



DOES A RELATIONSHIP EXIST BETWEEN PALAEOPATHOLOGIES AND INSULARITY ? A CASE STUDY OF SOME BONES OF *PROLAGUS SARDUS* (WAGNER, 1829) FROM SARDINIA (ITALY)

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ABSTRACT: This research describes pathological bones of *Prolagus sardus* (Lagomorpha, Ochotonidae) from four Middle-Late Pleistocene to Early Holocene sites of Sardinia (Italy), and presents a short inventory of the main Sardinian localities recording the species, with the intent to infer the viability of the Sardinian ochotonid populations during the Middle-Late Pleistocene and Early Holocene. The macroscopical analysis evidences that the pathologies were mostly of a traumatic origin, rather than due to other pathological conditions, which have been only observed in a few individuals inhabiting the Tavolara islet. The significance of the occurrence of palaeopathological signatures in bones of insular mammals and their usefulness in detecting the life-style, behaviour and niche occupancy of endemic mammalian species, and reconstructing some aspects of population dynamics in the peculiar island environments, are briefly discussed.

Keywords: palaeopathology, palaeoecology, Lagomorpha, Quaternary

Supplementary Appendices only online at <http://amq.aiqua.it>

1. INTRODUCTION

Fossil endemic Lagomorpha, including Ochotonidae, are known only on the Western Mediterranean islands, where endemic genera have been reported since the Miocene epoch from the Balearic islands (genus *Gymnesicolagus* from Majorca and Minorca) (Bover et al., 2014; Mas et al., 2018), and the Tusco-Sardinian palaeobioprovince (genus *Paludotona* from Baccinello Basin, Tuscany) (Dawson, 1959; Angelone et al., 2017). Moreover, some insular species of the genus *Prolagus* are recorded in the ?Early Pliocene in the Gargano palaeoarchipelago (Mazza, 1987), and in the Pliocene - Holocene of the Corsica-Sardinia Massif (Angelone et al., 2015). Representatives of the Sardinian endemic lineage are a quite common element in the Sardinian Late Pliocene - Holocene fossil record, and fossil remains are especially abundant in the Middle to Late Pleistocene Sardinian Local Faunal Assamblages (LFAs) (Dragonara Faunal Sub-Complex of the *Microtus* (*Tyrrhenicola*) FC) (cf. Palombo, 2009, 2018). The oldest remains, currently referred to *Prolagus* aff. *P. figaro* (Angelone et al., 2015), were collected in the Late Pliocene deposits of Mandriola (Capo Mannu, Sinis Peninsula) (Pecorini et al., 1974; López Martínez & Thaler, 1975; Angelone et al., 2015). *P. aff. P. figaro* of Mandriola probably originated from the mainland species *Prolagus sorbinii*, a taxon of eastern European origin, which migrated westwards during the early Messinian (Masini, 1989; Angelone et al., 2015). The ancestor of

the Corso-Sardinian *Prolagus* lineage (*P. figaro* - *P. sardus*) (Angelone et al., 2015) probably passively dispersed to the island at the Early/Late Pliocene transition, possibly taking advantage from a reduction of the mainland to island distance during a phase of sea-level lowering. Its direct descendant *Prolagus figaro* (Early Pleistocene - late Early Pleistocene) is reported at Capo Figari I and in several fissure fillings of Monte Tuttavista (López Martínez, 1975; Abbazzi et al., 2004; Palombo, 2009; Palombo & Rozzi, 2014; Moncunill-Solé et al., 2016). *P. figaro* likely survived until the end of the Orsei 2 Faunal Sub-Complex (Palombo & Rozzi, 2014; Palombo, 2018).

The last and most advanced representative of the Corso-Sardinian *Prolagus* lineage, *Prolagus sardus*, was the most common species in the Quaternary mammal fauna of Sardinia and Corsica (Zoboli & Caddeo, 2016). The species, erected by Wagner in 1829 on the basis of remains collected in the bone breccias of Monreale di Bonaria (Cagliari) (Wagner, 1829), was the first Pleistocene endemic mammal identified in Sardinia. The fossil remains of the large ochotonid, typically found in a number of LFAs of the Dragonara Faunal Sub-Complex (Palombo, 2009, 2018; Moncunill-Solé et al., 2016), are particularly abundant in caves and karst fissure fillings, but also quite frequent in the Early Holocene to Iron Age deposits, either recording or not a human presence (Comaschi Caria, 1968; Vigne et al., 1981; Wilkens, 2000; Zoboli & Pillola, 2017). The transition from *P. figaro* to *P. sardus*, which probably occurred during the

early Middle Pleistocene (Palombo & Rozzi, 2014), is marked by an increase of about 20% in BM (but not in dental dimensions) (average BM *P. figaro* = 398-436 gr; *P. sardus* = 504-525 gr) (Moncunill-Solé et al., 2016). *P. sardus* was very successful in colonising different environments of the Corsica-Sardinia Massif, as it can be inferred from the abundance of remains, the very wide distribution within the region and the chronology of fossiliferous deposits the species has been recorded from (see Appendix A).

In the course of the Holocene, however, population richness and abundance possibly declined. *P. sardus* probably disappeared in the Roman period, after the spread on the island of *Rattus rattus* (Vigne et al., 1981). The persistence of the ochotonid in Roman period seems to be confirmed by Polibio (206-124 B.C.), who mentioned a "small hare" in the Corsican fauna (Wilkins, 2000). The hypothesis of a survival of *Prolagus* on the Tavolara islet (NE Sardinia) until the late 18th is currently abandoned (Wilkins, 2000). It is still a matter of debate which among several factors could have been the main responsible for the ochotonid decline and extirpation. Some human's influence is, however, indubitable, whatever it could be direct (e.g. hunting) or indirect (e.g. active and passive introductions of alien species, including new predators and competitors, spread of pathogens, parasites, and in turn infectious diseases, and modification of the landscape by agricultural activities), or due to both factors (Vigne, 1996; Vigne et al., 1981, MacPhee & Preston, 1997; Palombo & Rozzi, 2014; Ucchesu et al., 2015; Melis et al., 2017).

