Thorn Lesions in a Modern Osteological Collection of Guanaco (*Lama guanicoe*): A New Paleoenviromental Proxy and Its Implications for Archaeofaunal Assemblages

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ABSTRACT

This paper provides a detailed analysis of thorn lesions found in lower limb elements of a modern osteological collection of guanaco (*Lama guanicoe*). Four types of lesions were recorded: (1) thorns visible on the bone surface, (2) bony reaction with relief, (3) small negative scars and (4) medium negative scars. The methods used to recognise, record and quantify these lesions are presented. As a result, 35 of the 36 individuals analyzed contained one or more types of lesions. The highest concentrations of lesions were recorded on the anterior view of the metacarpal shafts. All the age ranges were affected by lesions; however, individuals between the ages of 1 and 3 years were the most affected, whereas those between the ages of 0 and 1 year contained the least amount of lesions. To provide examples of how thorn lesions can be identified and used as a paleoenvironmental proxy in the fossil record, we analyzed two archaeological sites from different phytogeographic provinces: Bajo de la Quinta (Monte phytogeographic province) and Calera (Pampa phytogeographic province). Results found that 25% of the elements from the Bajo de la Quinta site contained lesions, whereas none of the elements from the Calera site showed evidence of lesions. When detectable in the fossil record, thorn lesions can provide an indirect approximation of the paleoenvironment. Copyright © 2011 John Wiley & Sons, Ltd.

Key words: guanaco; metacarpal; metatarsal; Monte; paleoenvironmental proxy; phalange; thorn lesions

Introduction

The main objective of this paper was to document the frequency, location and types of thorn lesions found in the lower leg elements of a modern osteological collection of guanaco (*Lama guanicoe*). The guanaco elements were also analyzed for any pathological reactions related to the lesions, which may have affected the health of the individual or its ability to operate normally. Results from this study can be used as an analytical reference to identify and differentiate in the fossil record these modifications from other pathological reactions or taphonomic agents affecting the bones surface and can provide an indirect approximation of the paleoenvironment.

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The guanaco (L. quanicoe) is one of the few native large herbivores that inhabit South America and the most abundant free-ranging wild ungulate of its arid environments (Franklin, 1982). It is a social species that, in their organisation, includes family groups, male groups, and single males (Franklin, 1983; Redford & Eisenberg, 1989). During pre-Hispanic times, the guanaco was one of the main resources for southern-South American hunter–gatherers. Remains of this species are commonly found in archaeological sites throughout the Patagonic steppes and Pampean grasslands and were the most frequently exploited taxa in both regions (Politis & Salemme, 1990; Mengoni Goñalons, 1999; Miotti & Salemme, 1999; De Nigris, 2004; Gutiérrez & Martínez, 2008). The extensive fossil record provides archaeologists with the opportunity to study diverse aspects of hunter-gatherer subsistence strategies and incorporate paleoenvironmental aspects to these studies.

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A thorn or spine is defined here as a modified plant organ that is normally straight tipped, curved or hook shaped. Although most spinescence has almost certainly evolved as a defence against herbivores, plant armature is also the result of environmental stimuli such as reducing sunlight or camouflage as well as for seed and vegetative dispersal (Grubb, 1992; Hanley et al., 2007). Published data regarding thorn lesions in or near bone have been limited to clinical symptoms of foreign bodies, normally wooden splinters found in the feet or hands of medical patients (Maylahn, 1952; Borgia, 1963; Reginato et al., 1990; Fakoor, 2006; among others). Pathological reactions include osteolytic (dissolution of bone), osteoblastic (the formation of bone) or a combination of both reactions (Reginato et al., 1990; Fakoor, 2006). These studies have focused mainly on how to treat, diagnose and detect foreign bodies during medical examination. Therefore, the following paper provides the first systematic analysis of thorn lesions on bones from a sample of a wild animal population.

For the purpose of this study, 177 bone elements from 36 guanacos of diverse age and sex groups were analyzed. To accurately record and quantify the lesions in the osteological collection, we used an image-based GIS approach (Marean *et al.*, 2001; Abe *et al.*, 2002). This method allowed us to visually and statistically summarise the thorn lesions on the different views of the skeletal elements. Finally, to provide examples of how thorn lesions can be identified and used as a paleoenvironmental proxy in the fossil record, metapodials and phalanges from two Late Holocene archaeological sites (Bajo de la Quinta and Calera) were analyzed for thorn lesions.

Materials and methods

The individuals analyzed here were selected from a reference collection of 158 guanacos, which were collected during actualistic research by one of the authors (C.K.) in the district of Río Negro, Argentina, and are currently being stored in the INCUAPA research centre (Universidad Nacional del Centro de la Provincia de Buenos Aires) (Kaufmann, 2009). The carcasses were collected from the Monte phytogeographic province, an extensive area from the northern subtropical regions of Argentina to the temperate northern areas of Patagonia (Figure 1). This province is characterised by a dry open landscape with small trees, shrubs and bushes of average height between 2 and 3 m (Cabrera & Willink, 1973; Morrone, 2001; Roig et al., 2009). The majority of the vegetation has natural thorns of 1 to 3cm in length. Some of the species which

currently inhabit the Monte with thorns include the alpataco (Prosopis alpataco), algarrobo patagónico (Prosopis denudaes), llaullín espinudo (Lycium gilliesianum), monte negro (Bougainvillea spinosa) and a variety of cactus (e.g. Maihueniopsis darwinii).

