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ORIGINAL PAPER

A taphonomic study of a carcass consumed by griffon vultures (*Gyps fulvus*) and its relevance for the interpretation of bone surface modifications

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Abstract Vultures are ubiquitous taphonomic agents in most biomes. However, taphonomic studies of vultures are scarce and very little is known of the damage they cause to bone surfaces when consuming carcasses. This study presents the results of a taphonomic analysis of bones modified by griffon vultures. Although some marks created by these agents are diagnostically unique, others are extremely similar to modifications caused by other biostratinomic processes. This renders interpretations of marks on bones very problematic when these modifications are considered in isolation rather than at the assemblage and contextual levels.

Keywords Bone surface modifications · Vultures · Taphonomy · Biostratinomy · Trampling marks

Introduction

Vultures are very conspicuous carcass-consuming agents in most biomes on Earth and yet most of their species have not been the focus of taphonomic research until recently. This remains so despite the fact that in South Africa, up to six species of vultures have been reported to collect and accumulate bones in their nests (Plug 1978). Only bearded vulture (*Gypaetus barbatus*) bone accumulations have been studied taphonomically and characteristics of the bones that they digest described (Robert and Vigne 2002). The effect that carcass consumption by vultures has on bone surface modifications remains unstudied. While Reeves (2009) in her study of carcass disarticulation by the American black vulture (*Coragyps atratus*) reported the presence of shallow linear scratches, some indicated by a change in the color of the bone surface, these were not described in detail. She mentioned that most scratches are linear and shallow and that some were indicated by a change in the color of the surface of the bone. This remains insufficient to create a diagnosis of vulture-made marks and to understand how they overlap with other types of bone surface modifications. Other forensic studies focus on the effects of vulture consumption of soft tissues (Komar and Beattie 1998; Pickering and Bachman 2009; Khan 2006), but this has limited application to prehistoric remains.

The present work aims at covering part of this knowledge gap by showing the results of a taphonomic study on a carcass consumed by griffon vultures (*Gyps fulvus*) and the resulting patterns of bone surface modification according to their frequency and anatomical distribution. A detailed discussion of mark morphology will also be provided, showing the uniqueness of some vulture-made bone modifications when compared to other carnivore-made marks, but also their similarity to other types of marks made by other biostratinomic processes. Previously, only Cáceres (2002) showed some preliminary examples of bone modifications by vultures.

Vultures are birds of prey classified as Falconiformes and further divided according to geographic provenience: the New World vultures—Cathartidae—and the Old World vultures—Accipitridae. The Old World and New World vultures have a similar morphology and both survive as scavengers, probably as a result of convergent evolution

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from two different evolutionary lines; but, they show several important differences in their respective biology and behavior.

Griffon vultures and other vulture taxa have been documented in prehistoric Eurasia during the Middle and Upper Pleistocene (Tyrberg 1998; Sánchez 2007). Therefore, they are a potential taphonomic agent in archaeofaunal assemblages preserved during the past 500 ka, either by directly accumulating bones (such as bearded vultures) or by consuming carcasses later accumulated by other taphonomic agents (e.g., carnivore mammals). They are gregarious and feed on carcasses of all sizes (Domínguez-Solera 2010). The Iberian Peninsula maintains one of the largest populations of griffon vultures in Eurasia with almost 50,000 individuals recorded (Iñigo and del Moral 2009). Therefore, Spain and Portugal are some of the best places to study this species, which is currently widespread, reaching central Asia and parts of Africa.

Robert and Vigne (2002) and Marín et al. (2009) reported on prehistoric assemblages accumulated by or contributed to by vultures in Gritulu (Corsica) and El Mirón Cave (Spain) during the Upper Pleistocene. Understanding how vultures modify bones during carcass consumption would better enable differentiation between palimpsests in which they contribute as accumulating agents versus assemblages entirely accumulated by them. This study addresses these questions and is the first taphonomic study undertaken on griffon vultures. Although griffon vultures do not accumulate bones (Mundy and Ledger 1976), they raise the question of whether other bone-accumulating taxa, such as the bearded vulture, may leave similar types of marks on the bones of the carcasses they consume given the overall similarity in beak morphology and carcass-consuming behavior. Furthemore, the study of the griffon vulture increases the referential framework for the understanding of potential taphonomic signatures in scenarios of hominins scavenging carcasses initially consumed by vultures.

