C. R. Palevol 15 (2016) 245–254

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Palaeontology, Systematics and Evolution (Palaeopathology)

# Surviving in a predator-free environment: Hints from a bone remodelling process in a dwarf Pleistocene deer from Crete

## *Survivre dans un environnement sans prédateurs : considérations sur un processus de remodelage osseux dans un cerf nain du Pléistocène de Crète*

Maria Rita Palombo[a,*], Marco Zedda[b]

[a] *Dipartimento di Scienze della Terra, Sapienza Università di Roma, P.le Aldo Moro 5, 00185, Roma, Italy*
[b] *Dipartimento di Medicina Veterinaria, Università degli Studi di Sassari, Sassari, Italy*

ARTICLE INFO

*Article history:*
Received 14 December 2014
Accepted after revision 24 March 2015
Available online 11 June 2015

Handled by Michel Laurin

*Keywords:*
*Candiacervus*
Dwarf deer
Bone fracture
Crete
Pleistocene

*Mots clés :*
*Candiacervus*
Cerf nain
Fracture osseuse
Crète
Pléistocène

ABSTRACT

Islands have been regarded by scientists as a living laboratory of evolution, and a prime target for the study of forces influencing evolution. This research aims to investigate whether a dwarf deer (*Candiacervus ropalophorus*), that suffered a traumatic fracture of its metatarsal, might have survived, despite the broken limb, in the Cretan free-predator environment for a time longer than commonly expected on mainland. The metatarsal shows a healed complete and oblique fracture at level of the distal part of the diaphysis. Both macroscopic and X-ray examinations show the impressive new bone formation that occurred in the post-trauma period. The size of osseous callus, covering the fracture line and the surface next to the lesion, suggests that the deer has survived several months after the traumatic injury. In a mainland context, an injured deer would hardly have survived for such a long period, because any movement constantly irritated the fracture, dramatically reducing performance or willingness to move and the gait speed, and hampering any escape.


RÉSUMÉ

Les îles ont été considérées comme des laboratoires vivants de la biodiversité et une cible pour l'étude des forces qui influent sur l'évolution. Cette recherche vise à déterminer si un cerf nain du Pléistocène de Crète (*Candiacervus ropalophorus*) qui a subi une fracture de son métatarsien aurait pu survivre, en dépit de sa jambe cassée, dans un environnement sans prédateurs pour un temps plus long que prévu sur le continent. L'os métatarsien montre une fracture complète et oblique au niveau de la diaphyse. Les examens macroscopiques et aux rayons X montrent l'impressionnante formation d'os nouveau qui s'est produite dans la période post-traumatique. La taille de ce cal osseux, couvrant la ligne de fracture, suggère que le cerf a survécu durant plusieurs mois au traumatisme, même si tout mouvement

* Corresponding author.
*E-mail address:* mariarita.palombo@uniroma1.it (M.R. Palombo).

http://dx.doi.org/10.1016/j.crpv.2015.03.003

irritait constamment la fracture, réduisant considérablement les performances locomotrices, la vitesse de marche et la possibilité d'échapper aux prédateurs.


## 1. Introduction

Studies on palaeopathology of fossil bones, dating back to the beginning of the last century, mainly deal with investigations on human and dinosaur bones or on domestic animals from archaeological sites, while only a few concern Pleistocene mammals (see e.g. Acosta Hospitaleche et al., 2012; Aufderheide and Conrado, 1998; Bartosiewicz, 2008; Bartosiewicz and Gal, 2013; Bell and Coria, 2013; Bishop, 2011; Bricknell, 1987; Brothwell, 2008; Buffetaut et al., 2007; De Boer et al., 2013; Duckler and Van Valkenburgh, 1998; Everhart, 2008; Fisk and Macho, 1992; Franklin, 2011; Johnson and Milburn, 1982; Jordana et al., 2011; Kallal et al., 2012; Kierdorf et al., 2012; Lingham-Soliar, 2004; Martin, 2013; Martin Sander, 1992; Moodie, 1917, 1923; Ortner, 2002; Rega et al., 2012; Rothschild and Martin, 1993; Salesa et al., 2014; Tanke and Rothschild, 2010; Tasnádi-Kubacska, 1962; Telldahl, 2012a,b; Vann and Thomas, 2006; Wu and Schepartz, 2009).

During the last two decades, studies on palaeohistology and palaeopathology have been receiving increasing attention, at least partially reflecting the recent development and changing emphasis in the field of palaeoecology. Studying factors causing pathological diseases in past wild animals could, indeed, provide valuable hints for a better understanding of their life-style, behaviour and niche occupancy, in turn providing additional data to reconstruct predator-prey relationships and some aspects of population/ecosystem dynamics (see among others Gardner and Smith, 2006; Katsura, 2004; Palmqvist et al., 1999; Rothschild and Tanke, 1992; Rothschild et al., 2001; Salesa et al., 2014; Tanke and Farke, 2006). In particular, "survival of animals with injuries or diseases limiting their mobility and function suggests the possibility of "a support system" which allowed their survival" (Rothschild and Tanke, 1992, p. 73).

Therefore, studies of palaeopathology in insular endemic mammals may help determining whether resources availability, and ecological interaction and displacement or the release from predator pressure are among the major factors driving evolution and survival in isolated environments (see e.g. Lomolino et al., 2013 and references therein).

Here, we present a case study of a healed fracture of a still undescribed metatarsal of *Candiacervus ropalophorus* (the smallest among the endemic Pleistocene deer species from Crete, eastern Mediterranean), found in the latest Middle (?) — Late Pleistocene (see below) deposits of Bate cave (Rethymnon, northern Crete) (Capasso Barbato, 1990, 1992; Kotsakis, 1977; Kotsakis et al., 1976).

## 2. Material and methods

### 2.1. Bate cave and its faunal record

The metatarsal (MPUR/V coll. Bate S50) is part of a rich fossil sample collected in the seventies by a team of Sapienza University of Rome (Italy) in an unexplored cavity (named "Bate cave" by the Italian discoverers), located in the north Cretan coast, not far from the Zourida gorge, in the cliffs below the Rethymnon-Chania National Road (Fig. 1). The material is currently stored in the Museum of Palaeontology, Department of Earth Sciences of Sapienza University (Rome, Italy).

The vertebrate fauna retrieved from the chaotic fossiliferous layers filling Bate cave includes a few remains of amphibians, reptiles (*Bufo* cf. *B. viridis*, *Testudo marginata cretensis*, *Lacerta* cf. *L. erhardi*, *Coluber* cf. *C. gemonensis* in Kotsakis, 1977), small mammals (*Mus minotaurus)* and four deer species: *Candiacervus* ex gr. *C. ropalophorus* (*sensu* Palombo et al., 2008), the smallest and the most abundant, and three larger deer species, *Candiacervus cretensis*, *Candiacervus dorothensis* (= *Candiacervus* sp. V, De Vos, 1979),


**Fig. 1.** (Color online.) Map of the island of Crete. Localization of caves cited in the text.
**Fig. 1.** (Couleur en ligne.) Carte de l'île de Crète. Localisation des grottes mentionnées dans le texte.