The aim of this research is two fold, i) to describe pathological bones of *P. sardus* found in Sardinia in four Middle Pleistocene - Early Holocene caves, including one anthropogenic deposit (Fig. 1); ii) to discuss the origin of such pathologies with the view to provide some information on the *P. sardus* population health. Congenital and/or non-traumatic pathologies may, indeed, increase in very small populations or in populations subjected to environmental stress. Stressful conditions may also increase inbreeding depression (the reduced biological fitness in a given population as a result of inbreeding) (e.g. Atmar, 1993; Frankham, 1998; Alcover et al., 1999; Roldan & Gomendio, 2009; Fox & Reed, 2011).

We also present a synthetic inventory (Appendix A) of the main Sardinian localities recording the species, with the intent to appraise the extent of the fossil record and infer the viability of the endemic ochotonid populations from the Middle Pleistocene to the Early Holocene.

2. MATERIAL AND METHODS

2.1. Material

Most of the material analysed herein was collected during archaeological excavations performed in 2008 by a University of Cagliari team at Su Carroppu (Carbonia, SW Sardinia), a site where the human presence seems to be documented since about 10 ka BP (Modi et al., 2017). Some other bones were recovered from the Middle Pleistocene sequence of Grotta dei Fiori (older than 500 ka) (Carbonia SW Sardinia) (Melis et al., 2013), and from a small fissure filling at "Surconis", a locality near

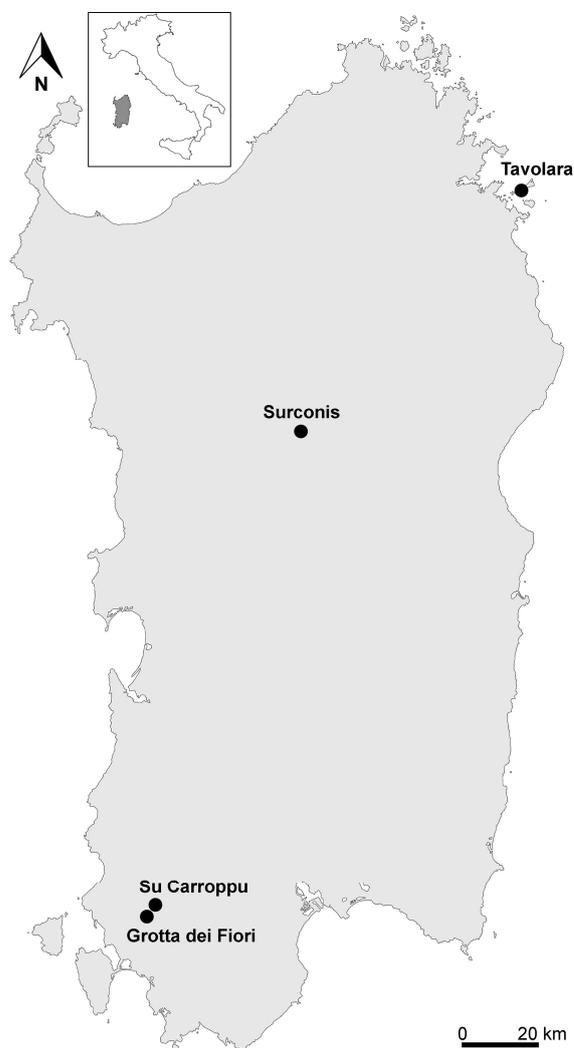


Fig. 1 - Location map of the studied localities.

the village of Bolotana (central Sardinia). The chronology of this deposit is uncertain, either Late Pleistocene or Early Holocene (Zoboli & Pillola, 2016).

The analysis also includes few remains belonging to the Major's Collection (Naturhistorisches Museum of Basel, Switzerland, NMB) found on the Tavolara islet (NE Sardinia) (Zoboli, 2017). A comparison was made with materials belonging to the collections stored in the Museo Sardo di Geologia e Paleontologia D. Lovisato (University of Cagliari, Italy, MDLCA), and using literature data (Appendix B).

2.2. Methods

Pathology - Each remain departing in some way from the normality has been carefully analysed. First of all, particular attention has been paid to distinguish lesions involving the whole bone, probably related to a systemic disease, from lesions affecting only limited areas of the bone surface. Among the later, a distinction between pathological signs present either on the bone or on the joint surface was made. The disease that

caused each pathological lesions was inferred by means of the diagnosis and classification of bone palaeopathologies provided in the specialized literature (Baker, 1978; Baker & Brothwell, 1980; Bendrey, 2014; Driesch, 1989). Living bone tissue is known to have a limited repertoire of responses to any prolonged/unusual stress, therefore, it often reacts in similar ways to different pathogenic factors (Bartosiewicz, 2008). Accordingly, we consulted texts on veterinary pathology and clinics to formulate a more compelling diagnosis and better inferring the factors causing the pathological lesions (Slatter, 2003; Tobias & Johnston, 2012).

Body mass (BM) estimate - It is well-known that body size (BS), and in turn the BM that generally has been regarded as its best proxy (Gingerich et al., 1982), are strictly related to animal life history, metabolic and reproductive rates, architecture and physiology, ecology and ethology (see among several others Blueweiss et al. 1978; McNab, 1990; Auer et al., 2018; Naya et al., 2018). Accordingly, BS/BM represents a pivotal aspect of mammal adaptive strategy, also limiting, for instance, the number of species to be found in a given area, intra- and interspecific relationships, exploitation of resources, and, indirectly, the population health.

Since the femur is the bone most frequently recording pathological signatures in the samples herein analysed, the BM estimate is herein based only on the femur dimensions, by means of the equations proposed for lagomorphs by Moncunill-Solé et al. (2015, 2016) ($\log \text{Body Mass, BM} = -1.11 + 2.229 \log \text{Femur Length, FL}$; and $\log \text{BM} = 0.318 + 2.481 \log \text{Distal Femoral Transversal diameter, FTd}$), and Quintana et al. (2011) ($\log \text{BM} = 2.487 \log \text{FTd} + 0.141$).