Sample and method

The present study was carried out in the Reserve of El Hosquillo in Cuenca (Spain). The reserve includes a feeding spot where carcasses are usually available for a large population of vultures that inhabit the nearby Serrania de Cuenca National Reserve. The experiment consisted of feeding a complete female adult deer carcass to vultures to document their feeding behavior and the resulting bone damage. The deer was provided by one of the reserve's rangers and was later discovered to contain a fetus. The carcass was deposited on the feeding spot at 9:30 a.m. An observation point was established 375 m from the feeding spot, so as not to disturb the vultures. Binoculars and cameras with high-powered lenses were used to observe and document the whole process.

Visual control of the carcass was complete throughout the experiment. The carcass attracted more than 50 vultures but was mostly consumed by a dozen individuals in less than 1 h. After consumption, the distribution of carcass elements was drawn to document disarticulation and dispersal of bones, and then the carcass was collected. Bones were subsequently cleaned by boiling them in a solution of water and neutral soap in two separate days. No tool was used for disarticulation so that, given the full control of the sample, marks present on bones can be directly attributed to vultures.

Bones were then carefully inspected for bone surface modifications, with the aid of ×15 hand lenses under strong light and then a binocular microscope (Motic) with magnifications of ×20–40 and an incorporated digital camera (MC V3), which transfers high-resolution images in .mix, .bmp and .jpeg formats into a computer. Marks were also observed under a handheld digital microscope (Dinolite AM413FVT) with magnifications of ×10–200 and analyzed using the microscope's (Dino Capture 2.0) software. Marks were defined following Binford (1981) for pits, scores, and punctures, Pickering and Egeland (2006) for striae fields, and Domínguez-Rodrigo et al. (2009) for microabrasion and intersecting striae.

The behavior documented in the consumption of the carcass analyzed in the present study has been observed in several other carcasses, therefore supporting that this behavior is common in this species. The other carcasses, reported in Domínguez-Solera (2010), were not included in this study either because complete control of the sample was not possible or because in some cases, carcasses were disarticulated with metal knives and some marks could be mistaken with those created by vultures.

Results

Most of the deer bones were dispersed along 30 m from the point where the carcass was initially deposited (Fig. 1). The rib cage, the skull, and the limbs were joined by skin. Some ribs and the mandible were detached from the carcass. Despite being attached by the skin, the skull, metatarsals, proximal femora, and humeri were disarticulated from the axial skeleton. The vertebral spine was also split at the thoracic–lumbar section (Fig. 1). The pelvis and the lumbar and caudal vertebrae were taken away from the feeding spot and were not found within a perimeter of 200 m. They ended up downslope with the large number of bones accumulated from previous recent feeding episodes. This disarticulation process produced while competing for