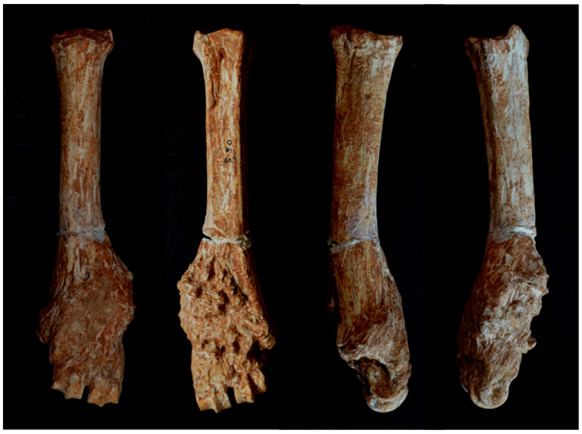

**Fig. 2.** Left metatarsal (MPUR/V coll. Bate S50) of *Candiacervus ropalophorus*, Bate cave. From left to right: anterior, posterior, medial and lateral view.

**Fig. 2.** Métatarse gauche (MPUR/V coll. Bate S50) de *Candiacervus ropalophorus*, Grotte Bate. De gauche à droite : vues antérieure, postérieure, médiale et latérale.

and *Candiacervus major* (= *Candiacervus* sp. VI, De Vos, 1979) (Capasso Barbato, 1989). The latest two species have been reported only from Bate cave, while in this cave a fifth endemic Cretan species, *Candiacervus rethymnensis*, seems to be absent. The fossil assemblage of Bate cave belongs to the youngest Pleistocene Cretan fauna complex, the so-called *Mus minotaurus* "sub-zone" (Mayhew, 1977). The age of the fossiliferous deposit is not firmly established because of the inconsistency of dates obtained by different authors/methodologies (see Lax, 1996). Belluomini and Delitala (1983, 1988) indicated an age from 63,500 ± 20% to 69,000 ± 20% years (Amino Acid Racemization, AAR, datings on deer bones), while Reese et al. (1966, p. 47) argue that AAR dates done on bones are "very much less reliable than tooth enamel". Two AAR dates on deer teeth are indeed significantly older: 152,000 ± 20% to 105,000 ± 20%, suggesting a late Middle to early Late Pleistocene age for the deposits of Bate cave (Reese et al., 1966).

The bone studied here (Fig. 2) is a left metatarsal belonging to the group of the smallest deer (cf. Capasso Barbato, 1989), whose dimensions partially overlap the dimensional range of the richest samples of the smallest deer found in Crete [i.e. samples from Simonelli (Malatesta, 1980), Gerani 4 and Liko caves (De Vos, 1979, 1984)]. This might make the identification of the sample from Bate cave questionable. The smallest Cretan deer, indeed, shows a large variation in size, proportions and in skull, teeth and especially antler morphology. This prompted some research to tentatively split them into four different species/morphotypes (*C. ropalophorus*, *Candiacervus* sp. IIa, *Candiacervus* sp. IIb, *Candiacervus* sp. IIc) (Dermitzakis et al., 1987 and De Vos, 1987; De Vos, 1979, 1984, 2000; Van der Geer et al., 2010). Such a high level of specific diversity seems, however, improbable, and the hypothesis that differences in skull and antler morphology could depend on increased intra-specific variation, as sometime observed in insular species, cannot be discarded (cf. e.g. Caloi and Palombo, 1995; Capasso Barbato, 1990; Van der Geer et al., 2014; Palombo et al., 2008 for a discussion).

Dimensions and proportions of the metatarsal studied here (see below) (Figs. 2, 3; Table 1) suggest it could be identified as *C. ropalophorus*, as supported by a comparison with the rich Late Pleistocene metatarsal samples from Gerani 4 (*C. ropalophorus*) (AAR date 70,000 ± 20% years, ESR date 100,600 ± 20% years, Reese et al., 1966) and Liko sites (with *Candiacervus* spp. II) (AAR dates from 85,000 ± 20% to 105,000 ± 20% years, Reese et al., 1966) (De Vos, 1979), as well as with the Late Pleistocene sample from Simonelli cave (= *"Megaceros cretensis"*, Malatesta, 1980) (AAR and ESR dates ranging from 21,500 ± 20% to 81,000 ± 20%, Reese et al., 1966).

### 2.2. Methods

Dimensions and proportion of the metatarsal (MPUR/V coll. Bate S50) (Figs. 2, 3; Table 1) were compared with those of the smallest deer from Bate cave (Capasso Barbato, 1989) and Simonelli cave (Malatesta, 1980) to confirm its specific identification (see above) and evaluate the extent of modifications caused by the fracture.

The morphological exam of the lesion was performed by direct observation (Figs. 2, 4) and by means of X-ray examination (Fig. 5). This approach permitted to study the inner part of the bone, visualizing the medullary cavity in the diaphysis and the possible fracture line in the bone structure and inferring factor causing the pathological bone alteration. Digital X-ray analysis was conducted in the Radiological Laboratory of the Veterinary Hospital, in the Department of Veterinary Medicine of Sassari University (Italy). Digital radiographic images were obtained through anterior-posterior and lateral-medial projections of X-rays using a Radiological Unit CR 30-X (Agfa, Mortsel, Belgium) with the following parameters: 120 kVp and 120 mA. In addition, a microtomographic analysis was made to study the inner part of the lesion area with particular attention to the shape of the medullary cavity and its three-dimensional reconstruction. The area of the osseous callus was scanned with a micro-CT scanner (Skyscan 1172, Aartselaar, Belgium) in the Biophysical Laboratory of the University of Sassari (Italy). The scanner was equipped with the X-ray detector: 11 Megapixel, 12 bit digital X-ray camera with 24 × 36 mm field of view.

## 3. Results

The left metatarsal of *Candiacervus ropalophorus* from Bate cave belongs to an adult individual, as it shows complete epiphyseal fusion (Fig. 2). Its dimensions indicate that the specimen is among the smallest and most robust specimens found at Bate cave, while at Simonelli cave a few specimens show smaller dimension and more robust proportions, confirming the large variation in size and proportion of bones of small-sized Cretan deer (Fig. 3, Table 1). Compared with the specimens from Bate cave, the metatarsal shows a more robust proximal epiphysis, sensibly expanded antero-posteriorly. This feature possibly relates to the modified general shape caused by the fracture that displaced the distal part of the bone.