A total of 36 guanacos where chosen from the reference collection on the basis of the individuals limb bone completeness and in order to have a representative sample of at least one individual from the different age groups (0-12 years) (Table 1). In total, 177 elements were analyzed, including 53 metacarpals, 47 metatarsals, 45 front proximal phalanges and 32 rear proximal phalanges. During processing of the carcasses, thorns were observed within the soft tissue and between the soft tissues of the bones and those that penetrated into the bone. The thorn lesions were found to be randomly located on the cortical surface of the bone, and although many were identifiable with the naked eye, classification was realised systemically with the assistance of a microscope (Motic ST-39, Motic, Richmond, British Columbia, Canada; ×20 and ×40 magnification). Four types of thorn lesions were classified in accordance to the pathological reaction processes: (1) thorns visible on the bone surface, (2) bony reaction with relief, (3) small negative scars and (4) medium negative scars.

When thorns are visible on the bones' cortical surface, they sometimes appear as very small black marks similar to magnesium stains (Shahack-Gross *et al.*, 1997; Marín-Arroyo *et al.*, 2008). Once viewed through the microscope, the actual form and size of the thorn can be recognised and differentiated. In many cases, the thorn had fractured during either penetration or the reaction process (Figure 2(A, B)).

Bony reaction with relief encapsulates the thorn and leaves a small localised granuloma as a result of the osteoblastic reaction. In the case of the modern osteological collection, some thorns were still visible beneath the granuloma, particularly during the initial stages of the reaction process. The lesions varied in size and shape but were generally small (<1 cm) and produced only a slight relief (Figure 2(C, D)).

When the thorn has detached or dissolved from the bones surface, it leaves a negative scar. Small negative scars appear as tiny circular or elliptic shaped pits (<1 cm). The edges are normally rounded, and they can present a U-like cross section (Figure 2(E, F)). Medium negative scars on the other hand are larger (>1 cm), irregularly shaped pits and normally parallel oriented with the major axis of the element (Figure 2(G)).

The large number of thorn lesions found in the osteological collection required developing an accurate way to organise and calculate the findings. We utilised the

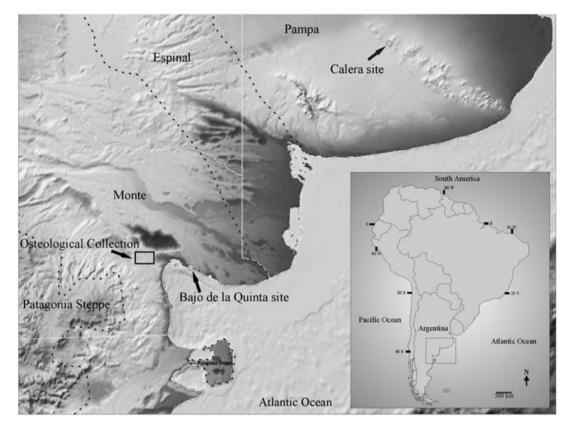


Figure 1. Geographical location of the guanaco osteological collection area and the Bajo de la Quinta and Calera sites. Also shown here are the limits of the phytogeographic provinces Patagonia Steppe, Monte, Espinal and Pampa.

method described in Abe *et al.* (2002) by using an image-based GIS approach to record and quantify lesions on the selected anatomical parts (Marean *et al.*, 2001; Izeta, 2005; Izeta & Scattolin, 2006; Izeta 2007). Each lesion was digitally drawn on the corresponding template (metacarpal, metatarsal, front proximal phalange and rear proximal phalange) and view (anterior, posterior, lateral and medial). Lesions were

Table 1. Sample of guanaco carcasses used for thorn lesion analysis

Age group	Age (years)	Male	Female	Indet.	Subtotal	Total
Newborn Juvenile	0-1 1-2 2-3	1 3	2	6 2 2	6 5 5	6 10
Adult	2-3 3-4 4-5 5-6 6-7	1	3 1 3 1	2	3 2 3 1	9
Senile	7–8 8–9 9–10 10–11 11–12	1	1 3 2 2 2		1 3 2 3	11
Total	11-12	6	20	10	36	36

then assigned a code number and theme name, which was stored in a database file format (.dbf). Each type was assigned a distinct symbol or colour for reference and presentation (Figure 3).

Beyond developing the methods used to recognise, record and quantify the thorn lesions during faunal analysis, the second objective of this paper was to discuss the potential of the thorn lesions as a paleoenvironmental proxy when studying the archaeological or paleontological record. To assess thorn lesions in the fossil record, we analyzed a sample of guanaco metapodial bones recovered from the archaeological sites Bajo de la Quinta (Monte phytogeographic province) and Calera (Pampa phytogeographic province). Results from the analysis of the modern osteological collection and these sites are presented in the succeeding section.