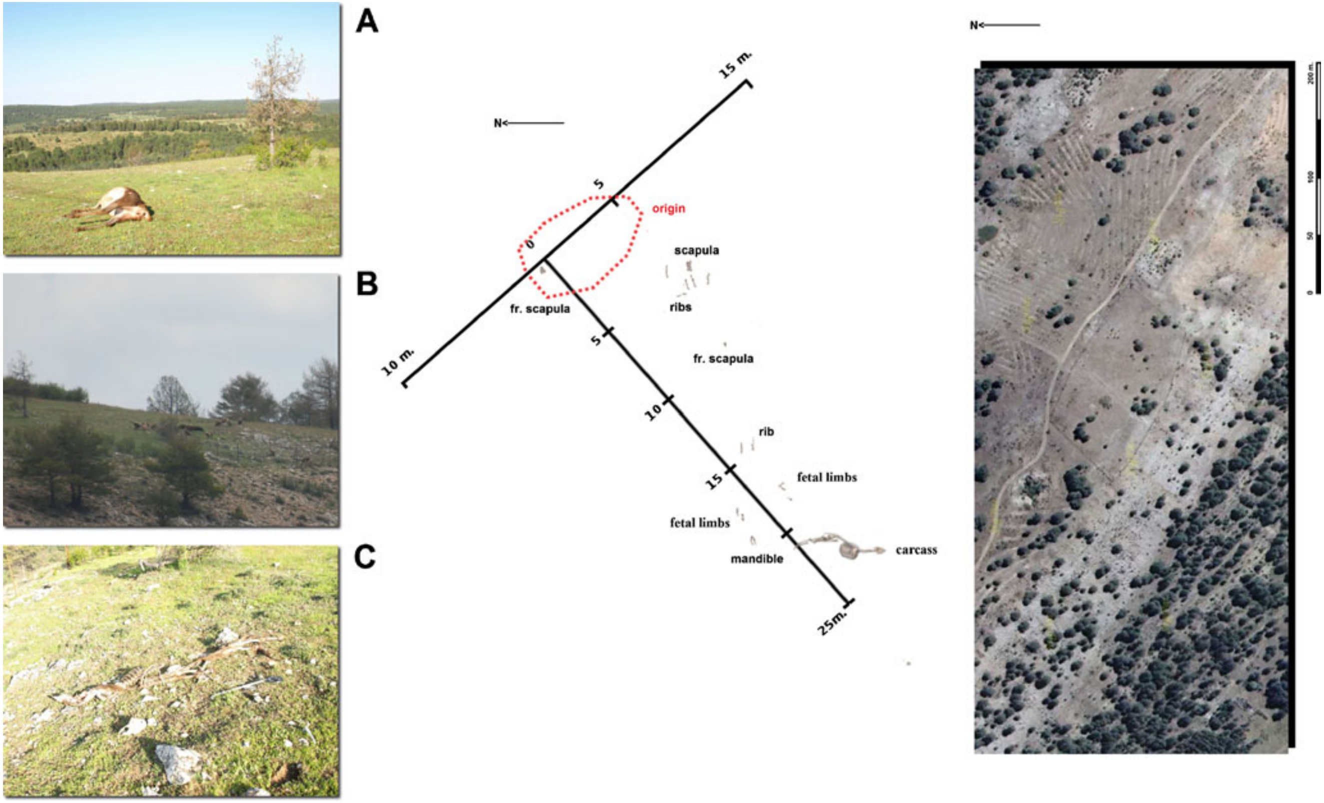

Fig. 1 Aerial view of the feeding place (*right*) and dispersal of the deer carcass remains after its consumption by vultures (*center*). **a** Location of the feeding spot right after placing the deer carcass. **b** Vultures starting carcass consumption and **c** carcass remains after consumption

access to meat is similar to that reported by Reeves (2009) for black and turkey vultures in America.

Upon recovery, all flesh had been consumed. Only metapodials were left undisturbed and skinned. All bones were abandoned by vultures unbroken, with the exception of the fetal bones, some of which were damaged on their ends. The analysis of bone surface modifications revealed extensive inconspicuous damage to bone surfaces, mostly in the form of shallow scores. A total of 110 elements were recovered, and almost 22% of them bore marks on their surfaces (Table 1). Most anatomical sections, except radii–ulnae, carpals, metapodials, and phalanges, are marked (Fig. 2). Marks created by vultures appear in low numbers on most marked elements, with a maximum of five marks per element documented. The exceptions to this are femora and humeri, where marks occur in greater abundance, if counting the extreme cortical exfoliation caused by vultures' beaks, where individual marks were overlapping to the extent of not being individually identifiable (Fig. 3). For these elements, mark tallying refers to individual marks. All marks on long bones occur where flesh is more abundant, with upper limb bones being more highly marked than intermediate limb bones. A distinctive feature of vulture bone marking is that most marks on long bones occur on the diaphyseal sections. Vultures abandon carcasses with long bones articulated and therefore, no damage is inflicted on epiphyseal portions,

Table 1 Anatomical distribution of marks created by griffon vultures

Elements	Elements with marks (%)	Number of marks
Skull	1 (100)	5
Mandible	2 (100)	5
Cervical vertebrae	2 (28.5)	2
Thoracic vertebrae	2 (16.6)	2
Lumbar vertebrae	–	–
Scapula	1 (50)	3
Pelvis	–	–
Ribs	8 (33.3)	17
Humeri	2 (100)	4
Femora	2 (100)	6
Radio-ulnae	0 (0)	0
Tibiae	2 (100)	7
Carpals	0 (0)	0
Tarsals	2 (25)	2
Metapodials	0 (0)	0
Phalanges	0 (0)	0
Total	24 (21.8)	53