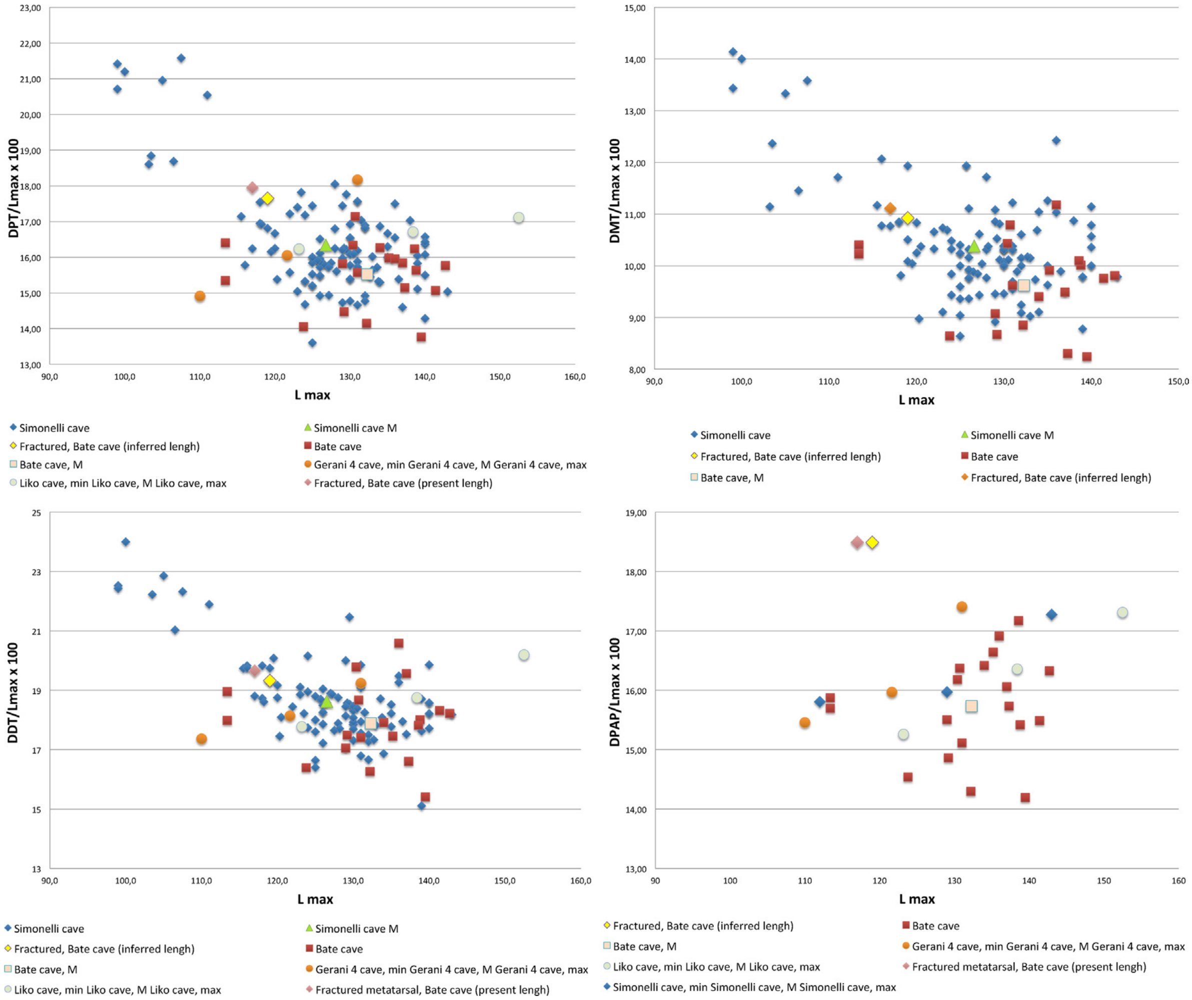


**Fig. 3.** (Color online.) Proportions of the *Candiacervus ropalophorus* metatarsal (MPUR/V coll. Bate S50) from Bate cave, as compared with samples of small-sized *Candiacervus* from Simonelli, Gerani 4 and Liko caves whose measurements were taken from Capasso Barbato (1989) (1), Malatesta (1980) (2), De Vos (1979) (3). Lmax: maximal length; DPAP: maximal antero-posterior breadth of the proximal articular surface; DPT: maximal medio-lateral breadth of the proximal articular surface; DMT: medio-lateral breadth at the half of the diaphysis; DDT: maximal medio-lateral breadth of the distal articular surface.

**Fig. 3.** (Couleur en ligne.) Proportions du métatarse de *Candiacervus ropalophorus* (MPUR/V coll. Bate S50) de la grotte Bate, comparées avec les échantillons de *Candiacervus* de petite taille des grottes Simonelli, Gerani 4 et Liko dont les mesures ont été publiées par Capasso Barbato (1989) (1), Malatesta (1980) (2), De Vos (1979) (3). Lmax : longueur maximale ; DPAP : largeur maximale antéro-postérieure de la surface articulaire proximale ; DPT : largeur maximale médio-latérale de la surface articulaire proximale ; DMT : largeur médio-latérale à la moitié de la diaphyse ; DDT : largeur médio-latérale maximale de la surface articulaire distale.

The bone presents a healed, complete oblique fracture of the diaphysis, slightly distal to the mid-shaft. The fractured area shows a considerable overriding of the two main fragments, the distal part of the diaphysis being positioned laterally and displaced posterior to the proximal one. As a result, the distal shaft and the epiphysis is misaligned by at least 22 degrees from the original axis in the cranial view and at least 19 degrees in the lateral view (Fig. 4). The slipping reduces the metatarsal length of about 2 cm. The misaligned axis of the bone ant the entity of the displacement of the two broken segments, on one hand confirms that a complete fracture occurred, on the other that the fracture was likely open and a tearing of soft tissues and skin occurred.

What was the accident that caused the fracture is difficult to say. However, it could be hypothesized that the fracture has been provoked by either a sudden twisting movement or an accidental fall after a jump, as may be supported by the hypothesis that *C. ropalophorus* inhabited rocky environments, similarly to the extant Cretan goat *Capra aegagrus cretica* (Van der Geer et al., 2006, 2010).

Considering the fact that at the level of the fracture, no musculature surrounds metapodial bones in deer (only tendons are present) and that the distal part of the metatarsal, where even tendons are present, significantly slipped laterally, the hypothesis that the fracture was open may be considered realistic. In the shank of long bones of most artiodactyls, indeed, the tendons are localized in the cranial side (terminal tendons of extensor muscles) and in the plantar side (terminal tendons of flexor muscles), and only a thin layer of subcutaneous connective tissue separates the skin from the metapodial bone in the lateral and

**Table 1**
Measurements of the *Candiacervus ropalophorus* metatarsal (MPUR/V coll. Bate S50) from Bate cave, as compared with small-sized *Candiacervus* samples from Simonelli, Gerani 4 and Liko caves whose measurements were taken from Capasso Barbato (1989) (1), Malatesta (1980) (2), De Vos (1979) (3).
**Tableau 1**
Mesures du métatarse (MPUR/V coll. Bate S50) de *Candiacervus ropalophorus* de la grotte Bate, comparées avec celles de *Candiacervus* de petite taille des grottes Simonelli, Gerani 4 et Liko dont les mesures sont tirées de de Capasso Barbato (1989) (1), Malatesta (1980) (2), De Vos (1979) (3).

| | Lmax | DPAP | DPT | DMAP | DMT | DDAP | DDT | DDT soprart |
|---|---|---|---|---|---|---|---|---|
| Factured metatarsal, Bate cave | 119.0 | 22.0 | 21.0 | 14.0 | 13.0 | 16.0 | 23.0 | 25.0 |
| Bate cave (1) | | | | | | | | |
| Bate cave, min | 113.4 | 17.8 | 17.4 | 10.8 | 10.7 | 10.0 | 20.3 | 19.4 |
| Bate cave, M | 132.3 | 20.8 | 20.6 | 12.3 | 13.4 | 14.7 | 24.2 | 23.9 |
| Bate cave, max | 142.7 | 23.8 | 22.5 | 15.0 | 15.2 | 20.0 | 30.0 | 31.6 |
| Simonelli cave (2) | | | | | | | | |
| Simonelli cave, min | 112.0 | 17.7 | 17.1 | 10.6 | 10.2 | – | 19.6 | – |
| Simonelli cave, M | 129.9 | 20.6 | 20.3 | 13.2 | 12.7 | – | 22.9 | – |
| Simonelli cave, max | 143.0 | 24.7 | 23.8 | 14.7 | 15.0 | – | 26.6 | – |
| Gerani 4 cave (3) | | | | | | | | |
| Gerani 4 cave, min | 110.0 | 17.0 | 16.4 | – | – | 12.2 | 19.1 | – |
| Gerani 4 cave, M | 121.6 | 19.4 | 19.5 | – | – | 13.8 | 22.1 | – |
| Gerani 4 cave, max | 131.0 | 22.8 | 23.8 | – | – | 15.5 | 25.2 | – |
| Liko cave (3) | | | | | | | | |
| Liko cave, min | 123.2 | 18.8 | 20.0 | – | – | 13.6 | 21.9 | – |
| Liko cave, M | 138.4 | 22.6 | 23.1 | – | – | 16.1 | 26.0 | – |
| Liko cave, max | 152.5 | 26.4 | 26.1 | – | – | 19.2 | 30.8 | – |