Results and discussion

Modern osteological collection

Of the 36 individuals analyzed, all but one contained thorn lesions. From the 35 individuals with lesions, a

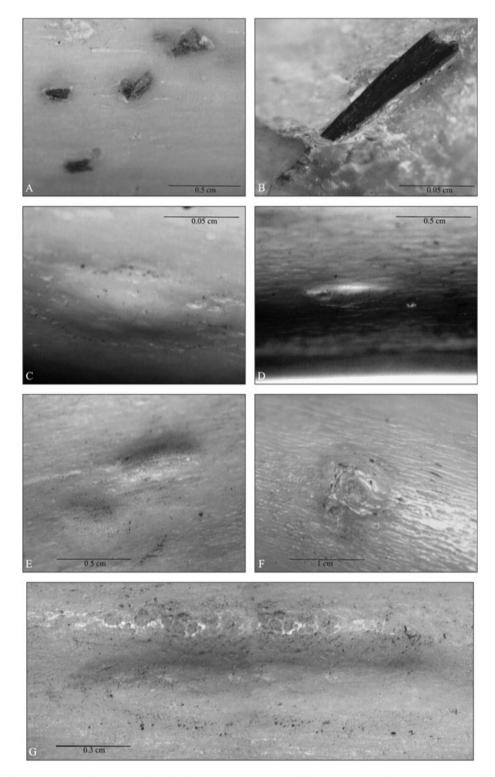


Figure 2. (A and B) Thorns visible on the bone surface. The foreign body inserts or adheres to the bones fibrous tissue. (C and D) Bony reaction with relief. The foreign body becomes encapsulated by the bones fibrous tissue. (E and F) Small negative scars. Depressions are left after the foreign body detached or dissolved. (G) Medium negative scars. Depressions are left after the foreign body detached or dissolved.

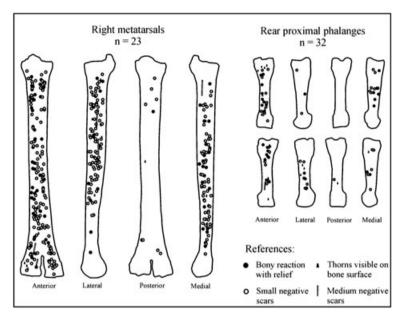


Figure 3. Image themes with thorn lesions recorded on the right metatarsals and rear proximal phalanges.

total of 1660 thorn lesions were recorded on the lower leg elements. The highest concentration of lesions were found on the metacarpals (n = 769; avg. 14.5 thorns per element) and metatarsals (n = 660; avg. 14 thorns per element). The phalanges showed a considerably lower frequency, with a combined total of only 231: front proximal phalanges (n = 144; avg. 3.2 thorns per element), rear proximal phalanges (n = 87; avg. 2.7 thorns per element) (Table 2).

Regarding the types of lesions, the total of each of the four categories was calculated (Table 2). Results showed a higher frequency in small negative scars (n = 1037; 62%), followed by bony reactions with relief (n = 372; 22%), thorns visible on the bone surface (n = 209; 13%) and lastly medium negative scars (n = 42; 3%).

Table 2. Frequency of thorn lesions from the guanaco osteological collection

Thorn lesions	Metacarpal	Metatarsal	Front proximal phalange	Rear proximal phalange	Total
Thorns visible on bone surface	105	55	31	18	209
Bony reaction with relief	170	137	34	31	372
Small negative scars	472	452	77	36	1037
Medium negative scars	22	16	2	2	42
Total	769	660	144	87	1660

The higher frequency of small negative scars, especially in the metapodials, may be the result of the physiological response of the organism to a foreign object. In other words, the thorns penetrate the bone tissue, leaving a small scar, but fewer thorns will remain on the bone (i.e. thorns visible on the bone surface) or have an inflammatory reaction (i.e. bony reaction with relief).

When considering the elements' view (anterior, posterior, lateral and medial), results for both metapodials and phalanges showed similar lesion frequencies. The higher percentages of lesions were found on the anterior perspective (between 45% and 56%), followed by the medial (between 18% and 32%), lateral (between 17% and 30%) and finally the posterior (between 2% and 3%) (Figure 4).

To quantify the location of the lesions on the bone surface, we considered three zones: proximal, shaft and distal. Given that the fossil record is generally found in a fragmented state, zooarchaeologists utilise these types of divisions for quantification and analysis (e.g. Morlan, 1994; Domínguez-Rodrigo, 1997). For the purpose of the thorn lesion quantification, the epiphysis included the epiphysis and the shaft ends (e.g. proximal shaft was combined with proximal epiphysis). As a result, given the overall surface area of the shafts, 72% of the lesions in the metapodial elements occurred in this zone, whereas 20% were encountered on the distal zone and only 8% on the proximal zone.