Numbers in parentheses show percentages

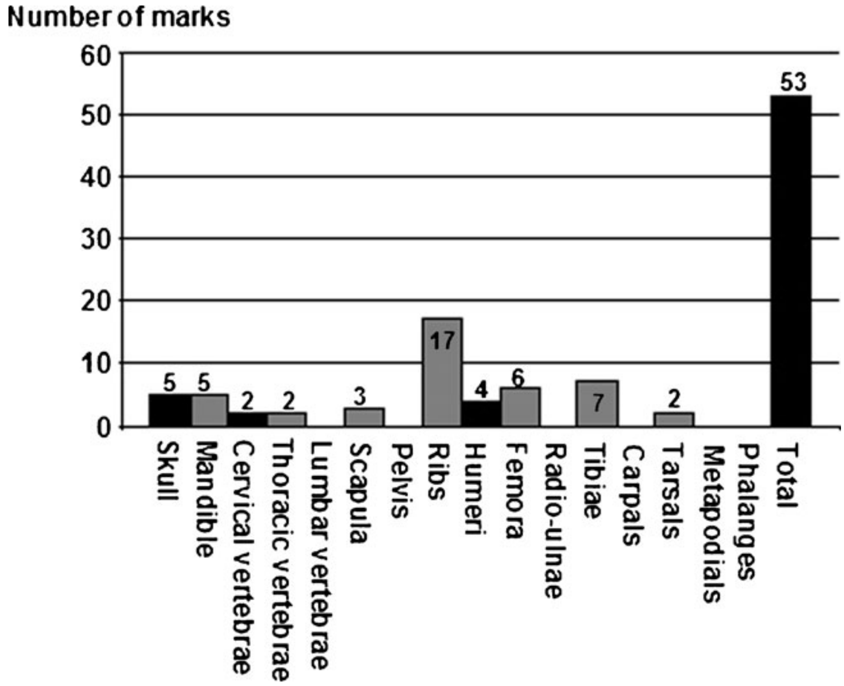

Fig. 2 Anatomical distribution of the number of isolated marks created by vultures

since they do not remove tendons or ligaments. Marks are also more frequent on the back and neck than on the rest of the axial skeleton. Ribs are marked on both the dorsal and ventral sides, with as many as 30% of them bearing at least one mark. The exposure of rib surfaces during defleshing is partly responsible for this frequency of damage. These marks can also be due to the very long and elastic neck of griffon vultures which allows them to put their head inside the rib cage and eat the internal organs. The cranium is also marked with low frequency of modifications. The most conspicuous damage is documented on the external/lateral bodies of mandibles.

Marks imparted by vultures on bones were of several types. Punctures were recorded on the cranial and scapular bones (Fig. 4). Pits occurred in low numbers, but the most conspicuous could easily be mistaken with mammalian carnivore tooth marks (Fig. 5). They consisted of roughly circular or oval pits, with wide U-shaped sections, containing crushed bone inside, especially around the perimeter of the mark, as is typical of mammalian carnivore tooth pits (Blumenschine 1988). The more oval pits contain a polished surface, also typical of carnivore tooth pits and scores. These are perfect cases of equifinality, since they cannot be differentiated from mammalian carnivore tooth marks.

