliffe, 2002: 90). The rays are useful for interpretation: their lengths show the relative amount of variation accounted for by each variable; they graphically show the contrast between variables for particular PC-scores (projections onto a PC-axis that are positive show they increase that PC-score, while negative projections show they reduce it); and variables that correlate closely have rays that lie close together (Jolliffe, 2002: 92).

We chose PCA over DFA or CVA for this study primarily because problems of functional interpretation are fewer and inferring causes for variation is simpler. PCA differs from DFA (a method for defining a formula that distinguishes two pre-defined groups), and canonical variate analysis (the extension of DFA used to distinguish more than two groups). Confusingly, CVA is sometimes also called DFA (as for example in Phillips *et al*., 2009).

0	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	PC	Eigenvalue	% variance
BL	0.2908	0.2782	0.1213	0.023	-0.06584	-0.01941	-0.06443	-0.2068	0.4532	0.7522	1	0.101366	93.889
BP	0.303	0.2723	0.1325	-0.0518	-0.01066	0.1877	-0.0833	-0.06591	0.6113	-0.6273	2	0.00317995	2.9454
B	0.2605	0.3604	0.4818	-0.04089	0.1314	0.4821	0.1383	0.3516	-0.4135	0.07113	3	0.000930978	0.86231
P4	0.2952	-0.1861	-0.3345	0.6492	0.5379	0.2157	-0.04257	0.06789	0.04118	0.03159	4	0.000666405	0.61725
SW	0.3569	-0.2668	-0.00189	-0.5317	0.4535	-0.02885	0.3444	-0.4287	-0.0984	-0.01287	5	0.000608249	0.56338
ZW	0.3063	-0.03318	0.2254	-0.1187	0.2557	-0.5542	-0.6197	0.2603	-0.1193	-0.04047	6	0.000433925	0.40192
RA	0.302	0.275	-0.04772	0.269	-0.1489	-0.5806	0.6023	0.134	-0.08007	-0.1103	7	0.000320207	0.29659
CP	0.3733	0.191	-0.7154	-0.3346	-0.2741	0.1605	-0.1582	0.2179	-0.1607	0.03392	8	0.000258853	0.23976
PW	0.3334	-0.705	0.2018	-0.00363	-0.3919	0.104	0.1325	0.3596	0.1888	0.06425	9	0.000150888	0.13976
PL	0.3251	-0.0499	0.1343	0.3044	-0.4088	0.06252	-0.2448	-0.6151	-0.3956	-0.1241	10	4.85E-05	0.044908

TABLE 1

Parameter loadings for PC analyses. The Lüps basicranial measurements for skulls (BL, BP, B) account for the most variable and the greatest discriminatory power, as does condyle with (CW) for jaw rami.

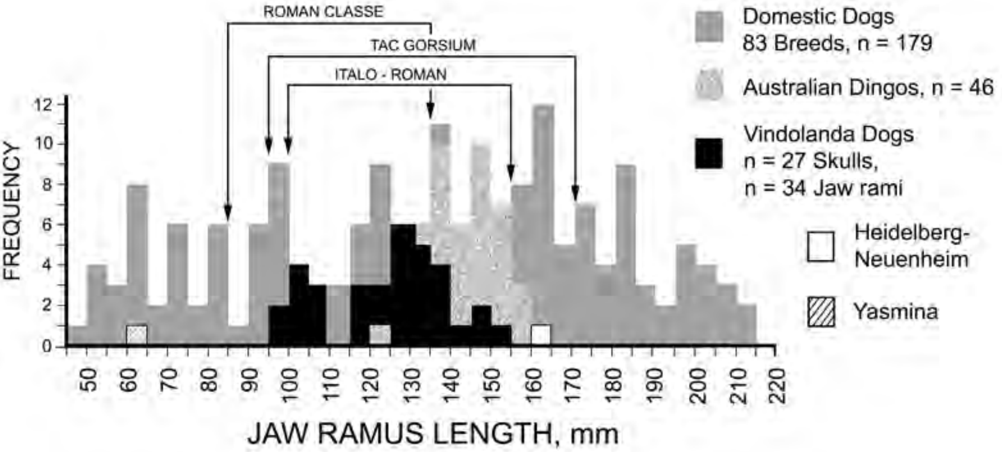

FIGURE 5

Raw size of skulls. Tac Gorsium data from Bökönyi (1984); Roman Italy from DeGrossi-Mazzorin & Tagliacozzo (2000); Classe from Farello (1995); Heidelberg–Neuenheim from Luttschwager (1965); Yasmina from MacKinnon & Belanger (2002).

In PCA the data for all the groups are pooled, the loadings for the variables are calculated to account for as much variability as possible regardless of group membership, and the analyst is left to assess the nature of the variability which might distinguish groups. In CVA the pre-defined groups are kept separate, the loadings for each variable on each canonical variate function (the functions are used as the axes in CVA plots) are calculated to maximize the differences in variability between the pre-defined groups compared to the variability within those groups (Reyment & Savazzi, 1999: 174), and the analyst uses the CV functions to assign individuals to the most appropriate group. This re-scaling to maximize group differences can mean that novel groups go unrecognised, the values of the loadings can be quite different even if the samples used to define the groups are similar, and the interpretation of the functions are obscure (Reyment & Savazzi, 1999: 173, 204).

Because dog morphotypology does not have the same basis as the assignment of breed identity, it is not appropriate on the basis of morphometric analysis to suggest that any ancient dog "belongs to" any modern breed. The present study focuses on differentiating the Vindolanda dog population *as a whole* from other canid groups. A range of dog morphotypes is certainly present in the Vindolanda dog collection; their particular characteristics and methods for distinguishing them are the subject of forthcoming papers (Bennett & Timm, in prep.).

RESULTS

Frequency of Skeletal Elements

A total of 520 bones of domestic dogs have been recovered from excavations carried out between 1960 and 2014 at Vindolanda (2.6% of all bones recovered). The collection includes 39 partial to nearly complete skulls (due to breakage, not every measurement could be taken on every skull). Six of the skulls have at least one associated jaw ramus; five have associated postcranial elements. There are 59 jaw rami, of which 9 (15%) are juvenile with evidence of erupting teeth. The total Vindolanda collection comprises a maximum number of 317 individuals distributed over a stratigraphic range of approximately 350 years [detailed stratigraphic analysis appears in Part II (Bennett & Timm, 2016)].

Raw Size Distribution

That more than one size-class of dog existed at Vindolanda has previously been demonstrated through study of pawprints impressed in ceramic building materials (Higgs, 2001; Bennett, 2012). In Figure 4, Vindolanda skulls complete enough to obtain a measurement of basal length are compared to a sample of 83 domestic dog breeds and to three

FIGURE 6

Series of humeri (to scale) demonstrating size range of Vindolanda dogs, with comparisons to wolf, Australian dingo, and seven modern domestic breeds. A, Dachshund LACM 30598, 74 mm; B, Pomeranian KU 51-Z, 78 mm; C, Vindolanda VH-102 29712, 92 mm (reversed); D Vindolanda E93-112 3190, 94 mm (estimated); E, Vindolanda V06-54A 5832, 96 mm (reversed); F, Scotch Terrier LACM 30541, 99 mm; G, Vindolanda V02-17016 (SF 8659), 120 mm; H, Cocker Spaniel UNSM ZM-15573, 136 mm; I, Vindolanda V14-33B 29151, 150 mm; J, Chow-chow LACM 30423, 151 mm; K, Vindolanda VI-82 10132, 153 mm; L, Dingo ANM M-7386, 164 mm; M, Greyhound UNSM ZM-14252, 172 mm; N, Vindolanda VI-24 10129, 179 mm; O, Vindolanda V04A 996, 188 mm (reversed); P, Vindolanda V1997-19 16742, 190 mm; Q, Great Pyrenees, KU 165573, 207 mm; R, Wolf UNSM-ZM 28814, 242 mm. Institutional abbreviations: ANM = Australian National Museum; KU = The University of Kansas; LACM = Los Angeles County Museum of Natural History; UNSM ZM = University of Nebraska Zoological Museum.

types of feral dogs. Most of the Vindolanda skulls range from 125–160 mm in basal length. The median size of modern feral dog skulls equals the size of the largest Vindolanda skulls, while the smallest modern feral dog skulls lie near the median size for Vindolanda skulls.

Dog jaw rami are far more frequently found on archaeological sites than skulls. As with the skulls, the Vindolanda jaws fall near the center of the very wide range represented by modern domestic dogs (Figure 5), and the median size of the Vindolanda dogs is smaller than the median size for Australian dingoes. The size range of Vindolanda dogs is less than that for Tac Gorsium site in Hungary (Bökönyi, 1984) and much less than Heidelberg–Neuenheim site in Germany (Luttschwager, 1965). The late-Roman site at Classe in Italy (Farello, 1995) contains some jaws significantly smaller than any so far found at Vindolanda. Baxter (2010 a, b) has reported small Romano–British dogs but the Yasmina skull (MacKinnon & Belanger, 2002) is smaller than any so far known from Roman Britain.

Baxter (2002, 2010a, 2010b) was the first to clearly distinguish between dwarfs (chondrodystrophic dogs; see Koch *et al*., 2003; Parker *et al.*, 2009), which have limb bones that are short, thick, broadened at both ends, and often twisted, vs. miniatures (whose smallness is due to pituitary or thyroid dysfunction; Crockford, 2000a; Sutter *et al*., 2007; Boyko *et al.*, 2010). The limb bones of miniatures, though small, are normally or almost normally proportioned and straight. Dwarf dogs are very common on Romano–British sites, with numerous finds of their distinctive limb bones. Baxter (2010b) points out that we know less about the miniatures; to date the only nearly-complete skeletons that have been published come from Yasmina (MacKinnon & Belanger, 2002) and Heidelberg–Neuenheim (Luttschwager, 1965). In Roman Britain, there appear to have been at least two different types of miniature dog, the smaller the size of a Chihuahua, Pomeranian, or Maltese (about 25–30 cm shoulder height), the larger about the size of a Miniature Poodle (around 30–35 cm shoulder height) (Baxter, 2010a, b).

The range in Vindolanda limb bone lengths (Figures 6–8) parallels the range in skull and jaw sizes. The tallest are shorter than small wolves, while the shortest are taller than some of the smallest modern dogs and also taller than Roman-era dogs from Neidelberg–Neuenheim (Luttschwager, 1965) or Yasmina (MacKinnon & Belanger, 2002). Neither pawprints in tile (Bennett, 2012) nor cranial material indicates the presence of the smallest form at Vindolanda, but a few small tibias and femurs (Figure 8A, B) are as small as the smallest Romano–British dogs reported by Harcourt (1974), Baxter (2002, 2010a, b) and Ayton (2011).

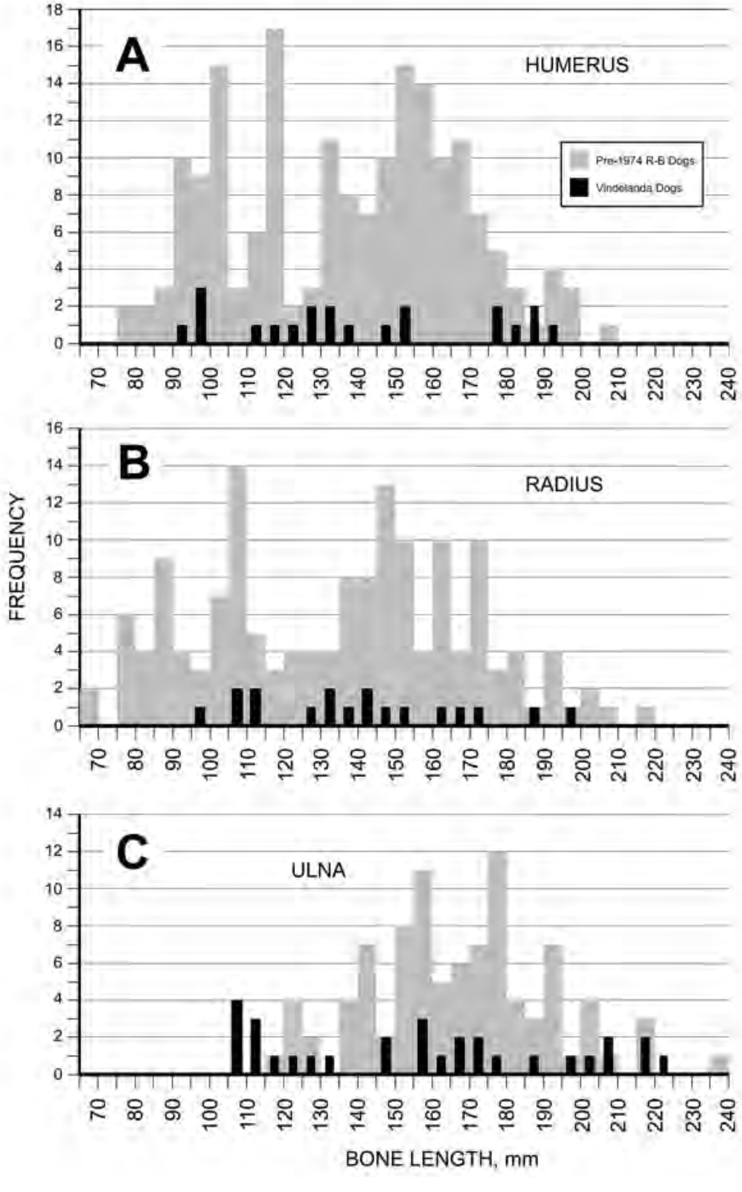

FIGURE 7

Raw size of long bones of the forelimb: humerus (A), radius (B), ulna (C).

Results of Morphometric Analysis

Cranial Index (Figure 9): The range represented by Vindolanda cranial and limb bone indexes is much less than those pertaining to domestic dogs (limb bone indexes are represented on the "y" axis in our MTA analyses, Figures 12–20). The range of skull indexes equals that of dingoes. Snout widths of Vindolanda dogs are greater, while snout length is less. Ratios describe conformation, so that overall it appears that the inhabitants of Vindolanda preferred dogs with broad heads, broad snouts, and muzzles proportionally somewhat shorter than those of dingoes.

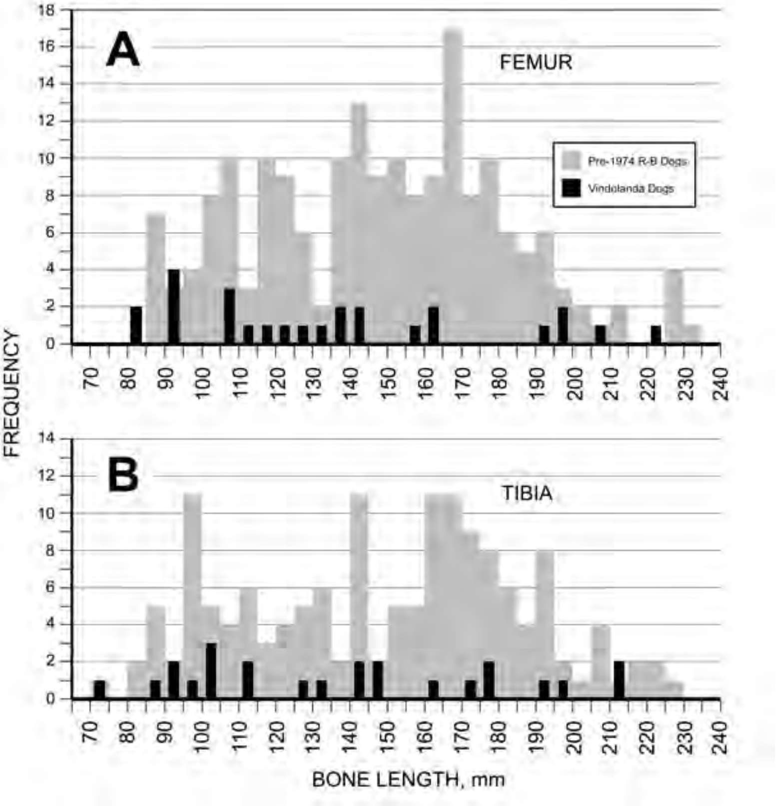

FIGURE 8
Raw size of long bones of the hind limb: femur (A), tibia (B).

Principal Components Analysis (PCA): The first principal component of the PCA on the four jaw parameters accounts for the great majority of the variation in the data (96.6%), and all the loadings are positive (all the biplot rays on Figure 10A are positive for PC1), making PC1 a rough allometric size measure for these canid types. Mandible depth (DP) is a good proxy for size, having a significant loading for PC1 but near-zero loading for PC2. The biplot shows foxes have the smallest jaws, dingoes are about average, wolves the largest, and Vindolanda dogs have a range of jaw sizes much greater than any other canid type, suggesting that Vindolanda dogs underwent greater directional selection than expected from natural environmental forces.

Components PC2 and PC3 accounted for comparable amounts of the remaining variation (1.6% and 1.1%, respectively). The biplot of PC2 and PC3 (Figure 10B) shows a considerable contrast between jaw length (TL) and condyle size (CW) (their biplot rays point in nearly opposite directions). The average positions for the canid types (the centers of their 95% confidence ellipses) were reasonably well-separated along this "axis of contrast", even the two types of wolf (which were not distinguished on Figure 10A). A jaw "shape" variation that contrasts between canid types is therefore likely to be expressed by a ratio of CW/TL. Since size is principally related to jaw depth, we use DP in an MTA plot with this ratio to discriminate canid types (Figure 12).

The first principal component of the PCA on 10 skull parameters accounts for the great majority of the variation (93.7%), and all the loadings are positive (all the biplot rays on Figure 11A are positive for PC1), making PC1 a rough allometric skull-size measure for these canid types generally. Zygomatic width (ZW) and palate length (PL) are the main measures of size, having significant loadings for PC1 but near-zero loadings for PC2; carnassial length (P4) might also be a workable

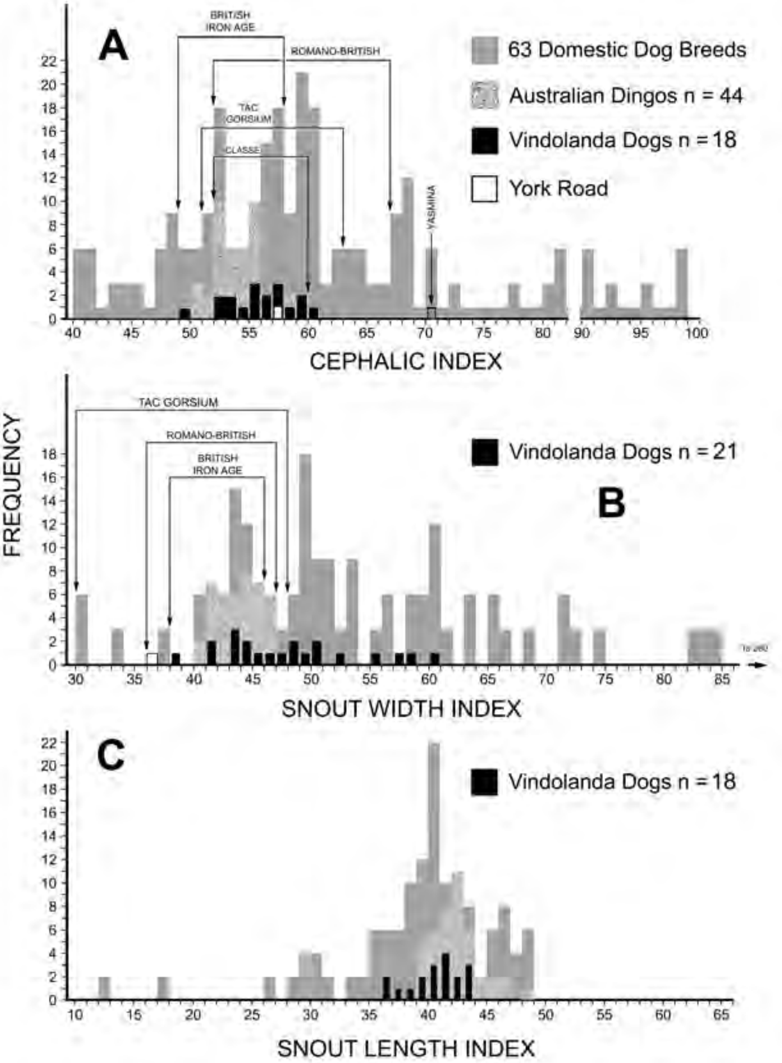

FIGURE 9

Harcourt's (1974) skull indexes applied to a sample of modern domestic dogs, Australian dingoes, the Vindolanda dogs, and several European dog-producing sites of Roman and Iron Age date. (A) Cephalic index, (B) Snout width index, (C) Snout length index. British Iron Age and Romano–British ranges from Harcourt (1974); Tac Gorsium (Bökönyi, 1984), Classe (Farello, 1995); York Road (Baxter, 2002).

general size measure, although its PC2 loading was somewhat larger. The biplot (Figure 11A) is similar to that for the jaws (Figure 10A): foxes are small-skulled, dingoes about average, wolves large, and Vindolanda dogs much more morphologically diverse than natural wild-type canids.

Component 2 accounted for considerably more of the remaining variation (2.9% of the total) than PC3 (0.9%); it is possible that PC3 principally represents natural variation (differences in skull size and shape expected between twins, for example) or measurement error (Figure 11B). The loadings of PC2 tend to be positive for parameters of the back of the skull (B, BP, RA) and negative for mouth parameters (PW, SW, perhaps P4) suggesting that brain-case shape contrasts with mouth shape. The conclusion that the fore-part and hind-part of the skull are fairly free to grow in different ways within domestic dogs (Drake & Klingenberg, 2010) may thus also be true for other canids.

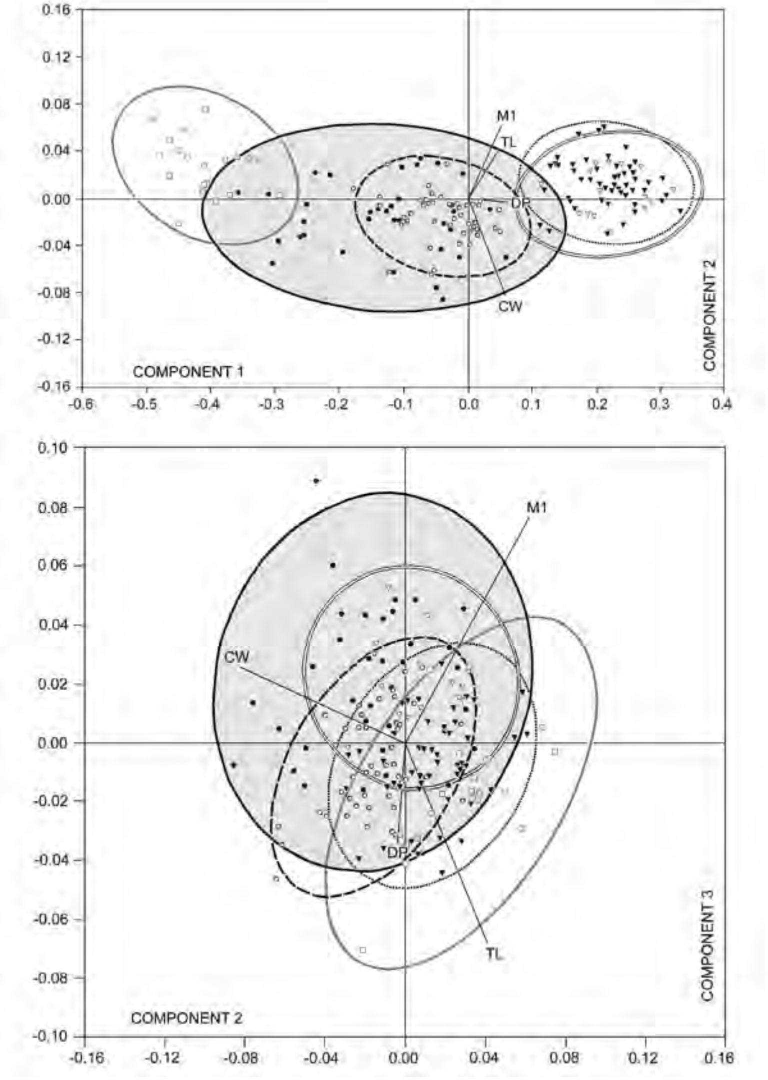

FIGURE 10

Principal component (PC) plots for jaw rami. Ellipses represent 95% confidence. See Figure 1 for measurement abbreviations.

The biplot of PC2 and PC3 (Figure 11B) shows a close relationship between palate width (PW) and snout width (SW); the greater loading of PW suggests that palate length tends to increase much faster than snout width. These two dimensions contrast with braincase dimensions, especially spine-articulation width (RA) (their biplot rays point in nearly opposite directions). The average positions for the canid types (the centers of their 95% confidence ellipses) are reasonably well-separated along this "axis of contrast". A skull "shape" variation that contrasts between canid types is therefore likely to be expressed by a ratio of RA/PW. Since palate length is the better preserved of the two comparable measures of "size", we used PL in an MTA plot with this ratio to discriminate canids with differing relative neck strength (Figure 13). The considerable contrast in allometry between SW and PW suggests that mouth shape may also alter significantly with mouth size; a ratio expressing the "pointedness" of the snout (SW/PW) was therefore plotted with mouth size (PL) as an MTA (Figure 14).

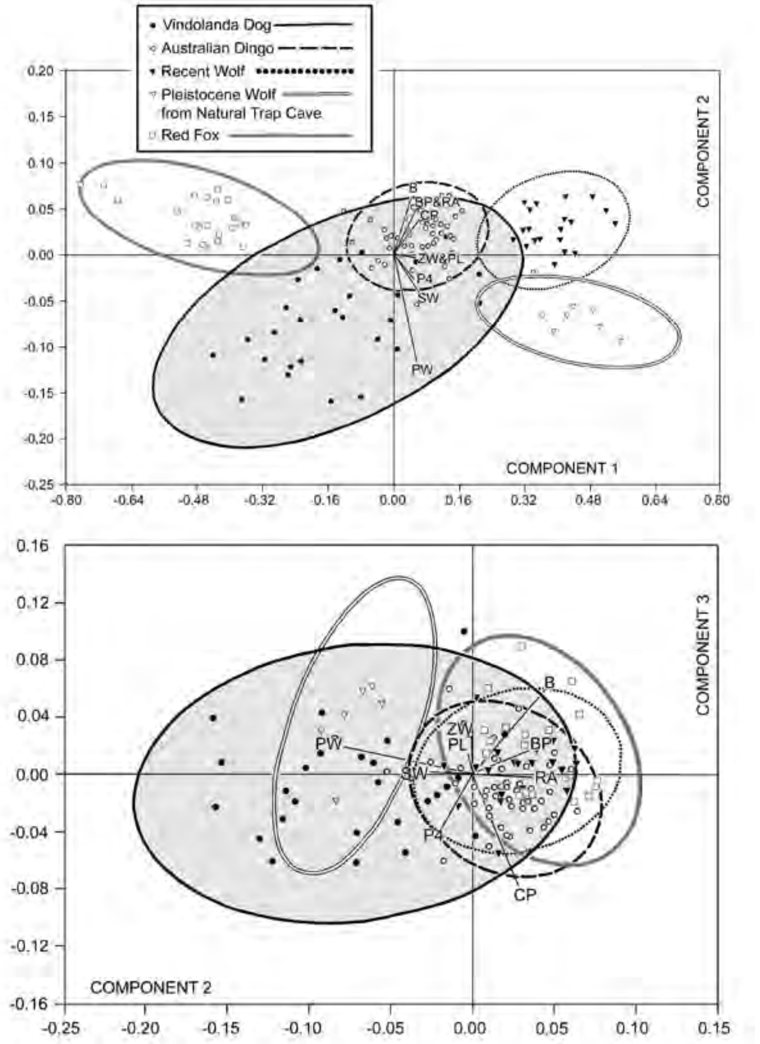

FIGURE 11

Principal component analysis (PCA) plots for skulls, based on 10 measured parameters. Ellipses represent 95% confidence. See Figure 1 for measurement abbreviations.

De Grossi Mazzorin–Tagliacozzo Analysis (MTA): The bones of wolves are clearly differentiated by MTA from those of dogs, and the analysis suggests that wolf bones are generally rare or absent from Roman-era archaeological sites across Europe. Limb elements of foxes, however, are more problematic. The postcranial elements of dogs most likely to be confused with red fox are the tibia and femur; indeed, there is no guarantee that some bones reported in the literature as dogs, and treated as such in our analyses, do not actually belong to foxes (particularly likely in the case of Romano–British tibias, Figure 17). Forelimb elements overlap much less (Figures 18–20). Limb bones of foxes can be differentiated on the basis of detailed morphology from those of small dogs, and in a forthcoming paper we contrast fox postcranials from Vindolanda with small dogs of modern times and the Roman era.

MTA plots make it clear that the Vindolanda dog population, like Roman-era collections from other localities, is much more morphologically

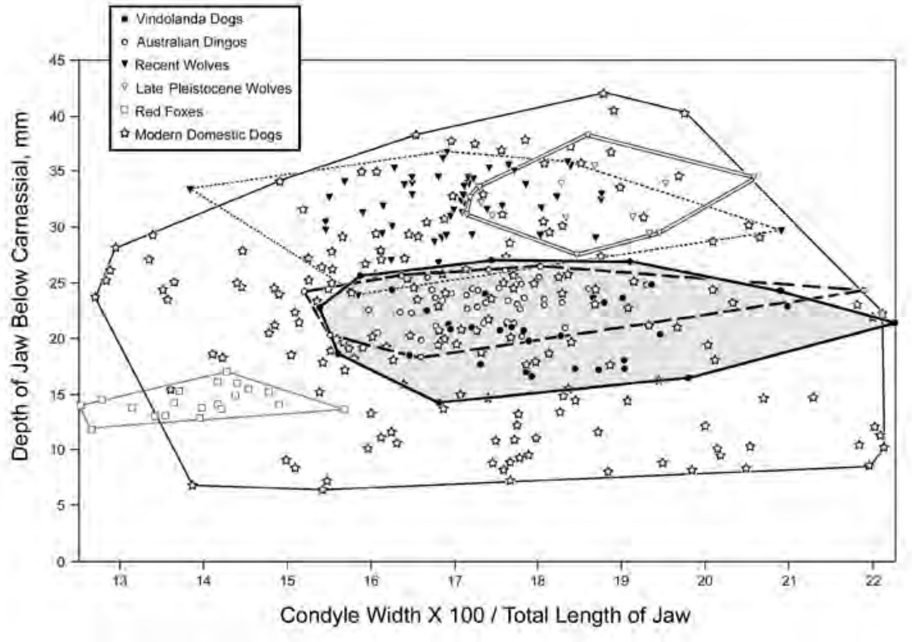

FIGURE 12

MTA plot for jaw grip strength. In this and subsequent figures, the Vindolanda hull is shaded gray for added clarity. Abbreviations as in Figure 2.

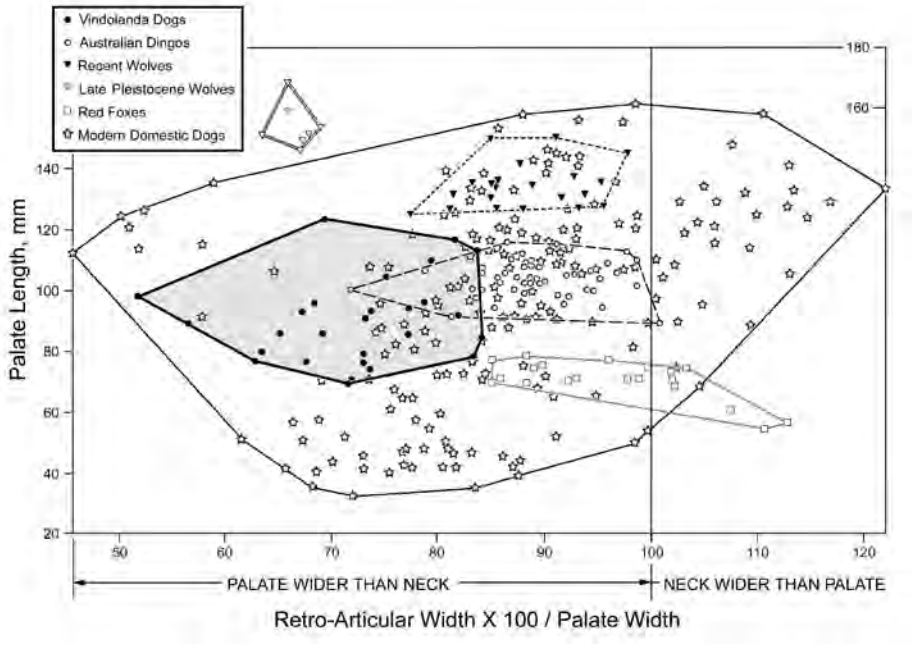

FIGURE 13

MTA plot for relative neck strength. Abbreviations as in Figure 2; symbol key as in Figure 12.

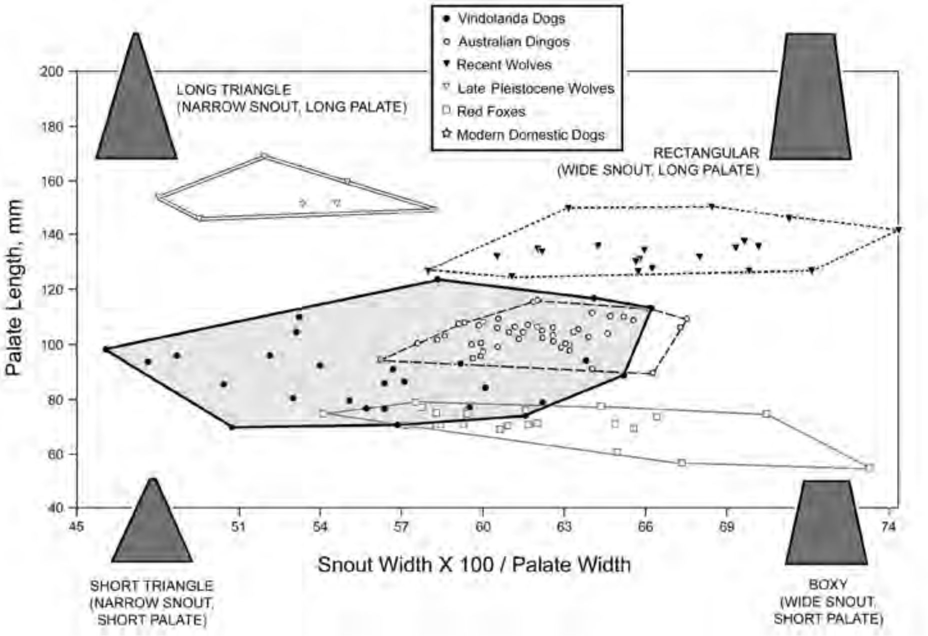

FIGURE 14

MTA plot for mouth shape. Abbreviations as in Figure 1; symbol key as in Figure 12.

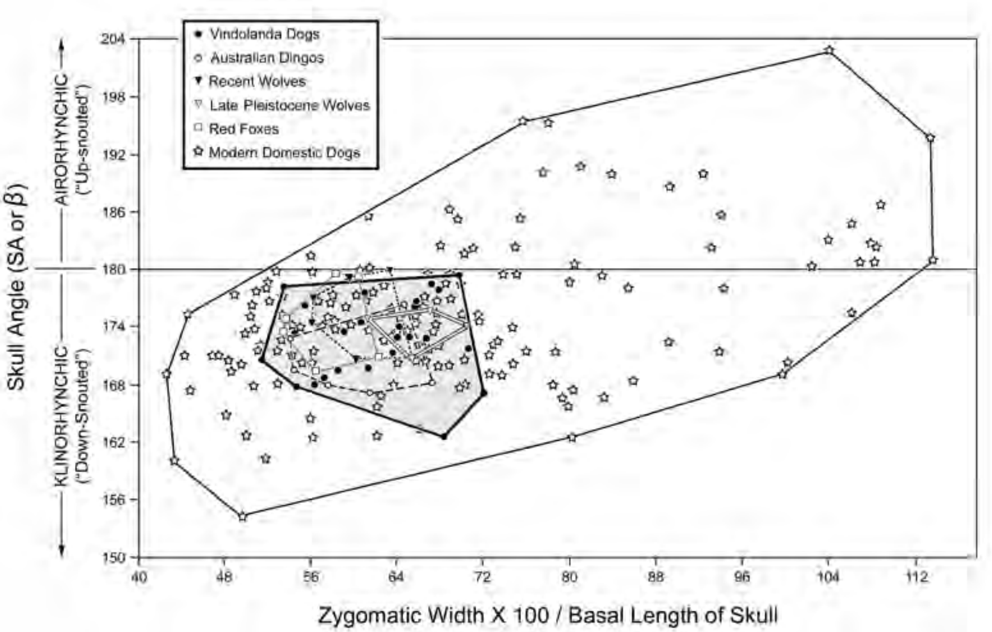

FIGURE 15

MTA plot for snout declination (SA or β), showing that all wild, feral, and ancient canids studied are klinorhynchic. The many airorhynchic modern dogs (stars above the 180° line) belong to such breeds as Pugs, Boston Terriers, English Bulldogs, Pekingese, Pomeranians, and Lhasa Apso.

diverse than the putative "primitive" dog morphotype represented by the Australian dingo. As predicted by Harcourt's (1974) work, we find that Romano–British dogs are also much more diverse than those of the British Neolithic, but interestingly there is no conformational overlap between "primitive" Australian Dingoes and our small sample of Neolithic dogs.

The Vindolanda population does not cover as great a morphologic range as that of the sample of modern domestic dogs included in this study, nor does the area of the Vindolanda hull in Figures 16–21 equal that of other Romano–British collections compared. The very large sample from Tac Gorsium equals or even (in presenting very stout radii, humeri, and femurs for dogs of medium height) exceeds the range for our sample of domestic dogs.

Snout Declination: Nussbaumer (1982) invented the measurement technique and gives valuable comparative data. Snout declination is measured

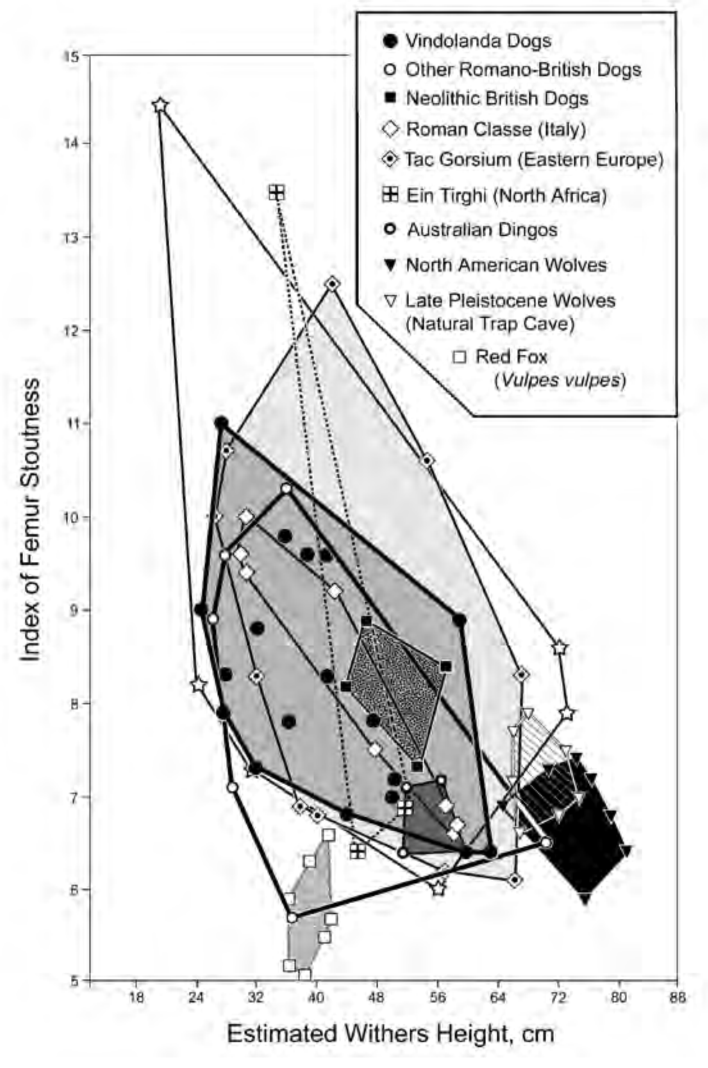

FIGURE 16

MTA plot for femurs. Index of femur stoutness computed as GL × 100/msd (see Figure 2 for anatomical abbreviation). Tac Gorsium data from Bökönyi (1984); Ein Tirghi (Churcher, 1963); Roman Classe (Farello, 1995); British dogs of the Neolithic (Burleigh *et al*., 1977). Romano–British data are all post-1974, reported by Baxter (2002, 2010a, b, and pers. comm.), Baxter & Nussbaumer (2009), Grimm (2007), and Ayton (2011). In this and next several figures, only extreme data points that define the various hulls are shown, except Vindolanda data points which are plotted as black dots. Stars = recent domestic dogs.

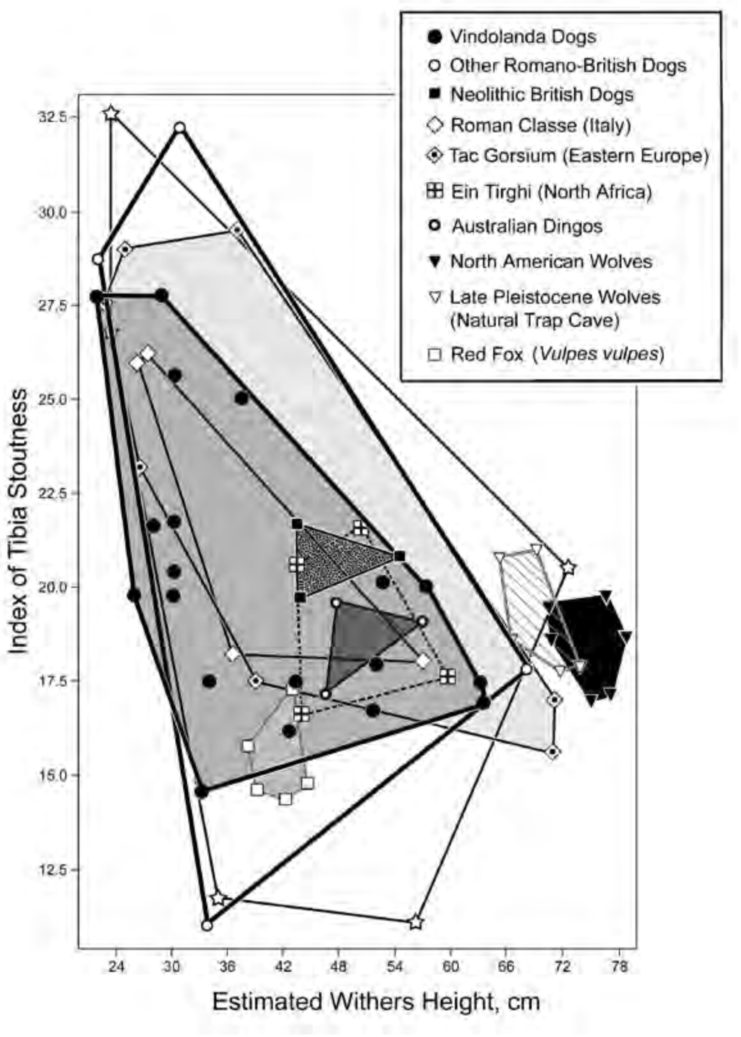

FIGURE 17

MTA plot for tibias. Vindolanda dogs are compared with several British and European continental dog-producing sites of Roman and Neolithic date. Index of tibia stoutness computed as GL × 100/Bp. Sources as in Figure 17; key to symbols as in Figure 16; anatomical abbreviations Figure 2.

by applying a carpenter's contour-gauge along the midline basicranium and caudal palate, transferring the resulting shape to paper, then using Photoshop tools to measure the angular difference between the basicranium and palate. Results are accurate to about +/- 1°. All Vindolanda dogs are klinorhynchic ("down-snouted"), with a few falling into the 0 to 10° range. The MTA plot (Figure 15) of cranial index vs. SA (called "β" by Nussbaumer, 1982 and Baxter & Nussbaumer, 2009) shows that the range in Vindolanda dog skulls is greater than in modern wolves, Pleistocene wolves, red foxes, or Australian dingoes; and that the range in modern dogs is in turn much greater than in the Vindolanda collection of skulls. The most klinorhynchic modern dogs are certain types of terriers, i.e. Bull, Scotch, and Bedlington, which can be as much as 26° "down-snouted". The total range of klinorhynchy among Vindolanda dogs is 0.8 to 17.5° "down", whereas the total range in the sample of modern domestic dogs included in our study is from 23° airorhynchic ("up-snouted") to 26° "down-snouted".

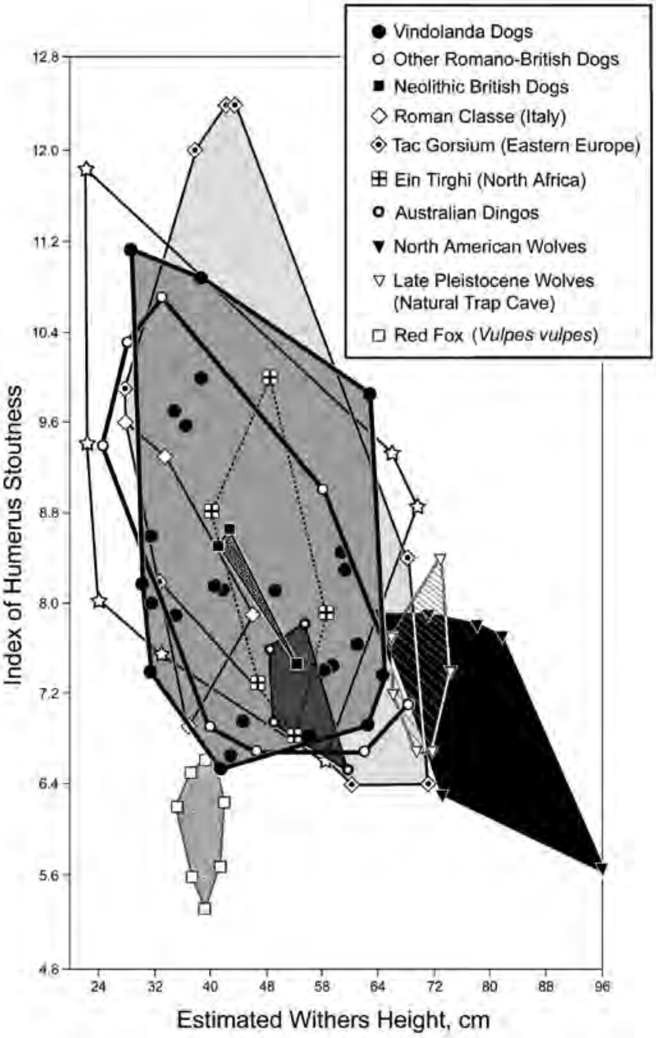

FIGURE 18

MTA plot for humeri. Vindolanda dogs are compared with several British and European continental dog-producing sites of Roman and Neolithic date. Index of humerus stoutness computed as GL × 100/msd. Sources as in Figure 17. Key to symbols as in Figure 16; anatomical abbreviations Figure 2.

DISCUSSION

The Study of Variability in Roman-Era Dogs

Several reports document dog diversity from Roman-era sites on the European continent and North Africa (Churcher, 1963; Luttschwager, 1965; Bökönyi, 1984; Farello, 1995; Bartosiewicz, 2000; De Grossi Mazzorin & Tagliacozzo, 2000; MacKinnon & Belanger, 2002). Using a sample of 1200 long bones, 154 skulls and 325 mandibles from 80 sites in Ireland and Britain ranging in age from Mesolithic to post-Roman, Harcourt (1974) demonstrated a dramatic increase in the range of British dog types—especially the advent of small dogs standing less than 35 cm high—coinciding approximately with the beginning of the Roman occupation of the British mainland. With more refined dating, Clark (1995) suggested that small dogs first appear in the British archaeological record somewhat earlier, in the late Iron Age. Our

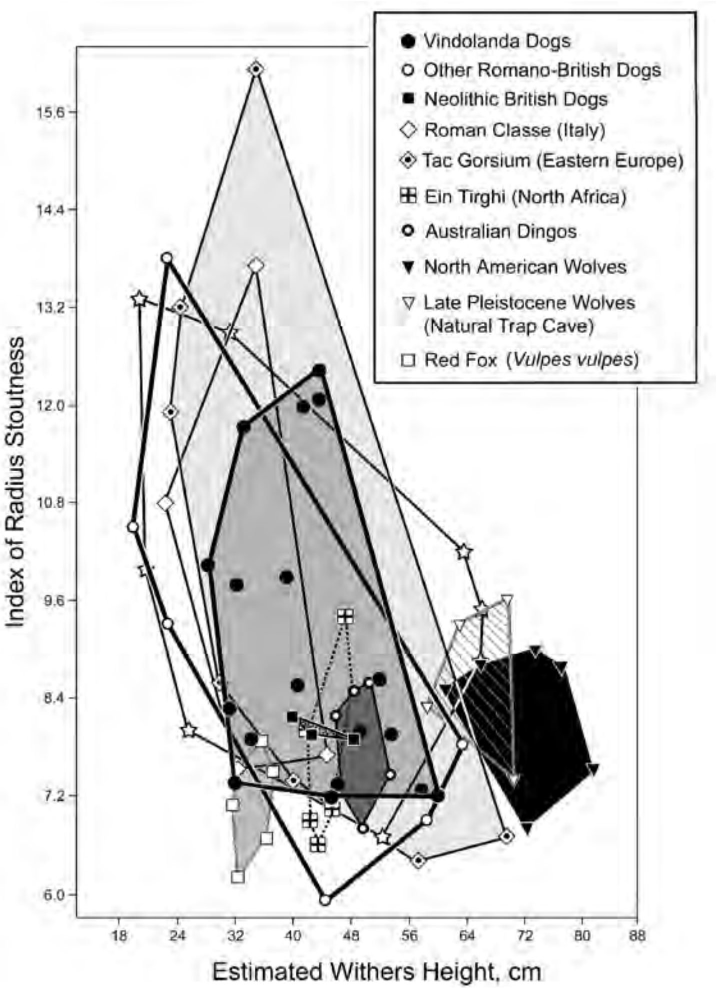

FIGURE 19

MTA plot for radii. Vindolanda dogs are compared with several British and European continental dog-producing sites of Roman and Neolithic date. Index of radius stoutness computed as GL × 100/msd. Sources and key to symbols as in Figure 16; anatomical abbreviations Figure 2.

results confirm that deliberate selection for phenotypes different from a putative dingo-like ancestor began no later than the Neolithic in Britain.

Harcourt's (1974) indexing technique proved useful in differentiating dog types, especially cranial length vs. zygomatic breadth (cephalic index), snout length vs. skull length (snout length index), and muzzle breadth vs. snout length (snout width index) (Figures 9A, B, C). His work primarily relies upon these factors plus raw size for differentiation. Harcourt (1974) also developed multiplication factors for the estimation of dog stature ("shoulder" or "withers" height) from length measurements of isolated limb bones. Because they were created from a population of dogs of normal ("eumorphic") build, these factors are most accurate for dogs of medium height but tend to overestimate withers height in short-statured dogs, especially the bandy-legged "brachymel" dwarfs such as modern Dachshunds and Corgis (Baxter, 2002). Harcourt (1974) also introduced the very useful concept of relative limb stoutness, the ratio of minimum shaft diameter to length.

De Grossi Mazzorin & Tagliacozzo (2000) built upon Harcourt's work by creating bivariate plots of limb stoutness index against projected withers

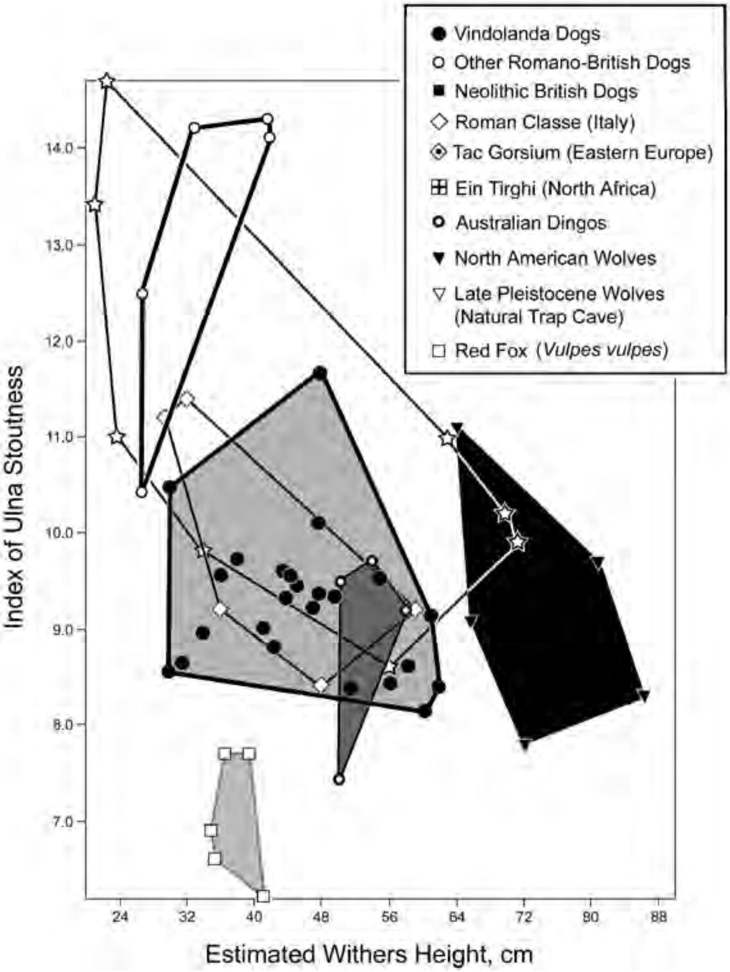

FIGURE 20

MTA plot for ulnas. Because Bpc is rarely reported, Vindolanda dogs are compared only with dwarf and miniature Romano–British specimens reported by Baxter (2002, 2010a, b, and pers. comm.); the hulls enclosing Baxter's specimens and those from Vindolanda are disjoint because very small dogs are rare at Vindolanda. Pleistocene wolves are omitted because no ulnas were available. Ulna stoutness computed as GL × 100/Bpc. Key to symbols as in Figure 16; anatomical abbreviations Figure 2.

height ("MT" analyses or MTA's). The resulting charts are easy to interpret and allow quick visual differentiation of long-bone material pertaining to dwarf, miniature, normal, gracile, and massive dogs (Figures 16–21). MTA shifts the emphasis away from heavy reliance upon skulls and jaws and is useful because archaeological cranial material is sometimes unavailable and often fragmentary, whereas limb bones often survive whole and in large numbers (Churcher, 1963; Bökönyi, 1984; Johnstone & Albarella, 2002; Grimm, 2007; Ayton, 2011).

Morphometric Techniques for Distinguishing Canids

This study responds to numerous pleas in recent literature (Clark, 1995; Baxter, 2000; Clutton-Brock, 2000; Cram, 2000; Crockford, 2000a, b) for new, practical approaches to the differentiation of canids. Multivariate analysis is not new –Clutton-Brock *et al*. (1976) applied it to the problem of differentiating dogs in the British archaeological record, and Morey (1992) used it for American ones– but it was otherwise essentially ignored in the study of archaeological dogs until studies by Baxter and

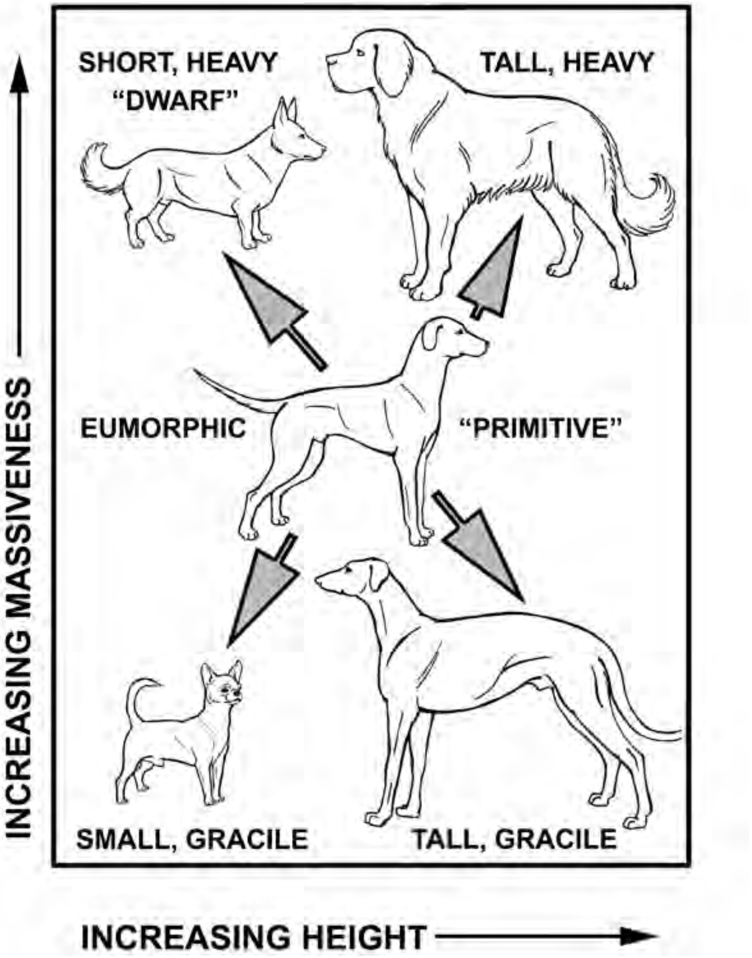

FIGURE 21

Visual key for the interpretation of Figures 15–19.

colleagues (Baxter & Nussbaumer, 2009; Phillips *et al*., 2009). Possibly because the results it produces are easier to interpret, Harcourt's (1974) indexing technique by contrast became standard.

Although less sophisticated than multivariate analysis, indexes remain useful in differentiating canids. In some cases –especially where the parameters which make up the index are likely to reflect different selective pressures and thus different rates of growth– individual linear measurements work better than indexes. For example, Clutton-Brock (1969) suggested that the length of the superior carnassial in wolves is typically greater than the combined length of the superior M2 and M3, the reverse being characteristic of domestic dogs. Our measurements demonstrate this to be true 65% of the time, with modern domestic dogs, Australian dingoes, modern wolves, and some of the Vindolanda dogs all presenting exceptions. However, PCA led us to realize that P4 length alone correctly identifies dog vs. wolf over 90% of the time (Figure 11; i.e., P4 length > 22 mm likely indicates a wolf).

A completely different approach has been taken by Nussbaumer (1982). His technique for measuring klinorhynchy–airorhynchy in dog skulls is both novel and useful, and Baxter & Nussbaumer (2009) applied it to a dog from Iron Age Britain. We find airorhynchy ("up-snoutedness") to be an excellent character which occurs only in certain types of modern dogs (Figure 15). No wild or feral dog we have so far examined is airorhynchic, although some are essentially straight-headed with skull angle (SA or “β”) = 180°. Low degrees of klinorhynchy (180 to 170°, i.e. from 0° to 10° of “down-snoutedness”) are characteristic of both wolves and certain breeds of large dog, for example German Shepherd/Alsatian, Mastiff, Newfoundland, Greenland Dog, and Wolfhound. Some small modern breeds which are “incipiently” or occasionally airorhynchic, for example Pekingese, Pug, and Spitz, also record in the 0° to 10° range. Airorhynchy does not, however, correlate merely with smallness; there are many breeds of small dog that are moderately to strongly klinorhynchic, for example Dachshund, Mexican Hairless, and miniature and toy Poodles (and see Nussbaumer, 1982). All Vindolanda dogs are klinorhynchic.

Like Harcourt’s (1974) technique, De Grossi-Mazzorin & Tagliacozzo’s (2000) innovative (MTA) method relies upon ratios but contrasts the ratio with a linear measurement. In contrast to PCA or DFA, MTA presents few interpretive difficulties, but especially when many parameters are measured it offers no guidance as to which should be compared. The MTA technique becomes more useful after PCA identifies which parameters have the greatest discriminatory power.

The PCA’s and MTA’s employed in this study demonstrate that the population of dogs from Roman Vindolanda encompass a far greater range in size and morphology than dogs from earlier archaeological periods. The Vindolanda dogs also far exceed a comparison sample of Australian dingoes, which represent the putative “primitive” morphology achieved by feral, pariah, and village dogs worldwide when they are allowed panmictic access to mates (Morey, 1992; Corbett, 1995; Cruz *et al*., 2008). The sample of dog skulls from Tac Gorsium (Bökönyi, 1984) in turn exceeds the range presented by Vindolanda, especially in containing numerous large dogs, while the Rothwell Haigh collection (Ayton, 2011) contains limb bones of very small “toy” dogs, which likely came from animals with skulls like that of the small dogs from Thistleton (Baxter, 2010a, b), Heidelberg–Neuenheim (Luttschwager, 1965), or Yasmina (MacKinnon & Belanger, 2002). These were lap-dogs, probably unable to survive without specialized human care (MacKinnon & Belanger, 2002). Dogs smaller than 35 cm shoulder height were certainly present at Vindolanda, but the majority had the stout-limbed morphology characteristic of dwarfs rather than the fine, straight limbs of miniatures.

Functional Implications of Morphological Differences

Small dogs, as well as a wide range of dog morphotypes, first appear in Britain in the late Iron Age (Harcourt, 1974; Cark, 1995). This is important, because it implies that the husbandry techniques required for the production and maintenance of phenotypic distinctiveness were not invented by the Romans, but were already widely known. Clark (1995) observes that phenotypic change in domestic dog populations is primarily due to changes in peoples’ attitudes and preferences; Ellis *et al*. (2009) agree and observe that “it is fair to expect that [selective breeding] has not followed the path that natural selection would have prescribed”. Driven by breeder selection, dog skull shape can be quickly altered; Drake & Klingenberg (2008) demonstrate marked change in a sample of skulls of St. Bernards that occurred over a time span of only 120 years. Such changes usually have functional significance; thus, phenotypic differences in the Vindolanda population of dogs compared to other canids are not likely to be due to random “drift” but rather to directional selection.

Stepwise PCA–MTA assists in identifying trends in phenotypic change, and the significance of such studies becomes greater when PCA identifies parameters that not only have discriminatory power but biomechanical significance. Our study highlights several instances of directional selection:

(1) The index of width between the retro–articular processes (RA) vs. palate width (PW). We term this comparison “neck strength” (Figure 13).

(2) The index of snout width (SW) vs. palate length (PL), which we term “mouth shape” (Figure 14).

(3) The index of jaw condyle width (CW) vs. depth of jaw below the carnassial, which describes the robustness of the jaw and is an indicator of grip strength (Figure 12).

(4) Increase of relative stoutness in all limb bones compared to wild canids, Australian dingoes, and Iron Age British dogs (Figures 16–20).

(5) Increase in the range of shoulder (or “withers”) height compared to wild canids, Australian dingoes, and Iron Age British dogs (Figures 6–8, 16–20).

The width between the retro–articular processes on the occiput is a measure of the strength of the attachment of the head to the neck and of the overall strength of the neck (Radinsky, 1981; Ellis *et al.*, 2009). In our MTA analysis (Figure 13), the small sample of Late Pleistocene wolves stands apart. They have long, wide palates –big “maws” (Figure 14)– but necks that are noticeably weaker than modern wolves or many Vindolanda dogs, which may imply that they were primarily scavengers (carcasses don’t wriggle). At the opposite extreme, red foxes are the most likely of the groups studied to have neck attachments wider than their palates, not necessarily because their necks are strong but because their skulls are very narrow. Domestic dogs with RA greater than 100% of PW are of two types: either they have been bred to be narrow-headed (English Collie, Greyhound, Borzoi, Afghan Hound), or they have been bred to have strong necks (German Shepherd/Alsatian, Deerhound, Wolfhound). Narrow-headed domestic breeds can be thought of functionally as fox analogs, but exceptionally broad-necked domestic breeds are a novelty (see Radinsky, 1981). There are many domestic breeds (Shar-Pei, Chow-Chow, English Bulldog, Mastiff, Cane Corso) that have historically been associated with dog-fighting; they fall below the 100% line even though they have strong necks because they also have exceptionally wide palates. The Vindolanda dog population overlaps Australian dingoes and represents development from an ancestral dingo-like morphology, with a definite trend toward proportionally wide palates.

There is more overlap in mouth shape (Figure 14), with some Vindolanda dogs having rather fox-like mouths. The Vindolanda population and the Australian dingo overlap almost completely, so that in this character also the Vindolanda population appears to be a development out of a dingo-like ancestral morphology. Both Late Pleistocene and modern wolves have relatively long heads and plot separately from dogs, but the Natural Trap wolves have less pointed snouts.

The width of the jaw condyle has not often been reported for dogs of the Roman era, but this parameter should be measured along with depth below the carnassial because both have obvious biomechanical significance: robustness in either parameter relates directly to grip strength (Radinsky, 1981). The wider the jaw condyle, the stronger and more stable is the attachment of the jaw to the skull, and the more difficult for large or wriggling prey to dislocate the articulation. At the same time, depth of jaw below the carnassial is a direct measure of the strength of the ramus, analogous to MSD for limb bones. MTA (Figure 12) separates wolves and foxes from dingoes and the Vindolanda dog population, which broadly overlap. Both of the latter trend toward broader condyles on jaws of only moderate stoutness. Overlap between dingoes and the Vindolanda dogs probably represents the primitive condition, but some directional selection is evident in the thinner-jawed Roman-era dogs.

The shoulder height of the dog, as well as the stoutness of its limb bones, strongly affects its locomotor capabilities and its potential utility as a courser, terrier, guard dog, war dog, or fighting dog. While the limb bones of most Vindolanda dogs are no stouter than those of Australian dingoes, 34% of Vindolanda forelimb elements and 43% of hindlimb elements are very stout indeed –stouter than dingoes or even the stoutest-limbed Pleistocene wolf. That this is a trend driven by directional selection, and not merely a characteristic of dogs bred on a dwarfing gene, is suggested by the fact that most humeri, femurs, and tibias of British dogs of the Iron Age are also stouter than those of either wolves or dingoes. Romano–British dogs from sites other than Vindolanda, as well as from sites in Continental Europe and North Africa, show the same trend.

The trend in withers height among Roman-era dogs is toward smallness; only the biggest dogs from Tac Gorsium equal the height of Pleistocene or modern wolves, while the great majority are smaller. 37% of Vindolanda dogs as predicted by forelimb elements, and 57% of hindlimb elements, come from animals that stood less than 40 cm high. Again, directional selection is suggested by the fact that British Iron Age dogs fall into the dingo size range, while many Roman-era dogs from Vindolanda and other sites are either smaller or larger than dingoes.

The Beginning of Dog Breed Differentiation

Dogs from the European Mesolithic and Neolithic appear to have originated from dingo-like ancestors (Morey, 2010; Sacks *et al.*, 2013). Dog morphotypes distinctively different from dingoes in height, limb stoutness, and skull shape become common in the Iron Age. Small dogs appear in the late Iron Age and become common in the Roman period. Several of these ancient morphotypes are similar to, but not exactly like, modern dog breeds. In some cases, reasons for differences between ancient and modern dog breeds can be historically documented; for example, the Irish Wolfhound (Phillips *et al.*, 2009), the Pug and the Dachshund (Dennis-Bryan & Clutton-Brock, 1988), and the St. Bernard (Drake & Klingenberg, 2008).

The advent of long-distance semen shipping since the 1970s has accelerated phenotypic change by permitting a limited number of popular sires to produce more than 1000 litters in their lifetime. The highly unequal contributions of a few males are not only the reason for unequal genetic contribution of the sexes in modern dogs (Sundqvist *et al.*, 2006), but are the functional equivalent of a genetic bottleneck. Consumer preference for phenotypic extremes of height, shortening of the muzzle, and stance or way of going fuel debate in many modern breeds (Sampson & Binns, 2006). Narrowly-defined dog breed standards (Crowley & Adelman, 1998) and the high commercial value of purebred dogs that strictly fit the definition (Cunliffe, 1999) create strong directional selective pressure (Sundqvist *et al.*, 2006). Phenotypic extremes achieved through inbreeding add to genetic load (Calboli *et al.*, 2008); many veterinarians and geneticists today define dog breeds not by appearance or behavior but by the suite of genetic disorders to which they are prone (Lindblad-Toh *et al.*, 2005; Cruz *et al.*, 2008).

Modern breeds of dog differ widely in conformation, size, pelage, color, behavior, physiology, and susceptibility to disease (Coppinger & Coppinger, 2002; Freedman *et al.*, 2013). Such is the range in domestic dog skull shape that it not only exceeds that of other domesticated species, but of the entire order Carnivora (Drake & Klingenberg, 2010). We demonstrate herein that neither the Vindolanda dogs, nor any other known population of Roman-era dogs, comes close to matching the huge morphological range of modern domestic dogs.

Distinctive forms of domestic dog are well attested by the Neolithic in the Middle East and by the Paleo-Indian period in the Americas (Turnbull & Reed, 1974; Lawrence & Reed, 1983; Olsen, 1985; Crockford & Pye, 1997; Schwartz, 2000; Barsh *et al.,* 2006). Because the gene complex for chondrodysplasia is inherited as an autosomal dominant, short, bandy-legged dogs may spontaneously appear in a population (Parker *et al.*, 2009), but once they do appear they can be –and have often been– maintained by isolation, as for example in both Aztec Mexico (Valadez Azúa, 2000) and by the ancient Egyptians (Churcher, 1963; Brewer *et al.*, 2001). By the late Iron Age, not only dwarf but miniature or "toy" dogs were being deliberately bred in Europe (Clark, 1995; Boyko *et al.*, 2010); such dogs were also then bred on, along with bigger sorts of dog, throughout the Roman Empire. An abundance of Roman writing and artwork attests to this and corroborates zooarchaeological studies of dog bones of diverse shapes and sizes found on many Roman-era sites in Great Britain and on the European continent (Part II, Dogs of Roman Vindolanda; Bennett & Timm, 2016).

Numerous genetic studies of dog breeds using autosomal markers demonstrate that the physical traits that distinguish dog breeds are inherited (Koskinen, 2003; DeNise *et al.*, 2004; Parker *et al.*, 2009; Vaysse *et al.*, 2011). Such studies led Parker *et al.* (2009) to conclude that most dog breeds have a very recent origin; this is supported by research utilizing mtDNA which also indicates that breeds have not been isolated for a very long time (Sundqvist *et al.*, 2006; Quignon, 2007). Parker *et al.* (2009) suggested that modern breeds may have developed from "less codified phenotypic varieties after the introduction of the breed concept and the creation of breed clubs in Europe in the 1800s."

These results contrast with the widespread view that many dog breeds have ancient origins (Crowley & Adelman, 1998). Naturalistic artwork going back as much as 4,000 years represents dogs with conformation, pelage, color, and behavior characteristics strikingly similar to that of some modern dog breeds (Toynbee, 1973; Clutton-Brock, 2000). Sundqvist *et al.* (2006) and Parker *et al.* (2009) posit the existence of distinctive phenotypes bred in widely-separated communities, and Larson *et al.* (2012) suggest that the failure of DNA studies to clearly differentiate most modern breeds of dog is due to repeated human-mediated mixing of lineages that had previously been maintained in isolation.

Harcourt (1974) demonstrated that Romano–British dogs exceed the range of variability of dogs of the British Neolithic, yet our analysis demonstrates almost no overlap in limb bone morphology between the latter and Australian dingoes (Figures 16–20). This suggests that cultural preferences, expressed through a degree of directional selection in Europe, were already at work during the Neolithic to make domestic dogs look and function differently from Australasian dingoes (and certainly differently than wolves). We demonstrate directional selection affecting the Vindolanda dog population in neck strength, mouth shape, jaw grip strength, and limb stoutness.

The Vindolanda collection of domestic dog remains is important not only because of its broad range of size and phenotype, but because it is approximately 1950–1600 years old, and thus lies near the beginning of dog breed diversification in Europe. Rather than representing the intermingling of formerly-separate dog bloodlines, the Vindolanda collection samples the initial diversification of modern domestic dog breeds, and thus has the potential to assist in identifying the point of origin in time and space of several modern dog lineages.

ACKNOWLEDGEMENTS

We gratefully acknowledge the financial support of the Vindolanda Trust and its Director, Patricia Birley. Andrew Birley and Justin Blake provided indispensable on-site guidance and redaction by Andrew and Anthony Birley greatly improved the manuscript. Ian Baxter generously provided discussion, measurements, and many photos. Barbara Birley, Louisa Gidney, Jessica Grimm, and Marc Nussbaumer supplied crucial photographs. Sarah Taylor assisted with measurements. We thank Helen Walker and Darren Plumb of the Australian Dingo Conservation Association for access to cranial material. Salvador Gonzales and Wilson Colón provided Spanish-language assistance. Collection access was provided by David Berman, University of Kansas Natural History Museum; Jacquie Huntley, Louisa Gidney, and Beth Upex, Durham University Department of Archaeology; Robert S. Voss, American Museum of Natural History; Jay Villamarette and Joey Williams, Skulls Unlimited, Inc.; Sandy Ingleby, The Australian National Museum; Tom Labedz, University of Nebraska State Museum; and Ken Thornton, Veterinary Department, Massey University.

REFERENCES

AYTON, G. 2011: Animal bone from a Roman well at Rothwell Haigh, West Yorkshire. *English Heritage Research Department Report Service* 66-2011: 1–62.

BARSH, R. L.; JONES, J. M. & SUTTLES, W. 2006: History, ethnography, and archaeology of the Coast Salish Woolly-Dog. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 1-11. Proceedings of the 9th I.C.A.Z. Conference, Durham. Oxbow Books.

BARTOSIEWICZ, L. 2000: Metric variability in Roman period dogs in Pannonia Province and the Barbaricum (Hungary). In: Crockford, S.J. (ed.): *Dogs through Time: an Archaeological Perspective*: 181-189. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

BAXTER, I. L. 2002: A dwarf hound skeleton from a Romano–British grave at York Road, Leicester, England, U.K., with a discussion of other Roman small dog types and speculation regarding their respective aetiologies. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 12-23. Proceedings of the 9th I.C.A.Z. Conference, Durham. Oxbow Books, Oxford.

— 2010a: Small Roman dogs. *Alexandria Archive* 901: 1–9. Available at: http://alexandriaarchive.org/bonecommons/items/show/901

— 2010b: A re-examination of the Thistleton canids. *Alexandria Archive* 885: 1–11. Available at: http://alexandriaarchive.org/bonecommons/items/show/885

BAXTER, I. L. & NUSSBAUMER, M. 2009: Evidence of morphometric variation in an Iron Age dog cranium from Trumpington, Cambridgeshire, U.K. *Archaeofauna* 18: 69–78.

BENNETT, D. 2005: Bones from the Severan ditch, Area A, 2004. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2003–2004*: 115-186. The Vindolanda Trust. Hexham, Northumberland.

— 2012: Life history information from tracks of domestic dogs (*Canis familiaris*) in ceramic building materials from a Roman bath-house at Vindolanda, Northumberland, England. *Archaeofauna* 21: 7–36.

— 2014: Faunal remains from third-century contexts at Vindolanda. In: Blake, J. (ed.): *Vindolanda Research: The Excavations of 2007–2012 in the* Vicus *or Extramural Settlement ('Area B')*: 197-216. Roman Army Museum Publications. Brampton, Greenhead.

BENNETT, D. & TIMM, R. M. 2013: Microfaunal remains from the East granary, Roman Vindolanda: Evidence for human–animal interactions. In: Birley, A. (ed.): *The Vindolanda Granary Excavations*: 72-98. Roman Army Museum Publications. Brampton, Greenhead.

— 2016: The dogs of Roman Vindolanda, Part II: time-stratigraphic occurrence, ethnographic comparisons, and biotype reconstruction. *Archaeofauna*. 25: 107-126.

Birley, A. 2003: *Vindolanda Research Report, 2003: The Excavations of 2001–2002, Volume I*. The Vindolanda Trust. Bardon Mill, Hexham.

Blake, J. 2014: *Vindolanda Research: The Excavations of 2007–2012 in the* Vicus *or Extramural Settlement ('Area B')*. Roman Army Museum Publications. Brampton, Greenhead.

Bökönyi, S. 1984. *Animal Husbandry and Hunting in Tac-Gorsium*. Budapest, Akadémiai Kiadó.

Boyko, A. R.; Quignon, P.; Li, L.; Schoenebeck, J. J.; Degenhardt, J. D.; Lohmueller, K. E.; Zhao, K.; Brisbin, A.; Parker, H. G.; Vonholdt, B. M.; Cargill, M.; Auton, A.; Reynolds, A.; Elkahloun, A. G.; Castelhano, M.; Mosher, D. S.; Sutter, N. B.; Johnson, G. S.; Novembre, J.; Hubisz, M. J.; Siepel, A.; Wayne, R. K.; Bustamante, C. D. & Ostrander, E. A. 2010: A simple genetic architecture underlies morphological variation in dogs. *PloS Biology* 8: e1000451.

Brewer, D.; Clark, T. & Phillips, A. 2001: *Dogs in antiquity: Anubis to Cerberus, The Origins of the Domestic Dog*. Aris and Phillips, Warminster.

Calboli, F. C. F.; Sampson, J.; Fretwell, N. & Balding, D. J. 2008: Population structure and inbreeding from pedigree analysis of purebred dogs. *Genetics* 179: 593–601.

Churcher, C. S. 1963: Dogs from Ein Tirghi cemetery, Balat, Dakleh Oasis, Western Desert of Egypt. In: Clason, A.; Payne, S. & Uerpmann, H-P. (eds.): *Skeletons in Her Cupboard: a Festschrift for Juliet Clutton-Brock*: 39-59. Oxbow Monographs 34. Oxford.

Clark, K. M. 1995: Neolithic dogs: a reappraisal based on evidence from the remains of a large canid deposited in a ritual feature. *International Journal of Osteoarchaeology* 6: 211–219.

Clutton-Brock, J. 1969: The origins of the dog. In: Brothwell, D.R. & Higgs, E.S. (eds.): *Science in Archaeology: a Survey of Progress and Research*: 303-309. Thames and Hudson, London.

— 2000: Introduction. In: Crockford, S.J. (ed.): *Dogs through Time: an Archaeological Perspective*: 3-7. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

Clutton-Brock, J.; Corbet, G. B. & Hills, M. 1976: A review of the family Canidae, with a classification by numerical methods. *Bulletin British Museum (Natural History)* 29: 117–199.

Coppinger, R. & Coppinger, L. 2002: *Dogs: a Startling New Understanding of Canine Origins, Behavior, and Evolution*. Scribner, New York.

Corbett, L. 1995: *The Dingo in Australia and Asia*. University of New South Wales Press, Sydney.

Cram, L. 2000: Varieties of dog in Roman Britain. In: Crockford, S.J. (ed.): *Dogs through Time: an Archaeological Perspective*: 171-180. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

Crockford, S. J. 2000a: Dog evolution: a role for thyroid hormone physiology in domestication changes. In: Crockford, S.J. (ed.): *Dogs through Time: an Archaeological Perspective*: 11-20. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

— 2000b: A commentary on dog evolution: regional variation, breed development and hybridization with wolves. In: Crockford, S.J. (ed.): *Dogs through Time*: *an Archaeological Perspective*: 295-312. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

Crockford, S. J. & Pye, C. J. 1997: Forensic reconstruction of prehistoric dogs from the Northwest Coast. *Journal Canadien d'Archéologie* 21: 149–153.

Crowley, J. & Adelman, B. (eds.) 1998: *The Complete Dog Book: Official Publication of the American Kennel Club*. 19th edition. Howell Book House, New York.

Cruz, F.; Vilá, C. & Webster, M. T. 2008: The legacy of domestication: accumulation of deleterious mutations in the dog genome. *Molecular Biology and Evolution* 25: 2331–2336.

Cunliffe, J. 1999: *The Encyclopedia of Dog Breeds*. Parragon Publishing, Bath.

Davis, S. J. M. & Valla, F. 1978: Evidence for the domestication of the dog 12,000 years ago in the Natufian of Israel. *Nature* 276: 608-610.

De Grossi-Mazzorin, J. & Tagliacozzo, A. 2000: Morphological and osteological changes in the dog from the Neolithic to the Roman period in Italy. In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 141-161. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

Denise, S.; Johnston, E.; Halverson, J.; Marshall, K.; Rosenfeld, D.; Mckenna, S.; Sharp, T. & Edwards, J. 2004: Power of exclusion for parentage verification and probability of match for identity in American Kennel Club breeds using 17 canine microsatellite markers. *Animal Genetics* 35: 14–17.

Dennis-Bryan, K. & Clutton-Brock, J. 1988: *Dogs of the Last Hundred Years at the British Museum (Natural History)*. British Museum, London.

Drake, A. G. & Klingenberg, C. P. 2008: The pace of morphological change: historical transformation of skull shape in St. Bernard dogs. *Proceedings of the Royal Society B: Biological Sciences* 275: 71–76.

— 2010: Large-scale diversification of skull shape in domestic dogs: disparity and modularity. *American Naturalist* 175: 289–301.

Driesch, A. von den 1976: A Guide to the Measurement of Animal Bones from Archaeological Sites. *Peabody Museum of Archaeology and Ethnology Bulletin* 1: 1–137.

Ellis, J. L.; Thomason, J.; Kebreab, E.; Zubair, K. & France, J. 2009: Cranial dimensions and forces of biting in the domestic dog. *Journal of Anatomy* 214: 362–373.

Farello, P. 1995: I cani tardo-antichi rinvenuti in un condoto fognario de Classe (RA). *Estratto da Padusa Quaderni* 1: 295–308.

Freedman, A. H.; Gronau, I.; Schweizer, R. M.; Ortega-Del Vecchyo, D.; Han, E.; Silva, P. M.; Galaverni, M.; Fan, Z.; Marx, P.; Lorente-Galdos, B.; Beale, H.; Ramirez, O.; Hormozdiari, F.; Alkan, C.; Vilà, C.; Squire, K.; Geffen, E.; Kusak, J.; Boyko, A. R.; Parker, H.g.; Lee, C.; Tadigotla, V.; Siepel, A.; Bustamante, C. D.; Harkins, T. T.; Nelson, S. F.; Ostrander, E. A.; Marques-Bonet, T.; Wayne, R. K. & Novembre, J. 2013: Genome sequencing highlights the dynamic early history of dogs. *PloS Genetics* 10(1)**:** e1004016. [doi: 10.1371/journal.pgen.1004016].