Measurements were taken by means of a digital electronic precision calliper (0.05 mm error) on femora of fully adult individuals (fused epiphyses). A comparison was made with the BM of *P. sardus* specimens for which measurements of femur are available in literature: Monte Tuttavista (Moncunill-Solé et al., 2016), Grotta dei Fiori, Cava Alabastro, Medusa-Dragonara Cave, S'omu S'Orcu (Boldrini & Palombo, 2010; Boldrini et al., 2010), Tavolara islet and Tramariglio breccias (van der Geer et al., 2013).

3. RESULTS

3.1. Pathology

The percentage of pathological bones is definitely low if compared to the number of healthy bones present in the analysed samples. In the Surconis and Su Carroppu samples (the only two samples for which the total number of limb bones collected during excavation is known), the percentage of bones showing pathological signatures is lower than 2%, and only ten lesions have been noticed in on the vertebrate and ribs of the analysed samples.

Among the pathological lesions detected in the samples, most could be referred to trauma, though a few likely depend on metabolic diseases and tumour. A list of the main pathological lesions is shown in Appendix C.

Fractures are present, for instance, on a rib (MDLCA 23786, Pl. 1, fig. 30) and an ulna (MDLCA

23774, Pl. 1, fig. 3) respectively found in the Grotta dei Fiori and Su Carroppu samples. Both fractures were fully healed as documented by the union of fragments through the formation of a well-evident bone callus. The fracture of the rib was complete, transverse and non-displaced. The great dimension of its callus is due to the breathing continuous movements. The fracture of the ulna was complete, oblique and displaced. As a result, the bone fragments remained separated even during the healing, forming a well visible groove. The lesion did not affect the radius that, therefore, represented a stable support permitting the ulna healing.

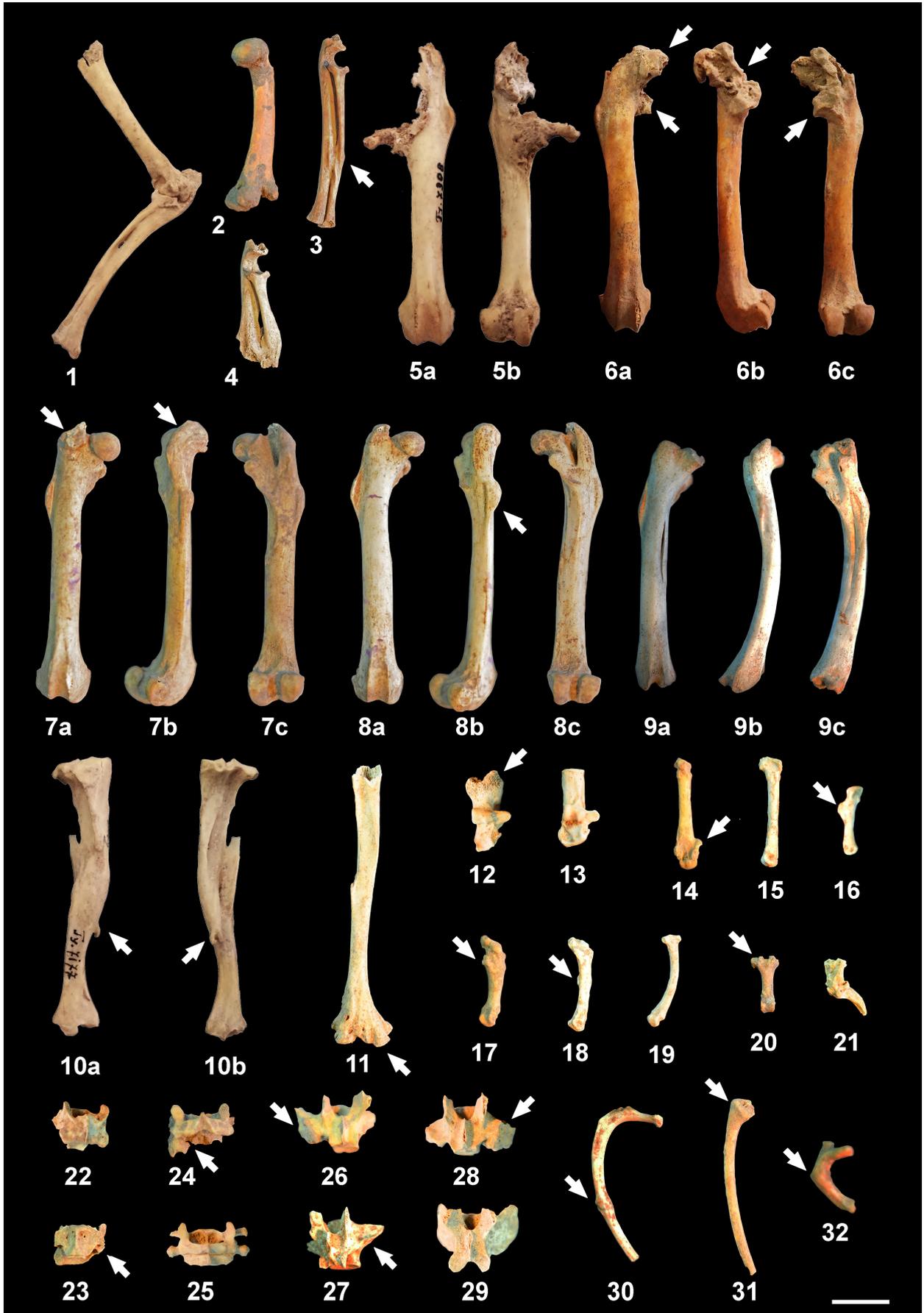
Some pathological lesions of traumatic origin have been detected in the distal epiphysis of a tibia (MDLCA 23776, Pl. 1, fig.11), a calcaneum (MDLCA 2377, Pl. 1, fig. 12), some metapodials (MDLCA 23779/1-5, Pl. 1, figs. 14-18), and phalanges (MDLCA 23781, MDLCA 23782, Pl. 1, figs. 20-21) collected at Su Carroppu. The bones show an extensive growth of bone tissue around and on the articular surfaces, likely caused by a chronic inflammation of the joint surface.