Lmax: maximal length; DPAP: maximal antero-posterior breadth of the proximal articular surface; DPT: maximal medio-lateral breadth of the proximal articular surface; DMAP: antero-posterior breadth at the half of the diaphysis; DMT: medio-lateral breadth at the half of the diaphysis; DDAP: maximal antero-posterior breadth of the distal articular surface; DDT: maximal medio-lateral breadth of the distal articular surface; DDT soprart: maximal medio-lateral breadth of the shaft just above the distal articular surface.

medial sides of the diaphysis. Therefore, the medial and lateral sides of metapodial bones may be more exposed to traumatic events.

The fracture of the *C. ropalophorus* metatarsal was entirely healed. Both a direct observation and X-ray examination show the impressive new bone formation that occurred in the post-trauma period (Figs. 2 and 5).

The localization, shape, size and symmetry of the osseous callus confirm it was a consequence of a traumatic fracture and that the bone remodelling process depends neither on a bone proliferative process as a consequence of a periosteum reaction due to chronic inflammatory events (e.g. periostitis or osteoperiostitis), nor on tumoral osteogenic process (e.g. osteoma and osteosarcoma, respectively benignant and malignant tumours of bones). In the case of any tumoral process, the surface of the osseous callus would be porous, whereas in the case of periosteum reaction the lesion would be quite localized.

X-ray images indicate that the remodelling process developed while biomechanical stresses continued to solicit movements at the fracture line level, suggesting that the animal was actively moving in spite of the important injury affecting its hint limb, because without movements the callus osseous would have been much less voluminous (Claes et al., 1998).

Assuming that the fracture was open with skin laceration, the hypothesis that the remodelling process was so important because of the simultaneous presence of an infection of the soft tissue surrounding the bone caused by pathogens seems reasonable (Urist et al., 1954). How long the stress of walking with a broken leg delayed the healing process it is difficult to hypothesize, though the size of the osseous callus suggests that the healing process lasted at least 4–5 months.

The extensive remodelling process modified the bone structure and the shape, position and direction of the diaphysis canals. The micro-CT images show a light passage from the canal typical of ruminants (doubled because the metapodial bone originated ontogenetically and phylogenetically from two distinct bones) in a labyrinth of canals becoming smaller (Fig. 5).

The rough surface of the callus and the extremely limited presence of smoothing signs indicate that the process of fracture remodelling had not appreciably progressed at the time when the deer died.

## 4. Discussion

Traumatic lesions constitute an important research field in the study of palaeopathology because they could provide useful insights in reconstructing animal behaviour and palaeoecology. Studies on this field go back to the 17 centuries, when the German naturalist Johann Friedrich Esper (1774) correctly described a fracture in a femur of a cave bear affected by osteosarcoma. Fractures in extinct animals have been reported ever since the Late Palaeozoic, as documented, for instance, by the healed fracture in a radius of the Permian synapsid *Dimetrodon* (Moodie, 1923).

In wild animals, fractures sometime occur as a result of accidental falls, though most long bone fractures are the result of bending and/or torsional loading, whose strengths scale similarly across a broad range of animals, in spite of differences in scaling of length and external diameter of bones (Selker and Carter, 1989).

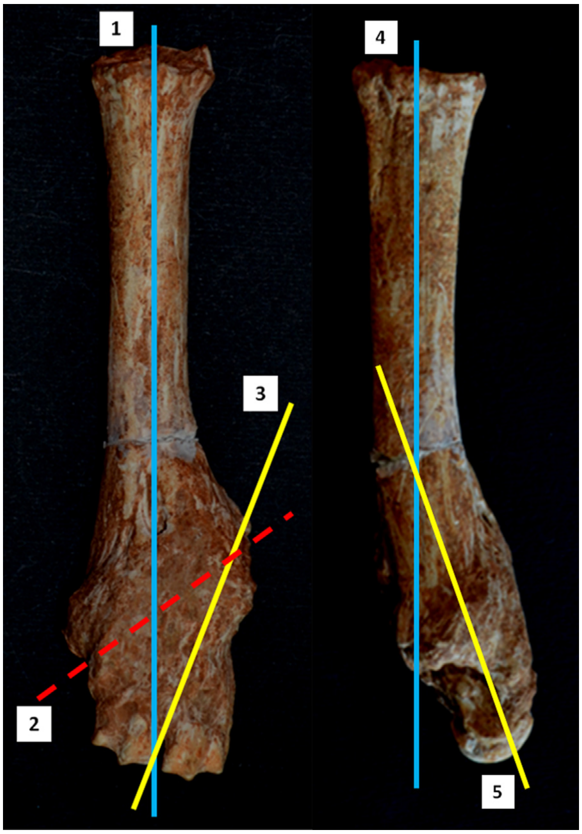


**Fig. 4.** (Color online.) Left metatarsal of *Candiacervus ropalophorus*, Bate cave, in anterior and medial view. 1 and 4: original axis of metatarsal; 2: oblique line of the fracture; 3 and 5: axis of the distal portion of fractured bone.

**Fig. 4.** (Couleur en ligne.) Métatarse gauche de *Candiacervus ropalophorus*, Grotte Bate, en vues antérieure et médiale. 1 et 4 : axe original du métatarse ; 2 : ligne oblique de fracture; 3 et 5 : axe de la portion distale de l'os.

Therefore, it would not be surprising if a traumatic lesion had occurred as a fracture that dramatically damaged the metatarsal of the small Cretan deer, though the size of the callus and the extent of processes involved in a fracture healing suggest a survival normally unexpected in deer living on mainland in structurally balanced community. A bone fracture, indeed, determines a reaction that causes the formation of new bone tissue in both endosteum and periosteum. The fracture repair involves various steps, including the formation of new bone tissue and the remodelling to normal bone (Aufderheide and Conrado, 1998; Grauer, 2012). Immediately after a fracture, a hematoma is produced and its blood coagulates in 6–8 hours. During this stage, connective cells migrate into the coagulating hematoma where they differentiate in fibroblasts, chondrocytes and osteoblats. Subsequently, a vasculoneogenesis initiates the repair at the level of periosteum. In mammals this reparative stage generally lasts about three weeks and it is initially characterized by a fibrous callus that subsequently calcifies (Grauer, 2012). The replacement of the fibrous callus with a bone callus is the slowest repair stage, requiring up to a few months. The time necessary for the complete replacement mainly depends on the age (faster in juvenile than adult individuals), the type of bone tissue (more rapid in cancellous bone, slower in compact cortical bone), the kind of bone (slower in tibia than other bones) and the fracture type (slower in horizontal fracture, more rapid in helicoidal fracture) (Newton and Nunamaker, 1985). As a result, the healing process in bone fractures is a complex process that requires good general health and nutrition to be achieved rapidly. The immobilization of the fractured bone accelerates healing, while any factor disturbing bone immobility, as well as infections and other pathological conditions, significantly delays the healing process.