Gould, S. J. 1966: Allometry and size in ontogeny and phylogeny. *Biological Reviews* 41: 587–640.

Grimm, J. 2007: A dog's life: Animal bone from a Romano–British ritual shaft at Springhead, Kent (UK). *Sonderdruck aus Beiträge zur Archäeozoologie und Prähistorischen Anthropologie* 6: 54–75.

Hambleton, E. 2003: Report on the remains of a dog (8659) from Vindolanda. In: Birley, A. (ed.): *Vindolanda Research Reports: the Excavations of 2001–2002*: 250-256. Vol. I. The Vindolanda Trust. Hexham, Northumberland.

Hammer, Ø. & Harper, D. A. T. 2006: *Paleontological Data Analysis*. Blackwell, Oxford.

Hammer, Ø.; Harper, D. A. T. & Ryan, P. D. 2001: PAST: Paleontological statistics software package for education and data analysis. *Paleontologica Electronica* 4: 1–9. Available at:http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Harcourt, R. A. 1974: The dog in prehistoric and early historic Britain. *Journal of Archaeological Science* 1: 151–175.

Higgs, W. 2001: Ichnology in Archaeology: Comparison of Two Recently Excavated Assemblages as a Case Study in the Recording and Analysis of Archaeological Footprints. Unpublished MSc. Thesis, University of York, York.

Hodgson, G. W. I. 1977: Vindolanda: the animal remains, 1970–1975. *Vindolanda Research Reports.* The Vindolanda Trust. Hexham, Northumberland.

Johnstone, C. & Albarella, U. 2002: The late Iron Age and Romano–British mammal and bird bone assemblage from Elms Farm, Heybridge, Essex (Site Code: Hyef 93–95). *English Heritage Centre for Archaeology Report* 45: 1–200.

Jolicoeur, P. 1963: Note: The multivariate generalization of the allometry equation. *Biometrics* 19(3): 497–499.

Joliffe, I. T. 2002: *Principal Component Analysis*. Springer–Verlag, New York.

Koch, D. A.; Arnold, S.; Hubler, M. & Montavon, P. M. 2003: Brachycephalic syndrome in dogs. *Compendium Continuing Education for Veterinarians* 25: 48–55.

Koskinen, M. T. 2003: Individual assignment using microsatellite DNA reveals unambiguous breed identification in the domestic dog. *Animal Genetics* 34: 297–301.

Larson, G.; Karlsson, E. K.; Perri, A.; Webster, M. T.; Ho, S. Y. W.; Peters, J.; Stahl, P. W.; Piper, P. J.; Lingaas, F.; Fredholm, M.; Comstock, K. E.; Modiano, J. F.; Schelling, C.; Agoulnik, A. L.; Leegwater, P. A.; Dobney, K.; Vigne, J. D.; Vilá, C.; Andersson, L. & Lindblad-Toh, K. 2012: Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences* 109: 1–6.

Lawrence, B. & Reed, C. A. 1983: The dogs of Jarmo. In: Braidwood, L. S.; Braidwood, R. J.; Howe, B.; Reed, C.A. & Watson, P. (eds.): *Prehistoric Archaeology along the Zagros Flats*: 485-494. University of Chicago Oriental Institute Publication 1.

Lindblad-Toh, K.; Wade, C. M.; Mikkelsen, T. S.; Karlsson, E. K.; Jaffe, D. B.; Kamal, M.; Clamp, M.; Chang, J. L.; Kulbokas, E. J. Iii; Zody, M. C.; Mauceli, E.; Xie, X.; Breen, M.; Wayne, R. K.; Ostrander, E. A.; Ponting, C. P.; Galibert, F.; Smith, D. R.; Dejong, P. J.; Kirkness, E.; Alvarez, P.; Biagi, T.; Brockman, W.; Butler, J.; Chin, C-W.; Cook, A.; Cuff, J.; Daly, M. J.; Decaprio, D.; Gnerre, S.; Grabherr, M.; Kellis, M.; Kleber, M.; Bardeleben, C.; Goodstadt, L.; Heger, A.; Hitte, C.; Kim, L.; Koepfli, K-P.; Parker, H. G.; Pollinger, J. P.; Searle, S. M. J.; Sutter, N. B.; Thomas, R.; Webber, C.; Broad Institute Genome Sequencing Platform & Lander, E. S. 2005: Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature* 438(8)**:** 803–819. Available at:doi:10.1038/nature 04338

Lüps, P. 1974: Biometrische Untersuchungen an der Schadelbasis des Haushundes. *Zoologischer Anzeiger* 192: 383–413.

Luttschwager, J. 1965: Ein zwerghund aus römischen Graberfeld and der Berliner Strasse zu Heidelberg–Neuenheim. *Zeitschrift für Säugetierkunde* 30: 24–30.

Mackinnon, M. & Belanger, K. 2002: In sickness and health: care for an arthritic Maltese dog from the Roman cemetery of Yasmina, Carthage, Tunisia. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 38-43. Proceedings of the 9th I.C.A.Z. Conference, Durham. Oxbow Books, Oxford.

Martin, L. D. & Gilbert, B. M. 1978: Excavations at Natural Trap Cave. *Transactions of the Nebraska Academy of Sciences* 6: 107–116.

Morey, D. F. 1992: Size, shape and development in the evolution of the domestic dog. *Journal of Archaeological Science* 19: 181–204.

— 2010: *Dogs: Domestication and the Development of a Social Bond.* Cambridge University Press, Cambridge. MA.

Nobis, G. 1979: Der älteste Haushund lebte vor 14000 Jahren. *UMSHAU* 19: 610.

Nussbaumer, M. 1978: Biometrischer vergleich der Topogenesemuster an der Schädelbasis kleiner und mittelgrosser Hunde. *Sonderdruck aus Zeitschrift für Tierzüchtung und Züchtungsbiologie* 95: 1–14.

— 1982: Über die Variabilität der dorso-basalen Schädelknickungen bei Haushunden [On the variability of dorso–basal curvatures in skulls of domestic dogs]. *Zoologischer Anzeiger* 209: 1–32.

Olsen, S. J. 1985: *Origins of the Domestic Dog: the Fossil Record*. University of Arizona Press, Tucson.

Parker, H. G.; Vonholdt, B. M.; Quignon, P.; Margulies, E. H.; Shao, S.; Mosher, D. S. & Spady, T. S. 2009: An expressed *Fgf4* retrogene is associated with breed-defining chondrodyspasia in domestic dogs. *Science* 325: 995–998.

Phillips, C.; Baxter, I. L. & Nussbaumer, M. 2009: The application of discriminant function analysis to archaeological dog remains as an aid to the elucidation of possible affinities with modern breeds. *Archaeofauna* 18: 51–64.

Quignon, P.; Herbin, L.; Cadieu, E.; Kirkness, E. F.; Hédan, B.; Mosher, D. S.; Galibert, F.; André, C.; Ostrander, E. & Hitte, C. 2007: Canine population structure: assessment and impact of intra-breed stratification on SNP-based association studies. *PloS ONE* 2, e1324**:** 1–8.

Radinsky, L. B. 1981: Evolution of skull shape in carnivores, 1. Representative modern carnivores. *Biological Journal of the Linnean Society* 15: 369–388.

Reyment, R. A. & Savazzi, E. 1999: *Aspects of MULTIVARIATE Statistical Analysis in Geology*. Elsevier, Amsterdam.

Sacks, B. N.; Brown, S. K.; Stephens, D.; Pedersen, N. C.; Wu, J-T. & Berry, O. 2013: Y chromosome analysis of dingoes and Southeast Asian village dogs suggests a Neolithic continental expansion from Southeast Asia followed by multiple Austronesian dispersals. *Molecular Biology and Evolution* 30(5): 1103–1118.

Sampson, J. & Binns, M. M. 2006: The Kennel Club and the early history of dog shows and breed clubs. In: Ostrander, E.A.; Giger, U. & Lindblad-Toh, K. (eds.): *The Dog and Its Genome*: 19-30. Cold Spring Harbor Laboratory Press, New York.

Schwartz, M. 2000: The form and meaning of Maya and Mississippian dog representations. In: Crockford, S.J. (ed.): *Dogs through Time: an Archaeological Perspective*: 217-226. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

Sundqvist, A-K.; Björnerfeldt, S.; Leonard, J. A.; Hailer, F.; Hedhammar, Å.; Ellegren, H. & Vilá, C. 2006: Unequal contribution of sexes in the origin of dog breeds. *Genetics* 172: 1121–1128.

Sutter, N. B.; Bustamante, C. D.; Chase, K.; Gray, M. M.; Zhao, K.; Zhu, L.; Padhukasahasram, B.; Karlins, E.; Davis, S.; Jones, P. G.; Quignon, P.; Johnson, G. S.; Parker, H. G.; Fretwell, N.; Mosher, D. S.; Lawler, D. F.; Satyaraj, E.; Nordborg, M.; Lark, K. G.; Wayne, R. K. & Ostrander, E. A. 2007: A single IGF1 allele is a major determinant of small size in dogs. *Science* 316: 112–115.

Toynbee, J. M. C. 1973: *Animals in Roman Life and Art*. Johns Hopkins University Press, Baltimore.

Turnbull, P. F. & Reed, C. A. 1974: The fauna from the terminal Pleistocene of Palegawra Cave, a Zarzian occupation site in northeastern Iraq. *Fieldiana Anthropology* 63(3): 81–146.

Valadez Azúa, R. 2000: Prehispanic dog types in Middle America. In: Crockford, S.J. (ed.): *Dogs through Time: an Archaeological Perspective*: 193-204. Proceedings of the 1st I.C.A.Z. Symposium on the history of the domestic dog. B.A.R. (International Series) 889. Oxford.

Vaysse, A.; Ratnakumar, A.; Derrien, T.; Axelsson, E.; Rosengren Pielberg, G.; Sigurdsson, S.; Fall, T.; Seppälä, E. H.; Hansen, M. S. T.; Lawley, C. T.; Karlsson, E. K.; The Lupa Consortium; Bannasch, D.; Vilá, C.; Lohi, H.; Galibert, F.; Fredholm, M.; Häggström, J.; Hedhammar, Å.; André, C.; Lindblad-Toh, K.; Hitte, C. & Webster, M. T. 2011: Identification of genomic regions associated with phenotypic variation between dog breeds using selection mapping. *PloS Genetics* 7(e1002316): 1–21.

Archaeofauna 25 (2016): 107-126

The dogs of Roman Vindolanda, Part II: Time-stratigraphic occurrence, ethnographic comparisons, and biotype reconstruction

DEB BENNETT[1*] & ROBERT M. TIMM[2]

[1]Deb Bennett, Director, Equine Studies Institute, P.O. Box 411, Livingston, CA, USA

[2]Department of Ecology and Evolutionary Biology & Natural History Museum,
University of Kansas, Lawrence, KS, USA

*Corresponding author: office@equinestudies.org

Equine Studies Institute, P.O. Box 411, Livingston, CA 95334 USA

(Received *8 September 2015*; Revised *29 November 2015*; Accepted *11 December 2015*)

ABSTRACT: The Roman fort-village complex at Vindolanda in northern England has yielded extensive well-preserved remains of domestic dogs, *Canis familiaris*. Herein, we pose the questions—did the Romans breed for distinctive dog morphotypes, or were dogs breeding panmictically; and if dogs were bred, was it for functionality. We address these questions utilizing remains that are correlated to age and context; morphometric analysis; dental wear stage; bone pathology; pawprints impressed in tiles, and contemporary written records and artwork. All age classes of dogs are represented. There is no evidence that dogs were butchered for food; survivorship curves suggest the typical U-shaped distribution found in populations at equilibrium. Small, medium-sized, and large dogs are represented with frequency changing over time and corresponding to change in the region of origin of the resident military cohort. Husbandry is confirmed on an individual with healed wounds and with the discovery of a beehive-shaped wattle doghouse. Dogs were used extensively in hunting wild game and bred for that activity. By integrating many diverse kinds of data we are able reconstruct biotypes of Roman dogs, greatly facilitating the interpretation of their functionality.

KEYWORDS: ANCIENT DOG HUSBANDRY, BIOTYPE RECONSTRUCTION, *CANIS FAMILIARIS*, DOMESTIC DOG, ROMANO–BRITISH, ROMAN DOG ETHNOGRAPHY, SURVIVORSHIP, VINDOLANDA

RESUMEN: El fuerte-poblado romano de Vindolanda en el norte de Inglaterra fue ocupado desde el 50 al 415 A.D. y ha proporcionado una importante colección de restos bien conservados de perro, *Canis familiaris*. En este trabajo se contesta a las preguntas acerca de si los romanos criaron perros con el propósito de obtener morfotipos específicos o si aquellos perros se cruzaron libremente y de modo aleatorio (panmixis). También, si los perros fueron criados, si tal cría repondía a razones funcionales. Utilizando restos caninos bien contextualizados, respondemos estas preguntas incorporando análisis morfométricos, estadíos de desgaste dentario, patologías óseas, huellas impresas en cerámica (tejas) y registros documentales e iconográficos. Todas las cohortes de perro se encontraban aquí documentadas y no existen evidencias de que los perros fuesen consumidos. Las curvas de supervivencia son las clásicas con forma de U constatadas en poblaciones en equilibrio. Se constatan asímismo perros pequeños, medianos y grandes cuyas frecuencias variaron según el lugar de origen de las guarniciones que se sucedieron en el asentamiento. El cuidado de los canes lo confirma una perrera con forma de colmena y un individuo con heridas cicatrizadas. Los perros fueron usados para la caza y criados con tal fin. Integrando todas las fuentes de datos se han podido reconstruir los biotipos caninos de los romanos, infiriendo con ello su funcionalidad.

PALABRAS CLAVE: CRIA CANINA ANTIGUA, RECONSTRUCCIÓN DE BIOTIPOS, *CANIS FAMILIARIS*, PERRO, ROMANO–BRITÁNICO, ETNOGRAFÍA DE PERROS ROMANOS, SUPERVIVENCIA, VINDOLANDA

INTRODUCTION

The Vindolanda fort and village complex situated 3 km south of Hadrian's Wall in northern England sits near the edge of the ancient Roman Empire, yet has yielded a large and diverse collection of Roman-era dogs. This paper represents Part II in a series on the dogs of Roman Vindolanda; for detailed site information and collection techniques, see Part I (Bennett *et al*., 2016).

Herein, we ask the question -did the Roman- era inhabitants of this remote garrison have distinctive morphotypes of dogs or were their dogs all of the "village dog" or dingo-like morphotype which likely represents panmictic breeding? If there are dogs of different sizes and shapes, do they resemble modern morphotypes? Much contemporary Roman artwork suggests that dogs resembling modern breeds were already in existence nearly 2,000 years ago. To evaluate potentially distinctive Roman-era dogs and determine whether they were bred for different purposes, we utilize morphometrics (Bennett *et al*., Part I of this series, 2016); dental wear stage; bone pathology; pawprints impressed in tile (Bennett, 2012); written records and contemporary artwork; and site geography, ecology, stratigraphy, and architecture. We present biotype reconstructions of the range of Roman dogs known from Vindolanda, created through integration of all these kinds of data in an effort to facilitate our understanding of the uses to which the dogs may have been put.

MATERIALS AND METHODS

For basic excavation techniques and site location map, please see Part I of this series (Bennett *et al*., 2016). Determination of context at Vindolanda has developed over fifty years of excavation at the site, which contains a complex succession of nine forts built one on top of the other over the whole period of its occupation (Birley, 2003; Birley & Blake, 2005, 2007; Birley, 2009; Blake, 2014). Associated with the forts through the earlier periods was an adjacent *vicus* or officially-recognized village, so that the total range of Vindolanda contexts encompasses both formal military and informal military or possibly civilian areas (Birley, 2003; Blake, 2003; Birley & Blake, 2007; Blake, 2014). Military areas include infrastructure such as the fort walls, defensive ditches, and roadways, as well as numerous types of buildings including the commandant's residence (*praetorium*), the administrative center (*principia*), barracks, hospital, granary, warehouse, stables, bath-houses, and latrines. Civilian areas include residences, workshops (butchery, tannery, tilery, jeweler, cobbler, tentmaker, bowmaker, armorer, wainwright, carpenter, blacksmith, bakery, brewery), market areas and shops, an inn, temples, mausolea, and a public spring and aqueduct system (Birley, 2003, 2013; Birley, 2009; Blake, 2014). Bones, including those of dogs, are found from every context and from every time period (Figure 1).

The succession of Vindolanda forts has given rise to a system of relative dating in which Vindolanda finds are grouped by period (Figures 2–4) (Birley, 2003). Absolute chronology by year (Figure 3) has been established through cross-comparison of coins (Brickstock, 2003, 2005, 2007, 2013, 2014) and pottery-makers' stamps (Marlière, 2003, 2007; Marlière & Torres Costa, 2005; Birley, 2007; Sheehan-Finn, 2013, 2014).

RESULTS

Frequency of Skeletal Elements; Juveniles

A total of 520 bones pertaining to domestic dogs have been recovered from excavations carried out

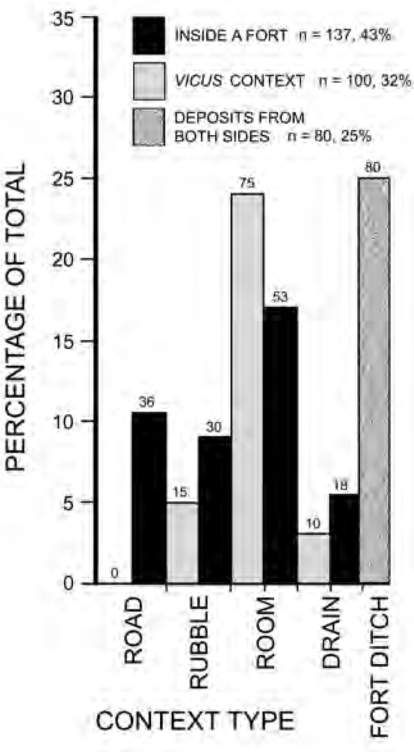

FIGURE 1

Dog bone finds by major context type. Percentages are of the maximum number of individuals (n = 317), with associated material counted as “1”. Numbers at tops of columns are actual number of items recovered.

between 1960 and 2014 (Figure 1). Dog remains comprise about 2.6% of the total Vindolanda collection. For purposes of this study, limb bones are considered “juvenile” if any major epiphyses are unfused, or if the central vertebral physis is detached. Maxillae or jaw rami are considered juvenile if deciduous teeth are present, or if the carnassial, premolar, or canine teeth are not fully erupted; or in jaws, if the horizontal ramus is swollen indicating the presence of unerupted teeth (Silver, 1970). Even by these rather broad criteria, only 67 of 520 elements whose maturity could be assessed, representing 12.9% of all dog bones, came from juveniles (Figure 5).

Size and Completeness of Skeletons

Study of pawprints impressed in ceramic building materials (Higgs, 2001: 51; Bennett, 2012; and see Cram, 2000) document that dogs of different sizes existed at Vindolanda. Our morphometric study of 27 relatively complete skulls, 61 jaws and 92 measurable limb bones confirm the presence of dogs ranging in “shoulder” or “withers” height from about 27 cm to 70 cm. While some Vindolanda dogs show phenotype similar to modern “village dogs” or Australian dingoes, the majority are morphologically different and the range of size and

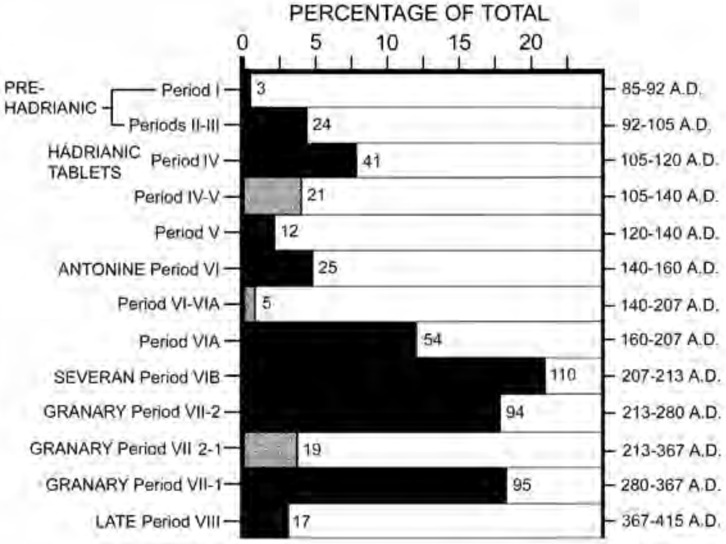

FIGURE 2

Bone counts by Vindolanda period and calendar year. Numbers to right of columns represent actual number of bones recovered. Dark gray bars are specimens with “fuzzy” dates which could be assigned to time periods either earlier or later. Total sample n = 520.

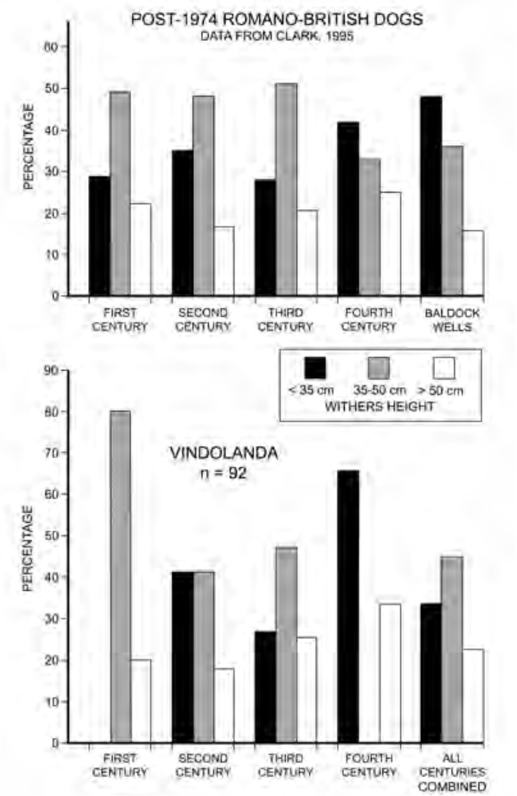

FIGURE 3

Frequency of large, medium, and small dogs by century. Vindolanda numbers (below) are compared with data from Clark Baldock Wells locality (1995, her Figure 14). Withers heights calculated by application of Harcourt's (1974) factors. Vindolanda n = 130, representing the total number of limb bones complete enough to permit calculation of withers height.

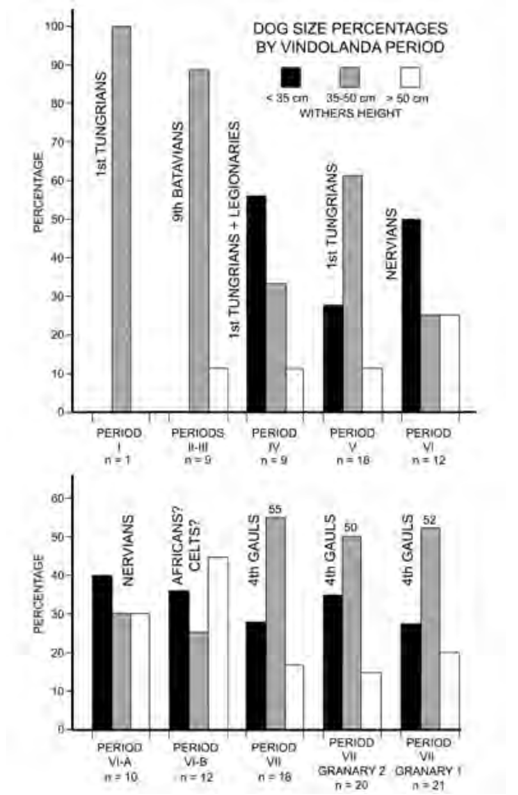

FIGURE 4

Frequency of large, medium, and small dogs by Vindolanda period. The cohort name or nationality thought to have been in residence at Vindolanda in any given period is shown. "Granary level 2" dates 213–280 A.D.; "Granary level 1" dates 280–400 A.D. Only bones complete enough to permit reasonably accurate estimation of withers height are represented, with n = 130.

phenotype is far greater than either dingoes or British dogs of the Neolithic (Bennett *et al*., 2016).

Of 39 dog skulls or partial skulls recovered to date from Vindolanda, five have been recovered in association with a significant portion of the postcranial skeleton. The bones were not interred but instead were recovered scattered on a surface or in a ditch with skeletal elements in proximity but for the most part not in normal anatomical position. Association has been assumed because of proximity, congruence among the bones as to size and maturity, and the absence of other dog bones from the same immediate area. The associated dogs include a juvenile excavated in 1993 from the floor of a room in a *vicus* building; an adult from the Severan Fort Ditch excavation of 2002 (Hambleton, 2003); an adult from a drainway ditch excavated in 2012; and an adult excavated in 2014 from the floor of a room in a fort. All these dogs are of medium to small size. The fifth dog was recovered in 1997 from a hypocaust channel under a heated room in the third-century (Period VII) *praetorium*; this adult dog is of large size. Unassociated dog bones have been recovered from most Vindolanda contexts, but as with the associated material, none had been interred, deposited in a well, or buried in association with a building cornerstone.

The maximum number of individual dogs indicated by bony remains is 317, an estimate based on the assumption that all dog bones not otherwise believed to be associated belong to different individuals. Minimum number of individuals was not calculated because material was usually excavated from widely separated contexts, so that all unassociated bones probably represent different dogs.

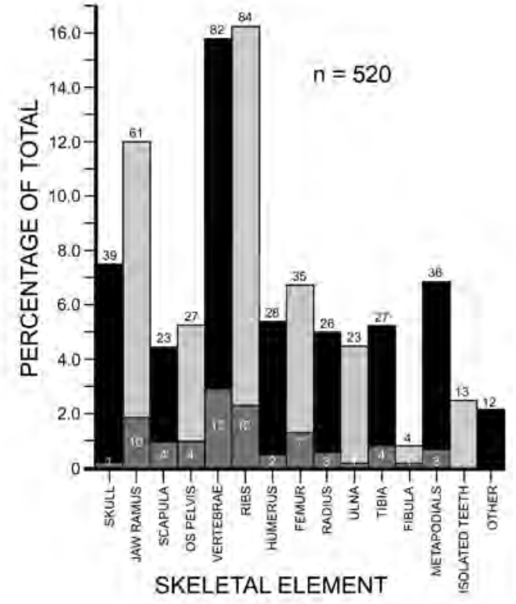

FIGURE 5

Comparative frequency of different skeletal elements of Vindolanda dogs. Juveniles are shown in dark gray at the base of each category in which they occur. Juveniles number 67 of 520 elements or 12.9% of the total. Black numbers at tops of columns are the total recovered, representing adults plus juveniles; white numbers at column bases are juveniles only.

Evidence for Butchery, Skinning, and Gnawing; Pathologies

Butchery marks, which usually manifest as V-shaped chop marks, chattering cuts, the ends of bones cloven cleanly away, or shattering and splintering, are very common on bones of “food species” from Vindolanda, including cattle (*Bos taurus*), goat (*Capra hircus*), sheep (*Ovis aries*), and pig (*Sus scrofa*). Bennett (2005) reported butchery marks on horse vertebrae at Vindolanda. However, butchery marks are extremely rare on dog bones there, with only one instance observed (Figure 15). Cut-marks, usually interpreted as an indication of skinning, were found on one juvenile dog metapodial and one humerus, representing less than one-half of one percent of all dog bones recovered.

Evidence of gnawing or digestion is rare also (Table 1); two geriatric inferior premolars from beneath the East Granary (Bennett & Timm, 2013) appear to have been partially digested. An associated radius and ulna from the 2013 roundhouse context (discussed below) were thoroughly gnawed (Figure 16), but they plus a partial proximal ulna collected in 2009 are the only gnawed dog bones in the collection. By contrast, pathologies are fairly common on Vindolanda dog bones, with more than 20 found (about 5% of all dog bones recovered). Herein, we highlight pathologies on the skull of an aged dog, presumed to be a boarhound (Figures 6–8).

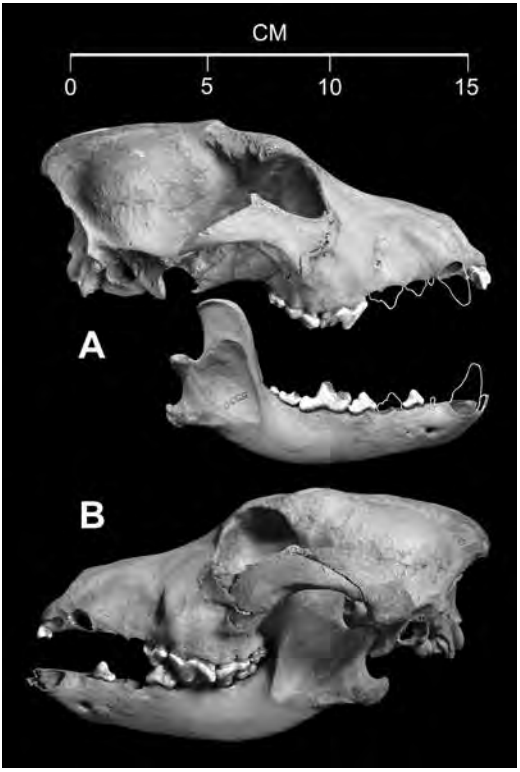

FIGURE 6

Vindolanda specimen CI-VI 10152 (SF 5530), right and left lateral views of the skull and associated mandible of an aged dog from a *vicus* ditch of the Antonine Period VI, 140–160 A.D. Note in this figure and following the bulldog-like stout build, with deep mandible, wide face, and slightly short muzzle. Profiles of missing teeth restored with white lines. Pathology due to blunt impact is evident on the right frontal, while the left frontal shows the healed wound from a boar’s tusk.

Survivorship Based on Tooth Wear Scores

We used the tooth-wear scoring system of Horard-Herbin (2000) to compare Vindolanda dogs with wild-killed Australian dingoes and with wolves from the late Pleistocene Natural Trap Cave in Wyoming. Survivorship curves for these three pop-

FIGURE 7

Vindolanda specimen CI-VI 10152 (SF 5530), dorsal view showing details of healed tusk-wound to left orbit and frontal, and cudgel wound which partially crushed the right frontal sinus.

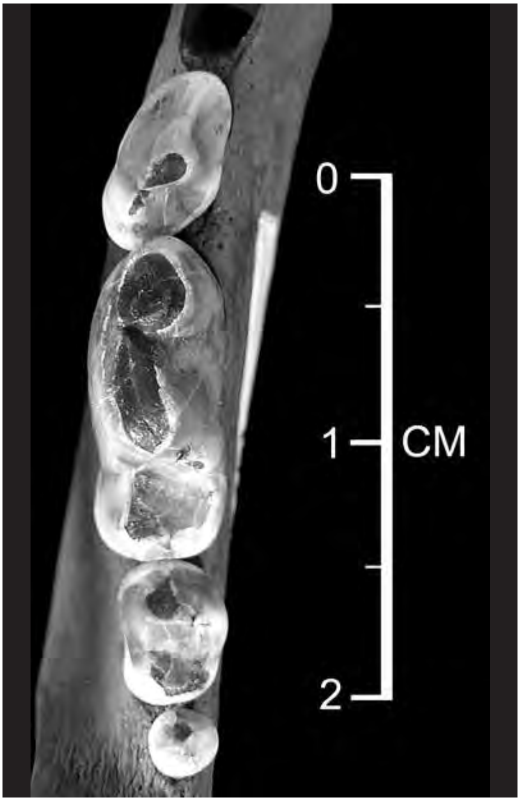

FIGURE 8

Vindolanda specimen CI-VI 10152 (SF 5530), closeup view of the right mandible to show the heavily worn teeth (Stage F of Horard-Herbin, 2000).

FIGURE 9

Reconstructed life appearance of Vindolanda specimen CI-VI 10152, after healing of wounds.

ulations are in sharp contrast and thus instructive. Australian government programs currently mandate the systematic removal of dingoes found outside the “dingo fence” (Corbett, 1995). Removal is either by trapping or hunting, and it is evident from the survivorship curve (Figure 10) that the naïve and curious young dingo is the most frequent casualty.

The survivorship curve for Pleistocene wolves from Natural Trap Cave is exactly the opposite. Aptly named, this cave is a flask-shaped, cathedral-sized hollow developed in limestone bedrock. It has a blind, funnel-shaped entrance at the top with a 25-m deadfall to a rocky floor below, with no egress. The smell of the rotting carcasses of entrapped animals probably attracted many geriatric carnivores; wolves, especially older individuals, are especially well represented. Hungry and with diminished ability to hunt (MacNulty *et al.*, 2009), they either fell or jumped into the cave in quest of an easy meal, but were subsequently unable to get out (Martin & Gilbert, 1978).

The Vindolanda dog survivorship curve contrasts with both of the above examples (Figure 10) representing the typical U-shaped distribution found in populations at equilibrium (Keeton, 1972). Death rate is high for puppies and young dogs, falls steadily to a low point during the prime of life (for dogs, this equates to about 1 ½ to 2 ½ years of age), and then rises again as the teeth become senescent (putatively, at age 4 years old or greater) (Figures

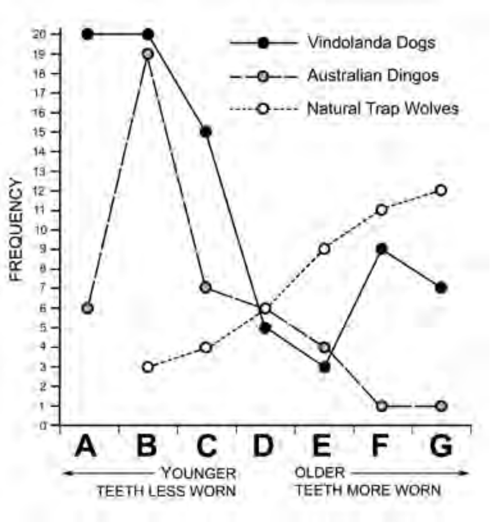

FIGURE 10

Survivorship curves determined by application of the tooth-wear scoring system of Horard-Herbin (2000) to a sample of jaws from Vindolanda, Australian dingoes, and late Pleistocene wolves from Natural Trap Cave, Wyoming. A–G represent tooth-wear categories.

6–8). In agreement with the above-noted lack of cutmarks or butchery marks, the Vindolanda survivorship curve indicates that dogs were neither raised nor utilized at this site to provide meat or hides as is documented elsewhere in the Iron Age (Méniel, 1992; Horard-Herbin, 2000).

Time-Stratigraphic Distribution and Cultural Association

Dog bones in the Vindolanda collection come from every period, from "pre-Hadrianic" levels dating to circa A.D. 85, to the twilight years of the Roman Empire in the early 5th century (Figures 3–5; Birley, 2009; Blake, 2014). Thanks to tight stratigraphic control achieved through careful excavation and cross-comparison of amphora stamps and coins (Marlière, 2003, 2007; Marlière & Torres Costa, 2005; Birley, 2007; Sheehan-Finn, 2013, 2014), we are able to track changes in the Vindolanda dog population through time.

With associated material counted as 1 individual, the maximum number of individuals is 307. Highest totals occurred in the Severan and Granary periods, VI-B and VII respectively, but totals are moderately high from the Hadrianic Period IV onward (Birley & Blake, 2005, 2007; Blake, 2003, 2014). Clark (1995) examined dog material from Romano–British sites excavated since Harcourt's survey (1974). Comparison with Clark's results (Figure 4) indicates that in most centuries, Vindolanda produces more dogs of both small and large size, though small dogs do not appear at Vindolanda until the second century.

Dog remains are broken out by "Vindolanda period" in Figure 5, a technique which relates the occurrence of dogs directly to the resident military cohort (Blake, 2014). Cohort change often coincides with cultural changes, because cohorts were drawn from disparate areas of the empire including Spain, North Africa, Belgium, France, and Italy (Birley, 2002). It is reasonable to believe that people of different cultures would have varying preferences for dog type. The native Celtic population also had an ongoing influence, for many soldiers were recruited locally (Birley & Blake, 2005, 2007). Dogs from Vindolanda periods I through III are almost all of middle size. Small dogs suddenly appear in the "tablet era," Period IV, and thereafter persist as a significant percentage of the total dog population. Large dogs seem to have been most popular during the Severan anomaly, period VI-B, but were first kept in significant numbers during the earlier Antonine era, period VI.

Occurrences by Context

Context association allows determination of the physical settings that most commonly produce dog remains at Vindolanda. Vindolanda dogs have not been found in wells, graves, near or under altars, or incorporated into building foundations, and it is thus unlikely that any so far recovered were ritually slaughtered or interred as has been observed at other sites (see Yvinec, 1987; Méniel, 1992; Davis, 1995; Murphy & Ó Baoill, 2000; Dunand & Lichtenberg, 2005; Smith, 2006; Snyder & Moore, 2006; Wilkens, 2006).

A higher percentage of Vindolanda dogs (43%) come from contexts within or directly associated with a fort, than from any *vicus* context (32%). Of *vicus* remains, the majority come from the floors of rooms or from the yards just outside those rooms (Figure 2). A significant fraction (25%) of dog material was recovered from the fort ditches, which were defenses ringing the forts. They had a V-shaped cross-section and averaged about 2–3 m wide at the top and about 1–2 m deep with an “ankle breaker” or cleanout slot cut into the bottom (Birley, 2003; Blake, 2014). Although constructed as part of the fort, the ditches were actually more accessible to people who worked and resided outside the fort walls and a large fraction of the artifacts of all classes recovered from the ditches were probably deposited from the *vicus* side (Andrew Birley, *pers. comm.*).

Evidence for Dog Husbandry and Use at Vindolanda

Direct evidence for the use of dogs in hunting comes from a skull with associated mandible (Figures 6–8) recovered from a ditch in the Antonine-era *vicus* (R. Birley, *pers. comm.*). Measuring 151.55 mm (basal length) by 107.14 mm (zygomatic width), the skull is slightly larger than the median size for Vindolanda dogs and of robust build. The teeth are stout and heavily worn. With a broad, relatively short face it is similar to a British Iron Age Shar-Pei analog reported by Baxter & Nussbaumer (2009).

Two pathologies are evident upon the anterior frontal bones. Upon the left side is a 5.5 cm grooved scar of 2–5 mm depth, whose width and flat-bottomed shape makes it most likely to have been made by the inferior tusk of a boar. The lesion skims the center of the superior rim of the left orbit, and there are changes in bone thickness and texture in the immediate area consistent with a healed abscess. There is also scarring on the inferior orbital rim which involves the eminence for the postorbital ligament. It seems from this that the boar probably did not take the dog’s eyeball but left him with the distinctively scarred face of an old campaigner (Figure 9).

A second pathology also appears upon the head of the same dog: crushing of the right frontal bone, due to downward impact from a blunt object, probably a wooden cudgel (Figures 6, 7). Damage is located primarily behind the right orbit, although there is bony proliferation upon the right postorbital process. Roman boar hunts often included a “master of hounds”—a servant or slave whose duties were to manage leashed dogs, to release them at the appropriate moment, and to call the dogs off the boar so that the hunter, rather than the dogs, would be credited for the kill. Once dogs engage prey, however, it can be difficult to get their attention—thus the master of hounds typically carried a cudgel, so that the dogs, which wore heavy leather collars as well as leather body armor, could be pulled out of the fight (Figure 14).

Since all the rather serious wounds upon this dog’s head healed completely, and the condition of its dentition shows that it lived to be at least four years old (probably longer), it is reasonable to conclude that boarhounds were valued at Vindolanda and that they received veterinary attention when injured (see MacKinnon & Belanger, 2002, and the Vindolanda tablets which mention an officer who functioned as a veterinarian; Bowman & Thomas, 1994, 2003; Birley, 2002; Birley, 2009). If “Scarface” was a bitch, she might have been valued as a breeder even if no longer able to hunt; the same might also have been true if the dog were male. From the find context it is probable that this dog did not die afield.

Still more about dog husbandry at Vindolanda is revealed by the unusual and interesting “roundhouse complex” excavated during 2012–2013. This consists of an oval structure associated with a rectangular structure immediately to the south (Figure 11; Blake, 2014). Both buildings were made of wattle, constructed by weaving thin, flexible sticks between upright poles which had been driven into the ground. Evidence from coin dating, amphora stamps, and ceramic analysis indicates that the complex may originally have been built as early as the very beginning of the 2nd century in Vindolanda period III (ca. AD 100–105). The complex continued in use into period IV and was demolished and remodeled between ca. AD 105–120 before being abandoned with the fort. A subsequent fort’s western defensive ditch (period V, ca. AD 120–130) cut out part of the complex of buildings and covered the rest below a meter of “boulder clay” which made up the ditch’s western berm. Throughout its history, the complex was located outside the western (period III) and northern (period IV) ditches of the Vindolanda forts (Blake, 2014).

In its first phase, the roundhouse averaged 4.67 m in diameter, yielding about 17 m^2 of interior floor space. The second phase was smaller, with an average diameter of 3.87 m and an interior area of about 12 m^2. The range of material culture found on the floor in each building, along with hearths and storage pits, suggest that they were used as a domestic dwelling (Blake, 2014).

FIGURE 11

Aerial photograph of the “roundhouse complex” excavated at Vindolanda in 2012 and 2013 (scale units in meters). Superstructures of both the rectangular and the round structures were made of wattle. White dots mark the tops of structural poles driven into the natural clay substrate. The circular “footprint” of the beehive-shaped doghouse within the larger elliptical structure can clearly be seen. Photo by Adam Stanford, courtesy The Vindolanda Trust.

Within the later oval building there is also a smaller, circular wattle feature measuring 98.2 cm (about one yard) in diameter (Figure 11). While the percentage of dog bones recovered from this complex is not, on average, different from other Vindolanda contexts that produce dog bone, the percentage of juvenile dog bones from the roundhouse context is about twice as high (9.5%) as the average for other Vindolanda contexts (Figure 18). Two thoroughly gnawed adult dog bones (Figure 16), along with high percentages of gnawed bones of goats, cattle, and pigs, also come from this complex. The punctate form of the toothmarks and their presence over virtually the entire surface of many of the bones confirm that they were chewed by dogs -probably puppies- and not pigs (Greenfield, 1988; Domínguez-Solera & Domínguez-Rodrigo, 2009). The fourth-century “Dominus Julius” floor mosaic from near ancient Carthage (Dunbain, 1978; Ben-Abed Ben-Khader *et al*., 1987; Blanchard-Lemee & Ennaifer, 1996; Bardo National Museum, 2014) (Figure 12) presents the image of a similar-sized beehive-shaped wattle doghouse in context of the daily routine of a prosperous Roman country estate. The evidence suggests that the small round structure was in fact a doghouse of this type, perhaps used to shelter bitches nursing puppies (Figure 17).

The Range of Dog Morphotypes at Vindolanda

Space limitations prevent us from presenting more than a few of the hundreds of dogs depicted in Roman painting, pottery, sculpture, and mosaics (see Figures 13, 14). Survey of artwork (Schefold, 1972; Dunbain, 1978; Joyce, 1981; Ben-Abed Ben-Khader *et al*., 1987; Guillaud & Guillaud, 1990; Blanchard-Lemee & Ennaifer, 1996; Wilson, 2005; Witts, 2005; Yućel, 2010; Bardo National Museum, 2014; Pompeii and Herculaneum mosaics and paintings, 2014; Sullivan, 2014) corroborates our osteological and tile-track studies in finding a broad size range, from toys shown sitting in peoples’ laps up through long-legged coursers standing as high as a man’s hips or a horse’s elbow.

FIGURE 12

A brindle-coated, bat-eared harrier wearing a collar, tied by a rope to a T-shaped stake in front of a beehive-shaped wattle doghouse. Detail from the Dominus Julius mosaic, dating to about 375 A.D. (Bardo Museum, Tunis (14cm)).

While a metric scale is obviously not provided in Roman artwork, there can be no question that the intention was to represent different sizes and phenotypes. In terms of apparent shoulder height and build, we classify these as follows:

1. Small dogs:
   (a) Toys (analogous to modern Maltese, Chihuahua, or Pomeranian).
   (b) Miniatures (somewhat larger than toys; analogous to Miniature Poodle, small Spitz, Miniature Schnauzer).
   (c) Dwarfs (analogous to "old fashioned" Dachshunds or to many modern terriers such as the Scottish or Patterdale).
2. Medium-sized dogs:
   (a) Harriers (analogous to the Ibizan or I'Siqha Hounds or the so-called "Pharaoh hound").
   (b) "Pack hounds" (dogs with body size and type similar to living pariahs, village dogs, and dingoes).
   (c) Boarhounds (analogous to the Cane Corso, Chow-Chow, or Shar-Pei).
3. Large dogs:
   (a) Coursers (analogous to the Scottish Deerhound or Irish Wolfhound)
   (b) Mastiffs (analogous to the Turkish Kuvash or several European and American mastiff breeds).

Each of these morphotypes is represented by bony remains in the Vindolanda collection, and on the basis of standard manual forensic reconstruction techniques (Crockford & Pye, 1997) we provide a "biotype reconstruction" (Valadez *et al.*, 2006) of the living appearance of each (Figure 19). It is important to note that reconstructions of head shape and body proportions are based strictly upon bony remains, and were made by the lead author prior to our survey of Roman artwork. The final reconstructions presented here convey typical stance, ear shape and carriage, tail carriage, and pelage length and thickness as suggested by contemporary Roman artwork. The reconstructions are labeled by category, with shoulder height calculated using Harcourt's (1974) factors.

The dwarf, harrier, and courser were reconstructed from complete or nearly complete associated material. They are clearly the products of selective breeding, as are the toy and miniature, the boarhound and mastiff. The pack hound/village dog represents a medium-sized eumorphic type,

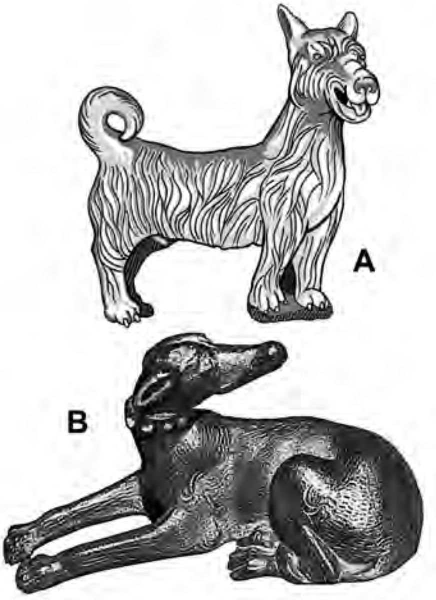

FIGURE 13

Facsimile drawings of two well-known Roman dog statuettes from Britain; approximate maximum dimension of dog image in (cm). A, a shaggy-haired dog with "dwarf" conformation, possibly representing the *Agassaean* breed as known to the Romans. From Coventina's Well situated less than 1.6 km (1 mi) from Vindolanda (4.8cm). B, a smooth-haired dog with long snout and long-legged, gracile conformation, from Lydney Park in Gloucestershire. As scale is impossible to determine, this statuette could represent either a harrier or a courser. It may represent the type of dog called *Vertragus* by the Romans (9.2cm).

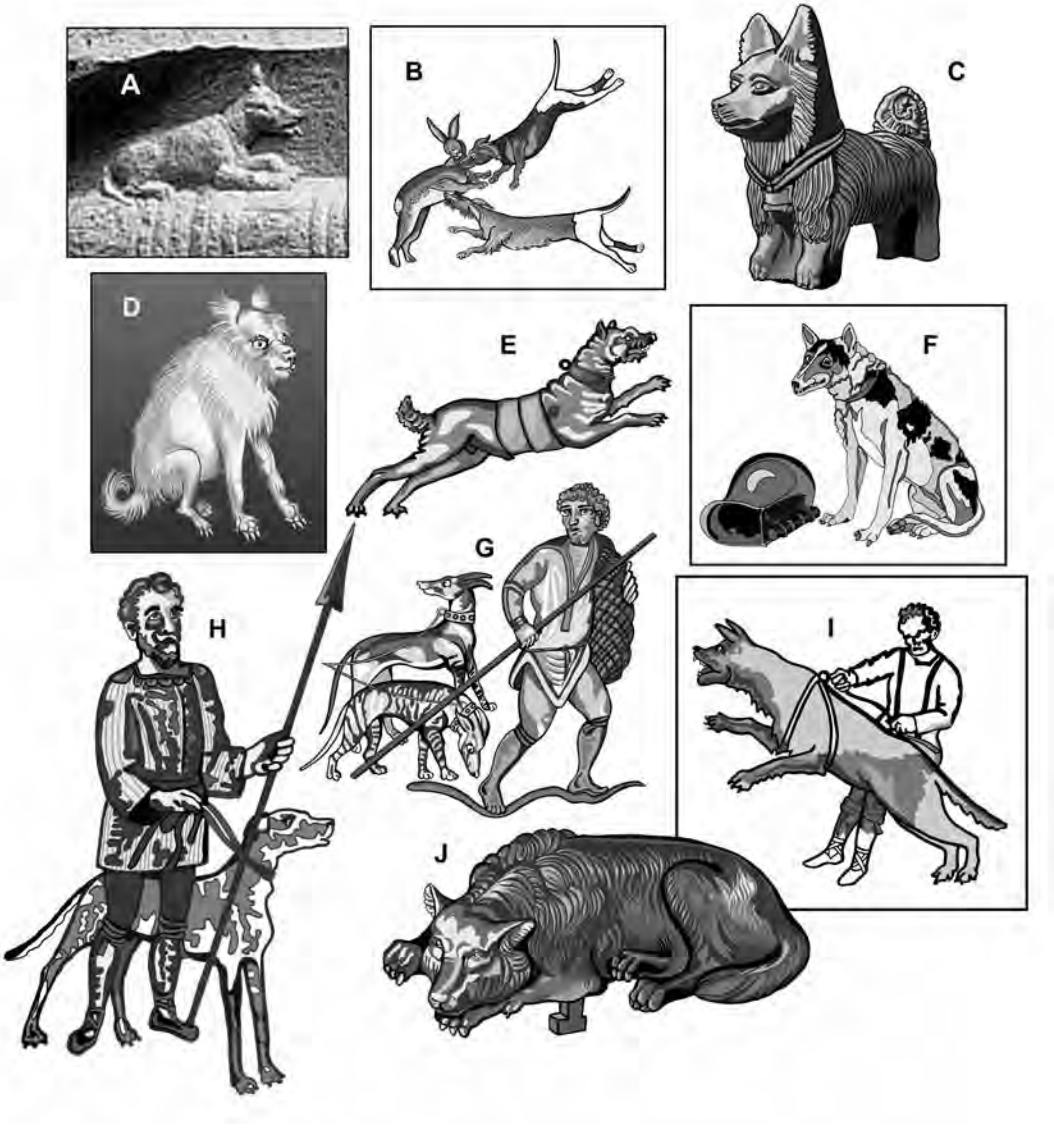

FIGURE 14

A sampling of Roman artwork representing dogs; facsimile drawings; approximate maximum dimension of dog image in (cm). A, a dog of dwarf-hound type riding atop beer barrels loaded upon an oxcart. Many works of art provide a scale by which the size of the dog may be judged (From a 2nd-century sarcophagus (15cm); British Museum). B, a pair of long-bodied, short-legged dwarf-hounds attacking a hare (detail from a floor mosaic in the Palace of Constantine, Alexandria, Egypt (40cm). C, statuette representing a toy dog similar to a Maltese (from Roman Egypt; British Museum (17.3cm). D, a wire-haired and snaggle-toothed toy dog (detail from a Pompeiian wall painting (35cm). E, a boarhound; this image is excerpted from a scene in which several such dogs are shown pursuing a boar. Note the stout build, docked tail and ears, and wrinkled skin. Roman boarhounds are frequently shown wearing armor consisting of a heavy, studded leather collar and leather straps wrapped around the midbody (from an apsidal mosaic in the Bardo Museum, Tunis (62cm). F, a common dog with dingo-like build, exquisitely rendered in microtesserae (from the Royal Palace at Alexandria (72cm). G, a brace of harriers, one brindled and the other fawn-colored. Note the gracile build, long, batlike ears and the height, less than the hunter's knees. Such dogs were used by the Romans to pursue hares, foxes, and birds (detail from the Dominus Julius mosaic, Bardo Museum, Tunis (44cm). H, a courser. Note the soft, flaplike ears and larger size, the dog being taller than the hunter's knees. The "deerhound" or "wolfhound" of Roman times was not as tall as modern dogs of these breeds (from a Gallo–Roman floor mosaic, Lillebonne Museum, Rouen (56cm). I, a mastiff. These massive, woolly dogs, known in antiquity as "Molossians", were used in war, as guard-dogs, and to pursue large or particularly dangerous prey (from a floor mosaic at Le Kef, near Carthage, Bardo Museum (35cm). J, tanged statuette of a mastiff from the lid of a treasure-box that shows the dog's thick, woolly coat (from Roman Syria, British Museum (24cm).

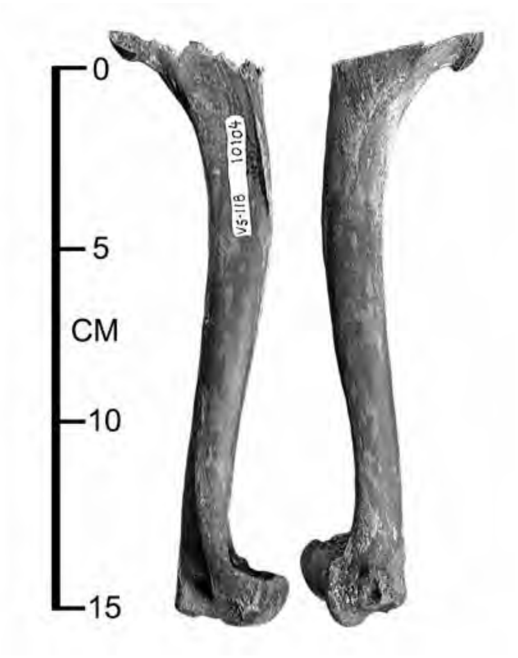

FIGURE 15

Vindolanda specimen VS-118 10104, humerus of a dog with dingo-like build, bearing evidence of butchery. The total length of this bone is estimated to be 170 mm, with a slenderness index (minimum shaft diameter × 100/estimated total length) of about 7.4.

but skulls in this size range are variable with some showing much more breadth of face and more "step" to the forehead than others which probably represent village dogs. While these biotype reconstructions illustrate general characteristics and the overall range of phenotypic variation, subsequent papers will analyze and document in detail the bony remains of each.

DISCUSSION

Ethnographic Evidence for Morphological Diversity in Roman-Era Dogs

Harcourt (1974) argues that "artistic evidence" should not be used in archaeological studies of dogs because "there is no way to know how true to life [artistic representations are] either in conformation or in scale". However, at the same time, he quotes Strabo—and we would add Cato and Varro (Anonymous, 1913); Columella (Forstner & Heffner, 1968); and the Vindolanda tablets themselves (Bowman & Thomas, 1994, 2003; Birley, 2002; Birley, 2009)—all of which attest the existence of various kinds of dog from different geographic areas of the ancient world. The almost fanatical naturalism of Roman artists whose reputation depended upon their ability to render their subjects with fidelity is well known (Figures 13, 14; Toynbee, 1973).

FIGURE 16

Vindolanda specimens V13-26B 23405 and V13-26B 23283, associated radius and ulna of a chondrodystrophic "dwarf" hound found near the roundhouse complex. The bones have been thoroughly gnawed. The ulna measures 111.61 mm, the radius 95.27 mm. The limb slenderness index of the radius is a relatively high 10.03, typical of dwarf dogs.

FIGURE 17

Vindolanda specimens V13-27B 22942 and V13-27B 23282, associated humerus and radius of a harrier, a dog of medium size with gracile conformation, whose bones were found near the roundhouse complex. The humerus measures 133.56 mm, with an index of 6.63; the radius measures 127.26 mm, with an index of 4.8.

FIGURE 18

Vindolanda specimens V13-2B 23516 (tibia), V13-11B 23170 (radius), associated limb bones of a puppy found in rubble just outside the roundhouse; and Vindolanda specimen V13-15B 26341, femur of a puppy found in a roundhouse drain. The limb bones of juvenile dogs are stouter than they will be at maturity, as circumferential growth somewhat outpaces lengthwise growth during puppyhood. These bones might thus pertain to a pup of boarhound type, but given their small size, they more probably pertain to a dwarf hound. Estimated length of femur 26341 = 100 mm with estimated index of 10.2; estimated length of tibia 23430 (center) = 97 mm with estimated index of 9.0; estimated length of radius 23170 = 81 mm with estimated index of 13.6.

Harcourt discounts a well-crafted statuette from Lydney Park in Gloucestershire (Figure 13B) as representing a Greyhound, saying “although nearly 100 skulls of the Roman period have been examined in the course of this study, not one has been found that bore the slightest resemblance to that of the Greyhound, thus casting further doubt upon the validity of such representations.” It is Harcourt himself, we note however, who says that the statuette resembles a Greyhound, and then argues against his own supposition. We consider it unlikely that any artist of Roman Britain would be capable of representing a type of dog that had probably not yet come into existence. We believe rather that the Lydney Park statuette, along with another quality statuette recovered from Coventina’s Well less than two miles from Vindolanda (Figure 13A), represent dogs for which we have ample osteological evidence, vis., dogs whose conformation was like that of the Scottish deerhound and the Scottish terrier, respectively (Walsh, 1878; Palmer, 1981; Phillips *et al*., 2009). Ancient names for these dogs are “Vertragus” and “Agassaean,” respectively (Birley, 2002).

Morphological similarity does not necessarily equate to affinity with any modern breed. The essential reason for this is that modern dog breeds are often founded upon particular known individuals, and all breeds are defined by physical characteristics and behavioral traits that are rarely or never preserved in the archaeological record (Crowley & Adelman, 1998). Nonetheless, we concur with Phillips *et al*. (2009) in the belief that it is “unreasonable to consider the comparison of archaeological dog remains to modern breeds as too problematic to be of use to zooarchaeological analysis.” Clark (1995: 11; italics ours) states, “The increase in variation of size and shape of the domestic dog over time is a phenomenon which is *inextricably bound to human attitudes*, and there is no valid reason why a skeleton cannot be said to derive from a dog of the same size as a particular modern breed, or [to avoid describing a skull] as being of a similar shape to that of a known breed.”

Ethnographic data are highly useful when applied with appropriate cautions—especially, that culturally-specific artistic style and iconographic convention are recognized, artistic context is taken into consideration, and over-interpretation is avoided (Toynbee, 1973; Clutton-Brock, 2000; Daróczi-Szabó, 2002; Trantalidou, 2006). In addition to morphological analysis of bones, we follow many other authors in surveying contemporary dog

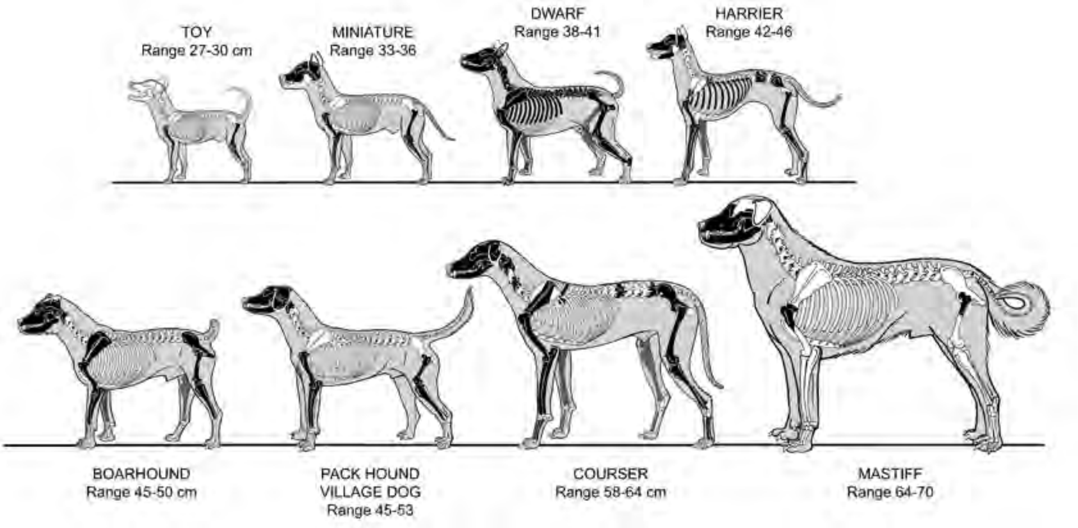

FIGURE 19

Biotype reconstructions of the eight dog morphotypes known from Roman Vindolanda. In characterizing them, we deliberately avoid using the names of modern breeds. Note that each occupies a height range of 3–8 cm, and that some ranges partially overlap; bones pertaining to different morphotypes are distinguished on the basis of slenderness index and anatomical details. Black color delineates bodyparts known from bones. The dwarf hound, harrier, boarhound, and courser are known from extensive associated material, and complete or nearly complete skull material is known from Vindolanda for all but the toy.

artwork (Toynbee, 1973; Manaserian & Antonian, 2000; Schwartz, 2000; Valadez Azúa, 2000; Brewer *et al.*, 2001; Daróczi-Szabó, 2002; Trantalidou, 2006). We consider this survey important because the naturalistic representations of Roman artists contain detailed and reliable information on "perishable" physical traits (Daróczi-Szabó, 2002).

Dog Size Distribution

Dogs whose living height ranged from about 27 to 70 cm are present in the Vindolanda collection (Figure 19). Harcourt (1974) reported a similar size range for dogs from British archaeological sites of all periods. Johnstone & Albarella (2002), Grimm (2007), and Baxter & Nussbaumer (2009) document more recent finds that likewise fall within Harcourt's (1974) reported range. Baxter (2010 a, b) and Ayton (2011) reported small dogs, but the total size range of Romano–British dogs, including those from Vindolanda, is less than that from some contemporaneous sites on the European continent: for example Heidelberg-Neuenheim in Germany (Luttschwager, 1965), Tac Gorsium (Bökönyi, 1984; Bartosiewicz, 2000), and Classe (Farello, 1995). A skull from a North African grave-field at Yasmina (MacKinnon & Belanger, 2002) is the smallest Roman-era dog yet reported.

Harcourt (1974) believed that the appearance of small (toy and dwarf) dog morphotypes in Britain coincided with the Roman invasion of the main British island in the last century B.C., but subsequent work by Clark (1995) suggests that they first appeared there somewhat earlier, in the late Iron Age. This implies that the husbandry techniques required for the production and maintenance of phenotypic distinctiveness were not invented by the Romans, but were already known to peoples whom the Romans conquered or with whom they traded.

References in the Vindolanda tablets (Bowman & Thomas, 1994, 2003), along with the wider corpus of Roman writing and record-keeping (Birley, 2002; Birley, 2009), allow us to ascertain something about the people occupying Vindolanda at any given period. So too do the thousands of non-osteological artifacts of every type that have been excavated from the site (Birley, 2003, 2009, 2013; Birley & Blake, 2005, 2007; Blake, 2003, 2014). The succession of soldiers and civilians who occupied Vindolanda originated in areas far from the site and came there by orders of the Emperor, following their tribal leaders whom the Romans designated as military commanders (Birley, 2002; Birley, 2009).

It is reasonable to assume that the type of dog most preferred by peoples of different culture and geographic area of origin might differ. Herein we document correlation of dog size with time period. Insofar as dogs of different sizes also tend to be of different phenotype, we can provide the following observations.

The "Vindolanda periods" correspond to changes in the cultural identity of the garrison (Figure 5; Birley, 2002; Birley, 2003). Cohorts drawn from at least five different geographic areas lived at Vindolanda over the more than three centuries during which Roman-allied people maintained it. The Tungrian and Batavian cohorts were recruited from areas in Belgium and the Netherlands not very far apart, and they appear to have been culturally similar (Birley, 2002). The Nervians (if indeed they were the site's occupants during Periods VI and VI-A; Birley, 2002) also came from Belgium. The Gauls, occupants for most of Periods VII and VIII, were from France. During Period VI-B, the Severan "anomaly", there may have been troops from North Africa on site, but also evidently a highly-disciplined elite corps who came directly from Italy, plus, in all likelihood, local Celts occupying the tightly-packed, ordered rows of roundhouses built at Vindolanda (Birley, 2002; Birley, 2003).

The most significant point evident in Figure 5 is the sudden advent of small dogs which occurs at the beginning of Period IV, and the persistent high frequency of small dogs at Vindolanda thereafter. That there were no small dogs on site during Periods I–III, but that the Tungrians kept them at high frequency during Periods IV and V when they returned after an absence of only a few years, argues for the idea that small dogs simply did not become available in the far north of England until the beginning of Period IV.

Large dogs, by contrast, were in Roman time either coursers or guard-dogs, whereas medium-sized dogs were harriers, boarhounds, or else village dogs with dingo-like conformation. Contemporary mosaics show that tall, swift dogs were used to pursue deer with the hunter and the master of hounds following upon horseback, while stout, strong bulldogs and mastiffs were used against wild boar (Toynbee, 1973). There are several references in the Vindolanda writing tablets to hunting activity by commanding officers (Bowman & Thomas, 1994: *Tab Vindol 233*; Bowman & Thomas, 2003: *Tabs Vindol 593*, *594*, *615*). Hunts requiring large dogs were high-status activities reserved for military officers and Legionaries (Alcock, 2001; Birley, 2003). Nonetheless the raising, keeping, training and use of hunting hounds was a complex activity which doubtless involved the efforts of many community members (Birley, 2003).

Nearly all dogs on site during Periods I through III were of medium size. We know from several indications in the Vindolanda Tablets that Flavius Cerialis, probably a Batavian chieftain who served as the Roman commandant of the garrison from about 100 through 105 A.D., was an avid hunter, and so in all likelihood was his predecessor Flavius Genialis (Birley, 2002). It is quite possible that the few large dogs recovered from Periods II–III were, in fact, members of an elite hunting pack belonging to one or both of these men.

Legionaries directly from Rome are thought to have been on site during the Severan Period VI-B (Birley, 2003 and *pers. comm.* 2014), and it is during this period that we find the highest percentage of large dogs. Next highest is associated with the Nervian periods VI and VI-A, but the Gauls who occupied Vindolanda in later periods also kept significant numbers of large dogs.

Ecological conditions in the vicinity of the site changed during the centuries that the Romans occupied it (Birley, 2003). Mature forest originally surrounded the site (Tyres, 2007, 2014), forming a patchwork with fields in late-successional stage (Huntley, 2007, 2014). The plateau upon which most of the Vindolanda forts were built is surrounded on three sides by streams margined by thick undergrowth, and less than one mile away, a reedy tarn lies across low ground in a moist, flowering meadow. To the east, heather-covered slopes stretch upwards to rocky heights. Originally, abundant game populated this richly diverse environmental mosaic, including deer, boar, foxes, hare and comestible wild birds, but the Romans gradually degraded their surroundings over time, and the frequency and diversity of the remains of game species declined (Hodgson, 1977; Bennett, 2005, 2007, 2014; Bennett & Timm, 2013; Birley, 2013). After the end of the Severan Period, however, garrison size as well as the total population at Vindolanda were less, and the bones of game animals rebound somewhat in frequency. The frequency of large dogs also probably reflects the relative wealth and prosperity of the Gaulish cohort (Alcock, 2001; Birley, 2003).

CONCLUSIONS

The Vindolanda dog collection demonstrates that a range of dog morphotypes was present at this remote garrison during most of its history. While some Vindolanda dogs show phenotype similar to modern village dogs or Australian dingoes, the majority are morphologically different and the range of size and phenotype is far greater than either dingoes or British dogs of the Neolithic. Dental wear documents that dogs of all ages were kept, while the skull of an old dog injured while boar-hunting but subsequently healed shows that “working” dogs were valued. The number of juvenile dogs is relatively low and evidence for skinning, butchering, or gnawing is rare. There is no evidence at Vindolanda that dogs were raised for slaughter, or interred in any ritual context.

Images from contemporary mosaics, as well as the wider Latin literature and specific tablet references, corroborate the idea that large and medium-sized dogs at Vindolanda were used to hunt deer, boar, birds, foxes, and hares. There were also miniature and dwarf dogs small enough to sit on peoples’ laps, but which might also have functioned in hunting small game or house mice. Mastiffs functioned as guard-dogs and war-dogs. That dogs were bred and raised at Vindolanda is indicated by the remains of a beehive-shaped wattle dog-house associated with juvenile and gnawed dog bones.

The frequency of large, medium, and small dogs changes with time at Vindolanda, corresponding to change in the region of origin of the resident cohort. Morphometric analysis (Bennett *et al*., 2016) and measurement of dog pawprints impressed in ceramic building materials (Bennett, 2012) provide size data, while documentation of contemporary Roman artwork provides insight regarding perishable characteristics of pelage, coloration, and carriage. Considered together, this evidence allows biotype reconstruction of eight different types of dog that were present at Roman Vindolanda.

The trading reach of the Roman Empire was vast, encompassing much of Eurasia. We demonstrate herein that a range of dog morphotypes were bred at Vindolanda and that they probably served many functions. Dogs were no doubt highly valued and some, perhaps, were obtained from great distances. The striking resemblance of the Trumpington dog reported by Baxter & Nussbaumer (2009) to the modern Chinese Shar-Pei, and of a toy dog reported by MacKinnon & Belanger (2002) to the modern Maltese—to cite only two examples—suggest that some Vindolanda dogs may also have originated far away. However, because dog morphotypology does not have the same basis as the assignment of breed identity, it is not appropriate on the basis of the evidence adduced here to suggest that any ancient dog “belongs to” any modern breed. Future DNA studies may demonstrate ancestor–descendant relationships (Larson *et al*., 2012); until then, the safest course is to understand ancient dogs as functional analogs of the modern dog breeds that they resemble.

ACKNOWLEDGEMENTS

We gratefully acknowledge the financial support of the Vindolanda Trust and its Director, Patricia Birley. Andrew Birley and Justin Blake provided indispensable on-site guidance, and Andrew kindly provided air photos of the “roundhouse complex”. Ian Baxter generously provided discussion, measurements, and many photos; he, Andrew Birley, and Anthony Birley read and improved our first drafts. Greg Campbell generously advised us in database design and multivariate analysis. Salvador Gonzales and Wilson Colón provided Spanish-language assistance. Barbara Birley, Louisa Gidney, Jessica Grimm, Geraldine Missig, and Marc Nussbaumer kindly supplied specimen photographs. Sarah Taylor assisted with measurements. Assistance and collection access was provided by David Berman, University of Kansas Natural History Museum.

REFERENCES

Alcock, J. P. 2001: *Food in Roman Britain.* Tempus Publishing, Stroud, Gloucestershire.

ANONYMOUS 1913: *Roman Farm Management: Cato and Varro, Done into English with Notes of Modern Instances.* The MacMillan Co., New York.

AYTON, G. 2011: Animal bone from a Roman well at Rothwell Haigh, West Yorkshire. *English Heritage Research Department Report Service* 66-2011: 1–62.

ANCIENT ROMAN MOSAICS IN THE BARDO NATIONAL MUSEUM (TUNIS) 2014: Available at: http://commons.wikimedia.org/wiki/Category:Ancient_Roman_mosaics_in_the_Bardo_National_Museum_(Tunis); and http://www.bardomuseum.tn

BARTOSIEWICZ, L. 2000: Metric variability in Roman period dogs in Pannonia Province and the Barbaricum (Hungary). In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 181-189. B.A.R. (International Series) 889. Oxford.

BAXTER, I. L. 2002: A dwarf hound skeleton from a Romano–British grave at York Road, Leicester, England, U.K., with a discussion of other Roman small dog types and speculation regarding their respective aetiologies. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 12-23. Oxbow Books 85. Oxford.

— 2010 a: Small Roman dogs. *Alexandria Archive* 901: 1–9.
Available at: http://alexandriaarchive.org/bonecommons/items/show/901

— 2010 b: A re-examination of the Thistleton canids. *Alexandria Archive* 885: 1–11.

Available at:http://alexandriaarchive.org/bonecommons/items/show/885

BAXTER, I. L. & NUSSBAUMER, M. 2009: Evidence of morphometric variation in an Iron Age dog cranium from Trumpington, Cambridgeshire, U.K. *Archaeofauna* 18: 69–78.

BEN-ABED BEN-KHADER, A.; SOREN, D. & COOPER, M. (eds.) 1987: *Carthage: a Mosaic of Ancient Tunisia.* American Museum of Natural History & W.W. Norton publishers, New York.

BENNETT, D. 2005: Bones from the Severan ditch, Area A, 2004. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2003–2004*: 115-186. The Vindolanda Trust, Hexham, Northumberland.

— 2007: Ongoing mammal bone research at Vindolanda: interim report on the 2005–2006 collections. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2005–2006*: 200-204. The Vindolanda Trust, Hexham, Northumberland.

— 2012: Life history information from tracks of domestic dogs (*Canis familiaris*) in ceramic building materials from a Roman bath-house at Vindolanda, Northumberland, England. *Archaeofauna* 21: 7–36.

— 2014: Faunal remains from third-century contexts at Vindolanda. In: Blake, J. (ed.): *Vindolanda Research: the Excavations of 2007–2012 in the* Vicus *or Extramural Settlement ('Area B')*: 197-216. Roman Army Museum Publications, Brampton, Greenhead.

BENNETT, D. & TIMM, R. M. 2013: Microfaunal remains from the East granary, Roman Vindolanda: Evidence for human–animal interactions. In: Birley, A. (ed.): *The Vindolanda Granary Excavations*: 72-98. Roman Army Museum Publications, Brampton, Greenhead.

BENNETT, D.; CAMPBELL, G. & TIMM, R. M. 2016: The dogs of Roman Vindolanda, Part I: morphometric techniques useful in differentiating domestic, feral, and wild canids. *Archaeofauna* 25: 79-106.

BIRLEY, A. 2002: *Garrison Life at Vindolanda: a Band of Brothers.* Tempus Publishing, Gloucestershire.

— (ed.) 2003: *Vindolanda Research Report, 2003: the Excavations of 2001–2002*. Volume I. The Vindolanda Trust, Bardon Mill, Hexham.

— (ed.) 2013: *The Vindolanda Granary Excavations.* Roman Army Museum Publications, Brampton, Greenhead.

BIRLEY, A. & BLAKE, J. (eds.) 2005: *Vindolanda Excavations, 2003–2004.* The Vindolanda Trust, Hexham, Northumberland.

— (eds.) 2007: *Vindolanda Research Report: the Excavations of 2005–2006*. The Vindolanda Trust, Hexham, Northumberland.

BIRLEY, R. 2007: Stamps on Samian and mortaria. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2005–2006*: 147-149. The Vindolanda Trust, Hexham, Northumberland.

— 2009: *Vindolanda: a Roman Frontier Fort on Hadrian's Wall.* Amberley Publishing, Gloucestershire.

BLAKE, J. 2003: The excavations of 2001–2002: The Romano–Celtic temple and other sites. In: Blake, J. (ed.): *Vindolanda Research Report 2003*: 1-95. Vol. II. Roman Army Museum Publications, Carvoran, Greenhead, Northumberland.

— 2014: *Vindolanda Research: the Excavations of 2007–2012 in the* Vicus *or Extramural Settlement ('Area B').* Roman Army Museum Publications, Brampton, Greenhead.

BLANCHARD-LEMEE, M. & ENNAIFER, M. 1996: *Mosaics of Roman Africa: Floor Mosaics from Tunisia*. George Braziller, New York.

BÖKÖNYI, S. 1984: *Animal Husbandry and Hunting in Tac-Gorsium*. Akadémiai Kiadó, Budapest.

BOWMAN, A. K. & THOMAS, J. D. 1994: *The Vindolanda Writing-tablets*: *Tabulae Vindolandenses II.* British Museum Press, London.

— 2003: *The Vindolanda Writing-tablets: Tabulae Vindolandenses III*. British Museum Press, London.

Boyko, A. R.; Quignon, P.; Li, L.; Schoenebeck, J. J.; Degenhardt, J. D.; Lohmueller, K. E.; Zhao, K.; Brisbin, A.; Parker, H. G.; Vonholdt, B. M.; Cargill, M.; Auton, A.; Reynolds, A.; Elkahloun, A. G.; Castelhano, M.; Mosher, D. S.; Sutter, N. B.; Johnson, G. S.; Novembre, J.; Hubisz, M. J.; Siepel, A.; Wayne, R. K.; Bustamante, C. D. & Ostrander, E. A. 2010: A simple genetic architecture underlies morphological variation in dogs. *PloS Biology* 8: e1000451.

Brewer, D.; Clark, T. & Phillips, A. 2001: *Dogs in antiquity: Anubis to Cerberus, the Origins of the Domestic Dog.* Aris and Phillips, Warminster.

Brickstock, R. 2003: The coins. In: Birley, A. (ed.): *Vindolanda Research Report 2003: the Excavations of 2001–2002*: 121-124. Vol. I. The Vindolanda Trust, Hexham, Northumberland.

— 2005: The coins. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2003–2004*: 204-209. The Vindolanda Trust, Hexham, Northumberland.

— 2007: The coins. In: Birley, A. & Blake, J. (eds.): *Vindolanda Research Report: the Excavations of 2005–2006*: 119-129. The Vindolanda Trust, Hexham, Northumberland.

— 2013: Vindolanda 2008: the coins. In: Birley, A. (ed.): *The Vindolanda Granary Excavations*: 121-167. Roman Army Museum Publications, Brampton, Greenhead.

— 2014: Coin identifications. In: Blake, J. (ed.): *Vindolanda Research: the Excavations of 2007–2012 in the* Vicus *or Extramural Settlement (‘Area B’)*: 125-128. Roman Army Museum Publications, Brampton, Greenhead.

Clark, K. M. 1995: The later prehistoric and protohistoric dog: the emergence of canine diversity. *Archaeozoologia* 2: 9–32.

Clutton-Brock, J. 2000: Introduction. In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 3-7. B.A.R. (International Series) 889. Oxford.

Corbett, L. 1995: *The Dingo in Australia and Asia.* University of New South Wales Press, Sydney.

Cram, L. 2000: Varieties of dog in Roman Britain. In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 171-180. B.A.R. (International Series) 889. Oxford.

Crockford, S. J. 2000: Dog evolution: a role for thyroid hormone physiology in domestication changes. In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 11-20. B.A.R. (International Series) 889. Oxford.

Crockford, S. J. & Pye, C. J. 1997: Forensic reconstruction of prehistoric dogs from the Northwest Coast. *Journal Canadien d’Archéologie* 21: 149–153.

Crowley, J. & Adelman, B. (eds.) 1998: *The Complete Dog Book: Official Publication of the American Kennel Club*. 19th ed. Howell Book House, New York.

Daróczi-Szabó, M. 2002: Variability in Medieval dogs from Hungary. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 95-105. Oxbow Books 85, Oxford.

Davis, S. J. M. 1995: *The Archaeology of Animals.* Yale University Press, New Haven.

Domínguez-Solera, S. D. & Domínguez-Rodrigo, M. 2009: A taphonomic study of bone modification and of tooth-mark patterns on limb bone portions chewed by suids. *International Journal of Osteoarchaeology* 19: 345–363.

Dunand, F. & Lichtenberg, R. 2005: Des chiens momifiés à El-Deir, Oasis de Kharga. *Bulletin de L’Institut Français d’Archéologie Orientale* 105: 75–88.

Dunbain, K. M. D. 1978: *Mosaics of Roman North Africa: Studies in Iconography and Patronage*. Clarendon Press, Oxford.

Farello, P. 1995: I cani tardo-antichi rinvenuti in un condoto fognario de Classe (RA). *Estratto da Padusa Quaderni* 1: 295–308.

Forstner, F. S. & Heffner, E. H. Trs. 1968: *Lucius Junius Moderatus Columella on Agriculture.* Vol. II. Heinemann Loeb Classical Library, London.

Greenfield, H. J. 1988: Bone consumption by pigs in a contemporary Serbian village: implications for the interpretation of prehistoric faunal assemblages. *Journal of Field Archaeology* 15: 473–479.

Grimm, J. 2007: A dog’s life: Animal bone from a Romano–British ritual shaft at Springhead, Kent (UK). *Sonderdruck aus Beiträge zur Archäeozoologie und Prähistorischen Anthropologie* 6: 54–75.

Guillaud, J. & Guillaud, M. 1990: *Frescoes in the Time of Pompeii.* Guillaud Editions, New York.

Hambleton, E. 2003: Report on the remains of a dog (SF8659) from Vindolanda. In: Birley, A. (ed.): *Vindolnda Research Reports: the Excavations of 2001–2002*: 250-256. Vol. I. The Vindolanda Trust, Hexham, Northumberland.

Harcourt, R. A. 1974: The dog in prehistoric and early historic Britain. *Journal of Archaeological Science* 1: 151–175.

Higgs, W. 2001: Ichnology in Archaeology: Comparison of Two Recently Excavated Assemblages as a Case Study in the Recording and Analysis of Archaeological Footprints. Unpublished MSc. Thesis. University of York, York.

Hodgson, G. W. I. 1977: Vindolanda: the animal remains, 1970–1975. *Vindolanda Research Reports*. The Vindolanda Trust, Hexham, Northumberland.

Horard-Herbin, M. P. 2000: Dog management and use in the late Iron Age: evidence from the Gallic site of Levroux (France). In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 115-121. B.A.R. (International Series) 889. Oxford.

Huntley, J. P. 2007: Interim report on plant remains and charcoal. In: Birley, A. & Blake, J. (eds.): *Vindolanda Research Report: the Excavations of 2005–2006*: 205-219. The Vindolanda Trust, Bardon Mill, Hexham, Northumberland.

Huntley, J. P. 2014: Vindolanda environmental samples. In: Blake, J. (ed.): *Vindolanda Research: the Excavations of 2007–2012 in the* Vicus *or Extramural Settlement (‘Area B’)*: 217-224. Roman Army Museum Publications, Brampton, Greenhead.

Johnstone, C. & Albarella, U. 2002: The late Iron Age and Romano–British mammal and bird bone assemblage from Elms Farm, Heybridge, Essex (Site Code: Hyef 93–95). *English Heritage Centre for Archaeology Report* 45: 1–200.