Some evidence of osteoarthritis are detectable at level of the crurotarsal joint, between the distal epiphysis of tibia and the proximal articular surfaces of tarsal bones, i.e. astragalus and calcaneum. The extent of the overproduction of bone tissue shown by the right tibia (MDLCA 23776, Pl. 1, fig. 11) may suggest that the osteoarthritis originated from a dislocation of the crurotarsal joint, probably due to a traumatic event, such as either a fall, a violent impact, or an excessive muscular effort. Analogous inflammation processes caused a pathological overproduction of bone tissue also in interphalangeal joints of phalanges and at level of metapodial bones (MDLCA 23779/1-5, Pl. 1, figs. 14-18). The osteoarthritis process was so pronounced to lead to ankylosis processes that caused the fusion of articulated bones and, thereby, the immobility of the distal interphalangeal joint (MDLCA 23782, Pl. 1, fig. 21).

Some cervical (MDLCA 23783/ 1-4, Pl. 1, figs. 22-25) and lumbar vertebrae (MDLCA 23784/1-3, Pl. 1, figs. 26-28) from Su Carroppu show pathological lesions likely caused by spondyloarthropathy.

In the pathological humerus from Su Carroppu (MDLCA 23773, Pl. 1, fig. 2) and femur from Surconis (MDLCA 23772, Pl. 1, fig. 9), the pathologies were likely caused by metabolic diseases. The diaphysis of both long bones, which belong to juvenile individuals (the distal epiphyses are not fused) are abnormally arched. This anomalous growth is attributable to a bone softening caused by an impaired bone metabolism, known as osteomalacia. The inadequate bone mineralization is generally caused by a deficiency of levels of calcium, phosphate and vitamin D. The pathological condition, named also "rickets", is more frequently reported among young individuals and is primary related to a malnutrition or insufficient sun light exposition. This pathological condition is also visible in a metapodial bone from Su Carroppu (MDLCA 23780, Pl. 1, fig. 19). The fact that all the three arched long bones belong to juvenile individuals confirms the diagnosis.

A zeugopodium (radius and ulna) (MDLCA 23775, Pl. 1, fig. 4) from Surconis shows interesting pathological lesions. A large mass of bone tissue surrounds the



middle part of the diaphysis. The irregular surface characterising this anomalous bone tissue accretion suggests a rapid and irregular growth, typical of a malignant bone tumour such as osteosarcoma. A collateral effect of this serious pathology is the bone fragility leading to spontaneous fractures, as it occurred to the zeugopodium from Surconis, where the lack of the distal part of both radius and ulna was likely caused by a fracture that separated them from the diaphysis.

The proximal epiphysis of a left femur (NMB Ty. 7308, Pl. 1, fig. 5) from Tavolara islet shows serious pathological bone erosion and bone remodelling. In the caput femoris, the part lacking bone tissue formation is surrounded by overabundant osteophytes, a phenomenon typical present in case of osteonecrosis pathology. The aetiology comprises a fracture at level of the femoral neck or a hip joint dislocation. This type of trauma, indeed, can provoke the interruption of blood supply in the femoral head, and, in turn the death of cells resulting in an avascular necrosis. It is interesting to note that a high level of steroids may represent a risk factor in the pathogenesis of this kind of lesion (Drescher et al., 2011). As regards to the ochotonid population confined on Tavolara islet, it could be speculate that this pathology was somehow related to the presence in the Mediterranean flora of species containing phytosteroids (cf. among others Desole, 1960; Bocchieri et al., 2011; Riccobono, 2016), that some *Prolagus* in Tavolara islet were forced or inclined to eat, increasing the steroid levels in their organism.

3.2. Body mass estimate

The average BM estimates for the *P. sardus* samples here studied, whose age ranges from older than to 500 ka (Grotta dei Fiori) to the late Early Holocene (Greenlandian stage, Mesolithic period) (Su Carroppu) (see Appendix A), highlights an extremely large range of variation in the selected samples. The variation is irrespective of the age and the size of the samples, as it appears, by comparing the range of the quite large sample of Monte Tuttavista Xlr fissure (52 specimens) with the small Tramariglio breccias sample (4 specimens), or the range of samples with no so different number of specimens (e.g. Monte Tuttavista Vlb6 fissure, 18 specimens, and Tavolara, 11 specimens) (Fig. 2). The average BM estimated for the Mesolithic site of Su Carroppu (about 412 gr) and the possibly older Surconis site (about 490 gr) would suggest that the size of *P. sardus*, slightly decrease during the Early Holocene. This hypothesis, however, has to be considered with a great caution because the uncertainty about the actual age of Surconis, the small number of specimens available for the analysis, and the extremely large range of the body mass variation shown by the analysed samples (Fig. 3).