Contrary to poikilothermic animals (amphibians and many reptiles) that can stay for weeks or months without eating (Janssens, 1970), in endotherm animals, such as mammals, the immobilization of fractured limb bones is virtually impossible in the wild due to the need of moving at least for the minimum resource exploitation necessary to survive. Under the best conditions (immobilization by a circular external fixator, juvenile age and good nutrition), a fracture of metapodial bones in a young deer in its first year heals in five weeks (Aitken-Palmer et al., 2012). In the wild, this period could be longer. Indeed, movements constantly irritate the fracture line, causing production of more callus. Moreover, fractures of limb bones, particularly autopodium bones more exposed to traumatic injuries, are the most common in terrestrial mammals. The fracture of the metatarsal of the Cretan deer is in line with the high frequency of this kind of fracture in cervids. Nisbet et al. (2010), for instance, reported in a clinical study on twenty roe deer (*Capreolus capreolus*) affected by traumatic injuries, that among the 11 identified fractures, 3 affected metapodials. All fractures of the metapodials were open, with a tearing of the surrounding soft tissue and skin. A case of a spontaneous complete healing of an open metatarsal fracture has been also described in an extant white-tailed deer (*Odocoileus virginianus*) (Withrow, 1982).

The extent of the complete fracture in the Cretan metatarsal, the displacement suffered by the two broken parts, and the enormous development of the callus suggest that also in this case the fracture was open. This condition certainly caused the entry of pathogens. As a result, a severe inflammatory process likely developed, further increasing the disease of the injured deer.

The complete healing of the extensive trauma in the Cretan specimen, long-lasting despite the functional impact of the pathological consolidation, is an indirect evidence of the peculiar life condition of the animal in its insular ecosystem where predators were absent and the pressure for resources was expected to be low because Cretan herbivores of *Mus* "biozone" (elephant, and large, middle-sized and small deer) likely differed in their niche specialization (see below).

The fracture did not cause the immobility of the dwarf deer that moved at least to find food, being facilitated in this by the high pain threshold the ruminants generally have (Waterman-Pearson, 2006). Any movement constantly irritated the broken metatarsal, delaying the healing of the fracture. This joined with the difficulty firstly to place the hind leg and then the lameness due to the shortening of the

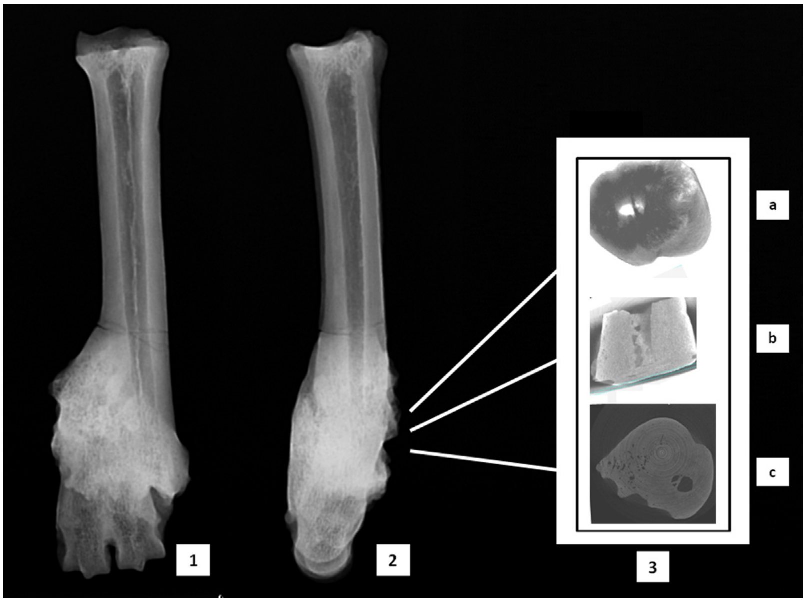


**Fig. 5.** (Color online.) X-rays images. 1: anterior projection; 2: lateral projection; 3: micro-CT scanned at different levels of the lesion: a: double diaphysis canal; b: 3D reconstruction of the end of the integrity of the diaphysis canal; c: reconstructed section of the vascular cavities in the osseous callus.
**Fig. 5.** (Couleur en ligne.) Images radiographiques. 1 : projection antérieure ; 2 : projection latérale ; 3 : images micro-CT scannées à différents niveaux : a : canal diaphysaire double ; b : reconstruction tridimensionnelle de la terminaison du canal diaphysaire ; c : section du cal osseux avec les cavitations vasculaires.

limb, dramatically reduced performance or willingness to move and the gait speed, hampering any escape and possibly reducing the animal's home range. A survival in such conditions would be highly problematic for a mainland deer having to compete for food and to face large carnivorous predators. The low biodiversity of insular faunas and the disharmonic ecological structure of mammalian communities, changing the common rules of competition-coevolution dynamics, may increase the chance of survival of individuals suffering from some diseases. In an insular species-poor biota lacking predators, where ecological release should be prevalent, a lower level of inter-specific competition might attenuate the effect on population density and intra-specific competition caused by the absence of predators (e.g. Abrams, 2000). This was likely true of the Pleistocene fauna of Crete, lacking large mammalian predators and with a low number of herbivore species competing each other for resources.

Crete has been isolated from surrounding mainland since the end of the Pliocene by large barriers (van Hinsbergen and Meulenkamp, 2006), and most, if not all, non-volant vertebrate settlers reached the island by over-sea, sweepstake dispersal (Sondaar, 1977). As a result, the island was inhabited throughout the Pleistocene by unbalanced, disharmonic and impoverished vertebrate faunas (i.e. lacking large terrestrial mammalian carnivores, the only documented carnivore on Crete being a Late Pleistocene otter *Lutrogale cretensis*), counting mammals that managed to survive active or passive overwater dispersal (rodents, insectivores, elephants, deer, hippopotamuses), which enabled them to establish viable populations on the island. In this peculiar island ecosystem, the presence of a number of available ecological niches, proper on mainland to species absent on the island, triggered the radiative evolution of deer settlers. A new competition-coevolution equilibrium developed, life-history traits of mammals evolved differently than in continental ecosystems. Deer partitioned resources and reduced competition by specializing for having different body size, habitat and trophic requirements as suggested by both the peculiar morphological traits of skulls, teeth, and limb bones and by the different Cretan deer species/morphotypes that coexisted on the same territory (Caloi and Palombo, 1995, 1996; De Vos, 2000; De Vos and Van der Geer, 2002; Van der Geer et al., 2010).

Key factors in interpreting the reason why *C. ropalophorus* from Bate cave survived for a fairly long time in spite of the severe injury of its hind limb depend on the interplay among resource availability and intra- and inter-specific competition that, in turn, affected the population density of the ecological group the small Cretan deer belongs to.