Joyce, H. 1981: *The Decoration of Walls, Ceilings, and Floor in Italy in the Second and Third Centuries A.D.* G. Bretschneider, Rome.

Keeton, W. T. 1972: *Biological Science*. 2nd edition. Norton, New York.

Koch, D. A; Arnold, S.; Hubler, M. & Montavon, P. M. 2003: Brachycephalic syndrome in dogs. *Compendium Continuing Education for Veterinarians* 25: 48–55.

Larson, G.; Karlsson, E. K.; Perri, A.; Webster, M. T.; Ho, S. Y. W.; Peters, J.; Stahl, P. W.; Piper, P. J.; Lingaas, F.; Fredholm, M.; Comstock, K. E.; Modiano, J. F.; Schelling, C.; Agoulnik, A. L.; Leegwater, P. A.; Dobney, K.; Vigne, J-D.; Vilá, C.; Andersson, L. & Lindblad-Toh, K. 2012: Rethinking dog domestication by integrating genetics, archeology, and biogeography. *PNAS* 109: 1–6.

Luttschwager, J. 1965: Ein zwerghund aus römischen Graberfeld and der Berliner Strasse zu Heidelberg–Neuenheim. *Zeitschrift für Säugetierkunde* 30: 24–30.

Mackinnon, M. & Belanger, K. 2002: In sickness and health: care for an arthritic Maltese dog from the Roman cemetery of Yasmina, Carthage, Tunisia. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 38-43. Proceedings of the 9th ICAZ Conference, Durham. Oxbow Books 85, Oxford.

Macnulty, D. R.; Smith, D. W.; Vucetich, J. A.; Mech, L. D.; Stahler, D. R. & Packer, C. 2009: Predatory senescence in ageing wolves. *Ecology Letters* 12: 1347–1356.

Manasarian, N. H. & Antonian, L. 2000: Dogs of Armenia. In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 227-238. B.A.R. (International Series) 889. Oxford.

Marliére, E. 2003: The wooden containers and amphorae, including the stamps. In: Birley, A. (ed.): *Vindolanda Research Report 2003: the Excavations of 2001–2002*: 125-180. Vol. I. The Vindolanda Trust, Hexham, Northumberland.

— 2007: Nouveaux timbres amphoriques a Vindolanda. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2005–2006*: 144-146. The Vindolanda Trust, Hexham, Northumberland.

Marliére, E. & Torres Costa, J. 2005: The amphorae and barrels. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2003–2004*: 214-236. The Vindolanda Trust, Hexham, Northumberland.

Martin, L. D. & Gilbert, B. M. 1978: Excavations at Natural Trap Cave. *Transactions of the Nebraska Academy of Sciences* 6: 107–116.

Méniel, P. 1992: *Les Sacrifices d’Animaux Chez les Galois.* Errance, Paris.

Murphy, E. & Ó Baoill, R. 2000: It’s a dog’s life: butchered medieval dogs from Carrickfergus, Co. Antrim. *Archaeology Ireland* 14: 24–25.

Palmer, J. 1981: *An Illustrated Guide to Dogs.* Arco Publishing, New York.

Phillips, C.; Baxter, I. L. & Nussbaumer, M. 2009: The application of discriminant function analysis to archaeological dog remains as an aid to the elucidation of possible affinities with modern breeds. *Archaeofauna* 18: 51–64.

Pompeii and Herculaneum Hosaics and Paintings 2014: Available at: http://mosaicartsource.wordpress.com/category/world-mosaics/italy/pompeii-herculaneum

Schefold, K. 1972: *La Peinture Pompéienne: Essai sur l’Évolution de sa Signification*. Latomus, Bruxelles.

Schwartz, M. 2000: The form and meaning of Maya and Mississippian dog representations. In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 217-226. B.A.R. (International Series) 889. Oxford.

Sheehan-Finn, K. 2013: Stamps on amphora, mortaria and terra sigillata (Samian). In: Birley, A. (ed.): *The Vindolanda Granary Excavations*: 168-173. Roman Army Museum Publications, Brampton, Greenhead.

— 2014: Stamps on amphorae, mortaria, and samian ware. In: Birley, A. (ed.): *Vindolanda Research: the Excavations of 2007–2012 in the* Vicus *or Extramural Settlement ('Area B')*: 129-144. Roman Army Museum Publications, Brampton, Greenhead.

Silver, I. A. 1970: The ageing of domestic animals. In: Brothwell, E. & Higgs, E. (eds.): *Science in Archaeology: a Survey of Progress and Research*: 283-302. Praeger Publishers, New York.

Smith, K. 2006: *Guides, Guards, and Gifts to the Gods: Domesticated Dogs in the Art and Archaeology of Iron Age and Roman Britain*: 1-84. B.A.R. (British Series) 422. Oxford.

Snyder, L. M. & Moore, E. A. (eds.) 2006: *Dogs and People in Social, Working, Economic or Symbolic Interaction.* Proceedings of the 9th ICAZ Conference, Durham. Oxbow Books, Oxford.

Sullivan, M. A. 2014: Bluffton University Index of Art Historical Sites. Piazza Armerina, Sicily. http://www.bluffton.edu/~sullivanm/armerina/armerina2.html

Sutter, N. B.; Bustamante, C. D.; Chase, K.; Gray, M. M.; Zhao, K.; Zhu, L.; Padhukasahasram, B.; Karlins, E.; Davis, S.; Jones, P. G.; Quignon, P.; Johnson, G. S.; Parker, H. G.; Fretwell, N.; Mosher, D. S.; Lawler, D. F.; Satyaraj, E.; Nordborg, M.; Lark, K. G.; Wayne, R. K. & Ostrander, E. A. 2007: A single IGF1 allele is a major determinant of small size in dogs. *Science* 316: 112–115.

Toynbee, J. M. C. 1973: *Animals in Roman Life and Art*. Johns Hopkins University Press, Baltimore.

Trantalidou, K. 2006: Companions from the oldest times: dogs in ancient Greek literature, iconography and osteological testimony. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 96-120. Oxbow Books, Oxford.

Tyres, I. 2007: Tree ring spot dates of archaeological samples: Vindolanda Roman fort, Northumberland—the 2006 excavation timbers. In: Birley, A. & Blake, J. (eds.): *Vindolanda Excavations 2005*–2006: 130-137. Roman Army Museum Publications, Bardon Mill, Hexham, Northumberland.

— 2014: Tree ring spot dates from archaeological samples: the Vindolanda 2007 excavation timbers. In: Blake, J. (ed.): *Vindolanda Research: the Excavations of 2007–2012 in the* Vicus *or Extramural Settlement ('Area B')*: 225-228. Roman Army Museum Publications, Brampton, Greenhead.

Valadez Azúa, R. 2000: Prehispanic dog types in Middle America. In: Crockford, S.J. (ed.): *Dogs Through Time: an Archaeological Perspective*: 193-204. B.A.R. (International Series) 889. Oxford.

Valadez, R.; Rodríquez, B.; Manzanilla, L. & Tejeda, S. 2006: Dog-wolf hybrid biotype reconstruction from the archaeological city of Teotihuacan in prehispanic central Mexico. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 38-43. Oxbow Books, Oxford.

Walsh, J. H. 1878: *Dogs of the British Islands, Being a Series of Articles on the Points of their Various Breeds, and the Treatment of the Diseases to which they are Subject*. 3rd ed. "The Field" Office, London.

Wayne, R. K.; Geffen, E.; Girman, D. J.; Koepfli, K. P.; Lau, L. M. & Marshall, C. R. 1997: Molecular systematics of the Canidae. *Systematic Biology* 46: 622–653.

Wilkens, B. 2006: The sacrifice of dogs in ancient Italy. In: Snyder, L.M. & Moore, E.A. (eds.): *Dogs and People in Social, Working, Economic or Symbolic Interaction*: 132-137. Proceedings of the 9th ICAZ Conference, Durham. Oxbow Books, Oxford.

Wilson, R. J. A. 2005: *Piazza Armerina*. BK Books, New York.

Witts, P. 2005: *Mosaics in Roman Britain: Stories in Stone*. Tempus Publishing, Stroud.

Yućel, E. 2010: *Great Palace Mosaic Museum*. Bilken Kulturgirisimi, Istanbul.

Yvinec, J-H. 1987: Découpe, pelleterie et consommation des chiens gaulois à Villeneuve-Saint-Germain, la découpe et le partage du corps à travers le temps et l'espace. *Anthropozoologica,* Premier Numéro Spécial 1987: 83–90.

Archaeofauna 25 (2016): 127-184

A Post-cranial Osteometrical Database for the Spanish ibex (*Capra pyrenaica* Schinz, 1838)

LAURA LLORENTE RODRÍGUEZ[1,2] & VICTORIA QUIRALTE[3]
[1]BioArCh-Department of Archaeology. University of York
Environment building, Wentworth Way YO10 5NG York. United Kingdom.
[2]Laboratorio de Arqueozoología, Universidad Autónoma de Madrid
C/ Darwin, 2 28049 Madrid. Spain
[3]Paleobiology Department, Museo Nacional de Ciencias Naturales
C/ José Gutierrez Abascal 2, 28006. Madrid. Spain.

(Received *9 June 2015*; Revised *30 September 2015*; Accepted *17 December 2015*)

ABSTRACT: Body size analyses in zooarchaeology require reliable osteometrical databases in order to evaluate phenomena such as the existence of diachronic and geographic changes and the estimation of the sex ratio. Despite it being a major hunting item in the Iberian Peninsula since Upper Palaeolithic times, the Spanish ibex presently lacks such a reference database. This paper intends to address such absence by offering a comprehensive overview of selected postcranial measurements of the Spanish ibex that includes data from the two extant sub-species, plus a compilation of measurements from Upper Pleistocene Basque Country sites and those retrieved at Sector C of the NE Iberian site of Cova Fosca.

KEYWORDS: OSTEOMETRY, SPANISH IBEX, INTRA-SPECIFIC VARIABILITY, DATABASE

RESUMEN: En Zooarqueología la evaluación del tamaño corporal, tanto para inferir cambios de talla espacio-temporales como para estimar la proporción de sexos, requiere de bases de datos que abarquen la variabilidad documentada para dicha especie. Siendo la cabra montés un recurso clave en la Península Ibérica desde el Paleolítico Superior, sorprende la falta de bases de datos osteométricos. Este trabajo pretende neutralizar tal ausencia para el caso del esqueleto postcraneal incorporando medidas de las dos subespecies existentes, así como una recopilación de medidas de yacimientos vascos del Pleistoceno Superior y las de la colección recuperada en el Sector C del abrigo levantino de Cova Fosca.

PALABRAS CLAVE: OSTEOMETRÍA, CABRA MONTÉS, VARIABILIDAD INTRAESPECÍFICA, BASE DE DATOS

INTRODUCTION

The Spanish ibex (*Capra pyrenaica* Schinz, 1838) is one of the most frequently hunted items in Iberian archaeological sites since the Upper Palaeolithic (Mariezkurrena, 1983; Straus, 1987; Aura Tortosa & Pérez Ripoll, 1992, 1995; Martínez-Valle, 1996). Despite its acknowledged importance in the assessment of the adaptive strategies of hunter-gatherers and agro-pastoralists, the Spanish ibex presently lacks a well-defined database that would allow zooarchaeologists to monitor, among others, sex ratios and body size changes through space and time. Without that tool attempts to recognize important features of the exploitation strategies, such as overhunting, "specialized hunting" or practices aimed at controlling the age and sex structure of the populations should be taken with caution. In addition, and prior to any interpretation, one needs to know how certain sources of variation, such as site location, environmental constraints or even sample size, affect the validity of inferences on body size through time and space. Included here are also some of the major biases that affect zooarchaeological analyses in general as is the case of preservation and retrieval biases and taxonomic miss-identification. A correct identification of the Spanish ibex is crucial in Iberia due the presence of another caprine species of very similar morphology since the middle Pleistocene as is the chamois (*Rupricapra rupricapra*, Linnaeus 1758). To it, one has to add the domestic sheep (*Ovis aries* Linnaeus, 1758) and goat (*Capra hircus* Linnaeus, 1758) from the Neolithic onwards (Altuna, 1978; Manceau *et al.*, 1999a, 1999b; Quiralte, 2001; Ureña *et al.*, 2011). This presence of several caprine species, even prior to the onset of the Neolithic, adds to the difficulty of correctly identifying caprine remains to species level in the Iberian Peninsula and constitutes a pressing problem for zooarchaeologists as substantial numbers of bones from middle-sized bovids end up in the category of unspecified caprines.

Osteometry allows one to address different archaeological problems, in particular changes in the size/shape of the elements that can, in turn, inform about different aspects of the populations from which those elements derived (Boessneck & Driesch, 1978; Albarella, 2002). Ideally, these analyses should be addressed with large osteometric datasets from known populations (extant or archaeological) that would allow one to clearly define standards against which data can be compared. In spite of the aforementioned importance of the Spanish ibex in Iberian zooarchaeology, one is baffled by the ludicrously low numbers of osteometric data that are available for comparison and by an absolute lack of standards.

Oteometrical analyses need to take into account three main sources of variation that, in the case of the Spanish ibex, include (Boessneck & Driesch, 1978; Payne & Bull, 1988):

Ontogenetic variation: referred to differences in size and proportions of the various age groups (i.e. cohorts) of a population.

Sexual variation: sexual variation constitutes a special kind of intra-specific variation that is often considered independently due of its relevance in dimorphic species as is the case of most ungulates. In the Spanish ibex, some differences between the sexes do not normally overlap. This would be the case of weight where adult females range between 30-40 kg and adult males between 50-70 kg with the largest males reaching to 100-120 kg (Granados *et al.*, 2001).

Intra-specific variation. Included here are variations due to genetic differences and differences fostered by environmental agents (temperature, fodder, altitude, etc.). Observer's errors when taking measurements, although representing a totally different kind of phenomenon, could be eventually added to this category. Although in most species intra-specific variation tends to be residual, under certain circumstances the environmental parameters become relevant due mainly to two phenomena:

- Temporal variation: different climatic conditions (or different exploitation strategies) occurred through time and body size is known to vary according to parameters such as temperature and moisture. Selective breeding and alternative exploitation strategies may also bring about changes in size and proportions (Albarella, 2002). Despite limitations, comparing diachronic samples from one cultural sequence often proves the best way to characterize size trends through time. The second best alternative would be to compare assemblages from different sites and periods within the same region.
- Geographical variation: animal populations from different regions may exhibit eco-morphotypes due to local adaptations and/or

genetic isolation. One needs always to be aware of the influence that regional differences may have had when comparing samples from different localities.

SIZE VARIATION IN THE SPANISH IBEX

Although osteometric analyses on the Spanish ibex bones require temporal variability to be considered, more so when dealing with Pleistocene and Early Holocene sites, one should never neglect geographic variation. This is due to the discontinuous distribution that the Spanish ibex, as is typical for species living in mountains, exhibits. It was this regional variation what led Ángel Cabrera to recognize four sub-species of *Capra pyrenaica* in 1911 by virtue of their coat colour, horn size and morphology, and body size. These four sub-species were defined as follows (Granados *et al.*, 2001; García-González, 2011) (Figure 1):

- *C. p. pyrenaic*a, Schinz (1838): Taken to be the holotype for the species, this sub-species featured long, twisted horns bearing a marked keel. Its coat was greyish-brown with large patches of black on the flanks of the body and the limbs. Located in the Pyrenean region, the last population became officially extinct in January 2000.
- *C. p. victoriae*, Cabrera (1911): Smaller than the holotypic populations, this sub-species exhibits a less developed black coat and slightly smaller and wider horns. It is presently distributed in the Sistema Central Mountains.
- *C. p. hispanica*, Schimper (1848): This is the smallest of the Spanish ibex sub-species and features black stripes that are mostly restricted to the limbs as well as a more reddish summer coat. Horns are here narrower and generally become more outward projecting, their keels less pronounced. *C. p. hispanica* occupies the south-eastern quarter of the Iberian Peninsula.
- *C. p. lusitanica*, Schlegel (1872): This sub-species was distributed in Western Iberia but became extinct around 1890. It combined the large size of the holotype and the colour patterning and horn morphology of *C. p. hispanica.*

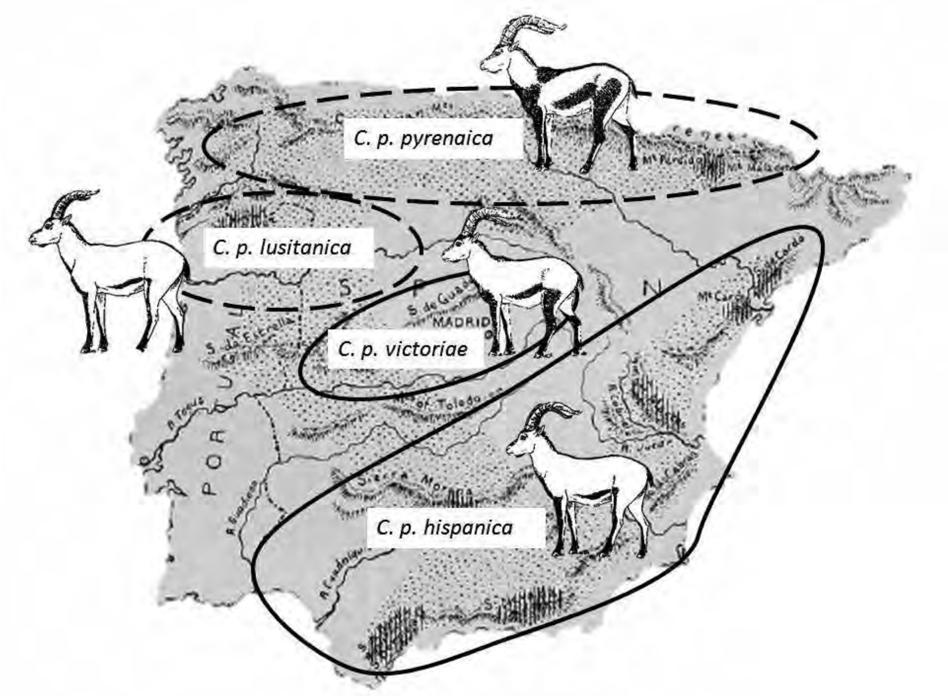

FIGURE 11
Distribution areas of the Spanish ibex sub-species according to Cabrera (1911, 1914). Map and drawings modified from Cabrera (1911).

The emergence and spreading of these sub-species postulated a sequential colonization from a founder population in Northern Spain that paleontological and biomolecular data suggest diverged after the migration and subsequent speciation of the extinct *Capra camburgensis* (Toepfer, 1934) from the Alpine ibex (*Capra ibex* Linnaeus, 1758) during the Riss-Würm interglaciar (Hartl *et al.*, 1990; Manceau *et al.*, 1999a, b; Pidancier *et al.*, 2006; Ureña *et al.*, 2011). The Spanish ibex thus colonized the Iberian Peninsula following a counterclockwise movement towards Portugal then downwards to the central mountain systems, the southern peninsula and finally upwards into the Iberian Levant (Cabrera, 1911; Hartl *et al.*, 1990; Manceau *et al.*, 1999a; García-González, 2011). This hypothesis still requires a reliable phylogenetic analysis incorporating archaeological and paleontological specimens in order to clarify the phylogeographic events that led to the sub-speciation of this species (Ureña *et al.*, 2011).

For this reason, zooarchaeologists cannot take it for granted that the sub-species that today occupies a particular region did so in the past or remained invariable through time. This variability as it pertains to size is crucial to evaluate any putative trends reporting size changes of Spanish ibexes in the archaeological record.

With these provisos in mind, in this paper we will present a preliminary osteometricaal database of *Capra pyrenaica* that not only incorporates measurements from the two extant modern subspecies but also from selected zooarchaological collections, in particular those from the Basque Country during prehistoric times and two additional ones from the Spanish Levant region,. Of these, the collection retrieved in Sector C of the Cova Fosca rock shelter (Ares del Maestrat, Castellón, Spain) holds the largest number of measurements for the species in Iberian soil, whereas the smaller collection is from the nearby site of Mas Nou.

MATERIALS, METHODS AND DATASET

Given that the main goal of this osteometrical tool is to provide a reference system for future studies on body size variability analyses, only selected elements have been taken into consideration. This include the elements from both girdles (i.e. scapula and pelvis), the major limb bones (humerus, radius, ulna, femur and tibia) plus the two ankle bones that are regularly present in archaeological sites (calcaneus and astragalus). Phalanges were intentionally excluded from the database as difficulties occasionally exist to assign them to the fore- or hind limb, or even parasagitally. In the case of other elements, as are most of the cranial bones and teeth the problem is of another nature for, as has been already said, these may even prove difficult to assign to the level of the species.

To address the problem of the natural size variability of the Spanish ibex, modern samples from the two extant subspecies (*Capra pyrenaica victoriae* and *Capra pyrenaica hispanica*) have been measured. Specimens of known sex and above 2 years of age were measured at the *Museo Nacional de Ciencias Naturales* (MNCN) and the *Laboratorio de Arqueozoología Universidad Autónoma de Madrid* (LAZ-UAM). In addition, Late Pleistocene samples from the Cantabrian region (assumed to represent the Pleistocene ancestors of the now extinct subspecies *C. pyrenaica pyrenaica*) were incorporated to the database. These measurements were mostly compiled in the papers of J. Altuna and P. M. Castaños by Quiralte (2002).

In the case of the dataset from Cova Fosca, bone identification was carried out with the help of the reference collection of Arturo Morales housed at LAZ-UAM along with diagnostic criteria taken from the bibliography to discriminate the species from sheep and goat (Altuna, 1978; Quiralte, 2001; 2002). Likewise, although only fused elements and non-porous elements (only criteria to set apart adult from non-adult specimens in bones without epiphyses) should have been measured, measurements of fusing and unfused bones have been also incorporated to the database for comparative purposes. These are highlighted in grey in the tables. For the same reason, elements that were only slightly eroded or mildly burned have been incorporated. Their values are provided within brackets in the tables.

Measurements were taken with either a standard calliper M or a digital calliper “Powerfix” (both with estimated errors ± 0.5 mm), and mainly follow Driesch (1976) and Davis (Davis, 1996, 2008). Additionally, some measurements originally defined for the Genus *Sus* by Payne & Bull (1988) have been adapted for the Spanish ibex.

Age estimation in archaeological bones is based on data taken from Vigal and Machordom (1985), Pérez Ripoll (1988) and Serrano *et al*. (2004). In the case of dates of closure of the epiphyses, only those elements that allow one to discriminate between the different age groups have been considered (Tables 1-3). Despite mandible and teeth measurements not being included in the dataset, a compilation of tooth eruption and tooth wear stages are included here to provide a standarization for age estimation methodologies in the species.

ACKNOWLEDGEMENTS

We want to thank Arturo Morales (LAZ-UAM, Madrid) for reviewing the manuscript. Carmè Olària is gratefully acknowledged for allowing Laura Llorente to study the faunas from Cova Fosca. L. Llorente research is supported by the European Comission under a Marie Curie-Slodowska IF Action 658072.

Tooth eruption	Age range (months)	Cohort
dp$_4$ (+/-)	1-2	Neonate (<2 months)*
M$_1$ (+/-)	2-4	Infantile (2-6 months)
M$_2$ (+/-)	9-12	Juvenile (6-12 months)
I$_1$ (+/-)	12-25	Subadult (12-24 months)
P$_3$ y P$_4$ (+/-)	19-31	
M$_3$ (+/-)	24	
P$_2$ (+/-)	26-40	Adult (24-72 months)
M$_3$ (+)	48	
M$_3$ (+++)	+72	Senile (+72 months)

TABLE 1

Spanish ibex: Dental eruption sequence of the main cohorts. *All newborns documented in the archaeological record are usually relocated into the undetermined caprine category given the difficulty to discriminate their bones to the level of the species.

Element	Epiphyseal fusion (months)		Cohort
	Fusing	Fused	
Scapula (coracoid)	12-24		Subadult (12-24 months)
Proximal radius			
Distal metacarpus			
Proximal phalanges			
Acetabulum			
Distal metacarpus		24-36	Adult (24-72 months)
Acetabulum		>24	
Proximal femur	24-72		
Trocanter femoris	24-60		
Distal femur	24-72		
Distal tibia	24-36	>36	
Calcaneus		48-60	
Distal metatarsus		24-36	
Vertebrae	72-83		Senile (+72 months)

TABLE 2

Spanish ibex: Post-juvenile cohort arrangement according to the epiphyseal calendar of the main postcranial bones.

Wear stages	Age range (months)	Cohort
dp_4: 0, a	1-2	Neonate (<2 months)*
dp_4: b, c	2-4	Infantile (2-6 months)
dp_4: g ; M_1:b, c	4-6	
dp_4: g, h; M_1:d,e	9-12	Juvenile (6-12 months)
dp_4: post g, M_1:g M_2:a,b	12-24	Subadult (12-24 months)
M_1:g-k M_2:g M_3: c, d	36	Adult (24-72 months)
M_1: l M_2:g M_3: g	48	
M_1:post m M_2:g M_3: g	48-60	
M_2: post g M_3: post h	+72	Senile (+72 months)

TABLE 3

Spanish ibex: Dental wear features of the main cohorts. * All newborns documented in the archaeological record are usually relocated into the undetermined caprine category given the difficulty to discriminate their bones to the level of the species.

REFERENCES

Albarella, U. 2002: Size matters: how and why biometry is still important in zooarchaeology. In: Brothwell, D. R.; Dobney, K. & O'Connor, T.P. (eds.): *Bones and the Man: Studies in Honour of Don Brothwell.* 51-62. Oxbow Books, Oxford.

Altuna, J. 1978: Dimorphisme sexual dans le squelette postcephalique de *Capra pyrenaica* pendant le Würm final. *Munibe* 30(201): 214.

Aura Tortosa, J. E. & Pérez Ripoll, M. 1992: Tardiglaciar y Postglaciar en la región mediterránea de la Península Ibérica (13.500-8.500 BP): transformaciones industriales y económicas. *SAGVNTVM* 25: 25-47.

— 1995: El Holoceno inicial en el Mediterráneo español (11.000-7.000 BP). Características culturales y económicas. In: Villaverde, V. (ed.): *Los últimos cazadores. Transformaciones culturales y económicas durante el Tardiglaciar y el inicio del Holoceno en el ámbito mediterráneo:* 119-146. Instituto de Cultura Juan Gil-Albert, Alicante.

Boessneck, J. & Driesch, A. von den 1978: The significance of measuring animal bones from archaeological sites. *Approaches to Faunal Analysis in the Middle East, Peabody Museum Bulletin* 2: 25-39.

Cabrera, A. 1911: The Subspecies of the Spanish Ibex. *Proceedings of the Zoological Society of London* 81(4): 963-977.

— 1914: *Fauna ibérica. Mamíferos.* Junta para Ampliación de Estudios e Investigaciones Científicas- Museo Nacional de Ciencias Naturales, Madrid.

Davis, S. J. M. 1996: Measurements of a Group of Adult Female Shetland Sheep Skeletons from a Single Flock: a Baseline for Zooarchaeologists. *Journal of Archaeological Science* 23: 593-612.

— 2008: Zooarchaeological evidence for Moslem and Christian improvements of sheep and cattle in Portugal. *Journal of Archaeological Science* 35(4): 991-1010.

Driesch, A. von den 1976: *A guide to the measurements of animal bones from archaeological sites.* Peabody Museum Bulletin, Yale.

García-González, R. 2011: Elementos para una filogeografía de la cabra montés ibérica (*Capra pyrenaica* Schinz, 1838). *Pirineos* 166: 87-122.

Granados, J. E.; Pérez, J. M.; Márquez, F. J.; Serrano, E.; Soriguer, R. C. & Fandos, P. 2001: La cabra montés (*Capra pyrenaica*, Schinz 1838). *Galemys* 13(1): 3-37.

Hartl, G. B.; Burger, H.; Willing, R. & Suchentrunk, F. 1990: On the biochemical systematics of the Caprini and the Rupicaprini. *Biochem. Syst. Ecol.* 18(2): 175-182.

Manceau, V.; Crampe, J.; Boursot, P. & Taberlet, P. 1999a: Identification of evolutionary significant units in the Spanish wild goat, *Capra pyrenaica* (Mammalia, Artiodactyla). *Anim.Conserv.* 2(1): 33-39.

Manceau, V.; Després, L.; Bouvet, J. & Taberlet, P. 1999b: Systematics of the Genus *Capra* Inferred from Mitochondrial DNA Sequence Data. *Molecular Phylogenetics and Evolution* 13(3): 504-510.

Mariezkurrena, K. 1983: Contribución al conocimiento del desarollo de la dentición y el esqueleto poscraneal de *Cervus elaphus*. *Munibe* 35: 149-202.

MARTÍNEZ-VALLE, R. 1996: *Fauna del Pleistoceno Superior en el País Valenciano: aspectos económicos, huellas de manipulación y valoración paleoambiental.* Universitat de València, Valencia.

PAYNE, S. & BULL, G. 1988: Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *Archaeozoologia* II (1.2): 27-66.

PÉREZ RIPOLL, M. 1988: Estudio de la secuencia del desgaste de los molares de la «*Capra pyrenaica*» de yacimientos prehistóricos. *Archivo de Prehistoria levantina* 18: 83-127.

PIDANCIER, N.; JORDAN, S.; LUIKART, G. & TABERLET, P. 2006: Evolutionary history of the genus *Capra* (Mammalia, Artiodactyla): discordance between mitochondrial DNA and Y-chromosome phylogenies. *Molecular phylogenetics and evolution* 40(3): 739-49.

QUIRALTE, V. 2001: *Osteología comparada de* Capra hircus *(cabra doméstica) y* Capra pyrenaica *(cabra montés). Tabla de fusiones epifisarias en* Capra pyrenaica. Memoria del Diploma de Estudios Avanzados. Universidad Autónoma de Madrid, Madrid.

— 2002: *Estudio de la variabilidad intraespecífica en el esqueleto postcraneal de la cabra montés* (Capra pyrenaica*, Schinz, 1838). Aplicaciones al registro fósil.* Museo Nacional de Ciencias Naturales-CSIC, Madrid.

SERRANO, E.; GÁLLEGO, L. & PÉREZ, J. M. 2004: Ossification of the apendicular skeleton in the Spanish ibex *Capra pyrenaica* Schinz, 1838 (Artiodactyla: Bovidae), with regard to determination of age. *Anatomy, Histology and Embriology* 33: 33-37.

STRAUS, L. G. 1987: Upper Paleolithic Ibex Hunting in Southwest Europe. *Journal of Archaeological Science* 14: 163-178.

UREÑA, I.; ARSUAGA, J. L.; GALINDO-PELLICENA, M. Á; GÖTHERSTRÖM, A. & VALDIOSERA, C. 2011: Filogenia y evolución local de la cabra montés (*Capra pyrenaica*) en el yacimiento Cuaternario de Chaves (Huesca, España). *Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica* 105 (1-4): 5-14.

VIGAL, C. R. & MACHORDOM, A. 1985: Tooth eruption and replacement in the Spanish wild goat. *Acta Theriologica* 30(19): 305-320.

APPENDIX

ATLAS											
Sub-species	**Sex**	**Age**	**Collection/ Site**	**Code**	**Location**	**Level**	**GB**	**GL**	**GLF**	**BFcr**	**BFcd**
C. p. hispanica	♂	6	AMM	656	S. Cazorla		94	82.5	31.5	59	57
C. p. hispanica	♀	5	AMM	AL-6	S. Cazorla		70	62.5	29.5	53	49
C. p. pyrenaica	♂	7	AMM	Cap pyr-15	Somiedo		109	84.5	37	64	63
			Cova Fosca		Ares del Maestrat	[-120/-130]		(31.5)			
			Cova Fosca		Ares del Maestrat	[-170/-177]	(86)	37	34	66.5	59
			Cova Fosca		Ares del Maestrat	[-170/-177]	70.5	36	29.5	60	54
			Cova Fosca		Ares del Maestrat	[-177/-196]		39			62
			Cova Fosca	1145	Ares del Maestrat	[-196/-211]	(105)	78	(35.5)	(62)	(53)
			Cova Fosca	1149	Ares del Maestrat	[-196/-211]	((94))		(38)	59	54
			Cova Fosca	1147	Ares del Maestrat	[-196/-211]				53.5	
			Cova Fosca	293	Ares del Maestrat	[-211/-220]			37.5		
			Cova Fosca	886	Ares del Maestrat	[-211/-220]	71		30	(50)	50.5
			Cova Fosca	71	Ares del Maestrat	[-220/-224]			26.5	52	((47.5))
			Cova Fosca		Ares del Maestrat	[-242/-255]	((88))				
			Cova Fosca		Ares del Maestrat	[-242/-255]	(56)	31	26	50	(46)

SCAPULA										
Sub-species	**Sex**	**Age**	**Collection/ Site**	**Code**	**Location**	**Level**	**GLP**	**SLC**	**BG**	**HS**
C. p. hispanica	♂	6	AMM	656	S. Cazorla		38.5	25.5	33.7	198
C. p. hispanica	♂	10	MNCN	18070	S. Cazorla		36.5	26	28.2	189
C. p. hispanica	♂	11	MNCN	18073	S. Cazorla		37	23.5	27.4	184.5
C. p. hispanica	♂	11	MNCN	18075	S. Cazorla		38	23.9	27.2	190
C. p. hispanica	♂	8	MNCN	18124	S. Cazorla		36.1	25.2	27.2	195
C. p. hispanica	♂	8	MNCN	18127	S. Cazorla		33.5	22.5	24.5	168
C. p. hispanica	♂	5	MNCN	18147	S. Cazorla		34	21.5	23.8	158.5

SCAPULA										
Sub-species	**Sex**	**Age**	**Collection/ Site**	**Code**	**Location**	**Level**	**GLP**	**SLC**	**BG**	**HS**
C. p. hispanica	♂	9	MNCN	18151	S. Cazorla		37.2	26.5	26.8	194
C. p. hispanica	♂	13	MNCN	18153	S. Cazorla		38.7	25	28.8	193
C. p. hispanica	♂	13	MNCN	18155	S. Cazorla		40	26	28.6	203.5
C. p. hispanica	♂	12	MNCN	18157	S. Cazorla		35	23	25.5	180.3
C. p. hispanica	♀	7	MNCN	18087	S. Cazorla		33.5	19	21.9	150
C. p. hispanica	♀	5	MNCN	18089	S. Cazorla		33	20.5	23	154
C. p. hispanica	♀	7	MNCN	18094	S. Cazorla		30	18.5	22.7	146
C. p. hispanica	♀	4	MNCN	18116	S. Cazorla		30.2	19	21.8	142.5
C. p. hispanica	♀	6	MNCN	18117	S. Cazorla		33	19	21.6	
C. p. hispanica	♀	4	MNCN	18207	S. Cazorla		30	18	24.5	168
C. p. hispanica	♀	5	MNCN	18216	S. Cazorla		31	19	22	147.3
C. p. hispanica	♀	5	AMM	AL-6	S. Cazorla		35.5	22.5	29	171
C. p. victoriae	♂	6	MNCN	18159	S. Gredos		37.8	23.8		165
C. p. victoriae	♂	4	MNCN	16163	S. Gredos		36.5	20.5		164
C. p. victoriae	♂	5	MNCN	18166	S. Gredos		40	26		176
C. p. victoriae	♂	6	MNCN	18170	S. Gredos		41.5	24.5		183
C. p. victoriae	♂	6	MNCN	18172	S. Gredos		39.8	23	29.5	180.5
C. p. victoriae	♂	4	MNCN	18174	S. Gredos		35	23		160
C. p. victoriae	♂	6	MNCN	18279	S. Gredos		44	27		187.5
C. p. victoriae	♂	8	MNCN	18281	S. Gredos		41.5	26		186
C. p. victoriae	♀	8	MNCN	18184	S. Gredos		37.5	24	26.5	169
C. p. victoriae	♀	8	MNCN	18189	S. Gredos		36.5	23	24.2	161
C. p. victoriae	♀	6	MNCN	18191	S. Gredos		34.5	23	24	155.3
C. p. victoriae	♀	5	MNCN	18197	S. Gredos		34	21	23.3	151
C. p. victoriae	♀	6	MNCN	18201	S. Gredos		36	22	24.5	162
C. p. victoriae	♀	7	MNCN	18222	S. Gredos		34	21	23.1	146

SCAPULA										
Sub-species	**Sex**	**Age**	**Collection/ Site**	**Code**	**Location**	**Level**	**GLP**	**SLC**	**BG**	**HS**
C. p. victoriae	♀	7	MNCN	18237	S. Gredos		31	19.5	22.4	148.9
C. p. victoriae	♀	5	MNCN	18252	S. Gredos		33.5	20	23.4	150
C. p. victoriae	♀	8	MNCN	18254	S. Gredos		33.5	21.5		166
C. p. victoriae	♀	5	MNCN	18271	S. Gredos		35.5	21		160
cf. *C. p. pyrenaica*	♀?		Atxuri	ATXU 1	Mañaria	V-VI	36.5	20.5	25	
cf. *C. p. pyrenaica*	♀?		Bolinkova	BO 1	Aradiano	VI	36.5	23.5	25.5	
cf. *C. p. pyrenaica*	♂?		Lumentxa	LU 1	Lekeitio	V	44	32	29.5	
cf. *C. p. pyrenaica*	2?		Lumentxa	LU 2	Lekeitio	V	32	21	21	
cf. *C. p. pyrenaica*	♂?		Lumentxa	LU 3	Lekeitio	VII	51	38	35	
cf. *C. p. pyrenaica*			Arenaza	P-1	Galdames		34		23	
cf. *C. p. pyrenaica*			Rascaño	P-10	Mirones		36.5		25	
cf. *C. p. pyrenaica*			Rascaño	P-11	Mirones		37		24.5	
cf. *C. p. pyrenaica*			Arenaza	P-12	Galdames		37		25	
cf. *C. p. pyrenaica*			Arenaza	P-13	Galdames		37		25	
cf. *C. p. pyrenaica*			Arenaza	P-14	Galdames		37		26	
cf. *C. p. pyrenaica*			Arenaza	P-15	Galdames		37.5		24.5	
cf. *C. p. pyrenaica*			Arenaza	P-16	Galdames		37.5		25	
cf. *C. p. pyrenaica*			Rascaño	P-17	Mirones		37.5		25.5	
cf. *C. p. pyrenaica*			Rascaño	P-18	Mirones		37.5		25.5	
cf. *C. p. pyrenaica*			Rascaño	P-2	Mirones		35		23	
cf. *C. p. pyrenaica*			Rascaño	P-21	Mirones		38		25.5	
cf. *C. p. pyrenaica*			Rascaño	P-23	Mirones		38		26	
cf. *C. p. pyrenaica*			Rascaño	P-25	Mirones		38.5		27	
cf. *C. p. pyrenaica*			Rascaño	P-26	Mirones		39		27	
cf. *C. p. pyrenaica*			Rascaño	P-27	Mirones		39.5		26	
cf. *C. p. pyrenaica*			Rascaño	P-31	Mirones		41.5		29	

SCAPULA										
Sub-species	**Sex**	**Age**	**Collection/ Site**	**Code**	**Location**	**Level**	**GLP**	**SLC**	**BG**	**HS**
cf. *C. p. pyrenaica*			Rascaño	P-32	Mirones		42.5		31	
cf. *C. p. pyrenaica*			Rascaño	P-34	Mirones		43		30	
cf. *C. p. pyrenaica*			Rascaño	P-35	Mirones		43		31.5	
cf. *C. p. pyrenaica*			Rascaño	P-36	Mirones		43		32	
cf. *C. p. pyrenaica*			Rascaño	P-37	Mirones		43		32.5	
cf. *C. p. pyrenaica*			Rascaño	P-38	Mirones		43.5		30	
cf. *C. p. pyrenaica*			Rascaño	P-39	Mirones		43.5		30	
cf. *C. p. pyrenaica*			Rascaño	P-40	Mirones		43.5		31.5	
cf. *C. p. pyrenaica*			Rascaño	P-41	Mirones		44		28.5	
cf. *C. p. pyrenaica*			Rascaño	P-42	Mirones		44		30.5	
cf. *C. p. pyrenaica*			Rascaño	P-43	Mirones		44		31	
cf. *C. p. pyrenaica*			Rascaño	P-44	Mirones		44		34	
cf. *C. p. pyrenaica*			Rascaño	P-45	Mirones		44.5		31	
cf. *C. p. pyrenaica*			Rascaño	P-46	Mirones		45		30	
cf. *C. p. pyrenaica*			Rascaño	P-47	Mirones		45		31	
cf. *C. p. pyrenaica*			Rascaño	P-48	Mirones		45		31.5	
cf. *C. p. pyrenaica*			Rascaño	P-49	Mirones		45		32	
cf. *C. p. pyrenaica*			Rascaño	P-50	Mirones		45.5		29.5	
cf. *C. p. pyrenaica*			Rascaño	P-51	Mirones		45.5		30.5	
cf. *C. p. pyrenaica*			Rascaño	P-52	Mirones		45.5		32.5	
cf. *C. p. pyrenaica*			Rascaño	P-53	Mirones		45.5		33	
cf. *C. p. pyrenaica*			Rascaño	P-54	Mirones		46		37	
cf. *C. p. pyrenaica*			Rascaño	P-55	Mirones		46.5		32	
cf. *C. p. pyrenaica*			Rascaño	P-56	Mirones		47		33.5	
cf. *C. p. pyrenaica*			Rascaño	P-57	Mirones		47		37	
cf. *C. p. pyrenaica*			Arenaza	P-20	Galdames		38		25	

SCAPULA										
Sub-species	**Sex**	**Age**	**Collection/ Site**	**Code**	**Location**	**Level**	**GLP**	**SLC**	**BG**	**HS**
cf. *C. p. pyrenaica*			Arenaza	P-22	Galdames		38		26	
cf. *C. p. pyrenaica*			Arenaza	P-24	Galdames		38.5		26.5	
cf. *C. p. pyrenaica*			Arenaza	P-28	Galdames		39.5		27	
cf. *C. p. pyrenaica*			Arenaza	P-29	Galdames		40		26	
cf. *C. p. pyrenaica*			Arenaza	P-35	Galdames		35		31.5	
cf. *C. p. pyrenaica*			Arenaza	P-30	Galdames		41		29.5	
cf. *C. p. pyrenaica*			Arenaza	P-33	Galdames		43		29.5	
cf. *C. p. pyrenaica*			Arenaza	P-4	Galdames		35		24.5	
cf. *C. p. pyrenaica*			Arenaza	P-6	Galdames		35.5		23	
cf. *C. p. pyrenaica*			Arenaza	P-7	Galdames		35.5		24	
cf. *C. p. pyrenaica*			Arenaza	P-8	Galdames		35.5		25	
cf. *C. p. pyrenaica*			Tito Bustillo	P-5	Ribadesella		35		24.5	
cf. *C. p. pyrenaica*			Riera	P-9	Llanes		36.5		25.5	
cf. *C. p. pyrenaica*	♀		Santimamiñe	SA 1	Kortezubi	VI	36.5	22.5	25.5	
cf. *C. p. pyrenaica*	♀		Santimamiñe	SA 2	Kortezubi	VI	36.5	23	27.5	
cf. *C. p. pyrenaica*	♀		Santimamiñe	SA 3	Kortezubi	VI	33.5	23.5	22	
cf. *C. p. pyrenaica*	♀		Santimamiñe	SA 4	Kortezubi	II	35.5		23	
cf. *C. p. pyrenaica*	♂		Santimamiñe	SA 5	Kortezubi	V	43.5		28	
cf. *C. p. pyrenaica*			Urtiaga	URT 1	Deba	D	35.9	23.4	25.6	
cf. *C. p. pyrenaica*			Urtiaga	URT 2	Deba	D	38.4	23	24	
cf. *C. p. pyrenaica*			Urtiaga	URT 3	Deba	D	41.2	29.1	30.1	
cf. *C. p. pyrenaica*			Urtiaga	URT 4	Deba	D	41.8	27.4	29.6	
cf. *C. p. pyrenaica*			Urratxa	URR 1	Orozko	III	43	27	31	
cf. *C. p. pyrenaica*			Urratxa	URR 2	Orozko	III	35	23.5	26	
cf. *C. p. pyrenaica*			Urratxa	URR 3	Orozko	III	42	25.5	31.5	
cf. *C. p. pyrenaica*			Urratxa	URR 4	Orozko	III	36	21.5	25	

SCAPULA										
Sub-species	**Sex**	**Age**	**Collection/ Site**	**Code**	**Location**	**Level**	**GLP**	**SLC**	**BG**	**HS**
cf. *C. p. pyrenaica*			Urratxa	URR 5	Orozko	III	38	21.5		
cf. *C. p. pyrenaica*			Urratxa	URR 6	Orozko	III	43	25.5	30.5	
			Mas Nou		Ares del Maestrat	1	(37)		(27)	
			Mas Nou		Ares del Maestrat	1		(22)		
			Mas Nou		Ares del Maestrat	2	34	21	23	
			Cova Fosca		Ares del Maestrat	[-150/-170]	(33.5)	(19.5)		
			Cova Fosca		Ares del Maestrat	[-150/-170]	33	19.5		
			Cova Fosca		Ares del Maestrat	[-170/-177]	40	23.5	28	
			Cova Fosca		Ares del Maestrat	[-170/-177]		(26)		
			Cova Fosca		Ares del Maestrat	[-177/-196]	39.5	23	27.5	
			Cova Fosca	75	Ares del Maestrat	[-196/-211]	(40)			
			Cova Fosca	1530	Ares del Maestrat	[-196/-211]	40	24,5		
			Cova Fosca	1051	Ares del Maestrat	[-196/-211]	37	21		
			Cova Fosca	1160	Ares del Maestrat	[-196/-211]	(38)	22		
			Cova Fosca	1447	Ares del Maestrat	[-196/-211]		20		
			Cova Fosca	804	Ares del Maestrat	[-196/-211]	(31)			
			Cova Fosca	800	Ares del Maestrat	[-196/-211]	(40)			
			Cova Fosca	1498	Ares del Maestrat	[-196/-211]	(32)			
			Cova Fosca	375	Ares del Maestrat	[-211/-220]		(18.5)		(140)
			Cova Fosca	484	Ares del Maestrat	[-211/-220]	32	19.5		
			Cova Fosca	98	Ares del Maestrat	[-211/-220]	37	20.5		
			Cova Fosca	568	Ares del Maestrat	[-211/-220]	(34.5)	19	(22.5)	147
			Cova Fosca	1066	Ares del Maestrat	[-211/-220]	36.5		24	
			Cova Fosca	506	Ares del Maestrat	[-211/-220]	39.5	25	26.5	
			Cova Fosca	901	Ares del Maestrat	[-211/-220]		24.5	28	
			Cova Fosca	532	Ares del Maestrat	[-211/-220]		(21)		
			Cova Fosca	118	Ares del Maestrat	[-211/-220]		(21)	(23)	
			Cova Fosca		Ares del Maestrat	[-220/-224]	34			

SCAPULA										
Sub-species	Sex	Age	Collection/ Site	Code	Location	Level	GLP	SLC	BG	HS
			Cova Fosca		Ares del Maestrat	[-220/-224]	33	24		
			Cova Fosca	453+461	Ares del Maestrat	[-220/-224]	33.5			
			Cova Fosca	204	Ares del Maestrat	[-220/-224]		21		
			Cova Fosca		Ares del Maestrat	[-298/-308]	40	28		
			Cova Fosca		Ares del Maestrat	[-319/-365]	(42)	(26)		
			Cova Fosca		Ares del Maestrat	[-365/-388]	(36)	(21)		
			Cova Fosca		Ares del Maestrat	[-365/-388]		15.6		
			Cova Fosca		Ares del Maestrat	[-380]		(20)		

HUMERUS														
Subspecies	Sex	Age (years)	Collection/ Site	Code	Location	Level	Ht	HTC	BT	Bd	GL	GLC	Bp	SD
C. p. hispanica	♂	6	AMM	656	S. Cazorla		23.2	17	37	39	210	185.5	54	19.5
C. p. hispanica	♂	3	AMM	661	S. Cazorla		21.5	15.2	36					
C. p. hispanica	♂	3	AMM	646	S. Cazorla		20.6	15	34.8					
C. p. hispanica	♂	10	AMM	629	S. Cazorla		21.6	16.6	36.3					
C. p. hispanica	♂	(≤3)	AMM	501	S. Cazorla		21	16.2	35.4					
C. p. hispanica	♂	6	AMM	662	S. Cazorla		21	16.1	36					
C. p. hispanica	♂	10	AMM	J-3	S. Cazorla		21.4	15	33.8					
C. p. hispanica	♂	2	AMM	624	S. Cazorla		21.6	15.15	33.8					
C. p. hispanica	♂	≤2	AMM	503	S. Cazorla		21	15.8	34.6					
C. p. hispanica	♀	5	AMM	AL-6	S. Cazorla		20	15	33	35	172.5	152	43.7	18
C. p. hispanica	♀	12	AMM	626	S. Cazorla		19.7	15.5	33	34.7	175.7	154.3	43.2	17
C. p. hispanica	♀	10	AMM	625	S. Cazorla		18.6	14	29.2	31.8	159.3	141.5	38.6	15

HUMERUS														
Subspecies	**Sex**	**Age (years)**	**Collection/ Site**	**Code**	**Location**	**Level**	**Ht**	**HTC**	**BT**	**Bd**	**GL**	**GLC**	**Bp**	**SD**
C. p. hispanica	♀	> 4	AMM	736	S. Cazorla		18	14.5	29.5	31	161.3	144.5	39	15.5
C. p. hispanica	♀	4	AMM	500	S. Cazorla			14.8	32					
C. p. hispanica	♀	4	AMM	735	S. Cazorla		18	13.4	29.2	31.7	159.7	141.5	37.9	15.5
C. p. hispanica	♀	3	AMM	651	S. Cazorla		18.6	14	30.6	32.1				
C. p. hispanica	♀	6	AMM	635	S. Cazorla		18.3	14.4	30.8	31.4	165	146.6	39.6	15.5
C. p. hispanica	♂	10	MNCN	18070	S. Cazorla						205.2	182.5	52	19
C. p. hispanica	♂	4	AMM	Cap pyr-14 (D)	S. Cazorla		21.3	15.2	36	37.5				
C. p. hispanica	♂	4	AMM	Cap pyr-14 (S)	S. Cazorla		21.5	15.2	36	37				
C. p. hispanica	♂	10	MNCN	18070	S. Cazorla		23.1	17.7	36.7	39.3	206	183.5	51.8	19.5
C. p. hispanica	♂	11	MNCN	18073	S. Cazorla		21.9	16.5	37	39	194	173.5	49.5	18.3
C. p. hispanica	♂	11	MNCN	18075	S. Cazorla		22.2	15.7	35.2	38	198	176	49.5	18.5
C. p. hispanica	♀	7	MNCN	18087	S. Cazorla		18.3	14.1	30.5	32	168.9	50	42	15.9
C. p. hispanica	♀	5	MNCN	18089	S. Cazorla		19.9	15.5	32	33	171	151.5	42	16
C. p. hispanica	♀	7	MNCN	18094	S. Cazorla		18.9	14.7	31	33	168	148	42	14.2
C. p. hispanica	♀	4	MNCN	18116	S. Cazorla		18.3	14.7	31.9	31				
C. p. hispanica	♀	6	MNCN	18117	S. Cazorla		19	14.8	32	33	170	151	44	16
C. p. hispanica	♂	7-8	MNCN	18124	S. Cazorla		23	16.5	36.5	38.8	202	178	51	20
C. p. hispanica	♂	8	MNCN	18127	S. Cazorla		21.5	15.5	34.6	35.5	185.5	164.4	52.6	17
C. p. hispanica	♂	7	MNCN	18130	S. Cazorla		22.6	16.6	35	37.1	197.5	175.2	49.7	18
C. p. hispanica	♂	7	MNCN	18146	S. Cazorla		23.1	17.4	37.5	39.5	204.5	181	51	18.7
C. p. hispanica	♂	5	MNCN	18147	S. Cazorla		21.2	15.6	33.3	35.4	180	161.5	45.5	16.5
C. p. hispanica	♂	8	MNCN	18151	S. Cazorla		24	17.5	38.1	40	207.5	184.9	54	21
C. p. hispanica	♂	13	MNCN	18153	S. Cazorla		23.8	18.9	36.2	40				19
C. p. hispanica	♂	13	MNCN	18155	S. Cazorla		23.9	17.5	38.9	40	208.5	184	53	21
C. p. hispanica	♂	12	MNCN	18157	S. Cazorla		21.8	16.7	34.5	37	198.8	170	50	17.5
C. p. hispanica	♀	4	MNCN	18207	S. Cazorla		18.5	14	30.5	31	161	143.5	38.8	14
C. p. hispanica	♀	5	MNCN	18216	S. Cazorla		19.8	15.2	34	32	165	147	41.2	15
C. p. victoriae	♂	6	MNCN	18159 (D)	S. Gredos		23.8	17.2	37.4	40.5	185	165	50.4	19.7

HUMERUS														
Subspecies	**Sex**	**Age (years)**	**Collection/ Site**	**Code**	**Location**	**Level**	**Ht**	**HTC**	**BT**	**Bd**	**GL**	**GLC**	**Bp**	**SD**
C. p. victoriae	♂	6	MNCN	18159 (S)	S. Gredos		23.7	16.8	37.2	40	185.2	164.2	50.9	19
C. p. victoriae	♂	5	MNCN	18166 (S)	S. Gredos		24	19.4	38.7	40.1				
C. p. victoriae	♂	6	MNCN	18170 (D)	S. Gredos		25.3	18.6	39	42.1				
C. p. victoriae	♂	6	MNCN	18170 (S)	S. Gredos		26	18.1	39	41.4				
C. p. victoriae	♂	6	MNCN	18172 (S)	S. Gredos		23.9	17.5	38.1	40.5				
C. p. victoriae	♀	8	MNCN	18184	S. Gredos				35.5	38.5	186.5	164.5	47	18
C. p. victoriae	♀	8	MNCN	18189	S. Gredos		21.5	16.4	36	37	175	154.5	49	16
C. p. victoriae	♀	6	MNCN	18191 (S)	S. Gredos		19.8	15.5	33.5	34	174	153	46.5	16.5
C. p. victoriae	♀	5	MNCN	18197 (D)	S. Gredos		21.8	15.5	34	35.8	170.6	150.5	46	16.6
C. p. victoriae	♀	6	MNCN	18201 (S)	S. Gredos		21.8	16.6	34.5	36.8	177.5	156.5	47.5	17
C. p. victoriae	♀	7	MNCN	18222 (D)	S. Gredos		20	14.8	32.8	34.5	165	145	45	15.5
C. p. victoriae	♀	7	MNCN	18237 (D)	S. Gredos		20	14.6	31.5	33.6	161	142.8	41	14.5
C. p. victoriae	♀	5	MNCN	18252 (D)	S. Gredos		20.7	20.1	32.5	35	171	149.5	43.5	15
C. p. victoriae	♀	8	MNCN	18254 (S)	S. Gredos		20.8	16.7	34.5	35.5	171.5	152	46	16
C. p. victoriae	♀	5	MNCN	18271 (D)	S. Gredos		20.8	16.4	35.3	36	173.5	154	45.5	16
C. p. victoriae	♂	8	MNCN	18281 (S)	S. Gredos		25	18						
C. p. victoriae	♂	8	AMM	Cap pyr-3	S. Gredos		23.5	16.3	37	40	187.2	162.4	51.7	
C. p. victoriae	♂	6	AMM	Cap pyr-10	S. Gredos			18	41	42	-	192.4	52.6	22.3
C. p. victoriae	♂	4	AMM	Cap pyr-11	S. Gredos			-	-	-	-			
cf. *C. p. pyrenaica*	♂	7	AMM	Cap-pyr 15 (S)	Somiedo		25.7	19.7	40.5	44.5	227.5	201	59	24
cf. *C. p. pyrenaica*	♂	7	AMM	Cap-pyr 15 (D)	Somiedo		26.7	19	41.4	44				
cf. *C. p. pyrenaica*			Aitzbitarte	AITZ 1	Renteria	Aziliense				43.3				
cf. *C. p. pyrenaica*	♂?		Atxuri	ATXU 1	Mañaria	II			44	45.5				
cf. *C. p. pyrenaica*	♀?		Bolinkova	BO 1	Aradiano	VI			37.5	39				
cf. *C. p. pyrenaica*	♀?		Bolinkova	BO 2	Aradiano	VI			37	38.5				
cf. *C. p. pyrenaica*	♀?		Lumentxa	LU 1	Lekeitio	IB			31	33				
cf. *C. p. pyrenaica*	♀?		Lumentxa	LU 2	Lekeitio	IV			29.5	32.5				
cf. *C. p. pyrenaica*	♂?		Lumentxa	LU 3	Lekeitio	VI			38.5	41				

HUMERUS														
Subspecies	**Sex**	**Age (years)**	**Collection/ Site**	**Code**	**Location**	**Level**	**Ht**	**HTC**	**BT**	**Bd**	**GL**	**GLC**	**Bp**	**SD**
cf. *C. p. pyrenaica*	♂?		Polvorin	PO 1	Carranza	V			47	50				
cf. *C. p. pyrenaica*	♂?		Santimamiñe	SA 1	Kortezubi	III			41.5	44				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 10	Kortezubi	VI			35.5	37				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 11	Kortezubi	VII			36.5	38				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 12	Kortezubi	VIII			41.5	37.5				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 13	Kortezubi	VIII			36.5	38				
cf. *C. p. pyrenaica*	♂?		Santimamiñe	SA 14	Kortezubi	I			41.5	46.5				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 15	Kortezubi	II			33.5	36				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 16	Kortezubi	III			37	40.5				
cf. *C. p. pyrenaica*			Santimamiñe	SA 17	Kortezubi	III			38.5	40.5				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 18	Kortezubi	IV			36.5	38.5				
cf. *C. p. pyrenaica*	♂?		Santimamiñe	SA 19	Kortezubi	V			39.5	40.5				
cf. *C. p. pyrenaica*	♂?		Santimamiñe	SA 2	Kortezubi	III			39.5	41.5				
cf. *C. p. pyrenaica*	♂?		Santimamiñe	SA 20	Kortezubi	V			39	41				
cf. *C. p. pyrenaica*	♂?		Santimamiñe	SA 21	Kortezubi	V			39	40				
cf. *C. p. pyrenaica*	♂?		Santimamiñe	SA 3	Kortezubi	V			44	48				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 4	Kortezubi	VI			36	37.5				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 5	Kortezubi	VI			29.5	32.5				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 6	Kortezubi	VI			35	37				
cf. *C. p. pyrenaica*			Santimamiñe	SA 7	Kortezubi	VI			38.5	39.5				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 8	Kortezubi	VI			31	33.5				
cf. *C. p. pyrenaica*	♀?		Santimamiñe	SA 9	Kortezubi	VI			32	34.5				
cf. *C. p. pyrenaica*	♂?		Urratxa	URR 1	Orozko	III			39	41				
cf. *C. p. pyrenaica*	♂?		Urratxa	URR 2	Orozko	III			40.5	43				
cf. *C. p. pyrenaica*	♂?		Urratxa	URR 3	Orozko	III			40	42				
cf. *C. p. pyrenaica*	♀?		Urratxa	URR 4	Orozko	III			35	36.5				
cf. *C. p. pyrenaica*	♂?		Urratxa	URR 5	Orozko	III			39.5	40.5				
cf. *C. p. pyrenaica*	♀?		Urratxa	URR 6	Orozko	III			36	36.5				

HUMERUS														
Subspecies	Sex	Age (years)	Collection/ Site	Code	Location	Level	Ht	HTC	BT	Bd	GL	GLC	Bp	SD
cf. *C. p. pyrenaica*	♂?		Urratxa	URR 7	Orozko	III			40	42				
cf. *C. p. pyrenaica*	♂?		Urratxa	URR 8	Orozko	III			41.5	43.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 1	Deba	D			37	39.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 2	Deba	D			39	40				
cf. *C. p. pyrenaica*			Urtiaga	URT 3	Deba	D			39	40.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 4	Deba	D			38.5	41				
cf. *C. p. pyrenaica*			Urtiaga	URT 5	Deba	D			39	41				
cf. *C. p. pyrenaica*			Urtiaga	URT 6	Deba	D			41.5	43.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 7	Deba	D			42	44				
cf. *C. p. pyrenaica*			Urtiaga	URT 8	Deba	D			45	45.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 9	Deba	D			43	46				
cf. *C. p. pyrenaica*			Urtiaga	URT 10	Deba	D			43	46				
cf. *C. p. pyrenaica*			Urtiaga	URT 11	Deba	D				46.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 12	Deba	D			43	46.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 13	Deba	D			45	46.5				
cf. *C. p. pyrenaica*			Urtiaga	URT 14	Deba	D			45	48.5				
			Mas Nou		Ares del Maestrat	2			(34)	37				
			Mas Nou		Ares del Maestrat	2			(28.5)					
			Cova Fosca		Ares del Maestrat	[-119]			28	29.5				
			Cova Fosca		Ares del Maestrat	[-120/-130]			30	32				
			Cova Fosca		Ares del Maestrat	[-120/-130]			39.5	44.5				
			Cova Fosca		Ares del Maestrat	[-125/-142]			35	37				
			Cova Fosca		Ares del Maestrat	[-150/-170]			33	34				
			Cova Fosca		Ares del Maestrat	[-150/-170]			(28.5)					
			Cova Fosca		Ares del Maestrat	[-150/-170]			38	41				
			Cova Fosca		Ares del Maestrat	[-170/-177]			38.5	41				
			Cova Fosca		Ares del Maestrat	[-170/-177]			38.7	41.5				
			Cova Fosca		Ares del Maestrat	[-170/-177]			35	38.5				

HUMERUS														
Subspecies	Sex	Age (years)	Collection/ Site	Code	Location	Level	Ht	HTC	BT	Bd	GL	GLC	Bp	SD
			Cova Fosca		Ares del Maestrat	[-170/-177]			38.5	43				
			Cova Fosca		Ares del Maestrat	[-170/-177]			(36)	(38)				
			Cova Fosca		Ares del Maestrat	[-177/-196]			(35)	39				
			Cova Fosca		Ares del Maestrat	[-177/-196]			37.5	40				
			Cova Fosca		Ares del Maestrat	[-177/-196]			36	39				
			Cova Fosca		Ares del Maestrat	[-177/-196]			(32)	32.5				
			Cova Fosca		Ares del Maestrat	[-177/-196]			33.5	36				
			Cova Fosca		Ares del Maestrat	[-177/-196]			31	33				
			Cova Fosca		Ares del Maestrat	[-177/-196]			(32.5)	36				
			Cova Fosca		Ares del Maestrat	[-177/-196]			(30)					
			Cova Fosca		Ares del Maestrat	[-177/-196]			(29)					
			Cova Fosca	1012	Ares del Maestrat	[-196/-211]		14.8	32.8	33.7				
			Cova Fosca	1394	Ares del Maestrat	[-196/-211]		16	32.4	34.7				
			Cova Fosca	815	Ares del Maestrat	[-196/-211]		14.8	31.8	33.5				
			Cova Fosca	807	Ares del Maestrat	[-196/-211]		16.2	34	35.6				
			Cova Fosca	257	Ares del Maestrat	[-211/-220]		16.5	39	41				
			Cova Fosca	706	Ares del Maestrat	[-211/-220]		18	37	40				
			Cova Fosca	611	Ares del Maestrat	[-211/-220]		15.5	32	34				
			Cova Fosca	28	Ares del Maestrat	[-211/-220]		17.5	39	41.5				
			Cova Fosca	704	Ares del Maestrat	[-211/-220]		14.7	32	33				
			Cova Fosca	78	Ares del Maestrat	[-211/-220]		17.3	39.5	42				
			Cova Fosca	317	Ares del Maestrat	[-211/-220]		15.6	31.5	34				
			Cova Fosca	393	Ares del Maestrat	[-211/-220]		15.2	33.5	34				
			Cova Fosca		Ares del Maestrat	[-211/-220]		15.8	32.5	34.5				
			Cova Fosca		Ares del Maestrat	[-211/-220]			33.5					
			Cova Fosca	628	Ares del Maestrat	[-211/-220]		16	33.5	36.5				
			Cova Fosca	158	Ares del Maestrat	[-211/-220]		16.5	34.5	36.5				
			Cova Fosca		Ares del Maestrat	[-211/-220]		14	31.5	32.5				

HUMERUS														
Subspecies	Sex	Age (years)	Collection/ Site	Code	Location	Level	Ht	HTC	BT	Bd	GL	GLC	Bp	SD
			Cova Fosca	705	Ares del Maestrat	[-211/-220]		16	32.5	34				
			Cova Fosca	591	Ares del Maestrat	[-220/-224]		16.8	34					
			Cova Fosca	188	Ares del Maestrat	[-220/-224]		15	33	34.5				
			Cova Fosca	285	Ares del Maestrat	[-220/-224]		15.3	32.1	37				
			Cova Fosca		Ares del Maestrat	[-224/-235]			30	30				
			Cova Fosca		Ares del Maestrat	[-224/-235]			(34.5)	(35)				
			Cova Fosca		Ares del Maestrat	[-224/-235]			(31)	(32)				
			Cova Fosca		Ares del Maestrat	[-255/-262]			(34)	(34)				
			Cova Fosca		Ares del Maestrat	[-255/-262]			33.5	34.5				
			Cova Fosca		Ares del Maestrat	[-279/-298]			33.4	33.5				
			Cova Fosca		Ares del Maestrat	[-298/-308]			32.7	34.3				
			Cova Fosca		Ares del Maestrat	[-319/-365]			(32)	38				
			Cova Fosca		Ares del Maestrat	[-365/-388]			34.5	(38.5)				
			Cova Fosca		Ares del Maestrat	[-365/-388]				(37)				
			Cova Fosca		Ares del Maestrat	[-365/-388]			(34.5)	35				
			Cova Fosca		Ares del Maestrat	[-385]			(38)					

RADIUS											
Sub-species	Sex	Age (years)	Collection / site	Code	Location	Level	GL	BP	BFp	SD	BD
C. p. hispanica	♂	6	AMM	656	S. Cazorla		197.5	39	36	22	37.5
C. p. hispanica	♂	10	MNCN	18070	S. Cazorla		196	39		20.5	36.5
C. p. hispanica	♂	11	MNCN	18073	S. Cazorla		184	39		21	37
C. p. hispanica	♂	11	MNCN	18075	S. Cazorla		188	38		20.2	36.5
C. p. hispanica	♂	8	MNCN	18124	S. Cazorla		189.5	40		20	36
C. p. hispanica	♂	8	MNCN	18127	S. Cazorla		179	37		19	33.5
C. p. hispanica	♂	7	MNCN	18130	S. Cazorla		190.5	37		20.9	35

RADIUS											
Sub-species	**Sex**	**Age (years)**	**Collection / site**	**Code**	**Location**	**Level**	**GL**	**BP**	**BFp**	**SD**	**BD**
C. p. hispanica	♂	7	MNCN	18146	S. Cazorla		188	39		21.5	36
C. p. hispanica	♂	9	MNCN	18151	S. Cazorla		200.5	40.5		22	38
C. p. hispanica	♂	13	MNCN	18153	S. Cazorla		190.5	40		22.5	38.5
C. p. hispanica	♂	13	MNCN	18155	S. Cazorla		197	39		23	38.5
C. p. hispanica	♂	12	MNCN	18157	S. Cazorla		182	37.5		19	35.5
C. p. hispanica	♀	7	MNCN	18087	S. Cazorla		161	32.8		16.5	29.3
C. p. hispanica	♀	5	MNCN	18089	S. Cazorla		163.5	33.5		17.3	30.5
C. p. hispanica	♀	7	MNCN	18094	S. Cazorla			32			30
C. p. hispanica	♀	6	MNCN	18117	S. Cazorla		158	35.6		17	30
C. p. hispanica	♀	4	MNCN	18207	S. Cazorla		150	31.8		15	28.5
C. p. hispanica	♀	5	MNCN	18216	S. Cazorla		155.6	32		16.9	29
C. p. hispanica	♀	5	AMM	AL-6	S. Cazorla		165.5	33.5	32	19	33
C. p. victoriae	♂	6	MNCN	18279	S. Gredos		187.5	44		22	40
C. p. victoriae	♂	8	MNCN	18281	S. Gredos		188.5	44		22.6	40.5
C. p. victoriae	♀	8	MNCN	18184	S. Gredos		168	38		19.5	35.2
C. p. victoriae	♀	8	MNCN	18189	S. Gredos		159	36.8		19	33.8
C. p. victoriae	♀	6	MNCN	18191	S. Gredos		163	35.5		18	32.5
C. p. victoriae	♀	5	MNCN	18197	S. Gredos		155	35		18	33.5
C. p. victoriae	♀	6	MNCN	18201	S. Gredos		158	36.5		19	34
C. p. victoriae	♀	7	MNCN	18222	S. Gredos		154	32		16.5	32
C. p. victoriae	♀	7	MNCN	18237	S. Gredos		148	34.5		16.5	31
C. p. victoriae	♀	5	MNCN	18252	S. Gredos		155	35		17.3	32
C. p. victoriae	♀	8	MNCN	18254	S. Gredos		156.5	35		18	32
C. p. victoriae	♀	5	MNCN	18271	S. Gredos		166	36		17.8	33

RADIUS											
Sub-species	**Sex**	**Age (years)**	**Collection / site**	**Code**	**Location**	**Level**	**GL**	**BP**	**BFp**	**SD**	**BD**
cf. *C. p. pyrenaica*	♂		AMM	Cap pyr-15	Somiedo		216.5	44.5	40.5	26	44
cf. *C. p. pyrenaica*			Urratxa	URT 1	Orozko	D		41.5	40		
cf. *C. p. pyrenaica*	♂		Atxuri	ATXU 1	Mañaria	I		41	39		
cf. *C. p. pyrenaica*			Atxuri	ATXU 2	Mañaria	II					38.5
cf. *C. p. pyrenaica*	♀		Bolinkova	BO 1	Aradiano	VI		36			
cf. *C. p. pyrenaica*	♂		Lumentxa	LU 1	Lekeitio	VII		43	40.5		
cf. *C. p. pyrenaica*			Santimamiñe	SA 1	Kortezubi	VI					30.5
cf. *C. p. pyrenaica*	♂		Santimamiñe	SA2	Kortezubi	VII		44.5	42.5		
cf. *C. p. pyrenaica*	♀		Santimamiñe	SA3	Kortezubi	VIII		37	35.5		
cf. *C. p. pyrenaica*	♂		Urratxa	URR 1	Orozko	III		42.5	41		
			Mas Nou		Ares del Maestrat	1		(30)	(30)		(34.5)
			Cova Fosca		Ares del Maestrat	[-119]		(41)			
			Cova Fosca		Ares del Maestrat	[-177/-196]		41.5	37		
			Cova Fosca		Ares del Maestrat	[-177/-196]		(31)	27.5		
			Cova Fosca		Ares del Maestrat	[-177/-196]		(39.5)	((35.5))		
			Cova Fosca	1392	Ares del Maestrat	[-196/-211]		35.1			
			Cova Fosca	1294	Ares del Maestrat	[-196/-211]					31.2
			Cova Fosca		Ares del Maestrat	[-196/-211]					33
			Cova Fosca	1230	Ares del Maestrat	[-196/-211]					37.3
			Cova Fosca	1421	Ares del Maestrat	[-196/-211]		(33.5)			
			Cova Fosca	1429	Ares del Maestrat	[-196/-211]					30.9
			Cova Fosca	1289	Ares del Maestrat	[-196/-211]		(33.5)			
			Cova Fosca	1145	Ares del Maestrat	[-196/-211]				13	
			Cova Fosca	1132	Ares del Maestrat	[-196/-211]				(17.7)	

RADIUS											
Sub-species	**Sex**	**Age (years)**	**Collection / site**	**Code**	**Location**	**Level**	**GL**	**BP**	**BFp**	**SD**	**BD**
			Cova Fosca		Ares del Maestrat	[-211/-220]		36	37.4		
			Cova Fosca	49	Ares del Maestrat	[-211/-220]		41	37		
			Cova Fosca	263	Ares del Maestrat	[-211/-220]		36.7	35		
			Cova Fosca	487	Ares del Maestrat	[-211/-220]					31.9
			Cova Fosca	927	Ares del Maestrat	[-211/-220]					34
			Cova Fosca	764	Ares del Maestrat	[-211/-220]					30
			Cova Fosca		Ares del Maestrat	[-211/-220]					21.3
			Cova Fosca	305	Ares del Maestrat	[-220/-224]					33.5
			Cova Fosca	166	Ares del Maestrat	[-220/-224]		(36)	(36)		
			Cova Fosca		Ares del Maestrat	[-220/-224]					
			Cova Fosca	305	Ares del Maestrat	[-224/-235]					(30.5)
			Cova Fosca		Ares del Maestrat	[-242/-255]					(42.5)
			Cova Fosca		Ares del Maestrat	[-304/-319]		(43)	(40)		

ULNA										
Sub-species	**Sex**	**Age (years)**	**Collection / site**	**Code**	**Location**	**Level**	**BPC**	**DPA**	**SDO**	**LO**
C. p. hispanica	♂	6	656	AMM	S. Cazorla		30	33.5	28.5	52
C. p. hispanica	♀	5	AL-6	AMM	S. Cazorla		24.5	29.5	24	46.5
C. p. pyrenaica	♂	7	Cap pyr-15	AMM	Somiedo		32.5	38.5	32	57
			Cova Fosca		Ares del Maestrat	1A		30		
			Cova Fosca		Ares del Maestrat	[-119]		(30.5)		
			Cova Fosca		Ares del Maestrat	[-120/-130]	24	25		
			Cova Fosca		Ares del Maestrat	[-111/-126]	24.5			
			Cova Fosca		Ares del Maestrat	[-177/-196]	26			

ULNA										
Sub-species	**Sex**	**Age (years)**	**Collection / site**	**Code**	**Location**	**Level**	**BPC**	**DPA**	**SDO**	**LO**
			Cova Fosca	517	Ares del Maestrat	[-196/-211]	(25.5)			
			Cova Fosca	1482	Ares del Maestrat	[-196/-211]	24			
			Cova Fosca	1271	Ares del Maestrat	[-196/-211]	(22.5)			
			Cova Fosca	1357	Ares del Maestrat	[-196/-211]	23			
			Cova Fosca	1464	Ares del Maestrat	[-196/-211]	24.5			
			Cova Fosca		Ares del Maestrat	[-211/-220]	24			
			Cova Fosca	385	Ares del Maestrat	[-211/-220]	24			
			Cova Fosca	417	Ares del Maestrat	[-211/-220]	19			
			Cova Fosca	87	Ares del Maestrat	[-211/-220]	22			
			Cova Fosca	682	Ares del Maestrat	[-211/-220]	19.5			
			Cova Fosca	657	Ares del Maestrat	[-220/-224]	(22.5)	(27)		
			Cova Fosca		Ares del Maestrat	[-262/-275]	(25)			

METACARPUS																		
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WCM**	**WCL**	**DEM**	**DVM**	**DIM**	**DIL**	**DVL**	**DEL**
C. p. hispanica	♂	6	656	AMM	Sierra de Cazorla		133	31.5	20	32.8	32.5	15	15	11.6	19.5	16.1	16	18.9	11.4
C. p. hispanica	♂	3	661	AMM	Sierra de Cazorla		129.4	27.8	18	33.2	30.5	14	13.8	11.5	18	15.3	15.3	17.5	10.9
C. p. hispanica	♂	3	646	AMM	Sierra de Cazorla		131.1	28	18	31.5	29.5	13.8	13.5	11.1	18.3	15.2	15.2	17.7	11.3
C. p. hispanica	♂	10	629	AMM	Sierra de Cazorla		130.8	30.3	21	34.3	33.5	15.1	14.9	11.5	18.9	15.5	15.2	18.2	11.1
C. p. hispanica	♂	3	501	AMM	Sierra de Cazorla		131	29.8	19.5	31.9	32	14.9	14.7	11.8	19.5	15.9	15.9	18.7	10.6

METACARPUS																			
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WC M**	**WCL**	**DE M**	**DV M**	**DIM**	**DIL**	**DVL**	**DEL**
C. p. hispanica	♂	6	662	AMM	Sierra de Cazorla		127.1	29.6	19	32.8	31.6	14.5	14.4	11.5	18.5	15.5	15.3	18	10.2
C. p. hispanica	♂	10	J-3	AMM	Sierra de Cazorla		124.2	26.7	16.8	29.4	29.8	13.9	13.4	10.2	16.4	13.6	13.6	15.9	10.7
C. p. hispanica	♂	2	624	AMM	Sierra de Cazorla		134	29.2	18.5	32.5	30.4	14	13.7	11.4	18.8	15.6	15.4	18.5	10.9
C. p. hispanica	♂	2	503	AMM	Sierra de Cazorla		132.7	29.3	18.5	33.7	31.4	14.4	14.1	11.4	18.5	15.4	15.3	18.8	10.3
C. p. hispanica	♀	5	AL-6	AMM	Sierra de Cazorla		122.8	27.4	18	30.5	29	13.8	13.5	10.8	17.7	14.8	14.6	17.1	9.8
C. p. hispanica	♀	10	625	AMM	Sierra de Cazorla		114.6	24.8	15.5	27.3	26	12.2	12.1	10.4	16.8	13.8	13.5	16.2	10.4
C. p. hispanica	♀	12	626	AMM	Sierra de Cazorla		120.6	27.4	17	29.6	28.3	13.2	13	11	18.3	14.9	15	17.5	9.6
C. p. hispanica	♀	??	736	AMM	Sierra de Cazorla		112.3	26.5	15.5	27.2	26.5	12.4	12.1	10.2	16.7	14.2	14.1	16.3	
C. p. hispanica	♀	3	651	AMM	Sierra de Cazorla		114.9	24.9	15.4	27.1	26.2	12.1	12	10.4	16.7	14	14	16.1	9.9
C. p. hispanica	♀	6	635	AMM	Sierra de Cazorla		117.5	25.6	16	28.4	26.3	12.2	12	10.5	16.7	13.9	13.9	16.1	10.4
C.p. hispanica	♂	4-5	Cap pyr-14 (D)	AMM	Sierra de Cazorla		132.7	37.9	18.5	31.5	30.5	14.1	13.9	11	18.2	15	15	17.8	10.5
C.p. hispanica	♂	4-5	Cap pyr-14 (S)	AMM	Sierra de Cazorla		132.4	38.1	18.3	31.6	30.4	14.1	14	11	18.3	15.1	15	17.8	11.5
C. p. pyrenaica	♂	7	Cap-pyr 15	AMM	Somiedo		147	35	22.4	38.2	36.4	17	17	13.3	22.7	18.2	22.2	17.7	11.7

METACARPUS																			
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WC M**	**WCL**	**DE M**	**DV M**	**DIM**	**DIL**	**DVL**	**DEL**
C. p. hispanica	♂	10	18070	MNCN	Sierra de Cazorla		139	30	21.5	32.5	30.4	14.7	14	11.7	19.2	15.9	15.8	16.6	10.7
C. p. hispanica	♂	11	18073	MNCN	Sierra de Cazorla		132	30	18	32	31.2	14.6	14.4	11.3	18.8	15.1	14.7	18.1	10.7
C. p. hispanica	♂	11	18075	MNCN	Sierra de Cazorla		135	29	17.5	32.5	30.6	14.1	13.7	11.1	18.4	15	14.7	17.7	9
C. p. hispanica	♀	7	18087	MNCN	Sierra de Cazorla		118.3	24.4	15	27.5	26.8	12.4	12.1	9.7	16.1	13	13	15.4	10.3
C. p. hispanica	♀	5	18089	MNCN	Sierra de Cazorla		121.5	26	16	29	28.2	13	12.5	10.8	18	14.4	14.4	17.3	9.4
C. p. hispanica	♀	7	18094	MNCN	Sierra de Cazorla		116	24.5	15	27.5	26.4	12.5	12	9.9	16.6	13.4	13.4	16.1	9.3
C. p. hispanica	♀	4	18116	MNCN	Sierra de Cazorla		117.5	23.8	15	26.5	26.3	12.3	11.8	9.9	16.5	13.5	13.5	16	9.4
C. p. hispanica	♀	6	18117	MNCN	Sierra de Cazorla		116.5	25	15	27	27.3	12.5	12.4	9.9	17	13.4	13.5	16.5	10.3
C. p. hispanica	♂	8	18124	MNCN	Sierra de Cazorla		136	29	17.5	33	32.1	15.2	14.4	10.9	19	15.2	15.2	18.4	10.4
C. p. hispanica	♂	8	18127	MNCN	Sierra de Cazorla		130	27.5	16.5	30	29.9	13.7	13.3	11.1	18	14.4	14.4	17.3	11.1
C. p. hispanica	♂	7	18130	MNCN	Sierra de Cazorla		133.5	29	18	33	32	14.4	14.2	11.6	19	15.3	15.3	18.2	10.8
C. p. hispanica	♂	7	18146	MNCN	Sierra de Cazorla		136	28.8	18	32.3	31.4	14.7	34	11.1	18.7	15.3	15.1	18.3	10.5
C. p. hispanica	♂	5	18147	MNCN	Sierra de Cazorla		130.5	27	16.5	30.5	30.3	14	13.6	11	18	14.8	14.9	17.5	11.5
C. p. hispanica	♂	9	18151	MNCN	Sierra de Cazorla		140.8	30	18.9	33.5	32.1	14.6	14.5	12	19.8	16.1	16	19.4	11.5