The morphological and dimensional analysis of the *Prolagus* samples from Monte Tuttavista, has already suggested that this species underwent an anagenetic evolution that involved both the morphology of dental elements, leading to an asymptotic increase in size of dental and postcranial elements (Angelone et al., 2008). The average BM of the samples analysed herein, conversely, fails to comply with the progressive increase in

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Plate 1 - Pathological bones of *Prolagus sardus* from different localities of Sardinia. 1) Left humerus, radius and ulna (NMB Ty. 8797, Major's Collection) in lateral view, showing a process of ankylosis of the elbow joint probably due to a serious arthrosis, and of the radioulnar joints probably due to an extensive process of periostitis. Tavolara islet, Holocene. 2) Left humerus of a juvenile individual (MDLCA 23773) in postero-medial view, showing a curvature of the diaphysis caused by a bone osteomalacia. Su Carroppu, Mesolithic. 3) Right ulna and radius (MDLCA 23774) in lateral view. A complete and displaced fracture involving the radius and the successive extensive bone remodelling process led to the fusion of the diaphysis of the two bones. The arrow indicates the groove corresponding to the space between the two bone fragments. Su Carroppu, Mesolithic. 4) Right ulna and radius (MDLCA 23775) in anterolateral view. The middle part of the diaphyses of both bones show a great mass of bone tissue possibly related to an osteosarcoma leading to contemporary phenomena of exuberant proliferation of bone tissue and bone resorption that induces bone fragility and predisposes to spontaneous fractures. Surconis, Late Pleistocene-Early Holocene. 5) Left femur (NMB Ty. 7308, Major's Collection) in anterior (a) and posterior (b) view. In the femoral head, the large areas of missing bone tissue are surrounded by exuberant osteophytes, which could be caused by osteonecrosis or chronic osteoarthritis. Tavolara islet, Holocene. 6) Right femur (MDLCA 23769) in anterior (a), medial (b) and posterior (c) view. The proximal epiphysis shows pathological signs consisting of bone erosion and bone remodelling, probably due to the osteoarthritis or osteonecrosis of the femoral head. Su Carroppu, Mesolithic. 7) Right femur (MDLCA 23770) in anterior (a), lateral (b) and posterior (c) view. The arrows indicate osteophytes due to a periostitis. Su Carroppu, Mesolithic. 8) Right femur (MDLCA 23771) in anterior (a), lateral (b) and posterior (c) view. The arrow indicates a presence of exuberant bone tissue probably related to a periostitis. Su Carroppu, Mesolithic. 9) Right femur (MDLCA 23772) of a juvenile individual in anterior (a), lateral (b) and posterior (c) view. The diaphysis shows a curvature likely caused by the one softening that often occurs during the osteomalacia. Surconis, Late Pleistocene-Early Holocene. 10) Right tibiofibula (NMB Ty. 7177, Major's Collection) in anterior (a) and posterior (b) view. The sample shows a complete, angulated and displaced fracture of the diaphysis healed by an extensive bone remodelling process. Tavolara islet, Holocene. 11) Right tibiofibula (MDLCA 23776) in anterior view. The arrow indicates a periarticular osteophyte that can be associated with a wide chronic inflammation of the crurotarsal joint. Su Carroppu, Mesolithic. 12-13) Comparison between a pathological (12) (MDLCA 23777) and a healthy (13) (MDLCA 23778) right calcaneus in anterior view. The arrow indicates an exuberant bone tissue probably due to the chronic inflammation of the nearby soft tissues. Su Carroppu, Mesolithic. 14-18) Metapodials (MDLCA 23779/1-5). The arrows indicate osteophytes nearby the joints. Su Carroppu, Mesolithic. 19) Metapodial bone (MDLCA 23780). The diaphysis shows a curvature caused by a bone softening that occurs during an osteomalacia process. Su Carroppu, Mesolithic. 20) First phalanx (MDLCA 23781) in plantar view. The arrow indicates a periarticular osteophyte. Su Carroppu, Mesolithic. 21) Second and third phalanges (MDLCA 23782) in lateral view, showing an ankylosis process affecting the distal interphalangeal joint. Su Carroppu, Mesolithic. 22-24) Cervical vertebrae (MDLCA 23783/1-3). The arrows indicate osteophytes related to chronic inflammation of the intervertebral joints (spondylarthritis). Su Carroppu, Mesolithic. 25) Sixth and seventh cervical vertebrae (MDLCA 23783/4) in dorsal view, showing an intervertebral ankylosis. Su Carroppu, Mesolithic. 26-28) Lumbar vertebrae (MDLCA 23784/1-3) in dorsal view. The arrows indicate osteophytes due to the chronic inflammation of the intervertebral joints. Su Carroppu, Mesolithic. 29) Healthy lumbar vertebrae (MDLCA 23785) in dorsal view (for comparison), Su Carroppu, Mesolithic. 30-32) Ribs showing a complete not displaced and healed fracture (30) (MDLCA 23786, Grotta dei Fiori, Middle Pleistocene) and some osteophytes (31, 32) (MDLCA 23787/1-2, Su Carroppu, Mesolithic). The arrows indicate the pathologies. Scale bar = 1 cm.

P. sardus BM during time. The results obtained show that the lower average BM value corresponds to the oldest *Prolagus* sample from Grotta dei Fiori (but followed by that of Su Corroppu and S'omu S'Orcu, the youngest among the analysed sites), while the highest average value corresponds to the sample from Cava Alabastro, a locality for which a Middle Pleistocene age cannot be excluded (Minieri et al., 1995; Boldrini & Palombo, 2010). The pattern of the minimum and maximum values of the BM estimated for each samples also fails to confirm any matching between the long bone size and their chronology.

In addition, the results of this work, and the new radiometrical data of Medusa-Dragonara Cave (Palombo et al., 2017), question the hypothesis that of a positive relationship may exist in *Prolagus* between increase in temperature and femur length (Boldrini & Palombo, 2010). Boldrini & Palombo (2010) made a preliminary analysis on a few *Prolagus* femurs to ascertain whether temperature would affect the femur length in the Sardinian ochotonid, following the Allen's rule (Allen, 1877) (animals living in cold geographical regions show limbs consistently shorter than those of related species living in warmer climatic conditions) or because temperature control the cartilage growth as it has been demonstrated for rodents (Serrat et al., 2008). It is worth noting, however, that Boldrini & Palombo (2010) based they suggestion of a possible positive correlation between femur dimensions and the temperature (inferred according to the $\delta^{18}\text{O}$ values obtained from teeth and bones of *P. sardus*) on the chronological assessment of the Sardinian sites as accepted at that time, but successively modified according to new studies and radiometric data (Palombo & Rozzi, 2014; Palombo et al., 2017).