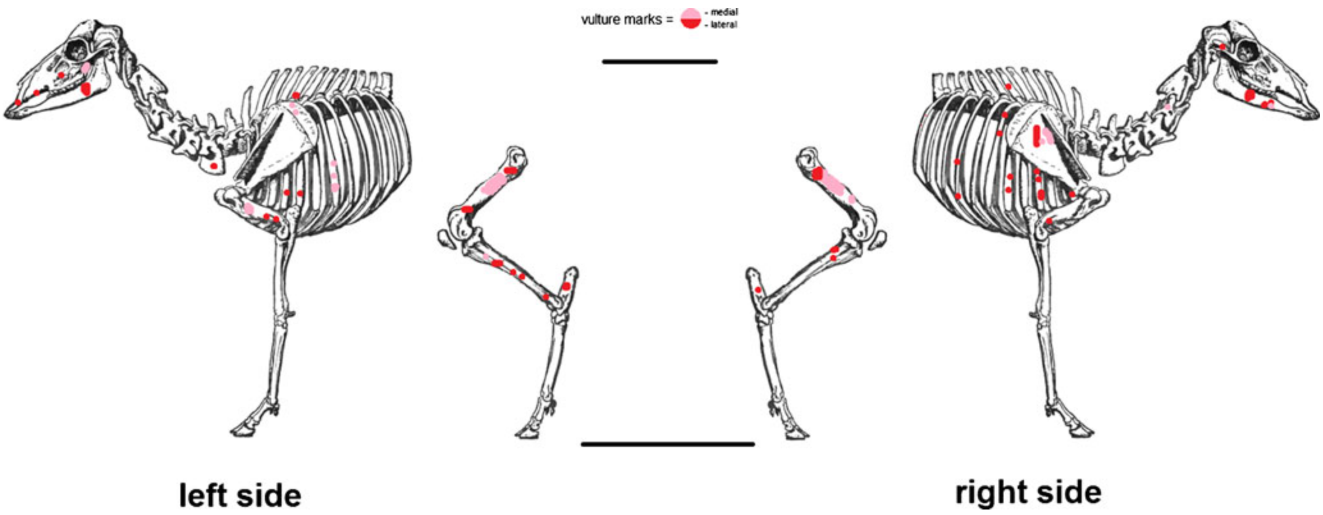

Fig. 3 Anatomical location of marks created by vultures on bones. *Dark color* shows lateral side; *light color* shows marks on the medial side

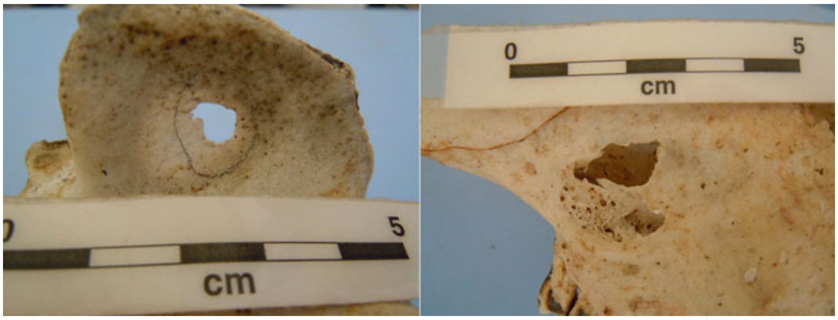

Fig. 4 Punctures made by vultures on vertebral apophysis (*left*) and maxillar bone (*right*)

The most common mark types made by vultures are shallow scores and striae, as initially documented by Reeves (2009). The striae can sometimes be irregular (Fig. 6a) and, more frequently, linear (Fig. 6b). The most striking feature documented in these striae is the presence of multiple parallel microstriations, which can be linear (Fig. 6b, d), curved (Fig. 6a), or with a winding trajectory (Fig. 6c), which perfectly mimics the array of forms in which striations caused by trampling have been documented (Domínguez-Rodrigo et al. 2009). Some of them even display shallower striae in the form of microabrasion, which are similar to those documented by trampling (Fig. 6d) or to some of the marks made by human incisors on bones as reported by Fernández-Jalvo and Andrews (2011). When some of these striations are very short, they also mimic the isolated striae fields observed on both trampled and hammerstone-percussed bones (Domínguez-Rodrigo et al. 2010).

Some marks combine different linear grooves into a tick (check)-shaped mark, although in some cases a single tick-shaped mark was reported (Fig. 7). These marks resemble some hook-shaped marks reported for crocodiles (Njau and Blumenschine 2006) and also look similar to some of the tick-shaped marks reported for the Pliocene Dikika fossils (McPherron et al. 2010).