At the time when *C. ropalophorus* broke its left hind limb, the mammalian fauna consisted of deer species with a different diet and inhabiting different environments, a dwarf elephant (*Palaeoloxodon creutzburgi*), a giant mouse (*Mus minotaurus*), and a shrew (*Crocidura zimmermanni*), the only Cretan Pleistocene mammal surviving today. Therefore, adult deer of *C.* ex gr. *C. ropalophorus* [having nearly the same size, similar dietary behaviour (e.g. grassy food or prickly bushes) and inhabiting similar environments (e.g. rocky hill), as suggested by De Vos and Van der Geer (2002)] had neither potential competitors nor predators, the impact of the endemic near-flightless (*Athene cretensis*) being negligible, and the presence of a second endemic raptor (*Aquila* according to Weesie, 1988, but Aves *incertae sedis* in Louchart et al., 2005) not substantiated because it is based on a single fragment, lacking diagnostic features. Accordingly, it is rational to suppose that inter-specific competition was low and individuals within each herbivorous species could efficiently exploit resources. More important (though difficult to ascertain) was the role of intra-specific competition, which regulates population growth in a density-dependent manner and tends to favor the individuals with high resource use efficiency and competition ability when resources are insufficient and competition occurs. Taking into account that available data on vegetation cover during the Late Pleistocene in the Aegean area indicate that forests were present even during the Last Glacial Maximum (i.e. on Lesbo island) (Bottema and Sarpaki, 2003; Digerfeldt et al., 2000; Fletcher et al., 2010; Margari et al., 2009), the hypothesis of a presence on Crete of diversified environments, including *Zelkova* forests (Kozlowski et al., 2014), an environment fairly rich in nutrients, seems reasonable. If so, it might be speculated that the competition among individuals of *Candiacervus* ex gr. *C. ropalophorus* was low, even though the absence of predators likely increased the population density. However, studies of mortality profile of small Cretan deer from both Gerani 4 (*C. ropalophorus)* and Liko (*Candiacervus* sp. II) caves carried out by Van der Geer et al. (2014), would suggest "a nutrient-poor environment supporting relatively few individuals" (Van der Geer et al., 2014, p. 21). Assuming as true this hypothesis, the competition would have increased, reducing the chance of survival of a severely crippled individual. The healed fracture of the metatarsal from Bate cave, however, indicates that the animal was reasonably healthy, as confirmed by the absence of any abnormal morphology of pathological origin, as conversely found in deer from Mavro Mouri cave (Rethymnon), most of which suffered of an osteopatia caused by a long-term malnutrition (Dermitzakis et al., 2006).

All things considered, the hypothesis that the crippled deer of Bate cave survived because throughout the time the fracture healed the competition for resources was low seems plausible. Moreover, taking into account that the reduced motility of *C. ropolophorus* from Bate cave limited its home range, the hypothesis that it died sometime after the fracture healed because a long dry season (or other unfavourable climatic conditions) negatively affected the vulnerable rocky environment it inhabited, thus triggering a starvation period, may be plausible. Other factors, however, could have caused the death of the draft deer before any conspicuous remodelling of the bony callus had occurred.

## 5. Conclusion

The complete and oblique fracture affecting a metatarsal of *C. ropalophorus* from Bate cave displaced laterally and posteriorly the distal epiphysis, reducing the metatarsal length of at least 2 cm (10,52% of the inferred total length). Both macroscopic observation and X-ray examination show the impressive new bone formation that occurred in the post-trauma period with the development of a massive callus with a coarse surface. The size of osseous callus suggests that the deer has survived several months after the traumatic injury, though any movement constantly irritated the open fracture. This, coupled with impaired locomotory ability due to the reduced length of the left hind limb, dramatically reduced performance or willingness to move and the gait speed, and hampering any escape. Survival in such a condition would be highly problematic for a deer having to compete for food and to face large carnivorous predators, as happens for species living on mainland. The loss of biodiversity of Pleistocene Cretan fauna and the unbalanced functional diversity of mammalian communities, in particular the absence of predators, the inferred low intra-guild competition, changing the common rules of competition-coevolution dynamics, likely increased the chance of survival of this small deer.

The size and extension of the bony callus indicate that the animal had survived the metatarsal fracture for some months in environmental conditions providing enough resources for permitting the bone tissue to regenerate, though the poor remodelling suggests that no long time elapsed between the fracture healing and the death of the deer. Which among various factors caused its death is difficult to say, though taking into account the reduced motility of *C. ropolophorus* from Bate cave limited its home range, the hypothesis that a contrasted seasonal climate induced a starvation that in turn caused its death, cannot be discarded.

## Acknowledgements

We thank D. Magri for her information on vegetation records in the Aegean area and the two anonymous reviewers for their comments. This work has been founded by Sapienza University of Rome (project C26A14BNRM, PI M.R. Palombo).

## References

Abrams, P.A., 2000. The evolution of predator-prey interactions: theory and evidence. Annu. Rev. Ecol. Syst. 31, 79–105.
Acosta Hospitaleche, C., Perez, L.M., Acosta, W., Reguero, M., 2012. A traumatic fracture in a giant Eocene penguin from Antarctica. Antarct. Sci. 24, 619–624.
Aitken-Palmer, C., Lewis, D.D., Kim, S.E., Reese, D.J., 2012. Use of a circular fixator construct for metacarpal fracture stabilisation in a fawn. Vet. Rec. 170, 444.
Aufderheide, A.C., Conrado, R.M., 1998. The Cambridge encyclopedia of human paleopathology. Cambridge University Press, Cambridge, UK.
Bartosiewicz, L., 2008. Taphonomy and palaeopathology in archaeozoology. Geobios 4, 69–77.
Bartosiewicz, L., Gal, E., 2013. Shuffling nags, lame ducks: the archaeology of animal disease. Oxbow Books.
Bell, P.R., Coria, R.A., 2013. Palaeopathological survey of a population of *Mapusaurus* (Theropoda: Carcharodontosauridae) from the Late Cretaceous Huincul formation, Argentina. PloS One 8, e63409.
Belluomini, G., Delitala, L., 1983. Datazione di resti ossei e denti del Pleistocene superiore e dell'Olocene dell'area mediterranea con il metodo della racemizzazione degli aminoacidi. Geografia Fisica e Dinamica Quaternaria 6, 21–30.
Belluomini, G., Delitala, L., 1988. Amino acid racemization dating of Quaternary deposits of central and southern Italy. Org. Geochem. 13, 735–740.
Bishop, K., 2011. Thule palaeopathology: the health concerns of an Arctic lifestyle. J. Anthropol. 19, 4 [Totem: The University of Western Ontario].
Bottema, S., Sarpaki, A., 2003. Environmental change in Crete: a 9000-year record of Holocene vegetation history and the effect of the Santorini eruption. The Holocene 13 (5), 733–749.

Bricknell, I., 1987. Palaeopathology of Pleistocene proboscideans in Britain. Mod. Geol. 11, 295–309.

Brothwell, D.R., 2008. Paleoradiology in the service of zoopaleopathology. In: Paleoradiology. Berlin Heidelberg, Springer, pp. 119–145.

Buffetaut, E., Li, J., Tong, H., Zhang, H., 2007. A two-headed reptile from the Cretaceous of China. Biol. Lett. 3, 81–82.

Caloi, L., Palombo, M.R., 1995. Functional aspects and ecological implications in Pleistocene endemic cervids of Sardinia, Sicily and Crete. Geobios 28, 247–258.

Caloi, L., Palombo, M.R., 1996. Functional aspects and ecological implications in Hippopotamuses and Cervids of Crete. In: Reese D.S. (Ed.), Pleistocene and Holocene fauna of Crete and its first settlers, monographs in world archaeology,. Prehistory Press of Madison 28, Madison Winsconsin, USA, pp. 125–152.