The results obtained herein by using as variable FTdD are poorly convincing as evidenced by the BM estimations obtained for Surconis and Su Carroppu samples, which sensibly differ depending on the applied regression equations (Fig. 4). The variable FTdD estimates a BM above the arithmetic mean of that obtained using FL following (Moncunill-Solé et al., 2016), (Surconis = 511.87-797.44, M 638.38 gr; Su Carroppu = 361.88-629.50, M 484.50 gr), while they are inferior following Quintana et al. (2011) (Surconis = 424.62-538.2, M 426.53 gr; Su Carroppu = 243.77424.62, M 326.17 gr). The correlation between value obtained considering FL and FTdD is low, especially as regards to Surconis, suggesting an intra-population variation of length vs distal articular transversal diameter of the femur that clearly exceeds the minimal variation potentially related to sexual dimorphism, known to be minimal in the extant *Ochotona* (Smith, 1988; Nowak, 1999).

All in all, the results obtained indicate that the BM can be hardly regarded as a useful indicator for providing specific information on the health condition of a *P. sardus* population.

4. DISCUSSION

The study of palaeopathology is an interesting research field that may provide valuable clues for inferring the life-style of animals in the past, their behaviour

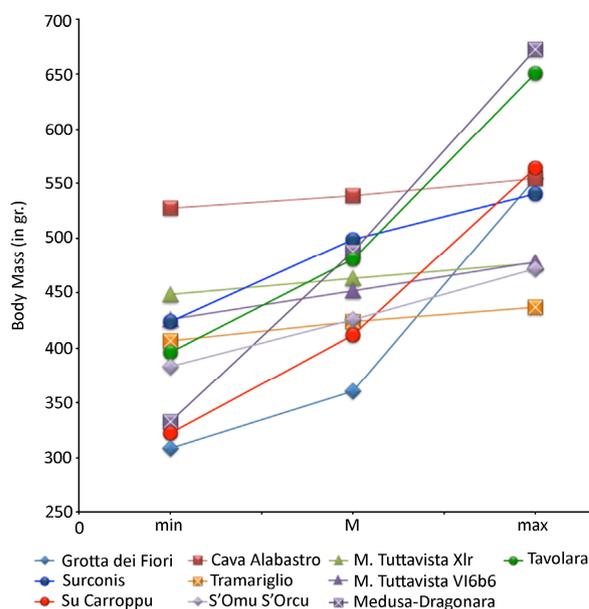


Fig. 2 - Comparison among the variation ranges of Body Mass in Sardinian *P. sardus* samples ranging in age from the Middle Pleistocene to the Early Holocene (see Appendix A).

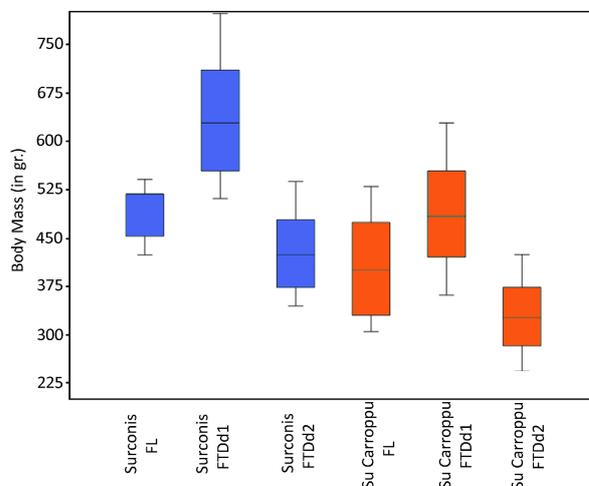


Fig. 3 - Box plots comparing the variation range of the Body Mass (estimated by using as variable the femur maximum length, FL, and the wide of the femur distal epiphysis, FTdD) in the *P. sardus* samples from Surconis (blue) and Su Carroppu (red).

and niche occupancy, the predator-prey relationships, and some aspects of population/ecosystem dynamics (Moodie, 1923; Baker & Brothwell, 1980; Rothschild & Tanke, 1992; Rothschild & Martin, 1993; Rothschild et al., 2001; Beatty & Rothschild, 2009; Tanke & Rothschild, 2010; Grauer, 2012; Salesa et al., 2014).

Palaeopathological studies, moreover, may be the starting point to evaluate the state of health of an animal population and to frame this in a palaeoecological perspective. The chance of surviving of a pathological individual depends on a number of factors, among which the quality of resources, food availability and the extent