However, the description of the modifications shown above should not indicate that a faunal assemblage created by vulture consumption of carcasses should reflect the same types of marks as a trampled assemblage. If one considers the combined characteristics of all bone modifications in both types of assemblages, instead of the characteristics of individual marks, some important differences can be documented, which can be used to differentiate between taphonomic agents.

At magnification lower than ×50, these are the main characteristics which can be used to identify bone damage caused by vultures: most damage on long bones is concentrated on the shafts of meat-bearing bones, it is not documented on epiphyses of adult individuals, and marks on most bones occur in low densities and without microabrasion which is typical of trampling. A further diagnostic feature of carcasses consumed by vultures is that all bones are unbroken and that long bones remain articulated after consumption. This latter characteristic can be biased if other biotic postdepositional agents (such as mammalian carnivores) intervene afterwards.

Discussion

The study of bone surface modifications has acquired a prominent role in interpretations of taphonomic agency in the formation and modification of faunal assemblages. It has contributed to differentiating carnivore tooth marks (Brain 1981; Binford 1981; Blumenschine 1988; see review in Fisher 1995) from hammerstone percussion marks (Blumenschine and Selvaggio 1988; Pickering and Egeland 2006) or biochemical marks (Domínguez-Rodrigo and Barba 2006; Domínguez-Rodrigo et al. 2007). It also made it possible to differentiate stone-tool cut marks (Bunn 1983;

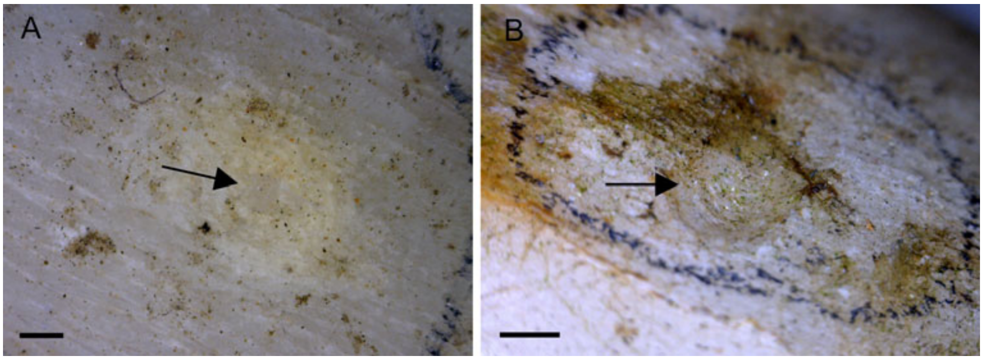

Fig. 5 **a** Pit created by vulture beak, showing irregular crushed bone on its contour (×20). **b** Oval pit (too short to be a score) with polished interior surface made by vultures (×35). Section and cortical shapes are similar to those made by mammalian carnivores. *Scale*, 1 mm