METACARPUS																			
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WC M**	**WCL**	**DE M**	**DV M**	**DIM**	**DIL**	**DVL**	**DEL**
C. p. hispanica	♂	13	18153	MNCN	Sierra de Cazorla		139.5	31	19	33.9	32.9	15.5	15	11.7	19.4	15.8	15.8	19	11.4
C. p. hispanica	♂	13	18155	MNCN	Sierra de Cazorla		141.6	31	20.5	34	32.9	14.9	14.7	12.1	19.7	16.3	16	19	10
C. p. hispanica	♂	12	18157	MNCN	Sierra de Cazorla		130.5	27.5	17	31	30.5	14	13.7	10.3	17.6	14.1	14.1	17.2	11.1
C. p. victoriae	♂	6	18159 (D)	MNCN	Sierra de Gredos		124	30	19.1	34.4	34.3	15.9	15.4	12.3	19.8	16	15.9	19	11.1
C. p. victoriae	♂	6	18159 (S)	MNCN	Sierra de Gredos		123.9	30.5	19	34.1	34.3	15.9	15.4	11.8	19.8	15.9	15.8	19	11.9
C. p. victoriae	♂	5	18166 (D)	MNCN	Sierra de Gredos		134	32	20	37	36.1	16.5	16.2	12.8	20.9	17.1	17	20.2	11.8
C. p. victoriae	♂	6	18170 (D)	MNCN	Sierra de Gredos		130	31.6	19.5	35	36.9	17	16.8	12	20.2	16.4	16.1	19.4	11.5
C. p. victoriae	♂	6	18170 (S)	MNCN	Sierra de Gredos		130.5	31.3	19.6	35.4	37.5	17.4	17	12	20.4	16.5	16.4	19.8	11.7
C. p. victoriae	♂	6	18172 (D)	MNCN	Sierra de Gredos		131.4	32	19	34	34.6	16.2	15.8	12.4	20.8	16.9	16.6	19.8	
C. p. victoriae	♀	8	18184	MNCN	Sierra de Gredos		126	29	18	33.5									10.9
C. p. victoriae	♀	8	18189 (D)	MNCN	Sierra de Gredos		116.5	28.5	17	31.3	32.7	15.1	14.9	11.6	19.2	15.8	15.5	18.5	10.7
C. p. victoriae	♀	6	18191 (S)	MNCN	Sierra de Gredos		119.5	28	17	30.7	31.5	14.6	14.2	11.3	19	15.3	15.2	18.3	10.2
C. p. victoriae	♀	5	18197 (S)	MNCN	Sierra de Gredos		113.8	28	17	30	31	14.4	13.9	10.6	18.6	14.9	14.9	18	11
C. p. victoriae	♀	6	18201 (S)	MNCN	Sierra de Gredos		117.5	27.9	17	31.5	31.2	14.3	13.9	11.6	18.9	15.4	15.3	18.5	9.2
C. p. hispanica	♀	4	18207	MNCN	Sierra de Gredos		115.2	24	14.5	25.9	26.5	12.1	11.8	9.8	16.7	13.4	13.3	16.1	10
C. p. hispanica	♀	5	18216	MNCN	Sierra de Gredos		120	25.3	15.5	27	26.6	12.5	11.8	10.8	17.3	14.1	14	16.6	9.4

METACARPUS																			
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WC M**	**WCL**	**DE M**	**DV M**	**DIM**	**DIL**	**DVL**	**DEL**
C. p. victoriae	♀	7	18222 (S)	MNCN	Sierra de Gredos		113	26.5	15.5	27.8	28.7	13.4	13	10.1	17.1	14	13.8	16.5	9
C. p. victoriae	♀	7	18237 (S)	MNCN	Sierra de Gredos		111.3	25	15	28.4	29	13.4	13	9.8	17.1	13.8	13.6	16.3	10.4
C. p. victoriae	♀	5	18252 (D)	MNCN	Sierra de Gredos		114	26	15.5	29.7	30.5	13.9	13.7	10.8	18	14.5	14.6	17.7	10.6
C. p. victoriae	♀	8	18254 (S)	MNCN	Sierra de Gredos		115	27.5	16.5	30	30	13.7	13.6	11.1	18	14.7	14.7	17.3	10.5
C. p. victoriae	♀	5	18271 (D)	MNCN	Sierra de Gredos		118	28	17	29.7	30.5	14.1	13.7	11.3	18.7	15.5	15.5	18	
C. p. victoriae	♂	6	18279	MNCN	Sierra de Gredos		133	34	20.8	38									12.8
C. p. victoriae	♂	8	18281 (S)	MNCN	Sierra de Gredos		129.4	34.2	20	38.2	38	17.6	16.6	12.8	21.2	17.4	17.4	21.1	10.9
C. p. victoriae	♂	8	Cap pyr-3	AMM	Sierra de Gredos		121.8	28.6	18.4	33.7	33.3	15.9	15.3	11.3	19	15.2	15.1	18.5	11.9
C. p. victoriae	♂	6	Cap pyr-10	AMM	Sierra de Gredos		143	36.1	23	40.4	39.6	18	17.9	12.9	22	17.8	17.8	21	9.9
C.p. victoriae	♂	4	Cap pyr-11	AMM	Sierra de Gredos		112.4	20.5	16.6	28.7	28	13.3	13.3	9.5	17	13.5	13.8	16.5	
cf. *C.p. pyrenaica*	♂		ATX 1	Atxuri	Mañaria	I-IV				28									
cf. *C.p. pyrenaica*	♂		BO 2	Bolinkoba	Aradiano	III				43.5									
cf. *C.p. pyrenaica*	♂		BO 3	Bolinkoba	Aradiano	IV				41									
cf. *C.p. pyrenaica*	♀		BO 5	Bolinkoba	Aradiano	V				33									
cf. *C.p. pyrenaica*	♂		LUM 1	Lumentxa	Lekeitio	IV	156.5			46									
cf. *C.p. pyrenaica*	♀		LUM 2	Lumentxa	Lekeitio	III				35									

METACARPUS																			
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WC M**	**WCL**	**DE M**	**DV M**	**DIM**	**DIL**	**DVL**	**DEL**
cf. *C.p. pyrenaica*	♀		OYA 1	Oyalkoba	Abadiño					34									
cf. *C.p. pyrenaica*			P-1	Rascaño	Mirones					31.5									
cf. *C.p. pyrenaica*			P-16	Rascaño	Mirones					36.5									
cf. *C.p. pyrenaica*			P-2	Rascaño	Mirones					32									
cf. *C.p. pyrenaica*			P-24	Rascaño	Mirones					39									
cf. *C.p. pyrenaica*			P-25	Rascaño	Mirones					39									
cf. *C.p. pyrenaica*			P-26	Rascaño	Mirones					39.5									
cf. *C.p. pyrenaica*			P-27	Rascaño	Mirones					39.5									
cf. *C.p. pyrenaica*			P-3	Rascaño	Mirones					32									
cf. *C.p. pyrenaica*			P-30	Rascaño	Mirones					40									
cf. *C.p. pyrenaica*			P-31	Rascaño	Mirones					40									
cf. *C.p. pyrenaica*			P-32	Rascaño	Mirones					40.5									
cf. *C.p. pyrenaica*			P-4	Rascaño	Mirones					32									
cf. *C.p. pyrenaica*			P-10	Tito Bustillo	Ribadesella					34									
cf. *C.p. pyrenaica*			P-17	Tito Bustillo	Ribadesella					37.5									
cf. *C.p. pyrenaica*			P-18	Arenaza	Galdames					38									
cf. *C.p. pyrenaica*			P-19	Arenaza	Galdames					38									

METACARPUS																			
Sub-species	Sex	Age (years)	Code	Collection / site	Location	Level	GL	BP	SD	BD	BFd	WC M	WCL	DE M	DV M	DIM	DIL	DVL	DEL
cf. *C.p. pyrenaica*			P-20	Arenaza	Galdames					38.5									
cf. *C.p. pyrenaica*			P-33	Arenaza	Galdames					41									
cf. *C.p. pyrenaica*			P-5	Arenaza	Galdames					33									
cf. *C.p. pyrenaica*			P-6	Arenaza	Galdames					33									
cf. *C.p. pyrenaica*			P-7	Arenaza	Galdames					33									
cf. *C.p. pyrenaica*			P-9	Arenaza	Galdames					33.5									
cf. *C.p. pyrenaica*			SA 1	Santimamiñe	Kortezubi	VI				34									
cf. *C.p. pyrenaica*			SA 2	Santimamiñe	Kortezubi	VI				35									
cf. *C.p. pyrenaica*			SA 3	Santimamiñe	Kortezubi	VII				41									
cf. *C.p. pyrenaica*			SA 4	Santimamiñe	Kortezubi	VIII				30.5									
cf. *C.p. pyrenaica*			SA 5	Santimamiñe	Kortezubi	V				36									
cf. *C.p. pyrenaica*	♀		URR 1	Urratxa	Orozko	III	123.5			29.5									
cf. *C.p. pyrenaica*	♀		URR 2	Urratxa	Orozko	III				29.5									
cf. *C.p. pyrenaica*	♀		URR 3	Urratxa	Orozko	III				28.5									
cf. *C.p. pyrenaica*			URR 7	Urratxa	Orozko	III				39.5									
cf. *C.p. pyrenaica*			URR 8	Urratxa	Orozko	III				38									
cf. *C.p. pyrenaica*			URT 1	Urtiaga	Deba	D	145	35.1		39									

METACARPUS																			
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WC M**	**WCL**	**DE M**	**DV M**	**DIM**	**DIL**	**DVL**	**DEL**
cf. *C.p. pyrenaica*			URT 10	Urtiaga	Deba	D				39.8									
cf. *C.p. pyrenaica*			URT 11	Urtiaga	Deba	D				40									
cf. *C.p. pyrenaica*			URT 12	Urtiaga	Deba	D				41.5									
cf. *C.p. pyrenaica*			URT 13	Urtiaga	Deba	F				41.7									
cf. *C.p. pyrenaica*			URT 2	Urtiaga	Deba	D				33									
cf. *C.p. pyrenaica*			URT 3	Urtiaga	Deba	D				34									
cf. *C.p. pyrenaica*			URT 4	Urtiaga	Deba	D				34.2									
cf. *C.p. pyrenaica*			URT 5	Urtiaga	Deba	D				34.3									
cf. *C.p. pyrenaica*			URT 6	Urtiaga	Deba	D				34.5									
cf. *C.p. pyrenaica*	♂		URT 7	Urtiaga	Deba	D				36									
cf. *C.p. pyrenaica*	♂		URT 8	Urtiaga	Deba	D				38.8									
cf. *C.p. pyrenaica*			URT 9	Urtiaga	Deba	D				39									
			133	Cova Fosca	Ares del Maestrat	[-120]				(30.5)									
				Cova Fosca	Ares del Maestrat	[-125/-143]				(27.)7	(26.6)								
				Cova Fosca	Ares del Maestrat	[-170/-177]					28.8	13.3	13	10.3	16.6	14.1	13.8	16	9.8
				Cova Fosca	Ares del Maestrat	[-170/-177]					30.2	14.5	14	12	18.7	16.4	15.8	18.1	11.7
				Cova Fosca	Ares del Maestrat	[-170/-177]					31.4								

METACARPUS																			
Sub-species	Sex	Age (years)	Code	Collection / site	Location	Level	GL	BP	SD	BD	BFd	WC M	WCL	DE M	DV M	DIM	DIL	DVL	DEL
				Cova Fosca	Ares del Maestrat	[-177/-196]		(29.5)											
			765	Cova Fosca	Ares del Maestrat	[-177/-196]		(26.5)											
			800	Cova Fosca	Ares del Maestrat	[-177/-196]				(29)	29.7	13.7	13.2	11.1	17.6	14.8	14.7		10.5
			1088	Cova Fosca	Ares del Maestrat	[-177/-196]				(34)									
			1283	Cova Fosca	Ares del Maestrat	[-177/-196]				(28.8)	(28.6)	13.1	12.8	10	(15.7)	(15.3)	13.8	13.8	10
			1410	Cova Fosca	Ares del Maestrat	[-177/-196]				34.9	(34.5)	(15.5)	(14.8)	(12.4)					(12.4)
				Cova Fosca	Ares del Maestrat	[-196/-211]				28.6	(27.8)	(13)	(13)	(10.9)					(10)
			1235	Cova Fosca	Ares del Maestrat	[-196/-211]					27.5	13	12.2	10.7	17	14.3	14.6	16.9	10.5
			185	Cova Fosca	Ares del Maestrat	[-196/-211]				(34.8)	34.6	16.6	15.9	12	(20.3)	16.9	16.5	(19.6)	11.7
				Cova Fosca	Ares del Maestrat	[-211/-220]				29.7	(28.3)		13.8			15.5	15.5	18	10.6
			707	Cova Fosca	Ares del Maestrat	[-211/-220]				(30.3)	30.3	13.5	13.5	11	18.1	14.9	14.7	(17.3)	(11.4)
				Cova Fosca	Ares del Maestrat	[-211/-220]				(33)	(32)	(14.9)	(14.1)	(11.8)	(19.1)	(15.5)	(15.9)	(18.7)	(10.7)
				Cova Fosca	Ares del Maestrat	[-211/-220]				(30)	28.1	13.3	13.1	11.1	16.4	14.7	14.7		
				Cova Fosca	Ares del Maestrat	[-211/-220]	(124)												
				Cova Fosca	Ares del Maestrat	[-211/-220]		(25)											
				Cova Fosca	Ares del Maestrat	[-211/-220]				30									
				Cova Fosca	Ares del Maestrat	[-211/-220]				30									

METACARPUS																			
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**BP**	**SD**	BD	BFd	**WC M**	**WCL**	**DE M**	**DV M**	**DIM**	**DIL**	**DVL**	**DEL**
				Cova Fosca	Ares del Maestrat	[-211/-220]				26.5									
				Cova Fosca	Ares del Maestrat	[-220/-224]				27.5	26.8	12.4	12.4	11.1	17.7	14.9	14.9	17.7	10.9
				Cova Fosca	Ares del Maestrat	[-220/-224]				31.7	31.2	15.1	14.4	12.1	16.8	16.7	16.2	17.5	11.9
				Cova Fosca	Ares del Maestrat	[-220/-224]				27.4	26.7	12.7	12.4	10.3	16.9	14.1	14.3	16.8	9.9
			309	Cova Fosca	Ares del Maestrat	[-220/-224]				27.2	27	11.8	11.8	9.2	16	13.9	13.3	16	9.2
				Cova Fosca	Ares del Maestrat	[-220/-224]				30	30.3	14	13.8	11.2	17	15.4	15.3	16.4	11.4
			100	Cova Fosca	Ares del Maestrat	[-220/-224]											15.1	(15.9)	11.3
			389	Cova Fosca	Ares del Maestrat	[-224/-235]				29.2	28.9	13.2	13	10.2	(18.4)	15	14.9	(17.8)	10.7
			584	Cova Fosca	Ares del Maestrat	[-235/-242]				29.5	29.6	14	13.3	10.9		(15)	(14.9)		10.7
			84	Cova Fosca	Ares del Maestrat	[-235/-242]					(30)	13.8	13.8	11.4					11.3
				Cova Fosca	Ares del Maestrat	[-242/-255]				29.7	(31.2)	(14.2)	(13.8)	(11.5)	(18.6)	(15.4)	(15.4)	(17.7)	(10.8)
			36	Cova Fosca	Ares del Maestrat	[-255/-262]		(28)											11.8
			53	Cova Fosca	Ares del Maestrat	[-279/-298]				34.1	33.3	15	14.6	12.5	(19.3)	16.3	15.9	(18.1)	(11.3)
			36	Cova Fosca	Ares del Maestrat	[-279/-298]				(24.5)	(25.5)	(11.4)	(11)	(9.9)	(14.7)	(13.4)	(13)	(16.1)	10
			46	Cova Fosca	Ares del Maestrat	[-298/-308]				26.9	27	12.2	11.8	10.4	(16.5)	(14.4)	13.6	16.1	(10.9)
				Cova Fosca	Ares del Maestrat	[-298/-308]				26.8	26.4	11.8	11.1	10.9	18	14.9	15	17.9	11.4
				Mas Nou	Ares del Maestrat	1				(35)									

METACARPUS																			
Sub-species	Sex	Age (years)	Code	Collection / site	Location	Level	GL	BP	SD	BD	BFd	WC M	WCL	DE M	DV M	DIM	DIL	DVL	DEL
				Mas Nou	Ares del Maestrat	1				(26)									
				Mas Nou	Ares del Maestrat	1				(34.5)									

PELVIS								
Sub-species	Sex	Age (years)	Code	Collection / site	Location	Level	SH	LA
C. p. hispanica	♂	6	656	AMM	S. Cazorla		19.4	31
C. p. hispanica	♀	5	AL-6	AMM	S. Cazorla		17	27.5
cf. *C. p. pyrenaica*	♂	7	Cap-pyr 15	AMM	Somiedo		22.4	34
				Cova Fosca	Ares del Maestrat	[-170/-177]		(29)
				Cova Fosca	Ares del Maestrat	[-170/-177]		(35)
				Cova Fosca	Ares del Maestrat	[-211/-220]	17	31
				Cova Fosca	Ares del Maestrat	[-211/-220]	21	33
				Cova Fosca	Ares del Maestrat	[-211/-220]	19	
				Cova Fosca	Ares del Maestrat	[-211/-220]	18.5	
				Cova Fosca	Ares del Maestrat	[-211/-220]	19	28
				Cova Fosca	Ares del Maestrat	[-211/-220]	19	29
				Cova Fosca	Ares del Maestrat	[-211/-220]	15	
				Cova Fosca	Ares del Maestrat	[-220/-224]		27
				Cova Fosca	Ares del Maestrat	[-220/-224]		25.8
				Cova Fosca	Ares del Maestrat	[-262/-275]		(30)
				Cova Fosca	Ares del Maestrat	[-298/-308]		(29.2)
				Cova Fosca	Ares del Maestrat	[-298/-308]		(32)

FEMUR												
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**GL**	**Bp**	**Ac**	**DC**	**SD**	**Bd**
C. p. hispanica	♂	6	656	AMM	S. Cazorla		234	55.5	27.5	25.5	22	48
C. p. hispanica	♀	5	AL-6	AMM	S. Cazorla		198.5	47.5	23.3	23.5	18	39
cf. *C. p. pyrenaica*	♂	7	Cap-pyr 15	AMM	Somiedo		253	64	30	30.5	24	53
				Cova Fosca	Ares del Maestrat	[-119]				26.5		
				Cova Fosca	Ares del Maestrat	[-170/-177]				24		
				Cova Fosca	Ares del Maestrat	[-170/-177]				(22)		
				Cova Fosca	Ares del Maestrat	[-196/-211]			18.73	26		
				Cova Fosca	Ares del Maestrat	[-196/-211]			14	24		
				Cova Fosca	Ares del Maestrat	[-196/-211]			16	22		
				Cova Fosca	Ares del Maestrat	[-211/-220]					19.5	38.5
				Cova Fosca	Ares del Maestrat	[-211/-220]				23.5		
				Cova Fosca	Ares del Maestrat	[-211/-220]				(22.5)		
				Cova Fosca	Ares del Maestrat	[-211/-220]				(21.5)		
				Cova Fosca	Ares del Maestrat	[-211/-220]				26		
				Cova Fosca	Ares del Maestrat	[-242/-255]				(26.5)		
				Cova Fosca	Ares del Maestrat	[-242/-255]						47
				Cova Fosca	Ares del Maestrat	[-298/-308]			23	22.4		
				Cova Fosca	Ares del Maestrat	[-262/-275]				26		
				Mas Nou	Ares del Maestrat	1				(23)		
				Mas Nou	Ares del Maestrat	1				(22.5)		
				Mas Nou	Ares del Maestrat	1				(23)		
				Mas Nou	Ares del Maestrat	1				(21)		
				Mas Nou	Ares del Maestrat	1				(23.5)		
				Mas Nou	Ares del Maestrat	1A				(26.5)		
				Mas Nou	Ares del Maestrat	1A						35
				Mas Nou	Ares del Maestrat	1B				(26.5)		

TIBIA											
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**Bd**	**GL**	**Bp**	**SD**	**Dd**
C. p. hispanica	♂	6	656	AMM	S. Cazorla		32	271.5	51.5	20	
C. p. hispanica	♀	5	AL-6	AMM	S. Cazorla		28	238.5	45.5	17	
C. p. hispanica	♂	10	18070	MNCN	S. Cazorla		31	272	50.5	18	
C. p. hispanica	♂	11	18073	MNCN	S. Cazorla		30.5	261	51	19	
C. p. hispanica	♂	11	18075	MNCN	S. Cazorla		31.5	267	50	17.5	
C. p. hispanica	♂	11	18124	MNCN	S. Cazorla		30.5	270	50.5	19.5	
C. p. hispanica	♂	8	18130	MNCN	S. Cazorla		30.8	269	50	18.2	
C. p. hispanica	♂	7	18146	MNCN	S. Cazorla		31.5	267	52	19	
C. p. hispanica	♂	7	18151	MNCN	S. Cazorla		31.5	273.8	53	20	
C. p. hispanica	♂	5	18153	MNCN	S. Cazorla		32.5	271	52	20	
C. p. hispanica	♂	9	18155	MNCN	S. Cazorla		32	273	54	20.5	
C. p. hispanica	♂	13	18157	MNCN	S. Cazorla		28.7	254	48.5	18	
C. p. victoriae	♂	8	18281	MNCN	S. Gredos		33	278.5	55	18.5	
C. p. hispanica	♀	7	18087	MNCN	S. Cazorla		25.5	229.1	42	15.5	
C. p. hispanica	♀	5	18089	MNCN	S. Cazorla		27	232	44	16.5	
C. p. hispanica	♀	7	18094	MNCN	S. Cazorla		26.5	220	42.8	15.3	
C. p. hispanica	♀	6	18117	MNCN	S. Cazorla		27	228.5	43.9	15.5	
C. p. hispanica	♀	4	18207	MNCN	S. Cazorla		25	215	41.5	15	
C. p. hispanica	♀	5	18216	MNCN	S. Cazorla		26.5	224	43	16	
C. p. hispanica	♀	7	18222	MNCN	S. Cazorla		26.7	231	45.5	15	
C. p. victoriae	♀	8	18184	MNCN	S. Gredos		31	248	50	18	
C. p. victoriae	♀	8	18189	MNCN	S. Gredos		28	233.5	49	16.5	
C. p. victoriae	♀	6	18191	MNCN	S. Gredos		28.2	239.5	47	16.5	
C. p. victoriae	♀	5	18197	MNCN	S. Gredos		28	230	46	17.2	

TIBIA											
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**Bd**	**GL**	**Bp**	**SD**	**Dd**
C. p. victoriae	♀	6	18201	MNCN	S. Gredos		28.7	232	48	17	
C. p. victoriae	♀	7	18237	MNCN	S. Gredos		26	220.5	43.5	14.6	
C. p. victoriae	♀	5	18252	MNCN	S. Gredos		28	229	47	15.5	
C. p. victoriae	♀	8	18254	MNCN	S. Gredos		29	230.5	46.8	17	
C. p. victoriae	♀	5	18271	MNCN	S. Gredos		28.5	239	47.5	17.5	
cf. *C. p. pyrenaica*	♂	7	Cap-pyr 15	AMM	Somiedo		37	302.5	59	23.5	
cf. *C. p. pyrenaica*	♀		ATX 1	Atxuri	Mañaria	I-IV	34.5				28.5
cf. *C. p. pyrenaica*	♀		ATX 2	Atxuri	Mañaria	IV	35				29.5
cf. *C. p. pyrenaica*	♀		ATX 3	Atxuri	Mañaria	V-VII	35				26.5
cf. *C. p. pyrenaica*	♀		LUM 1	Lumentxa	Lekeitio	V-VII	29.5				22
cf. *C. p. pyrenaica*	♀		LUM 2	Lumentxa	Lekeitio	V-VII	29				22
cf. *C. p. pyrenaica*			SA 1	Santimamiñe	Kortezubi	II	34				
cf. *C. p. pyrenaica*	♂		SA 2	Santimamiñe	Kortezubi	VI	38.5				
cf. *C. p. pyrenaica*			SA 3	Santimamiñe	Kortezubi	VII	33.5		45.5		
cf. *C. p. pyrenaica*			URR 1	Urratxa	Orozko	III			42.5		
cf. *C. p. pyrenaica*			URR 2	Urratxa	Orozko	III			47.5		
cf. *C. p. pyrenaica*	♂		URR 3	Urratxa	Orozko	III	36				27
cf. *C. p. pyrenaica*	♀		URR 4	Urratxa	Orozko	III	32.5				26
cf. *C. p. pyrenaica*	♂		URR 5	Urratxa	Orozko	III	34				25.5
cf. *C. p. pyrenaica*	♀		URR 6	Urratxa	Orozko	III	31.5				24.5
cf. *C. p. pyrenaica*	♀		URR 7	Urratxa	Orozko	III	30				24.5
cf. *C. p. pyrenaica*	♀		URR 8	Urratxa	Orozko	III	30.5				25.5
cf. *C. p. pyrenaica*	♀		URR 9	Urratxa	Orozko	III	30				23
cf. *C. p. pyrenaica*	♀		URR 10	Urratxa	Orozko	III	29				21
cf. *C. p. pyrenaica*	♀		URR 11	Urratxa	Orozko	III	30.5				21

TIBIA											
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection / site**	**Location**	**Level**	**Bd**	**GL**	**Bp**	**SD**	**Dd**
				Cova Fosca	Ares del Maestrat	[-111/-126]	33.6				
				Cova Fosca	Ares del Maestrat	[-111/-126]	(26.6)				
				Cova Fosca	Ares del Maestrat	[-120/-130]	(32)				
				Cova Fosca	Ares del Maestrat	[-125/-142]	30.5				
				Cova Fosca	Ares del Maestrat	[-150/-170]	31				
				Cova Fosca	Ares del Maestrat	[-170/-177]	30				
				Cova Fosca	Ares del Maestrat	[-177/-196]	(28)				
				Cova Fosca	Ares del Maestrat	[-177/-196]	25				
				Cova Fosca	Ares del Maestrat	[-177/-196]	32				
				Cova Fosca	Ares del Maestrat	[-196/-211]	29				
			1069	Cova Fosca	Ares del Maestrat	[-196/-211]	29.5				
			738	Cova Fosca	Ares del Maestrat	[-196/-211]	29.5				
			902	Cova Fosca	Ares del Maestrat	[-196/-211]	28				
			1461	Cova Fosca	Ares del Maestrat	[-196/-211]	28				
			819	Cova Fosca	Ares del Maestrat	[-196/-211]	29.4				
				Cova Fosca	Ares del Maestrat	[-211/-220]	34				
			405	Cova Fosca	Ares del Maestrat	[-211/-220]	32.5		(20.5)		
			440	Cova Fosca	Ares del Maestrat	[-211/-220]	32				
				Cova Fosca	Ares del Maestrat	[-211/-220]	30				
				Cova Fosca	Ares del Maestrat	[-211/-220]	27				
				Cova Fosca	Ares del Maestrat	[-211/-220]	27.5				
			332	Cova Fosca	Ares del Maestrat	[-211/-220]	(28)				
			53	Cova Fosca	Ares del Maestrat	[-211/-220]	28.5				
			273	Cova Fosca	Ares del Maestrat	[-211/-220]	28				
			899	Cova Fosca	Ares del Maestrat	[-211/-220]	28				

TIBIA											
Sub-species	Sex	Age (years)	Code	Collection / site	Location	Level	Bd	GL	Bp	SD	Dd
			577	Cova Fosca	Ares del Maestrat	[-211/-220]	29				
				Cova Fosca	Ares del Maestrat	[-211/-220]	25.5				
			777	Cova Fosca	Ares del Maestrat	[-211/-220]		(52.5)			
			255	Cova Fosca	Ares del Maestrat	[-220/-224]	(30)				
				Cova Fosca	Ares del Maestrat	[-220/-224]	(30.5)				
			382	Cova Fosca	Ares del Maestrat	[-220/-224]	29.5				
			653	Cova Fosca	Ares del Maestrat	[-220/-224]	29				
				Cova Fosca	Ares del Maestrat	[-224/-235]	32.4				
				Cova Fosca	Ares del Maestrat	[-224/-235]	28.5				
				Cova Fosca	Ares del Maestrat	[-242/-255]	(29)				
				Cova Fosca	Ares del Maestrat	[-242/-255]	(29.5)				
				Cova Fosca	Ares del Maestrat	[-242/-255]	(32.5)				
				Cova Fosca	Ares del Maestrat	[-255/-262]	28.1				
				Cova Fosca	Ares del Maestrat	[-255/-262]	30				
				Cova Fosca	Ares del Maestrat	[-304/-319]	30				

ASTRAGALUS										
Sub-species	Sex	Age (years)	Code	Collection/ Site	Location	Level	GLl	GLm	Dl	Bd
C. p. hispanica	♂	10	18070	MNCN	S. Cazorla		33.5	32	18	21.5
C. p. hispanica	♂	11	18073	MNCN	S. Cazorla		33	32	18.5	21.5
C. p. hispanica	♂	11	18075	MNCN	S. Cazorla		32.5	31	17.8	21
C. p. hispanica	♂	11	18124	MNCN	S. Cazorla		34.5	32.6	18.5	21.5
C. p. hispanica	♂	8	18127	MNCN	S. Cazorla		32	30	17.5	20
C. p. hispanica	♂	8	18130	MNCN	S. Cazorla		32.8	31.5	18	22
C. p. hispanica	♂	7	18147	MNCN	S. Cazorla		33	31.2	18	20
C. p. hispanica	♂	8	18151	MNCN	S. Cazorla		34	32	19	21.8

ASTRAGALUS										
Sub-species	Sex	Age (years)	Code	Collection/ Site	Location	Level	GLl	GLm	Dl	Bd
C. p. hispanica	♂	5	18153	MNCN	S. Cazorla		34	32.2	19	22
C. p. hispanica	♂	9	18155	MNCN	S. Cazorla		34.5	32.5	18.5	23
C. p. hispanica	♂	13	18157	MNCN	S. Cazorla		31	30	17	20
C. p. victoriae	♂	12	18159	MNCN	S. Gredos		34	32.2	19	23.2
C. p. victoriae	♂	6	18163	MNCN	S. Gredos		34	31.3	18	21.9
C. p. victoriae	♂	4	18166	MNCN	S. Gredos		36	33.5	19	23
C. p. victoriae	♂	5	18170	MNCN	S. Gredos		35	33.5	19.8	23.5
C. p. victoriae	♂	6	18172	MNCN	S. Gredos		35.5	33	19	22.5
C. p. victoriae	♂	6	18174	MNCN	S. Gredos		34	31.2	18.5	21
C. p. victoriae	♂	4	18233	MNCN	S. Gredos		32.6	31.6	18.6	22.8
C. p. victoriae	♂	2	18240	MNCN	S. Gredos		32.5	30.7	18.4	21.2
C. p. victoriae	♂	3	18246	MNCN	S. Gredos		34.9	32.1	19.4	23
C. p. victoriae	♂	2	18248	MNCN	S. Gredos		33	30.5	18.2	22
C. p. victoriae	♂	6	18279	MNCN	S. Gredos		36	33	20	24.5
C. p. victoriae	♂	8	18281	MNCN	S. Gredos		36	33	20.5	24.5
C. p. hispanica	♀	7	18087	MNCN	S. Cazorla		27.3	27	15	18.5
C. p. hispanica	♀	5	18089	MNCN	S. Cazorla		32	3	17.5	19.5
C. p. hispanica	♀	7	18094	MNCN	S. Cazorla		30.5	29	16.5	18.5
C. p. hispanica	♀	4	18116	MNCN	S. Cazorla		30	29	15.7	19
C. p. hispanica	♀	4	18207	MNCN	S. Cazorla		30	28	15	19
C. p. hispanica	♀	5	18216	MNCN	S. Cazorla		31	30.3	16.8	19
C. p. victoriae	♀	8	18184	MNCN	S. Gredos		34.5	32	18.6	22
C. p. victoriae	♀	6	18191	MNCN	S. Gredos		33	31	18	21
C. p. victoriae	♀	2	18195	MNCN	S. Gredos		30	27.5	16.5	19.8
C. p. victoriae	♀	5	18197	MNCN	S. Gredos		33	31	17.9	21
C. p. victoriae	♀	6	18201	MNCN	S. Gredos		31.9	30	19	21.5
C. p. victoriae	♀	7	18222	MNCN	S. Gredos		31	28.5	17	19.7
C. p. victoriae	♀	3	18230	MNCN	S. Gredos		31.5	29.4	17.8	20.3
C. p. victoriae	♀	7	18237	MNCN	S. Gredos		31	30.7	18.4	19.5
C. p. victoriae	♀	3	18244	MNCN	S. Gredos		33.9	31.9	18.6	21.2

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
C. p. victoriae	♀	5	18252	MNCN	S. Gredos		31	29	17	20
C. p. victoriae	♀	2	18253	MNCN	S. Gredos		29.9	28.1	17.1	18.9
C. p. victoriae	♀	8	18254	MNCN	S. Gredos		31.5	29	17	20.5
C. p. victoriae	♀	5	18271	MNCN	S. Gredos		34	31	18	21
C. p. hispanica	♂	6	656	AMM	S. Cazorla		34.5	32.5	24	23.2
C. p. hispanica	♀	5	AL-6	AMM	S. Cazorla		31.5	31	22.4	20.5
cf. *C. p. pyrenaica*	♂	7	Cap-pyr 15	AMM	Somiedo		37.3	34.7	28.5	24.5
cf. *C. p. pyrenaica*			ATXU 1	Atxuri	Mañaria	Atxuri I	37.5	38.5	21.5	24
cf. *C. p. pyrenaica*	♂?		ATXU 2	Atxuri	Mañaria	Atxuri I	39	37	21.5	24.5
cf. *C. p. pyrenaica*	♂?		ATXU 3	Atxuri	Mañaria	Atxuri II	38	35	22	25.5
cf. *C. p. pyrenaica*			ATXU 4	Atxuri	Mañaria	Atxuri II		36.5		
cf. *C. p. pyrenaica*			ATXU 5	Atxuri	Mañaria	Atxuri II	36.5	34.5	20	24
cf. *C. p. pyrenaica*			ATXU 6	Atxuri	Mañaria	Atxuri III		32.5	19.3	24.5
cf. *C. p. pyrenaica*			ATXU 7	Atxuri	Mañaria	Atxuri I-IV	39	36.5	21	26
cf. *C. p. pyrenaica*			ATXU 8	Atxuri	Mañaria	Atxuri I-IV	37	33.5	19.6	23.5
cf. *C. p. pyrenaica*			ATXU 9	Atxuri	Mañaria	Atxuri I-IV	35.5	33.5	19.3	23
cf. *C. p. pyrenaica*	♂?		ATXU10	Atxuri	Mañaria	Atxuri V-VII	41.5	38.5	23.5	29
cf. *C. p. pyrenaica*	♀?		ATXU 11	Atxuri	Mañaria	Atxuri V-VII	35	33		22
cf. *C. p. pyrenaica*			ATXU 12	Atxuri	Mañaria	Atxuri V-VII		32.5		22.5
cf. *C. p. pyrenaica*	♂?		ATXU 13	Atxuri	Mañaria	Atxuri V-VII	41.5	38.5	23	28
cf. *C. p. pyrenaica*			ATXURI 14	Atxuri	Mañaria	Atxuri V-VII	37.5	35	20	25.5
cf. *C. p. pyrenaica*			ATXURI 15	Atxuri	Mañaria	Atxuri V-VII	39.5	33	22	25
cf. *C. p. pyrenaica*			ATXURI 16	Atxuri	Mañaria	Atxuri V-VII	35	32.5	19.1	23.5
cf. *C. p. pyrenaica*			ATXURI 17	Atxuri	Mañaria	Atxuri V-VII		30.5		
cf. *C. p. pyrenaica*	♂?		BOLIN 1	Bolinkova	Aradiano	I-III	38.5	34.5	21	26.5
cf. *C. p. pyrenaica*	♀?		BOLIN 2	Bolinkova	Aradiano	I-III	34.5	31.5	18.2	21
cf. *C. p. pyrenaica*	♂?		BOLIN 3	Bolinkova	Aradiano	I-III	38.5	36	20.5	25.5
cf. *C. p. pyrenaica*	♂?		BOLIN 4	Bolinkova	Aradiano	I-III	40.5	37.5	22.5	27.5
cf. *C. p. pyrenaica*	♂?		BOLIN 5	Bolinkova	Aradiano	I-III	38	36.5	20.5	25
cf. *C. p. pyrenaica*	♂?		BOLIN 6	Bolinkova	Aradiano	I-III	39	36.5	22	27

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
cf. *C. p. pyrenaica*	♂?		BOLIN 7	Bolinkova	Aradiano	I-III	38.5	36	20	
cf. *C. p. pyrenaica*			BOLIN 8	Bolinkova	Aradiano	I-III	37	33	18.8	23.5
cf. *C. p. pyrenaica*	♀?		BOLIN 9	Bolinkova	Aradiano	I-III	35	32	19	22.5
cf. *C. p. pyrenaica*			BOLIN 10	Bolinkova	Aradiano	IV	37	34	19.5	23
cf. *C. p. pyrenaica*	♀?		BOLIN 11	Bolinkova	Aradiano	IV	34.5	33.5	39.9	25
cf. *C. p. pyrenaica*	♀?		BOLIN 12	Bolinkova	Aradiano	IV	35	32.5	18.4	22
cf. *C. p. pyrenaica*			BOLIN 13	Bolinkova	Aradiano	IV	36.5	34.5	19.8	24
cf. *C. p. pyrenaica*			BOLIN 14	Bolinkova	Aradiano	IV	37.5	34.5	20.5	23
cf. *C. p. pyrenaica*	♀?		BOLIN 15	Bolinkova	Aradiano	V	35	34	18.8	23
cf. *C. p. pyrenaica*			BOLIN 16	Bolinkova	Aradiano	V	38	36	21	24
cf. *C. p. pyrenaica*			BOLIN 17	Bolinkova	Aradiano	V	37	34.5	20.5	23
cf. *C. p. pyrenaica*	♂?		BOLIN 18	Bolinkova	Aradiano	V	39	37	21.5	27
cf. *C. p. pyrenaica*	♀?		BOLIN 19	Bolinkova	Aradiano	VI	34	31	18.3	21.5
cf. *C. p. pyrenaica*	♀?		BOLIN 20	Bolinkova	Aradiano	VI	33.5	31.5	19	22
cf. *C. p. pyrenaica*	♀?		BOLIN 21	Bolinkova	Aradiano	VI	35	34	19.6	24
cf. *C. p. pyrenaica*	♀?		BOLIN 22	Bolinkova	Aradiano	VI	35	32	18.1	22.5
cf. *C. p. pyrenaica*	♂?		BOLIN 23	Bolinkova	Aradiano	VI	38.5	36	21	25
cf. *C. p. pyrenaica*	♀?		BOLIN 24	Bolinkova	Aradiano	VI	35	33.5	19	24
cf. *C. p. pyrenaica*	♀?		BOLIN 25	Bolinkova	Aradiano	VI	36	33	19.4	23.5
cf. *C. p. pyrenaica*	♂?		BOLIN 26	Bolinkova	Aradiano	VI	40	16.5	21.5	25
cf. *C. p. pyrenaica*	♀?		BOLIN 27	Bolinkova	Aradiano	VI	36	34	19	21.5
cf. *C. p. pyrenaica*	♀?		BOLIN 28	Bolinkova	Aradiano	VI	35.5	33.5	19.2	23.5
cf. *C. p. pyrenaica*	♀?		BOLIN 29	Bolinkova	Aradiano	VI	35	32.5	18.7	23
cf. *C. p. pyrenaica*			BOLIN 30	Bolinkova	Aradiano	VI	36			
cf. *C. p. pyrenaica*			BOLIN 31	Bolinkova	Aradiano	VI		32		
cf. *C. p. pyrenaica*			BOLIN 32	Bolinkova	Aradiano	VI		33.5		
cf. *C. p. pyrenaica*	♀?		LUM 1	Lumentxa	Lekeitio	III	33.5	32.5	18.7	21.5
cf. *C. p. pyrenaica*	♀?		LUM 2	Lumentxa	Lekeitio	IV	33.5	31.5	18.1	23
cf. *C. p. pyrenaica*	♀?		LUM 3	Lumentxa	Lekeitio	IV	30.5	29	16.9	18.5
cf. *C. p. pyrenaica*	♀?		LUM 4	Lumentxa	Lekeitio	V	32.5	31.5	18.3	22.5

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
cf. *C. p. pyrenaica*	♀?		LUM 5	Lumentxa	Lekeitio	V	31	28.5	15.5	19.5
cf. *C. p. pyrenaica*	♀?		LUM 6	Lumentxa	Lekeitio	V	32	31.5	18.1	21
cf. *C. p. pyrenaica*	♀?		LUM 7	Lumentxa	Lekeitio	V	33	31.5	18	21.5
cf. *C. p. pyrenaica*	♀?		LUM 8	Lumentxa	Lekeitio	V	30.5	28.5	15.1	19.5
cf. *C. p. pyrenaica*			LUM 9	Lumentxa	Lekeitio	V			18.9	22.5
cf. *C. p. pyrenaica*			OYAL 1	Oyalkoba	Abadiano	III		33	19	21
cf. *C. p. pyrenaica*			OYAL 2	Oyalkoba	Abadiano	III	37	35		23
cf. *C. p. pyrenaica*			P-1	Lezetxiki	Mondragón	IIIa	37.2	35.2		21.6
cf. *C. p. pyrenaica*			P-2	Lezetxiki	Mondragón	IIIa	34.3			21.5
cf. *C. p. pyrenaica*			P-3	Urtiaga	Deba	D	34.3			21.5
cf. *C. p. pyrenaica*			P-4	Urtiaga	Deba	D	34.7			22.4
cf. *C. p. pyrenaica*			P-5	Urtiaga	Deba	D	34.8	32.9	19.5	22.7
cf. *C. p. pyrenaica*			P-6	Urtiaga	Deba	D	35		19.4	
cf. *C. p. pyrenaica*			P-7	Urtiaga	Deba	D	35	32.6	19.4	21.5
cf. *C. p. pyrenaica*			P-8	Urtiaga	Deba	D	35.1	32.8	18.9	22.7
cf. *C. p. pyrenaica*			P-9	Urtiaga	Deba	D	35.2	33.1	19.5	22.6
cf. *C. p. pyrenaica*			P-10	Urtiaga	Deba	D	35.2	33.4	19.2	22.7
cf. *C. p. pyrenaica*			P-11	Urtiaga	Deba	D	36	34.9	19.5	23.2
cf. *C. p. pyrenaica*			P-12	Urtiaga	Deba	D	36	33.9	20	23
cf. *C. p. pyrenaica*			P-13	Urtiaga	Deba	D	36.1	34	19.9	23.9
cf. *C. p. pyrenaica*			P-14	Urtiaga	Deba	D	36.3	33.9	19.5	23.7
cf. *C. p. pyrenaica*			P-15	Urtiaga	Deba	D	36.3	34.3	20	23.3
cf. *C. p. pyrenaica*			P-16	Urtiaga	Deba	D	37	35.4		
cf. *C. p. pyrenaica*			P-17	Urtiaga	Deba	D	34.2	34.8	20	25
cf. *C. p. pyrenaica*			P-18	Urtiaga	Deba	D	37.2	34.8	19.7	23.6
cf. *C. p. pyrenaica*			P-19	Urtiaga	Deba	D	37.3	34	19.7	23.7
cf. *C. p. pyrenaica*			P-20	Urtiaga	Deba	D	37.3	34.2	20.9	23.7
cf. *C. p. pyrenaica*			P-21	Urtiaga	Deba	D	37.6	34.4	21.2	24.2
cf. *C. p. pyrenaica*			P-22	Urtiaga	Deba	D	37.7	35	20.6	24
cf. *C. p. pyrenaica*			P-23	Urtiaga	Deba	D	38.2	36	20.9	25.4

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
cf. *C. p. pyrenaica*			P-24	Urtiaga	Deba	D	38.4	36.4	21.1	25.2
cf. *C. p. pyrenaica*			P-25	Urtiaga	Deba	D	38.6	38	21.1	24.7
cf. *C. p. pyrenaica*			P-26	Urtiaga	Deba	D	38.7	36	21.5	25.7
cf. *C. p. pyrenaica*			P-27	Urtiaga	Deba	D	39	35.5	22.1	26.1
cf. *C. p. pyrenaica*			P-28	Urtiaga	Deba	D	39.4	36.2	21.5	26.2
cf. *C. p. pyrenaica*			P-29	Urtiaga	Deba	D	37.5	37.6	21.4	27
cf. *C. p. pyrenaica*			P-30	Urtiaga	Deba	D	40	31.7	18.7	25.5
cf. *C. p. pyrenaica*			P-31	Urtiaga	Deba	D	40.5	36.7	22.3	28
cf. *C. p. pyrenaica*			P-32	Urtiaga	Deba	E	37.3	38.2	23.3	23.8
cf. *C. p. pyrenaica*			P-33	Urtiaga	Deba	E	40.6	34.7	20	27.4
cf. *C. p. pyrenaica*			P-34	Urtiaga	Deba	F	34	37.5	22.1	21.5
cf. *C. p. pyrenaica*			P-35	Urtiaga	Deba	F	38.3	35.3	21	24.1
cf. *C. p. pyrenaica*			P-36	Urtiaga	Deba	F	38.8	36.5	21.1	24.8
cf. *C. p. pyrenaica*			P-37	Urtiaga	Deba	F	39.3	37	21.1	26.4
cf. *C. p. pyrenaica*			P-38	Ermittia	Deba	Azilian	33.5	31.3	19	22.1
cf. *C. p. pyrenaica*			P-39	Ermittia	Deba	Magdalenian	34.5	32.5	18.5	22.1
cf. *C. p. pyrenaica*			P-40	Ermittia	Deba	Magdalenian	36.4	33.2	19.2	23.7
cf. *C. p. pyrenaica*			P-41	Ermittia	Deba	Magdalenian	37	35	20.3	23.5
cf. *C. p. pyrenaica*			P-42	Ermittia	Deba	Solutrean	37.7	35	20.3	24.5
cf. *C. p. pyrenaica*			P-43	Ermittia	Deba	Solutrean	39.2	37.5	21.2	27
cf. *C. p. pyrenaica*			P-44	Rascaño	Mirones		31.5			23
cf. *C. p. pyrenaica*			P-45	Rascaño	Mirones		32			21
cf. *C. p. pyrenaica*			P-46	Rascaño	Mirones		32.5			20
cf. *C. p. pyrenaica*			P-47	Rascaño	Mirones		32.5			23.5
cf. *C. p. pyrenaica*			P-48	Rascaño	Mirones		33			22
cf. *C. p. pyrenaica*			P-49	Riera	Llanes		33			22.5
cf. *C. p. pyrenaica*			P-50	Rascaño	Mirones		33.5			22
cf. *C. p. pyrenaica*			P-51	Rascaño	Mirones		33.5			22.5
cf. *C. p. pyrenaica*			P-52	Rascaño	Mirones		33.5			24
cf. *C. p. pyrenaica*			P-53	Rascaño	Mirones		34			21.5

ASTRAGALUS										
Sub-species	Sex	Age (years)	Code	Collection/ Site	Location	Level	GLl	GLm	Dl	Bd
cf. *C. p. pyrenaica*			P-54	Rascaño	Mirones		34			22
cf. *C. p. pyrenaica*			P-55	Rascaño	Mirones		34			22
cf. *C. p. pyrenaica*			P-56	Rascaño	Mirones		34			22
cf. *C. p. pyrenaica*			P-57	Rascaño	Mirones		34.5			21
cf. *C. p. pyrenaica*			P-58	Rascaño	Mirones		34.5			21.5
cf. *C. p. pyrenaica*			P-59	Rascaño	Mirones		34.5			21.5
cf. *C. p. pyrenaica*			P-60	Riera	Llanes		34.5			21.5
cf. *C. p. pyrenaica*			P-61	Tito Bustillo	Ribadesella		34.5			23
cf. *C. p. pyrenaica*			p-62	Riera	Llanes		34.5			23
cf. *C. p. pyrenaica*			p-63	Rascaño	Mirones		35			23.5
cf. *C. p. pyrenaica*			p-64	Rascaño	Mirones		35			21.5
cf. *C. p. pyrenaica*			p-65	Rascaño	Mirones		35			21.5
cf. *C. p. pyrenaica*			p-66	Rascaño	Mirones		35			22
cf. *C. p. pyrenaica*			P-67	Rascaño	Mirones		35			22
cf. *C. p. pyrenaica*			P-68	Rascaño	Mirones		35			22.5
cf. *C. p. pyrenaica*			P-69	Rascaño	Mirones		35			22.5
cf. *C. p. pyrenaica*			P-70	Rascaño	Mirones		35			23
cf. *C. p. pyrenaica*			P-71	Rascaño	Mirones		35			23.5
cf. *C. p. pyrenaica*			P-72	Rascaño	Mirones		35			24
cf. *C. p. pyrenaica*			P-73	Rascaño	Mirones		35.5			24.5
cf. *C. p. pyrenaica*			P-74	Rascaño	Mirones		35.5			21.5
cf. *C. p. pyrenaica*			P-75	Rascaño	Mirones		35.5			22
cf. *C. p. pyrenaica*			P-76	Rascaño	Mirones		35.5			22
cf. *C. p. pyrenaica*			P-77	Rascaño	Mirones		35.5			22
cf. *C. p. pyrenaica*			P-78	Rascaño	Mirones		35.5			23
cf. *C. p. pyrenaica*			P-79	Tito Bustillo	Ribadesella		35.5			23.5
cf. *C. p. pyrenaica*			P-80	Rascaño	Mirones		36			22
cf. *C. p. pyrenaica*			P-81	Rascaño	Mirones		36			22
cf. *C. p. pyrenaica*			P-82	Rascaño	Mirones		36			22.5
cf. *C. p. pyrenaica*			P-83	Rascaño	Mirones		36			22.5

ASTRAGALUS										
Sub-species	Sex	Age (years)	Code	Collection/ Site	Location	Level	GLl	GLm	Dl	Bd
cf. *C. p. pyrenaica*			P-84	Tito Bustillo	Ribadesella		36			23
cf. *C. p. pyrenaica*			P-85	Rascaño	Mirones		36			23.5
cf. *C. p. pyrenaica*			P-86	Rascaño	Mirones		36			24
cf. *C. p. pyrenaica*			P-87	Rascaño	Mirones		36			25
cf. *C. p. pyrenaica*			P-88	Tito Bustillo	Ribadesella		36			22.5
cf. *C. p. pyrenaica*			P-89	Tito Bustillo	Ribadesella		36			23.5
cf. *C. p. pyrenaica*			P-90	Riera	Llanes		36			24
cf. *C. p. pyrenaica*			P-91	Rascaño	Mirones		36.5			22
cf. *C. p. pyrenaica*			P-92	Rascaño	Mirones		36.5			22.5
cf. *C. p. pyrenaica*			P-93	Rascaño	Mirones		36.5			23.5
cf. *C. p. pyrenaica*			P-94	Rascaño	Mirones		36.5			24.4
cf. *C. p. pyrenaica*			P-95	Rascaño	Mirones		36.5			25
cf. *C. p. pyrenaica*			P-96	Rascaño	Mirones		36.5			25
cf. *C. p. pyrenaica*			P-97	Riera	Llanes		36.5			24
cf. *C. p. pyrenaica*			P-98	Lezetxiki	Mondragón		37			21.5
cf. *C. p. pyrenaica*			P-99	Rascaño	Mirones		37			22.5
cf. *C. p. pyrenaica*			P-100	Rascaño	Mirones		37			23
cf. *C. p. pyrenaica*			P-101	Rascaño	Mirones		37			23
cf. *C. p. pyrenaica*			P-102	Rascaño	Mirones		37			23
cf. *C. p. pyrenaica*			P-103	Rascaño	Mirones		37			24
cf. *C. p. pyrenaica*			P-104	Rascaño	Mirones		37			25
cf. *C. p. pyrenaica*			P-105	Arenaza	Galdames		37			26
cf. *C. p. pyrenaica*			P-106	Rascaño	Mirones		37.5			23
cf. *C. p. pyrenaica*			P-107	Rascaño	Mirones		37.5			23.5
cf. *C. p. pyrenaica*			P-108	Rascaño	Mirones		37.5			24
cf. *C. p. pyrenaica*			P-109	Rascaño	Mirones		37.5			25.5
cf. *C. p. pyrenaica*			P-110	Rascaño	Mirones		37.5			24.5
cf. *C. p. pyrenaica*			P-111	Rascaño	Mirones		37.5			24.5
cf. *C. p. pyrenaica*			P-112	Rascaño	Mirones		37.5			26.5
cf. *C. p. pyrenaica*			P-113	Rascaño	Mirones		38			23.5

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
cf. *C. p. pyrenaica*			P-114	Rascaño	Mirones		38			23.5
cf. *C. p. pyrenaica*			P-115	Rascaño	Mirones		38			24
cf. *C. p. pyrenaica*			P-116	Rascaño	Mirones		38			24
cf. *C. p. pyrenaica*			P-117	Rascaño	Mirones		38			24.5
cf. *C. p. pyrenaica*			P-118	Rascaño	Mirones		38			24.5
cf. *C. p. pyrenaica*			P-119	Rascaño	Mirones		38			24.5
cf. *C. p. pyrenaica*			P-120	Rascaño	Mirones		38			25
cf. *C. p. pyrenaica*			P-121	Rascaño	Mirones		38			25
cf. *C. p. pyrenaica*			P-122	Rascaño	Mirones		38			25
cf. *C. p. pyrenaica*			P-123	Rascaño	Mirones		38			25.5
cf. *C. p. pyrenaica*			P-124	Rascaño	Mirones		38			25.5
cf. *C. p. pyrenaica*			P-125	Rascaño	Mirones		38			26
cf. *C. p. pyrenaica*			P-126	Rascaño	Mirones		38			27
cf. *C. p. pyrenaica*			P-127	Rascaño	Mirones		38.5			25.5
cf. *C. p. pyrenaica*			P-128	Rascaño	Mirones		38.5			25.5
cf. *C. p. pyrenaica*			P-129	Rascaño	Mirones		38.5			26.5
cf. *C. p. pyrenaica*			P-130	Rascaño	Mirones		38.5			25.5
cf. *C. p. pyrenaica*			P-131	Arenaza	Galdames		38.5			25.5
cf. *C. p. pyrenaica*			P-132	Rascaño	Mirones		38.5			26
cf. *C. p. pyrenaica*			P-133	Rascaño	Mirones		38.5			26
cf. *C. p. pyrenaica*			P-134	Rascaño	Mirones		39			24.5
cf. *C. p. pyrenaica*			P-135	Rascaño	Mirones		39			24.5
cf. *C. p. pyrenaica*			P-136	Rascaño	Mirones		39			26
cf. *C. p. pyrenaica*			P-137	Rascaño	Mirones		39			26
cf. *C. p. pyrenaica*			P-138	Rascaño	Mirones		39			26.5
cf. *C. p. pyrenaica*			P-139	Rascaño	Mirones		39			25.5
cf. *C. p. pyrenaica*			P-140	Rascaño	Mirones		39.5			25.5
cf. *C. p. pyrenaica*			P-141	Rascaño	Mirones		39.5			25.5
cf. *C. p. pyrenaica*			P-142	Rascaño	Mirones		39.5			25.5
cf. *C. p. pyrenaica*			P-143	Rascaño	Mirones		39.5			26

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
cf. *C. p. pyrenaica*			P-144	Rascaño	Mirones		39.5			26
cf. *C. p. pyrenaica*			P-145	Rascaño	Mirones		39.5			27
cf. *C. p. pyrenaica*			P-146	Rascaño	Mirones		40			26
cf. *C. p. pyrenaica*			P-147	Rascaño	Mirones		40			26
cf. *C. p. pyrenaica*			P-148	Tito Bustillo	Ribadesella		40			27
cf. *C. p. pyrenaica*			POL 1	Polvorin	Carranza	VI	38	35.5	20.5	23.5
cf. *C. p. pyrenaica*			POL 2	Polvorin	Carranza	VI	38	36	21.5	24.5
cf. *C. p. pyrenaica*			SANTI 1	Santimamiñe	Kortezubi	II	37.5	34.5	20.5	23.5
cf. *C. p. pyrenaica*			SANTI 2	Santimamiñe	Kortezubi	II	39	36	22.5	27.5
cf. *C. p. pyrenaica*			SANTI 3	Santimamiñe	Kortezubi	IV	37.5	34.5	20.5	25
cf. *C. p. pyrenaica*			SANTI 4	Santimamiñe	Kortezubi	V	30.5	28.5	17.8	19.4
cf. *C. p. pyrenaica*			SANTI 5	Santimamiñe	Kortezubi	V	30	28	17.1	20
cf. *C. p. pyrenaica*			SANTI 6	Santimamiñe	Kortezubi	VI	36	34.5	19.8	22.5
cf. *C. p. pyrenaica*			SANTI 7	Santimamiñe	Kortezubi	VI	33	30.5	18.5	21
cf. *C. p. pyrenaica*			SANTI 8	Santimamiñe	Kortezubi	VI	35.5	33.5	19.7	22.5
cf. *C. p. pyrenaica*			SANTI 9	Santimamiñe	Kortezubi	VIII	39.5	36.5	21.5	26.5
cf. *C. p. pyrenaica*			SANTI 10	Santimamiñe	Kortezubi	VIII	40.5	37	22.5	26.5
cf. *C. p. pyrenaica*			SANTI 11	Santimamiñe	Kortezubi	S	32	31	18.6	21.5
cf. *C. p. pyrenaica*			SANTI 12	Santimamiñe	Kortezubi	III	38	36	20.5	26
cf. *C. p. pyrenaica*			URRA 1	Urratxa	Orozko	III	38.5			
cf. *C. p. pyrenaica*			URRA 2	Urratxa	Orozko	III	35.5	34.5	19.3	
cf. *C. p. pyrenaica*			URRA 3	Urratxa	Orozko	III	33	32	18.2	22
cf. *C. p. pyrenaica*			URRA 4	Urratxa	Orozko	III	33.5	32.5	18.8	23
cf. *C. p. pyrenaica*			URRA 5	Urratxa	Orozko	III	31		16.8	19.7
cf. *C. p. pyrenaica*			URRA6	Urratxa	Orozko	III	40	36.5	21.5	27
cf. *C. p. pyrenaica*			URRA 7	Urratxa	Orozko	III		35	21.5	26
cf. *C. p. pyrenaica*			URRA 8	Urratxa	Orozko	III	36.5	34.5	21	23.5
cf. *C. p. pyrenaica*			URRA 9	Urratxa	Orozko	III	33.5	31	18.2	21.5
cf. *C. p. pyrenaica*			URRA 10	Urratxa	Orozko	III		30.5		19.2
cf. *C. p. pyrenaica*			URRA 11	Urratxa	Orozko	III				23

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
cf. *C. p. pyrenaica*			URRA 12	Urratxa	Orozko	III				21.5
				Mas Nou	Ares del Maestrat	1				(21)
				Mas Nou	Ares del Maestrat	1A		(30)		
				Mas Nou	Ares del Maestrat	2	(33.5)	(32)		
				Mas Nou	Ares del Maestrat	S	(36.5)	(35)	(20)	(22)
				Cova Fosca	Ares del Maestrat	[-120]	(35)	(33.5)	(19)	(22.5)
				Cova Fosca	Ares del Maestrat	[-89/-128]	35	33	18.5	22
				Cova Fosca	Ares del Maestrat	[-119]	33	31		
				Cova Fosca	Ares del Maestrat	[-120/-130]	31.5		17.5	20
				Cova Fosca	Ares del Maestrat	[-120/-130]	(32.5)	(30.5)	(18.5)	(22)
				Cova Fosca	Ares del Maestrat	[-170/-177]	(36.5)	(33.5)	(20)	(24)
				Cova Fosca	Ares del Maestrat	[-170/-177]	(35)	(24)	(19)	(22)
				Cova Fosca	Ares del Maestrat	[-170/-177]	(32)	(30)	(18)	(20)
				Cova Fosca	Ares del Maestrat	[-177/-196]	(35.5)	(34.5)	(19.5)	(22.5)
				Cova Fosca	Ares del Maestrat	[-177/-196]	(35.2)			(22.5)
				Cova Fosca	Ares del Maestrat	[-177/-196]	(35)	(33)	(19)	(22.5)
				Cova Fosca	Ares del Maestrat	[-177/-196]	(34.5)	(33)	(19.5)	(22.5)
				Cova Fosca	Ares del Maestrat	[-177/-196]	(33.5)	(32)	(18.5)	(21)
			1274	Cova Fosca	Ares del Maestrat	[-196/-211]	(31)	(29)	(16.4)	(19)
			1991	Cova Fosca	Ares del Maestrat	[-196/-211]	(31.4)	(29.3)	(17.7)	(18.7)
			934	Cova Fosca	Ares del Maestrat	[-196/-211]	(32.8)	(31)	(17.5)	(18.2)
			872	Cova Fosca	Ares del Maestrat	[-196/-211]	32.4	30.3	17.5	20
			1448	Cova Fosca	Ares del Maestrat	[-196/-211]	33.9	32.4	18.8	21.7
			766	Cova Fosca	Ares del Maestrat	[-196/-211]	32	30.3	17.3	21.5
			1261	Cova Fosca	Ares del Maestrat	[-196/-211]	28.5	27	16.8	19.2
			1290	Cova Fosca	Ares del Maestrat	[-196/-211]	28.9	27	16	18
			1256	Cova Fosca	Ares del Maestrat	[-196/-211]	31.8	(29.9)	17	20
			999	Cova Fosca	Ares del Maestrat	[-196/-211]	31.4	29.3	17.2	19.3

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
			1416	Cova Fosca	Ares del Maestrat	[-196/-211]	(32)	(39)	(17.6)	(20.1)
			1417	Cova Fosca	Ares del Maestrat	[-196/-211]	34	31.8	18.3	20.6
			1270	Cova Fosca	Ares del Maestrat	[-196/-211]	(35.6)	(33)	(19.8)	(21.5)
			583	Cova Fosca	Ares del Maestrat	[-211/-220]	36	(34)	(20)	(23)
			27	Cova Fosca	Ares del Maestrat	[-211/-220]	30.5	29	(17.5)	19
			766	Cova Fosca	Ares del Maestrat	[-211/-220]	31	29	17.5	19.5
				Cova Fosca	Ares del Maestrat	[-211/-220]	31	29.5	16.5	21
				Cova Fosca	Ares del Maestrat	[-211/-220]	32	30.5	17.5	20
			407	Cova Fosca	Ares del Maestrat	[-211/-220]	(32.5)	(31.5)	(18)	(21)
			722	Cova Fosca	Ares del Maestrat	[-211/-220]	33	31.5	17.5	20.5
			195	Cova Fosca	Ares del Maestrat	[-211/-220]	33	31		20.5
			510	Cova Fosca	Ares del Maestrat	[-211/-220]	34.5	32	18.5	22.5
			739	Cova Fosca	Ares del Maestrat	[-211/-220]	(36.5)	(33.5)		(22.5)
			331	Cova Fosca	Ares del Maestrat	[-211/-220]	33.5	31.5	18.5	23
			800	Cova Fosca	Ares del Maestrat	[-211/-220]	33	31	18	22
				Cova Fosca	Ares del Maestrat	[-211/-220]	32	29.5	17	20
				Cova Fosca	Ares del Maestrat	[-211/-220]	31.5	29.5	17	20.5
			596	Cova Fosca	Ares del Maestrat	[-211/-220]	(31.5)	(30)	(16)	(20)
			144	Cova Fosca	Ares del Maestrat	[-211/-220]	30.5	29.5	(16)	19.5
			428	Cova Fosca	Ares del Maestrat	[-211/-220]	(31)	29.5	(16.5)	20
			551	Cova Fosca	Ares del Maestrat	[-211/-220]	(32.5)		(20.5)	
			160	Cova Fosca	Ares del Maestrat	[-211/-220]	31	29		
			281	Cova Fosca	Ares del Maestrat	[-220/-224]	32	30.2	17	20.9
			263	Cova Fosca	Ares del Maestrat	[-220/-224]	35	32.3	18.5	(21)
			266	Cova Fosca	Ares del Maestrat	[-220/-224]				(16)
			68	Cova Fosca	Ares del Maestrat	[-220/-224]	33.6	32.5	18.7	26
			284	Cova Fosca	Ares del Maestrat	[-220/-224]	34	32	18.4	25
				Cova Fosca	Ares del Maestrat	[-220/-224]				(16)

ASTRAGALUS										
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ Site**	**Location**	**Level**	**GLl**	**GLm**	**Dl**	**Bd**
				Cova Fosca	Ares del Maestrat	[-220/-224]				(19)
			575	Cova Fosca	Ares del Maestrat	[-220/-224]	32	29.6	16.7	19.2
				Cova Fosca	Ares del Maestrat	[-220/-224]				(18)
				Cova Fosca	Ares del Maestrat	[-220/-224]				(20)
				Cova Fosca	Ares del Maestrat	[-242/-255]	(36)	33	19.5	(23)
				Cova Fosca	Ares del Maestrat	[-242/-255]	34	31.8	19	23
				Cova Fosca	Ares del Maestrat	[-242/-255]	(35.8)	(33.5)	(19)	(23.2)
				Cova Fosca	Ares del Maestrat	[-242/-255]	(31.5)	29.5	(16.5)	(19.5)
				Cova Fosca	Ares del Maestrat	[-255/-262]	34	31.3	18.3	20
				Cova Fosca	Ares del Maestrat	[-255/-262]	33	31.4	17.5	20.4
				Cova Fosca	Ares del Maestrat	[-304/-319]	32.5	31.5		
				Cova Fosca	Ares del Maestrat	[-365/-388]	33.7	33	18.5	22.5
				Cova Fosca	Ares del Maestrat	[-365/-388]	33.5	32		

CALCANEUS								
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ site**	**Location**	**Level**	**GL**	**GB**
C. p. hispanica	♂	6	656	AMM	S. Cazorla		72.5	24
C. p. hispanica	♂	10	18070	MNCN	S. Cazorla		71.5	24
C. p. hispanica	♂	11	18073	MNCN	S. Cazorla		67	26
C. p. hispanica	♂	11	18075	MNCN	S. Cazorla		70.5	24.5
C. p. hispanica	♀	7	18087	MNCN	S. Cazorla		60.5	19
C. p. hispanica	♀	5	18089	MNCN	S. Cazorla		62.5	21
C. p. hispanica	♀	7	18094	MNCN	S. Cazorla		58.5	21.5
C. p. hispanica	♀	4	18116	MNCN	S. Cazorla		59	21.5
C. p. hispanica	♂	8	18124	MNCN	S. Cazorla		70.1	24.5
C. p. hispanica	♂	8	18127	MNCN	S. Cazorla		68	23

CALCANEUS

Sub-species	Sex	Age (years)	Code	Collection/ site	Location	Level	GL	GB
C. p. hispanica	♂	7	18130	MNCN	S. Cazorla		69.5	23.5
C. p. hispanica	♂	5	18147	MNCN	S. Cazorla		65.5	20.9
C. p. hispanica	♂	9	18151	MNCN	S. Cazorla		72	25.8
C. p. hispanica	♂	13	18153	MNCN	S. Cazorla		71	25.5
C. p. hispanica	♂	13	18155	MNCN	S. Cazorla		71.5	27
C. p. hispanica	♂	12	18157	MNCN	S. Cazorla		67	23
C. p. hispanica	♀	4	18207	MNCN	S. Cazorla		57.5	20
C. p. hispanica	♀	5	18216	MNCN	S. Cazorla		59.5	20
C. p. hispanica	♀	5	AL-6	AMM	S. Cazorla		64.5	22.4
C. p. victoriae	♂	5	18166	MNCN	S. Gredos		69	24
C. p. victoriae	♂	6	18170	MNCN	S. Gredos		69.2	28
C. p. victoriae	♀	8	18184	MNCN	S. Gredos		66	25
C. p. victoriae	♀	8	18189	MNCN	S. Gredos			
C. p. victoriae	♀	6	18191	MNCN	S. Gredos		64	22
C. p. victoriae	♀	2	18195	MNCN	S. Gredos			19.8
C. p. victoriae	♀	5	18197	MNCN	S. Gredos		63	23.2
C. p. victoriae	♀	6	18201	MNCN	S. Gredos		63	25
C. p. victoriae	♀	7	18222	MNCN	S. Gredos		60.5	21.5
C. p. victoriae	♀	3	18230	MNCN	S. Gredos			21
C. p. victoriae	♂	2	18233	MNCN	S. Gredos			22.6
C. p. victoriae	♀	7	18237	MNCN	S. Gredos		58.9	21.3
C. p. victoriae	♂	2	18240	MNCN	S. Gredos			21.8
C. p. victoriae	♀	3	18244	MNCN	S. Gredos		65.1	22.5
C. p. victoriae	♂	3	18246	MNCN	S. Gredos			23.6
C. p. victoriae	♂	2	18248	MNCN	S. Gredos			21.4
C. p. victoriae	♀	5	18252	MNCN	S. Gredos		61.5	20.5
C. p. victoriae	♀	2	18253	MNCN	S. Gredos			19.8
C. p. victoriae	♀	8	18254	MNCN	S. Gredos		60.8	23.5
C. p. victoriae	♀	5	18271	MNCN	S. Gredos		65	24
C. p. victoriae	♂	6	18279	MNCN	S. Gredos		73	27

CALCANEUS								
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ site**	**Location**	**Level**	**GL**	**GB**
C. p. victoriae	♂	8	18281	MNCN	S. Gredos		72	26.5
cf. *C. p. pyrenaica*	♂	7	Cap-pyr 15	AMM	Somiedo		79.3	28.5
cf. *C. p. pyrenaica*			AITZ 1	Aitzbitarte	Rentería	Aziliense	86.2	
cf. *C.p. pyrenaica*			ATXU 1	Atxuri	Mañaria	I	90	30.5
cf. *C.p. pyrenaica*			ATXU 2	Atxuri	Mañaria	II	71	24.5
cf. *C.p. pyrenaica*			ATXU 3	Atxuri	Mañaria	V-VII	82.5	28
cf. *C.p. pyrenaica*			ATXU 4	Atxuri	Mañaria	V-VII	72.5	25
cf. *C.p. pyrenaica*			BO 1	Bolinkoba	Aradiano	I-III	71.5	
cf. *C.p. pyrenaica*			BO 2	Bolinkoba	Aradiano	III	82.5	29.5
cf. *C.p. pyrenaica*			BO 3	Bolinkoba	Aradiano	III	84	30
cf. *C.p. pyrenaica*			BO 4	Bolinkoba	Aradiano	III	82.5	29
cf. *C.p. pyrenaica*			BO 5	Bolinkoba	Aradiano	III	65	22.5
cf. *C.p. pyrenaica*			BO 6	Bolinkoba	Aradiano	IV	82.5	30
cf. *C.p. pyrenaica*			BO 7	Bolinkoba	Aradiano	V	69	22.5
cf. *C.p. pyrenaica*			BO 8	Bolinkoba	Aradiano	VI	71.5	23.5
cf. *C.p. pyrenaica*			BO 9	Bolinkoba	Aradiano	VI	70	23
cf. *C.p. pyrenaica*			BO10	Bolinkoba	Aradiano	VI		23.5
cf. *C.p. pyrenaica*			BO 11	Bolinkoba	Aradiano	VI		20
cf. *C.p. pyrenaica*			LUM 1	Lumentxa	Lekeitio	V	67	23.5
cf. *C.p. pyrenaica*			LEZ 1	Lezetxiki	Mondragón	IV c	87	
cf. *C.p. pyrenaica*			P-1	Arenaza	Galdames		65.5	22.5
cf. *C.p. pyrenaica*			P-2	Rascaño	Mirones		66	23
cf. *C.p. pyrenaica*			P-3	Rascaño	Mirones		66.5	24.5
cf. *C.p. pyrenaica*			P-4	Riera	Llanes		68.5	23.5
cf. *C.p. pyrenaica*			P-5	Riera	Llanes		69.5	25
cf. *C.p. pyrenaica*			P-6	Rascaño	Mirones		70	23.5
cf. *C.p. pyrenaica*			P-7	Arenaza	Galdames		70	24.5
cf. *C.p. pyrenaica*			P-8	Urtiaga	Deba		71	24
cf. *C.p. pyrenaica*			P-9	Urtiaga	Deba		71.5	25
cf. *C.p. pyrenaica*			P-10	Urtiaga	Deba		72	25

CALCANEUS								
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ site**	**Location**	**Level**	**GL**	**GB**
cf. *C.p. pyrenaica*			P-11	Urtiaga	Deba		72	24
cf. *C.p. pyrenaica*			P-12	Urtiaga	Deba		73.5	25
cf. *C.p. pyrenaica*			P-13	Riera	Llanes		74.5	23
cf. *C.p. pyrenaica*			P-14	Urtiaga	Deba		74.5	24
cf. *C.p. pyrenaica*			P-15	Rascaño	Mirones		75	25.5
cf. *C.p. pyrenaica*			P-16	Rascaño	Mirones		78.5	27
cf. *C.p. pyrenaica*			P-17	Rascaño	Mirones		78.5	28.5
cf. *C.p. pyrenaica*			P-18	Rascaño	Mirones		78.5	28.5
cf. *C.p. pyrenaica*			P-19	Arenaza	Galdames		79	26.5
cf. *C.p. pyrenaica*			P-20	Rascaño	Mirones		79	29.5
cf. *C.p. pyrenaica*			P-21	Rascaño	Mirones		79.5	28
cf. *C.p. pyrenaica*			P-22	Rascaño	Mirones		80	27.5
cf. *C.p. pyrenaica*			P-23	Rascaño	Mirones		80.5	28.5
cf. *C.p. pyrenaica*			P-24	Arenaza	Galdames		81.5	27
cf. *C.p. pyrenaica*			P-25	Rascaño	Mirones		81.5	28.5
cf. *C.p. pyrenaica*			P-26	Rascaño	Mirones		81.5	29
cf. *C.p. pyrenaica*			P-27	Urtiaga	Deba		81.5	27.5
cf. *C.p. pyrenaica*			P-28	Urtiaga	Deba		84.5	29
cf. *C.p. pyrenaica*			P-29	Aitzbitarte	Rentería	IV	86	29
cf. *C.p. pyrenaica*	♀?		SA 1	Santimamiñe	Kortezubi		70	23
cf. *C.p. pyrenaica*	♀?		SA 2	Santimamiñe	Kortezubi		71.5	24
cf. *C.p. pyrenaica*	♂?		SA 3	Santimamiñe	Kortezubi		77.5	29
cf. *C.p. pyrenaica*	♂?		SA 4	Santimamiñe	Kortezubi		77.5	27.5
cf. *C.p. pyrenaica*			URT 1	Urtiaga	Deba		68.5	
cf. *C.p. pyrenaica*			URT 2	Urtiaga	Deba		70.5	
cf. *C.p. pyrenaica*			URT 3	Urtiaga	Deba		71	
cf. *C.p. pyrenaica*			URT 4	Urtiaga	Deba		71.6	
cf. *C.p. pyrenaica*			URT 5	Urtiaga	Deba		72	
cf. *C.p. pyrenaica*			URT 6	Urtiaga	Deba		72	
cf. *C.p. pyrenaica*			URT 7	Urtiaga	Deba		73.5	

CALCANEUS								
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ site**	**Location**	**Level**	**GL**	**GB**
cf. *C.p. pyrenaica*			URT 8	Urtiaga	Deba		74.5	
cf. *C.p. pyrenaica*			URT 9	Urtiaga	Deba		81.5	
cf. *C.p. pyrenaica*			URT 10	Urtiaga	Deba		84.5	
				Cova Fosca	Ares del Maestrat	[-111/-118]	(72.5)	(28.5)
				Cova Fosca	Ares del Maestrat	[-170/-177]	(71)	(27)
				Cova Fosca	Ares del Maestrat	[-170/-177]		(26.5)
				Cova Fosca	Ares del Maestrat	[-177/-196]	(70)	(26)
				Cova Fosca	Ares del Maestrat	[-177/-196]	63	22
			1268	Cova Fosca	Ares del Maestrat	[-196/-211]	70.5	26.5
			940	Cova Fosca	Ares del Maestrat	[-196/-211]	61.5	22
			930	Cova Fosca	Ares del Maestrat	[-211/-220]	(75)	(29)
			307	Cova Fosca	Ares del Maestrat	[-211/-220]	(65)	(23.5)
			650	Cova Fosca	Ares del Maestrat	[-211/-220]	62.5	(19)
			318	Cova Fosca	Ares del Maestrat	[-211/-220]	(73)	(25)
				Cova Fosca	Ares del Maestrat	[-211/-220]	(60.5)	(20)
			494	Cova Fosca	Ares del Maestrat	[-211/-220]		(19.5)
			379	Cova Fosca	Ares del Maestrat	[-220/-224]		(23.9)
			107	Cova Fosca	Ares del Maestrat	[-220/-224]	60.5	21.5
			612	Cova Fosca	Ares del Maestrat	[-220/-224]	(65)	26.5
				Cova Fosca	Ares del Maestrat	[-224/-235]	(64)	(23.3)
				Cova Fosca	Ares del Maestrat	[-224/-235]	(62.5)	(21)
				Cova Fosca	Ares del Maestrat	[-242/-255]		(24.5)
				Cova Fosca	Ares del Maestrat	[-242/-255]		(25)
				Cova Fosca	Ares del Maestrat	[-298/-308]		(19.3)
				Cova Fosca	Ares del Maestrat	[-255/-262]	64	22

METATARSUS																				
Sub-species	Sex	Age (years)	Code	Collection/ site	Location	Level	GL	Lt	BP	SD	BD	BFd	WCM	WCL	DEM	DVM	DIM	DIL	DVL	DEL
C. p. hispanica	♂	6	656	AMM	S. Cazorla		140.9	146.6	26.5	16	30	29.4	13.1	12.5	11.1	19	15.7	15.5	18.1	11.1
C. p. hispanica	♂	3	646	AMM	S. Cazorla		139	142.6	24	15.3	29.4	27.3	12.1	11.4	10.6	17.8	14.8	14.8	16.8	10.7
C. p. hispanica	♂	10	629	AMM	S. Cazorla		139	142.5	25.7	18.4	30.2	29	13	12.7	11	18.3	15.1	14.8	17.4	11.8
C. p. hispanica	♂	≤3	501	AMM	S. Cazorla		139	144.5	24.7		29	29.4	13	12.6	11.4	19.2	15.7	15.7	18.2	11.1
C. p. hispanica	♂	6	662	AMM	S. Cazorla		134.4	138.1	25.3	15.2	29.5	28.7	12.7	12.1	10.9	18.9	14.8	14.8	16.9	10.4
C. p. hispanica	♂	10	J-3	AMM	S. Cazorla		129.7	133.1	22.5	13.6	26.6	26.5	11.4	11.4	9.8	16.4	13.5	13.5	15.4	9.7
C. p. hispanica	♀	4	735	AMM	S. Cazorla		118.2	121.8	20.8	12.5	24.1	23	11	10.3	9.9	16	13.3	13.2	15.1	9.4
C. p. hispanica	♀	3	651	AMM	S. Cazorla		125.2	122.4	21.5	12.5	24.5	23	10.7	10.1	9.8	15.9	13.3	13.3	15.2	9.7
C. p. hispanica	♀	6	635	AMM	S. Cazorla		127.2	123.8	20.9	14	25.5	23	10.8	10.3	10	16.2	13.3	13.3	15.3	9.6
C. p. hispanica	♀	10	625	AMM	S. Cazorla		124.5	120.5	20.5	13.1	24.2	22.8	10.9	10.2	9.9	16.2	13	12.9	15.2	9.5
C. p. hispanica	♀	12	626	AMM	S. Cazorla		132.4	129.3	23.3	14	27	25.2	11.5	11.2	10.4	17.5	14.3	14.3	16.6	10.1
C. p. hispanica	♀	??	736	AMM	S. Cazorla		124.6	121.7	21.2	12.8	24.5	23	10.8	10.4	10.3	16.1	13.5	13.3	15.4	9.2
C. p. hispanica	♂	4-5	Cap pyr-14	AMM	S. Cazorla		142	146	23.8	15.3	28.4	28	12	11.8	10.5	17.5	14.5	14.5	16.7	10.5
cf. *C.p. pyrenaica*	♂	7	Cap-pyr 15	AMM	Somiedo		155.5	162	29	19	34.5	34	15	14.3	12.4	22	17.5	17.5	21.4	12.4
C. p. hispanica	♂	10	18070	MNCN	S. Cazorla		147	152.5	25	16	29	27.4	12.7	11.9	11.2	18.9	15.8	15.4	18	11.2
C. p. hispanica	♂	11	18073	MNCN	S. Cazorla		143	147	26	15.5	30	28.1	13.2	12.3	10.4	18.4	14.6	14.7	17.4	10.5
C. p. hispanica	♂	11	18075	MNCN	S. Cazorla		143	147.5	25	15	29.5	26.5	12.4	11.9	10.7	17.8	14.7	14.6	16.7	10.4
C. p. hispanica	♀	7	18087	MNCN	S. Cazorla		124.5	130.5	21.5	13	25.5	23.4	10.9	10	9.1	15.7	12.8	12.6	14.7	8.9
C. p. hispanica	♀	5	18089	MNCN	S. Cazorla		129	133	22.6	13.5	26.5	25.6	11.6	10.7	10.5	18	14.6	14.1	16.6	10.1
C. p. hispanica	♀	7	18094	MNCN	S. Cazorla		123	126	24.5	12.5	25.5	24.1	10.8	10.1	9.3	16.1	13	13.1	15.3	9.3
C. p. hispanica	♀	4	18116	MNCN	S. Cazorla		124	128	21	12.5	24	23.7	11	10.4	9.3	16.4	13.3	13.3	15.4	9.2
C. p. hispanica	♀	6	18117	MNCN	S. Cazorla		124.5	129	21.5	13	26	25	11.2	10.4	9.4	16.6	13.3	13.2	15.7	9.7
C. p. hispanica	♂	8	18124	MNCN	S. Cazorla		144.5	149	26	14.5	30	28.5	13.1	12.3	10.6	19.1	15.4	15.1	18.8	10.4
C. p. hispanica	♂	8	18127	MNCN	S. Cazorla		138.5	141.5	24.5	14.5	27.8	26.6	12	11.2	10.4	17.7	14.4	14.1	16.6	10.3
C. p. hispanica	♂	7	18130	MNCN	S. Cazorla		145	149	27	15.5	30	28.9	12.7	12	11.1	18.5	15.1	15	17.5	10.9
C. p. hispanica	♂	7	18146	MNCN	S. Cazorla		144	149	25.5	15.5	29.5	28	12.6	12.2	10.7	18.4	15	15	17.8	10.8
C. p. hispanica	♂	5	18147	MNCN	S. Cazorla		137	142	23	13.9	27.9	26.5	12.2	11.6	10.8	18.9	14.6	14.7	17.1	10.3
C. p. hispanica	♂	8	18151	MNCN	S. Cazorla		146.5	152.3	27	16	29.5	28.3	12.6	12.2	11.1	19.2	16	16	18.3	11

METATARSUS																					
Sub-species	**Sex**	**Age (years)**	**Code**	**Collection/ site**	**Location**	**Level**	**GL**	**Lt**	**BP**	**SD**	**BD**	**BFd**	**WCM**	**WCL**	**DEM**	**DVM**	**DIM**	**DIL**	**DVL**	**DEL**
C. p. hispanica	♂	13	18153	MNCN	S. Cazorla		149	155	27	16	30	28.6	13	12.6	11.6	19.3	15.8	15.4	18.3	11.5
C. p. hispanica	♂	13	18155	MNCN	S. Cazorla		150	156	27	17	31.5	30.3	13.1	12.5	11.7	19.2	15.7	15.7	18.1	11.1
C. p. hispanica	♂	12	18157	MNCN	S. Cazorla		138.2	142.5	24	14.5	28	27.1	12.2	11.6	9.9	17.5	14.2	14.2	16.7	9.9
C. p. victoriae	♂	6	18159 (D)	MNCN	S. Gredos		130.5	135	25.8	15	31	30.6	13.7	13	10.6	18.8	15.3	15.2	18.1	10.7
C. p. victoriae	♂	6	18159 (S)	MNCN	S. Gredos		130.1	134.4	25.2	15.5	30.5	29.7	13.8	13	11	18.8	15.3	15.3	18	10.7
C. p. victoriae	♂	5	18166 (D)	MNCN	S. Gredos		140	144.6	25.3	16	31.3	31	14.2	13.4	11.9	19.8	16.4	16	18.7	11.1
C. p. victoriae	♂	6	18170 (D)	MNCN	S. Gredos		135	141	26.5	16.5	32.3	31.3	14.4	14	11.6	20.1	16.2	16	18.8	11.1
C. p. victoriae	♂	6	18170 (S)	MNCN	S. Gredos		137.3	140.5	26.4	16.3	31.6	31.4	14	14	11.3	20	15.4	15.4	19.1	11.1
C. p. victoriae	♂	6	18172 (S)	MNCN	S. Gredos		140	143.5	26	15.5	30.5	30	14.2	13.9	11	19.8	16.4	16	18.8	11
C. p. victoriae	♀	8	18189 (D)	MNCN	S. Gredos		122.6	126.5	23.2	14	28	28	12.7	12.3	10.9	18.4	15	14.8	17.4	10.4
C. p. victoriae	♀	6	18191 (S)	MNCN	S. Gredos		126.1	130.2	23.8	14	28	27.7	12.6	11.7	10.6	18.4	15.1	14.8	17.3	10.2
C. p. victoriae	♀	5	18197 (D)	MNCN	S. Gredos		120.6	124.5	23.3	14.3	27.7	28	12.5	11.7	9.9	18	14.4	14.7	17	9.8
C. p. victoriae	♀	6	18201(D)	MNCN	S. Gredos		124.3	129	24	14	28.3	28	12.1	11.8	10.8	18.3	15	14.7	17.4	10.2
C. p. hispanica	♀	4	18207	MNCN	S. Cazorla		120	125	20	11.9	24.2	23.5	10.8	10.3	9.2	16.5	13.3	13.2	15.5	9
C. p. hispanica	♀	5	18216	MNCN	S. Cazorla		127	132	22	13	25	24.2	11.1	10.4	10	17.1	13.7	13.7	16	10
C. p. victoriae	♀	7	18222 (S)	MNCN	S. Gredos		118.7	122.4	22	13.1	25.2	25	11.5	11.1	9.1	16.6	13.4	13.3	15.8	8.7
C. p. victoriae	♀	7	18237 (S)	MNCN	S. Gredos		116.2	119.5	21.9	12	26	25.5	11.8	11.5	9.4	16.7	13.4	13.3	15.9	9.1
C. p. victoriae	♀	8	18252 (D)	MNCN	S. Gredos		118.7	121.4	23	13	27	26.9	12	12	9.9	17.5	14	13.9	16.6	9.5
C. p. victoriae	♀	8	28254 (S)	MNCN	S. Gredos		120.9	124.4	23.8	14	27.3	26.5	11.7	11.6	10.2	17.7	14.4	14.2	16.6	9.9
C. p. victoriae	♀	5	18271 (S)	MNCN	S. Gredos		125	128.8	23.6	14.3	27.7	27.1	12.6	11.9	10.3	18.1	14.9	14.8	17.2	10.3
C. p. victoriae	♂	8	18281 (D)	MNCN	S. Gredos		140.5	144.5	27.4	16	32.8	33	14.8	14.4	11.6	20.2	16.7	16.6	19.2	11.6
C. p. victoriae	♂	8	Cap pyr-3 (D)	AMM	S. Gredos		130.5	133	24	14.6	29.9	31	13	13	10.4	18.3	14.6	14.4	17.4	10.3
C. p. victoriae	♂	8	Cap pyr-3 (S)	AMM	S. Gredos		129.5	132.8	23.8	14.6	30.3	31.4	13.5	13	10.8	18.6	15	14.9	17.5	10.4
				Cova Fosca	Ares del Maestrat	[-126]					31									
				Cova Fosca	Ares del Maestrat	[-177/-196]					25.8	25	15.2	10.6	15.7	14.6	13.9	10.9	10.5	11
				Cova Fosca	Ares del Maestrat	[-177/-196]					26.8	25.8	15.5	10.3	16.5	15.2	14.4	10.4	11	11.8
			789	Cova Fosca	Ares del Maestrat	[-196/-211]					32.5	32.7	20.5	14	19.7	17.5		12.7	14.4	14.5
			502	Cova Fosca	Ares del Maestrat	[-196/-211]					32.2	31	18	11.6	19	16.1	16.7	11.8	13.5	14.7

METATARSUS																				
Sub-species	Sex	Age (years)	Code	Collection/ site	Location	Level	GL	Lt	BP	SD	BD	BFd	WCM	WCL	DEM	DVM	DIM	DIL	DVL	DEL
			1395	Cova Fosca	Ares del Maestrat	[-196/-211]					30.3	29.9	16.9	11.7	18.1	15.5	15.4	12	12.4	12.5
			869	Cova Fosca	Ares del Maestrat	[-196/-211]					26.4	26	14.6	10.1	16	13.6	14	10.3	10.9	11.4
			956	Cova Fosca	Ares del Maestrat	[-196/-211]					25.8									
				Cova Fosca	Ares del Maestrat	[-211/-220]					30.5	29.4	18	11.4	18.8	15.7	15.7	12	12.7	13.5
			555	Cova Fosca	Ares del Maestrat	[-211/-220]					27	26.8	16.5	10.7	15.9	14.3	14.2	10.7	11.3	12
				Cova Fosca	Ares del Maestrat	[-211/-220]						30.8	19.5	12.3	20.7	16.7	16.5	12.4	13.2	14.1
			631	Cova Fosca	Ares del Maestrat	[-211/-220]						30.2	19	12	20.3	16.5	15.7	12.5	12.5	13.4
			620	Cova Fosca	Ares del Maestrat	[-211/-220]			20.5	11.3										
			481	Cova Fosca	Ares del Maestrat	[-220/-224]			24											
			334	Cova Fosca	Ares del Maestrat	[-220/-224]					27.7	27.4	15.7	11.4	16.8	15	14.7	11.3	12.2	12.5
			110	Cova Fosca	Ares del Maestrat	[-220/-224]				15.5	27	26.7	17	10.8	18.6		14.8	11.5	11.3	12.2

Archaeofauna 25 (2016): 185-204

Presencia de felinos *(Felis, Lynx y Panthera)* en el registro arqueológico de la Península Ibérica durante el Pleistoceno Superior

ARITZA VILLALUENGA
MONREPOS Research Centre and Museum for Human Behavioural Evolution-RGZM.
Schloss Monrepos, Monrepos 2, D-56567, Neuwied, Deutschland.
villaluenga@rgzm.de

(Received *03 December 2015*; Revised *26 January 2016*; Accepted *28 January 2016*)

RESUMEN: Este artículo tiene por objetivo el análisis de la distribución biogeográfica de felinos *(Felis, Lynx y Panthera)* en la Península Ibérica durante el Pleistoceno Superior. Este periodo comprende fases climáticas rigurosas, última fase glacial, y templadas. Estas cambiantes condiciones afectaron en la distribución geográfica de la fauna, propiciando la presencia de especies adaptadas a medios fríos en el tercio norte. La Península Ibérica es el territorio europeo situado más al Suroeste, su situación hace que en este territorio existan diversas áreas climáticas, esto unido a un complejo relieve afectaron en la distribución biogeográfica de las especies durante el Pleistoceno Superior.