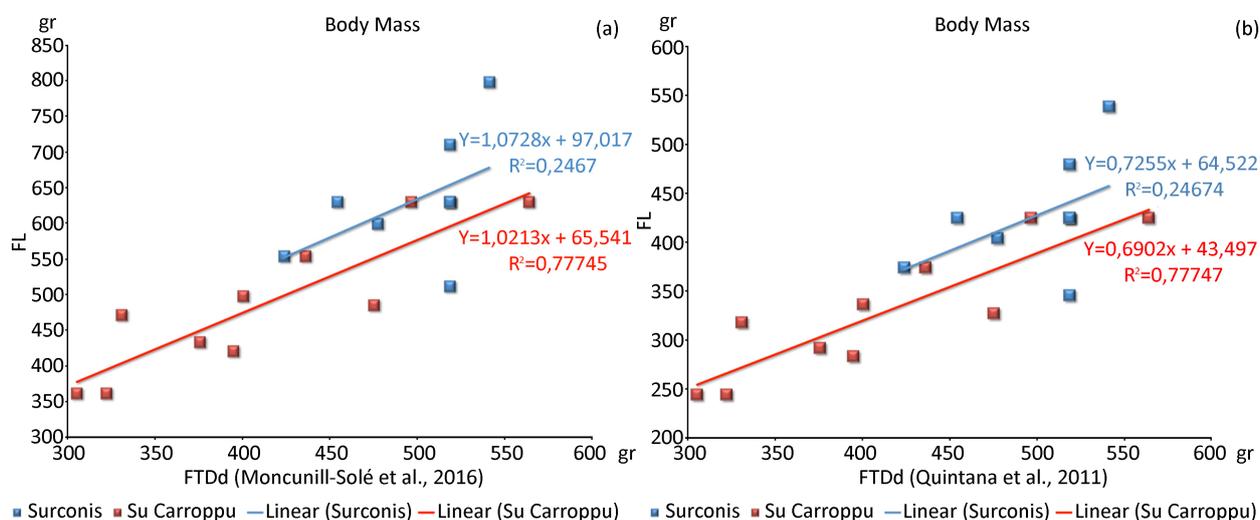


Fig. 4 - Scatter diagrams comparing, in the *P. sardus* samples from Surconis and Su Carroppu, the relationship between the maximum length (FL) of femur and the values of Body Mass obtained by using as variable the wide of the femur distal epiphysis (FTDd) according to the regression equations proposed by Moncunill-Solé et al. (2016) (a) and Quintana et al. (2011) (b).

of predation and competition pressure are the most influential. Accordingly, analysing palaeopathologies and their origin may be a useful tool for reconstructing the ecological balance of a region, particularly as regards to poorly diversified, disharmonic and unbalanced vertebrate faunas, like those characterising isolated ecosystems, such as islands.

A variety of factors, in addition to traumatic injuries, may induce the presence of skeletal pathologies in wild animals (endogamy, disease, congenital degenerative lesions, malnutrition due to either low forage quantity or high population density, low predator pressure etc.). The inbreeding depression, the reduced biological fitness in a given population as a result of breeding of related individuals in small, isolated populations, has been sometimes hypothesised as a concurrent phenomenon in the modifications shown by endemic species. Insular populations are expected to suffer increased inbreeding with respect to their ancestor populations living on mainland, because of the lower number of colonisers and the subsequent small population sizes, and the bottleneck effect likely occurring at their establishment on the island. As regards to human populations, for instance, it has been argued that the combined action of founder effect, genetic drift, and inbreeding may increase the frequency of detrimental rare variants, leading to an overall worsening of population health (Rudan et al., 2006). In the case of wild mammals, the survival of animals with injuries or diseases limiting their mobility and function suggests the possibility of "a support system" which allowed their survival (Rothschild & Tanke, 1992). This may be particularly true as the survival in insular environments, due to the reduced predator and competitor pressure. Conversely, the augment of inter-guild and intraspecific competition for resources, which may be related to overpopulation, likely hampers the survival of animals affected by some kind of physical illness. Therefore, studies of palaeopathology in insular endemic mammals may help in answering questions

whether resources availability, and ecological interaction and displacement are among the major factors driving evolution and survival in isolated environments (Lomolino et al., 2013).

Moreover, the active or passive introduction by humans of mainland species may expose native taxa to exotic pathogens to which the insular species had no opportunity to develop a reasonable resistance (MacPhee & Preston, 1997).

Pathological modifications of the bone tissues can even be caused by congenital diseases/disorder genetically inherited. The genetic defects may be related to the increase of individuals homozygous and therefore the increase of the appearances of recessive traits in small populations and marked inbreeding. This may be not the case of the Sardinian ochotonid due its incredibly rich fossil records, both in abundance of remains, number and geographical distribution of fossiliferous sites, and longevity of the species. The notable abundance of *Prolagus* remains accounts for a persistent high population density during time (see Appendix A). This, joined with the differences in morphology and the increased BM of *P. sardus* with respect to its ancestors may indicate that the species characteristics correspond to those of vertebrate isolated populations showing the so-called "island syndrome" (or "insular syndrome") (Thiollay, 1993). Accordingly, it may be speculated that, in line with the syndrome, the Sardinian ochotonid may have had a behaviour different from those characterising the mainland populations, and a higher reproductive output, and demography, as shown in small mammals (Mappes et al., 2008), but still questioned in large mammals (Köhler and Moyà-Solà, 2009).

The relative low number of pathological bones present in the analysed samples and, perhaps, the large range of the dimensional variation may suggest that pathologies due to traumatic events were more frequent in *P. sardus* bones than those related to disease. This hypothesis cannot be adequately supported by data on

the frequency of pathological bones in fossil and extant lagomorphs. Although, indeed, some osteopathologies due to traumatic injuries (e.g. Jordana et al., 2011; Palombo & Zedda, 2016; Lyras et al. 2016), osteoarthritis (Peterson et al., 2010), and metabolic diseases (Dermitzakis et al., 2006) are reported in island large mammals, such kind of pathologies are poorly known as regards to wild mainland and insular lagomorphs. Most of studies and researches deal with dental and cranial anomalies (e.g. among others Suchentrunk, et al., 1992; Jekl & Redrobe, 2013; Böhmer & Böhmer, 2017), or with domestic animals, rarely with wild rabbits and hares (e.g. among others Eriksson et al., 1984; DeSanto, 1997; Batiste et al., 2004; Okuda et al., 2007; Delaney et al., 2018).

It is worth noting, however, that accidental fractures of limb bones, as for instance those observed in the *P. sardus* samples analysed herein (Pl. 1, figs 3, 10, 30), could be somehow related to either the structural characteristic of the skeleton or to a peculiar locomotory aptitude.

In extant Ochotonidae, for instance, some ecological specialisation based on different locomotory adaptation are known (Smith, 1988, 1990, 2008; Reese et al., 2013). Two skeletal ecotypes have been recognised corresponding to different behaviour and life-style: i) meadow-dwellers, specialised in burrowing and characterised by a short, highly fecund and highly social life; ii) rock-dwellers, specialised in leaping and characterised by a long, asocial and lower fecund life. The meadow-dweller ochotonid first use forelimbs to scratch and dig more or less deep cavities, then both fore limbs and hind limbs are involved to move backwards out of the burrow. The rock-dwellers ochotonid usually jump among rocks covering horizontal and vertical distances from a few centimetres to a more than three times their body length.