Elements were also quantified by their lateral side (left or right). Consequently, there were no significant differences found in the type or quantity of thorn lesions for this variable. For example, the right metacarpal had 398 lesions, whereas the left metacarpal had only slightly

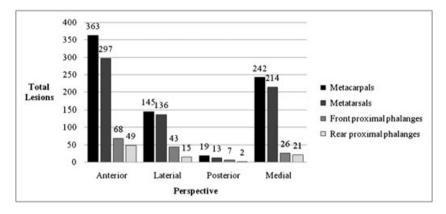


Figure 4. Frequency of thorn lesions and their locations in the osteological collection.

less with 371. A similar pattern was found with the metatarsals (right = 362; left = 298). Because of the low number of lesions on the phalanges, this variable was not considered relevant at this stage of analysis.

In reference to the sex categories (male, female and indeterminate), the average total number of thorn lesions for each category was calculated. As a result, only a slightly higher percentage of lesions were found in female individuals (39%), followed by male (34%) and indeterminate individuals (27%).

To quantify the number of thorn lesions per age group, we divided the sample into four categories on the basis of the behavioural activity of the guanaco during their regular life span (Raedeke, 1979; Franklin, 1982; Larrieu *et al.*, 1982; Merino & Cajal, 1993; Ortega & Franklin, 1995). The four categories were as follows: 0–1, 1–3, 3–7 and 7–12 years. As shown in Figure 5, the thorn frequency in metatarsals and metacarpals is similar. In both elements, the age categories with lower frequencies of lesions per individual are the newborns (0–1 year) and the adults (3–7 years), whereas the greater frequencies of lesions were found in the juvenile (1–3 years) and the senile individuals (7–12 years).

Although the greater frequency of lesions in the senile individuals may be related to the gradual accumulation during the regular life span, this does not explain the lower frequency in adult individuals compared with juvenile individuals. The number of lesions per age group may be related with the natural conduct of the guanaco. In their organisation, the guanaco are a social species that includes family groups, male groups and single males (Franklin, 1983; Redford & Eisenberg, 1989). The family groups represent the centre of the social system and integrate adult males, females and juvenile individuals as young as 13 months (Raedeke, 1979; Franklin, 1982; Larrieu *et al.*, 1982; Ortega & Franklin, 1995).

Each family group possesses a defined territory that is permanently occupied (Franklin, 1982, 1983). The individuals that make up the family groups are primarily newborns (0-1 year) and reproductive adults (3-7 years). Consequently, these are the age groups that presented the lowest frequency of thorn lesions in the sample. On the other hand, a male-only group is represented by non-territorial and dynamic open formations. These groups are usually made up of mature individuals older than 1 year (Franklin, 1982, 1983; Fritz, 1985). It is within this age range that the highest frequencies of lesions were found. The male groups are highly mobile, and members normally will separate and then reunite during the course of their daily activities. They occupy marginal areas of the landscape, and the group size fluctuates from day to day, always maintaining both social and geographic distance from the family groups (Raedeke, 1979; Franklin, 1982, Larrieu et al., 1982; Wilson, 1982). As a result, it may be suggested that the animals that form part of the family groups are more familiar with their territory and possible escape routes from predators and thus reduce the risk of direct contact with thorns, whereas the animals that form part of the male group are less familiar with their territory and highly mobile, thus increasing the risk of contact with thorn vegetation.

In synthesis, the morphology and size of the guanaco, as well as the environmental characteristics of the Monte, are coherent with the results presented above. The distribution, frequency and location of the lesions in the osteological collection also indicate what one would come to expect from the natural locomotive and behavioural activities of the guanaco. The lower leg elements are more vulnerable to direct impact with shrubs and bushes, thus resulting in a higher frequency in the anterior view and distal zone. These

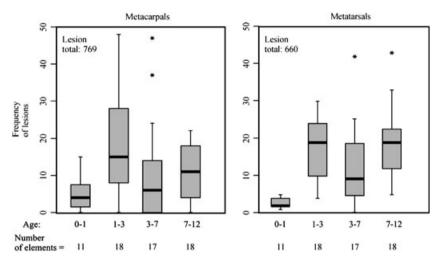


Figure 5. Box-pot frequencies of thorn lesions by age groups.

elements also contain low amounts of muscular and fat content to protect them from foreign bodies.

Finally, we analyzed the sample for any pathological modifications directly related to the thorn lesions (e.g. degeneration of the joint, infection). In medical cases, if a wooden splinter enters into the bone and is not removed immediately, or is not phagocytosed during acute inflammatory reaction, it can cause an inflammatory tissue reaction, ranging from a localised granuloma (Borgia, 1963), during which time the thorn becomes encapsulated with fibrous tissue (Bouajina et al., 2006), to significant synovitis (Sugarman et al., 1977; Carandell et al., 1980; Kchir et al., 1994) and osseous lesions (Croochiolo & Goldberg, 1997). Penetrating thorn injuries have also been associated with a number of bacterial and fungal infections including Enterobacter agglomerans, Sporothrix schenkii and Actinomycosis, which produces a sinus that discharges sulphur granules (Mangat & Jawad, 2007: 17). Although thorns can cause pathological modifications, the thorn lesions in the modern osteological collection do not appear to have affected the health of the individuals. Furthermore, it can be stated that the organisms have adapted to these foreign bodies in two ways: (1) the direct expulsion of the thorns or (2) the integration of the thorn to the bony tissue through an osteoblastic reaction, encapsulation and disintegration.