En la Península Ibérica han sido identificados tres géneros de felino, desde un pequeño carnívoro como el gato montés, al lince de tamaño medio, hasta grandes carnívoros como el leopardo y el león. El análisis de esta familia de carnívoros permite realizar un repaso diacrónico y geográfico a las adaptaciones de los carnívoros al cambiante medio ambiente del Pleistoceno Superior. Sin embargo, esta investigación ha de considerarse como un trabajo preliminar, futuros trabajos podrían modificar la actual distribución biogeográfica, especialmente en aquellas regiones en las que ciertas especies están ausentes.

PALABRAS CLAVE: FELINOS, *FELIS, LYNX, PANTHERA*, BIOGEOGRAFÍA, PENÍNSULA IBÉRICA, PLEISTOCENO SUPERIOR

ABSTRACT: This paper aims to introduce the biogeographic distribution of felids (*Felis, Lynx* and *Panthera*) in Iberian Peninsula during Upper Pleistocene. These period hold in last glacial phases, changing climatic conditions affected spatial distribution of fauna. Furthermore, Iberian Peninsula is the Southwestern most European territory, this region has different climatic and environmental influence areas, in addition to a complex geography these factors affected species biogeographic distribution.

Three felid genus have been identified in Iberian Upper Pleistocene archaeological sites, from small wildcat to middle size lynx, until big leopard and lion. Analysis of this carnivore family allows an overview on diachronic and geographic carnivore adaptation to changing environments, however this research should be considered as a preliminary work, information proceeding from future research could modify current perspective on felids biogeographic distribution, especially in those areas where some species have not been identified.

KEYWORDS: FELIDS, *FELIS, LYNX, PANTHERA*, BIOGEOGRAPHY, IBERIAN PENINSULA, UPPER PLEISTOCENE

INTRODUCCIÓN

Este artículo desea profundizar en la distribución biogeográfica de los felinos (*Panthera*, *Lynx* y *Felis*) a través de los restos óseos hallados en contextos arqueológicos de la Península Ibérica. Estos medios se localizan en abrigos y cuevas, habiendo sido alternativamente ocupados por carnívoros y humanos, entre ellos los felinos quienes en ciertos lugares han jugado un importante rol en la formación de los conjuntos arqueológicos (Yravedra, 2007a, b; Sanchis *et al*., 2015).

Antes de profundizar en la presencia de estas especies en la Península Ibérica han de realizarse algunas consideraciones. Primero, los restos óseos sólo se han preservado en determinados ambientes, siendo especialmente abundantes en áreas kársticas; cuevas, abrigos y simas han permitido la conservación de restos de fauna. Segundo, la aparición de grupos de Espeleología y los trabajos exploratorios de cavidades han permitido el descubrimiento de yacimientos arqueológicos y paleontológicos. En tercer lugar, el desarrollo de la Arqueología Prehistórica y Paleontología del Cuaternario, junto a la aparición de especialistas en el estudio de restos de fauna cuaternaria impulsó el desarrollo de estudios regionales acerca de la distribución biogeográfica de macro-mamíferos (Estévez, 1979; Castaños, 1987; Altuna, 1992 a, b).

El marco cronológico considerado en este artículo es el Pleistoceno Superior, este periodo comenzó tras el interglacial Eemiense (OIS 5e) hace 126.000 ± 5.000 Ka y terminó con el Holoceno (OIS 1) hace 9.700 años. La glaciación de Würm (OIS 4, 3 y 2) fue una fase climática irregular en la que se alternaron fases frías (estadiales) con momentos más benignos (Interestadiales). Ello propició que a diferencia del norte del continente la Península Ibérica nunca resultó despoblada e incluso pudo convertirse, al igual que las otras penínsulas del Sur del continente, en áreas de refugio para homínidos y animales (Sommer & Nadachowski, 2006).

En este trabajo han sido considerados tres géneros de felino (*Felis*, *Lynx* y *Panthera*). Tradicionalmente la adscripción taxonómica de cada especie ha sido realizada siguiendo criterios biométricos y cronológicos. Ello ha provocado durante décadas una amplia controversia científica que ha llegado hasta nuestros días. El león de las cavernas (*Panthera spelaea*) de gran talla y *Panthera leo clueti* de tamaño comparable al actual león africano o asiático (>200 kg) (Burger *et al*., 2004). Esta distinción ha estado sustentada en un cambio en el tamaño y contexto crono-cultural asociado a cada resto (Ballesio, 1980; Castaños, 2005). Por último otros autores atribuyen tal diferencia al dimorfismo sexual existente entre los grandes felinos, ya que este puede alcanzar hasta un 30% (Turner, 1984). Sin embargo, gracias al desarrollo de nuevas técnicas de ADN antiguo se ha producido un importante avance en la asignación taxonómica de los restos óseos de carnívoros pleistocenos. Hoy día ya no se puede mencionar la existencia de dos especies de león durante el Pleistoceno Superior en el oeste de Europa, sino de una sola especie que paulatinamente redujo su talla (Burger *et al*., 2004; Ersmark *et al*., 2014).

Junto al león, en Europa han sido identificadas hasta cuatro subespecies de leopardo siendo los ejemplares del Pleistoceno Superior adscritos a la subespecie *Panthera pardus spelaea* con características morfológicas craneales próximas al leopardo persa (*Panthera pardus ciscaucasica*) (Diedrich, 2013). Otros autores defienden la existencia de una única especie de leopardo (*Panthera pardus*) con una amplia variabilidad interespecífica (Ghezzo & Rook, 2015), dentro de la cual se hallarían los restos hallados en la Península (Sanchis *et al*., 2015). Una segunda problemática es acerca de la extinción del leopardo. En Europa continental parece situarse en el MIS 3/2 (32.000-26.000 BP), mientras que en la Península Ibérica ha sido certificada su supervivencia hasta el fin del último periodo glacial e incluso el Holoceno Inicial (Castaños, 1987; Sauqué & Cuenca-Bescós, 2013), esto supondría que este depredador se habría adaptado a varios medio ambientes, glaciares y templados desde su aparición en Europa durante el Pleistoceno Medio, hasta su extinción.

La identificación de tres especies de lince (*Lynx lynx*, *Lynx spelaea* y *Lynx pardina*) también ha sido causa de gran controversia. El desarrollo de técnicas de ADN antiguo ha permitido dilucidar la adscripción taxonómica. Recientemente ha sido confirmada, vía ADN antiguo, la presencia de lince europeo (*Lynx lynx*) en la Cornisa Cantábrica, aunque tal vez más importante es la identificación como perteneciente a una misma especie del lince de las cavernas (*Lynx spelaea*) y del lince ibérico (*Lynx pardinus*) (Rodríguez-Varela *et al*., 2015a, b).

El gato montés (*Felis silvestris*) colonizó Europa durante un momento impreciso del Pleistoceno Medio (450.000-200.000 años BP) (Sommer & Benecke, 2006). Recientes análisis han confirmado la extinción de la especie en Europa continental durante los periodos glaciares y una recolonización desde los refugios situados en las tres penínsulas meridionales (ibérica, itálica y balcánica) durante las fases interglaciares (Zachos & Hackänder, 2011). Este fenómeno parece que se repitió al final de la última glaciación, en paralelo a la reforestación del paisaje, la existencia de subespecies regionales o una sola forma continental (*Felis silvestris silvestris*) es objeto de debate. Así mismo, como consecuencia de la presión antrópica e hibridación con ejemplares domésticos hace complejo discernir el verdadero origen de las actuales poblaciones europeas (Mattucci *et al*., 2015).

La mayoría de las referencias incluidas en este artículo corresponden con restos hallados en excavaciones arqueológicas de contextos deposicionales del Pleistoceno Superior. Durante este periodo muchas cavidades kársticas fueron alternativamente ocupadas por carnívoros y homínidos (Villaluenga, 2013), en cronologías más recientes, final del Pleistoceno Superior, la presencia de restos óseos de carnívoros de talla pequeña y mediana en ciertos casos se debe a la caza de estos animales por parte del ser humano con objeto de explotar la piel y carne (Charles, 1997; Díez *et al*., 1998; Arribas & Jordá, 1999; Yravedra, 2005).

La publicación de modo periódico de nuevos estudios arqueozoológicos ha hecho incrementar de modo incesante los lugares y el número de restos de felinos hallados en la Península Ibérica. En este artículo deseamos realizar un Estado de la Cuestión pero reiterando la provisionalidad de este artículo fruto de un extenso análisis bibliográfico que sin embargo ha podido pasar por alto descubrimientos accidentales de restos óseos de felinos, publicados hace décadas o hallazgos paleontológicos dados a conocer en publicaciones de carácter divulgativo. Finalmente, consideramos que este artículo debía ser realizado, ya que durante las últimas décadas se ha producido un aumento exponencial de trabajos arqueológicos y paleontológicos. Ello ha propiciado la aparición y generalización de restos de felinos en la totalidad de la Península Ibérica por ello considerábamos necesario acometer un amplio estudio biogeográfico.

CONTEXTO GEOGRÁFICO

La Península Ibérica es el territorio situado más al Oeste del continente europeo, con una longitud media (Norte-Sur) de 865 km y una anchura (Este-Oeste) de 1.155 km. Este territorio se encuentra rodeado por tres de sus lados por dos mares, el Sur y Este por el Mar Mediterráneo, mientras que el Suroeste, Oeste y Norte limitan con el Mar Cantábrico y Océano Atlántico, en total la existen 3.313 km de costa. Finalmente, al Noreste los Pirineos (Aneto 3.404 m) hacen de frontera natural con el sur de Europa.

La Península Ibérica es tras los Alpes el territorio europeo con mayor desnivel, sin embargo el centro está dominado por la Meseta Central, de altitud media situada entre los 610 y los 760 m sobre el nivel del mar. Alrededor de esta se encuentran varias cadenas montañosas y sierras, en las que nacen los principales ríos (Miño, Duero, Tajo, Guadiana, Guadalquivir, Segura, Júcar y Ebro) cuyo curso hacia el mar ha erosionado las principales elevaciones. La descripción y conocimiento de la geografía, orogenia e hidrografía son fundamentales para comprender la distribución biogeográfica de la fauna ibérica (Vera-Torres, 2004).

El sustrato geológico de la Península Ibérica está compuesto por materiales formados desde el periodo Ediacara (635 millones) hasta el Cuaternario (2,5 millones-actualidad), existiendo ejemplos de materiales de prácticamente todas las eras geológicas. Sin embargo, el núcleo de las formaciones aparecieron durante la era Terciaria y Mesozoica, así mismo la Orogenia Alpina ha modelado el territorio, ejemplo de ello son la Cordillera Bética y los Pirineos, estos macizos fueron creados por la presión ejercida por la placa tectónica africana en su movimiento hacia el Norte. Finalmente el área Noroccidental está compuesta de material magmático formado en el fondo del Océano Atlántico. Posteriormente, diversos procesos erosivos han modelado la superficie de la Península, entre ellos materiales del Paleozoico, Mesozoico y Cenozoico, que sufrieron procesos de karstificación (Durán-Valsero & Robledo-Ardila, 2009), incluyendo abrigos bajo roca y cavidades que homínidos y carnívoros ocuparon durante el Pleistoceno Superior (Jordá-Pardo, 2009).

BIOLOGÍA Y ETOLOGÍA DE LOS FELINOS

En este apartado deseamos aportar una serie de datos acerca de la etología de las especies incluidas en este trabajo. Consideramos que a pesar de tratarse en muchos casos de información actual, su consideración es necesaria para comprender la presencia o ausencia de algunas especies en ciertas regiones de la Península Ibérica.

GATO MONTÉS (*Felis silvestris*)

El gato montés (*Felis silvestris*) es un carnívoro solitario, nocturno, territorial, además del felino de menor talla de Europa. Los machos (7,5 kg) son algo más grandes que las hembras (5 kg), su distribución actual va desde el Cáucaso en el Este, hasta la Península Ibérica en el Oeste (Macdonald & Barrett, 2002). Actualmente, en la Península Ibérica habitan dos subespecies, en la mitad Norte *Felis silvestris silvestris* (Mattucci *et al*., 2015) y en el Sur y área mediterránea *Felis silvestris tartessia* (Purroy & Varela, 2009), siendo esta última subespecie de mayor tamaño y con un pelaje de coloración más contrastada. Ambas subespecies habitan en entornos forestales donde hallan múltiples refugios y recursos alimenticios entre los que se incluyen microvertebrados, aves, peces e insectos.

LINCE (*Lynx pardinus, Lynx spelaea, Lynx lynx* y *Lynx* sp.)

Actualmente Europa está habitada por dos especies de Lince, en el centro y Sur de la Península Ibérica habita el Lince ibérico o Lince pardela (*Lynx pardinus*), su talla es mucho menor (9-13 kg) que la del Lince europeo (*Lynx lynx)* (18-30 kg). El Lince ibérico es un depredador especializado en la caza de conejos, aspecto que junto a la presión antrópica lo ha colocado al borde de la extinción, 156 individuos adultos en 2014 (Rodríguez & Calzada, 2015). Por otro lado, el hábitat del Lince Europeo se extiende desde el norte hasta la parte meridional del continente, habiéndose documentado la recolonización de Europa Occidental, área en la que fue cazado hasta su extinción en el siglo XIX. La dieta de esta especie es variada, desde pequeñas presas hasta ejemplares juveniles de ungulados (Macdonald & Barrett, 2002; Lloveras *et al*., 2007; Rodríguez-Hidalgo *et al*., 2013).

LEOPARDO (*Panthera pardus*)

El Leopardo es un cazador solitario que emplea la técnica de acecho y emboscada para cazar, los leopardos transportan a sus presas a cuevas y abrigos para proteger la comida de carroñeros (De Ruiter & Berger, 2000; Yravedra, 2007a, b; Sauqué *et al*., 2014). Este comportamiento también ha sido identificado entre los leopardos pleistocenos, algunos conjuntos arqueo-paleontológicos del Pleistoceno Superior han sido interpretados como lugares de consumo, caracterizados por la abundancia de restos óseos cabra (*Capra pyrenaica*) y rebeco o sarrio (*Rupicapra pyrenaica*) con evidencias tafonómicas propias de la actividad de este animal (Yravedra, 2007a; Sauqué *et al*., 2014).

LEÓN (*Panthera spelaea* y *Panthera leo clueti*)

Durante largo tiempo no ha quedado claro el árbol filogenético de los grandes félidos, hoy día se considera que leopardos, jaguares, leones y tigres tuvieron un ancestro común hace 4,5 millones de años, la *Panthera gombaszoegensis*. Hace 3 millones de años surgió en el Este de África el ancestro común (*Panthera leo fossilis*) de los leones actuales (*Panthera leo*) y león de las cavernas (*Panthera spelaea goldfuss*). Posteriormente, hace 900.000 años emigró a Eurasia la *Panthera leo fossilis*, desde entonces los leones africanos y euroasiáticos evolucionaron de manera independiente divididos en cuatro especies: León Africano (*Panthera leo*), León de las cavernas (*Panthera spelaea goldfuss*) en el Oeste de Eurasia, León asiático (*Panthera leo persica*) y León Americano (*Panthera leo youngi*). Este último migró hasta America del Norte durante el Pleistoceno Medio (400,000-300,000 años) y evolucionó hacia el León (*Panthera leo atrox*) del Pleistoceno Superior (Barnett *et al*., 2009; Ersmark *et al*., 2014).

Por otro lado, la presencia de restos de león en contextos arqueo-paleontológicos durante el Pleistoceno Superior final y Holoceno inicial de la Península Ibérica, se debe a otra forma de león distinta al león de las cavernas, extinto hace 10.000 años en el Este de Eurasia y precedentemente en el Oeste (Stuart & Lister, 2011). Durante el Pleistoceno Superior final otra especie de león (*Panthera leo europaea*), posiblemente descendiente del león asiático (*Panthera leo pérsica*) o africano (*Panthera leo*) colonizó el Sur del continente, nuevos análisis son necesarios en este punto. Esta forma de león (*Panthera leo europea*) pobló el Suroeste de Europa, desde la Península Ibérica, hasta los Balcanes (Figura 5). Esta especie constituyó un preciado trofeo de caza entre los pueblos griegos, macedonios y romanos, documentos gráficos y escritos datan la extinción, a causa de una caza excesiva, en torno al 100 DC.

La apariencia y etología del león de las cavernas también ha sido objeto de estudio. El arte rupestre y mobiliar ha sido durante largo tiempo la única fuente de información. El mejor ejemplo son las representaciones pictóricas de la cueva Chauvet (Ardèche, Francia). Una característica común a todas las imágenes de leones durante el Paleolítico Superior es la ausencia de melena. Algunos autores han apuntado la posibilidad de que sólo las hembras hubiesen sido representadas, mientras que otros autores defienden que los machos de león de las cavernas, al igual que el león asiático (*Panthera leo persica*) careciese de melena (Azéma, 2009, 2010). Así mismo, las representaciones de la Cueva Chauvet indican un comportamiento gregario similar al de los leones actuales, en los que el núcleo de cada manada se compone de hembras y sus crías junto a uno o dos machos dominantes. El hallazgo en verano de 2015 de dos cachorros de león de las cavernas helados en el río Uyandina (Siberia, Rusia) datados en al menos 12.000 años aportará nuevos y relevantes datos acerca de las adaptaciones a condiciones glaciales y en cuanto a la apariencia física de estos animales. Análisis de la dieta, a través del estudio de los isótopos estables, sitúan al león de las cavernas en la cima de la pirámide trófica, en directa competición con la hiena de las cavernas (*Crocuta crocuta spelaea*) y homínidos (*Homo neanderthalensis y Homo sapiens*). La dieta de los leones estaba compuesta por caballos, bisontes, uros, ciervo y megafauna, incluyendo subadultos de rinoceronte lanudo (*Coelodonta antiquitatis*) y mamut (*Mammuthus primigenius*) (Bocherens *et al*., 2011), la extinción del león de las cavernas estaría relacionada con la desaparición de estas especies.

RESULTADOS

La presencia de restos óseos de felinos depende de múltiples factores. Primero, la presencia de cavidades que potencialmente pudiesen ser ocupadas. Segundo, la existencia de un entorno adecuado a las exigencias etológicas de cada especie, haciendo que la distribución biogeográfica de estas especies alcanzase la Península Ibérica de modo parcial o total. Tercero, la diversidad de sustratos, ambientes sedimentarios (fluvio-lacustres o kársticos) y climatología, ha favorecido o perjudicado la conservación de restos orgánicos entre los que se encuentran los restos óseos. Cuarto, la existencia de una tradición en los estudios de Arqueología Prehistórica o Paleontología del Cuaternario, ha sido diferente a lo largo de la Península Ibérica, haciendo que en ciertas áreas exista una mayor cantidad de yacimientos arqueológicos. Considerando en conjunto estos cuatro criterios, es posible corregir la sobrerrepresentación de yacimientos y restos óseos en ciertas regiones, frente a la escasez en otras áreas peninsulares (Sala-Ramos *et al*., 2014).

La distribución biogeográfica de los felinos (gato montés, lince europeo, lince ibérico, leopardo y león) en la Península Ibérica durante el Pleistoceno Superior no es uniforme. Algunas especies, como el gato montés (*Felis silvestris*), el Lince ibérico (*Lynx pardinus*) y el leopardo (*Panthera pardus*) estuvieron presentes en todo el territorio. La distribución de otras especies es parcial, el lince europeo (*Lynx lynx*) se restringe al Noroeste, y ambas formas de león (*Panthera spelaea goldfuss* y *Panthera leo clueti*) están ausentes en el tercio Sur. La presencia de especies de macro-mamíferos en sólo parte del territorio no es exclusiva de los felinos o carnívoros, es más se encuentra ligada a la existencia de condiciones ambientales similares a las del centro del continente europeo. Por ejemplo, la distribución del reno, rinoceronte lanudo, mamut (García & Arsuaga, 2003), oso de las cavernas (Villaluenga, 2009), zorro ártico (Altuna & Mariezkurrena, 2004) y glotón (Altuna, 1963; Altuna & Baldeón, 1986) se reduce a la mitad norte peninsular durante episodios estadiales. Al contrario, la ausencia de estas especies en la mitad Sur y costa Mediterránea estarían ligadas a condiciones ambientales más benignas, con presencia de especies arbóreas termófilas (Fierro-Enrique *et al*., 2011).

En este estudio han sido incluidas 143 cavidades, mediante el estudio de este amplio conjunto es posible realizar algunas consideraciones acerca de la distribución biogeográfica de los felinos en la Península Ibérica. Sin embargo, para poder profundizar y acometer este análisis la Península Ibérica ha sido dividida en cinco unidades geográficas:

N°	YACIMIENTO	LOCALIDAD	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.	REFERENCIAS
1	Cueva Eirós	Triacastela, Lugo						X				Lombera-Hermida *et al*., 2014
2	Las Caldas	Priorio, Asturias						X				Corchón, 2002
3	La Güelga	Cangas de Onís, Asturias						X				Menéndez *et al*., 2014
4	La Riera	Posada de Llanes, Asturias						X	X	X		Álvarez-Lao, 2003
5	Llonín	Peñamera Alta, Asturias						X				Fortea *et al*., 1992, 1995, 1999
6	La Paloma	Soto de Regueras, Asturias	X						X			Castaños, 1980
7	Colombres	Ribadeva, Asturias	X									Altuna, 1972
8	Cueto de la Mina	Llanes, Asturias	X									Castaños, 1982
9	Tudela Veguín	Grado, Asturias	X									Altuna, 1972
10	Sima del Sueve	El Sueve, Asturias				X						Altuna, 1972
11	Tito Bustillo	Ribadesella, Asturias			X							Altuna, 1972
12	Balmorí	Llanes, Asturias									X	Altuna, 1972; Castaños, 2005
13	Quintanal	Llanes, Asturias									X	Castaños, 2005
14	La Parte	Siero, Asturias								X		Castaños, 2005
15	Hornos de la Peña	S.F. de Buelna, Cantabria				X		X				Yravedra, 2010
16	Castillo	Puente Viesgo, Cantabria						X	X	X		Cabrera, 1984; Landry & Burke, 2006
17	El Juyo	Igollo, Cantabria						X			X	Castaños, 2005
18	Morín	Villaescusa, Cantabria	X		X	X		X				Altuna, 1972
19	El Mirón	Ramales, Cantabria	X								X	Castaños, 2005; Marín-Arroyo, 2008
20	El Otero	Voto, Cantabria	X									Altuna, 1972
21	Covalejos	Arce, Cantabria	X									Castaños, 2005
22	Valle	Ramales, Cantabria	X									Altuna, 1972
23	Rascaño	Miera, Cantabria				X						Altuna, 1981
24	Altamira	Santillana del Mar, Cantabria				X	X		X			Altuna & Straus, 1976
25	Cueva San Juan	Arredondo, Cantabria						X				Altuna, 1992
26	El Pendo	Camargo, Cantabria							X		X	Altuna, 1980
27	Covacho Arenillas	Islares, Cantabria						X				Altuna, 1992
28	El Cuco	Castro Urdiales, Cantabria						X				Castaños, 2007
29	Las Pajucas	Lanestosa, Bizkaia				X		X				Castaños, 1987
30	Arlanpe	Lemoa, Bizkaia						X			X	Arceredillo et al., 2013
31	Atxuri	Mañaria, Bizkaia						X				Castaños, 1987
32	Oyalkoba	Abadiano, Bizkaia						X				Castaños, 1987
33	Bolinkoba	Abadiano, Bizkaia		X				X				Castaños, 1984
34	Axlor	Dima, Bizkaia				X		X				Altuna, 1981; Castaños, 2005
35	Goikolau	Mañaria, Bizkaia	X									Castaños, 1987
36	Lumentxa	Lekeitio, Bizkaia	X			X	X					Castaños, 1987
37	Santimamiñe	Kortezubi, Bizkaia	X			X			X			Castaños, 1984
38	Lamiñak II	Berriatua, Bizkaia	X									Castaños, 1987
39	Urratxa III	Gorbea, Bizkaia				X						Castaños, 1987
40	Venta Laperra	Carranza, Bizkaia		X								Castaños, 1987
41	El Polvorín	Carranza, Bizkaia		X								Castaños, 1987
42	Arrillor	Zigoitia, Araba-Álava	X	X		X						Castaños, 2005
43	Peñas de Oro	Zuia, Araba-Álava	X									Altuna, 1972
44	Praileaitz I	Deba, Gipuzkoa						X				Castaños 2010
45	Astigarraga	Deba, Gipuzkoa	X			X		X				Villaluenga, 2013
46	Ekain	Deba, Gipuzkoa						X				Altuna & Mariezkurrena, 1984; Villaluenga *et al*., 2012b
47	Amalda	Zestoa, Gipuzkoa		X	X			X	X	X		Altuna, 1990; Yravedra, 2007

48	Lezetxiki	Arrasate, Gipuzkoa	X	X		X		X		X		Altuna, 1972; Villaluenga, 2015; Villaluenga *et al*., 2012 a
49	Labeko Koba	Arrasate, Gipuzkoa	X									Arrizabalaga & Altuna, 2000
50	Aitzbitarte III	Errenteria, Gipuzkoa						X				Altuna & Mariezkurrena, 2011
51	Marizulo	Urnieta, Gipuzkoa	X									Altuna, 1972
52	Urtiaga	Deba, Gipuzkoa	X	X		X			X	X		Altuna, 1972
53	Ermittia	Deba, Gipuzkoa		X								Altuna, 1972
54	Aitzbitarte IV	Errenteria, Gipuzkoa								X		Altuna, 1970, 1972
55	Abauntz	Arraitz, Navarra	X					X	X			Altuna & Mariezkurrena, 2002
56	Coscobilo	Olazagutia, Navarra						X				Altuna, 1992 a, b
57	Zatoya	Abaurrea Alta, Navarra		X								Altuna & Mariezkurrena, 2002

TABLA 1

Yacimientos arqueológicos de la Cornisa Cantábrica, localización y presencia de félidos.

N°	**YACIMIENTO**	**LOCALIDAD**	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.	**REFERENCIAS**
58	Prado Vargas	Cornejo, Burgos						X				Arceredillo, 2010
59	Valdegoba	Huérmeces, Burgos	X	X	X			X			X	Díez *et al*., 1988-1989
60	Cueva de la Ermita	Hortigüela, Burgos						X				Delibes, 1972; Yravedra, 2007
61	Caballón	Oña, Burgos	X	X			X	X				Yravedra, 2005
62	La Blanca	Oña, Burgos	X	X								Yravedra, 2005
63	Cueva Millán	Hortigüela, Burgos	X		X							Yravedra, 2005
64	Cueva de Aguilón	Aguilón, Zaragoza						X				Sauqué et al., 2014
65	Zarzamora-Buho	Perogordo, Segovia						X				Sala *et al*., 2011, 2012
66	Camino	Pinilla del Valle, Madrid						X				Alférez *et al*., 1982; Arsuaga et al., 2012
67	Cueva de los Torrejones	Tamajón, Guadalajara						X				Arribas & Jordá, 1999
68	Cueva de los Casares	Riba de Saelices, Guadalajara	X	X	X		X	X			X	Altuna, 1973
69	Moros de Gabasa	Peralta de Calasanz, Huesca	X		X	X		X			X	Blasco-Sancho, 1995
70	Cova dels Muricecs	Llimiana, Lleida		X	X			X				Estévez, 1979
71	Estebanvela	Ayllón, Segovia	X	X								Yravedra, 2005, 2007b
72	Congosto	S. Andrés del Congosto, Guadalajara	X		X		X					Arribas & Jordá, 2002
73	Chaves	Casbas de Huesca, Huesca		X								Castaños, 1993
74	Gato II	Épila, Zaragoza		X								Utrilla *et al*., 2006
75	Jarama VI	Valle del Jarama, Guadalajara									X	Castaños, 2005

TABLA 2

Yacimientos arqueológicos de la zona Centro y Pirineos, localización y presencia de félidos.

Cornisa Cantábrica, Centro y Pirineos, Costa Mediterránea, Sur y Oeste peninsular (Tablas 1, 2, 3 y 4). La Cornisa Cantábrica alberga la mayor parte de los conjuntos (57) además del mayor número de restos y especies (Altuna, 1992a, b; Castaños, 1987, 2005) (Tabla 1). El sector central de la Península Ibérica y el Pirineo estarían poblados por homínidos y carnívoros desde el Pleistoceno Medio, sin embargo el número de conjuntos es limitado, 18 yacimientos, tal vez porque en su mayoría se trata de abrigos bajo roca o cuevas de reducida extensión en la que fenómenos post-deposicionales pudieron afectar en la conservación de los restos orgánicos (Blasco-Sancho *et al*., 1996; Yravedra, 2007b; Sauqué *et al*., 2014) (Tabla 2). La costa mediterránea se está convirtiendo en la zona que durante los últimos años ha mostrado un mayor crecimiento en el número de yacimientos (40). Este aumento se debe al trabajo realizado por múltiples grupos de investigación (Estévez, 1979; Sanchis, 2015; Sanchís *et al*., 2015) (Tabla 3), revelándose dos áreas con una importante concentración de ya-

N°	YACIMIENTO	LOCALIDAD	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	Panthera leo sp.	REFERENCIAS
76	Cova de S'Espasa	Oix-Sardenes, Girona						X				Estévez, 1975-1976
77	Cova dels Ermitons	Sales de Llierca, Girona			X			X				Estévez, 1979; Maroto, 1993
78	Cova de l'Arbreda	Serinyá, Girona	X	X	X	X		X			X	Estévez, 1987; Nadal *et al*., 2002
79	Bora Gran	Serinyá, Girona	X				X					Estévez, 1979; Yravedra, 2005
80	Mollet I	Serinyá, Girona			X	X		X			X	Rueda, 1993
81	Mollet III	Serinyá, Girona			X							Rueda, 1993
82	Reclau Viver	Serinyá, Girona			X						X	Maroto, 1987
83	Olopte	Isobol, Girona			X	X						Yravedra, 2005
84	Cau del Duc	Torroella de Montgrí, Girona		X	X	X		X				Estévez, 1979
85	Abric Romaní	Capellades, Barcelona	X	X				X				Cáceres, 1995
86	Cova del Gegant	Sitges, Barcelona		X	X			X				Daura et al., 2005
87	Cau de Coçes	Sitges, Barcelona		X								Yravedra, 2005
88	Musclé	Sitges, Barcelona		X	X							Yravedra, 2005
89	Terrasses de la Riera dels Canyars	Gavá, Barcelona						X				Daura et al., 2013
90	Toixoneres	Toixoneres, Barcelona	X		X							Estévez, 1979
91	Toll	Moiá, Barcelona	X	X	X	X					X	Estévez, 1979
92	Cingle Vermell	Vilanova de Sau, Barcelona					X					Estévez, 1979
93	Parco	Alos de Llobregat, Barcelona					X					Mangado *et al*., 2002
94	Cova Foradada	Calafell, Tarragona						X				Sanchis *et al*., 2015
95	Cova de L'Olla	Marmellar, Tarragona		X		X						Estévez, 1979
96	Balma de la Griega	Calafell, Tarragona					X					Martínez, 1996
97	Matutano	Vilafamés, castellón	X	X			X					Olaria et al., 1997
98	Cueva Horadada	Azuebar, Castellón						X				Sanchis *et al*., 2015
99	Cueva de les Meravelles	Alzira, Valencia						X				Sanchis *et al*., 2015
100	Bolomor	Tavernes de Valldigna, Valencia						X			X	Sanchis *et al*., 2015
101	Mallaetes	Barx, Valencia					X	X				Sanchis *et al*., 2015
102	Cova Negra	Xátiva, Valencia	X	X				X			X	Royo, 1942
103	Cova de Racò del Duc I	Vilallonga, Valencia						X				Sanchis *et al*., 2015
104	Parpalló	Gandía, Valencia	X				X					Davidson, 1989
105	Abrigo de la Quebrada	Chelva, Valencia					X					Real C. comunicación personal
107	Cova Foradada	Xàbia, Alicante						X				Pantoja *et al*., 2011
108	Cova de les Calaveres	Benidoleig, Alicante						X				Aparicio *et al*., 1982
109	Cova del Parat	Tollos, Alicante						X				Sanchis *et al*., 2015
110	Cova del Salt	Alcoi, Alicante						X				Sanchis *et al*., 2015
111	Abric del Pastor	Alcoi, Alicante						X				Sanchis *et al*., 2015
112	Cendres	Teulada-Moraira, Alicante	X				X					Villaverde & Pérez Ripoll, 2010
113	Beneito	Muro de Alcoy, Alicante	X				X					Martínez, 1996
114	Sima de las Palomas	Torre Pacheco, Murcia						X				Walker *et al*., 2012
115	Cueva del Niño	Ayna, Albacete					X					García-Moreno *et al*., 2014
116	Cueva Negra	Caravaca de la Cruz, Murcia		X								Pérez Ripoll, 1977; Martínez, 1996

TABLA 3

Yacimientos arqueológicos en la Costa Mediterránea, localización y presencia de félidos.

cimientos, en las provincias de Girona y Alicante. La región Sur es un territorio con una importante diversidad, desde ambientes de gran aridez, a medios de la Costa Atlántica y hábitats a gran altitud en la Cordillera Bética (Barroso *et al*., 2014; Finlayson *et al*., 2014) (Tabla 4), dado que algunos de estos entornos no son propicios para la conservación de restos óseos y a pesar de existir abundantes

N°	YACIMIENTO	LOCALIDAD	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo sp.*	REFERENCIAS
117	Cueva Ambrosio	Vélez Blanco, Almería	X	X			X					Yravedra, 2005
118	Cueva de la Carigüela	Darro, Granada					X	X				Bouchud, 1969
119	Cueva Horá	Darro, Granada		X								Yravedra, 2005
120	Campana de Piñar	Piñar, Granada						X				Sanchis *et al*., 2015
121	Cueva de Nerja	Nerja, Málaga	X	X			X					Riquelme *et al*., 2005
122	Boquete de la Zafarraya	Alcaucín, Malaga		X				X				Barroso *et al*., 2014
123	Devil's Tower	Gibraltar		X				X				Currant, 2000
124	Genista Cave	Gibraltar		X				X				Currant, 2000
125	Vanguard Cave	Gibraltar						X				Stringer *et al*., 2008
126	Gorham's Cave	Gibraltar	X				X	X				Currant, 2000
127	Gruta do Escoural	Montemor-o-novo	X		X			X			X	Cardoso, 1993
128	Gruta da Figueira Brava	Brava, Setubal	X					X			X	Cardoso, 1993
129	Pego do Diabo	Loures	X		X			X				Zilhao *et al*., 2010 a, b
130	Pedreira da Salemas	Loures	X		X			X			X	Antunes *et al*., 1989
131	Salemas	Peniche	X		X							Antunes *et al*., 1989
132	Gruta das Fontaìnhas	Cadaval	X					X				Cardoso, 1993
133	Furninha	Peniche	X		X			X				Cardoso, 1993
134	Casa da Moura	Óbidos						X				Valente, 2004
135	Gruta da Oliveira	Torres Novas						X				Zilhao *et al*., 2010 a, b
136	Gruta do Caldeirao	Tomar	X		X			X				Davis, 2002; Davis *et al*., 2007, 2010
137	Lorga do Dine	Vinhais						X			X	Castaños, 2005
138	Lapa da Rainha	Leira	X		X							Cardoso, 1993
139	Columbeira	Bombarral	X		X							Cardoso, 1993
140	Casa da Moira	Peniche		X								Cardoso, 1993
141	Algar do Joao Ramos	Peniche		X	X							Cardoso, 1993
142	Algar do Cascais	Lisboa			X							Cardoso, 1993
143	Maltravieso	Cáceres, Extremadura		X								Rodríguez Hidalgo *et al*., 2008, 2010

TABLA 4

Yacimientos arqueológicos en las zonas Sur y Oeste de la Península Ibérica, localización y presencia de félidos.

sitios en cueva, sólo diez han conservado restos óseos. Finalmente la región Oeste presenta una concentración (17 yacimientos) de sitios arqueológicos alrededor del tramo inferior y desembocadura del río Tajo (Cardoso, 1993) (Tabla 4).

El recuento de restos de felinos rebela la existencia de restos de gato montés (*Felis silvestris*) en 53 yacimientos. Restos de lince (*Lynx lynx*, *Lynx spelaea* y *Lynx pardinus*) han sido mencionados en 80 cavidades. El leopardo (*Panthera pardus*) está presente en 76 sitios y el león (*Panthera spelaea Panthera leo* y *Panthera leo* sp.) en 31 cavidades.

Finalmente, creemos necesario acometer el comentario individualizado de cada una de las especies incluidas en este artículo. En primer lugar, el gato montés (*Felis silvestris*) se distribuye por toda la Península Ibérica, en un total de 53 yacimientos arqueológicos (Figura 1) desde la Cornisa Cantábrica, hasta el extremo Sur peninsular, pasando por la Fachada atlántica (10 sitios) y la costa mediterránea (11 sitios). A pesar de ello la distribución es desigual, la Cornisa Cantábrica alberga 21 localizaciones, sin embargo el porcentaje de presencia de gato montés comparado al número de sitios en una de las cinco zonas geográficas. Es en el Oeste de la Península (58%) el área en la que la presencia del gato montés es más elevada. En la zona Mediterránea el conejo (*Oryctolagus cuniculus*) constituye la presa principal.

La distribución biogeográfica del Lince (*Lynx pardinus*, *Lynx spelaea*, *Lynx lynx* and *Lynx* sp.) ha sido dividida para su mejor comprensión en dos figuras (Figuras 2 y 3). El primer mapa incluye la presencia de Lince ibérico (*Lynx pardinus*) y Lince

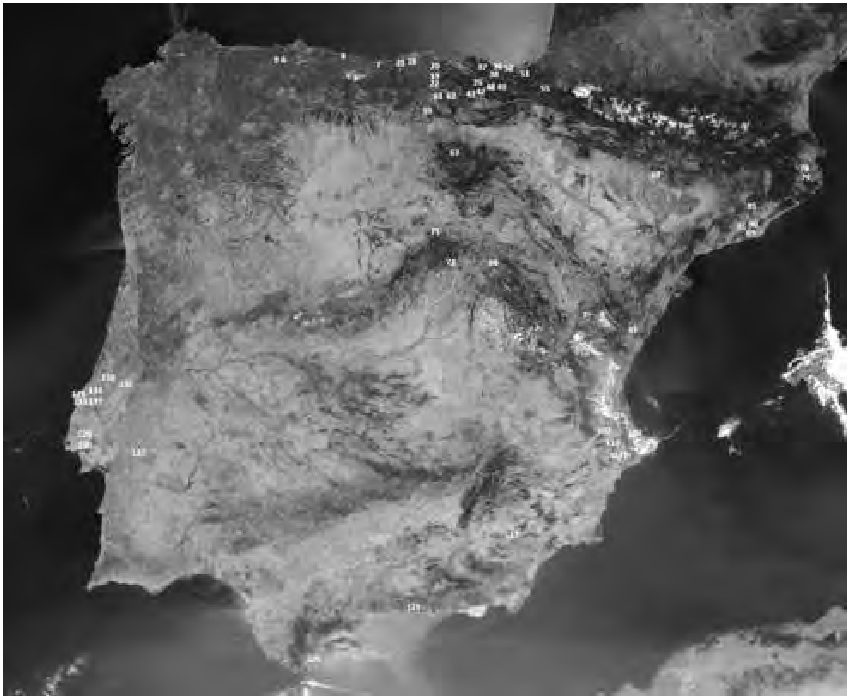

FIGURA 1

Gato montés *(Felis silvestris)* distribución biogeográfica. La numeración sigue las Tablas 1 a 4.

FIGURA 2

Lince Ibérico *(Lynx pardinus)* y Lince de las cavernas *(Lynx spelaea)*, distribución biogeográfica. La numeración sigue las Tablas 1 a 4.

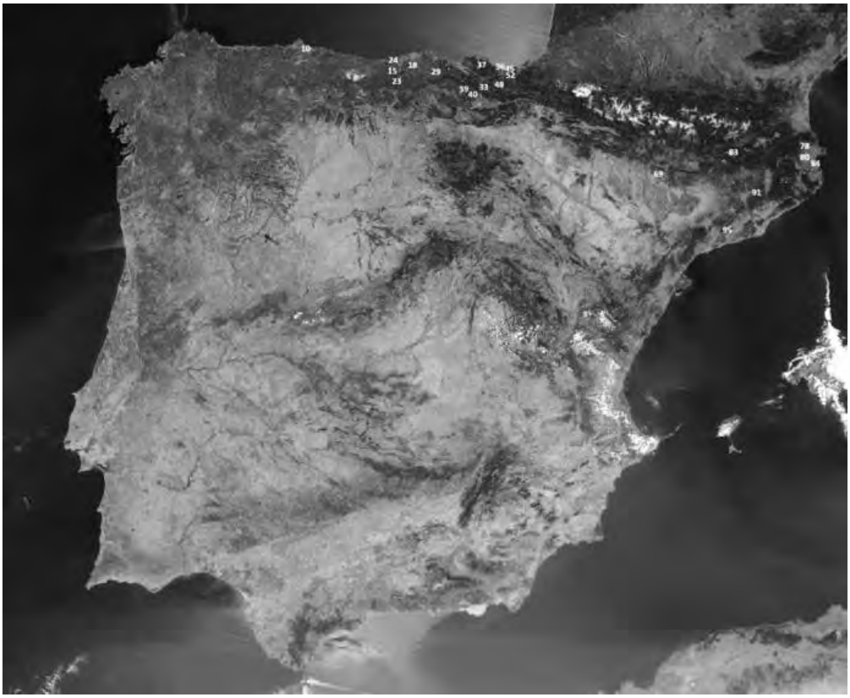

FIGURA 3

Lince europeo *(Lynx lynx)* y Lince indeterminado *(Lynx sp.)* distribución biogeográfica. La numeración sigue las Tablas 1 a 4.

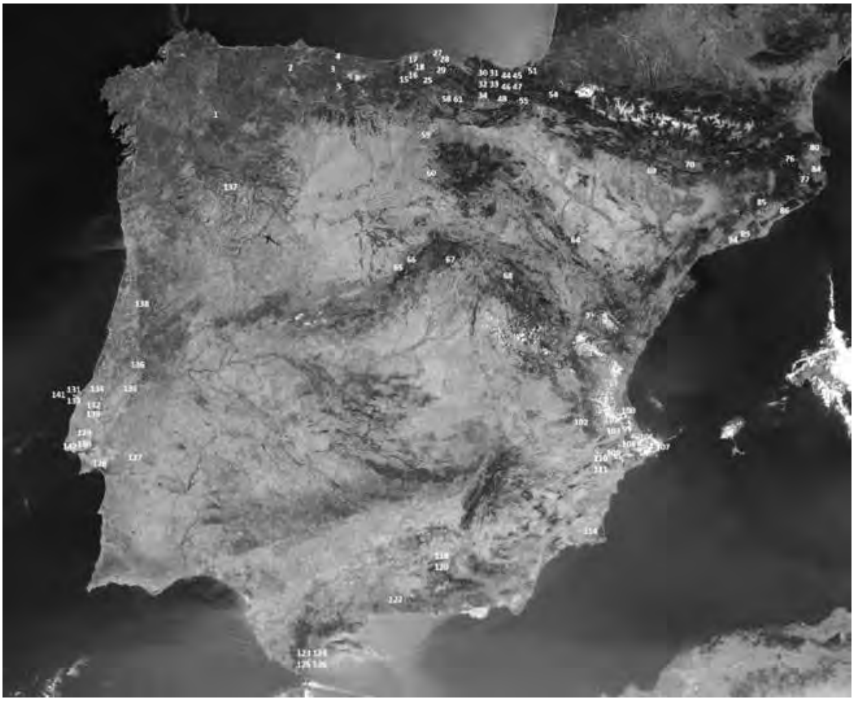

FIGURA 4

Leopardo *(Panthera pardus)* distribución biogeográfica. La numeración sigue las Tablas 1 a 4.

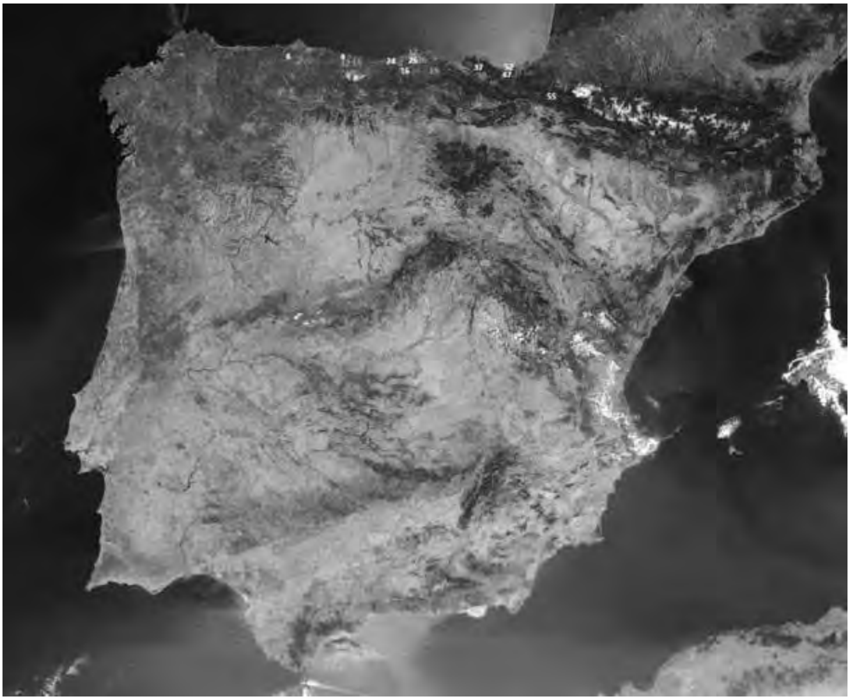

FIGURA 5

Distribución biogeográfica de tres formas de león en yacimientos arqueológicos del Pleistoceno Superior de la Península Ibérica. *Panthera leo clueti*, *Panthera spelaea* y Panthera sp. La numeración sigue las Tablas 1 a 4.

de las cavernas (*Lynx spelaea*). Los dos últimos estudios han descrito que ambos morfotipos pertenecen a una sola especie (Rodríguez-Varela *et al*., 2015a), sin embargo se ha decidido mantener esta distinción ya que sin un estudio taxonómico detallado no consideramos prudente modificar cada adscripción. Así la presencia de Lince Ibérico ha sido documentada en 57 yacimientos. 16 situados en la zona Noroeste y 14 en la Costa Mediterránea (Figura 2). Sobresale la ausencia de citas de Lince Ibérico o de las cavernas en el cuarto Noroeste de la Península, consideramos que las causas de esta ausencia han de ser analizadas.

En contextos arqueológicos y paleontológicos del Pleistoceno Superior en la Península Ibérica han sido descritas tres especies de lince (*Lynx pardinus*, *Lynx spelaea*, *Lynx lynx* y *Lynx* sp.). El Lince de las cavernas (*Lynx spelaea*) fue descrito por primera vez tomando como modelo los restos óseos descubiertos en las cuevas de Grimaldi (Boule, 1919) y L'Observatoire (Mónaco) (Boule & Villeneuve, 1927). Sin embargo la presencia de esta especie siempre fue controvertida, habiéndose extendido su uso a partir de la década de los ochenta del siglo veinte. En este trabajo hemos decidido mantener ambas nomenclaturas, ya que por el momento a falta de un estudio genético amplio no consideramos prudente generalizar tal asunción. Así mismo, ha sido constatada la amplia distribución biogeográfica que alcanzó esta especie tras la última fase glacial (Figura 2) extendiéndose hasta el norte de la península itálica (Rodríguez-Varela *et al*., 2015b).

Por otro lado, el Lince Europeo (*Lynx lynx*) presenta un patrón de distribución biogeográfica y cronológica propia. La presencia de esta especie se limita al tercio norte peninsular (Figura 3). La distribución de esta especie estuvo posiblemente ligada, como la de otras especies de fauna fría (García & Arsuaga, 2003) a fases estadiales. Las primeras citas de Lince europeo en la Península Ibérica se deben a los trabajos de J. Altuna en las cuevas de Rascaño (González-Echegaray & Barandiarán, 1981) y Erralla (Altuna *et al*., 1985), posteriormente otros restos han sido identificados en la Cornisa Cantábrica y el Norte de la costa mediterránea, constituyendo el valle del Ebro el límite Sur para la presencia de este taxón.

La densidad de ocupaciones en la Cornisa Cantábrica (Tabla 1) parece reforzar la hipótesis de una posible colonización a través del extremo Oeste del Pirineo, dada su mayor frecuencia en el tercio Este de la Cornisa (8 sitios), frente a cinco yacimientos en el centro y tan sólo una cita en el tercio Oeste. Por otro lado en el extremo Este peninsular (Tabla 2), existen siete citas, emplazamientos todos ellos situados al Norte del río Ebro.

La existencia de restos óseos determinados taxonómicamente como lince no determinables (*Lynx* sp.) han sido mencionados en 20 sitios; tres en la Cornisa Cantábrica (Tabla 1), dos en el Macizo Central (Tabla 2), cuatro en el Sur peninsular (Tabla 4) y diez yacimientos a lo largo de la Costa Mediterránea (Tabla 3). Finalmente, ha de mencionarse la total ausencia de cualquier resto de lince en el Noroeste de la Península Ibérica, área que si bien no posee una alta densidad de yacimientos arqueológicos, sí ha sido descrita la presencia de otros felinos (Figura 3).

El leopardo (*Panthera pardus*) es el carnívoro con mayor número de registros en la yacimientos arqueológicos peninsulares, habiendo sido identificado en 76 localidades (Figura 4) durante el Pleistoceno Superior, si bien su presencia en este territorio ha sido constatada desde el Pleistoceno Medio (Sanchis *et al*., 2015) hasta el Holoceno inicial (Castaños, 1987; Sauqué & Cuenca-Bescós, 2013). Del total de 76 localizaciones, 26 en la Cornisa Cantábrica (Tabla 1) y 22 en la Costa Mediterránea (Tabla 2), esto supone porcentualmente una presencia muy similar, 36 y 35% respectivamente de presencia de restos de leopardo con respecto al total de yacimientos existentes en cada zona. La presencia de leopardo es significativamente más elevada en el resto del territorio. En la zona Oeste, ha sido identificado en diez sitios (Tabla 4), lo que significa la existencia de leopardo en el 58% de los yacimientos identificados. En la zona Centro (Tabla 3), son once yacimientos, el 61% del total y el Sur peninsular (Tabla 4), estando el Leopardo presente en siete sitios, es decir el 70% de los conjuntos. Como ha sido anteriormente mencionado, la alta frecuencia de restos de leopardo (*Panthera pardus*) podría deberse a la etología de esta especie. Este cazador solitario, especializado en la caza de ungulados de media y pequeña talla, emplea las cuevas como refugio y cubil. En la Península Ibérica los leopardos pudieron focalizarse en la caza de la cabra (*Capra pyrenaica* y *Capra pyrenaica hispanica*) y rebeco (*Rupicapra rupicapra*) o sarrio (*Rupicapra pyrenaica*), especies adaptadas a los biotopos rocosos (Yravedra, 2007a; Sauqué & Cuenca-Bescós, 2013; Sanchis *et al*., 2015).

El león (*Panthera leo clueti, Panthera spelaea* y *Panthera sp*.) fue el mayor carnívoro presente en la Península Ibérica, aunque es la especie de felino más escasa en contextos arqueológicos (36 yacimientos) (Figura 5). De estos sitios tan sólo en la Cornisa Cantábrica han sido identificados taxonómicamente los restos óseos de león. En 9 cavidades los restos corresponden a *Panthera leo clueti* y 7 a *Panthera spelaea* (Tabla 1) (Castaños, 2005). Así mismo, tras la extinción de esta especie (Stuart & Lister, 2011) otra especie de león (*Panthera leo*) colonizó el Sur de Europa, incluyendo la Península Ibérica durante un breve periodo.

En el resto de la Península Ibérica los restos de gran felino han sido identificados como *Panthera* sp. o *Panthera leo* sp. en 20 cavidades (Figura 5). Las ocupaciones situadas más al Sur se localizan al Oeste en torno a la desembocadura del río Tajo (Gruta do Escoural) y en el Este en la provincia de Valencia (Cova Negra), mientras que en la zona centro ha sido determinada la presencia de león en la Cueva de los Casares y en Jarama VI. Por tanto, parece ser que el león nunca estuvo presente en el tercio Sur peninsular.

CONCLUSIONES

En este artículo ha sido descrita la distribución biogeográfica de los felinos (*Felis silvestris, Lynx pardinus, Lynx lynx, Lynx* sp., *Panthera pardus, Panthera leo clueti, Panthera spelaea* y *Panthera* sp.) en 143 yacimientos arqueológicos del Pleistoceno Superior de la Península Ibérica, este estudio ha tratado de realizar un estado de la cuestión acerca de la biogeografía y etología de estos carnívoros.

Ha sido posible establecer una relación entre diversos factores que han permitido la preservación de esta familia de carnívoros: La existencia de abrigos bajo roca y cuevas, principalmente en áreas kársticas, un medio ambiente al que se adaptasen las exigencias ecológicas de determinadas especies de carnívoro y sus presas. Por ejemplo, el Lince Ibérico *(Lynx pardinus*) al habitar en medios mediterráneos se adaptó morfológicamente mediante una reducción de talla y se especializó en la caza de la presa más abundante en ese entorno, el conejo. Al contrario, esta misma especie, durante el Pleistoceno Superior gozaba de mayor tamaño y probablemente su dieta pudiera ser más genérica, lo que permitió que colonizase áreas más extensas de la cuenca mediterránea.

Otro interesante fenómeno es la existencia de especies que sólo poblaron puntualmente y parcialmente la Península Ibérica, caso del Lince europeo (*Lynx lynx*) y del león pleistoceno (*Panthera leo clueti, Panthera spelaea* y *Panthera* sp.). Esta presencia en tal sólo parte de la Península estaría relacionada con las adaptaciones a distintas condiciones ambientales. Así la distribución del Lince europeo se limitó a la Cornisa Cantábrica y el tercio Norte de la Costa Mediterránea, mientras que el área de distribución del león ocupó los dos tercios septentrionales.

Si bien este trabajo es tan sólo un primer paso en el estudio biogeográfico de la fauna pleistocena en la Península Ibérica, creemos que ha podido constatarse como esta clase de trabajo es un interesante instrumento en los estudios de Paleontología, Arqueología Prehistórica y análisis del medio ambiente del Cuaternario en general. El presente trabajo se ha focalizado en una única familia de carnívoros, los felinos o félidos, debido a que las especies identificadas abarcan desde un carnívoro de pequeño tamaño, hasta el más grande de los carnívoros pleistocenos, pasando por varias especies de carnívoros de talla media.

Finalmente, son varias las cuestiones que han quedado sin respuesta, futuros estudios podrán clarificar el porqué de la no presencia de algunos taxones en determinadas áreas. La Península Ibérica en términos geográficos y ambientales es un territorio de reducidas dimensiones, aunque de gran diversidad, tanto en el Pleistoceno, como en la actualidad. Esta variedad tuvo reflejo en la elevada diversidad de especies identificadas, todo ello convierte a la Península Ibérica en un medio único para analizar la adaptación de las especies a las cambiantes condiciones ambientales.

AGRADECIMIENTOS

Este trabajo ha sido posible gracias a la financiación recibida por el programa de Becas de Investigación Predoctorales del Gobierno Vasco – Eusko Jaurlaritza, junto al apoyo recibido por *MONREPOS Research Centre and Museum for Human Behavioural Evolution-RGZM*, el Departamento de Geografía, Prehistoria y Arqueología de la Universidad del Pais Vasco - Euskal Herriko Unibertsitatea (UPV-EHU) y a la Asociación de Ciencias Aranzadi.

REFERENCIAS

ALFÉREZ, F.; MOLERO, G.; MALDONADO, E.; BUSTOS, V.; BREA, P. & BUITRAGO, A. M. 1982: Descubrimiento del primer yacimiento cuaternario (Riss-Würm) de vertebrados con restos humanos en la provincia de Madrid (Pinilla del Valle). *Colpa* 37: 15-32.

ALTUNA, J. 1963: Primer hallazgo de glotón (*Gulo gulo* L.) en la Península Ibérica. *Munibe* 15: 128.

— 1970: Fauna de mamíferos del yacimiento prehistórico de Aitzbitarte IV (Rentería, Guipúzcoa), *Munibe* 22: 3-41.

— 1972: *Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. Con catálogo de los mamíferos Cuaternarios del Cantábrico y del Pirineo Occidental. Munibe* 24. Sociedad de Ciencias Aranzadi, San Sebastián.

— 1973: Fauna de mamíferos del yacimiento prehistórico de Los Casares (Guadalajara). In: Barandiarán, I. (ed.): *La Cueva de los Casares*: 97-116. San Sebastián.

— 1980: Hallazgo de un Lince Nórdico (*Lynx lynx* L. Mammalia) en la sima de Pagolusieta, Gorbea (Vizcaya) *Munibe* 32: 317-324.

— 1981: Restos óseos del Yacimiento Prehistórico de Rascaño. In: González Echegaray, J. & Barandiarán, I. (eds.): *El Paleolítico Superior de la Cueva del Rascaño Santander*. Centro de Investigaciones del Museo de Altamira. Monografías. Santillana del Mar, Santander.

— 1990: Caza y alimentación procedente de macromamíferos durante el Paleolítico de Amalda. In: Altuna, J.; Baldeón, A. & Mariezkurrena, K. (eds.): *La Cueva de Amalda (Zestoa, País Vasco). Ocupaciones paleolíticas y postpaleolíticas*: 149-192. Eusko Ikaskuntza, San Sebastián.

— 1992a: Asociaciones de macromamíferos del Pleistoceno Superior en el Pirineo Occidental y Cantábrico. In: Cearreta, A. & Ugarte, F.M. (eds.): *The late Quaternary in the western Pyrenean Region.* UPV-EHU.

— 1992b: El medio ambiente durante el Pleistoceno Superior en la región cantábrica con referencia especial a sus faunas de mamíferos. *Munibe (Arkeologia-Antropologia)* 43: 13-29.

ALTUNA, J. & BALDEÓN, A. 1986: Resultados del sondeo estratigráfico practicado en la cueva de Mairulegorreta XI, Gorbea (Álava). *Estudios de Arqueología alavesa* 13: 47-62.

ALTUNA, J. & MARIEZKURRENA, K. 1984: Bases de subsistencia de origen animal en el yacimiento de Ekain. In: Altuna J. & Merino, J.M. (eds.): *El yacimiento prehistórico de la cueva de Ekain (Deba, Guipúzcoa)*: 211-280. Eusko Ikaskuntza, Sociedad de Estudios Vascos, San Sebastián.

— 2004: Los hallazgos de zorros (*Vulpes vulpes* Linnaeus y *Alopex lagopus* Linnaeus) en yacimientos paleolíticos de la región cantábrica. *Zona Arqueológica* 4 (Miscelánea en homenaje a Emiliano Aguirre), vol. II, Paleontología: 50-54. Madrid.

— 2011: Estudio de los macromamíferos del yacimiento de Aitzbitarte III (Excavación de la entrada). In: Altuna, J.; Marriezkurrena, K. & Ríos, J. (eds.): *Ocupaciones humanas en Aitzbitarte III (País Vasco) 33.600e18.400 BP (Zona de entrada de la cueva)*: 395-480. Vol. 5. EKOB, San Sebastián.

ALTUNA, J. & STRAUS, L. G. 1976: The Solutrean in Altamira. The artefactual and faunal evidence. *Zephyrus* 26-27: 175-182.

ALTUNA, J.; BALDEON, A. & MARIEZKURRENA, K. (Coord.) 1985: *Cazadores Magdalenienses en Erralla*. *Munibe* 37. Vols. 1-4: 7-206. San Sebastián.

ALTUNA, J.; MARIEZKURRENA, K. & ELORZA, M. 2001-2002: Arqueozoología de los niveles paleolíticos de la cueva de Abauntz (Arraiz, Navarra), *Saldvie* II: 1-26.

ÁLVAREZ-LAO, D. 2003: Macromamíferos fósiles del Pleistoceno de Asturias. Revisión bibliográfica y datos actuales. *Nat. Cantab*. 2: 11-23.

ANTUNES, M. T.; CABRAL, J. M. P.; CARDOSO, J. L.; PAIS, J. & SOARES, A. M. 1989: Paleolítico medio e superior em Portugal: datas 14C, estado actual dos conhecimentos, síntese e discussao. *Ciencias Terra* (UNL) 10: 127e138.

APARICIO, J.; PÉREZ, M.; VIVES, E.; FUMANAL, M. P. & DUPRÈ, M. 1982: La Cova de les Calaveres (Benidoleig, Alicante). Serie de Trabajos Varios del SIP, Vol. 75. Valencia.

ARCEREDILLO, D. 2010: Los macromamíferos del yacimiento del Pleistoceno superior de Prado Vargas (Burgos, España). In: Meléndez, G. (ed.): *III Congreso Ibérico de Paleontología. XXVI Jornadas de la Sociedad Española de Paleontología*: 63-66. Vol. 9. Publicaciones del Seminario de Paleontología de Zaragoza.

ARCEREDILLO, D.; GÓMEZ-OLIVENCIA, A. & SAN PEDRO-CALLEJA, Z. 2013: La fauna de micromamíferos de los niveles pleistocénicos de la Cueva de Arlanpe (Lemoa, Bizkaia). In: Ríos-Garaizar, J.; Garate, D. & Gómez-Olivencia, A. (eds.): *La Cueva de Arlanpe (Lemoa): ocupaciones humanas desde el Paleolítico medio antiguo hasta la prehistoria reciente*. *Kobie* BAI 3: 123-160.

ARRIBAS, A. & JORDÁ, J. F. 1999: Los macromamíferos del Cuaternario kárstico de Guadalajara (Castilla la Mancha). In: Aguirre, E. & Rubano, I. (eds.): *La huella del pasado. Fósiles de Castilla la Mancha*: 329-349. Patrimonio Arqueológico Histórico Castilla la Mancha.

ARRIZABALAGA, A. & ALTUNA, J. 2000: Labeko Koba (País Vasco) Hienas y Humanos en los albores del Paleolítico Superior. *Munibe (Antropologia-Arkeologia*) 52: 1-395.

ARSUAGA, J. L.; BAQUEDANO, E.; PÉREZ-GONZÁLEZ, A.; SALA, N.; QUAM, R. M.; RODRÍGUEZ, L.; GARCÍA, R.; GARCÍA, N.; ÁLVAREZ-LAO, D. J.; LAPLANA, C.; HUGUET, R.; SEVILLA, P.; MALDONADO, E.; BLAIN, H. A.; RUIZ-ZAPATA, M. B.; SALA, P.; GIL-GARCÍA, M. J.; UZQUIANO, P.; PANTOJA, A. & MARQUEZ, B. 2012: 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. *Quaternary International* 275: 55-75.

AZÉMA, M. 2009: *L'Art des cavernes en action. Tome 1: Les animaux modèles aspect. Locomotion, comportement*. Errance, Paris.

— 2010: *L'Art des cavernes en action. Tome 2: Les animaux figurés*. *Animation et mouvement, l'illusion de la vie*. Errance, Paris.

BALLESIO, R. 1980: Le gisement pléistocène supérieur de la grotte de Jaurens à Nespouls, Corrèze, France: les Carnivores (Mammalia, Carnivora). II. Felidae. *Nouv. Hist. nat. Lyon* 13: 68-97.

BARNETT, R.; SHAPIRO, B.; BARNES, I.; HO, S. Y. W.; BURGER, J.; YAMAGUCHI, N.; HIGHAM, T. F. G.; WHEELER, H. T.; ROSENDAHL, W.; SHER, L. V.; SOTNIKOVA, M.; KUZNETSOVA, T.; BARYSHINOKOV, G. F.; MARTIN, L. D.; HARINGTON, R.; BURNS, J. A. & COOPER, A. 2009: Phylogeography of lions (*Panthera leo* ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Molecular Ecology* 18(8):1668-1677.

BARROSO, C.; CAPARRÓS, M.; BARSKY, D.; MOIGNE, A. M. & MONCLOVA, A. 2014: Cueva del Boquete de Zafarraya: un yacimiento de neandertales en el sur Iberia. In: Sala Ramos, R.; Carbonell, E.; Bermúdez De Castro, J.M. & Arsuaga, J.L. (eds.): *Los cazadores recolectores del Pleistoceno y del Holoceno en Iberia y el Estrecho de Gibraltar, estado actual del conocimiento del registro arqueológico*: 463-472. Universidad de Burgos & Fundación Atapuerca, Burgos.

Blasco-Sancho, M. F. 1995: *Hombres, fieras y presas, estudio arqueológico y tafonómico del yacimiento del Paleolítico Medio en la cueva de los Moros de Gabasa 1 Huesca.* Universidad de Zaragoza, Zaragoza.

Blasco-Sancho, M. F; Montes, L. & Utrilla, P. 1996: Deux modeles de strategie occupationelle dans le Mousterien tardif de la Vallee de l'Ebre: les grotes de Peña Miel et Gabasa. In: Carbonell, E. & Vaquero, M. (eds.): *The last neandertals, the first anatomically modern humans.*

Bocherens, H.; Drucker, D. G.; Bonjean, D.; Bridault, A.; Conard, N. J.; Cupillard, C.; Germonpré, M.; Höneisen, M.; Münzel, S. C.; Napierala, A.; Patou-Mathis, M.; Stephan, E.; Uerpmann, H-P.; Ziegler, R. 2011: Isotopic evidence for dietary ecology of cave lion (*Panthera spelaea*) in North-Western Europe: Prey choice, competition and implications for extinction. *Quaternary International* 245(2): 249-261.

Bouchud, J. 1969: La faune mousterienne de Carigüela (Pinar, Grenade). *L'Anthropologie* 73(3-4): 361-364.

Boule, M. 1919: Les grottes de Grimaldi (Baoussé-Roussé) I: 237-362. Imprimerie de Monaco.

Boule, M. & Villeneuve, L. De 1927: La grotte de L'observatoire à Monaco. *Archives de l'Institut de Paléontologie Humaine* 1: 113.

Burger, J.; Rosendahl, W.; Loreille, O.; Hemmer, H.; Eriksson, T.; Götherström; Hiller, J.; Collins, M. J.; Wess, T. & Alt, K. W. 2004: Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Molecular Phylogenetics and Evolution* 30: 841-849.

Cabrera, V. 1984: El yacimiento de la Cueva del Castillo (Puente Viesgo, Santander). *Bibliotheca Praehistorica Hispana* 22: 11-485.

Cáceres, I. 1995: Estudios tafonómicos de los procesos de formación del nivel I del Abric Romaní, (Capellades, Barcelona). La influencia de la actividad antrópica. Tesis de Licenciatura Inédita. Depto. de Historia y Geografía. Facultad de Letras. Universitát Rovira i Virgili.

Cardoso, J. L. 1993: *Contribuçao para o Conhecimento dos grandes Mamíferos do Pleistoceno Superior de Portugal.* Comarca Municipal de Oeiras, Lisboa.

Castaños, P. M. 1980: La macrofauna del yacimiento de La Paloma. In: Hoyos Gómez, M. & Martínez Navarrete, M.I. (eds.): *La Cueva De La Paloma. Soto de Regueras Asturias. Excavaciones Arqueológicas en España* 116: 65-100.

— 1982: Estudio de los Macromamíferos del yacimiento prehistórico de Cueto de la Mina (Asturias). *Boletín del Instituto de Estudios Asturianos:* 105-106: 43-63.

— 1984: Estudio de macromamíferos de la cueva de Santimamiñe (Vizcaya). *Kobie (Serie Paleoantropología y Ciencias Naturales*) 14: 235-318.

— 1987: Los carnívoros prehistóricos de Vizcaya. *Kobie (Serie Paleoantropología)* XVI: 7-50.

– 1993: Estudio de los macromamíferos de los niveles Paleolíticos de Chaves. *Bolksan* 10: 9-30.

— 2005: Estudio paleontológico de un esqueleto de león, *Panthera leo* de la Sima de Azoleta, Gorbeia, Alava. *Munibe* 57: 123-129.

— 2010: Nuevas cavidades con carnívoros y humanos en el cantábrico oriental. In: Baquedano, E. & Rosell, J. (eds.): *Actas de la* 1^{a} *reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica. Zona Arqueológica* 13: 262-269.

Castaños, P. M. & Castaños, J. 2007: Estudio de la fauna del Abrigo del Cuco. In: Muñoz, E. & Montes, R. (eds.): Intervenciones arqueológicas en Castro Urdiales 3: 161-170.

Charles, R. 1997: The Exploitation of Carnivores and Other Fur-bearing Mammals during the North-western European Late and Upper Paleolithic and Mesolithic. *Oxford Journal of Archaeology*: 253-277.

Corchón, M. S. 2002: El tardiglaciar y la transición al postglaciar en la Meseta Norte Española. Una visión de síntesis. *Zephiru*s 55.

Currant, A. P. 2000: A review of the quaternary mammals of Gibraltar. In: Stringer, C.B.; Barton, R.N.E. & Finlayson, J.C. (eds.): *Neanderthals on the Edge*: 201-205. Oxbow Books, Oxford.

Daura, J.; Sanz, M.; Subira, M. E.; Quam, R.; Fullola, J. M. & Arsuaga, J. L. 2005: A neanderthal mandible from the Cova del Gegant (Sitges, Barcelona, Spain). *J. Hum. Evol*. 49(1): 56-70.

Daura, J.; Sanz, M.; García, N.; Allue, E.; Vaquero, M.; Fierro, E.; Carrión, J. S.; López-García, J. M.; Blain, H. A.; Sánchez-Marco, A.; Valls, C.; Albert, R. M.; Fornós, J. J.; Juliá, R.; Fullola, J. M. & Zilhao, J. 2013: Terrasses de la Riera dels Canyars (Gav_a, Barcelona): the landscape of Heinrich Stadial 4 north of the "Ebro frontier" and implications for modern human dispersal into Iberia. *Quat. Sci. Rev*. 60: 26-48.

Davidson, I. 1989: *La economía del final del Paleolítico en la España oriental*. Servicio de Investigación Prehistórica de la Diputación de Valencia, Serie de Trabajos Varios del SIP 85, Valencia.

Davis, S. J. M. 2002: The mammals and birds from Gruta do Caldeirao, Portugal. *Revista Portuguesa de Arqueologia* 2(5): 29-98.

Davis, S. J. M; Robert, I. & Zilhao, J. 2007: Caldeirao Cave (central Portugal)-whose house? Hyaena, man bearded vulture..." *Cour. Forsch-Inst. Senckenberg* 259: 213-226.

— 2010: La cueva de Caldeirão, (Portugal Central) -¿el hogar de hienas, hombres, quebrantahuesos…?, In: Baquedano, E. & Rosell, J. (eds.): *1ª Reunión de científicos sobre cubiles de hienas (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica*. *Zona Arqueológica* 13: 282-297.

Delibes, G. 1972: Informe paleontológico de la fauna de la Cueva de la Ermita. In: Moure Romaníllo, A. & Delibes De Castro, G. (eds.): *El Yacimiento Musteriense de la Cueva de la Ermita*.

De Ruiter, J. D & Berger, L. R. 2000: Leopard as taphonomic agents in dolomitic caves. Implications for bone accumulations in the hominid bearning deposits of South Africa. *Journal of Archeological Science* 27: 665-684.

Diedrich, C. G. 2013: Late Pleistocene leopards across Europe-northernmost European German population, highest elevated records in the Swiss Alps, complete skeletons in the Bosnia Herzegowina Dinarids and comparison to the ice age cave art. *Quaternary Science Reviews* 76: 167-193.

Díez, C.; García, M. A.; Gil, E.; Jordá Pardo, J. F.; Ortega, A. I.; Sánchez, A. & Sánchez, B. 1988-1989: La Cueva de Valdegoba (Burgos) Primera campaña de excavaciones. *Zephirus* XLI-XLII.

Díez, C.; Arribas, A. & Jordá, J. F. 1998: Torrejones (Tamajón, Guadalajara). A hyena den on human occupation. In: *Economie préhistorique: Les comportements de subsistence au Paléolitique*. XVIII Recontre Internationale d’Archeologie et d’Historie d’Antibes. APDECA, Sophia Antipolis.

Durán-Valsero, J. J. & Robledo-Ardila, P. A. 2009: Carbonate and Evaporite karst systems of the Iberian Peninsula and the Balearic Islands. In: García-Cortés, A.; Águeda-Villar, J.; Palacio Suárez-Valgrande, J. & Salvador González, C.I. (eds.): *Spanish Geological frameworks and Geosites, an approach to Spanish geological Heritage of International Relevance*: 200-215. Instituto Geológico y Minero de España, Madrid.

Ersmark, E.; Orlando, L.; Sandoval-Castellanos, E.; Barnes, I.; Barnett, R.; Stuart, A.; Lister, A. & Dálen, L. 2014: Population demography and Genetic Diversity in the Pleistocene cave lion. *Open Quaternary* DOI: 10.5334.oq.aa.

Estévez, J. 1975-1976: Hallazgo de una pantera en el Pleistoceno catalán. *Speleon* 22: 171-178.

— 1979: La Fauna del Pleistoceno catalán. Tesis doctoral inédita. Universidad Autónoma de Barcelona, Barcelona.

— 1987: La fauna de L’Arbreda (s. alfa) en el conjunt de faunes del pleistoce superior. *Cypsela* VI: 73-87.

Fierro-Enrique, E.; Munuera-Giner, M.; Fernández-Jiménez, S.; Arribas-Herrera, A. & Carrión García, J. S. 2011: Cambios en el paisaje vegetal de la región andaluza durante el Pleistoceno Superior y Holoceno. *Revista de Prehistoria de Andalucía* 2: 15-34.