Capasso Barbato, L., 1989. Cervidi endemici del pleistocene di Creta. Vol. I and II [Unpublished PhD thesis. Dottorato in Palaeontologia, Modena-Bologna].

Capasso Barbato, L., 1990. Les cervidés endémiques de Crète. Quaternaire 1 (3-4), 265–270.

Capasso Barbato, L., 1992. Nuova specie di cervide del pleistocene di Creta. Atti della accademia Nazionale dei Lincei, Memorie Lincee. Scienze Fisische e Naturali 1, 183–220.

Claes, L.E., Heigele, C.A., Neidlinger-Wilke, C., Kaspar, D., Seidl, W., Margevicius, K.J., et al., 1998. Effects of mechanical factors on the fracture healing process. Clin. Orthop. Relat. Res. 355, 132–147.

De Boer, H.H., Van der Merwe, A.E., Maat, G.J.R., 2013. The diagnostic value of microscopy in dry bone palaeopathology: a review. Int. J. Paleopathol. 3, 113–121.

De Vos, J., 1979. The endemic Pleistocene deer of Crete. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, 1., pp. 59–90 [Series B 82].

De Vos, J., 1984. The endemic Pleistocene deer of Crete. Verhandelingen Koninklijke Nederlandse Akademie van Wetenschappen, afd Natuurkunde, Eerste Reeks, 31., pp. 1–100.

De Vos, J., 2000. Pleistocene Deer fauna in Crete: its adaptive radiation and extinction. Tropics 10 (1), 125–134 [Special issue].

De Vos, J., Van der Geer, A.A.E., 2002. Major patterns and processes in biodiversity: taxonomic diversity on islands explained in terms of sympatric speciation. In: Waldren, B., Ensenyat, J.A. (Eds.), World islands in prehistory, international insular investigations, V Deia International Conference of prehistory. Bar International Series, 1095, pp. 395–405.

Dermitzakis, M.D., De Vos., J., 1987. Faunal succession and the evolution of mammals in Crete during the Pleistocene. Neues Jahrb. Geol. Paläontol. Abh. 173, 377–408.

Dermitzakis, M., Van der Geer, A., Lyras, G., 2006. Palaeopathological observations on a population of fossil deer from the late Pleistocene of Crete, chapter: 2. In: Kaofourtis, A., Papadopoulos, N., Spiliopoulou, C., Marabellas, K., Chatzioannou, A. (Eds.), Volume in honor of Prof. A.S. Koutselinis. Athens Editors, pp. 43–51 [in Greek with English summary].

Digerfeldt, G., Olsson, S., Sandgren, P., 2000. Reconstruction of lake-level changes in lake Xinias, central Greece, during the last 40 000 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 158 (1), 65–82.

Duckler, G.L., Van Valkenburgh, B., 1998. Osteological corroboration of pathological stress in a population of endangered Florida pumas (*Puma concolor coryi*). Anim. Conserv. 1, 39–46.

Esper, J.F., 1774. Description des Zoolithes nouvellement découvertes d'animaux quadrupèdes inconnus et des cavernes [Knorr G.W.].

Everhart, M.J., 2008. A bitten skull of *Tylosaurus kansasensis* (Squamata: Mosasauridae) and a review of mosasaur-on-mosasaur pathology in the fossil record. Trans. Kansas Acad. Sci. 111, 251–262.

Fisk, G.R., Macho, G.A., 1992. Evidence of a healed compression fracture in a Plio-Pleistocene hominid talus from Sterkfontein, South Africa. Int. J. Osteoarchaeol. 2, 325–332.

Fletcher, W.J., Goni, M.F.S., Allen, J.R., Cheddadi, R., Combourieu-Nebout, N., Huntley, B., et al., 2010. Millennial-scale variability during the last glacial in vegetation records from Europe. Quat. Sci. Rev. 29 (21), 2839–2864.

Franklin, R.D., 2011. The recognition, frequency and taxonomic association of skeletal pathology from selected Plio-Pleistocene-aged sites from the Cradle of Humankind, Witwatersrand, South Africa [Doctoral dissertation].

Gardner, J.C., Smith, F.H., 2006. The paleopathology of the Krapina Neandertals. Period. Biol. 108 (4), 471.

Van der Geer, A., Dermitzakis, M., De Vos, J., 2006. Relative growth of the metapodals in a juvenile island deer: *Candiacervus* (Mammalia, Cervidae) from the Pleistocene of Crete. Hellenic J. Geosci. 41, 119–125.

Van der Geer, A., Lyras, G., De Vos, J., Dermitzakis, M., 2010. Evolution of island mammals. Adaptation and extinction of placental mammals on islands. Wiley-Blackwell, London.

Van der Geer, A., Lyras, G., MacPhee, R.D.E., Lomolino, M.V., Drinia, H., 2014. Mortality in a predator-free insular environment: the dwarf deer of Crete, 3807. American Museum novitiates.

Grauer, A.L. (Ed.), 2012. A companion to paleopathology. Wiley-Blackwell, Hoboken, New Jersey.

van Hinsbergen, D.J., Meulenkamp, J.E., 2006. Neogene supradetachment basin development on Crete (Greece) during exhumation of the South Aegean core complex. Basin Res. 18, 103–124.

Janssens, P.A., 1970. Palaeopathology, diseases and injuries of prehistoric man. Royal Opera Arcade. The Curwen Press, London.

Johnson, G.D., Milburn, S.E.I., 1982. Pathological evidence of an injuried equid and associated fossil of Late Blancan (?) age from the Bon Homme Gravel, Yankton County, 63. PNAS, South Dakota, pp. 77–84.

Jordana, X., Galtés, I., Isidro, A., Malgosa, A., Köhler, M., 2011. Estudio macroscópico, radiológico y histológico de una fractura tibial de *Myotragus balearicus*. In: Gonzales Martin, A., Cambra-Moo, O., Rascòn Pérez, J., Campo Martin, M., Robledo Acinas, M., Labajo Gonzales, E., Sanchez Sanchez, J.A. (Eds.), Paleopatologia: ciencia multidisciplinar., pp. 435–439.

Kallal, R.J., Godfrey, S.J., Ortner, D.J., 2012. Bone reactions on a Pliocene cetacean rib indicate short-term survival of predation event. Int. J. Osteoarchaeol. 22, 253–260.

Katsura, Y., 2004. Paleopathology of *Toyotamaphimeia machikanensis* (Diapsida Crocodylia) from the Middle Pleistocene of central Japan. Hist. Biol. 16 (2–4), 93–97.

Kierdorf, U., Kahlke, R.D., Flohr, S., 2012. Healed fracture of the tibia in a bison Bison menneri from the late Early Pleistocene site of Untermassfeld (Thuringia, Germany). Int. J. Paleopathol. 2, 19–24.

Kotsakis, T., 1977. I resti di anfibi e rettili pleistocenici della grotta "Bate" (Rethymnon, Creta). Rend. Accad. Naz. Lincei. 8 (63), 571–582 [Ser].

Kotsakis, T., Melentis, J., Petronio, C., Sirna, G., 1976. Seconda spedizione paleontologica lincea nell'isola di Creta (1975). Rend. Accad. Naz. Lincei. 223, 3–10.

Kozlowski, G., Frey, D., Fazan, L., Egli, B., Bétrisey, S., Gratzfeld, J., et al., 2014. The Tertiary relict tree *Zelkova abelicea* (Ulmaceae): distribution, population structure and conservation status ion Crete. Oryx 48, 80–87.