Fossil record

The Bajo de la Quinta site

The Bajo de la Quinta site is located approximately 80km from the guanaco osteological collection area along the shoreline of the Atlantic coast, Gulf of San Matías,

Province of Río Negro (Borella et al., 2007; Favier Dubois & Borella, 2007; Favier Dubois et al., 2009) (Figure 1). The Bajo de la Quinta site is part of a large locality made up of various sectors and shell middens, which contain human burials, faunal remains, ceramics and stone tools (Borella et al., 2007; Favier Dubois et al., 2009). The modern climate and vegetation in the locality corresponds to that of the Monte. The Gulf of San Matías is also relatively more temperate and humid with respect to other areas of the Patagonian coast. With an elevated biodiversity of marine fauna and abundant secondary deposits of rock for the manufacture of stone tools, the conditions of this locality during the Middle and Late Holocene were adequate for northern Patagonian hunter-gatherers (Favier Dubois et al., 2009).

For the purpose of this study, we analyzed a sample of guanaco metapodial fragments recovered from two excavation units (separated by approximately 8m) from the sector Bajo de la Quinta-LNE (125 and 126), dated from ca. 450 to 1040 years BP (Favier Dubois et al., 2009). The sample consisted of five metatarsals, three metacarpals and four indeterminate metapodial fragments. None of the elements were complete, and two were identified as juvenile individuals. As a result, a total of eight small negative scars and one bony reaction with relief were recorded in three of the elements. Seven of the nine lesions were found on the anterior shaft of one juvenile metapodial (Figure 6), whereas the remaining two lesions were recorded on the posterior view of a metatarsal and the anterior shaft of an indeterminate metapodial.

Weathering and chemical deterioration of the bone surface were considered as a probable factor interfering with thorn lesion identification. In two of the 12 specimens, taphonomic modifications had heavily affected the cortical surface of the elements. With better preservation of the elements, the frequency of lesions is expected to increase. Although the sample was highly fragmented with poor surface preservation, 25% of the specimens from the Bajo de la Quinta site contained lesions.

The Calera site

The Calera site is located approximately 600km north of the modern osteological collection area at the base of the Tandilia sierra in the Province of Buenos Aires (Figure 1). The site is interpreted as a ritual deposit formed as a consequence of ceremonies and feasts, dated from *ca.* 1700 to 3400 years BP (Politis *et al.*, 2005; Kaufmann *et al.*, 2006; Messineo & Politis, 2007; Álvarez, 2009). The guanaco bones present excellent bone surface preservation, and the majority of the elements are complete or semi-complete (Álvarez, 2009).

Although vegetation in the Pampas fluctuated during the Holocene, over the last 4000 years, the region was dominated by different Poaceae genera (flowering plants and grasses). The natural vegetation of the Pampa grasslands lacks trees; however, some areas contain small shrubs and bushes. As a result of extensive agricultural activity, many native species have become extinct (León, 1991; Soriano *et al.*, 1992; Tonello & Prito, 2008).

For the purpose of this study, 15 metapodial elements were analyzed. The sample consisted of five

right and four left metacarpals, as well as three right and three left metatarsals. Three of the elements were complete, whereas the remaining were semi-complete. All of the elements had their proximal ends and shafts intact, and none of them had been heavily affected by taphonomic modifications (e.g. weathering, chemical deterioration); however, none of the 15 metapodials showed signs of thorn lesions.

Conclusion

The analysis of the modern osteological collection, which originated from an environment characterised by the presence of abundant communities of thorny vegetation (Monte phytogeographic province), permitted the identification of distinct lesions and reactions caused during the penetration of thorns in the bone tissue. The description of these phenomena constitutes the first of its kind for an animal population and contributes to the differentiation of these modifications from the effects of other taphonomic agents and processes, such as chemical dissolution (Nicholson, 1996; Johnson et al., 1997; Gutiérrez, 2004), carnivore furrowing or pitting (Binford, 1981; Haynes, 1981; Beherensmeyer, 1990), root marks (Beherensmeyer, 1978; Grayson, 1989) or pathological processes such as localised depressions caused by trauma (Baker & Brothwell, 1980), among others. Clearly, in the fossil record, the

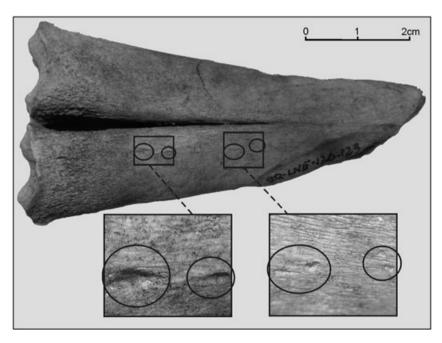


Figure 6. Fragment of juvenile guanaco metapodial from the Bajo de la Quinta site with multiple small negative scars.

presence of thorns visible on the bone surface (type 1) is a phenomenon highly dependent on the preservation of this organic matter. Although the scars and bone reactions described above present a certain equifinality with other taphonomic or pathological modifications, the detailed macroscopic description as well as the identification of the frequency and location of these lesions by anatomical region and portion, as shown here, helps contribute significantly to the recognition of these processes in the fossil record.