Finlayson, C.; Blasco, R.; Rodríguez-Vidal, J.; Giles-Pacheco, F.; Finlayson, G.; Gutiérrez, J. M.; Jennings, R.; Fa, D. A.; Rosell, J.; Carrión, J. M.; Sánchez-Marco, A.; Finlayson, S. & Bernal, M. A. 2014: Excavaciones en Gibraltar: especial referencia a Gorham´s cave y Vanguard Cave. In: Sala Ramos, R.; Carbonell, E.; Bermúdez De Castro, J.M. & Arsuaga, J.L. (eds.): *Los cazadores recolectores del Pleistoceno y del Holoceno en Iberia y el Estrecho de Gibraltar, estado actual del conocimiento del registro arqueológico*: 506-514. Universidad de Burgos & Fundación Atapuerca, Burgos.

Fortea, J.; De La Rasilla, M. & Rodríguez, V. 1992: La cueva de Llonín (Llonín, Penamera Alta). Campañas de 1987 a 1990. In: Excavaciones arqueológicas en Asturias 1987e1990. 2: 9-18.

— 1995: La cueva de Llonín (Llonín, Penamera Alta). Campañas de 1991 a 1994. In: Excavaciones arqueológicas en Asturias 1991e1994. 3: 33-43.

— 1999: La cueva de Llonín (Llonín, Peñamera Alta). Campañas de 1995 a 1998. In: Excavaciones arqueológicas en Asturias 1995-1998. 4: 59-73.

García, N. & Arsuaga, J. L. 2003: Last Glaciation cold-adapted faunas in the Iberian Peninsula. In: Reumer, J.W.F.; De Vos, J. & Mol, D. (eds.): *Advances in mammoth research (Proceedings of the Second International Mammoth Conference), Rotterdam, May 16-20 (1999)*: 159-169. *DEINSEA* 9.

García-Moreno, A.; Ríos-Garaizar, J.; Arroyo-Marín, A. B.; Ortíz, J. E.; De Torres, T. & López-Dóriga, I. 2014: La secuencia musteriense de la Cueva de El Niño (Aýna, Albacete) y el poblamiento neandertal en el sureste de la Península Ibérica. *Trabajos de Prehistoria* 71(2).
Doi: 10.3989/tp.2014.12132.

Ghezzo, E. & Rook, L. 2015: The remarkable *Panthera pardus* (Felidae, Mammalia) record from Equi (Massa, Italy): taphonomy, morphology, and paleoecology. *Quaternary Science Reviews* 110: 131-151.

González Echegaray, J. & Barandiarán, I. 1981: *El Paleolítico Superior de la Cueva del Rascaño, Santander*. Centro de Investigaciones del Museo de Altamira, Monografías. Santillana del Mar, Santander.

Jordá-Pardo, J. F. 2009: Vertebrate deposits of the Spanish Pliocene and Pleistocene. In: García-Cortés, A.; Águeda-Villar, J.; Palacio Suárez-Valgrande, J. & Salvador González, C.I. (eds): *Spanish Geologi-*

cal frameworks and Geosites, an approach to Spanish geological Heritage of International Relevance: 171-183. Instituto Geológico y Minero de España, Madrid.

Landry, G. & Burke, A. 2006: El Castillo: The Obermaier faunal collection. *Zona Arqueológica* 7. Homenaje a Victoria Cabrera: 104-113. Vol. 1.

Lloveras L.; Moreno-García, M. & Nadal, J. 2008: Taphonomic analysis of leporid remains obtained from modern Iberian lynx (*Lynx pardinus*) scats. *Journal of Archaeological Science* 35: 1-13.

Lombera Hermida, A.; Rodríguez, X. P. & Fábregas-Valcarce, R. 2014: El yacimiento arqueo-paleontológico de Cova Eirós (Triacastela, Lugo). In: Sala Ramos, R.; Carbonell, E.; Bermúdez De Castro, J.M. & Arsuaga, J.L. (eds.): *Los cazadores recolectores del Pleistoceno y del Holoceno en Iberia y el Estrecho de Gibraltar, estado actual del conocimiento del registro arqueológico*: 18-25. Universidad de Burgos & Fundación Atapuerca, Burgos.

Macdonald, D. W. & Barrett, P. 2002: *Mammals of Europe*. Princenton University Press, New Jersey.

Mangado, X.; Petit, M. A.; Fullola, J. M. & Bartrolí, R. 2002: El paleolític superior final de la cova de El Parco (Alòs de Balaguer, La Noguera). *Revista d'Arqueología de Ponent*: 45-62.

Marin Arroyo, A. B. 2008: El yacimiento paleolítico de la Cueva del Mirón: resultados de la aplicación de nuevas metodologías arqueozoológicas. In: Díez, J.C. (ed.): *Zooarqueología hoy*: 69-87. Encuentros Hispano Argentinos, Burgos.

Maroto, J. 1993: La cueva de los Ermitons (Sales de Llierca, Girona): un yacimiento del Paleolítico medio final. *Espacio, Tiempo y Forma*. Serie I. Prehist. Arqueol. 6: 13-30.

Martínez, R. 1996: Fauna del Pleistoceno superior en el País Valenciano: aspectos económicos, huella de manipulación y valoración paleoambiental. Tesis Doctoral inédita. Universitat de Valencia, Valencia.

Mattucci, F.; Oliveira, R.; Lyons, L. A.; Alves, P. C. & Randi, E. 2015: European wildcat populations are subdivided into five main biogeographic groups: consequences of Pleistocene climate changes or recent anthropogenic fragmentation?. *Ecology and Evolution* doi:10.1002/ece3.1815.

Menéndez, M.; Weniger, G. Ch.; Álvarez-Alonso, D.; De Andrés-Herrero, M.; García, E.; Jordá, J. F.; Kehl, M.; Rojo, J.; Quesada, J. M. & Schmidh, I. 2014: La Cueva de la Güelga. Cangas de Onís. Asturias. In: Sala Ramos, R.; Carbonell, E.; Bermúdez De Castro, J.M. & Arsuaga, J.L. (eds.): *Los cazadores recolectores del Pleistoceno y del Holoceno en Iberia y el Estrecho de Gibraltar, estado actual del conocimiento del registro arqueológico*: 60-63. Universidad de Burgos & Fundación Atapuerca, Burgos.

Olaria, C.; Gusi, F. & Watson, J. 1997: El asentamiento magdaleniense de Cova Matutano (Villafanes, Castellón) en el contexto sociocultural del Würm final del área mediterránea peninsular. In: Fullola, J.M. & Soler, N. (ed.): *El Món Mediterraní després del Pleniglacial (18-12000 Bp)*: 375-382. Serie Monográfica 17. Museu de Arqueología de Catalunya, Girona.

Pantoja, A.; Sala, M. T. N.; García, N.; Ruiz, B.; Gil, M. J.; Aranburu, A.; Arsuaga, J. L. & Casabó, J. 2011: Análisis paleontológico del yacimiento del Pleistoceno superior de Cova Foradada (Xábia, Alicante, España). *Bol. R. Soc. Esp. Hist. Nat. Sec. Geol*. 105(1-4): 53-66.

Pérez Ripoll, M. 1977: *Los mamíferos del yacimiento Musteriense de Cova Negra*. Servicio de Investigación prehistórica nº 53: 1-149.

Purroy, F. J. & Varela, J. 2009: *Guía de los mamíferos de España. Península, Baleares y Canarias.* Lynx Ediciones, Madrid.

Riquelme Cantal, J. A. *et al*. 2005: La fauna de mamíferos del Solutrense en la Cueva de Nerja. *Munibe (Antropología-Arkeologia)* 57: 255-263.

Rodríguez, A. & Calzada, J. 2015: *Lynx pardinus*. The IUCN Red List of Threatened Species 2015: e. T12520A50655794. http://dx.doi.org/10.2305.

Rodriguez-Hidalgo, A. J.; Muñoz Encinar, L. & Canals i Salomó, A. 2008: *Una aproximación zooarqueológica al yacimiento de la cueva de Maltravieso 50 años después* 2006. Museo de Cáceres, Cáceres.

Rodríguez-Hidalgo, A. J.; Canals, A.; Saladié, P. & Carbonell, E. 2010: Los cubiles de *Crocuta crocuta* como contenedores de información paleoeconómica. El caso de las Sala de los Huesos, Cueva de Maltravieso (Cáceres). In: Baquedano, E. & Rosell, J. (eds.): *1ª Reunión de científicos sobre cubiles de hienas (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica*. *Zona Arqueológica* 13: 246-261.

Rodríguez-Hidalgo, A.; Lloveras, L.; Moreno-García, M; Saladié, P.; Canals, A. & Nadal, J. 2013: Feeding behaviour and taphonomic characterization of non-ingested rabbit remains produced by the Iberian *Lynx* (*Lynx pardinus*). *Journal of Archaeological Science* 40: 3031-3045.

Rodríguez-Varela, R.; García, N.; Nores, C.; Álvarez-Lao, D.; Barnett, R.; Arsuaga, J. L. & Valdiosera, C. 2015a: Ancient DNA reveals past existence of Eurasian Lynx in Spain. *Journal of Zoology* DOI: 10.1111/jzo.12289.

Rodríguez-Varela, R.; Tagliacozzo, A.; Ureña, I.; García, N.; Crégut-Bonnoure, E.; Mannino, M. A.; Arsuaga, J. L. & Valdiosera, C. 2015b: Ancient DNA evidence of Iberian *Lynx* palaeoendemism. *Quaternary Science Reviews* 112: 172-180.

Rueda, J. M. 1993: L'acció antrópica sobre les matéries dures animáis durant el Pleistocé del Nord-est de Catalunya. Tesis Doctoral inédita. Universidad de Girona.

Sala, M. T. N.; Arsuaga, J. L.; Laplana, C.; Ruiz, B.; Gil, M. J.; García, N.; Aranburu, A. & Algaba, M. 2011: Un paisaje de la Meseta durante el Pleistoceno Superior. Aspectos paleontológicos de la Cueva de la Zarzamora (Segovia, España). *Bol. R. Soc. Esp. Hist. Nat. Sec. Geol.* 105(1-4): 67-85.

Sala, M. T. N.; Algaba, M.; Arsuaga, J. L.; Aranburu, A. & Pantoja, A. 2012: A taphonomic study of the Búho and Zarzamora caves. Hyenas and humans in the Iberian plateau (Segovia, Spain) during the Late Pleistocene. *J. Taphon*. 10(3-4): 477-497.

Sala-Ramos, R.; Carbonell, E.; Bermúdez De Castro, J. M. & Arsuaga, J. L. 2014: *Los cazadores recolectores del Pleistoceno y del Holoceno en Iberia y el Estrecho de Gibraltar, estado actual del conocimiento del registro arqueológico*. Universidad de Burgos & Fundación Atapuerca, Burgos.

Sanchis, A. 2015: *Un món de Feres Grans carnívors en la prehistòria valenciana-Un mundo de Fieras, Grandes Carnívoros en la Prehistoria Valenciana*. Diputació de València-Museo de Prehistoria de Valencia, Valencia.

Sanchis, A.; Tormo, C.; Sauqué, V.; Sanchis, V.; Díaz, R.; Ribera, A. & Villaverde, V. 2015: Pleistocene leopards in the Iberian Peninsula: New evidence from palaeontological and archaeological contexts in the Mediterranean region. *Quaternary Science Reviews* 124: 175-208.

Sauqué, V. & Cuenca-Bescós, G. 2013: The Iberian Peninsula, the last european refugium of *Panthera pardus* Linnaeus, 1758 during the Upper Pleistocene. *Quaternaire* 1: 45-38.

Sauqué, V.; Rabal-Garcés, R.; Sola-Almagro, C. & Cuenca-Bescós, G. 2014: Bone accumulation by leopards in the Late Pleistocene in the Moncayo Massif (Zaragoza, NE Spain). *PLoSOne* 9(3): e92144.
doi:10.1371/journal.pone.0092144.

Soler, N. & Maroto, J. 1987: Els nivells d'ocupació del Paleolític Superior a la cova de l'Arbreda (Serinyà, Girona). *Cypsela* 6: 221-228.

Sommer, R. S. & Benecke, N. 2006: Late Pleistocene and Holocene development of the Felid fauna (Felidae) of Europe: a review. *Journal of Zoology* 269*:* 7–19.

Sommer, R. S. & Nadachowski, A. 2006: Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Review* 36(4): 251-265.

Straus, L. G.; Altuna, J.; Jakes, M. & Kunst, M. 1988: New Excavations in Casa da Moura (Serra d'El Rei, Peniche) and at the Abrigos de Bocas (Rio Maior), Portugal. *Arqueologia (Porto)* 18: 65-94.

Stringer, C.; Finlayson, J. C.; Barton, R. N. E.; Cáceres, I. & Fernández-Jalvo, Y. 2008: Neanderthal exploitation of marine mammals in Gibraltar. *PNAS* 105(38): 14319-14324.

Stuart, J. A. & Lister, A. M. 2011: Extinction chronology of the cave lion *Panthera spelaean*. *Quaternary Science Reviews* 30(17-18): 2329-2340.

Turner, A. 1984: Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications. *Annales Zoologici Fennici* 21(1): 1-8.

Utrilla P.; Blasco, F. & Rodanés J. M. 2006: Entre el Ebro y la Meseta: El Magdaleniense de la Cuenca del Jalón y la Placa de Villalba. In: Delibes De Castro, G. & Díez Martín, F. (eds.): *El paleolítico Superior en la Meseta Norte española*: 173-213. Fundación Studia Archaeologica 94.

Vera Torres, J. A. 2004: *Geología de España*. Sociedad Geológica de España e Instituto Geológico y Minero de España, Madrid.

Villaluenga, A. 2009: Yacimientos del Pleistoceno Superior en la Península Ibérica con presencia de restos de oso. *Munibe (Antropología-Arkeologia*) 60: 17-33.

— 2013: *La Evaluación de los Úrsidos en Medios Kársticos la Cornisa Cantábrica.* UPV-EHU. Tesis Doctoral Internacional, 704 pp.
http://hdl.handle.net/10810/16468.

Villaluenga, A.; Castaños, P. M.; Arrizabalaga, A. & Mujika, J. A. 2012a: Cave Bear (*Ursus spelaeus* Rosenmüller Heinroth, 1794) and humans during the early Upper Pleistocene (Lower and Middle Palaeolithic) in Lezetxiki, Lezetxiki II and Astigarragako Kobea (Basque country, Spain). Preliminary approach. *J. Taphon.* 10(3-4): 521-543.

Villaluenga, A.; Arrizabalaga, A. & Rios-Garaizar, J. 2012b: Multidisciplinary approach to two Chatelperronian series: lower IX layer of Labeko Koba and X Level of Ekain (Basque country, Spain). *J. Taphon*. 10(3-4): 499-520.

Villaverde, V. & Pérez Ripoll, V. 2010: Los estudios arqueozoológicos y tafonómicos en los yacimientos del Paleolítico medio y superior de la región mediterránea ibérica. Algunos apuntes y reflexiones. In: Baquedano, E. & Rosell, J. (eds.): *1ª Reunión de científicos sobre cubiles de hienas (y otros grandes* *carnívoros) en los yacimientos arqueológicos de la Península Ibérica*. *Zona Arqueológica* 13: 480-493.

WALKER, M. J. 2001: Excavations at Cueva Negra del Estrecho del Rio Quipar and Sima de las Palomas del Cabezo Gordo: two sites in Murcia (south-east Spain) with Neanderthal skeletal remains, Mousterian assemblages and late Middle to early Upper Pleistocene fauna. In: Milliken, S. & Cook, J. (eds.): *A Very Remote Period Indeed: Papers on the Palaeolithic Presented to Derek Roe*. Oxbow Books, Oxford.

WALKER, M. J.; LÓPEZ-MARTÍNEZ, M. V.; ORTEGA-RODRIGUAÑEZ, J.; HABER-URIARTE, M.; LÓPEZ-JIMÉNEZ, A.; AVILÉS-FERNÁNDEZ, A.; POLO-CAMACHO, J. L.; CAMPILLO-BOJ, M.; GARCÍA-TORRES, J.; CARRIÓN-GARCÍA, J. S.; SAN NICOLÁS-DEL TORO, M. & RODRÍGUEZ-ESTRELLA, T. 2012: The excavation of buried articulated Neanderthal skeletons at Sima de las Palomas (Murcia, SE Spain). *Quat. Int*. 259: 7-21.

YRAVEDRA, J. 2005: Aprovechamiento cárnico de lince (*Lynx pardina*) durante el Pleistoceno Superior en el interior de la Península Ibérica. *Munibe (Arkeologia-Antropologia*) 57: 303-311.

— 2007a: Nuevas contribuciones en el comportamiento cinegético de la cueva de Amalda. *Munibe (Antropologia-Arkeologia)* 43: 3-85.

— 2007b: Aproximaciones tafonómicas a los cazadores de la segunda mitad del Pleistoceno Superior de la mitad norte del interior de la Península Ibérica. *Arqueoweb*. Revista sobre arqueología en Internet 9(1).

— 2010: Zooarqueología y tafonomía del yacimiento de Hornos de la Peña (San Felices de Buelna, Cantabria). *Complutum* 21(1): 69-86.

ZACHOS, F. E. *&* HACKLÄNDER, K. *(eds.)* 2011: Genetics and conservation of large mammals in Europe. *Mammal Review* 41*:* 85–174.

ZILHAO, J.; DAVIS, S. J. M.; DUARTE, C.; SOARES, A. M. M.; STEIER, P.; WILD, E. 2010a: Pego do Diabo (Loures, Portugal): dating the Emergence of anatomical Modernity in Westernmost Eurasia. *Plos One* 5(1): 1e22.

ZILHAO, J.; ANGELUCCI, D. E.; ARGANT, J.; BRUGAL, J. P.; CARRIÓN, J. S.; CARVALHO, R.; FUENTES, N. & NABAIS, M. 2010b: Humans and hyenas in the Middle Paleolithic of Gruta da Oliveira (Almonda System, Torres Novas, Portugal). *Zona Arqueol*. 13: 298e309.

Archaeofauna 25 (2016): 205-232

Faunal Remains from an Almohad (Ad XII/XIII) Silo at the Castle of Aljezur (Portugal)

DIOGO MOTA[1] & J. L. CARDOSO[2]

[1] MSc (Paleontology). Universidade Nova de Lisboa, Faculdade de Ciências e Tecnologia.
mota.d.m.m@gmail.com
[2] Universidade Aberta. Centro de Arqueologia da Universidade de Lisboa.
cardoso18@netvisao.pt

(Received *03 December 2015*; Revised *26 January 2016*; Accepted *29 January 2016*)

ABSTRACT: The analysis of a faunal collection from a storage silo found in the castle of Aljezur, dating from the Almohad period (XII/XIIIth centuries AD), is presented. It appears that the community occupying the castle concentrated on hunting species such as the rabbit, wild boar, red deer and Iberian lynx, while evidences of stockbreeding were scarce and centered upon caprines with horses and chicken playing minor role. The presence of a large dog has been assumed to be an aid for hunting but possibly also in herd keeping. With the exception of the lynx, all large mammals evidenced traces of consumption. The domestic cat is taken to represent a pet whereas the lynx had probably a role as a fur provider. It should be noted that equids and the pond turtle were probably food items. Rodents are taken to represent commensals whereas the toad of the Genus *Bufo* probably represented an intrusive element.

KEYWORDS: ZOOARCHAEOLOGY, ISLAMIC, ALMOHAD, ALJEZUR, ALGARVE, PORTUGAL

RESUMEN: Se presenta el estudio de un conjunto faunístico recogido en un silo del castillo de Aljezur en época Almohade (siglos XII/XIII d.C.). Se atestigua una notable actividad cinegética centrada sobre el conejo con aportes secundarios de ciervos, jabalíes y lince ibérico. Las evidencias pecuarias, centradas sobre caprinos y con équidos y gallinas como grupos secundarios, son marginales. Se asume que el perro actuó como auxiliar de caza y no tanto en la vigilancia de rebaños. En el caso de los macromamíferos, con excepción hecha del lince, las evidencias apuntan al consumo de la carne. El gato probablemente representó un animal de compañía en tanto que la presencia de lince se justificaría por su interés peletero. Tanto los équidos como el galápago parecen representar elementos de consumo. Frente a ellos, los restos de roedores representan animales comensales en tanto que los de sapo del género *Bufo* representan intrusivos

PALABRAS CLAVE: ZOOARQUEOLOGÍA, ÉPOCA ISLÁMICA, ALMOHADES, ALJEZUR, ALGARVE, PORTUGAL

INTRODUCTION. CONTEXTS, STRUCTURES AND CRONOLOGY

The fortification of Aljezur (Figure 1) integratedthe defensive system of the Silves territory during the XIIth and XIIIth centuries A.D. (Silva & Gomes, 2002: 347, Figure 2). Archaeological excavations carried in the interior of this fortification between 1990 and 1997 under the direction of Carlos Tavares da Silva, allowed the excavation of contexts from moments that date from Late Bronze Age, the Iron and Medieval ages to the XVIth century A.D.

The materials studied in this paper date from Medieval times of occupation and derive from one of the 2 negative structures (i.e. “silos”, labelled A and B) excavated on the geological substratum, on the inner quarters of a series of housing spaces dating from Muslim times. Both were covered by late Medieval structures, attributed to the cantonment of that time, that were abandoned by the early XVIth century A.D. (Figure).

The infilling of these structures represents the last stage of Muslim the occupation of the *Alcazaba*, correlated with layer 3 of the general stratigraphic sequence of the excavated area (Silva & Gomes, 2002). According to the characteristics and typology of the ceramics therein recovered this stage has been attributed to XII/XIIIth centuries A.D. The faunal assemblage comes exclusively from structure A, that corresponded to a storage area for cereals or possibly dry fruits filled with domestic refuse. From a stratigraphic perspective, the filling of the silo revealed a sequence that, from top to bottom, incorporated the following layers (Figure 4):

Layer 3 A – (thickness ≈ 0.15m). It corresponds to a level of lime mortar and sand of soil leveling.

Layer 3 B – (thickness ≈ 0,30m). Corresponds to a yellowish-brown sand-clay sediments, incorporating disperse coal, shale blocks, ceramics and abundant faunal remains.

Layer 3 C – (thickness ≈ 1,10m), formed by dark-brown sand-clay sediments, featured dispersed coal, numerous shale blocks, abundant faunal remains and ceramics;

Layer 3 D – (thickness ≈0.05m to 0.10m) featuring light-brown sand-clay sediments lying on the bottom of the structure, incorparated faunal remains and ceramics.

FIGURE 1

The Castle of Aljezur (photo C. M. Aljezur).

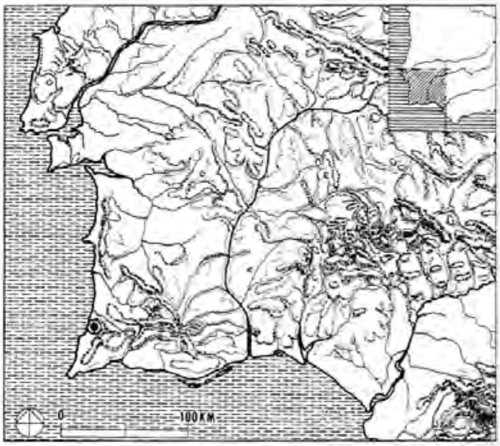

FIGURE 2

Location of the castle of Aljezur (Silva & Gomes, 2002, Figure 1).

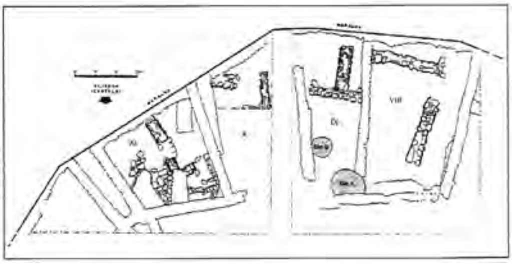

FIGURE 3

Location of structure A (silo) in the excavated area. Structures from Muslim times are represented with their respective stone elements drawn. Compartments VIII to XI (schematically represented) are late-medieval and should belong to a cantonment (Silva & Gomes, 2002: fig. 3).

The filling of this structure represent a rapid episode given that no levels of interrupted sedimentation were reported (i.e. films of fine-grained deposits), and the bone remains were found throughout the whole deposit.

MATERIALS AND METHODS

All specimens were retrieved by hand as no sieving operations were carried out during the excavations. Identifications were carried out with the help of the reference collection housed at the *Laboratório de Arqueociências* (LARC) of the DGPC in Lisbon, Portugal. These were additionally assessed with the help of the pertinent literature (e.g. Ellenberger, 1901; Schmid, 1972; Popesko, 1986; Cohen & Serjeantson, 1996; Goldfinger, 2004).

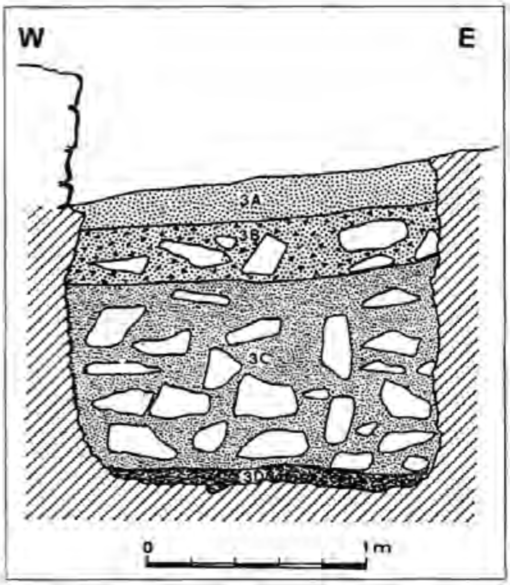

FIGURE 4

Stratigraphy of structure A (Silva & Gomes, 2002: fig. 5).

To estimate abundances, the number of specimens (NSP), number of identified specimens (NISP), minimal number of elements (MNE) and minimal number of individuals (MNI) were calculated following the protocols and limitations discussed by Valente (1997) and Lyman (2008). The number of unidentified specimens has been referred to as NUSP. Other symbols used in the text and tables appear in Table 1.

Butchery marks were grouped into 10 categories (i.e. hacked/chopped; cut; sawed; percussion/blow; torsion; flexion; scrape; puncture: polish; pathology; see Reitz & Wing, 2008:127). Fractures were grouped into 6 categories (i.e. transverse; oblique; spiral; columnar/stepped; splintered; regular; irregular; see Reitz & Wing, 2008: 169).

Taxa were allocated to four size classes, namely: very small (e.g. Muridae); small [e.g. Leporidae and Felidae]; medium (e.g. Canidae, Suidae and Caprini), and large (e.g. Cervidae and Equidae).

RESULTS AND DISCUSSION

The faunal assemblage from structure A offered an NSP = 1478, for an NISP = 811 (i.e. ≈55% of the NSP). Almost 90% of the NISP (i.e. 724 re-

	Symbol	REFERS TO
General	Indet.	Indeterminate
	N/a	Not applicable
Side	R	Right
	L	Left
	Up	Upper
	Low	Lower
	A	Anterior
	P	Posterior
Gender	M	Male
	F	Female
Bone Portions	+	Present
	(+)	Present but incomplete
	–	Absent
Quantification	NSP	Number of specimens
	%NSP total	% relative to the total NSP of the assemblage
	NISP	Number of Identified Specimens
	%NISP total	% relative to the total NISP of the assemblage
	MNE	Minimal number of elements
	MNI	Minimal number of individuals
	%MNI total	% relative to the total MNI of the assemblage

TABLE 1

Codes used in this paper.

mains) derived from mammals (Table 2). The only non-mammalian taxa were the chicken (*Gallus gallus domesticus*), the Iberian pond turtle, *Mauremys leprosa,* and an undetermined species of the Genus *Bufo* in the case of amphibians. The rabbit (*Oryctolagus cuniculus*), representing ca. 70% of the NISP, was the dominant taxon (MNI= 55 for a combined total of 81) (Figure 5). Red deer (*Cervus elaphus*) represented an additional 10% of the NISP and the pond turtle a further 6%. The remaining 14% of the NISP was represented by marginal taxa none of which exhibited MNIs above 4 (Figure). The NUSP (45%) was mainly represented by splinters from two size categories (i.e. small/medium-size and medium/large-size) that apparently represented remains of ungulates and lagomorphs for the most part.

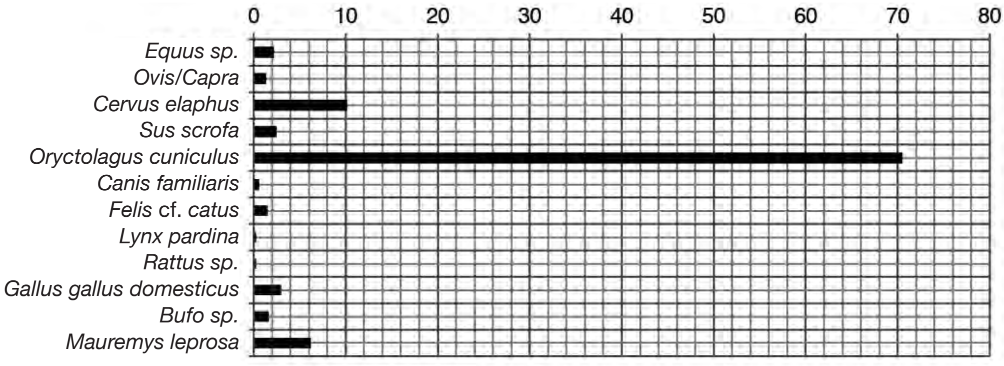

FIGURE 5

NISPs of the identified taxa expressed as percentage of the total NISP.

Taxon/Skeletal portion		Structure A										
		NSP				NISP				MNI		
		#		%NSP total		#		%NISP total		#	% NSP	%MNI total
Mammals	*Equus sp.*	18	799	1.2	54.1	18	724	2.2	89.3	4	22.2	4.9
	Ovis/Capra	11		0.7		11		1.4		2	18.2	2.5
	Cervus elaphus	82		5.5		82		10.1		3	3.7	3.7
	Sus scrofa	20		1.4		20		2.5		2	10.0	2.5
	Oryctolagus cuniculus	572		38.7		572		70.5		55	9.6	67.9
	Canis familiaris	5		0.3		5		0.6		1	20.0	1.2
	Felis cf. *catus*	12		0.8		12		1.5		1	8.3	1.2
	Lynx pardina.	2		0.1		2		0.2		1	50.0	1.2
	Rattus sp.	2		0.1		2		0.2		1	50.0	1.2
	Vertebrae *(medium)*	12		0.8		N/a		N/a		N/a	N/a	N/a
	Ribs *(medium or large)*	63		4.3		N/a		N/a		N/a	N/a	N/a
Birds	Gallus gallus domesticus	24		1.6		24		3.0		3	12.5	3.7
Anphibians	*Bufo sp.*	13		0.9		13		1.6		4	30.8	4.9
Reptiles	*Mauremys leprosa*	50		3.4		50		6.2		2	4.0	2.5
Medium or large sized vertebrates		234		15.8		N/a		N/a		N/a	N/a	N/a
Small or medium sized vertebrates		213		14.4		N/a		N/a		N/a	N/a	N/a
Anatomical remains	Mammal scapula	1		0.1		N/a		N/a		1	100.0	1.2
	Bird sternum	1		0.1		N/a		N/a		1	100.0	1.2
Unidentified specimens		143		9.7		N/a		N/a		N/a	N/a	N/a
Total		1478		100.0		811		100.0		81	5.5	100.0

TABLE 2

Castle of Aljezur: Overview of remains.

The Aljezur assemblage was intensively fragmented and this contributed to raise the number of unidentified specimens. Within the identified fraction, anthropic activities revealed butchery, cooking and consumption. Butchery marks with cleavers and knives, aimed at disarticulating carcasses and remove the meat, were abundant and particularly visible on the larger mammal remains. These activities to no small extent explain the degree of fragmentation that the sample exhibited. Activities reflecting hunting or secondary uses of animals, on the other hand, did not leave clear evidences. On the unidentified specimens no modifications that differed from those already mentioned were evident but the extent of a fragmentation that generated oblique fractures in fresh bone to reach to the medullar cavity again testified to an intensive use of the carcasses (Heinrich, 2014). No carbonization on the surface of any bone was recorded. In general, it can be said that these traces and the activities one may infer from them are similar to those proposed by Antunes (1996), Cardoso (1995), Gomes & Cardoso (1996) and Cardoso & Fernandes (2012) where first of all meat was stripped of bones, then boiled. Such interpretation requires culinary artifacts to be confirmed (Gomes & Cardoso,1996).

Modifications due to biological agents (e.g. bite marks, etc.) were present but infrequent and no mark of abiotic origin, as would be the case of diagenesis, appeared to have been relevant.

DESCRIPTIVE BY GROUP

Equids (*Equus* Linnaeus, 1758)

It is possible to distinguish between horse and donkey by the size and morphology of the pattern of wear of the flexids between the enamel and the dentine, but the state of preservation of the molar/premolar teeth from Aljezur precluded a clear-cut species identification. This distinction is also possible through the metapodials and the 1st phalange, which tend to be more robust in horse (Davis *et*

Ref.	Description				Quantification		
	Anatomy	Side	Cohort	Gender	NISP	MNE	MNI
1	Milk incisor (i_1/i^1?)	Indet.	Infant-juvenile	Indet.	1	1	4
2-3	Premolar/molar	Indet.	Indet.	Indet.	2	1	
4	Scapula	L	Infant-juvenile	Indet.	1	1	
5	Metacarpal	R	Infant-juvenile	Indet.	1	1	
6-8	Femur	R	Infant-juvenile	Indet.	3	3	
9		Indet.	Indet.	Indet.	1		
10	Tibia	R	Subadult-adult	Indet.	1	1	
11		L	Subadult-adult	Indet.	1	2	
12		L	Infant-juvenile	Indet.	1		
13	Metatarsal	R	Subadult-adult	Indet.	1	1	
14	Knee-cap	L	Indet.	Indet.	1	1	
15-16	Calcaneum	L	Infant-juvenile	Indet.	2	2	
17	1st phalanx	L	Subadult-adult	Indet.	1	2	
18		Indet.	Indet.	Indet.	1		
Total					18	16	

TABLE 3

Equids (*Equus* sp.): Overview of remains.

al., 2008: 198). In the phalanges, biometry can be particularly useful when one combines measure GL (greatest length), SD (smallest breadth of the diaphysis) and BFd (breadth of the distal diaphysis) (Driesch, 1976). In our study, the preservation and number of specimens precluded a conclusive answer on the determination issue. Lastly, according to Davis *et al.* (2008: 198), to separate equid species one calculates the BFd/GL x 100 value and plots this index vs. SD. Horse should have an SD > 30 mm thus a BFd/GL x 100 < 49. The value of SD = 33 for specimen 17 in our collection, could thus represent a horse (*vide* Mota, 2014). Although overall this assemblage could not be identified to species level due to the absence of the pertinent elements, the size and shape of the phalanges and metatarsals suggest that the species present might have been *E. caballus.*

The equids (*Equus* sp.) were represented by 18 specimens (*ca.* 2% of the NISP) and an MNI=4 (3 infantile/juvenile, on account of the three right femora, and an adult) (Table 3). In terms of age estimations, specimens were allocated into broad age classes (i.e. cohorts). Infantile and juvenile were broadly determined through the presence of a scapula, a metacarpal, 3 femora, one tibia and two calcanei exhibiting porous surfaces, absence of epiphyseal fusions (tibia), lack of the distal tuberosity (calcanei). The presence of a milk incisor (less elongated morphology and underdeveloped root) completed the assemblage of non-adult specimens.

In terms of bone modifications, those associated with carcass butchery were the most prevalent, with some cases of intense manipulation of the specimens (e.g. metatarsal, femur), leaving a significantly striated surface (Table). Some fractures suggested torsion and flexion of the bones after impact, while others simple percussion without butchery marks (e.g. scapula). One of the femora featured a groove and prominence that have been interpreted as a healed wound. The abundance of certain limb bones, mostly represented by 1-2 specimens per element and of butchery marks on these and certain vertebrae, suggest hypophagy thus also

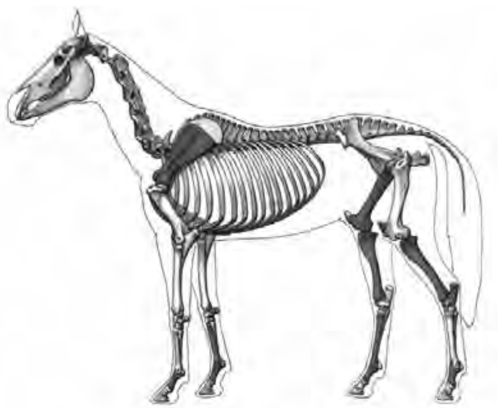

FIGURE 6

Horse skeleton highlighting the elements identified at Aljezur (taken from Goldfinger, 2004).

Element	Butchery Marks				Other
	Chop	Cut	Torsion	Flexion	Pathology
Mandible	2/4	-	-	-	-
Atlas	-	1/1	-	-	-
Axis	-	1/1	-	-	-
Cervical V.	-	2/2	-	-	-
Ulna	2/2	-	-	2/2	-
Radius	1/1	-	-	1/1	-
Metatarsal	3/6	-	2/6?	2/6?	1/6

TABLE 4
Butchery marks recorded on the equid bones.

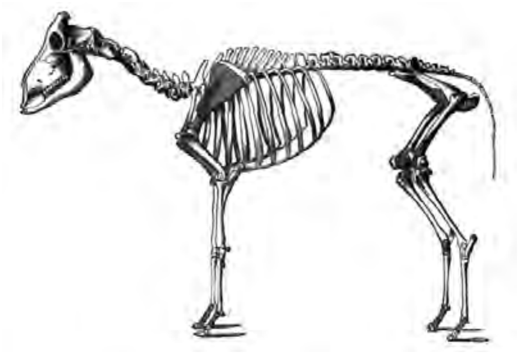

FIGURE 7
Sheep skeleton highlighting the elements identified at Aljezur (taken from Chauveau, 1857).

that these elements were probably selected for their food value (Figure 6; Table 4). Elements of lower meat value, such as metacarpals and phalanges, were also dismantled, as the chop marks and fragmentation patterns (flexion, torsion, percussion) suggest (Figure 26 on the Appendix). Cut marks and scrape marks, on the other hand, are most likely due to skinning and flesh stripping operations.

In connection with hypophagy, the study by Ramalho *et al*. (2001) mentions the importance given to juvenile horse meat for consumption in the Islamic world and this coincides with the cohort structure of this assemblage. Davis (2006: 41) also mentions that, in Islamic culture, whereas mule and ass meat was only consumed in times of famine, consumption of horse meat was not taboo. He also stresses the fact that horse meat was also given to hounds and dog packs during their days of rest, probably in the belief that, by virtue of it being considered a vigorous food, it would make the dogs stronger. This might explain the marks observed in the metatarsal and in one of the femora, where the dense groove/striated pattern appears coincident with biting made by a carnivore (dog?).

Sheep (*Ovis aries* Linnaeus, 1758) and Goat (*Capra hircus* Linnaeus, 1758)

Caprines were represented by 11 specimens (1,4% of NISP) (Table 5; Figure 7). The MNI and age determination were estimated via two isolated molars (Figure) and revealed two specimens aged 1-2 and 4-8 years, respectively (Payne 1973; Grant 1982).

Although pioneer studies on the identification of caprines, such as those of Boessneck (1969) and Payne (1973), are based on non-iberian materials

Ref.	Description								Quantification	
	Anatomy		Side	Cohort				Gender	NISP	MNI
-	Cranial skeleton	M3	-	Payne (1973)	Grant (1982)	#	General	-	-	2
19			Low. L	G-H	g	4-8 years	Adult	Indet.	1	
20			Upp. L	n/a	n/a	ind.	Adult	Indet.	1	
21		M2	Low. R	D	d-e	1-2 years	Subadult	Indet.	1	
22-23	Apendicular skeleton	Scapula	R	Subadult - adult				Indet.	2	
24-25			L	Subadult - adult				Indet.	2	
26		Astragalus	R	Subadult - adult				Indet.	1	
27		1st phalanx	L	Subadult - adult				Indet.	1	
28			R	Subadult - adult				Indet.	1	
29		2nd phalanx	R	Subadult - adult				Indet.	1	
Total									11	

TABLE 5
Sheep/goat *(Ovis/Capra)* Overview of remains

FIGURE 8

Caprine mandibular teeth: Right M2 (left); Left M3 (middle); Left M3 (right).

and studies in Portugal by have revealed important morphological variation in sheep and goat during Islamic times Davis (2008), at Aljezur, sheep/goat remains were of poor quality thus the distinction between species was essentially based on the method of Boessneck (1969), regarding the morphology of the astragalus (Figure), which is not always conclusive. The absence of horns and metapodials, and the small size of the assemblage did not contribute to raise the level of certainty. Thus, although the morphology and biometry of an astragalus (GLm=30,1 mm; GLi=31,6 mm) was coincident with a sheep, it is possible that also goat was present in these deposits.

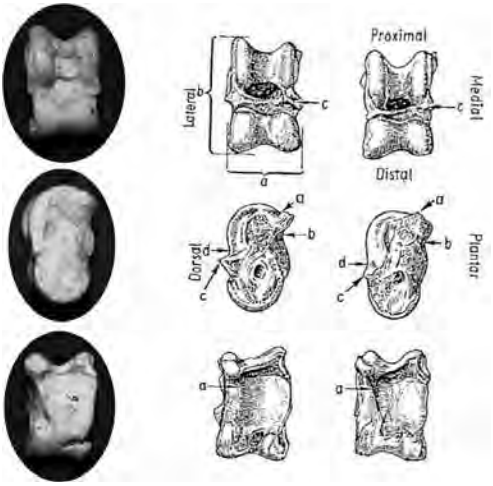

FIGURE 9

Caprine astragalus compared with specimens from goat (left) and sheep (right) (taken from Boessneck, 1969).

In the context of Aljezur, as expected for a fortification, the importance of caprines seems to be related with the consumption of meat (specimen aged 1-2 years), also considering the butchered bones of high food value, such as the scapulae. Indeed, in terms of bone modifications, only the scapulae exhibited meaningful marks. The butchering process here left regular fragmentation surfaces related to deep cuts (i.e. chop marks) made by some kind of cleaver, as well as superficial cut marks near the glenoid fossa and along the cranial and caudal edges of the blade. These seem to be related to skinning and/or defleshing operations. But the older specimen, above 4 years of age, speaks of a secondary use of caprines of a yet undetermined nature (milk, wool? cheese?).

Red deer **(***Cervus elaphus* Linnaeus, 1758)

Red-deer is represented by 82 specimens (10% of the NISP) (Table 6). The most numerous remains were those from antlers, that allowed for a straightforward identification (Lister, 1996) (Figure 10; see also Figure 27 on the Appendix). At least 3 individuals were represented, namely two adult males (2 right burrs) and one infantile. The infant was aged from a mandible and the eruption stage of its milk teeth. The *in situ* teeth were p_2 and p_3, but the crypt of the permanent M_1, the first perma-

FIGURE 10

Red deer skeleton highlighting the elements identified at Aljezur (taken from Lydekker, 1894).

Ref.	Description						Quantification		
		Anatomy	Side	Cohort		Gender	NISP	MNE	
30-32	Cranial skeleton	Antler	R	Subadult - adult		M	3	2	3
33-39		Antler (tine)	Indet.	Subadult - adult		M	7		
-		Antler splinters	Indet.	Subadult - adult		M	61	Indet.	
-		Mandible		Azorit et al. (2002)	General	-	-	-	
40			L	4 - 5 months	Infantile	Indet.	1	2	
41				Indet.	Subadult - adult	Indet.	1		
42	Apendicular skeleton	Pelvis	R	Subadult - adult		Indet.	1	1	
43-44			L	Subadult - adult		Indet.	2	2	
45		Femur	R	Subadult - adult		Indet.	1	1	
46		Tibia	R	Infantile-juvenile		Indet.	1	1	
47-48		Metacarpal	L	Subadult - adult		Indet.	2	2	
49		Metatarsal	L	Subadult - adult		Indet.	1	1	
50		1st phalanx	AL	Subadult - adult		Indet.	1	1	
Total							83	13	

TABLE 6

Red deer *(Cervus elaphus)*: Overview of remains.

nent tooth to erupt, was also evident (Azorit *et al*., 2002). According to these authors, this individual should have been 4 to 5 months old. The state of preservation of a second mandible doesn't allow for a precise determination of age.

The two specimens that could be measured were the metatarsal (Bd = 41.8 mm; Dd = 26.7 mm) and the first phalanx (GLpe = 55.3 mm; Bp = 20.2 mm; Bd = 18.6 mm; Bm = 16,2 mm; Dp = 25.2 mm; Dd = 15.7 mm).

In terms of bone modifications, butchery marks done with a cleaver are the most frequent category, particularly evident on both the articulations and diaphyses of the major limb bones (esp. metapodials), where they left regular and irregular fragmentation surfaces. Superficial cut marks were occasionally observed (Table). Antlers show considerable fragmentation and seem to have been involved in an intense dismantling (chop marks), percussion and flexion process aimed at removing the tines. Superficial cutmarks and scrape marks again reflected skinning and meat removal operations.

The presence of an infantile individual in this assemblage is worth remarking as the stage of the milk teeth indicated that this foal had been hunted intentionally. Could it be that, as was the case with horses at Aljezur, the tender meat of deer young was a sought after commodity? Since this was a 4-5 months old individual, in this species the rut ranges from the end of August until early November, and the gestation period of Red deer lasts for 210-250 days, this animal must have been born in the Spring or early Summer and killed around either late Summer or Autumn (Hutchins & Olendorf, 2004). As for adults, one of the antlers should have at least 4 tines on each side, indicating more than 3 years of age, which suggests an adult in its prime and a significant amount of meat. Beyond representing a food source, the hunting of red deer in this castle, as was the norm throughout medieval Iberia both for Christians and Muslims alike, may reflect a hunting not just related to meat procurement but also as training for the warriors stationed on the castle (Cardoso, 1995). One way or the other, this community had no particular interest in antlers as trophies, as suggested by the intensive butchery marks left on them and their discard in an offal deposit.

Element	Butchery Marks				
	Chop	Cut	Blow	Flex.	Scrap.
Antler	6/71	-	Indet.	Indet.	-
Mandible	-	-	1/2?	-	-
Pelvis (ilium)	1/3	1/3	-	-	-
Femur	-	1/1	-	-	-
Tibia	1/1?	-	-	1/1?	-
Metacarpal	1/2	1/2	-	2/2	1/2
Metatarsal	1//1	1/1	-	1/1	-
1st phalanx	-	-	-	-	-

TABLE 7

Butchery marks recorded on the red deer bones.

Suids (*Sus scrofa* Linnaeus, 1758 and *Sus* sp.)

Suids were represented by 20 specimens (2,5% of the NISP) (Table 8). The MNI=2 was obtained through the presence of left specimens from the 3rd metatarsal and the ulna. Based on size differences in the ulnae and canines these two were adult animals, probably a male and a female.

Although the size of the canines (Figure 28 on the Appendix) confirmed the presence of wild boar, most remains appeared to represent the agriotype and no domestic pig remain could be positively identified, the presence of the domestic variety should not be excluded despite the context being exclusively Islamic. The osteometric and odontometric distinction made by Payne & Bull (1988) between wild boar and domestic pig cannot be reliably applied in our case as suids from the Iberian Peninsula, wild and domestic alike, show a distinct morphology. Likewise, the specimens from Aljezur didn't allow for a comparison with the data of Albarella *et al*. (2005) as the scarce measurable specimens did not provide a clear distinction between domestic and wild (Table).

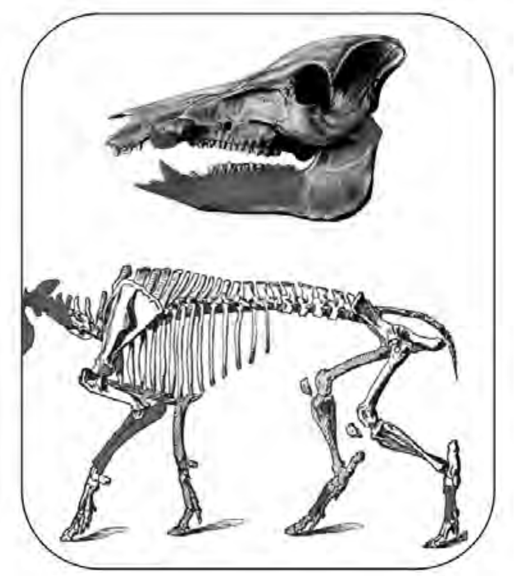

FIGURE 11
Wild boar skeleton highlighting the elements identified at Aljezur (taken from Lydekker, 1894).

The distinction between wild and domestic is important here as the presence of boar evidenced

Ref.	Description					Quantification		
	Anatomy		Side	Cohort	Gender	NISP	MNE	MNI
51	Cranial skeleton	Mandible	R	Adult	Indet.	1	1	2
52					M	1		
53			L	Adult	F	1	1	
54					Indet.	1		
55		Canine	Upper	Adult	M	1	1	
56			Indet.	Subadult - adult	F	1	1	
57		Incisor	Indet.	Subadult - adult	Indet.	1	1	
58	Axial skeleton	Atlas	N/a	Subadult - adult	Indet.	1	1	
59		Axis	N/a	Subadult - adult	Indet.	1	1	
60		3rd cervical v.	N/a	Subadult - adult	Indet.	1	1	
61		4th cervical v.	N/a	Subadult - adult	Indet.	1	1	
62	Apendicular skeleton	Ulna	L	Subadult - adult	Indet.	1	1	
63				Adult	Indet.	1	1	
64		Radius	L	Adult	Indet.	1	1	
65-66		metatarsal III	R	Subadult - adult	Indet.	2	2	
67			L	Subadult - adult	Indet.	1	1	
68		Metatarsal IV	R	Subadult - adult	Indet.	1	1	
69			L	Subadult - adult	Indet.	1	1	
70		Metatarsal V	R	Subadult - adult	Indet.	1	1	
Total						20	18	

TABLE 8
Wild boar: Overview of remains.

Ref.	Element	Measurement						
		H	BFcr	GL	LeP	Bp	B	Bd
58	Atlas	64.9	67.2	N/a	N/a	N/a	N/a	N/a
65	Metatarsal III	N/a	N/a	94.9	91.5	17.1	15	19.9
66		N/a	N/a	-	-	18.4	16.5	-
67		N/a	N/a	-	-	18.7	-	22
68	Metatarsal IV	N/a	N/a	103.8	98.7	18.4	15	19.2
69		N/a	N/a	104.1	101.7	18.9	14.8	19.7

TABLE 9

Biometry of the atlas and metatarsals of wild boar (measurements taken from Driesch, 1976).

hunting, not stockbreeding. Hunting would not only indicate training of warriors as previously postulated for red deer, but also consumption. Indeed, the butchery marks left on several of these bones (see below) suggested meat consumption, and whereas pork is forbidden to Muslims by their religion, wild boar is consumed under certain circumstances (Cardoso, 1995). At Aljezur the impression conveyed is that the Quran prohibition of pork consumption might have been taken more flexibly than at places such as Mértola (Antunes, 1996) and Almodôvar (Cardoso, 1995), and this might simply imply different interpretations of the rule. But other alternatives might exist. Since the remains of suids are scarce, it seems clear that, if at all consumed, this may not reflect Muslims who didn't abide Quranic rules, as Almohads in particular were good observers of the rules, but that, at some point, the community, in the face of starvation, could have consumed wild boar. One also needs to contend with the possibility of a culturally mixed deposit with Christian influence (Pereira, 2014). In the castle from Palmela it was possible to set apart the differences between the Christian and Muslim food patterns through the presence and absence of suids remains (Cardoso & Fernandes, 2012). But taking suid remains as proxies of cultural food patterns may not always work. This was the case of roman city of Conimbriga in Central Portugal, where the differences between the late roman and the Muslim levels were not evident probably due to the presence of an important Mozarabic community at the time the Muslims ruled the city (Detry *et al*., 2014).

As said, bone modifications (Table 10) exhibited a predominance of butchery marks with cleavers. These marks were most often recognized as deep cuts or impact zones close to the articulations (e.g. metatarsals) and by regular fragmentation surfaces (e.g. ulnae). They also suggested flexion of the bones on the cut zone that generated either stepped or irregular fragmentation surfaces. The cervical vertebrae featured very superficial marks of difficult interpretation, that may be due to damage done during excavation. In terms of pathologies only specimen 67 featured a bone thickening of the diaphysis probably reflecting inflammation.

Element	Butchery Marks						
	Chop	Cut	Saw	Blow	Tors.	Flex.	Scrap.
Mandible	2/4	-	-	-	-	-	-
Atlas	-	1/1	-	-	-	-	-
Axis	-	1/1	-	-	-	-	-
Cervical v.	-	2/2	-	-	-	-	-
Ulna	2/2	-	-	-	-	2/2	-
Radius	1/1	-	-	-	-	1/1	-
Metatarsal	3/6	-	-	-	2/6?	2/6?	-

TABLE 10

Butchery marks on wild boar bones.

Dog (*Canis familiaris* Linnaeus, 1758)

The dog (*Canis familiaris*) was represented by 5 specimens (0,6% of the NISP) that could have belonged to one individual (Figure 12; Table 11). The intense wear of the mandibular teeth revealed an individual of considerable age, possibly a senile (Figure 13). This appears to be a more likely condition in a domestic animal than in an animal living in the wild. In fact, keeping animals to an old age is often taken as evidence of a strong bond existing between a beast and its owner.

The distinction between wolf and dog was carried out with the biometric data on the M_1 pro-

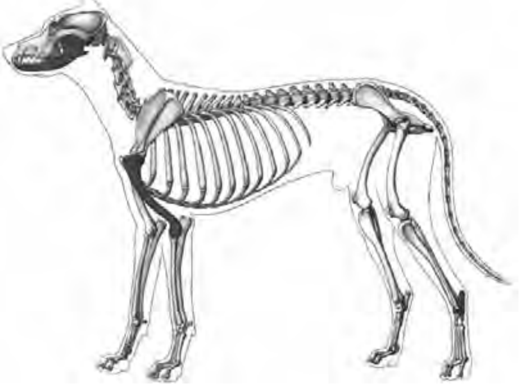

FIGURE 12

Dog skeleton highlighting the elements identified at Aljezur (taken from Goldfinger, 2004).

Ref.	Description				Quantif.	
	Element	Side	Cohort	Gender	NISP	MNI
643	Mandible	R	Senile	Indet.	1	1
644	Canine	R	Indet.	Indet.	1	
645	Humerus	L	Indet.	Indet.	1	
646	Astragalus	L	Indet.	Indet.	1	
647	Calcaneum	L	Indet.	Indet.	1	

TABLE 11

Dog *(Canis familiaris)*: Overview of remains.

vided by Detry & Cardoso (2010). This dataset shows that the M_1 of Portuguese wolves exhibit lengths at the crown ranging between 24-30 mm, the width ranging between 9,5-13,5 mm (Figure). The M_1 on the mandible specimen from Aljezur (Table 12) had a length of 24 mm and a width of 10 mm. Although both values fall within the lowermost boundary for wolf, the archaeological context and old age of the specimen make it more likely that this individual represented a large breed of dog of the kind that were normally used to hunt large animals (a molosser, such as the mastiff). Indeed, in view of the scarce representation of caprines at Aljezur, one may consider that a sheepdog would be a far less likely alternative.

FIGURE 13

Right mandible of *Canis familiaris*.

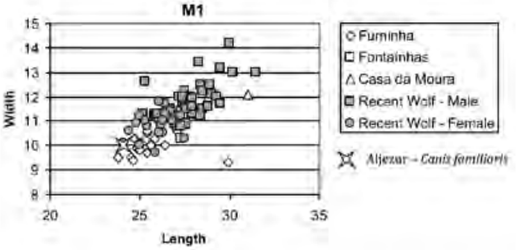

FIGURE 14

Length and width of the lower carnassial (M_1) from the canid mandible at Aljezur plotted against values of female and male Portuguese wolves, *Canis lupus* (Adapted from Detry & Cardoso, 2010).

Domestic Cat (*Felis* cf. *catus* Linnaeus, 1758)

Small felids were represented by 12 specimens (1,5% of the NISP) for an MNI = 1 that, on account of the archaeological context and age of most specimens, have been parsimoniously attributed to the domestic cat with reservations (Table 13).

The distinction between wild and domestic cat at Aljezur was complicated because of the comparatively large number of infantile/juvenile specimens that lacked the epiphyseal fusion in bones such as the humeri and femur (Table 13). This fact precluded clear cut comparisons with adults and also through biometrical means.

Measurements, in particular the height behind the carnassial (M_1; measurement 9), were taken on the mandibles (Table xx). These evidenced a developing mandible with teeth still growing. Compared with the data from Davis *et al.* (2008), measurements taken on M_1 (i.e. measurements 6a and 6b), with values of 8,8 mm (length) and 4,2 mm (width) were placed in the area of *F. silvestris* (*vide* Mota, 2014). The length measurements of the P_3-M_1 toothrow, with values of 21,9 mm and 20,6 mm, plotted closer to the overlapping zone between *F. catus* and *F. silvestris*, (*vide* Mota, 2014). The Pleistocene data from Portugal (Cardoso, 1993:

Canis familiaris	Measurement (mm)																				
	1	2	3	4	5	6	7	8	9	10	11	12	13a(L)	13b(W)	14	15	16	17	18	19	20
Driesch (1976)	-	-	-	-	-	-	-	82.2	75.8	39.2	41.9	36.7	24.0	10.0	-	-	-	-	-	29.6	24.6
Detry & Cardoso (2010)	-	-	-	-	30.1	23.9	-	26.4	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 12

Biometry of the dog mandible from Aljezur [measurements taken from Driesch (1976) and Detry & Cardoso (2010)].

Ref.	Description						Quantification	
	Element		Side	Epiphysal fusion	Cohort	Gender	NISP	MNI
602	Cranial skeleton	Mandible	R	N/a	Infantile-juvenile	Indet.	1	1
603			L		Infantile-juvenile	Indet.	1	
604	Apendicular skeleton	Scapula	R	Complete	Infantile-juvenile	Indet.	1	
606		Humerus	R	Absent	Infantile-juvenile	Indet.	1	
607			L	Absent	Infantile-juvenile	Indet.	1	
608		Ulna	R	Complete	Infantile-juvenile	Indet.	1	
609		Radius	R	Complete	Infantile-juvenile	Indet.	1	
610			L	Complete	Infantile-juvenile	Indet.	1	
611		Femur	Indet.	Absent	Infantile-juvenile	Indet.	1	
614		Calcaneum	R	Complete	Indet.	Indet.	1	
615		Metatarsal IV	L	Indet.	Indet.	Indet.	1	
616		Metatarsal V	L	Indet.	Indet.	Indet.	1	
-	Total						12	

TABLE 13
Cat *(Felis sp.)*: Overview of remains.

Ref.	Element	Side	Measurement (mm)										
			1	2	3	4	5	6a (L)	6b (B)	7	8	9	10
602	Mandible	Right	-	-	46.8	44.6	21.9	8.8	4.2	9.8	-	10.2	11.1
603		Left	54.2	52	47	44.7	20.6	8.8	4.2	8.9	21.5	10.5	-

TABLE 14
Biometry of the mandibles of *Felis* sp. from Aljezur (measurements taken from Driesch, 1976).

429) for the maximum length of the mandible (measurement 1), P$_3$-M$_1$ toothrow (measurement 5) and height behind M$_1$ (measurement 9) are, in average, above those from the specimens of Aljezur evidencing that adult *F. silvestris* were larger in the Pleistocene. To sum up, although we are dealing with a non-adult specimen, it was a large individual thus the possibility exists that this animal might have been a wildcat, not a domestic cat.

But such conclusion does not gain weight when the general context is taken into consideration. In this way Pereira (2014: 5) comments on the fondness of Muslims for cats as pets by comparison to dogs, that would have had always more utilitarian uses. The presence of the wildcat (*F. silvestris*), of which hunting is documented in Muslim sites, on the other hand, may instead have reflected some kind of commensalism that seems unlikely on account of the nature of this species. What one cannot rule out is the hybridization of local wildcats

FIGURE 15
Domestic cat skeleton highlighting the elements identified at Aljezur (taken from Goldfinger, 2004).

FIGURE 16
Left and right mandibles of a cat.

with the domestic variety, in places where domestic animals were allowed to roam free outside of the urban environment. This fact alone is known to compromise the distinction between the two populations (Driscol & Nowell, 2010), as documented for domestic and wildfowl in Asia.

Iberian lynx (cf. *Lynx pardinus* Temminck, 1824)

The identification of a larger felid, represented by 2 specimens (0,2% of the NISP) for an MNI = 1, has been taken to represent the Iberian lynx but remains open given the number and preservation state of bones that didn't allow for any conclusive biometry to be carried out (Table 15). Particularly distressful was the lack of teeth that precluded a comparison with the data from Cardoso (1993: 436). The preserved portion of the mandible could still be measured at the cheek teeth alveolar zone, but it was poorly preserved, offering values of small significance (Figure 17).

Ref.	Description				Quantification	
	Element	Side	Age	Gender	NISP	MNI
617	Mandible	L	Adult	Indet.	1	1
618	Metacarpal IV	R	Adult	Indet.	1	
-	Total				2	

TABLE 15
Cat *(Felis sp.)*: Overview of remains.

Extinct in Portugal in very recent times and in opposition to the wild cat, lynx has been greatly affected by human presence. Absence of traces does not allow one to state if it was meat, rather than the fur what people were looking for when they hunted this individual.

FIGURE 17
Cranium of European lynx (Lynx lynx) highlighting the portion retrieved at Aljezur (taken from Heptner, 1992).

Rabbit (*Oryctolagus cuniculus* Linnaeus, 1758)

With 572 specimens rabbit represented *ca.* 70% of the NISP. Even in terms of NSP, it represented 40% of the whole assemblage, which is a high figure considering that rabbit bones were far less fragmented than those from other mammals. In terms of MNI this is also the largest assemblage (i.e. 55 individuals).

Despite the idea of complete individuals being present in the deposits, the anatomical spectra evidenced partial skeletons devoid of the smallest elements as would be the case of carpals, tarsals and phalanges (Figure 18; Table 16). This bias is undoubtedly due to the defective method of retrieval by hand. For such reason, the absence of these smaller elements cannot be taken at face value to indicate an anthropic selection of bones with a higher meat content as would be the case of the major limb bones (19). Vertebrae were very abundant but less so than mandibles that provided the minimum number of 55 individuals. The high frequency of mandibles may have been due to a combination of hardness and easy detection in the sediment. The specimens from the zonal skeleton (i.e. scapula and pelvis) tended to be slightly more frequent and the smaller elements tend to be completely absent.

The majority of these specimens represented adults, but some without epiphyseal fusion belonged to younger cohorts (subadult and juvenile). The absence of infantile specimens and the sealed nature of the deposit allow us to postulate that all

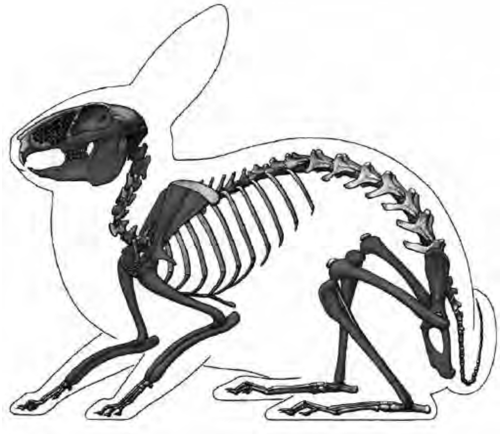

FIGURE 18
Rabbit skeleton highlighting the elements identified at Aljezur (taken from Goldfinger, 2004).

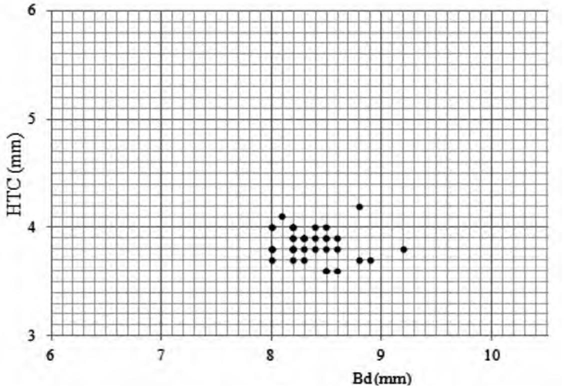

FIGURE 19

Humerus: Minimum diameter of the distal trochlea (HTC) plotted against the maximum breadth of the distal articulation (Bd) in rabbits from Aljezur.

these rabbits were accumulated as the result of human activity (i.e. hunting and consumption).

Given the number of specimens per element, the recognition of the portions from each element proved useful to estimate the MNE. In some cases, the NME did not equal the NISP because opposing portions of the same element might have belonged to the same specimen before it fragmented.

Most of the rabbit remains derived from adult/subadult individuals, thus it was easy to set them apart from remains of the Iberian hare (*Lepus granatensis*). To check further on this issue we compared two measurements taken on the distal humerus namely the minimum diameter of the distal trochlea (HTC) and the maximum breadth of the distal articulation (Bd) (see Davis *et al*., 2008). The analysis of the biometric data from 46 humeri revealed the sole species present in the samples to be *O. cuniculus* (Table 17; Figure 20). Although the obtained values were fully within the boundaries developed in Davis *et al.* (2008), the Bd were slightly higher (i.e. 8-9 mm *vs.* 7-8 mm). Such fact might be due to the measuring technique.

The abundance of rabbits is here taken to reflect the abundance of the species in the region.

Ref.	Description					Bone portion			Quantification		
	Element		Side	Gender	Cohort	-			NISP	MNE	MNI
71-82	Cranial skeleton	Cranium (Braincase)	R	Indet.	Subadult - adult	N/a			12	12	55
83-90			L	Indet.	Subadult - adult	N/a			8	8	
91-102		Upper jaw	R	Indet.	Subadult - adult	N/a			12	12	
103-117			L	Indet.	Subadult - adult	N/a			15	15	
-		Mandible				Articulation	Alveolar (molars/ premolars)	Alveolar (incisors)	-	-	
118-119			R	Indet.	Subadult - adult	(+)	-	-	2	55	
120-127						(+)	+	-	8		
128-174						(+)	+	+	47		
175						-	-	+	1		
176			L	Indet.	Subadult - adult	(+)	-	-	1	38	
177-178						(+)	(+)	-	2		
179-212						(+)	+	(+)	34		
213-214						-	(+)	+	2		
-		Premolar	Indet.	Indet.	Subadult - adult	N/a			36	36	
-		Incisor	Indet.	Indet.	Subadult - adult	N/a			4	4	
215-217	Axial skeleton	Atlas	N/a	Indet.	Subadult - adult	N/a			3	3	
218		Axis	N/a	Indet.	Subadult - adult	N/a			1	1	
219-289		Vertebra	N/a	Indet.	Subadult - adult	N/a			71	71	
290-294		Sacrum	N/a	Indet.	Subadult - adult	N/a			5	5	

Tabla 16 (continuación)

Ref.	Description					Element				Quantification		
		Element	Side	Ep. fusion	Cohort					NISP	MNE	MNI
295-324	Apendicular skeleton	Scapula	R	Total	Subadult - adult	N/a				30	30	55
325-346			L	Total	Subadult - adult	N/a				22	22	
-		Humerus				Prox. Art.	Proximal diaphysis	Distal diaphysis	Distal articulation	-		
347-351			R	Total	Subadult - adult	Complete				5	21	
352-361				Total	Subadult - adult	-	(+)	+	+	10		
362-364				Parcial	Juvenile/ subadult	Complete				3		
365-366				Ausente	Juvenile	Complete				2		
367				Ausente	Juvenile	+	+	+	-	1		
368-370			L	Total	Subadult - adult	+	+	(+)	-	3	25	
371-378				Total	Subadult - adult	Complete				8		
379-391				Indet.	Subadult - adult	-	(+)	+	+	13		
392				Ausente	Juvenile	Complete				1		
393-405		Ulna	R	Total	Subadult - adult	Complete				13	13	
406-418			L	Total	Subadult - adult	Complete				13	13	
419-426		Radius	R	Total	Subadult - adult	Complete				8	8	
427-431			L	Total	Subadult - adult	Complete				5	5	
-		Pelvis				Ílium	Articulation		Ísquium	-		
432-433			R	N/a	Subadult - adult	+	(+)		-	2	29	
434-460						(+)	+		(+)	27		
461-462						-	(+)		+	2		
463-464			L	N/a	Subadult - adult	+	(+)		-	2	22	
465-483						(+)	+		(+)	19		
484-486						-	(+)		+	3		
-		Femur				Prox. Art.	Diáfase proximal	Diáfase distal	Articulation o distal	-		
488-496			R	Total	Subadult - adult	+	(+)	-	-	9	17	
497						+	+	(+)	-	1		
498-502						Completo				5		
503						-	(+)	+	+	1		
504-507						-	-	(+)	+	4		
612				Ausente	Infantile/ juvenile	-	-	(+)	+	1		
508-515			L	Total	Subadult - adult	+	(+)	-	-	8	23	
516-522						Completo				7		
523						-	+	+	-	1		
524							(+)	+	+	1		
525-530						-	-	(+)	+	6		
531-533				Ausente	Infantile/ juvenile	+	(+)	-	-	3		
534						Completo				1		
613						-	(+)	+	+	1		
-		Tibia				Articulação proximal	Diáfise proximal	Diáfise distal	Articulação distal	-	-	
535-550			R	Total	Subadult – adult	+	+	(+)	-	16	21	
551-553						+	(+)	-	-	3		
554-557				Ausente	Infant-juvenile	+	+	(+)	-	4		
558-560						+	(+)	-	-	3		
561-569				Indet.	Indet.	-	(+)	(+)	-	9		
570-578			L	Total	Subadult - adult	+	+	(+)	-	9	25	
579-581						+	(+)	-	-	3		
582-587				Parcial	Juvenile	+	+	(+)	-	6		
588-590				Ausente	Infantile/juvenile	+	+	(+)	-	3		
591-600				Indet.	Indet.	-	(+)	(+)	-	10		
601		Metat. II	R	Total	Subadult - adult	Completo				1	1	
-		Total								572	535	

TABLA 16.
Rabbit *(Oryctolagus cuniculus)*: Overview of remains.

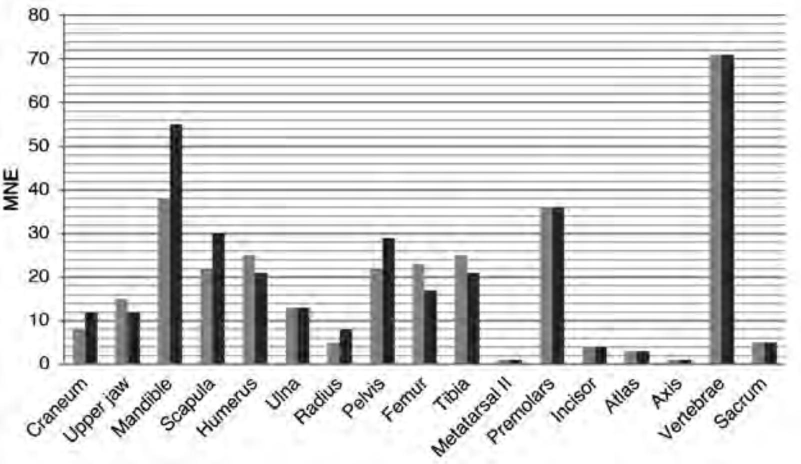

FIGURE 20

Anatomical distribution of O. *cuniculus* remains identified. The 2 columns for each element represent the left and right sides/portions of the element, respectively.

Ref.	Measurement (mm)		Ref.	Measurement (mm)	
	HTC	Bd		HTC	Bd
347	3.6	8.3	370	-	-
348	3.9	8.2	371	4.0	8.6
349	-	-	372	3.8	8.3
350	3.8	8.3	373	3.9	9.2
351	3.8	8.2	374	3.8	8.2
352	3.6	8.0	375	3.8	8.5
353	3.9	8.1	376	3.9	8.3
354	3.7	8.0	377	4.0	8.9
355	3.9	8.6	378	3.7	8.2
356	3.7	8.2	379	4.0	8.8
357	3.7	8.0	380	3.9	8.3
358	3.8	8.2	381	3.8	8.0
359	-	-	382	3.9	8.8
360	4.2	8.6	383	3.8	8.2
361	-	-	384	3.8	8.2
362	3.8	8.4	385	4.1	8.5
363	3.9	8.0	386	3.7	8.2
364	3.9	8.2	387	3.9	8.5
365	4.0	8.4	388	4.0	8.5
366	3.6	8.3	389	4.0	8.5
367	-	-	390	4.0	8.5
368	-	-	391	3.8	8.4
369	-	-	392	3.8	8.0

TABLA 17

Biometry of the rabbit humeri from Aljezur [measurements taken from Driesch (1976) and Davis *et al.* (2008)].

Rat (*Rattus* sp. G. Fischer, 1803)

This was one the less abundant taxa in this study with only 2 specimens (0,2% of the NISP) for an MNI of one (Table 18; Figure 21). The femur and pelvis could not be identified either as black rat (*Rattus rattus*) or brown rat (*Rattus norvegicus*), a far later intrusive species. Black rats were identified on the Almohad levels from Mertola (Morales & Rodriguez, 1997) so it is possible that this is also the species at Aljezur.

The complete epiphyseal fusion of the femur evidenced an adult individual (i.e. above 18 months).

FIGURE 21

Rat *(Rattus norvegicus)* skeleton highlighting the elements identified at Aljezur (taken, with modifications, from Van de Graaf *et al.*, 2012).

Ref.	Description				Quantification	
	Element	Side	Age	Gender	NISP	MNI
712	Femur	R	Adult	Indet.	1	1
487	Pelvis	L	Adult	Indet.	1	
-					2	

TABLE 18
Rat *(Rattus sp.)*: Overview of remains.

Chicken *Gallus gallus domesticus* Linnaeus, 1758

The domestic chicken was represented by 24 specimens (3% of the NISP) that the metatarsals indicated belonged to a minimum of 3 individuals (Figure 22; see also Figure 29 in the Appendix). These were all adults, and probably females as the metatarsals were devoid of spurs. The presence of hens suggests a primary emphasis on eggs, yet the cut marks documented on the coracoid evidence that use of the meat was also done.

The anatomical distribution, except for some major wing bones as is the case of the humerus, was restricted to the larger elements of the skeleton (Table 19). Although most of these bones have a high meat content the fact that most specimens were complete may simply reflect a retrieval bias of no further cultural connotation. As such, one cannot specify how the disarticulation of the carcasses took place.

FIGURE 21
Chicken skeleton highlighting the elements identified at Aljezur (taken, with modifications, from Coutureau, 2004).

Pond turtle (*Mauremys leprosa* Schwieegger, 1812)

The Pond turtle was represented by 50 specimens (6% of the NISP) most of which were plates (Table 20, Figure 23). A tentative MNI = 2 has been recorded on account of two almost complete plastrons that could be reconstructed (Figure 24; only a reconstruction of the upper carapace plates could confirm the validity of such MNI). This is still a substantial number of remains for an Iberian

Ref.	Description					Quantif.	
	Element		Side	Age	Gen.	NISP	MNI
619	Esqueleto axial	Clavicle	N/a	Adult	Indet.	1	3
620-622		Sternum	N/a	Adult	Indet.	3	
623		Thoracic vertebra	N/a	Adult	Indet.	1	
624-625		Lumbo-sacral vertebra	N/a	Adult	Indet.	2	
626	Esqueleto apendicular	Coracoid	E	Adult	Indet.	1	
627-629		Ulna	E	Adult	Indet.	3	
630		Metacarpal II + III	E	Adult	Indet.	1	
631-632		Pelvis	D	Adult	Indet.	2	
633			E	Adult	Indet.	1	
634		Femur	E	Adult	Indet.	1	
635-637		Tibia	D	Adult	Indet.	3	
638			E	Adult	Indet.	1	
639		Metatarsal	D	Adult	F	1	
640-642			E	Adult	F	3	
-	Total					24	

TABLE 19
Chicken *(G. gallus domesticus)*: Overview of remains.

Ref.	Description				Quantif.	
	Element	Side	Age	Gend.	NISP	NMI
661-662	Plastron	N/a	Adult	Indet.	2	2
663-707	Isolated plates	Indet.	Adult	Indet.	45	
708	Femur	L	Adult	Indet.	1	
709	Humerus	L	Adult	Indet.	1	
710		R	Adult	Indet.	1	
-	Total				50	

TABLE 20

Pond turtle *(Mauremys leprosa)*: Overview of remains.

archaeological site and, on account on the location of the castle, it would seem that these animals had been transported by people from the nearby "*ribeira de Aljezur*" which flows through the town below, rather than being intrusive or caught by people within the castle enclosure. There exist historical evidences for the consumption of pond turtles in late medieval contexts, the species being mentioned as a delicacy in Silves (Algarve, Portugal) (Cardoso & Gomes, 1996: 262). Muslims also seem to have appreciated this species.

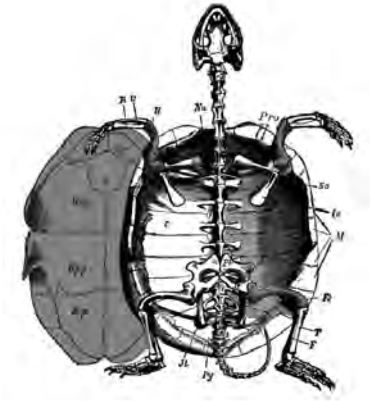

FIGURE 23

European pond turtle *(Emys orbicularis)* skeleton highlighting the elements identified at Aljezur (taken from Parker & Haswell, 1900).

FIGURE 24

Plastrons of Pond turtle *(Mauremys leprosa).*

Toad (*Bufo* sp. Laurenti, 1768)

The toad was represented by 13 appendicular bones (1,6% of the NISP) representing no less than 4 individuals on account of the number of pelves (Table 21; Figure 25). The identification of the genus *Bufo* is easy to carry out with the limb bones found at Aljezur due to the diagnostic traits that bones such as the tibio-fibula and radius-ulna feature. However, to determine the species (in this case either *B.bufo* or *B. calamita*) is far more difficult to accomplish.

Ref.	Description			Quantif.	
	Element	Side	Age	NISP	MNI
648	Urostyle	N/a	Adult	1	4
649-650	Pelvis (Ilium)	R	Adult	2	
651-654		L	Adult	4	
655	Femur	Indet.	Adult	1	
656	Tibio-fíbula	Indet.	Adult	1	
657-658	Humerus	R	Adult	2	
659		L	Adult	1	
660	Radio-ulna	Indet.	Adult	1	
	Total			13	

TABLE 21

Toad (*Bufo* sp.): Overview of remains.

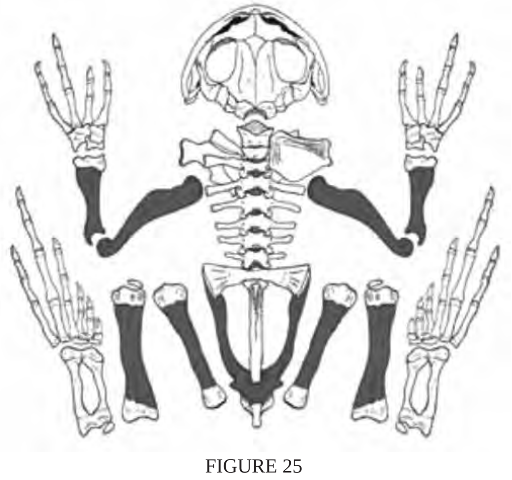

FIGURE 25

Frog (*Rana* sp.) skeleton highlighting the elements identified at Aljezur (taken from Kellogg, 1901).

Although the consumption of a toad debatable, one would think that the rocky hill where the castle rests does not appear to be a suitable environment for toads, thus one might feel prone to argue for human intervention of some kind to explain the presence of these animals in the assemblage. In fact, toads of the Genus *Bufo* are quite terrestrial outside their breeding season and also fond of occupying crevices in rocks. The castle would thus have been a perfectly acceptable environment for them and their nature as intrusives, as mentioned for the rat, seems as the most plausible hypothesis with the data at hand.

PALEOECOLOGY

Studies on faunas from Almohad sites in the Algarve region, as are the cases of Silves (Davis *et al.*, 2008), Mesas do Castelinho, Almodôvar (Cardoso, 1995) and the eastern Algarve (Catarino, 1997/98; Pereira, 2014) refer a woodland and scrubland that, on account of the presence of the same game species, in particular wild boar and red deer, seems to apply in general terms to the region of Aljezur but not quite. Indeed, both the presence of caprines and, to a smaller extent, of rabbits suggests the presence of more open lands including grasslands around the castle.

The Early Holocene (10-8 kya BP), was characterized in this region by a relatively wet climate that fostered a maximum development of woodlands (Pais, 2013). Pine forests of *Pinus pinaster* (cluster pine) and *P. pinea* (stone pine) covered most of the coastal and continental areas where, nowadays, evergreen oaklands (*Quercus* sp.) flourish (Pais, 2013). Probably most of these Mediterranean communities of pine forests managed to resist the advance of the oak forests until the onset of pastoral practices, in combination with the use of fire and a reduction of rainfall with its concomitant increase in seasonality, did away with many of them (Pais, 2013). Mining and naval construction from AD XV onwards also played their role in the demise of this woodland ecosystem, making the present day vegetation an unreliable proxy to interpret faunas from former times (Cardoso, 1995).

Barbosa (2000: 12) mentions that phyto-toponyms of places from southern Portugal help one to track down these changes, pointing out species typical of pastoral ecosystems since post-Reconquest (i.e. medieval) times. These would be the Portuguese terms that point out the presence of “carrasco” (*Quercus coccifera*), “sobreiro” (*Quercus suber*) and “zambujeiro” (*Olea europea*). But one does not know whether these names already existed in this region in the XII/XIII centuries.