Lax, E.M., 1996. A gazetteer of Cretan paleontological localities. In: Reese, D.S. (Ed.), Pleistocene and Holocene fauna of Crete and its first settlers, monographs in world archaeology. Prehistory Press of Madison 28, Madison Winsconsin, USA, pp. 1–32.

Lingham-Soliar, T., 2004. Palaeopathology and injury in the extinct mosasaurs (Lepidosauromorpha Squamata) and implications for modern reptiles. Lethaia 37, 255–262.

Lomolino, M.V., Geer, A.A., Lyras, G.A., Palombo, M.R., Sax, D.F., Rozzi, R., 2013. Of mice and mammoths: generality and antiquity of the island rule. J. Biogeogr. 40, 1427–1439.

Louchart, D.A., Bedetti, C., Pavia, D.M., 2005. A new species of eagle (Aves: Accipitridae) close to the Steppe Eagle, from the Pleistocene of Corsica and Sardinia, France and Italy. Palaeontographica Abteilung A, 121–148.

Malatesta, A., 1980. Dwarf deer and other late Pleistocene fauna of the Simonelli cave in Crete. Quaderni Accad. Naz. Lincei 249, 1–100.

Margari, V., Gibbard, P.L., Bryant, C.L., Tzedakis, P.C., 2009. Character of vegetational and environmental changes in southern Europe during the last glacial period; evidence from Lesvos Island. Greece Quat. Sci. Rev. 28 (13), 1317–1339.

Martin, J.E., 2013. Surviving a potentially lethal injury? Bite mark and associated trauma in the vertebra of a dyrosaurid crocodilian. Palaios 28, 6–8.

Martin Sander, P., 1992. The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 93, 255–299.

Mayhew, D.F., 1977. Endemic Pleistocene murids of Crete. 1. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, 80., pp. 182 [Series B-Palaeontology Geology Physics Chemistry Anthropology].

Moodie, R.L., 1917. Studies in paleopathology: general consideration of the evidences of pathological conditions found among fossil animals. Ann. Med. Hist. 1, 374–393.

Moodie, R.L., 1923. Palaeopathology: an introduction to the study of ancient evidences of disease. University of Illinois Press, Urbana, IL, USA.

Newton, C.D., Nunamaker, D.M., 1985. Textbook of small animal orthopaedics. J B Lippincott Company, Philadelphia, Pennsylvania.

Nisbet, H.O., Ozak, A., Yardimci, C., Sirin, Y.S., 2010. Treatment results of traumatic injuries in 20 roe deer (*Capreolus capreolus*): a retrospective study. Kafkas Universitesi Veteriner Fakultesi Dergisi 16, 617–622.

Ortner, D.J., 2002. Palaeopathology in the twenty-first century. Bones and the man: studies in honour of Don Brothwell. Oxbow, Oxford, UK, pp. 5–13.

Palombo, M.R., Köhler, M., Moya Sola, S., Giovinazzo, C., 2008. Brain versus body mass in endemic ruminant artiodactyls; a case studied of *Myotragus balearicus* and smallest *Candiacervus* species from Mediterranean islands. Quat. Int. 182 (1), 160–183.

Palmqvist, P., Arribas, A., Martinez-Navarro, B., 1999. Ecomorphological study of large canids from the Lower Pleistocene of southeastern Spain. Lethaia 32 (1), 75–88.

Reese, D.S., Belluomini, G., Ikeya, M., 1966. Absolute dates for the Pleistocene fauna of Crete. In Reese DS (ed), Pleistocene and Holocene fauna of Crete and its first settlers, monographs in world archaeology. Prehistory Press of Madison 28, Madison Winsconsin, USA, pp. 47–51.

Rega, E.A., Noriega, K., Sumida, S.S., Huttenlocker, A., Lee, A., Kennedy, B., 2012. Healed fractures in the neural spines of an associated skeleton of Dimetrodon: implications for dorsal sail morphology and function. Fieldiana Life Earth. Sci., 104–111.

Rothschild, B.M., Martin, L.D., 1993. Paleopathology. Disease in the fossil record. CRC Press, Boca Raton, FL, USA.

Rothschild, B.M., Tanke, D.H., 1992. Paleoscene 13. Paleopathology of vertebrates: insights to lifestyle and health in the geological record. Geosci. Canada 19 (2).

Rothschild, B., Tanke, D.H., Ford, T.L., 2001. Theropod stress fractures and tendon avulsions as a clue to activity. In: Tanke, D.H., Carpenter, K. (Eds.), Mesozoic vertebrate life. Indiana University Press, pp. 331–336.

Salesa, M.J., Antón, M., Siliceo, G., Pesquero, M.D., Alcalá, L., 2014. First evidence of pathology in the forelimb of the late Miocene Saber-toothed felid *Promegantereon ogygia* (Machairodontinae Smilodontini). Anat. Rec. 297, 1090–1095.

Selker, F., Carter, D.R., 1989. Scaling of long bone fracture strength with animal mass. J. Biomec. 22 (11), 1175–1183.

Sondaar, P.Y., 1977. Insularity and its effect on mammal evolution. In: Hecht, M.K., Goody, P.C., Hecht, B.M. (Eds.), Major patterns in vertebrate evolution. Plenum Press, New York, pp. 671–707.

Tanke, D.H., Rothschild, B.M., 2010. Paleopathologies in Albertan ceratopsids and their behavioral significance. New perspectives on horned dinosaurs. Indiana University Press, Bloomington and Indianapolis, Indiana, pp. 355–384.

Tanke, D.H., Farke, A.A., 2006. Bone resorption, bone lesions and extra cranial fenestrae in ceratopsid dinosaurs: a preliminary assessment. In: Galton, P.M. (Ed.), Horns and beaks: ceratopsian and ornithopod dinosaurs. Indiana University Press, Bloomington, pp. 319–347.

Tasnádi-Kubacska, A., 1962. Paläopathologie. Gustav Fischer Verlag, Jena, Germany.

Telldahl, Y., 2012a. Working animals and skeletal lesions: paleopathology of cattle and horse in Iron Age and Medieval Öland, Sweden.

Telldahl, Y., 2012b. Skeletal changes in lower limb bones in domestic cattle from Eketorp ringfort on the Öland island in Sweden. Int. J. Paleopathol. 2, 208–216.

Urist, M.R., Mazet, R., McLean, F.C., 1954. The pathogenesis and treatment of delayed union and non-union: a survey of eighty-five ununited fractures of the shaft of the tibia and one hundred control cases with similar injuries. J. Bone Joint Surg. Am. 36 (931), 980.

Vann, S., Thomas, R., 2006. Humans, other animals and disease: a comparative approach towards the development of a standardised recording protocol for animal palaeopathology, 20 [Internet Archaeology, http://intarch.ac.uk/journal/issue20/vannthomas_index.html].

Waterman-Pearson, A., 2006. Pain management in ruminants. Vet. Anaesth. Analg. 33, 137.

Weesie, P.D.M., 1988. The Quaternary avifauna of Crete, Greece. Palaeovertebrata 18, 1–94.

Withrow, S.J., 1982. Spontaneous healing of an open, comminuted metatarsal fracture in a white-tail reed. Vet. Med. Small Anim. Clin. 77, 50.

Wu, X., Schepartz, L.A., 2009. Application of computed tomography in paleoanthropological research. Prog. Nat. Sci. 19, 913–921.