In reference to the osteological collection, the high frequency in both metapodials and phalanges demonstrates that the guanacos were clearly living and interacted with vegetation containing thorns. Considering the results of the quantification of the sample, fossil records originating from a thorny environment would present the following patterns. (1) Frequency of lesions in the sample: a high percentage of lesions are expected. In the case of the modern osteological collection, 97% of the individuals contained one or more type of lesion. (2) Location of the lesions: the anterior view and the shafts of the elements will have the highest frequency of thorn lesions, whereas the posterior perspective and metaphysis have lower percentages. (3) Frequency of lesions by age group: all the age groups can be affected by thorn lesions. Individuals between the ages of 1 and 3 years are the most affected. whereas those between the ages of 0 and 1 year contained the least amount of lesions. Finally, as a premise, we expect that the distribution of the thorn lesions is constrained to the lower leg elements, principally the phalanges, metapodials, articulating bones and the distal segments of the radius-ulna and the tibia. The low soft tissue content associated with these elements permits the penetration of foreign bodies such as thorns.

The four types of lesions observed in the collection represent the different bone reaction processes during the penetration of the thorn: adherence, encapsulation, detachment and dissolution. When preserved in the fossil record, the lesions have the potential to be established as a third order proxy (sensu Caran, 1998) of the paleovegetation, which together with other proxies helps to reconstruct the paleoenvironment of archaeological and paleontological localities. Although the ability to recognise and distinguish thorn lesions in the fossil record is highly dependent on taphonomic modifications, which may have affected the bone surface, as observed here, even in a highly modified fossil record like the Bajo de la Quinta site, the preservation of thorn lesions were identifiable. Whereas the sample analyzed here was small, the presence of thorn lesions in the archaeofaunal assemblage constitutes indirect evidence that the guanacos that inhabited the locality from ca. 450 to 1040 years BP interacted with thorny vegetation.

The work presented here provides the direction for quantifying and interpreting thorn lesions in the fossil record. These data can be applied to any number of environmental settings as well as a variety of animal species. The implications of this research will improve our knowledge of the past by advancing our ability to recognise key indicators of the paleovegetation. Future work should incorporate the analysis of the remainder of the appendicular and axial skeleton, as well as the analysis of other modern osteological collections from distinct environmental settings.

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References

Abe Y, Marean CW, Nilssen PJ, Assefa Z, Stone EC. 2002. The analysis of cutmarks on archaeofauna: A review and critique of quantification procedures, and a new image-analysis GIS approach. *American Antiquity* 67: 643–63.

Álvarez MC. 2009. Análisis de los restos faunísticos del sitio Calera (Sierras Bayas, partido de Olavarría). Un aporte a su funcionalidad a través del estudio de los mamíferos. Relaciones de la Sociedad Argentina de Antropología 44: 29–51.

Baker JR, Brothwell D. 1980. Animal Diseases in Archaeology. Academic Press: London.

Beherensmeyer AK. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 473–578.

Beherensmeyer AK. 1990. Transport-hydrodynamics: Bones. Paleobiology: A Synthesis, D Briggs, P Crowther (eds.). Blackwell Scientific Publications: Oxford, 232–235.

- Binford LR. 1981. Bones: Ancient Men and Modern Myths. Academic Press: Nueva York.
- Borella F, Mariano C, Favier Dubois CM. 2007. Procesos tafonómicos en restos humanos de la localidad arqueológica de Bajo de la Quinta, golfo San Matías (Río Negro), Argentina. Arqueología de Fuego-Patagonia. Levantando piedras, desenterrando buesos...y develando arcanos, F Morello, M Martinic, A Prieto, G Bahamonde (eds.). Ediciones CEQUA: Punta Arenas, Chile; 403–410.
- Borgia CA. 1963. An unusual bone reaction to an organic foreign body in the hand. Clinical Orthopaedics and Related Research 30: 188–93.
- Bouajina E, Harzallah L, Ghannouchi M, Hamdi I, Rammeh N, Hamida RB, Kraiem C. 2006. Foreign body granuloma due to unsuspected wooden splinter. *Joint, Bone, Spine* 73: 329–337.
- Cabrera A, Willink A. 1973. Biogeografía de América Latina. Monografía 13. Serie Biología. OEA. Secretaria General de la OEA: Washington, DC.
- Caran SC. 1998. Quaternary paleoenvironmental and paleoclimatic reconstruction. *Plains Anthropologist* 43(164): 111–124.
- Carandell M, Roig D, Benasco C. 1980. Plant thorn synovitis. *Journal of Rheumatol* 7: 567–569.
- Croochiolo A, Goldberg L. 1997. Local and systemic reaction to puncture injuries by the sea urchin spine and the date palmar thorn. *Artbritis and Rheumatism* **20**: 1206–1212.
- De Nigris ME. 2004. El consumo en grupos cazadores recolectores. Un ejemplo zooarqueológico de patagonia meridional. Sociedad Argentina de Antropología: Buenos Aires.
- Domínguez-Rodrigo M. 1997. Meat-eating by early hominids at the FLK Zinjanthropus Site, Olduvai Gorge (Tanzania): An experimental approach using cut-mark data. *Journal of Human Evolution* 33: 669–690.
- Fakoor M. 2006. Prolonged retention of an intra medullary wooden foreign body. *Pakistan Journal of Medical Sciences* 22: 78–79.
- Favier Dubois CM, Borella F. 2007. Consideraciones acerca de los procesos de formación de concheros en la costa Norte del golfo San Matías (Río Negro, Argentina). Cazadores-Recolectores del Cono Sur 2: 151–165.
- Favier Dubois CM, Borella F, Tykot RH. 2009. Explorando tendencias en el uso humano del espacio y los recursos en el litoral rionegrino (Argentina) durante el Holoceno medio y tardío. Arqueología de la Patagonia—Una mirada desde el último confín, M Salemme, F Santiago, M Álvarez, E Piana, M Vázquez, ME Mansur (eds.). Utopías: Ushuaia; 985–997.
- Franklin WL. 1982. Biology, ecology and relationship to man of the South American camelids. *Mammalian Biology* in South America, Pymatuning Symposia in Ecology, Vol. 6, MA Mares, HH Genoways (eds.). Special Publication Series, University of Pittsburgh: Pittsburgh, PA, 457–489.
- Franklin WL. 1983. Contrasting socioecologies of South America's wild camelids: The vicuña and guanaco. Advances in the Study of Mammalian Behaviour, JF Eisemberg,