SOCIOECONOMIC INFERENCES

For any reliable comparisons to be established among these Islamic sites, one first needs to assess the nature of the deposits themselves. At Aljezur castle, remains date from a short time window set between AD XII/XIII that probably reflects an essentially continuous deposition yet other Islamic sites from the Algarve not only date to far earlier times (e.g. AD VIII) but also feature wide temporal windows (centuries) with intervals between the archaeological deposits. Likewise, islamic peasants undoubtedly experienced different socio-economic pressures, depending on the time and region, from the ruling classes. The Reconquest fight between Muslims and Christians, for example, aggravated after the fall of Lisbon (1147), shortly before the Almohads invaded Iberia, and the fall of Aljezur itself, around 1249, that signalled the end of Islamic rule in Portugal, shortly after the Almohads left the Peninsula (Silvério, 2001: 22). Also relevant for comparative purposes is the fact that the bone accumulation at Aljezur suggests a more focalized provenience, restricted to a presumably upper class community, that would in principle not allow one to establish general qualifications of certain socioeconomic aspects, as could be done on deposits reflecting the activities of a larger sectors of society.

Be it as it may, the Aljezur faunal assemblage suggests the importance that hunting had in the lives of the castle inhabitants during Almohad times, with the hunting of red deer, wild boar and, in particular, rabbit complemented with secondary resources ranging from lynxes to pond turtles. We believe that, notwithstanding meat procurement, hunting was important here to train soldiers and noblemen alike. Taken as a whole, this faunal assemblage seems to reflect the presence of a dominant social class, in contrast with the situation in other Islamic sites (Antunes, 1996; Cardoso, 1995), seemingly in times of economical crisis. The hunting activity itself may have been carried only by those social strata capable of investing in such activity, which requires appropriate means. Such phenomenon is recorded since Roman times when hunting, as a leisure or social activity, became linked to the manorial status of the proprietors of hunting zones (Cardoso & Detry, 2005).

In the Islamic levels from Almodôvar hunting of red deer was particularly important as a means of subsistence, not leisure. At Mértola and Silves, urban contexts par excellence, an opposed tendency was recorded, with scarce hunting and stressing husbandry and pastoralism.

As mentioned by Antunes (1991), and was corroborated by Silvério (2001), it is possible that the absence of hunting at Silves is due to urban development coupled with an intensive farming in the region, that shunned game animals to peripheral forested areas, like those of Monchique and Aljezur though a study by Davis *et al*., (2008) on the suburbs of Silves at the AD XII/XIII boundary, revealed hunted species. This shows that it was the socio-economic contrivances of those communities, coupled with the availability of wild fauna in adjacent areas, what determined the characteristics of the faunal spectrum in each case,.

Noteworthy at Aljezur is the total absence of cattle (*Bos taurus*). This contrasts with the situation recorded on other Islamic assemblages as are those from Almodôvar (Cardoso, 1995), Mértola (Antunes, 1996), Silves (Antunes, 1991), and those evidenced by Pereira (2014). The contrast is revealing as cattle were a major item of the farmland economies in those times. Given the social status of the castle inhabitants, as also suggested by Catarino (1997/98: 748), it may be that the domestic animal component in this site is probably connected to tributes paid by the town of Aljezur to the ruling class.

CONCLUSIONS

There exist several constraints that render it questionable to draw definitive conclusions from the faunal assemblages from structure A at Aljezur. The first one is that this collection is not only rather small but also exhibiting an intensive fragmentation that dictated that almost half of the remains could not be identified. Likewise, with the exception of the rabbit, both the number of identified remains and the MNI were so small that one remains unsure on whether comparing abundances among taxa is a reliable or even methodologically sound exercise (e.g. the "large" sample of the pond tortoise is due to the presence of loose plates from the carapace that are not strictly comparable to the conventional skeletal elements of the vertebrate skeleton; Table 20). Lastly, although the deposit appeared to be closed and of a primary nature and no infantile rabbits were found that would question those characters, the retrieval of potentially intrusive taxa, as would be case of the rat and, possibly also, of toads warn us that contamination cannot be ruled out completely.

Such restraints notwithstanding, and despite their apparently conventional nature, the faunas from structure A are atypical for the region and time for several reasons. The first one was the relevance of hunting, not so much in the case of the rabbit as for the presence of large and (in the case of adult wild boars) dangerous animals. Coupled with it, and equally revealing, was the marginal character of the domestic species of which one needs to stress the total absence of cattle. This peculiar combination suggests that whereas hunted items might have been actively and routinely brought to the castle by the people inhabiting it, domesticates may reflect an indirect and more erratic route of arrival that one, at this point, can only speculate about (i.e. payment of tributes/taxes?).

Complementary data add to this scenario of a non-peasant society. In this way, the presence of infantile horses and red deer not only reveals a targeting on tender meat but also –in the case of colts- a deliberate choice to consume a meat that was highly esteemed in the Islamic world. The same goes for the pond turtle and chicken. Add to it the presence of pets, such as the cat, and that of a large, molossid-like, dog that was allowed to live until very old age (i.e. was probably protected by its owner until death) and one cannot escape the idea of an affluent sector of society that, on account of the cultural identity (Almohad) and occupation of a castle, one can postulate to be the ruling sector of that society.

If this was the case, then one must strive to find parallels of the structure A faunas in order to attempt meaningful interpretations, and none apparently exist. Indeed, most Islamic faunal deposits from the Iberian peninsula not only reflect the doings of the lower sectors of society but are often mixed and the faunal elements accumulated by Muslims, Christians, or Jews, next to impossible to set apart as of this writing (Morales *et al*. 2011).

ACKNOWLEDGMENTS

The authors would like to express their gratitude to Carlos Tavares da Silva for granting them the opportunity to study this collection.

REFERENCES

ALBARELLA, U.; DAVIS, S. J.; DETRY, C. & ROWLEY-CONWY, P. 2005: Pigs of the 'Far West': the biometry of *Sus* from archaeological sites in Portugal. *Anthropozoologica* 40(2): 27-54.

ANTUNES, M.T. 1991: Restos de animais no castelo de Silves (séculos VIII-X). Contribuição para o conhecimento da alimentação em contexto islâmico. *Estudos Orientais* 2: 103-144.

— 1996: Alimentação de origem animal em regime islâmico – Alcaria Longa e Casa II da Alcáçova de Mértola. *Arqueologia Medieval* 5: 267-276.

BARBOSA, P. 2000: *Aljezur: entre o Islão e a Cristandade*. Câmara Municipal de Aljezur.

BOESSNECK, J. 1969: Osteological differences between sheep (*Ovis aries* Linné) and goat (*Capra hircus* Linné). *Science in archaeology* 331: 58.

CARDOSO, J. L. 1993: Contribuição para o conhecimento dos grandes mamíferos do Plistocénico Superior de Portugal. Tese de doutoramento apresentada à FCT/UNL. Câmara Municipal de Oeiras, Oeiras.

— 1995: A fauna de mamíferos da época muçulmana das Mesas do Castelinho (Almodôvar). Materiais das campanhas de 1989-1992. *Arqueologia Medieval* 3: 201-220.

CARDOSO, J. L. & DETRY, C. 2005: A lixeira baixo-imperial da uilla da Quinta das Longas (Elvas): análise arqueozoológica e significado económico-social. *Revista Portuguesa de Arqueologia* 8(1): 369-386.

CARDOSO, J. L. & FERNANDES, I. C. 2012: A economia alimentar dos muçulmanos e dos cristãos do Castelo de Palmela: um contributo. *Arqueologia Medieval* 12: 211-244.

CARDOSO, J. L. & GOMES, M. V. 1996: Contributo para o estudo das faunas encontradas no poço-cisterna de Silves (séculos XV-XVI). *XELB* 3: 207-268.

CHAUVEAU, A. 1857: *Traité d'anatomie comparée des animaux domestiques*. JB Baillière et Fils, Paris.

CATARINO, H. 1997/1998: *O Algarve Oriental durante a ocupação islâmica: Povoamento rural e recintos fortificados*. *Al-Ulya*, *6*/2. Câmara Municipal de Loulé.

COHEN, A. & SERJEANTSON, D. 1996: *A manual for the identification of bird bones from archaeological sites*. Archetype Publications.

DAVIS, S. J. 2006: *Faunal remains from Alcáçova de Santarém, Portugal*. *Trabalhos de Arqueologia* 43. Instituto Português de Arqueologia, Lisboa.

— 2008: Zooarchaeological evidence for Moslem and Christian improvements of sheep and cattle in Portugal. *Journal of Archaeological Science* 35(4): 991-1010.

DAVIS, S. J.; GONÇALVES, M. J. & GABRIEL, S. 2008: Animal remains from a Moslem period (12th/13th century AD) lixeira (garbage dump) in Silves, Algarve, Portugal. *Revista Portuguesa de Arqueologia* 11(1): 183-258.

DETRY, C. & CARDOSO, J. L. 2010: On some remains of dog (*Canis familiaris*) from the Mesolithic shell-middens of Muge, Portugal. *Journal of Archaeological Science* 37(11): 2762-2774.

DETRY, C.; CARDOSO, J. L.; CORREIA, V. H. 2014: What did the Romans ans Moslems eatin Conimbriga (Portugal)? The animal bones from the 1990´s excavations. *Proceedings of the First Zooarchaeology Conference in Portugal (Lisbon, 2012)*: 97-110. B.A.R. (International Series) 2662.

DRIESCH, A. VON DEN 1976: *A Guide to the Measurement of Animal Bones from Archaeological Sites. Peabody Museum Bulletin 1. Peabody Museum of Archaeology and Ethnology*. Harvard University Press, Cambridge MA.

DRISCOLL, C. & NOWELL, K. 2010: *Felis silvestris*. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org>

ELLENBERGER, W.; DITTRICH, H. & BAUM, H. 1901: *Handbuch der Anatomie der Tiere für Künstler*. Dieterich'sche Verlag.

GOLDFINGER, E. 2004: *Animal Anatomy for Artists: The Elements of Form*. Oxford University Press, Oxford.

GOMES, M. V.; GOMES, R.; CARDOSO, J. L. 1996: Aspectos do quotidiano numa casa de Silves, durante o século XV. *XELB* 3: 33-78.

GOMES, R. V. & DA SILVA, C. T. 2002: Primeiros resultados das intervenções arqueológicas no Castelo de Aljezur. In: *Mil Anos de Fortificaçoes na Península Ibérica e no Magreb (500-1500): Simpósio Internacional sobre Castelos 2000 Castelos*: 347-356.

GRANT, A. 1982: The use of tooth wear as a guide to the age of domestic ungulates. *Ageing and sexing animal bones from archaeological sites* 109: 91-108.

HEINRICH, A. R. 2014: The Archaeological Signature of Stews or Grease Rendering in the Historic Period:

Experimental Chopping of Long Bones and Small Fragment Sizes. *Advances in Archaeological Practice: A Journal of the Society for American Archaeology* 2(1): 1-12.

Hutchins, M. & Olendorf, D. 2004: *Grzimek's Animal Life Encyclopedia*. 2nd Edition. Volume 15: Mammals IV. Gale/Cengage Learning.

Kellogg, V. L. 1901: *Elementary zoology*. H. Holt and company.

Lister, A. M. 1996: The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). *International Journal of Osteoarchaeology* 6(2): 119-143.

Lydekker, R. 1894: *The Royal Natural History*. Vol. 2. Frederick Warne & Company.

Lyman, R. L. 2008: *Quantitative Paleozoology*. Cambridge manuals in archaeology. Cambridge University Press, Cambridge.

Heptner, V. G. (ed.) 1992: *Mammals of the Soviet Union*. Volume 2, Part 2: Carnivora (Hyenas and Cats). Brill.

Morales, A. & Rodriguez, J. 1997: Black rats (*Rattus rattus*) from medieval Mértola (Baixo Alentejo, Portugal). *Journal of Zoology* 241(4): 623-642.

Morales, A.; Moreno, M.; Roselló, E.; Llorente, L. & Morales, D. C. 2011: 711 Ad: ¿El Origen de una Disyunción Alimentaria? *Zona Arqueológica* 15(2): 301-319.

Mota, D. M. M. 2014: Estudo zooarqueológico de restos faunísticos de época islâmica (séculos XII/XIII) de um silo do castelo de Aljezur. MSc thesis, Universidade Nova de Lisboa and Universidade de Évora.

Parker, T. J. & Haswell, W. A. 1900: Scientific Books: A Manual of Zoology. *Science* 11: 821-822.

Pereira, V. 2014: Zooarchaeological perspective of the Islamic sites in Algarve - current state of knowledge. *Proceedings of the First Zooarchaeology Conference in Portugal*: 111-117. B.A.R. (International Series*)* 2662. Oxford.

Popesko, P. & Getty, R. 1971: *Atlas of topographical anatomy of the domestic animals*. Volumes I-III.

Pais, J. 2013: Apontamentos da Cadeira de Arqueobotânica e Arqueozoologia. Mestrado em Paleontologia. Faculdade de Ciências e Tecnologia. Universidade Nova de Lisboa.

Payne, S. 1973: Kill-off patterns in sheep and goats: the mandibles from Aşvan Kale. *Anatolian studies* 23: 281-303.

Payne, S. & Bull, G. 1988: Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *Archaeozoologia* 2(1).

Ramalho, M. M.; Lopes, C.; Custódio, J. & Valente, M. J. 2001: Vestígios da Santarém Islâmica – Um silo no Convento de S. Francisco. *Arqueologia Medieval* 7: 147-183.

Reitz, E. J. & Wing, E. S. 2008: *Zooarchaeology*. Cambridge manuals in archaeology. Cambridge University Press, Cambridge.

Silvério, S. 2001: *Silos Islâmicos de Alcaria – Aljezur (Séculos VIII-XII)*. Associação de Defesa do Património Histórico e Arqueológico de Aljezur, Câmara Municipal de Aljezur, Aljezur.

Schmid, E. 1972: *Atlas of Animal Bones*. Elsevier Publishing Company, New York.

Valente, M. J. 1997: A quantificação faunística: principais unidades, alguns parâmetros, regras e problemas. *Estudos do Quaternário* 1: 83-96.

Van De Graaff, K. M.; Morton, D. A. & Crawley, J. L. 2012: *A photographic atlas for the anatomy and physiology laboratory*. Morton Publishing Company.

APPENDIX

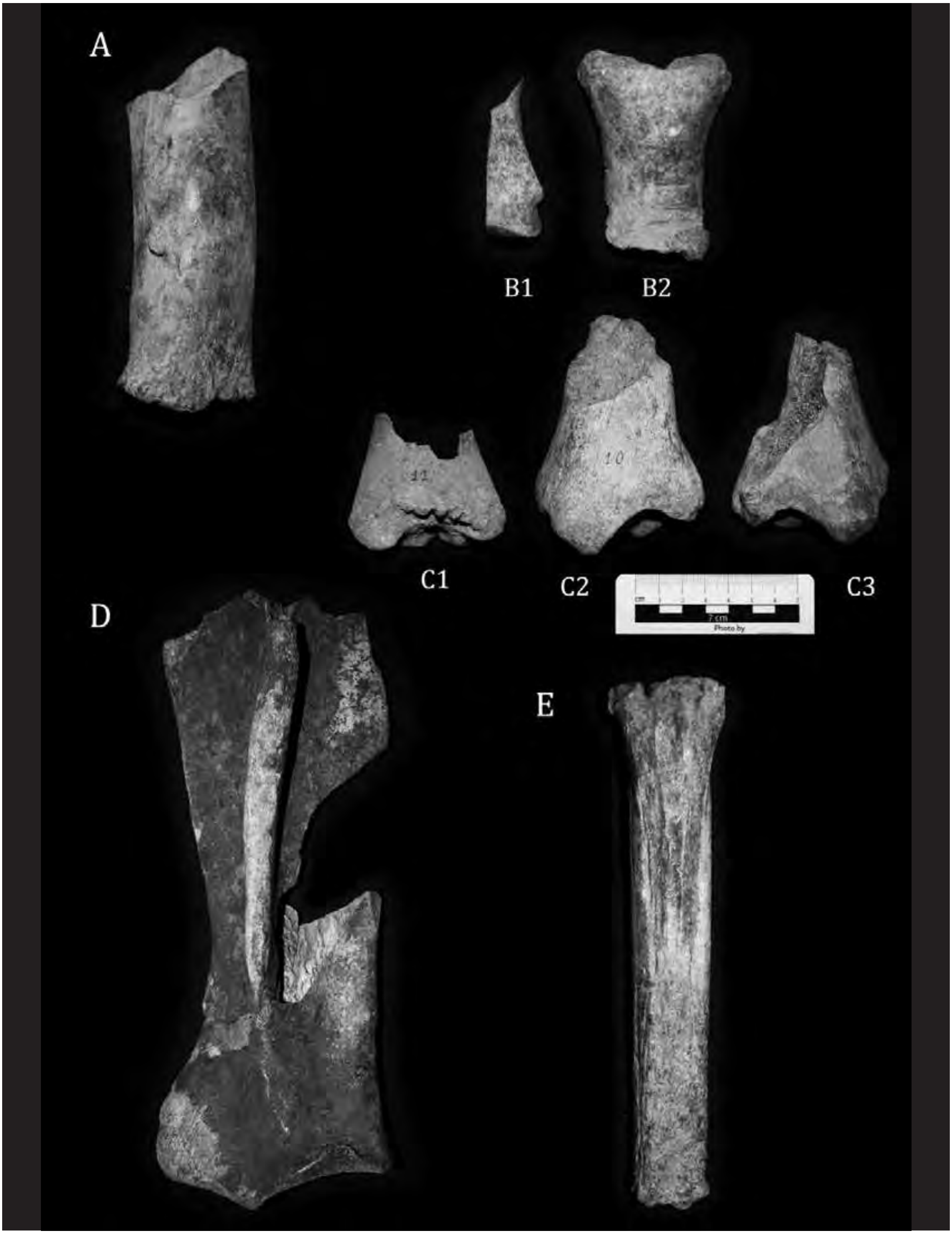

FIGURE 26

Equid remains. A – Right femur; B – 1st phalanges (B2 – right); C1 – Left tibia; C2 – Left tibia; C3 – Right tibia; D – Left scapula; E – Right metatarsal.

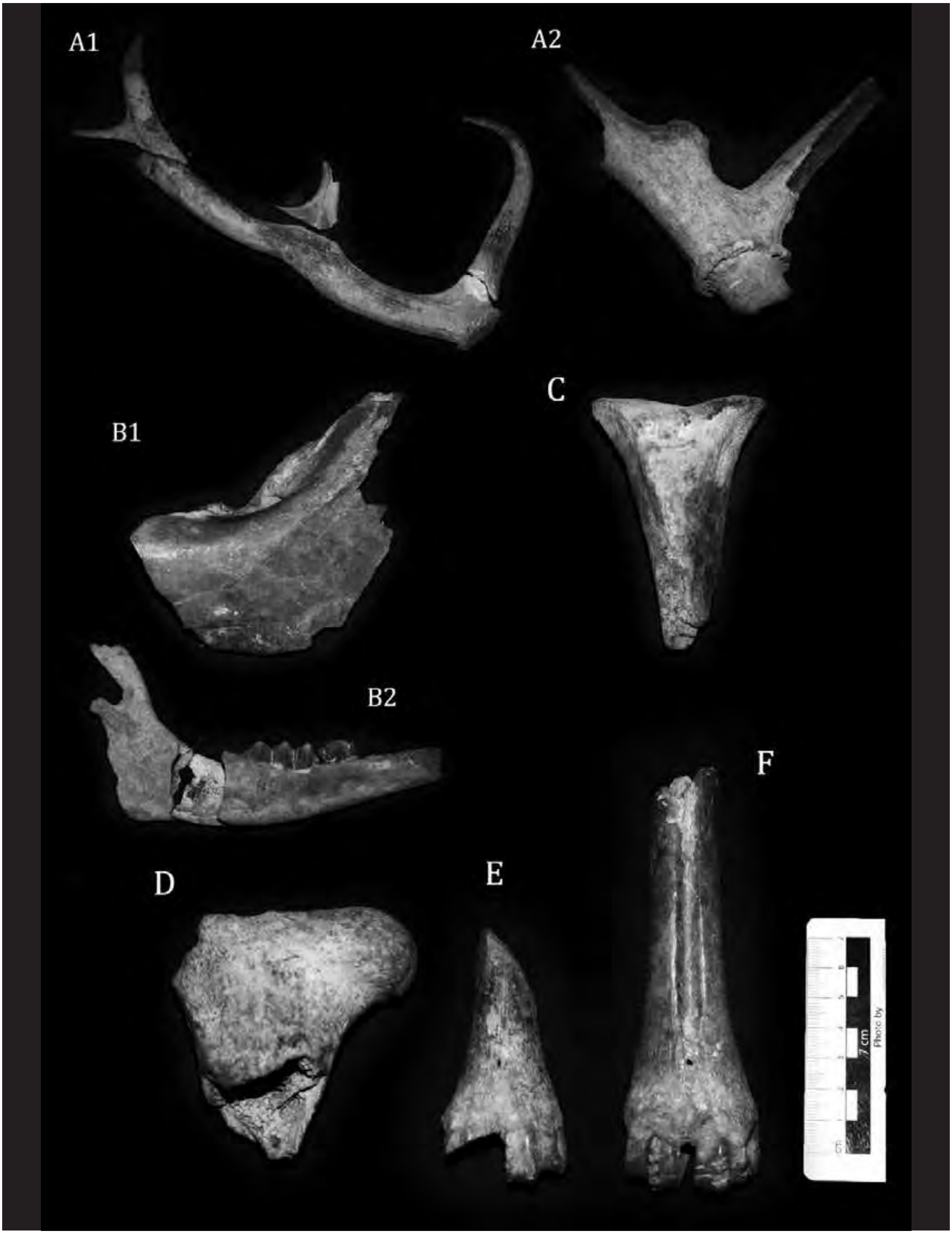

FIGURE 27

Red deer remains. A(1-2) – Right antlers; B – (1) Left mandible of an adult, (2) right mandible of an infant; C – Right tibia of a juvenile; D – Right femur; E – Metacarpal; F – Metatarsal.

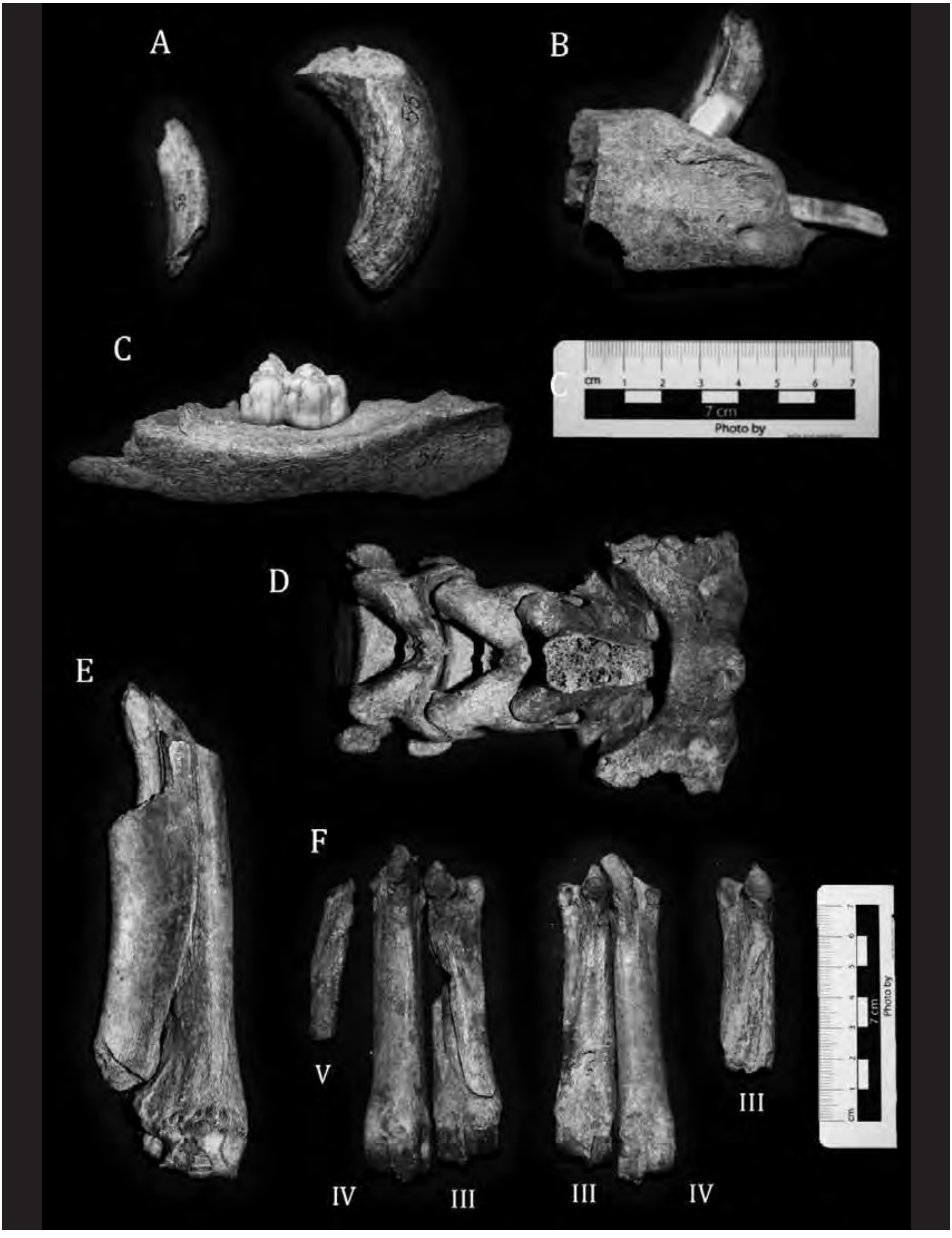

FIGURE 28

Suid remains. A – Canines; B – Alveolar zone of the incisors and of the canine of the right mandible; C – Alveolar zone of M_3 of the left mandible; D – Cervical vertebrae; E – Left radius and ulna; F – Metatarsals.

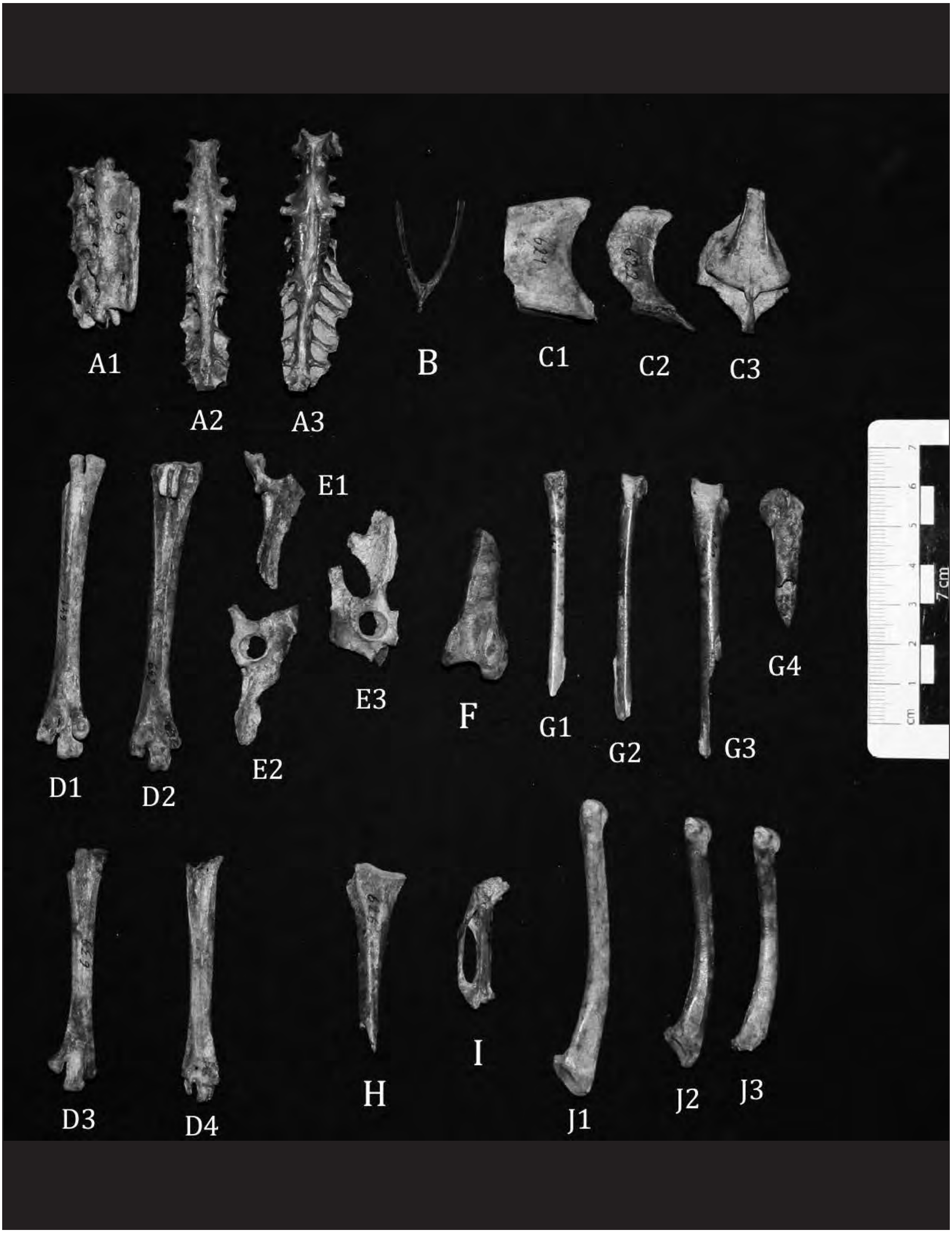

FIGURE 29

Chicken remains. A – Lombossacral; B – Clavicule; C – Sternum; D – Metatarsal, (1-2) left, (3-4) right; E – Pelvis, (1-2) right, (3) left; F – Left femur; G – Tibia, (1) left, (2-4) right; H – Left coracoid; I – Left metacarpals II and III; J – Right ulna.

Archaeofauna 25 (2016): 233-264

Patterns of ancient animal use at El Mirador: evidence for subsistence, ceremony and exchange

ERIN KENNEDY THORNTON & KITTY F. EMERY
Department of Anthropology, Washington State University, PO Box 644910, Pullman, WA 99164-4910
Florida Museum of Natural History, University of Florida, Gainesville, FL 32611-7800

(Received *6 February 2013*; Revised *1 February 2016*; Accepted *4 February 2016*)

ABSTRACT: El Mirador is among the largest Preclassic settlements in the Maya lowlands. The site has attracted attention due to its size and antiquity, but also for its location within a region containing few perennial water sources such as lakes and rivers. This report presents a preliminary and largely descriptive analysis of faunal remains recovered during early excavation of the site between 1978 and 1983. The zooarchaeological assemblage provides baseline information regarding past patterns of animal use, acquisition and exchange at El Mirador that may be compared with other Preclassic faunal assemblages from across the Maya lowlands. Intra-site temporal comparisons are also drawn between animal use during the site's primary Late Preclassic occupation, and a less extensive period of settlement during the Classic Period.

KEYWORDS: EL MIRADOR, MAYA PRECLASSIC, GUATEMALA, ZOOARCHAEOLOGY

RESUMEN: El Mirador es uno de los mayores asentamientos Preclásicos de las tierras bajas maya. El yacimiento atrajo la atención debido a su tamaño y antigüedad así como por su localización en una región con escasas fuentes de agua perenne como lagos y ríos. Este informe refiere un análisis preliminar y, en gran medida descriptivo, de los restos faunísticos recuperados durante las primeras excavaciones llevadas a cabo entre 1978 y 1983. La muestra zooarqueológica proporciona información de base referida a antiguos patrones de aprovechamiento e intercambio de animales en El Mirador. Estos pueden así ser comparados con otros conjuntos faunísticos Preclásicos de las tierras bajas maya. Comparaciones diacrónicas dentro del yacimiento se infieren también de los usos animales en el bloque de la ocupación del Preclásico Tardío y un momento de menor entidad del yacimiento que se corresponde con el periodo Clásico.

PALABRAS CLAVE: EL MIRADOR, MAYA, PRECLÁSICO, GUATEMALA, ZOOARQUEOLOGÍA

INTRODUCTION

This report presents the results of an analysis of the vertebrate and invertebrate faunal remains recovered from the site of El Mirador, Petén, Guatemala during investigations directed by Drs. Bruce Dahlin and Ray Matheny from 1978–1983. The faunal remains provide the first baseline information regarding the patterns of animal use and acquisition at this large and important site in the central Maya lowlands (Figure 1). In this report we identify the relative abundance of various taxa in the assemblage with particular emphasis on variations between residential and ceremonial contexts and an exploration of change in animal use patterns between the Late Preclassic (~350 BC–AD 150) and Late Classic (~AD 600-850). Through the analyses we also discuss habitat use and evidence for long distance exchange of animal resources as explanations for some of the variation observed. In addition, we report on the effects of taphonomy, recovery methods, and quantification as sources of bias, and present a brief discussion of artifactually modified remains.

SAMPLE DESCRIPTION AND ANALYSIS METHODS

The El Mirador faunal assemblage contains 3313 identifiable specimens (NISP: number of identified specimens), representing 65 MNI (minimum number of individuals) and 32 taxa. These tallies do not include land snails (NISP = 123) and small rodents (NISP = 38, MNI = 3), which may be intrusive. Identifiable human remains (NISP = 301) found intermingled with the zooarchaeologi-

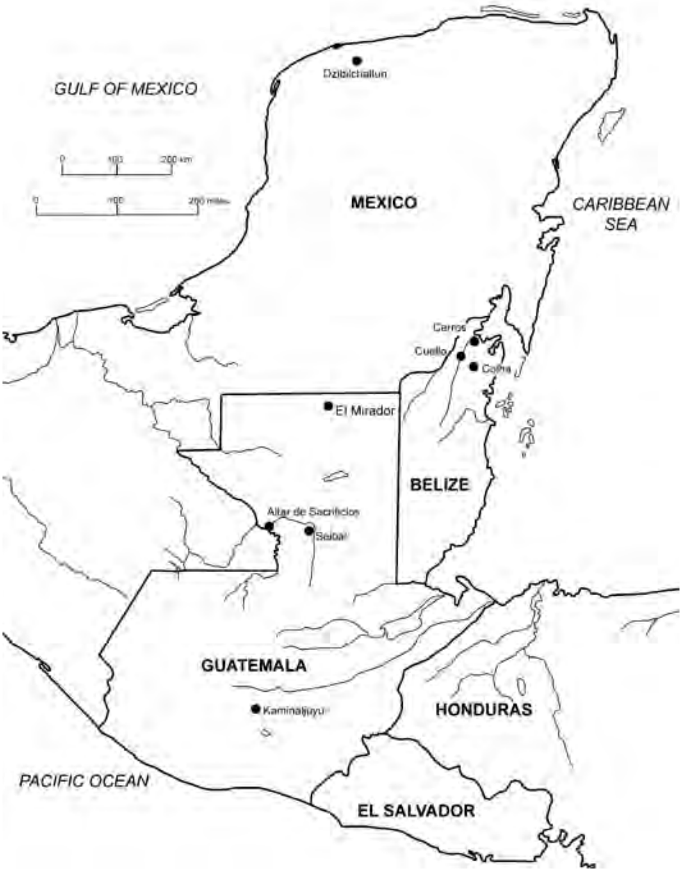

FIGURE 1

Map of the ancient Maya world showing the location of El Mirador and other sites mentioned in the text. Map by Thornton and Emery.

cal materials were also were excluded from NISP and MNI tabulations, but are reported in brief at the end of this article.

Sample Recovery

The El Mirador faunal assemblage was recovered using trowel and ¼-inch gauge screen. Zooarchaeological research has shown that the use of finer-gauge screens (1/8-1/16-inch) will increase the recovery of juvenile individuals and smaller sized taxa such as fish (e.g., Gordon, 1993; James, 1997; Cannon, 1999; Quitmyer, 2004; Wake, 2004). Recovery method tests conducted within the Maya region by Emery and Thornton (Emery, 2012; Thornton, 2012) confirm these previous finding and show that fish, reptiles, amphibians and small marine shells may also be better represented in fine-screened samples (see also Masson, 2004: 104). Consideration of sample recovery methods is of particular importance when comparing the El Mirador faunal sample to other contemporary assemblages.

Identification and Quantification

The El Mirador faunal remains were identified by Thornton under Emery's supervision using the modern comparative specimens housed in the Florida Museum of Natural History Environmental Archaeology Program (FLMNH-EAP) collections. More specialized identifications were made using the museum's Ornithology and Malacology collections with the assistance of Curator David Steadman and collection manager John Slapcinsky, respectively. Specimens were identified to a more generalized taxonomic level when the complete range of comparative specimens was not available in the collections. The lack of comparative material had the greatest effect on the identification of small Kinosternid turtle remains, which were often identified only to the family level.

FIGURE 2

Rodent gnawed mammal long bone shaft fragment (631.0002;21/I1/7– Early Classic)

The assemblage was quantified according to specimen or fragment counts (NISP) and MNI tallies. Contemporary proveniences in close proximity (e.g., within the same plaza group) were aggregated into single units for MNI quantification. Since the remains of a single carcass may have been distributed among households or disposal areas within a particular area (Emery, 2004b), this method was used to prevented MNI inflation. However, well-dated faunal materials from separate time periods were considered to be independent in terms of MNI calculations even when in close proximity. The results of both NISP and MNI calculations are presented whenever possible, as neither method of quantification is ideal for presenting measures of relative abundance (Grayson, 1984; Ringrose, 1993). MNI estimates are based on the presence of paired or unique elements, with regard to age, sex and size (Reitz & Wing, 1999: 194-197). MNI results are often preferable when quantifying the relative abundance of animals from different phyla that have widely different numbers of skeletal elements. However, many Maya faunal assemblages have high taxonomic diversity, and low element redundancy, which results in very low MNI counts for each species, which may not accurately reflect relative taxonomic abundance (Emery, 2004b: 28).

ANIMAL USE AT EL MIRADOR: RESULTS AND DISCUSSION

Appendix 1 presents a full list of the El Mirador zooarchaeological remains organized by provenience. This list includes the scientific name and skeletal elements identified for each taxa. Table 1 provides the scientific and common names for all of the species identified in the assemblage and quantifies them according to NISP and MNI tallies.

Scientific Name	**Common Name**	**NISP**	**%NISP**	**MNI**	**%MNI**
Mollusca	mollusc	56	1.7	-	-
Bivalvia	bivalve	2	0.1	-	-
Gastropoda	gastropod	40	1.2	-	-
Scaphopoda	tusk/tooth shell	1	<0.1	1	1.5
Cerithiidae	cerith	2	0.1	2	3.0
cf. Strombidae	cf. conch	1	<0.1	-	-
Strombus sp.	conch	1	<0.1	1	1.5
Conus spurius	alphabet cone	1	<0.1	1	1.5
Crassostrea virginica	eastern oyster	8	0.2	2	3.0
Spondylus cf. *calcifer*	Pacific spiny oyster	1	<0.1	1	1.5
Spondylus sp.	spiny oyster	3	0.1	2	3.0
cf. *Spondylus* sp.	cf. spiny oyster	1	<0.1	-	-
Pomacea flagellata	applesnail	11	0.3	6	9.0
cf. Unionidae	river clam	3	0.1	2	3.0
Vertebrata	vertebrate	1595	47.6	-	-
Osteichthyes	fish	1	<0.1	1	1.5
Sparisoma sp.	parrot fish	1	<0.1	1	1.5
Rhinella cf. *marina*	cane toad	1	<0.1	1	1.5
Testudines	turtle	70	2.1	-	-
Kinosternidae	mud/musk turtle	3	0.1	2	3.0
Staurotypus triporctatus	giant musk turtle	1	<0.1	1	1.5
Emydidae	slider/pond turtle	13	0.4	4	6.0
Dermatemys mawii	Central American river turtle	12	0.4	1	1.5
cf. *Dermatemys mawii*	cf. Central American river turtle	10	0.3	-	-
Colubridae	colubrid snake	1	<0.1	1	1.5
Lacertilia	lizard	1	<0.1	1	1.5
cf. Aves	cf. bird	1	<0.1	-	-
Aves	birds	5	0.2	-	-
Aves (medium)	bird (e.g., duck, gull)	2	0.1	-	-
Aves (medium/large)	bird (e.g., duck, turkey)	2	0.1	-	-
Aves (large)	bird (e.g., turkey, vulture)	24	0.7	2	3.0
Meleagris gallopavo	wild/domestic turkey	4	0.1	2	3.0
Meleagris sp.	turkey	2	0.1	-	-
Crax rubra	great curassow	1	<0.1	1	1.5
Ortalis vetula	plain chachalaca	3	0.1	1	1.5
Mammalia	mammals	360	10.8	-	-
Mammalia (small)	mammal (e.g., rat, squirrel)	29	0.9	-	-
Mammalia (small/medium)	mammal (e.g., squirrel, racoon)	20	0.6	-	-
Mammalia (medium)	mammal (e.g., raccoon, dog)	92	2.8	-	-
Mammalia (medium/large)	mammal (e.g., dog, deer)	144	4.3	-	-
Mammalia (large)	mammal (e.g., deer, puma)	527	15.7	-	-
Didelphis sp.	opossum	1	<0.1	1	1.5
Dasypus novemcinctus	nine-banded armadillo	3	0.1	1	1.5
Sylvilagus sp.	rabbit	2	0.1	2	3.00
Sciuridae	squirrel	1	<0.1	1	1.5

Table 1. Continuation

Muridae*	mouse/rat	23	0.7	1	1.5
*Ototylomys phyllotis**	big-eared climbing rat	15	0.5	2	3.0
Dasyproctidae/Cuniculidae	agouti/paca	3	0.1	-	-
cf. Cuniculidae	cf. paca	3	0.1	-	-
Cuniculus paca	paca	7	0.2	1	1.5
Dasyprocta punctata	Central American agouti	3	0.1	1	1.5
cf. Carnivora	cf. carnivores	1	<0.1	-	-
Felidae (medium) (cf. *Leopardus pardalis*)	felid (cf. ocelot)	1	<0.1	-	-
Felidae (large)	puma/jaguar	3	0.1	2	3.0
cf. Canidae	cf. canid (dog/coyote/fox)	5	0.2	-	-
Canidae	dog/coyote/fox	3	0.1	-	-
Canis lupus familiaris	domestic dog	28	0.8	3	4.5
cf. *Canis lupus familiaris*	cf. domestic dog	10	0.3	-	-
Artiodactyla	artiodactyl	4	0.1	-	-
Tayassuidae	peccary	20	0.6	4	6.0
cf. Tayassuidae	cf. peccary	1	<0.1	-	-
Pecari tajacu	collared peccary	4	0.1	1	1.5
Cervidae	cervid	19	0.6	1	1.5
Mazama sp.	brocket deer	43	1.3	5	7.5
Odocoileus virginianus	white-tailed deer	89	2.7	5	7.5
cf. *Odocoileus virginianus*	cf. white-tailed deer	3	0.1	-	-
	TOTAL =	**3351**	**100**	**68**	**100.0**

NOTE: Human remains and landsnails have been excluded
* = species likely intrusive

TABLE 1

Taxonomic composition of the El Mirador faunal assemblage

Taxonomic Level	**NISP**	**%NISP**
Above class	1595	50.1
Class or below*	1587	49.9
Family or below**	301	9.5

* includes remains identified to class, family, genus or species

** includes remains identified to family, genus or species

TABLE 2

Portion of the vertebrate El Mirador faunal assemblage identified to particular taxonomic levels

Sample Preservation

Although specimen preservation varied greatly in the assemblage, many of the remains were highly fragmented and eroded. Approximately 50% of the vertebrate faunal assemblage (based on NISP) was not identifiable to the level of taxonomic class (Table 2). Over two-thirds of these unidentified vertebrate remains came from unknown proveniences where the level of weathering and fragmentation was significantly greater than observed for other contexts. Large mammal long bone shafts were also highly fragmented in all proveniences, precluding their identification below the level of taxonomic class, and resulting in a large number of unidentified mammal remains. These preservational conditions are common for lowland Maya assemblages (Emery, 2004a). However, the MNI comparisons for the El Mirador assemblage may be skewed due to the relatively small sample size (Grayson, 1981), and the better preservation of the invertebrate remains (MNI/NISP ratio = 0.13) in comparison to the vertebrate remains (MNI/NISP ratio = 0.01).

Analysis of both the vertebrate and invertebrate faunal components revealed little evidence for

BURNT/CHARRED:

NISP	Provenience	Taxonomy	Skeletal Element
1	Operation 17 B-5, Lot 10	Mammalia (medium)	long bone shaft fragment
1	Operation 17 B-1, Lot 6	*Mazama* sp.	ulna
2	Operation 31, Lot 5	Mammalia (large)	long bone shaft fragment
2	Operation 31 A, Lot 6	*Odocoileus virginianus*	ischium (subadult)
4	Operation 32 Trench A, Lot 6	Vertebrata	unidentified bone
1	Operation 32 D-1, Lot 3	Mammalia	unidentified bone
1	Operation 32 D-1, Lot 4	Mammalia	unidentified bone
4	Unknown	Mammalia (large)	unidentified bone

RODENT GNAWED:

NISP	Provenience	Taxonomy	Skeletal Element
1	Operation 17 A-4, Lot 4	*Mazama* sp.	metatarsal
1	Operation 17 C-4, Lot1	*Canis lupus familiaris*	radius
1	Operation 21 I-1, Lot 7	Mammalia	femur? shaft fragment
1	Operation 26 K, Lot 4	*Meleagris* sp.	femur
1	Operation 32, Lot 11	*Canis lupus familiaris*	mandible

TABLE 3
El Mirador faunal remains with evidence of burning or gnawing

TAXA	NISP	%*	MNI	%
Marine Molluscs	19	1.2	10	15.4
Freshwater Molluscs	14	0.9	8	12.3
Fish	2	0.1	2	3.1
Reptiles/Amphibians	111	6.9	11	16.9
Birds	45	2.8	6	9.2
Mammals	1429	88.2	28	43.1
TOTAL =	1620	100	65	100

* percent of NISP identified to taxonomic class or lower

TABLE 4
Taxonomic distribution of the identified El Mirador faunal remains

natural modification. Less than 1% of the remains showed signs of either burning (0.5%) or rodent gnawing (0.2%), and no evidence for carnivore gnawing was observed (Table 3, Figure 2). The lack of extreme weathering, burning and gnawing on the remains from known proveniences suggests that the El Mirador faunal remains were rapidly buried after deposition, perhaps by being incorporated into architectural fill.

Taxonomic Composition of the Assemblage

According to NISP tallies, mammals are the most commonly identified animals in the assemblage (88%), followed by reptiles (7%), and birds (3%) (Table 4). The remaining 2% of the assemblage is composed of marine (1%) and freshwater molluscs (1%). Taxonomic distribution according to MNI also shows the dominance of mammalian taxa (43%) in the assemblage, but marine (15%) and freshwater molluscs (12%) appear to be almost as abundant as reptiles (17%) and birds (9%). This is likely due to the better preservation of the mollusc remains as opposed to their true abundance in the assemblage. The dominance of terrestrial mammals in the sample, regardless of quantification method, is not surprising considering El Mirador's inland location, and the lack of large rivers and lakes nearby. Overall, the most commonly identified animals at El Mirador according to NISP, are the white-tailed deer (*Odocoileus virginianus*), brocket deer (*Mazama* sp.), peccary (Tayassuidae), domestic dog (*Canis lupus familiaris*), and various species of turtles (Testudines). The specific species identified in the assemblage are listed in Table 1

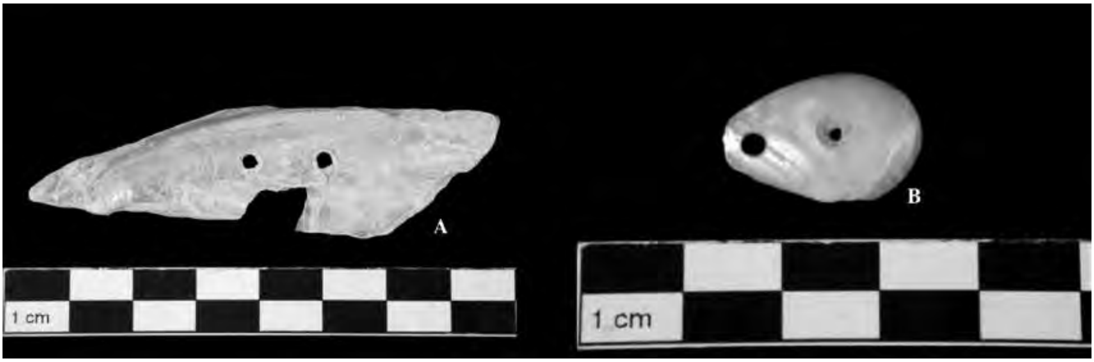

FIGURE 3

A. Bivalve (cf. Unionidae) shell fragment with two perforations below hinge (631.0316;17/B3/5/112 – Late Classic?); B.Teardrop-shaped shell pendant (cf. Unionidae) perforated twice along midline (631.0405; 32/D/2/96 – Late Preclassic/Protoclassic)

and Appendix 1, and are described in more detail in the following sections.

Molluscs

Terrestrial land snails account for a large portion of the mollusc remains in the El Mirador assemblage (see Appendix 1) and are considered separately from the molluscs more likely used by the El Mirador residents. Ten separate taxa of terrestrial snails, representing 123 individuals, were identified. Although these species have the potential to yield valuable environmental data, reliable information regarding their burrowing behavior and habitat requirements is lacking in the literature. The apple snail (*Pomacea flagellata*) is the most common freshwater mollusc identified in the sample. This species could have been harvested from the *bajo* (seasonal wetland) and *aguada* habitats (constructed water reservoirs) found near the site. In contrast, other freshwater mollusc species commonly present in Maya zooarchaeological assemblages, such as jute (*Pachychilus* sp.) and freshwater clams (Unionidae) are absent, or rare in the sample. This is likely due to the site's distance from major lacustrine and riverine habitats. When found, the Unionid clams are primarily modified as decorative artifacts, reinforcing their use and non-local acquisition primarily as adornments rather than subsistence resources (Figure 3).

Various species of marine molluscs were recovered at El Mirador including the eastern oyster (*Crassostrea virginica*), spiny oyster (*Spondylus* sp.), conch (*Strombus* sp.), tusk shell (Scaphopoda), olives (*Oliva* sp.) and alphabet cone (*Conus spurius*) (Figure 4). All of these species indicate trade of animal resources between the coast (primarily the Atlantic) and the interior of the Maya lowlands. One large articulated and unmodified specimen of *Spondylus* cf. *calcifer* was also present in the assemblage (Figure 5). This species of spondylus is significant because it is only found in the Pacific. The diversity of marine resources at El Mirador therefore indicates that the site was connected to Maya communities via multiple long distance trade routes. Many of the marine shells show evidence of artifactual modification, and it is likely that most were imported for ritual or craft production purposes. Most of the marine shells were recovered from elite ritual/ceremonial structures within the one of the site's main plazas (Tigre Plaza: Operations 26, 35, and 36), but two nearly whole eastern oyster shells where also found associated with an elite residential compound southwest of the main acropolis (Operation 46B).

Fish

Fish account for a very small proportion of the site's faunal remains (NISP =2), which is not unexpected based on the absence of perennial lakes and river within the El Mirador Basin. A scarcity of fish remains in the zooarchaeological record is also a typical of many inland lowland Maya sites. However, the near absence of fish in many Maya faunal assemblages may be partially due to recovery techniques and preservation bias (Chase *et al.*, 2004; Emery, 2004 a, b). The only species of fish

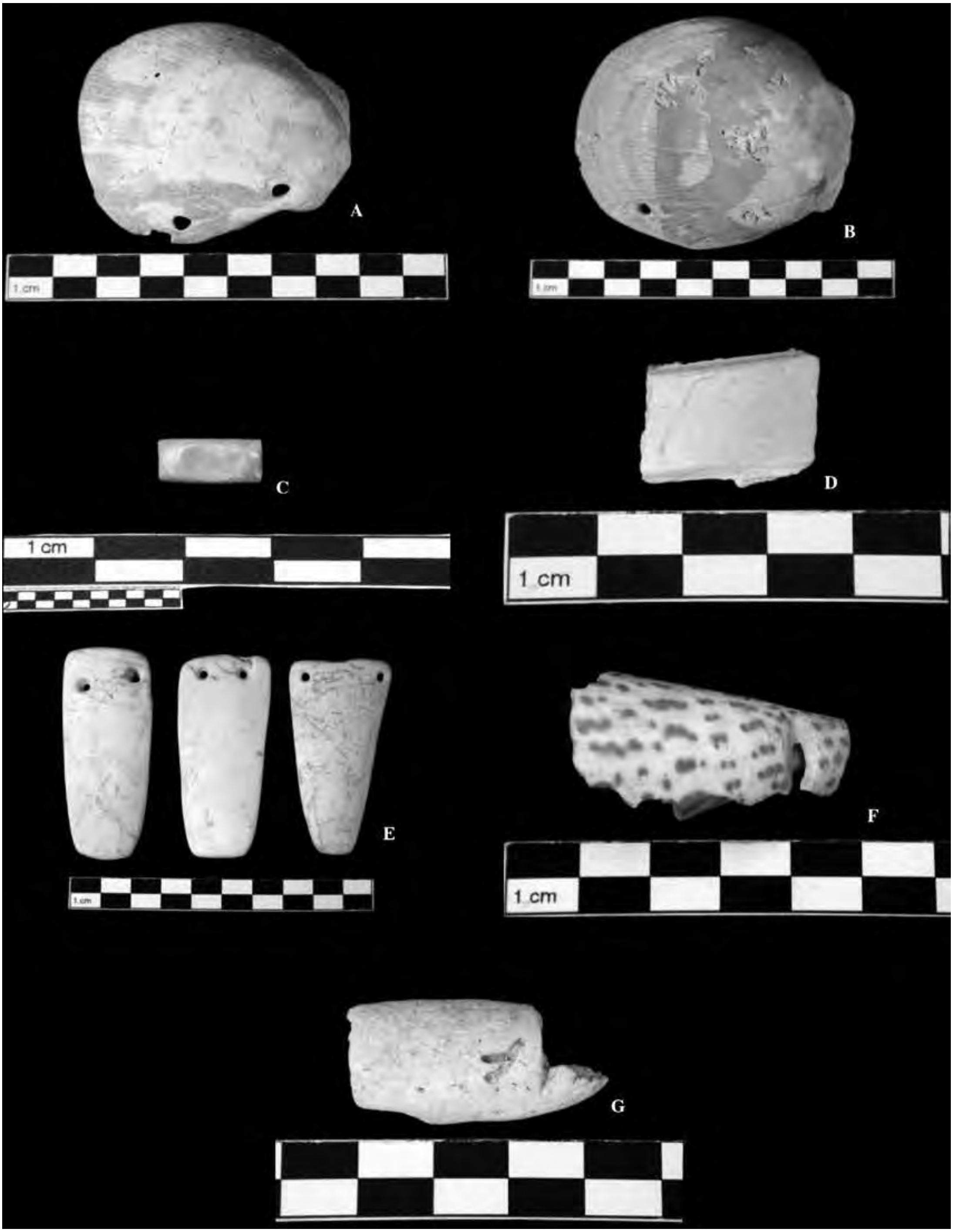

FIGURE 4

A. Perforated *Spondylus* sp. shell with spines abraded off (631.0019;26/K/4 – Late Preclassic); B. Perforated *Spondylus* sp. shell with spines abraded off(631.0276;32/D1/4/121 – Late Preclassic/Protoclassic); C. Cylindrical *Spondylus* sp. shell bead (631.0331; 26/A/9/216 – Late Preclassic); D. Thick cube of marine shell (cf. Strombidae) cut on four sides – likely debitage from shell artifact production(631.0186; 36/A/10/24 – Late Preclassic); E.Three perforated shell (cf. Strombidae) pectorals (631.0406;36/A/13/84 – unknown date); F. *Conus spurius* shell tinkler fragment (631.0329; 26/O/5/246 – Late Preclassic); G.*Oliva* sp. shell tinkler fragment (631.0039;47/D/6 – Late Preclassic).

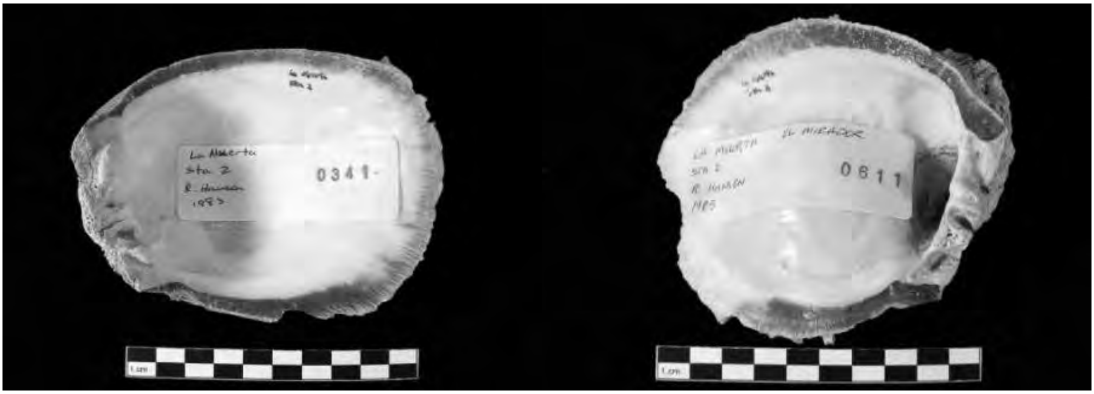

FIGURE 5

Unmodified *Spondylus* cf. *calcifer* shell (right (a) and left (b) valves) (631.0290; La Muerta, Sta. 2 (acc.# 611)).

identified in the El Mirador sample is the parrotfish (*Sparisoma* sp.), a colorful Atlantic coast species commonly found near coral reefs. The non-local nature of this species supports the hypothesis of El Mirador's participation in coastal-inland trade networks. Although it is not uncommon to identify small amounts of marine resources at Preclassic sites (Wing, 1977; Moholy-Nagy, 1985; Shaw, 1999; Fradkin & Carr, 2003; Teeter & Chase, 2004), the presence of marine fish remains at El Mirador is significant due to the site's distance from both the coast and major waterways used for transportation from the coast into the interior.

The well-preserved fish remains at El Mirador were found in a fill deposit sealed below a stucco floor in the Structure 34 Sub-complex (Operation 26J) located at the south end of the Tigre Plaza. Based on its location and architectural form, this building was likely used for elite ceremonial activities (Hansen, 1990). It is unclear whether the fish were imported for dietary consumption (including feasting) or for non-dietary ceremonial/ritual use. It is also impossible to determine whether the fish were imported in salted or unsalted form, although the site's distance from the coast suggests that salt would have been used to ensure preservation during transport. It is clear, however, that the fish were not brought into the site as processed fillets (i.e. with the heads removed) since all of the recovered fish bones are cranial fragments.

Including the fish remains, a total of 121 bone fragments were recovered from the sediments below the stucco floor. Other species present in association with the fish remains include deer, dog and turkey (*Meleagris* sp.). These species are common inclusions in Maya burial and cache deposits, and also may have been used for ritual feasting (Pohl & Feldman, 1982; Pohl, 1983, 1985; LeCount, 2001; Emery, 2003). The marine fish at El Mirador may therefore have formed part of a suite of species used in public ritual, ceremonial or feasting activities carried out in association with Structure 34.

Reptiles

Reptiles, primarily freshwater turtles, are also present in the El Mirador assemblage. A large portion of the turtle carapace fragments are not identifiable since many do not have diagnostic markers, but the identified turtle remains include the giant musk turtle (*Staurotypus triporctatus*), Central

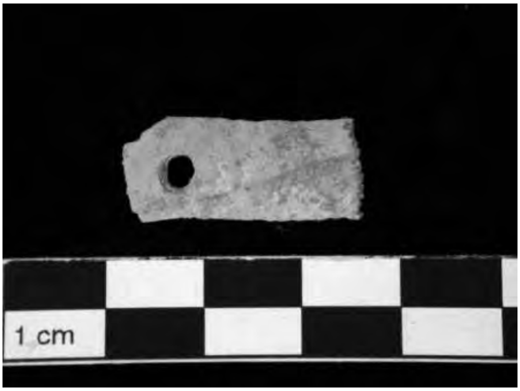

FIGURE 6

Perforated turtle carapace fragmen t(631.0403; 32/B/21/52– Late Preclassic)

American river turtle (*Dermatemys mawii*), pond/box turtles (Emydidae), and small mud and musk turtles (Kinosternidae). Single elements from other non-turtle reptiles, including an unidentified lizard and colubrid snake, were also identified in the sample. While the small lizard and snake could be incidental inclusions, the turtles were probably consumed or otherwise used by the residents. Over 90% of the turtle remains were recovered from a probable elite residential compound located 50 meters east of the West Wall System (Operation 17). The concentration of turtle remains in the site's residential areas suggests that the turtle remains represent food waste. However, turtle carapaces could also have been used in these contexts as bowls, or musical instruments such as drums and rattles. One perforated fragment of turtle carapace found in Operation 32 supports the secondary use of at least some of the remains as modified artifacts (Figure 6).

Most of the turtle species in the El Mirador assemblage could have been acquired in the nearby forest and *bajo* environments, but the Central American river turtle may have been acquired some distance from the site. This species is highly aquatic, requiring large water-bodies such as major rivers and lakes, and cannot easily disperse long distances away from major watercourses (Campbell, 1998). The meat of *Dermatemys* is still highly valued today and a single specimen can yield a significant amount of meat, which may have made the extra procurement effort worthwhile. The large carapace of this species could also have been desired for use as an instrument, or container.

Birds

Birds are not common in the El Mirador assemblage, and all of the avian species identified are large, ground-dwelling galliforms including the turkey, great curassow (*Crax rubra*), and plain chachalaca (*Ortalis vetula*). These are commonly identified game species in lowland Maya faunal assemblages. Although galliforms were likely targeted because of their large body size and meat weight yields, the absence of smaller avian species could also be due to taphonomic factors. Survivorship of bird skeletal remains varies between species and elements due to differences in bone density (Ericson, 1987; Livingston, 1989; Nicholson, 1996; Dirrigl, 2001). All of the El Mirador avian remains represent species and elements with greater survivorship potential in archaeological contexts (see density data in Dirrigl, 2001). The prehistoric use of smaller avian species may therefore be under-estimated based on the recovered zooarchaeological assemblage.

Avian remains are distributed across the site in both residential (Op. 17, 31) and probable public ritual or ceremonial contexts (Op. 26, 27, 32, 35). Three individuals (one curassow, one chachalaca, and one probable turkey) are subadults. Although subadult and juvenile fauna are often preferentially used for ceremonial purposes (Pohl, 1983; Carr, 1996; Emery, 2003), subadult avian remains are present in both elite residential and public ceremonial contexts at El Mirador.

An unexpected finding was the presence of *Meleagris gallopavo* (wild/domestic turkey) in the site's avian assemblage. Prior archaeological and ornithological research has suggested that during pre-Colombian times, the natural range of this species did not extend south of central Mexico (Leopold, 1959: 269; Schorger, 1966: 49; Steadman, 1980; Thornton & Emery, 2015). To date, remains of *M. gallopavo* have not been identified in Maya archaeological contexts dating to before the Postclassic period (ca. A.D. 1000-1500) when it was likely introduced as a domesticated species (Hamblin, 1984). With the assistance of Dr. David Steadman (Curator of Ornithology, FLMNH), we identified five possible specimens of *M. gallopavo* from Late Preclassic deposits in Operations 26 and 35. To confirm the osteological identifications, we submitted four of the five specimens for ancient DNA analysis by Dr. Camilla Speller and Dr. Dongya Yang at the Simon Fraser Department of Archaeology Ancient DNA Lab. The fifth specimen was too small to be tested. Three of the four turkey bones were positively identified through aDNA analysis as *M. gallopavo*, while the fourth sample was inconclusive (Thornton *et al*., 2012). The Late Preclassic date of the deposits containing *M. gallopavo* remains was reconfirmed with AMS radiocarbon dating of associated faunal remains in 2009. Therefore, this significant finding represents the earliest presence of this species (in either wild or domesticated form) within the Maya lowlands (Thornton & Emery 2015).

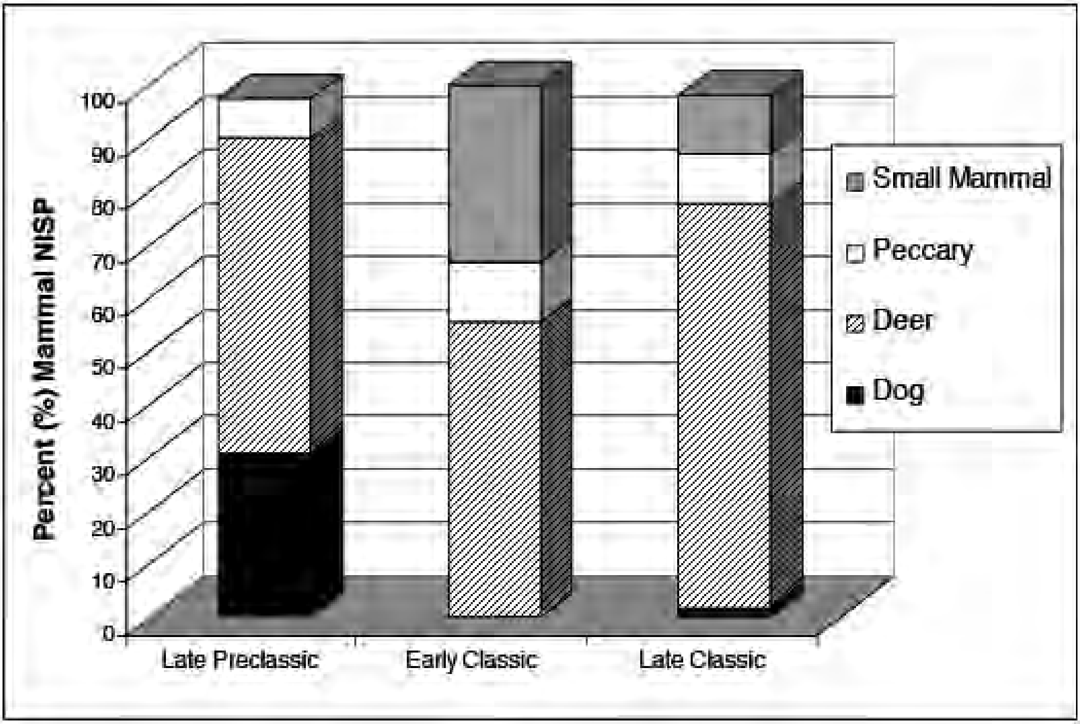

FIGURE 7

Distribution of mammalian faunal remains at El Mirador (based on percent of mammal NISP identified below the level of taxonomic class).

Mammals

Of the twelve mammalian taxa identified, the white-tailed deer was the most commonly encountered species. Brocket deer, peccaries and domestic dogs were also prevalent in the sample, while oppossom (*Didelphis* sp.), armadillo (*Dasypus novemcinctus*), rabbit (*Sylvilagus* sp.), squirrel (Sciuridae), paca (*Cuniculus paca*), agouti (*Dasyproctca punctata*), and felid (e.g., *Leopardus pardalis, Panthera onca, Puma concolor*) remains were less frequently encountered (Figure 7). The very well-preserved remains of two big-eared climbing rats (*Oyotylomy phyllotis*) were also present in the sample, but this species is probably intrusive.

Domestic dogs are primarily represented in the sample by teeth and jaw fragments, although several long bones were also recovered. The presence of a cut mark on the distal end of a tibia indicates butchery and probable consumption of domestic dog at El Mirador (Figure 8), as suggested for other Preclassic sites (Wing, 1978; Clutton-Brock & Hammond, 1994; Shaw, 1999; Emery *et al*., 2013). The butchered element was recovered from a Late Preclassic floor fill deposit within the Tigre Plaza (Op. 32B, Lot 22). Nineteen other cranial and post-cranial *Canis lupus familiaris* elements were found in this operation.

Most of the remaining canid remains were recovered from Late Preclassic fill deposits in the

FIGURE 8

Dog *(Canis lupus familiaris)* tibia with cutmark at distal end (631.0362;32/B/22/55– Late Preclassic)

Anatomical Region +	Observed	Expected	O/E Ratio
Cranial	39.0	63	0.62*
Axial	18.0	73	0.25
Forelimb	21.0	8	2.63
Hindlimb	25.0	16	1.56
Distal	44.0	104	0.42*

+ Cranial = skull, mandible, teeth, antler; Axial = vertebrae, ribs; Forelimb = scapula, humerus, ulna, radius; Hindlimb = pelvis, sacrum, femur, patella, tibia; Distal = metapodials, carpals/tarsals, phalanges

* Difference is not statistically significant as determined by a binomial test for differences of proportion at a significance level of 0.05.

TABLE 5

Observed vs. expected artiodactyl skeletal element distribution

nearby Structure 34 Sub-complex (Op. 26J, 26O, 26P). All of these contexts represent public ceremonial areas located within the site's architectural core. In the Maya area the use of dogs as feast foods, ritual sacrifices, and as burial and cache offerings is well-documented (Pohl, 1983; Hamblin, 1984; Shaw, 1995; Masson, 1999; Emery, 2003; Kozelsky, 2005; White *et al*., 2004; Emery *et al*., 2013). In some cases, dogs may have even been intentionally fattened on maize for elite feasts and ritual use (White *et al*., 2001, 2004). While none of the dog bones at El Mirador were associated with burials or caches, they were likely deposited in middens within and around the Tigre Plaza before being quickly incorporated into structural fill deposits during building construction (Hansen, 1990: 84). The Late Preclassic El Mirador dog remains may therefore represent general refuse associated with feasting, sacrifice, or other ceremonial activities taking place in the Tigre Plaza. The religious and dietary importance of this species appears to have been greatest during the Preclassic period. The only canid remain dating to a later time period is a radius found in a Late Classic elite residential group (Op. 17C-4, Lot1).

Unlike dogs, large bodied artiodactyls (deer and peccaries) are found in relatively equal numbers in both elite residential and public ceremonial areas at El Mirador. An analysis of the skeletal element distribution of these important species is presented to examine butchery and carcass distribution patterns across the site. This is accomplished by comparing the observed skeletal distributions to expected distributions based on the number of identifiable elements in a complete artiodactyl skeleton (Reitz & Wing, 1999: 211). Values greater than 1 tend to indicate over-representation of a particular body portion and statistical significance is assessed using a binomial test for differences of proportion at a significance level of 0.05. At El Mirador, major limb sections, which bear the most edible meat, are present in greater than expected proportions, while cranial, axial and distal elements appear to be under-represented (Table 5). However, the under-representation of distal and cranial elements is not statistically significant. This pattern did not change when the calculations were done separately for residential and non-residential contexts. These results suggest dietary use of deer and peccary, with initial butchery occurring primarily outside of the elite residential and public ceremonial proveniences represented by this sample. The major meat-bearing fore and hind limb elements of these species may be present in greater numbers due to their preferential distribution to the El Mirador elite for dietary or artifact production purposes. Similar element distribution patterns have been observed at other Maya sites (Pohl, 1985, 1994).

Artiodactyl age class and element side distributions can provide additional information about animal use and the differential access to resources. Subadult animals are often more common in ritual and elite deposits, suggesting some degree of elite control over access to young individuals (Pohl, 1983; Wing & Scudder, 1991; Carr, 1996). Skeletal elements from the left side of the body also tend to be more prevalent in ritual assemblages, perhaps due to the preferential use of one body side in ceremonial contexts (Pohl, 1985; Emery, 2003). Based on these observations, we might expect to see a greater number of left elements and subadult animals associated with the site's main public ceremonial areas. Although we did not observe any differences in artiodactyl element side (right versus left) distribution across the site, subadult deer and peccaries were present in greater numbers in residential contexts (Ops. 17 and 31) than in public ceremonial areas (Ops. 26 and 32). Sample size is small, but young animals at El Mirador may have been preferentially used for elite dietary consumption although their use in elite domestic rituals cannot be completely ruled out.

TEMPORAL CHANGE IN ANIMAL USE

Approximately 45% of the El Mirador faunal remains were recovered from well-dated contexts. All chronological comparisons in faunal use are based on the subset of dated assemblages within the site's complete faunal sample. Chronological assessments for the faunal assemblage were provided by Ray Matheny and were based on ceramic and carbon-14 data.

Over 57% of the faunal materials assigned to a particular time period at El Mirador date to the Late Preclassic period, while 12% and 30% of the sample date to the Early Classic and Late Classic respectively (Table 6). Due to the small size of the Early Classic sample, discussion of chronological change in animal use patterns will focus on contrasting animal use during the Late Preclassic and Late Classic, although Early Classic trends will be shown for comparison.

Preclassic animal use patterns at El Mirador are similar to those identified at other Preclassic sites within the Maya lowlands. Prior to the Late Preclassic, Maya animal use emphasized the use of aquatic resources such as fish and turtles (Wing & Scudder, 1991; Fradkin & Carr, 2003), while during the Late Preclassic animal use shifted towards greater reliance on larger terrestrial species including deer and dog. This Late Preclassic pattern has been observed at the sites of Cerros, Cuello, Dzibilchaltun, Colha, Seibal, Altar de Sacrificios and Kaminaljuyu (Wing & Steadman, 1980; Carr, 1985; Cliff & Crane, 1989; Pohl, 1990; Wing & Scudder, 1991; Shaw, 1999; Masson, 2004; Emery *et al*., 2013). Although similar in its overall pattern of Late Preclassic animal use, El Mirador differs from many of these sites in its extremely limited use of aquatic resources including fish and pond turtles prior to the Late Classic. This difference could be explained by variation in the local habitats surrounding each site. Cerros is located on the coast, while Seibal, Altar de Sacrificios, Cuello, Colha, and Kaminal-

Time Period	**NISP**	**%NISP**
Late Preclassic	794	57.6
Early Classic	166	12.0
Late Classic	418	30.3
	1378	100.0

TABLE 6

Distribution of dated El Mirador faunal remains by chronological period

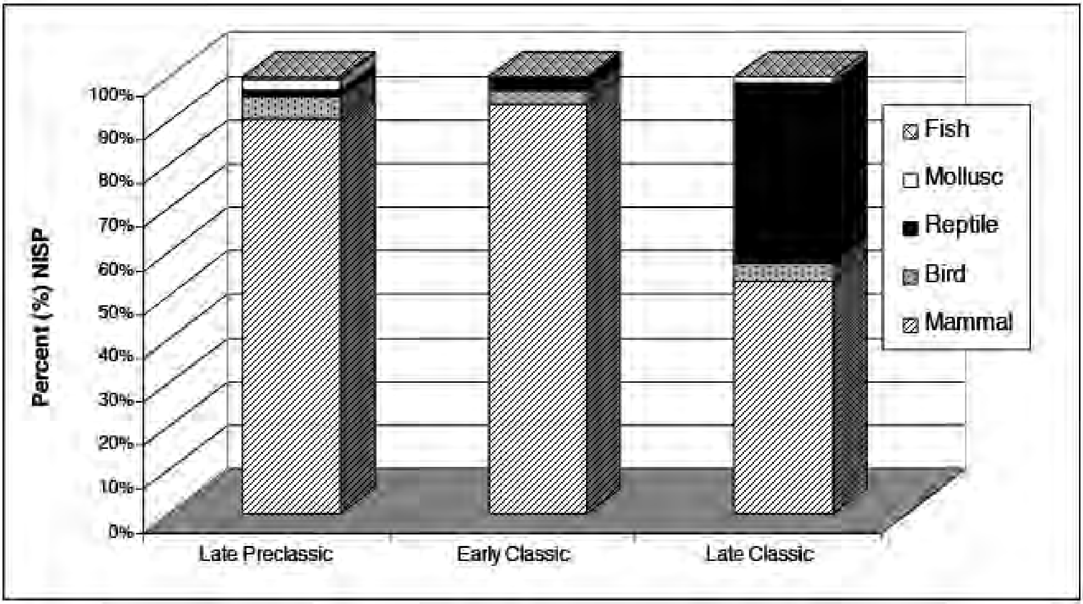

FIGURE 9

Temporal change in distribution of faunal remains according to taxonomic class (based on percent NISP). Tallies do not include unidentified vertebrate remains and marine molluscs juyu are all located near or adjacent to major lakes or rivers. The El Mirador region lacks perennial water sources, but interdisciplinary environmental reconstruction at the site indicates the presence of extensive wetland marshes (*civales*), which were used for agricultural purposes during the Preclassic Period (Hansen *et al*., 2002). Fauna from these wetland habitats appear to be under-represented in the Preclassic zooarchaeological assemblage from El Mirador. This could be due to cultural selection of terrestrial species, recovery method bias, or over-representation of ceremonial faunal (e.g., deer and dog) from non-residential contexts within the site's core. More research is needed to determine the extent to which animal use at El Mirador differs from other contemporary sites based on cultural and/or environmental heterogeneity.

When the Late Preclassic and Late Classic faunal samples from El Mirador are compared, several major trends can be discerned. Animal use during the Late Preclassic is characterized by significant use of mammalian resources, especially deer and dogs. Between the Late Preclassic and Late Classic the importance of deer, turtles and small mam-

Provenience	Time Period	Quantity	Description
17/A(Tr2)/4	Late Preclassic (mixed)	1	Bone spatula or perforator - large mammal long bone shaft fragment scored and snapped longitudinally and polished
17/A(Tr2)/6/122	Late Preclassic (mixed)	1	Bone perforator - large mammal long bone shaft fragment scored and snapped longitudinally and polished
17/B1/4/34	Late Classic	1	Medium/large mammal long bone shaft fragment – snapped longitudinally and polished
17/B3/5/112	Late Classic?	1	Bivalve (cf. Unionidae) shell fragment with two perforations below hinge
17/C5/5/59	Late Classic?	1	Mammal long bone shaft fragment – split longitudinally; polished on exterior surface
19/A1/9	Late Preclassic	1	Shell fragment – possibly polished
26/A/9/216	Late Preclassic	1	Cylindrical *Spondylus* sp. shell bead
26/J/2/104	Late Preclassic	1	Large mammal long bone shaft fragment cut longitudinally and polished exterior surface
26/J/4/106	Late Preclassic	1	*Odocoileus virginianus* proximal phalanx - proximal epiphysis removed and polished, and interior hollowed out
26/J/19/4	Late Preclassic	1	Tubular bone bead – large mammal long bone (humerus?) shaft cut through horizontally at proximal and distal ends, and polished
26/J/19/4	Late Preclassic	1	Bone tube – large mammal long bone shaft cut through horizontally at proximal and distal ends
26/K/4	Late Preclassic	1	Perforated *Spondylus* sp. shell – two perforations along dorsal edge, and exterior spines removed
26/O/5/246	Late Preclassic	1	*Conus spurius* shell tinkler fragment – horizontal slit cut in anterior body whorl
26/O/25-27/281	Late Preclassic	1	Large mammal long bone shaft fragment – snapped longitudinally and polished
31/A/1/95	Late Classic	1	*Odocoileus virginianus* femur shaft fragment cut through horizontally at distal end
31/A/5/125	Late Classic	1	Bone tube – large mammal tibia shaft cut horizontally at proximal and distal ends and polished
31/A/8/158A	Late Classic	1	Bone tube/bead - large mammal long bone shaft cut horizontally at proximal and distal ends, polished and blackened on interior and exterior surfaces
32/B/11/29	Late Preclassic	1	Turtle carapace fragment – possibly polished along one edge
32/B/11/29	Late Preclassic	1	Deer (Cervidae) phalanx distal epiphysis fragment – possibly polished/worked
32/B/12/32	Late Preclassic	1	Small cylindrical bone bead with two fine decorative grooves around circumference

Table 7. Continuation

32/B/14/38	Late Preclassic	1	Tubular bone bead – large avian long bone shaft cut through horizontally at proximal and distal ends; exterior polished
32/B/21/52	Late Preclassic	1	Perforated turtle carapace fragment
32/D/2/96	Late Preclassic/ Protoclassic	1	Teardrop-shaped shell pendant – highly nacreous shell (cf. Unionidae) perforated twice along midline
32/D1/2/102	Protoclassic	1	Perforated peccary (Tayassuidae) canine tooth – biconical perforation through root
32/D1/3/85	Late Preclassic/ Protoclassic	1	Large mammal long bone shaft fragment grooved longitudinally at one end
32/D1/4/121	Late Preclassic/ Protoclassic	1	Perforated *Spondylus* sp. shell – two perforations along dorsal edge and exterior spines removed
35/A/12/17	Late Preclassic	1	*Spondylus* sp. shell fragment – spines abraded, cut on all sides; possible mosaic inlay?
36/A/10/24	Late Preclassic	1	Thick non-nacreous cube of marine shell (cf. Strombidae) cut on four sides; likely debitage from marine shell artifact production
36/A/13/84	Unknown	3	Rectangular marine shell (cf. Strombidae) pectoral pendants with two perforations at one end
47/D/6	Late Preclassic	1	*Oliva* sp. shell tinkler fragment – horizontal slit cut in anterior body whorl; apex/spire removed just below shoulder
	TOTAL =	32	NOTE: drawings of some of these artifacts appear in Hansen (1990: 198-200)

TABLE 7

El Mirador bone and shell artifacts listed by provenience

malian game such as opossums, rabbits, agoutis, pacas and armadillos increases while the use of dog decreases (Figure 9). Exotic and important ritual species such as marine shells and large felids also decrease over time and are present in greatest quantities in the Late Preclassic assemblage. This may be due to differences in sample size, or it may reflect the site's greater political power and trade connections during the Preclassic. It is also important to note that the Late Preclassic and Late Classic faunal assemblages at El Mirador are not equal in terms the types of the contexts represented. Most of the Late Preclassic remains come from public ceremonial areas, while the Late Classic sample is dominated by remains excavated from elite residential compounds. The abundance of deer, dogs, and other large-bodied terrestrial mammals in the Late Preclassic sample may represent their preferred use for ritual or ceremonial purposes, rather than a reliance on these taxa for subsistence purposes.

FIGURE 10

Perforated peccary (Tayassuidae) canine tooth (631.0332;32/D1/2/102–Protoclassic)

FIGURE 11

A. Highly polished and blackened bone bead/tube made from a large mammal long bone shaft (631.0001; 31/A/8/158A – Late Classic); B. Bone tube made from a large mammal tibia shaft cut through horizontally at proximal and distal ends and polished (631.0006; 31/A/5/125 – Late Classic); C. Cylindrical bone bead with two fine grooves around circumference (631.0198; 32/B/12/32 – Late Preclassic); D. Bone tube made from a large mammal long bone shaft (631.0401;26/J/19/4– Late Preclassic).