The burrowing species show a well-developed, strong olecranon process (Hildebrand, 1985), while rock-dwelling species generally have proportionally longer limb bones and feet that are helpful in frequent leaping from rock to rock (Reese et al., 2013).

The morphology of *P. sardus* pelvis and limb bones suggest that the species had a powerful limb muscles, hind-limbs likely adapted to jump, but also a limb maneuverability wider than those shown by most of extant leporids (Dawson, 1969). More detailed studies and comparison among skeletal morphological features of *Prolagus* samples coming from sites having different physiographical location (e.g. rocky mountains, flat grasslands, and coastal dunary sites) are, however, necessary to verify whether in Sardinia only one, both or additional ecotypes were present. Results of our ongoing researches dealing with these questions will be present elsewhere.

Whatever the behaviour of ochotonid Sardinian populations was and the fact that only one or both ecotypes were present on the island, back and hind-limb bones of *Prolagus* were likely prone to fracture, due to their structure similar to the lagomorph skeleton. In rabbits, for instance, the skeleton represents only 7% to 8% of the body weight (opposed to the 12% to 13% in cats), and fractures of the back and hind-limbs are not so in-

frequent because of the hindlimb musculature and the delicate nature of the skeleton (Graham & Mader, 2012). This could explain the origin of the traumatic lesions observed in specimens found in different localities. A some higher frequency of pathological lesions in the hind-limb than fore-limb bones could be seen as a hint of the jumping aptitude of *Prolagus* and a confirmation of the pivotal role that the hind limbs had in the hypothesis has to be confirmed by further investigations, its locomotion, as it typically occurs in jumping animals.

Some lesions among those described in bones from all the sites analysed are, however, related to diseases, although apparently they are not congenital. The deformation shown by the zeugopodium (radius and ulna) (Pl. 1, fig. 4) from Surconis, for instance, was caused by an osteosarcoma, leading to the spontaneous fractures of both radius and ulna. However, considering its quite large size, the osteosarcoma onset cannot be related to a poor health condition of the population the pathological individual belongs to.

Some environmental constrains could be, conversely, conjectured as regards to the pathological bone erosion and an bone remodelling shown by the *P. sardus* femur from the Tavolara islet (Pl. 1, fig. 5). The hypothesis that the pathology may be related to a high level of steroids accumulated by this individual because of a peculiar feeding behaviour focused on Mediterranean plant species containing a high quantity of phyto-steroids, cannot, indeed, ruled out. It is, however, difficult to hypothesise about factors that may have led to this peculiar feeding propensity.

All things considered, and taking into account the low percentage of pathological bones in the analysed samples, the fact that the lesions of traumatic origin (fractures and periostites) were definitely more frequent than those related to malnutrition or tumours, and that all the observed lesions were compatible with life, it seems reasonable to hypothesise that the Sardinian *P. sardus* populations did not suffered any kind of marked environmental stress. During the Middle-Late Pleistocene, the maintenance of a healthy population status was possibly permitted on the one hand by the predator pressure (raptors and the small canid *Cynotherium*, the most common terrestrial predator, specialised to hunt and eat the Sardinian ochotonid), which contributes to limit the increasing in size of *Prolagus* population (e.g. López Martínez, 2001; Robert & Vigne, 2002; Lyras & van der Geer, 2006; Novelli & Palombo, 2007; Novelli et al., 2008; Lyras et al., 2016), on the other hand by the lack of effective competitors. The coeval non-predatory mammals (the megacerine *Praemegaceros cazioti*, the vole *Microtus (Tyrrhenicola) henseli*, the murid *Rhagamys orthodon*, the insectivores "*Nesiotites similis* and *Talpa tyrrhenica*), had indeed, a different feeding behaviour and ecological requirements. Lagomorphs, to which *Prolagus* belonged, are moreover used to ingest up to 80% of their feces (cecotropes animals), which are rich in vital nutritious elements, such as vitamins, produced by the intestinal bacteria flora. This behaviour probably allowed *Prolagus* to balance their nutritional requirement and in turn to survive also in the event of starvation periods.

5. CONCLUSIONS

The results obtained by this study (performed in the attempt to scrutinise the health status of *P. sardus* Sardinian populations), although preliminary, suggest that during the Middle-Late Pleistocene to the Early Holocene the specie did not suffer any serious environmental stress. The percentage of pathological bones found in the analysed samples is low and the observed pathologies on the one hand were mainly caused by traumatic/accidental factors, on the other hand no evidence of pathologies related to congenital disease have been detected. Accordingly, it is reasonable to suppose that the size of *P. sardus* populations maintained itself enough large to prevent any kind of inbreeding and related pathological risks. The conformity of *Prolagus* physical characteristics to those regarded as typical of rodent populations showing the so-called "island/ insular syndrome" would imply a high reproductive rate. The extraordinary rich fossil record of the Sardinian ochotonid, whose remains are definitely more abundant than those of all the other endemic Pleistocene mammalian species (including rodents) as the number of remains and sites where the remains were present may support this hypothesis.

The pathologies shown by the analysed bones provide some indirect hints as regard to the role (if any) that the changes underwent by the *Prolagus* body structure as a result of insular isolation may have had in facilitating the breakage of limb bones especially during jumping. *P. sardus*, indeed, had a musculoskeletal systems, especially as regard the posterior limbs, much more massive than those of extant pikas, as underlined by the pioneering study of Dawson (1969). The powerful muscles, therefore, possibly caused to bones tension/torsion stress higher than that compatible with the bone tissue elasticity.

The present research also evidences the wide range of intra-population variation of *P. sardus* dimensions, as well as the fluctuation in the average BM throughout time, which is apparently unrelated either to the chronology or to climate.

All in all, results obtained on th one hand highlight that *P. sardus* despite the amount of its remains, is still a poorly known species, on the other hand may represent a start point for further investigations.

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