- DG Kleiman (eds.). The American Society of Mammalogists. Special Publication *7*, 573–629.
- Fritz MA. 1985. Population dynamics and preliminary estimates of harvestibility of a Patagonian guanaco. Unpublished Master's thesis. Iowa State University, Ames, Iowa.
- Grayson DK. 1989. Bone transport, bone destruction, and reverse utility curves. *Journal of Archaeological Science* 16: 643–652.
- Grubb PJ. 1992. A positive distrust in simplicity—lessons from plant defenses and from competition among plants and among animals. *Journal of Ecology* **80**: 585–610.
- Gutiérrez MA. 2004. Análisis tafonómicos en el Área Interserrana (provincia de Buenos Aires). Unpublished Ph.D. thesis. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.
- Gutiérrez MA, Martínez G. 2008. Trends in the faunal human exploitation during the Late and Early Holocene in the Pampean region (Argentina). *Quaternary International* 191: 53–68.
- Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM. 2007.
 Plant structural traits and their role in anti-herbivore defense. Perspectives in Plant Ecology, Evolution and Systematics 8: 157–178.
- Haynes G. 1981. Bone modifications and skeletal disturbances by natural agencies: studies in North America. Unpublished Ph.D. thesis. Catholic University of America, Washington, DC.
- Izeta AD. 2005. Southamerican Camelid bone density: what are we measuring? Comments on datasets, values their interpretation and application. *Journal of Archaeological Science* 32: 1159–1168.
- Izeta AD. 2007. Zooarqueología del sur de los valles Calchaquíes (Provincias de Catamarca y Tucumán, República Argentina): Análisis de conjuntos faunísticos del primer milenio A.D. British Archaeological Research International Series \$1612. John & Erica Hedges Co. Ltd.: Oxford, UK.
- Izeta AD, Scattolin MC. 2006. Zooarqueología de una unidad doméstica formativa. El caso de Loma Alta (Catamarca, Argentina). *Intersecciones en Antropología* 7: 193–205.
- Johnson E, Gutiérrez MA, Politis G, Martinez G, Hartwell W. 1997. Holocene Taphonomy at Paso Otero 1 on the Eastern Pampas of Argentina. *Proceedings of the 1993 Bone Modification Conference, Hot Spring, South Dakota*, LA Hannus, L Rossum, RP Winham (eds.). Ocassional Publication 1, Archaeology Laboratory, Augustana College: Sioux Fall; 105–121.
- Kaufmann CA. 2009. Estructura de edad y sexo en guanaco. Estudios actualísticos y arqueológicos en Pampa y Patagonia. Sociedad Argentina de Antropología: Buenos Aires.
- Kaufmann CA, Messineo P, Politis G, Álvarez MC. 2006. Sitio Calera: un depósito ritual de huesos en las llanuras pampeanas de Argentina. Paper presented at the *International* Council for Archaeozoology, 10th Conference, D. F. Mexico; 94–95
- Kchir MM, Snoussi H, Kochbati S, Zouari R, Ben Jilani S, Hila A. 1994. Synovitis caused by plant thorn and chronic

polyarthritis. Apropos of a case and review of the literature. Revue du rhumatisme (French Edited) 61: 53-5.