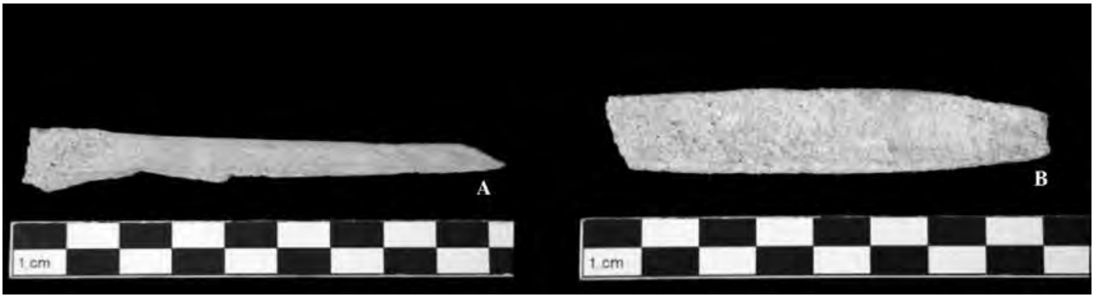

FIGURE 12

A. Polished bone perforator made from a mammal long bone shaft fragment (631.0025;17/A(Tr 2)/6/122 – Late Preclassic (mixed); B. Bone spatula or perforator made from a large mammal long bone shaft fragment (631.0056; 17/A (Tr2)/4 – Late Preclassic (mixed).

Bone and Shell Artifacts

A total of thirty-two bone (n=19) and shell (n=13) artifacts were recovered from the El Mirador excavations. A full list of artifact proveniences and descriptions is provided in Table 7. At El Mirador, modified bone artifacts were recovered from the Tigre chultun (Op. 32D), fill deposits in Structure 34 (Op. 26) and the Tigre Plaza (Op. 32B), as well as in elite residential groups within the Danta Complex (Op. 31) and outside the West Group wall system (Op. 17). Worked shell artifacts were primarily found in association with fill deposits within the Tigre Complex (Structures 34, 4D2-1, 4D3-2) and in elite residential groups located in Op. 17 and southwest of the great acropolis (Op. 47). Most of the bone and shell artifacts were not associated with discrete burial or cache deposits. Exceptions to this include a peccary tooth pendant (Figure 10) and one teardrop-shaped shell pendant (Op. 32D, Lot 2, Figure 3b), which may be associated with Protoclassic human skeletal remains found in the Tigre plaza chultun (Hansen, 1990: 89).

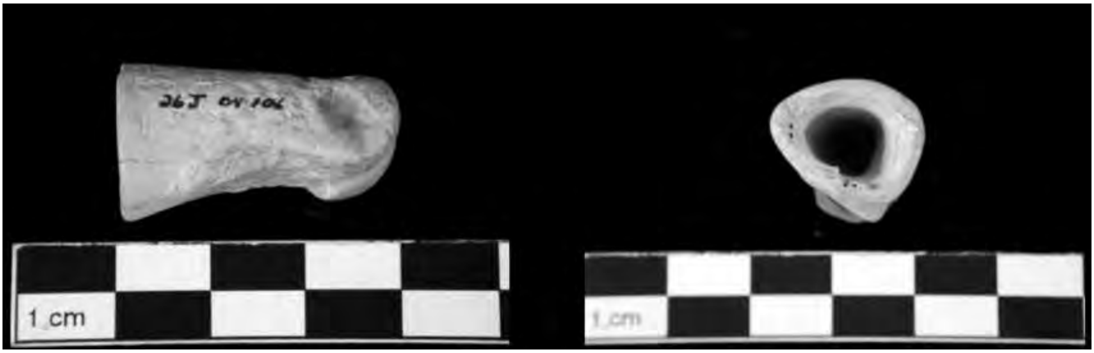

FIGURE 13
White-tailed deer *(Odocoileus virginianus)* proximal phalanx cut (a) and polished at proximal end (b) (631.0404; 26/J/4/106 – Late Preclassic).

Artifactually modified bones at El Mirador represent items intended for both personal adornment and utilitarian use. The most common bone adornments in the sample are large tubular beads created from short sections of hollow bone cut transversely at each end and polished on the exterior surface (Figure 11). In one instance, the tube was also coated in black paint (Op. 31A, Lot 8). Most of the tubular beads were made from mammalian long bone shafts, but the tibiatarsus of a large galliform bird (likely turkey) was also modified in a similar manner. Specimens of this type were recovered from Late Preclassic fill deposits in Structure 34 and beneath the Tigre Plaza (Op. 32B, Lot 14), and from Late Classic residential groups. A much smaller cylindrical bone bead decorated with two transverse incisions was also found in Op. 32B.

Several thin, tapered and polished fragments of thick cortical bone are also present in the sample (Figure 12). Many of these artifacts are broken and they likely represent fragments of bone awls or picks. At El Mirador, these artifacts are primarily associated with Op. 17, a Late Classic residential group, but in many cases it is difficult to distinguish fragments of bone awls/picks from slightly modified bone debitage. Other bone artifacts found at the site include a white-tailed deer phalanx that has been hollowed out and polished at the proximal end (Figure 13), and one perforated fragment of turtle carapace that may have been part of a drum, rattle or pendant (Figure 7).

The assortment of shell objects are all items of personal adornment, and are primarily made from non-local marine species. Spondylus shell artifacts include a small pink, cylindrical bead (Op. 26A), two almost complete perforated valves with the exterior spines and ridges removed (Op. 26K, 32D), and one shaped flat piece of shell that may have been a mosaic inlay (Op. 35A). Tinklers made from alphabet cone and olive shells are also present at the site. Shell tinklers are common artifacts in

FIGURE 14
A. White-tailed deer *(Odocoileus virginianus)* femur shaft cut through horizontally at distal end (631.0004;31/A/1/95 – Late Classic); B: Large mammal long bone shaft cut horizontally at proximal and distal ends (631.0402;26/J/19/4– Late Preclassic).

Provenience (Op./Sub. Op./Lot)	Time Period	Quantity (fragments)	Description (age/sex: elements identified) * most elements are fragmentary
17/C1/00	Late Preclassic or Late Classic	9	**1 adult:** Cranial fragments
21/I/9	Early Classic?	2	Ulna
21/I/11	Early Classic?	2	Cranial fragments, phalanx
21/I/14	Early Classic?	1	Patella (right)
21/I/15	Early Classic?	1	Second cuneiform
21/I/27	Early Classic?	3	Metacarpal/metatarsal, phalanx, humerus (right)
32/B/24	Late Preclassic	2	**1 adult:** humerus (right)
32/D/3-4	Late Preclassic/ Protoclasic	159	**2 adults – 1 male/1 indeterminate sex:** cranial fragments,mandible (enamel very worn), upper first molar (left), vertebrae, clavicle (2 - right), scapula (right), ribs (right/left), humerus (right/left), ulna (right/left), radius (left), capitate (left), triquetral, os coxa (right), femur, tibia (right/left), fibula, talus (2 right), calcaneus (2 right, 1 left), navicular, first metatarsal (left), second metatarsal, third metatarsals (2 left, 1 right), fifth metatarsal (left), phalanges
unknown	unknown	130	**1 juvenile (1-3 years old):** temporal (right/left), zygomatic (left), occipital, mandible, atlas, axis, cervical vertebrae, thoracic vertebrae, ribs (right/left), clavicle (left), radius (left), os coxa (left), femur (left), metacarpals/metatarsals
	TOTAL =	**309**	NOTE: It is unclear how many individuals are represented by the isolated human remains recovered in Operation 21 (salvage excavations in a plaza group near the Mono Complex)

TABLE 8

Human skeletal elements identified among the El Mirador zooarchaeological remains

Maya assemblages. They are made from modified marine gastropod shells with the spire removed and with a transverse slit perforation cut into the anterior body whorl. Broken tinklers were found in both public ceremonial (Op. 26O) and elite residential contexts (Op. 47D). Other marine shell artifacts from El Mirador include a set of three rectangular pectoral pendants likely made from the shell of a large species of conch (Op. 36A, Lot 13), and a thick cube of marine shell cut on all four sides (Op. 36A, Lot10). Despite their highly nacreous shell, freshwater clams (Unionidae) were used to a much lesser extent as shell artifacts. Examples include one freshwater clam shell that was perforated along the hinge area (Op. 17B3), one fragment of a shaped and perforated adornment (Op. 17B1), and one teardrop-shaped pendant from the Tigre chultun (Op. 32D).

Overall, there is little shell debitage at El Mirador, which suggests that the marine shells were imported to the site as finished artifacts, or that shell artifact production was taking place in an area of the site not yet excavated. In contrast, bone working appears to have been taking place on-site (Figure 14). Small amounts of bone debitage is found in Late Preclassic and Late Classic deposits across the site including units in Operations 17, 26, 31, 32 and 47. Evidence of bone and shell artifact production appears in both elite residential and ceremonial areas, but residential compounds have a slightly higher ratio of debitage to finished artifacts.

HUMAN REMAINS

The remains of at least four adults and one child (approximately 1-3 years old) were identified in the El Mirador assemblage. A summary of the human remains found among the zooarchaeological materials is presented in Table 8. Isolated adult human bones of unknown sex were recovered from a plaza group near the Monos Complex (Op. 21), and from a floor fill deposit in the Tigre Plaza (Op.

32B). Skeletal remains of two adults were also found in the lower levels of the Tigre plaza chultun (Op. 32D, Lots 3-4). One of the adults is known to be a male based on the shape and breadth of the greater sciatic notch, but the other individual is of indeterminate sex. No evidence of disease or injury was observed on the relatively complete skeletons found in the chultun, but the single mandible showed extensive wearing of the tooth enamel. The juvenile remains at El Mirador are of unknown provenience.

SUMMARY AND CONCLUSIONS

The El Mirador faunal assemblage provides information regarding the role of faunal resources in subsistence, ritual and exchange networks in the Central Maya lowlands from Late Preclassic to Late Classic times. Throughout the site's occupation, large terrestrial mammal species such as white-tailed deer, brocket deer, and peccaries were used intensively. Domestic dogs were also kept at the site and may have also been consumed particularly during the Late Preclassic. A diversity of other medium to small-bodied terrestrial mammals and large galliform birds, such as the turkey and curassow, also fit into the highly terrestrial pattern of subsistence observed at El Mirador. Although on-site reservoirs, or wetland habitats, surrounding the site could have provided easy access to aquatic resources such as apple snails and small turtles, these habitats do not appear to have been a significant source of faunal resources for the site's elite until the Late Classic. This seems to argue against suggestions of anthropogenic *bajo* alteration to create increased habitat for aquatic species during the primary period of site occupation. However, since the faunal remains analyzed in this report were excavated exclusively from elite contexts, it is possible that we are only seeing one part of the larger animal use patterns practiced at El Mirador.

Intra-site differences between residential and ceremonial contexts also suggest preferential use of particular species for public ritual or elite feasting. Dogs were primarily found in association with public ceremonial architecture within the Tigre Plaza, while other important taxa such as deer, peccaries and large galliform birds were more evenly distributed across the site. Late Preclassic dog use at El Mirador may therefore have focused on using this reliable resource as a feasting component or sacrificial animal. This finding, however, should be interpreted with caution. Dogs at El Mirador are primarily associated with Late Preclassic deposits, which come primarily from the site's public ceremonial areas. The association of dogs with ceremonial structures may therefore be an artifact of intra-site sampling.

Access to marine resources through trade is evidenced by the presence of a parrotfish and multiple species of marine molluscs. The parrotfish may have been imported as a subsistence resource, but the other marine fauna were likely exploited purely for ornamental and ritual use. The lack of marine shell debitage at the site suggests that these exotic resources were imported as finished artifacts from coastal localities. The extent of coastal trade is difficult to assess from the present sample. The diversity and abundance of marine fish present at the site is not likely to be represented by the El Mirador assemblage due to lack of fine screen recovery techniques. In addition, the specimens analyzed for this report do not represent the entire invertebrate assemblage recovered from the site. However, it is interesting to note that the El Mirador inhabitants imported marine resources from both the Atlantic and Pacific coasts. This animal resource acquisition pattern reinforces earlier propositions of El Mirador's importance in north-south, as well as east-west, trade interactions between the coasts and the interior Maya lowlands (Hansen, 1990: 211). The identification of *Melagris gallopavo* at El Mirador provides additional evidence for the site's role in long distance exchange networks. Although the ocellated turkey (*Meleagris ocellata*) was locally available, tamed or domesticated wild turkeys may have been obtained through trade connections with northern or central Mexico. These animals could have been raised on-site in domesticated form for use as subsistence or ritual resources. The identification of *Meleagris gallopavo* in Late Preclassic deposits at El Mirador represents the earliest record of this species within the Maya region.

ACKNOWLEDGEMENTS

Funding for this project and permission to identify the remains was generously provided by Dr. Ray Matheny and Dr. John Clark, New World Archaeological Foundation, Brigham Young University, and the Museum of Peoples and Cultures. Dr. Matheny provided chronological and contextual information important to the full analysis of the remains. The Florida Museum of Natural History provided access to comparative collections used to complete the faunal analysis, and special acknowledgement is due to David Steadman, John Slapcinsky, Camilla Speller, and Dongya Yang for their assistance in identifying the avian and molluscan remains.

REFERENCES

Campbell, J. A. 1998: Amphibians and Reptiles of Northern Guatemala, the Yucatan and Belize. University of Oklahoma Press, Norman.

Cannon, M. D. 1999: A Mathematical Model of the Effects of Screen Size on Zooarchaeological Relative Abundance Measures. *Journal of Archaeological Science* 26: 205-214.

Carr, H. S. 1985: Subsistence and ceremony: faunal utilization in the Late Preclassic community at Cerros, Belize. In: Pohl, M. (ed.): *Prehistoric Lowland Maya Environment and Subsistence*: 115-132. Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA.

— 1996: Precolumbian Maya exploitation and management of deer populations. In: Fedick, S.L. (ed.): *The Managed Mosaic: Ancient Maya Agriculture and Resource Use*: 251-261. University of Utah Press, Salt Lake City.

Chase, A.; Chase, D. & Teeter, W. G. 2004: Archaeology, faunal analysis, and interpretation: lessons from Maya studies. *Archaeofauna* 13: 11-18.

Cliff, M. B. & Crane, C. J. 1989: Changing subsistence economy at a Late Preclassic Maya community. In: McAnany, P.A. & Isaac, B.L. (eds.): *Prehistoric Maya Economies of Belize*: 295-324. JAI Press, Greenwich.

Clutton-Brock, J. & Hammond, N. 1994: Hot dogs: comestible canids in Preclassic Maya culture at Cuello, Belize. *Journal of Archaeological Science* 21: 819-826.

Dirrigl, F .J. Jr. 2001: Bone mineral density of wild turkey (*Meleagris gallopavo*) skeletal elements and its effects on differential survivorship. *Journal of Archaeological Science* 28: 817-832.

Emery, K. F. 2003: Animals in the Maya underworld: reconstructing elite Maya ritual at the Cueva de los Quetzales, Guatemala. In: O'Day, S.J.; Van Neer, W. & Ervynck, A. (eds.): *Behavior Behind Bones: the Zooarchaeology of Religion, Ritual, Status and Identity*: 101-113. Oxbow Books, London.

— 2004a: In search of the "Maya diet": is regional comparison possible in the Maya tropics? *Archaeofauna* 13: 37-56.

— 2004b: In search of assemblage comparability: methods in Maya zooarchaeology. In: Emery, K.F. (ed.): *Maya Zooarchaeology: New Directions in Method and Theory*: 15-33. Monograph 51. Cotsen Institute of Archaeology, University of California, Los Angeles.

— 2012: In: Foias, A.E. & Emery, K.F. (eds.): *Motul de San José: Politics, History and Economy in a Classic Maya Polity*: 291-325. University of Florida Press, Gainesville.

Emery, K. F.; Thornton, E. K.; Cannarozzi, N. R.; Houston, S. & Escobedo, H. 2013: Archaeological Animals of the Southern Maya Highlands: Zooarchaeology of Kaminaljuyu. In: Gotz, Ch.M. & Emery, K.F. (eds.): *The Archaeology of Mesoamerican Animals*: 381-416. Lockwood Press, Atlanta.

Emery, K. F. & Thornton, E. K. in prep.: Fine-gauge screening tests of recovery of zooarchaeological materials at sites in the Motul Polity. Manuscript in preparation.

Ericson, P. G. 1987: Interpretations of archaeological bird remains: a taphonomic approach. *Journal of Archaeological Science* 14: 65-75.

Fradkin, A. & Carr, H. S. 2003: Middle Preclassic landscapes and aquatic resource use at Cuello, Belize. In: King, F.W. & Porter, Ch.M. (eds.): *Zooarchaeology: Papers to Honor Elizabeth S. Wing Bulletin of the Florida Museum of Natural History* 44: 35-42.

Gordon, E. A. 1993: Screen Size and Differential Faunal Recovery: A Hawaiian Example. *Journal of Field* Archaeology 20: 453-459.

Grayson, D. K. 1981: The effects of sample size on some derived measures in vertebrate faunal analysis. *Journal of Archaeological Science* 8(1): 77-88.

— 1984: *Quantitative Zooarchaeology*: *Topics in the Analysis of Archaeological Faunas*. Academic Press, Orlando.

Hamblin, N. 1984: *Animal Use by the Cozumel Maya*. University of Arizona Press, Tucson.

Hansen, R. D. 1990: Excavations in the Tigre Complex El Mirador, Peten, Guatemala. *Papers of the New World Archaeological Foundation*. Volume 62. Brigham Young University, Provo.

Hansen, R. D.; Bozarth, S.; Jacob, J.; Wahl, D. & Schreiner, T. 2002: Climatic and environmental variability in the rise of Maya civilization. *Ancient Mesoamerica* 13: 273–295.

James, S. R. 1997: Methodological Issues Concerning Screen Size Recovery Rates and Their Effects on Archaeofaunal Interpretations. *Journal of Archaeological Science* 24: 385-397.

KOZELSKY, K. 2005: Identifying social drama in the Maya region: Fauna from the Lagartero Basurero, Chiapas, Mexico. Unpublished MA Thesis. Department of Anthropology, Florida State University, Tallahassee.

LECOUNT, L. J. 2001: Like water for chocolate: feasting and political ritual among the Late Classic Maya at Xunantunich, Belize. *American Anthropologist* 103(4): 935-953.

LEOPOLD, A. S. 1959: *Wildlife of Mexico: The Game Birds and Mammals*. University of California Press, Berkeley.

LIVINGSTON, S. D. 1989: The taphonomic interpretations of avian skeletal part frequencies. *Journal of Archaeological Science* 16: 537-547.

MASSON, M. 1999: Animal resource manipulation in ritual and domestic contexts at Postclassic Maya communities. *World Archaeology* 31: 93-120.

— 2004: Faunal exploitation from the preclassic to the postclassic periods at four Maya settlements in northern Belize. In: Emery, K.F. (ed.): *Maya Zooarchaeology: New Directions in Method and Theory*: 97-122. Monograph 51. Cotsen Institute of Archaeology, University of California, Los Angeles.

MOHOLY-NAGY, H. 1985: The social and ceremonial uses of marine molluscs at Tikal. In: Pohl, M. (ed.): *Prehistoric Lowland Maya Environment and Subsistence Economy*: 147-158. Papers of the Peabody Museum of Archaeology and Ethnology. Vol. 77. Harvard University, Cambridge, MA.

NICHOLSON, R. A. 1996: Bone degradation, burial medium and species representation: debunking the myths, an experiment-based approach. *Journal of Archaeological Science* 23: 513-533.

POHL, M. 1983: Maya ritual faunas: vertebrate remains from burials, caches, caves and cenotes in the Maya lowlands. In: Kolata, A. (ed.): *Civilization in the Ancient Americas*: 55-103. University of New Mexico Press, Albuquerque.

— 1985: The privileges of Maya elites: prehistoric vertebrate fauna from Seibal. In: Pohl, M. (ed.): *Prehistoric Lowland Maya Environment and Subsistence Economy*: 133-145. Papers of the Peabody Museum of Archaeology and Ethnology. Vol. 77. Harvard University, Cambridge, MA.

— 1990: The ethnozoology of the Maya: fauna remains from five sites in Peten, Guatemala. In: Wiley, G.R. (ed.): *Excavations at Seibal*: 144-174. Memoirs of the Peabody Museum of Archaeology and Ethnology. Vol. 17(3). Harvard University, Cambridge, MA.

— 1994: The economics and politics of Maya meat eating. In: Brumfiel, E.M. (ed.): *The Economic Anthropology of the State*: 121-149. Monographs in Economic Anthropology, no. 11. University Press of America, New York.

POHL, M. D. & FELDMAN, L. H. 1982: The traditional role of women and animals in the lowland Maya economy. In: Flannery, K.V. (ed.): *Maya Subsistence: Studies in Memory of Dennis E. Puleston*: 295-311. Academic Press, New York.

QUITMYER, I. R. 2004: What kind of data are in the back dirt? An Experiment on the Influence of screen size on optimal data recovery. *Archaeofauna* 13: 109-129.

REITZ, E. J. & WING, E. S. 1999: *Zooarchaeology*. Cambridge Manuals in Archaeology. Cambridge University Press, New York.

RINGROSE, T. J. 1993: Bone counts and statistics - a critique. *Journal of Archaeological Science* 20(2): 121-157.

SCHORGER, A. W. 1966: *The Wild Turkey: Its History and Domestication*. University of Oklahoma Press, Norman.

SHARER, R. J. 1994: *The Ancient Maya*. 5th edition. Stanford University Press, Stanford.

SHAW, L. C. 1995: The importance of dog in ritual freasting in the Maya Preclassic. Paper presented at the 60th Annual Meeting of the Society for American Archaeology, May 4, 1995, Minneapolis, MN.

— 1999: Social and ecological aspects of Preclassic Maya meat consumption at Colha, Belize. In: White, Ch. (ed.): *Reconstructing Ancient Maya Diet*: 83-100. University of Utah Press, Salt Lake City.

STEADMAN, D. W. 1980: A review of the osteology and paleontology of turkeys (Aves: Meleagridae). *Contribution of the Science and Natural History Museum of Los Angeles County, California* 330: 131-207.

TEETER, W. G. & CHASE, A. F. 2004: Adding flesh to bones: using zooarchaeology research to answer the big-picture questions. *Archaeofauna* 13: 155-172.

THORNTON, E. K. 2012: Animal resource use and exchange at an inland Maya port: Zooarchaeological investigations at Trinidad de Nosotros. In: Foias, A.E. & Emery, K.F. (eds.): *Politics, History, and Economy at the Classic Maya Center of Motul de San Jose, Guatemala*: 326-356. University of Florida Press.

THORNTON, E. K. & EMERY, K. F. 2015: The Uncertain Origins of Mesoamerican Turkey Domestication. *Journal of Archaeological Method and Theory* published on-line 11 December 2015. DOI 10.1007/s10816-015-9269-4.

THORNTON, E. K.; EMERY, K. F.; STEADMAN, D.; SPELLER, C.; MATHENY, R. & YANG, D. 2012: Earliest Mexican turkey (*Meleagris gallopavo*) in the Maya region found at the Preclassic site of El Mirador, Peten, Guatemala. *PLoS 1* 7(8):e42630.

WAKE, T. A. 2004: On the Paramount Importance of Adequate Comparative Collections and Recovery Techniques in the Identification and Interpretation of Vertebrate Archaeofaunas: A Reply to Vale & Gargett (2002). *Archaeofauna* 13: 173-182.

WHITE, CH. D.; POHL, M.; SCHWARCZ, H. P. & LOHGSTAFFE, F. J. 2001: Isotopic evidence for Maya patterns of deer and dog use at Preclassic Colha. *Journal of Archaeological Science* 28: 89-107.

— 2004: Field and forest: deer and dog diets at Lagarto and Copan. In: Emery, K.F. (ed.): *Maya Zooarchaeology: New Directions in Method and Theory*: 141-158. Monograph 51. Cotsen Institute of Archaeology, University of California, Los Angeles.

WING, E. S. 1977: Factors influencing exploitation of marine resources. In: Benson, E.P. (ed.): *The Sea in the Precolumbian World*: 47-66. Dumbarton Oaks Research Library, Washington, D.C.

— 1978: Use of dogs as food: an adaptation to the coastal environment. In: *Preclassic Coastal Adaptations: the Economy and Ecology of Maritime Middle America*: 29-41. Academic Press, New York.

WING, E. S. & QUITMYER, I. R. 1985: Screen size for optimal data recovery: a case study. In: Adams, W.H. (ed.): *Aboriginal Subsistence and Settlement Archaeology of the Kings Bay Locality*. *Volume 2: Zooarchaoelogy*. University of Florida, Department of Anthropology, Gainesville.

WING, E. S. & SCUDDER, S. J. 1991: The exploitation of animals. In: Hammond, N. (ed.): *Cuello: An Early Maya Community in Belize*: 84-97. Cambridge University Press, Cambridge.

WING, E. S. & STEADMAN, D. 1980: Vertebrate faunal remains from Dzibilchaltun. In: Andrews, E.W.I. & Andrews, E.W.V. (eds.): *Excavations at Dzibilchaltun, Yucatan, Mexico*: 326-331. Middle American Research Institute Publication, no. 48, New Orleans.

APPENDIX 1

*** = terrestial landsnail (likely intrusive)**

LIST OF EL MIRADOR ZOOARCHAEOLOGICAL REMAINS BY PROVENIENCE

Provenience: Operation/Sub-Operation/Lot/Bag – predominant period

16/A1/2 – Late Preclassic

1 Tayassuidae: lower fourth premolar, anterior 0.75

16/A1/4 – Late Preclassic

1 Mammalia (medium/large): long bone shaft fragment

16/A2/8

13 Mammalia (large): long bone shaft fragment

4 *Odocoileus virginianus:* antler fragment

16/A2/13/57 – Early Classic

4 Aves (large): tibiotarsus (left) distal 0.3 of shaft, in four fragments

16/A2/19/72 – Late Preclassic

2 *Canis lupus familiaris*: upper fourth premolar (right), in two fragments

17A(Tr2)/4 – Late Preclassic (mixed)

11 Vertebrata: 7 unidentified bone fragments, 4 long bone shaft fragments

1 Mammalia (large): long bone shaft fragment

1 Mammalia (large): long bone shaft fragment, snapped longitudinally and polished (bone spatula or perforator)

4 Tayassuidae [subadult]: parietal (left and right); radius/ulna (right) proximal 0.75; canine

1 *Odocoileus virginianus* [subadult]: long bone epiphysis fragment

17/A(Tr2)/5 – Early Classic

1 Vertebrata: long bone shaft fragment

4 Emydidae: hyoplastron (right), rib (right?)

15 Mammalia: long bone shaft fragment

1 Mammalia: maxilla/mandible tooth row fragment

7 Mammalia (large): long bone shaft fragment

3 cf. *Cuniculus paca* [subadult]: parietal (left), in three fragments

1 Cervidae: zygomatic (right)

1 *Mazama* sp.: zygomatic (right)

1 *Odocoileus virginianus*: metapodial shaft fragment

3 Tayassuidae: maxilla (left) fragment, in three fragments

17/A(Tr2)/6/122 – Late Prelassic (mixed)

1 Kinosternidae: seventh marginal (right)

1 Mammalia (large): long bone shaft fragment, snapped longitudinally and polished (bone perforator)

1 *Sylvilagus* sp.: femur (right) proximal 0.75

1 *Dasyprocta punctata*: radius (left)

1 Felidae (large) [subadult]: metapodial, proximal 0.75 of shaft

1 Cervidae (cf. *Odocoileus virginianus*): lumbar vertebra

3 *Odocoileus virginianus*: proximal phalanx (left), humerus (right) distal epiphysis, patella (right)

17/A1/1/11 – Late Classic

7 Mammalia (medium/large): unidentified bone fragment

17/A1/6/29 – Late Classic

1 *Mazama* sp.: upper molar (right)

17/A1/5/26 – Late Classic?

1 Bivalvia: valve fragment

17/A3/4/78 – Late Classic

1 Mammalia (large): long bone shaft fragment

2 cf. *Odocoileus virginianus*: femur (left?) proximal/anterior 0.25 of shaft, in two fragments

17/A4/3/90 – Late Classic

4 Vertebrata: unidentified bone fragments

8 Mammalia (medium/large): 4 long bone shaft fragments; 4 unidentified bone fragments

17/A4/4/93 – mixed

1 *Mazama* sp.: metatarsal (right) proximal 0.5, rodent gnawed

17/B1/1/18 – Late Classic

1 *Mazama* sp.: mandible (left) posterior 0.5 of tooth row

17/B1/4/34 – Late Classic

5 Mammalia (medium/large): 1 cranial fragment; 1 long bone shaft fragment (snapped longitudinally and polished); 3 unidentified bone fragments

2 *Mazama* sp.: metatarsal (left) proximal 0.5, in two fragments

17/B1/5/38 – Late Classic?

1 Mollusca: shell fragment

17/B1/5/42 – Early Classic

9 Mammalia: 2 rib fragments; 7 unidentified fragments

1 Mammalia (large): rib fragment

1 *Dasyprocta/Cuniculus* sp.: rib (right) medial 0.5

3 *Mazama* sp.: sixth lumber vertebra, in 3 fragments

17/B1/6/46 – Classic (mixed)

Mammalia: 1 vertebra fragment; 5 unidentified bone fragments

Mazama sp.: lower third molar (left); ulna (right) proximal 0.25, burnt

17/B1/6/152 - mixed

4 cf. *Canis lupus familiaris*: second, third and fifth metatarsals; phalanx

4 *Mazama* sp.: humerus (right) distal 0.75; radius (right) (unfused distal epiphysis)

17/B1/7/54 – Late Classic

2 Mammalia (large): long bone shaft fragment

17/B1/10/65 – Late Preclassic

2 Mammalia: unidentified bone fragment

1 Cervidae (cf. *Mazama* sp.): rib (right) medial 0.3

1 *Mazama* sp.: calcaneus (left)

17/B1(TP2)/4/115 – Late Classic

3 Vertebrata: unidentified bone fragments

5 Mammalia: 1 cranial fragment; 4 unidentified bone fragments

5 Mammalia (medium): long bone shaft fragment

3 Mammalia (large): long bone shaft fragment

2 *Mazama* sp.: astragalus (right), in two fragments

17/B1(TP2)/5/144 – Early Classic

9 Mammalia: 6 cranial fragments; 1 sacrum fragment; 2 unidentified bone fragments

6 Mammalia (large): 1 rib fragment; 4 long bone shaft fragments; 1 tibia proximal shaft fragment

5 *Cuniculus paca* [subadult]: 2 thoracic vertebrae; 2 lumbar vertebrae; 1 sacral vertebra

3 Cervidae: femur (right) distal epiphysis (right) unfused, in two fragments; proximal phalanx distal 0.75

6 *Mazama* sp.: femur (right) distal 0.25 of shaft; humerus (left) middle 0.75 of shaft and proximal epiphysis; os coxa (right) middle 0.75; middle phalanx

17/B3/5/112 – Late Classic?

1 cf. Unionidae: hinge fragment, two perforations below hinge

17/B3/5/119 – Late Classic

1 Cervidae: metapodial, anterior/distal 0.5 of shaft

1 *Odocoileus virginianus:* thoracic vertebra

17/B4/9/195 – Late Classic

Vertebrata: unidentified bone fragments

32 Testudines: carapace/plastron fragments

2 Emydidae: third neural; fifth neural

1 Aves: tibiotarsus? shaft fragment

2 Mammalia: unidentified bone fragment

17/B5/7/168 – Late Classic

54 Vertebrata: unidentified bone fragments

1 Testudines: carapace/plastron fragment

1 *Dermatemys mawii:* hyoplastron (left)

10 cf. *Dermatemys mawii*: hypoplastron (right); neural fragment; rib fragment

17/B5/10/180 – Late Classic

1 Mammalia (medium): long bone shaft fragment

17/B5/18/200 – Late Classic

1 cf. Carnivora: mandible (left) ascending ramus fragment

17/B5/5/130 – Late Classic

Vertebrata: unidentified bone fragments

3 Testudines: carapace fragment

17/B5/7/141 – Late Classic

11 Vertebrata: unidentified bone fragments

28 Testudines: carapace fragments

4 Emydidae: first rib; fifth rib; epiplastron; plastron fragment

17/B5/7/167 – Late Classic

2 Testudines: carapace fragments

11 *Dermatemys mawii*: second rib (right); third rib (right and left); second neural; third neural; hyoplastron (left); hypoplastron (right); 2 marginal fragments; 2 rib fragments

17/C1/0/1 – Late Preclassic/Late Classic (mixed)

12 Vertebrata: unidentified bone fragments

17/C2/1/30 –Late Classic

1 Aves (large): proximal phalanx

17/C2/2/27 –Classic?

1 Mammalia (small): long bone shaft fragment

1 *Ototylomys phyllotis*: mandible (right)

17/C4/1/32 – unknown (Late Classic?)

1 *Didelphis* sp.: mandible (left)

1 *Dasypus novemcinctus*: seventh cervical vertebra

1 *Canis lupus familiaris*: radius, middle 0.7 of shaft, rodent gnawed

1 Tayassuidae: upper first incisor (left)

17/C5/5/59 (floor 2) – unknown (Late Classic?)

4 Vertebrata: unidentified bone fragments

10 Mammalia: long bone shaft fragments

1 Mammalia: long bone shaft fragment, split longitudinally and polished, in two fragments

19/A1/9 – Late Preclassic?

1 Mollusca: shell fragment, possibly polished

19/B/12 – mixed

1 Mammalia (large): long bone shaft fragment

21/I/1/2 – Classic

1 Mammalia (large): long bone shaft fragment, heavily eroded

21/I1/7 - Early Classic

1 Mammalia: femur? shaft fragment, rodent gnawed

21/I1/11/26 – Classic

25 Vertebrata: unidentified bone fragments

21/I1/14 – mixed

1 Gastropoda: shell fragment

21/I1/14/34 – mixed

3 Vertebrata: unidentified bone fragments

21/I1/9/19 – Classic/Early Classic

1 Mammalia: long bone shaft fragment

21/I1/11/26 – Classic

4 Mammalia: unidentified bone fragments

21/I1/13/30 – Early Classic

8 Mammalia: unidentified bone fragments

21/I1/14/34 – Early Classic

10 Mammalia: 5 long bone shaft fragments;

5 unidentified bone fragments

21/I1/27 – Early Classic

29 Vertebrata: unidentified bone fragments

24 Mammalia: unidentified bone fragments

6 Mammalia (large): long bone shaft fragments

21/--/1 – mixed

5 Mammalia: unidentified bone fragments

4 Mammalia (large): 3 long bone shaft fragments; 1 unidentified bone fragment

3 Mammalia (medium): long bone shaft fragments

1 Tayassuidae: metapodial, middle 0.5 of shaft

26/1/4/107 – Late Preclassic

1 *Pomacea flagellata*: shell

26/A/4 – Late Preclassic

1 *Pomacea flagellata:* shell

26/A/9/216 – Late Preclassic

1 *Spondylus* sp.: cylindrical shell bead

26/B/10/32 – Late Preclassic

18 Vertebrata: unidentified bone fragments

13 Mammalia (small/medium): long bone shaft fragments

1 Mammalia (medium/large): long bone shaft fragments

2 Mammalia (medium): metapodial, distal 0.25, in two fragments

26/C/4/61 – Late Preclassic

4 Mollusca: shell fragments

26/D/12/261 – Late Preclassic

3 *Pomacea flagellata*: shell fragments

26/H/3/81 – Late Preclassic

1 *Mazama* sp.: calcaneus (left)

26/J/2/104 – Late Preclassic

Mammalia (large): long bone shaft fragment, cut longitudinally and polished

26/J/4/106 – Late Preclassic

30 Vertebrata: unidentified bone fragments

1 *Sparisoma* sp.: dentary

1 Aves (large): long bone shaft fragment

1 *Meleagris gallopavo* [male]: tarsometatarsus (right), distal 0.5 of shaft

14 Mammalia: unidentified bone fragments

4 Mammalia (medium/large): long bone shaft fragments

1 Mammalia (large): long bone shaft fragment

3 *Canis lupus familiaris*: lower canine; phalanx; radius, middle 0.25 of shaft

1 Cervidae: metapodial shaft fragment

2 *Odocoileus virginianus*: middle phalanx; proximal phalanx, cut through horizontally and polished at proximal end

26/J/14/120 – Late Preclassic

33 Vertebrata: unidentified bone fragments

1 Tayassuidae: maxilla (right), anterior/lateral fragment

1 *Meleagris gallopavo* [male?]: ulna (left), middle 0.3 of shaft

2 Mammalia: unidentified bone fragments

2 *Canis lupus familiaris*: canine, in two fragments

1 Tayassuidae: humerus (left), distal 0.25

1 *Odocoileus virginianus*: proximal phalanx (right)

26/J/19/4 – Late Preclassic

3 Vertebrata: unidentified bone fragments

1 Aves: long bone shaft fragment

1 Aves (large) (cf. *Meleagris* sp.): ulna (right), middle 0.3 of shaft

10 Mammalia: 2 long bone shaft fragments; 8 unidentified bone fragments

1 Mammalia (large): long bone shaft fragment, shaft cut horizontally at proximal and distal ends, polished exterior

1 Mammalia (large): long bone shaft fragment, cut horizontally along at proximal and distal ends

3 *Canis lupus familiaris*: maxilla (right); upper canine (right); upper third incisor (left)

3 *Mazama* sp.: 1 metacarapal (left); 2 distal metapodial fragments

26/K/4 – Late Preclassic

1 *Spondylus* sp.: valve (right), spines abraded off, two perforations along on edge. Very similar to valve in found in 32/D1/4/121.

26/K/4/96 – Late Preclassic

1 *Meleagris* sp.: femur (left) shaft fragment, rodent gnawed

26/O/5/246 – Late Preclassic

1 *Conus spurius*: shell tinkler – horizontal slit cut through anterior body whorl

26/O/8/259

1 *Euglandina* sp.*

26/O/24/273 – Late Preclassic

2 *Canis lupus familiaris*: mandible (right), in two fragments

26/O/25-27/281 – Late Preclassic

4 Vertebrata: unidentified bone fragments

1 Aves (large): long bone shaft fragment

1 *Meleagris* sp.: carpometacarpus (left)

1 *Meleagris gallopavo* [male]: ulna (right)

1 *Meleagris cf. gallopavo* [female?]: tarsometatarsus (right)

1 Mammalia (small/medium): radius, middle shaft fragment

1 Mammalia (large): long bone shaft fragment, one end snapped longitudinally, polished

1 Mammalia (large): long bone shaft fragment

1 *Canis lupus familiaris*: radius (right), proximal 0.3

26/P/9/29 – Late Preclassic

1 Mammalia: long bone shaft fragment

2 Mammalia (large): long bone shaft fragment, in two fragments

26/P/17/286 – Late Preclassic

36 Vertebrata: unidentified bone fragments

4 Aves (large): long bone shaft fragment

5 Mammalia: unidentified bone fragment

4 *Mazama* sp.: ox coxa (left), middle 0.75, in four fragments

26/P/25/292 – Late Preclassic

4 Mammalia: 2 long bone shaft fragments; 2 unidentified bone fragments

1 *Canis lupus familiaris*: upper canine (left)

1 cf. *Odocoileus virginianus*: ischium (left) fragment

26/P/25/295 – Late Preclassic

2 Vertebrata: unidentified bone fragments

8 Mammalia: unidentified bone fragments

2 Mammalia (large): femur? shaft fragments

1 *Canis lupus familiaris*: upper canine (left)

1 *Odocoileus virginianus*: femur, proximal 0.25

26/P/26/246 –

1 *Bulimulus unicolor**

27/B3/1 – Late Preclassic

1 *Crax rubra* [subadult]: coracoid (right)

30/A/15/40 – unknown (Late Classic?)

1 Lacertilia: quadrate

24 Mammalia (small): 4 caudal vertebrae; 6 rib fragments; 1 scapula, 13 unidentified bone fragments

23 Muridae: 1 temporal; 1 incisor; 2 maxilla fragments; 2 humerus (left); 3 ulna (left); 1 femur (right); 1 tibia (right); 1 thoracic vertebra; 5 lumbar vertebrae; 4 metapodials; 2 phalanges. Likely intrusive

12 *Ototylomys phyllotis*: 2 mandible (left); 1 occipital; 1 atlas; 1 scapula (left); 2 femurs (left); 1 tibia (left); 2 os coxae (left); 2 os coxae (right). Likely intrusive

31/A/1/95 – Late Classic

1 *Mazama* sp.: calcaneus (left)

2 *Odocoileus virginianus*: femur (right) shaft cut through horizontally at distal end; ischium (right) posterior fragment

31/A/2/97 – Late Classic

1 Aves (large): long bone shaft fragment

1 *Sylvilagus* sp.: tibia (left) proximal 0.3

31/A/3/101 – Late Classic

1 Emydidae: eighth rib (right)

31/A/4/107 – Late Classic

1 *Odocoileus virginianus*: lumbar vertebra

31/A/5/125 – Late Classic

1 Mammalia (large): tibia (right), shaft cut through horizontally at proximal and distal ends, polished

31/A/5/124 – Late Classic

13 Mammalia (large): long bone shaft fragments, 1 fragment burnt

5 *Odocoileus virginianus*: femur (right), metatarsal, proximal phalanx

31/A/6/138 – Late Classic

17 *Odocoileus virginianus* [subadult]: 1 me-

tacarpal (right); 6 os coxae (left and right) fragments; 4 sacrum fragments; 6 lumbar vertebrae fragments

31/A/8/158A – Late Classic

1 Mammalia (large): long bone shaft fragment, tubular bone bead polished and blackened

31/D/19/165 – Late Classic

4 Tayassuidae: mandible (left and right), in four fragments

31/D/20/166 – Late Classic

1 Aves [subadult]: tarsometatarsus, middle shaft fragment

1 cf. Aves [subadult]: coracoid? fragment

2 Aves (medium): tibiotarsus (left)

3 *Ortalis vetula*: femur (left and right); tibiotarsus (left)

1 Sciuridae: tibia (left)

32/B/10/23 – unknown

12 Mollusca: shell fragments

5 Gastropoda: shell fragments

3 *Pomacea flagellata*: shell fragments

2 cf. *Chondropoma* sp.*

2 *Euglandina gheisbreghti**

2 *Euglandina* sp.*

3 *Orthalicus princeps**

6 *Praticolella* cf. *griseola**

2 *Neocyclotus dysoni**

32/B/11/29 – Late Preclassic

8 Vertebrata: 1 long bone shaft fragment; 7 unidentified bone fragments

1 *Rhinella* cf. *marina*: thoracic vertebra

1 Testudines: rib fragment, possibly polished on one edge

1 Emydidae: eleventh? marginal (left)

1 Colubridae: thoracic vertebra

6 Mammalia: unidentified bone fragments

3 Mammalia (medium): 2 long bone shaft fragments; 1 femur (cf. *Cuniculus paca*), middle shaft fragment

7 Mammalia (large): long bone shaft fragment

6 *Canis lupus familiaris*: mandible (left) middle 0.5; lower canine (right); canine fragment; ulna (left) proximal 0.75, in three fragments

1 Cervidae: phalanx

2 *Mazama* sp.: metacarpal (right) proximal/lateral 0.6 of shaft; radius (left) proximal 0.75

2 *Odocoileus virginianus*: femur (right) proximal epiphysis (unfused); femur shaft fragment

32/B/11/30 – unknown

1 Mollusca: shell fragment

3 *Orthalicus princeps**

1 Polygyridae or Sagidae*

32/B/12/32 – Late Preclassic

1 Vertebrata: cylindrical bone bead with two fine grooves around circumference

32/B/13/34 – unknonwn

2 Bivalvia: valve fragments

32/B/13/37 – Late Preclassic

1 Aves: long bone shaft fragment

4 Mammalia (large): long bone shaft fragments

2 *Canis lupus familiaris*: mandible (right); upper canine (right)

2 cf. *Canis lupus familiaris*: rib (right); metapodial fragment

3 Cervidae: metapodial shaft fragment

1 *Mazama* sp.: metacarpal, middle 0.5 of shaft

2 *Odocoileus virginianus*: astragalus (left); metatarsal shaft fragment

32/B/14/38 – Late Preclassic

1 Aves (large): tibiotarsus (right), distal shaft fragment, grooved and snapped at proximal end

1 *Odocoileus virginianus*: proximal phalanx (left)

32B/18/49 – Late Preclassic

1 *Staurotypus triporcatus*: neural

1 Felidae (large): canine

32/B/21/52 – Late Preclassic

2 Testudines: carapace fragments; one fragment is perforated

1 Kinosternidae: rib fragment

1 Emydidae: third rib (left)

2 Aves (medium/large): radius (left) distal 0.25; tibiotarsus (left) shaft fragment

1 Aves (large) – cf. *Meleagris* sp.: tibiotarsus? shaft fragment

6 Mammalia: unidentified bone fragments

5 Mammailia (medium): long bone shaft fragments

22 Mammalia (large): 1 frontal (left) fragment; 21 long bone shaft fragments

3 Canidae.: femur (right) proximal fragment; metapodial shaft fragment; radius (left) middle shaft fragment

4 *Canis lupus familiaris*: second metatarsal (left); lower second premolar (left); maxilla with upper first molar (right)

5 Cervidae: os coxa (right) middle 0.5; metapodial distal shaft fragment

4 *Odocoileus virginianus*: molar; 2 tibia (left) fragments; phalanx

32/B/22/55 – Late Preclassic

18 Vertebrata: unidentified bone fragments

8 Mammalia (large): unidentified bone fragments

1 *Canis lupus familiaris*: tibia (right) distal 0.25, cut mark above distal epiphysis on anterior surface

6 *Odocoileus virginianus*: scapula (right) in three fragments; femur (right) shaft fragment; middle phalanx; proximal phalanx

32/B/24/60 – Late Preclassic

5 Mammalia (large): 1 scapula fragment; 2 long bone shaft fragments; 2 unidentified bone fragments

6 *Odocoileus virginianus*: 3 scapula (right and left) fragments; humerus (left) distal 0.75; humerus (right) distal 0.2; os coxa (right)

32/B1/15/41 – Late Preclassic

4 Vertebrata: unidentified bone fragments

3 Mammalia: long bone shaft fragments

1 Felidae (large): humerus (right) shaft fragment

2 *Canis lupus familiaris*: canine; humerus (left) distal 0.5 of shaft

2 *Odocoileus virginianus*: radius (right) proximal 0.3; femur (left) proximal 0.5, possible cutmarks on femur head

32/C/2/47 - unknown

4 Mollusca: shell fragments

32/D/2/96 - Late Preclassic/Protoclassic

1 cf. Unionidae: teardrop-shaped shell pendant, perforated twice along midline

32/D/4/91 – Late Preclassic

1 Mammalia: unidentified bone fragment

32/D/4/96(103?) – Late Preclassic

7 Vertebrata: unidentified bone fragments

1 Aves: long bone shaft fragment

2 Mammalia: unidentified bone fragments

1 Mammalia (large): long bone shaft fragment

1 Tayassuidae: temporal (left) petrous portion

32/D1/3/80 - Late Preclassic/Protoclassic

10 Mollusca: shell fragment

32/D1/2/102 – Protoclassic

1 Tayassuidae: lower canine, perforated through root

32/D1/3/82 – Protoclassic

1 Vertebrata: unidentified bone fragment

1 Mammalia (large): long bone shaft fragment

32/D1/3/85 – Late Preclassic/Protoclassic

4 Vertebrata: unidentified bone fragments

9 Mammalia (large): 3 long bone shaft fragments; 1 vertebra fragment; 4 unidentified bone fragments, 1 fragment grooved longitudinally at one end

32/D1/3/92 – Late Preclassic/Protoclassic

10 Mollusca: shell fragments

12 Gastropoda: shell fragments

1 *Pomacea flagellata*: shell fragment

6 cf. *Chondropoma* sp.*

3 Spiraxidae*

9 *Euglandina gheisbreghti**

7 *Euglandina* sp.*

1 *Bulimulus* sp.*

28 *Praticoella* cf. *griseola**

2 *Neocyclotus dysoni**

17 Mammalia (large): long bone shaft fragments

32/D1/3/98 - Late Preclassic/Protoclassic

1 Mollusca: shell fragment

18 Gastropoda: shell fragments

3 cf. *Chondropoma* sp.*

3 *Euglandina* sp.*

1 *Bulimulus unicolor**

2 *Orthalicus princeps**

12 *Praticoella* cf. *griseola**

4 *Neocyclotus dysoni**

7 Mammalia (large): long bone shaft fragments

32/D1/3/104 - Late Preclassic/Protoclassic

16 Mammalia (medium/large): unidentified bone fragments

48 Mammalia (large): 22 rib fragments; 2 vertebrae fragments; 19 long bone shaft fragments, 1 burnt; 5 unidentified bone fragments

32/D1/4/82 - Late Preclassic/Protoclassic

3 Mollusca: shell fragments

1 Gastropoda: shell fragment

2 *Pomacea flagellata*: shell fragments

1 *Helicina* sp.*

2 Sprixidae*

2 *Orthalicus princeps**

10 *Praticoella* cf. *griseola**

2 *Neocyclotus dysoni**

32/D1/4/87 - Late Preclassic

20 Vertebrata: unidentified bone fragments

18 Mammalia: unidentified bone fragments

25 Mammalia (large): 20 long bone shaft fragments; 5 rib fragments

1 Felidae (cf. *Leopardus pardalis*): femur (right) shaft fragment

1 Cervidae [male]: antler fragment

16 *Odocoileus virginianus* [large adult male]: antler fragment; cranial/antler fragment

32/D1/4/88 - Late Preclassic

6 Vertebrata: unidentified bone fragments

7 Aves (large): long bone shaft fragments

3 Mammalia (medium): long bone shaft fragments

6 Mammalia (medium/large): 1 sternum fragment; 5 long bone shaft fragments

151 Mammalia (large): 14 rib fragments; 4 vertebrae fragments; 46 long bone shaft fragments; 87 unidentified bone fragments. Some remains are likely human.

32/D1/4/91 – Late Preclassic

10 Vertebrata: unidentified bone fragments

14 Mammalia: 2 long bone shaft fragments; 12 unidentified bone fragments

32/D1/4/121 – Late Preclassic/Protoclassic

1 *Spondylus* sp.: valve (right), spines abraded off, two perforations along on edge. Very similar to valve found in 26K/4.

32/D1/4/122 – Late Preclassic

5 Vertebrata: unidentified bone fragments

65 Mammalia (large): 1 vertebra fragment; 2 long bone shaft fragments; 23 unidentified bone fragments

1 *Odocoileus virginianus*: atlas

32/D1/4/123 – Late Preclassic

6 Mammalia (large): unidentified bone fragments

32/E/3/113 – Late Preclassic

2 Mollusca: shell fragments

1 Scaphopoda: shell bead

3 Gastropoda: 1 body whorl fragment; 2 spire fragments

35/A/12/17 – Late Preclassic

1 cf. *Spondylus* sp.: cut fragment of valve with spines removed, possible mosaic inlay

35/B/5/22 – Late Preclassic

9 Vertebrata: unidentified bone fragments

1 *Meleagris* sp.: carpometacarpus (right), middle 0.5 of shaft

8 Mammalia (medium/large): long bone shaft fragment

1 *Canis lupus familiaris*: canine

36/A/10/24 – Late Preclassic

1 cf. Strombidae: cut cube of shell, polished (likely debitage from marine shell artifact production)

36/A/13/84 – unknown

3 cf. Strombidae: rectangular shell pectorals perforated twice along edge

39/A/1 – unknown

1 Mollusca: shell fragment

2 Subulinidae*

40/IL1/4/32 – Late Preclassic?

1 Mollusca: shell fragment

1 *Strombus* sp.: spire

46/B/14 – Late Preclassic

8 *Crassostrea virginica*: 2 valves (left); 6 valve fragments

47/D/6 – Late Preclassic

1 *Oliva* sp.: shell tinkler fragment, horizontal slit cut in anterior body whorl, apex/spire removed

La Muerta, Sta. 2 (acc.# 611)

1 *Spondylus* cf. *calcifer*: whole articulated valves (right and left)

Unknown provenience

1119 Vertebrata: unidentified bone fragments

1 Testudines: carapace fragment

1 Kinosternidae: marginal (right)

1 Aves (large): vertebra fragment

178 Mammalia: unidentified bone fragments

8 Mammalia (small/medium): 1 metapodial; 1tibia; 1rib; 1 femur; 4 vertebrae

69 Mammalia (medium): 1 thoracic vertebra fragment; 55 rib fragments; 13 long bone fragments

95 Mammalia (medium/large): 83 cranial fragments; 11 vertebra fragments; 1 unidentified bone fragment

109 Mammalia (large): 34 cranial fragments; 4 rib fragments; 6 carpal/tarsal fragments; 34 long bone shaft fragments; 31 unidentified bone fragments

2 *Dasypus novemcinctus*: femur (right); dermal scute

2 *Dasyprocta/Cuniculus* sp.: vertebra fragments

2 *Cuniculus paca*: rib; thoracic vertebra

2 *Dasyprocta punctata*: tibia (left), in two fragments (unfused proximal epiphysis)

5 cf. Canidae: 1 femur shaft fragment; 4 humerus shaft fragments

4 Artiodactyla: lumbar vertebra fragments

6 Tayassuidae: cuneiform (left); unciniform (left); scaphoid (right); carpal/tarsal; metapodial; ulna (right) distal epiphysis

1 Cervidae: radius (right) distal ephiphysis

6 *Mazama* sp.: radius (left and right) distal 0.25; metacarapal (left) proximal 0.5; 3 proximal phalanges

9 *Odocoileus virginianus*: 2 lumbar vertebra fragments; 2 metapodial distal epiphysis fragments; cubonavicular (right); 3 distal phalanges; phalanx fragment

Archaeofauna 25 (2016): 265-272

Erstnachweise des Feldhamsters als Beigabe in Grabbefunden der Thüringerzeit (Thüringer Königreich, 5/6. Jh. n. Chr.) von Thüringen

HANS-VOLKER KARL
Friedrich-Schiller-Universität Jena. Bereich Ur- und frühgeschichtliche Archäologie
Löbdergraben 24a. 07743 Jena, Deutschland

(Received *19 January 2014*; Revised *28 January 2016*; Accepted *5 February 2016*)

ABSTRACT: Hamster (*Cricetus cricetus* Linnaeus, 1758) remains from Thuringian Age graves from Merxleben/ Unstrut Hainich county and Gotha-Boilstedt are presented. The field data from Boilstedt proved crucial to rule out an independent burying event of these animals and constitute one of the few instances of rodents being intentionally deposited in a funerary context.

KEYWORDS: ARCHAEOZOOLOGICAL ANALYSIS, HAMSTERS, *Cricetus cricetus*, GRAVE GOODS, THURINGIAN KINGDOM, 5TH – 6TH CENTURY A.D., THURINGIA

RESUMEN: Se describen restos de hamster (*Cricetus cricetus* Linnaeus, 1758) recuperados en sepulturas de época Turingia en los yacimientos de Merxleben/ Unstrut Hainich y Gotha-Boilstedt. Los datos de campo de Boilstedt han sido cruciales para desechar la posibilidad de un evento natural de incorporación de estos animales a los depósitos haciendo de ellos uno de los excasos hallazgos de roedores depositados intencionalmente en contexto funerario.

PALABRAS CLAVE: ANÁLISIS ARQUEOZOOLÓGICO, HAMSTER, *Cricetus cricetus*, OFRENDA FUNERARIA, REINO DE TURINGIA, Siglos V-VI A.D., TURINGIA

EINLEITUNG

Nach dem Rückweichen des Inlandeises am Ende des Pleistozäns folgte eine Phase ganz lichten Birken- Kiefernwaldes, der aber auch eine Reihe von Steppenpflanzen und mit ihnen Steppentiere aufnehmen konnte. Neben dem Feldhamsters (Linnaeus, 1758) als ökologischem Indikator der großen Lößgebiete sind hier auch die die Saigaantilope (*Saiga tatarica*), die Ziesel (*Spermophilus* sp.) die Lerchen (Alaudidae) und die Trappen (Otididae) zu nennen, die beiden Letzten hatten gemeinsam mit dem Feldhamster bis in die Neuzeit einen Verbreitungsschwerpunkt im Thüringer Becken (Knorre *et al*., 1986).

Die Gattung *Cricetus* Leske 1779 ist seit dem Unterpliozän (Pontium) von Europa bzw. Pliopleistozän von Asien bis zum rezenten Eurasien bekannt (Schaub, 1930; Müller, 1970). Der Feldhamster breitete sich als Kulturfolger aus den Steppen Osteuropas mit der Landwirtschaftsausweitung bis nach Westeuropa aus. Der Feldhamster ist bereits seit dem Pleistozän sicher in Mitteldeutschland nachgewiesen, das würde aber den Rahmen hier sprengen. In Zentraleuropa kommen sie rezent gebietsweise recht häufig vor, besonders im Lößkörper der Magdeburger Börde und im Thüringer Becken (Stubbe *et al*., 1997; Weinhold & Kayser, 2006; Karl, 2012/2013).

Die Reste des Hamsters sind im archäologischen Befund leicht zu identifizieren. Bislang konnten aber nur die Hamsterreste aus einer römischen Brunnenwandung in Ladenburg im Landkreis Mannheim als stratigraphisch gesichert gelten (Lüttschwager, 1968). Mittlerweile wurden auch Hamsterreste der Thüringerzeit aus einem Grabbefund von Merxleben (Stadt Bad Langensalza), Unstrut-Hainich-Kreis bekannt. So konnten bereits 1968 mehrere Knochenreste des Feldhamsters in zwei Gräbern des 6. Jh. n.Chr. geborgen werden (TLDA 121/68A), welche vorerst für natürliche Eindringlinge angesehen wurden (Baumann, 2007: Abb. 4-5). Erst während der letzten Grabungskampagne konnte im Sommer 2013 der erste Feldhamster als sichere Beigabe in einem Frauengrab der Thüringerzeit (Thüringer Königreich, 5/6. Jh. n.Chr.) von Gotha-Boilstedt festgestellt werden (Abb. 1). Hierbei ist die Grabungsdokumentation brauchbar um ein selbständiges Eingraben dieses Nagetiers auszuschließen.

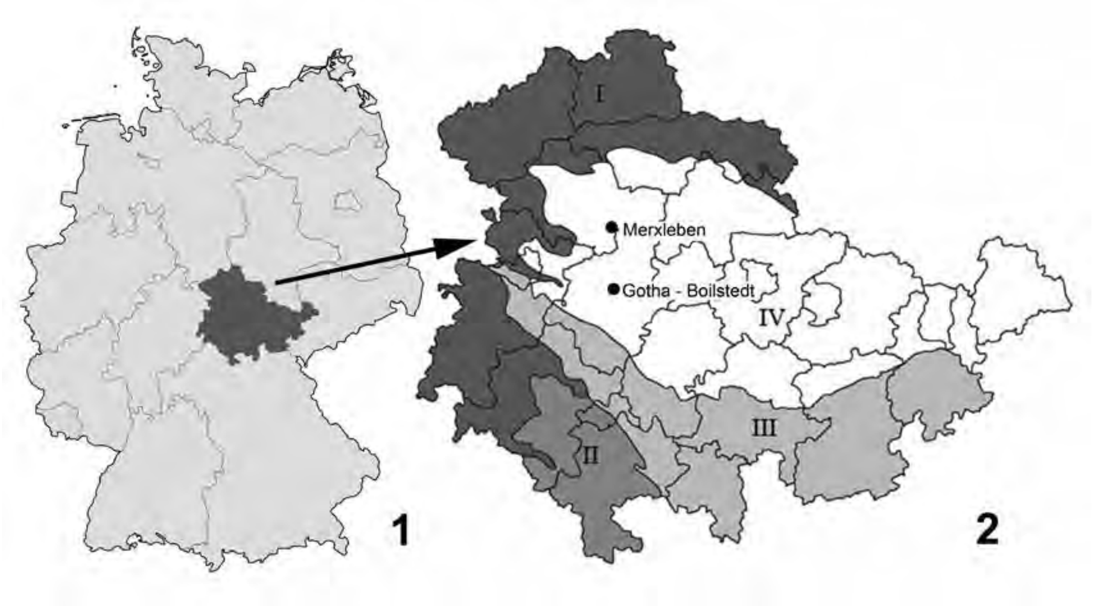

ABBILDUNG 1

1) Umrißkarte von Deutschland mit den Grenzen der Bundesländer, Thüringen dunkel markiert. 2) Geographische Position der Grabbefunde des 6. Jh. n. Chr. von Merxleben und Boilstedt in Thüringen. Klima- und Landschaftsgliederung in Thüringen: I= Harz und Rhön, II= Grabfeld, III= Thüringer Wald und Schiefergebirge, IV= Thüringer Becken. Kartengrundlage nach Potsdam-Institut für Klimafolgenforschung (PIK): http://www.tlug-jena.de/umweltdaten/umweltdaten2006/klima/klima_01.html

ALLGEMEINER ARCHÄOLOGISCHER KONTEXT

Bei baubegleitenden Ausgrabungen des TLDA an der Ortsumfahrung Sundhausen zwischen Leina und Boilstedt wurden mehrere Gräber aus der Zeit des Thüringer Königreiches geborgen. Das Grab eines um 480 n. Chr. bestatteten Fürsten gehört mit seinen reichen Beigaben zu den bedeutendsten Funden aus dem Thüringer Königreich. Das Grab eines weiteren Kriegers mit Lanzenspitze befand sich in unmittelbarer Nähe hierzu. Unweit davon befand sich eine Mehrfachbestattung von zwei Hunden und einem Pferd. Ein weiteres Pferd ohne Kopf wurde abseits bestattet. Solche Pferdebestattungen waren im Königreich üblich, die Kombination mit Hunden, vermutlich Jagdhunden, waren typisch für das Thüringer Königreich. Des Weiteren fand sich ein in prähistorischer Zeit ausgeraubtes Grab, in dem sich noch eine bronzene Gürtelschnalle befand, sowie ein Grab, in dem zwei vermutliche Männerskelette übereinander, aber wohl nicht gleichzeitig, bestattet wurden. Somit könnte es sich um einen Kriegerfriedhof handeln, der über ein bis zwei Generationen existierte. Spuren von Gewalt finden sich an mehreren Befunden, wie ein auf der Hüfte liegender Schädel als Zeichen für eine Enthauptung, aber auch der Schädel des auf dem Rücken liegenden Fürsten ist sehr weit nach hinten geklappt, was ebenfalls eine Enthauptung oder eine schwere Kriegsverletzung nahelegt. In diesem Kontext und der reichen Grabausstattung wegen, könnte es sich bei dem Frauengrab um eine hoch gestellte Person, wenn nicht die Fürstin handeln.

BEFUNDBESCHREIBUNG DES FRAUENGRABES

TLDA Vorgangs-Nummer 13/172-157: Frauengrab von Gotha-Boilstedt auf Fläche 1, Planum 2/ 1,25 Meter unter Planum 1, 6. Jh. (Abb. 4)

In der Befundbeschreibung des Ausgräbers Andreas Meyer vom 03.09.2013 wird eine im Planum langrechteckige, grob NO-SW orientierte Verfärbung mit abgerundeten Ecken und dort vier Pfostenlöchern von 6-7 cm Durchmesser vermerkt. Die Ausmaße sind von maximal 2,30 x 0,80 Metern bei scharf umrissener Befundgrenze. Das Profil zeigt sich kastenförmig mit steilen Wandungen und abgerundeten Ecken zur Grabbasis, Holzreste waren bei dieser Bestattung nicht nachweisbar. Mit Grabbasis ist die Sohle der Grabgrube gemeint. Die Menschenbestattungen sind noch unter Bearbeitung durch den Anthropologen. Die Pfostenlöcher müssen als gegeben hingenommen, werden die sind archäologischer Befund. Das Skelett lag 1,20 Meter unter Planum 1 in gestreckter Rückenlage. Es war insgesamt ungestört bei guter Knochenerhaltung, der Schädel war rechts gekippt. Die Länge betrug in situ 1,50 Meter. Die Abbildung 4 des Grabbefundes zeigt im Einzelnen die zwei Öffnungen eines Tierganges [1], welcher über das darüber liegende Planum verlief, vier Pfostenlöcher [2], einen Spinnwirtel aus Ton [3], ein Keramik-Standgefäß [4], Reste eines Dreilagenkammes [5] und ein Hamsterskelett [6] (Abb. 2) letzteres vergrößert in Abbildung 3 dargestellt. Der Hamster liegt direkt neben dem Fuß auf gleicher Ebene wie das Skelett, das Gefäß und der Dreilagenkamm. Die Ablagestellen der einzelnen Grabbeigaben (grave goods) folgen keiner Regel. Insgesamt kann der Befund als ungestört im Sinne von Alt *et al.* (2013) gelten.

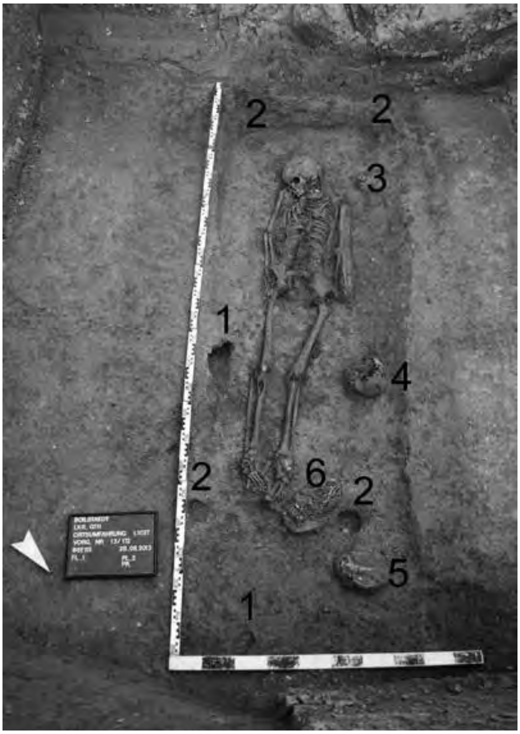

ABBILDUNG 2

TLDA Vorgangs-Nummer 13/172-157: Frauengrab von Gotha-Boilstedt auf Fläche 1, Planum 2/ 1,25 Meter unter Planum 1, 6. Jh. Photo Christian Tannhäuser.

ABBILDUNG 3

Das Hamsterskelett (6) aus Abbildung 2 vergrößert dargestellt. Photo Christian Tannhäuser.

FRÜHERE HINWEISE

TLDA Vorgangs-Nummer 121/68 A: Gräber 1/68 (Fundstelle Hühnerfarm) und 4/68 (Fundstelle 3/ Nordrand des Ortes) von Merxleben, 6. Jh., MTB 4830-Pkt 3, H 66 600 - R 07 200 (Abb. 1)

Laut Grabungsbericht von Dr. Wolfgang Timpel befanden sich in Grab 1/68 ein rechtsseitiger Hocker in W-O-Lage (Abb. 2), dessen Schädel beschädigt und der Unterkiefer weggerutscht war. Als Beigaben fanden sich 1 Eisenschüssel auf dem Becken im Rücken des Toten, 1 Glasperle im Beckenbereich und 2 kleine Leichenbrandstücke neben der Glasperle. Das Grab 4/68 (Abb. 3) erbrachte ein gut erhaltenes, gestrecktes Skelett in W-O-Lage, linker Unterarm verlagert. An Beigaben konnten 1 Knochenkamm über dem Schädel, 1 Pfeilspitze neben dem linken Oberarm (Spitze zum Schädel zeigend), 1 Eisenmesser unmittelbar rechts neben dem Schädel, 1 Eisenrest unter dem rechten Unterschenkel sowie 1 Pfeilspitze unter der Bestattung in der Rückengegend geborgen werden. Der Denkmalpfleger Günter Möbes erwähnt in seinem Grabungsbuch noch ein stark zerstörtes,

ABBILDUNG 4

TLDA Vorgangs-Nummer 121/68 A: Grab 1/68 (Fundstelle Hühnerfarm) von Merxleben, 6. Jh., MTB 4830-Pkt 3, H 66 600 - R 07 200. Photo Archiv TLDA.

verziertes Gefäß links neben dem Schädel, welches entnommen wurde. In beiden Gräbern wurden auch Hamsterknochen gefunden (Abb. 5).

BESCHREIBUNG DER HAMSTERKNOCHEN

Der Schädel ist nach Müller (1970) stark differenziert, wobei besonders das große Rostrum und die kräftigen Supraorbitalkämme auffallen. Der Postorbitalbereich ist hingegen schmal und das Interparietale klein. Der Processus coronoideus ist ausgezogen und deutlich posteriorwärts gekrümmt (Abb. 6).

Aus dem Frauengrab von Gotha-Boilstedt sind der Schädel in 14 Fragmenten, beide Mandibulae sowie von beiden Seiten die Scapulae, Humeri, Radii, Ulnae, Femora, Tibiae/1 Fibula und Pelvishälften sowie 1 Calcaneus/ 1 Fragment, 3 Phalangen, 1 Metacarpus/ Metatarsus, 30 Wirbel+Fragmente und 33 Rippenfragmente (MIZ= 1). Die abnehmbaren Maße sind in Tabelle 1 zusammengefaßt und Abb. 6 dargestellt. Die Hamsterknochen aus Grab 1/68 umfassen 2 Calvarienhälften, 2 Maxillahälften mit Zahnreihen (OZR) und einen Humerus ohne proximale Epiphyse (MIZ= 1). Der Knochen aus Grab 4/68 ist ein erodierter Metacarpus/ Metatarsus vom Ferkel.

ABBILDUNG 5

TLDA Vorgangs-Nummer 121/68 A: Grab 4/68 (Fundstelle 3/ Nordrand des Ortes) von Merxleben, 6. Jh., MTB 4830-Pkt 3, H 66 600 - R 07 200. Photo Archiv TLDA.

ABBILDUNG 6

Schematische Darstellung der Hamsterskelette mit Verteilung der erhaltenen Knochentypen von Merxleben Grab 1/68 (121/68 A) und Boilstedt (13/172-157). Original.

	OZR	UZR	HL	FL	RL	TL
121/68 A	7,76 / 7,74	-	30,41	-	-	-
13/172-157	7,66 / 7,68	8,48 / 7,84	35,27 / 35,29	40,73 / 50,52	29,48 / 29,43	38,91

TABELLE 1

DISKUSSION

Auf die Schwierigkeit der eindeutigen Zuordnung von Resten grabender Tieren zum Ausgrabungsbefund wurde schon hingewiesen (Karl, 2012/2013). Es konnten keine weiteren publizierten Daten beigebracht werden, da wir erst am Beginn der Aufarbeitung dieser Problematik stehen. Gewöhnlich wurden nur Reste für datiert angesehen, die ungestört mindestens 1 Meter tief unter der Erdoberfläche bzw. aus Mauerritzen oder Hohlräumen unter Steinen und Ziegeltrümmern stammen, die sicher nicht gezielt ergraben werden konnten (Lüttschwager, 1968; Karl, 2012/2013). Auch die Konsistenz und die Färbungen der verschiedenen Knochenreste sind variabel und reichen von heller und fester Knochensubstanz bis zu gelblich- bräunlichen und stark erodierten Zuständen, was aber nicht aussagefähig für Altersbestimmungen generell und vom Sediment abhängig ist. Erfahrungsgemäß gibt es besonders im Thüringer Becken Grabungsflächen die stellenweise von Gangsystemen regelrecht infiltriert waren (Abb. 7) und Keramik-Scherben bis zu 1 Meter und mehr von Grubeninhalten entfernt in Gangausfüllungen verfrachtet wurden (Karl, 2012/2013). Die Löcher des Tierganges von Boilstedt zeigen keine Beziehungen zu dem Hamsterskelett, was durch den Ausgräber ausdrücklich betont wurde. Die Distanz zwischen dem Gang und dem Hamsterskelett beträgt mindestens einen halben Meter, außerdem zeigt der Gang eine ganz andere Richtung. Die übrigen Vertiefungen sind die erwähnten Pfostenlöcher eines Kammergrabes. Ein Nagetier hat sich sicher nicht freiwillig in den verwesenden Inhalt einer solchen nahezu abgeschlossenen Gärkammer eingegraben und in Schlafposition gebracht. Die Möglichkeit der Bekämpfung grabender Kleinsäuger in Gärten mittels verwesenden Fisches ist bekannt, auch das Gangbereiche mit abgestorbenen Artgenossen vom Gangsystem abgeschnitten werden, erst verschlossen dann umgraben. Neben Fliegenmaden und weiteren Insekten (Leichenfauna) hinterlassen auch Wirbeltiere Fraßspuren an Leichen, insbesondere Ratten, Mäuse, Vögel, Füchse, Wildschweine, gelegentlich auch Hunde und Katzen (Wirth, 2010). Unter den Nagetieren scheinen nur Wanderratten (*Rattus norvegicus*) und gelegentlich Mäuse (Murinae) Aasgeruch zu tolerieren. Nagetierfraßspuren

ABBILDUNG 7

Grabungsbefund (1997) eines bronzezeitlichen Grubenhauses der Wüstung Sulze nördlich von Erfurt mit starker Störung durch Hamstergrabgänge. Photo Hans-Volker Karl.

sind besonders an Knochen nachweisbar, welche zum eigenen Calziumbedarf gefressen werden. An vielen archäozoologischen Materialien, besonders in Höhlen sind Nagespuren nachgewiesen. Im Kammergrab von Boilstedt gibt es keine derartigen Nachweise. Der Hamster muß demnach schon tot in den Fundzusammenhang gekommen sein. Hätte er sich aktiv zu diesem Zeitpunkt in diese Taphozönose eingegraben, müßte er zur Leichenfauna gezählt werden.

Der Typ des Kammergrabes macht etwa 10% der ausgegrabenen Bestattungen in Boilstedt aus (mdl. Chr. Tannhäuser). In einem weiteren Kammergrab einer wohlhabenden Frau der Merowingerzeit (7/8. Jh. n. Chr.) von Sondershausen-Bebra in Thüringen wurde ein Hundeskelett gefunden (Karl, 2013). Das Skelett liegt rechts des Menschenskelettes kopfunter im Bereich der unteren Extremitäten. Auch der Hamster von Boilstedt liegt im Bereich der Beine.

Während von den Nagetieren gelegentlich Biberreste (*Castor fiber*) aus Gräbern bekannt wurden, gehören Kleinsäugerreste zu den Seltenheiten, selbst bei gründlicher Suche und bei Anwendung von Sieben und Schlämmmethoden (Karl, 2012/2013). Siebenschläfer (*Glis glis*) wurden schon von den Römern und im Mittelalter gegessen. Mittermeier (1986) führt einen Nachweis des Eichhörnchens (*Sciurus vulgaris*) in einem Kindergrab aus dem 4. Jahrhundert von Thoraise in Frankreich nach Pilloy (1895) sowie fünf awarischen Kindergräbern von Keszthely in Ungarn an. Eichhörnchenreste treten vereinzelt in ur-und frühgeschichtlichen Grubenbefunden auf, sie wurden des Felles und Fleisches wegen gejagt aber auch zahm gehalten. Auch Hamster spielen als Fellieferanten und als Nahrungsquelle für den Menschen eine Rolle. Noch vor rund 20-50 Jahren waren Feldhamster eine Plage und galten als Ernteschädlinge. So wurden gebietsweise deren Getreidevorräte, welche bis zu 20 kg im Spätherbst zusammengetragen werden, wie auch das Fleisch selbst genutzt, besonders in Osteuropa und Asien (Gromow & Jerbajewa, 1995; Feaver & Zhang, 2010). Dieses Brauchtum könnte ein Hinweis auf die Vorfahren der Thüringer Könige sein.

Der Name Musahar des nordindischen Volkes der Bundesstaaten Bihar und Uttar Pradesh ist abgeleitet vom Wort für Ratte und auf ihren traditionellen Beruf als Rattenfänger zurückzuführen (Singh, 2008). Auch sie beuten die Getreidevorräte dieser Tiere aus, die beträchtlich sein können. Gewöhnlich hortet der Hamster bis 5 kg. Historische „Meldungen“ über Hamstervorräte von mehreren Zentnern Getreide in einem Hamsterbau gehören in das Reich der Fabel und waren rein rhetorische Mittel der Hamsterbekämpfung. In vielen Teilen Deutschlands mit ehemals hohen Hamstervorkommen ist der Feldhamster heute vom Aussterben bedroht. Seit 1994 wird er in der Roten Liste der BRD als „stark gefährdet“ geführt. Nach der Bundesartenschutzverordnung, Kategorie B, gehört er zu den besonders geschützten Arten und durch die europäische Flora-Fauna-Habitat-Richtlinie, Anhang IV, ist er streng geschützt (Weinhold & Kayser, 2006). Somit sind sehr viele Hamsterknochen aus Grabungsbefunden mittlerweile historisches Material und können zur Rekonstruktion der Arealdynamik dienen. Auf Grund der hier vorgestellten Ergebnisse sollten Hamsterreste künftig regelrecht dokumentiert werden, da eine Ablage oder Beigabe wenn auch nicht sicher nachgewiesen, doch auch nicht ausgeschlossen werden kann.

Der Fund von Gotha-Boilstedt kann als sichere Grabbeigabe gelten, da es das bislang mit Abstand vollständigste Hamsterskelett in Situ eines direkten Befundzusammenhanges darstellt und eine unmittelbare Verbindung zu einem Tierbau ausgeschlossen ist. Auch Hunde und portionierte Fleischbeigaben wurden in der Vorgeschichte am Fussende abgelegt. Im vorliegenden Fall ist diese Lage dahin gehend bedeutend, das auch hier eine Fleischgabe und kein Lieblingstier mit bestattet wurde.

ABKÜRZUNGEN

OZR= Obere Zahnreihen= Dentes praemolares et molares superior sinister / dexter; UZR= Untere Zahnreihen= Dentes praemolares et molares inferior sinister /dexter; HL= Humeruslänge; FL= Femurlänge; RL= Radiuslänge; TL= Tibialänge; MIZ= Mindestindividuenzahl.

DANKSAGUNG

Dem Grabungsleiter Christian Tannhäuser M.A. danke ich für die Überlassung des Materials zur Bearbeitung sowie die Vorlagen für die Abbildungen 2 und 3. Den Herren Dr. Ulrich Weinhold, Institut für Faunistik in Heiligkreuzsteinach und Dr. Klaus Wirth, Reiss-Engelhorn-Museen in Mannheim wird für die Unterstützung mit Informationen gedankt. Ganz besonders danke ich Frau Dr. Irene Mittermeier aus Osterhofen für die Bereitstellung ihrer Dissertation zur Auswertung. Zwei anonyme Reviewer gaben hilfreiche Hinweise zu einer früheren Version dieser Arbeit.

LITERATUR

ALT, K. W.; HELD, P. & NICKLISCH, N. 2013: Forensische Feldmethoden. *Rechtsmedizin* 23: 85-91.

BAUMANN, N. 2007: Das merowingische Gräberfeld von Merxleben, Unstrut-Hainich-Kreis. Ungedr. Magisterarbeit, Universität Jena; 216 S., 38 Taf.

FEAVER, J. & ZHANG ZHI-BIN 2010: Hamsters. In: MacDonald, D.W. (ed.): *The Encyclopedia of Mammals*: 204-205. Oxford University Press, Oxford.

GROMOW, I. M. & JERBAJEWA, M. A. 1995: Die Säugetiere Russlands und angrenzender Gebiete. Hasenartige und Nagetiere. — Russische Akademie der Wissenschaften (Zoologisches Institut), Sankt Petersburg (russ.). http://zoomet.ru/grom/gromov_oglav.html

KARL, H.-V. 2012/2013: Die Kleinwirbeltiere aus der mittelalterlichen Kirchenruine der Wüstung Sulza bei Erfurt. *Alt-Thüringen* 43: 215-217.

— 2013: Pferd und Hund: zum Verhältnis der Bestattungen von Mensch und Tier auf dem spätmerowingerzeitlichen Separatfriedhof von Sondershausen-Bebra. *Sondershäuser Beiträge Püstrich,* Beiheft 2: 145-151.

KNORRE, D. V.; GRÜN, G.; GÜNTHER, R. & SCHMIDT, K. 1986: *Avifauna der DDR* — Die Vogelwelt Thüringens. — 1. Aufl., 339 S.; Gustav Fischer Verlag, Jena.

LÜTTSCHWAGER, J. 1968: Hamster- und Hausrattenfunde im Mauerwerk eines römischen Brunnens in Ladenburg, Landkreis Mannheim. *Säugetierk. Mitt*. 16: 37-38.

MITTERMEIER, I. 1986: Speisebeigaben in Gräbern der Merowingerzeit. — Teil I: Text, 595 S.; Teil II: Karten, 147 Karten m. Erläuterungen; Teil III: Katalog, 495 S.; Unpubl. Diss. (Univ. Würzburg 1986).

MÜLLER, A. H. 1970: Lehrbuch der Paläozoologie, Bd. III Vertebraten, Teil 3 Mammalia. — 855 S.; Fischer, Jena.

PILLOY, J. 1895: Études sur d´anciens lieux de sépultures dans l´Aisne. — Bd. II, 343 ff. (occ. cit.).

SCHAUB, S. 1930: Quartäre und Jungteriäre Hamster. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*. 2: 1–49.

SINGH, K. S. (ed.) 2008: People of India: Vol. XVI. Bihar Including Jharkhand. *Anthropological Survey of India*, 2 Teile, 1094 S.; Seagull Books.

STUBBE, M.; SELUGA, K. & WEIDLING, A. 1997: Bestandssituation und Ökologie des Feldhamsters *Cricetus cricetus* (L., 1758). *Tiere im Konflikt* 5, 60 S.; Martin-Luther-Universität Halle-Wittenberg.

WEINHOLD, U. & KAYSER, A. 2006: Der Feldhamster *Cricetus cricetus*. Die Neue Brehm-Bücherei Bd. 625, 128 S; Westarp Wissenschaften, Hohenwarsleben.

WIRTH, I. 2010: Tierfraß (S. 574-575). In: Wirth, I. (ed.): Kriminalistik-Lexikon. 4. völlig neu bearbeitete und erweiterte Auflage, 668 S.; Kriminalistik Verlag.