- Larrieu E, Bigatti R, Lukovich R, Eddi C, Banazzi E, Gómez E, Niec R, Oporto N. 1982. Contribución al estudio del parasitismo gastrointestinal en guanacos (*Lama guanicoe*) y llamas (*Lama glama*). *Gaceta Veterinaria* 44: 958–960.
- León RJC. 1991. Geographic limits of the region, geomorphology and geology, regional subdivisions, floristic aspects, description of the vegetation. *Natural Grasslands: Introduction and Western Hemisphere*, RT Coupland (ed.). Elsevier: Amsterdam. The Netherlands: 369–387.
- Mangat P, Jawad ASM. 2007. A case of rose thorn tenosynovitis. *Grand Rounds* 7: 16–17.
- Marean CW, Abe Y, Nilssen PJ, Stone EC. 2001. Estimating the minimum number of skeletal elements (MNE) in zooarchaeology: a review and a new image-analysis GIS approach. *American Antiquity* **66**: 333–48.
- Marín-Arroyo A, Ruiz ML, Bernabeu GV, Román RS, Morales MG, Straus L. 2008. Archaeological implications of human-derived manganese coatings: a study of blackened bones in El Mirón Cave, Cantabrian Spain. *Journal of Archaeological Science* 25: 801–813.
- Maylahn DJ. 1952. Thorn induced "tumors" of bone. The Journal of Bone and Joint Surgery 34: 386–388.
- Mengoni Goñalons GL. 1999. Cazadores de guanaco de la estepa patagónica. Sociedad Argentina de Antropología: Buenos Aires
- Merino ML, Cajal JL. 1993. Estructura Social de la Población de Guanacos (*Lama guanicoe* Muller, 1776) en la costa norte de Península Mitre, Tierra del Fuego, Argentina. *Studies on Neotropical Fauna and Environment* 28: 129–138.
- Messineo PG, Politis GG. 2007. El sitio Calera. Un depósito ritual en las Sierras Bayas (sector noroccidental de Tandilia). Arqueología en las Pampas: Tomo II, C Bayón, A Pupio, MI González, N Flegenheimer, M Frère (eds.). Sociedad Argentina de Antropología: Buenos Aires; 697–720.
- Miotti L, Salemme M. 1999. Biodiversity, taxonomic richness and specialists—generalists during Late Pleistocene/ Early Holocene times in Pampa and Patagonia (Argentina, Southern South America). *Quaternary International* 53/54: 53–68.
- Morlan RE. 1994. Bison bone fragmentation and survivorship: A comparative method. *Journal of Archaeological Science* 21: 797–807.
- Morrone JJ. 2001. Biogeografía de América Latina y Caribe, Vol. 3. Manuales & Tesis SEA: Zaragoza.

- Nicholson RA. 1996. Fish bone diagenesis in different soils. *Archaeofauna* 5: 79–91.
- Ortega IM, Franklin WL. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. *Revista Chilena de Historia Natural* **68**: 489–500.
- Politis G, Salemme M. 1990. Pre-Hispanic mammal exploitation and hunting strategies in the Eastern Pampas Subregion of Argentina. *Hunters of the Recent Past*, LB Davis, BOK Reeves (eds.). Unwin: London; 352–372.
- Politis G, Messineo P, Kaufmann C, Barros MP, Álvarez MC, Di Prado V, Scalise R. 2005. Persistencia ritual entre cazadores-recolectores de la llanura pampeana. *Boletín de Arqueología PUCP* 9: 67–90.
- Raedeke K. 1979. Populations dynamics and socio-ecology of the guanaco (*Lama guanicoe*) of Magallanes, Chile. Unpublished Ph.D. Thesis. University of Washington, Seattle, USA.
- Redford KH, Eisenberg JF. 1989. Mammals of the Neotropics. The Southern Cone, Vol 2. University of Chicago Press: Chicago.
- Reginato AJ. Ferreiro JL, O'Connor CR, Barbasan C, Arasa J, Bednar J, Soler J. 1990. Clinical and pathologic studies of twenty-six patients with penetrating foreign body injury to the joint, bursae and tendon sheths. *Arthritis & Rheumatology* 33: 1753–1762.
- Roig FA, Roig Juñent S, Corbalán V. 2009. Biogeography of the Monte Desert. Journal of Arid Environments 73: 164–172.
- Shahack-Gross R, Bar-Yosef O, Weiner S. 1997. Black-colored bones in Hayonim Cave, Israel: differentiating between burning and oxide staining. *Journal of Archaeological Science* **24**: 439–446.
- Soriano A, León RJC, Sala OE, Lavado RS, Deregibus VA, Cahuepe MA, Scaglia OA, Velázquez CA, Lemcoff JH. 1992. Río de la Plata Grasslands. *Natural Grasslands*, RT Couplant (ed.). Ecosystems of the World, vol. 8. Elsevier: Amsterdam; 367–407.
- Sugarman M, Stobie DG, Quismorio FP, Terry R, Hanson V. 1977. Plant thorn synovitis. Arthritis and Rheumatism 20: 1125–8.
- Tonello MS, Prito AR. 2008. Modern vegetation-pollenclimate relationships for the Pampa grasslands of Argentina. *Journal of Biogeography* **35**: 926–938.
- Wilson PE. 1982. An analysis of male–male aggression in guanaco male groups. Unpublished Master thesis. Iowa State University, Ames, Iowa.