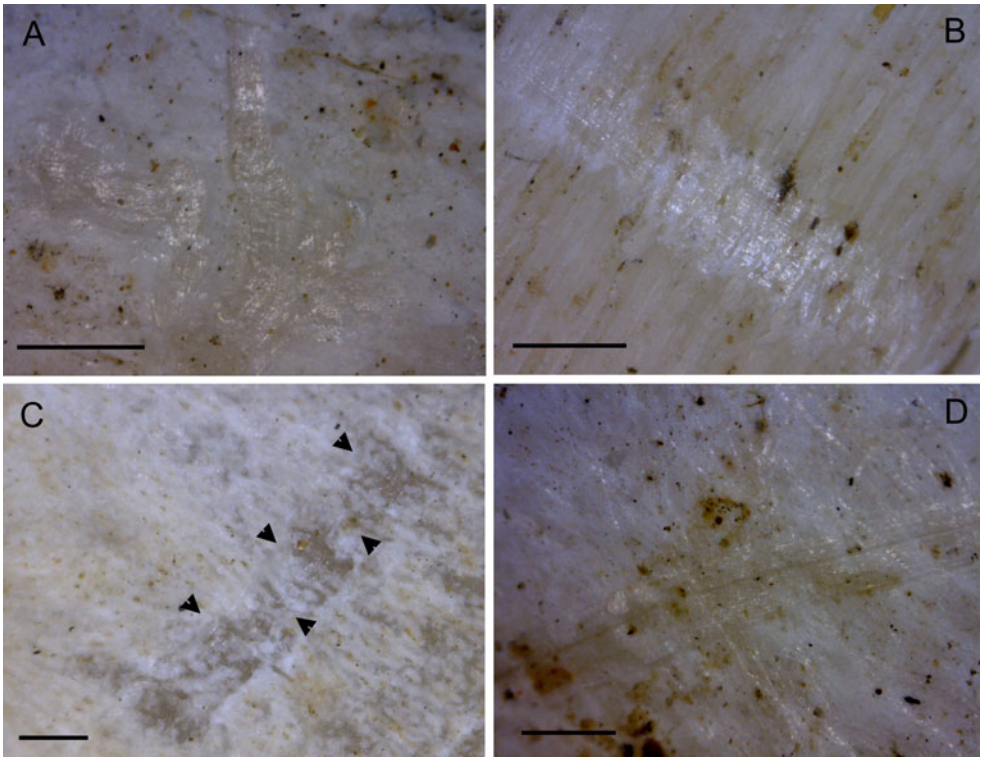

Fig. 6 **a** Irregular scoring of the bone surface. **b** Shallow striation with multiple linear microstriations. **c** Same as **b** but with winding trajectory of the microstriations, with *arrows* indicating a change of directionality. **d** Striation with multiple parallel microstriations overlaid by multiple, shallower striae with multiple orientations, similar to the microabrasion documented in trampling

Potts and Shipman 1981) from cut marks created with bamboo (Jolee et al. 2007) or metal (Greenfield 1999) and from trampling marks (Domínguez-Rodrigo et al. 2009 and references therein).

Some authors argue that the taphonomic knowledge gained in the past few years, mainly through experimental research, enables taphonomists to go further in each of the previous types of bone surface modifications and differentiate among carnivore types (Domínguez-Rodrigo and Piqueras 2003; Pobiner 2008)—including humans (Fernández-Jalvo and Andrews 2011)—stone tool types (Bello et al. 2009; Domínguez-Rodrigo et al. 2009; de Juana et al. 2009), and metal tool types (Lewis 2008). All this is of utmost relevance, for example, for discerning order of access to carcass remains when human–carnivore interactions are documented (see review in Domínguez-Rodrigo et al. 2007).

However, such optimism should be taken with precaution, since the more taphonomists broaden their referential frameworks, the greater the risk of potential equifinality becomes. For instance, some authors differentiating mark types emphasize the presence of overlap among marks created by different agents and, therefore, that mark differentiation is only statistically reliable at the assemblage level (Domínguez-Rodrigo et al. 2009). This can be noticed when comparing cut marks made with simple flakes to those made with retouched flakes and to trampling marks. A high number of marks can be attributed to agent, but the identification of every single mark in some cases remains probabilistic. This problem is even more noticeable when trying to identify marks on specimens that have undergone modifications by several agents on the same fragment, creating a palimpsest effect. Confidence in identification in such a situation decreases. This is why very optimistic interpretations of isolated marks or identification of agents through specific mark types could potentially be controversial. For instance, the double arch puncture on the edge of long bone shafts presented by Fernández-Jalvo and Andrews (2011) as typical of human chewing can also be documented in more than one carnivore type—namely, canids (unpublished). The same critique can be applied to the shallow microstriated linear marks created by human incisors, which are also similar to those created by suid incisors (Domínguez-Solera and Domínguez-Rodrigo 2009) and vultures (see above); and the same can be said of triangular tooth pits, also documented in suids. Pobiner's (2008) optimism about identifying carnivore type by using the properties of individual tooth marks was counterbalanced by those arguing that only the identification of carnivore size (large, medium, and small) could be approached (Domínguez-Rodrigo and Piqueras 2003), and even this has also been challenged (Delaney-Rivera et al. 2009).

Mark identification has to be carried out with utmost care. Identifications overlooking potential cases of equifinality are not scientifically supported. The recent discovery of a couple of Pliocene bones at Dikika (Ethiopia) with some marks resembling stone-tool marks (McPherron et al. 2010) produced a controversy because some of the marks are

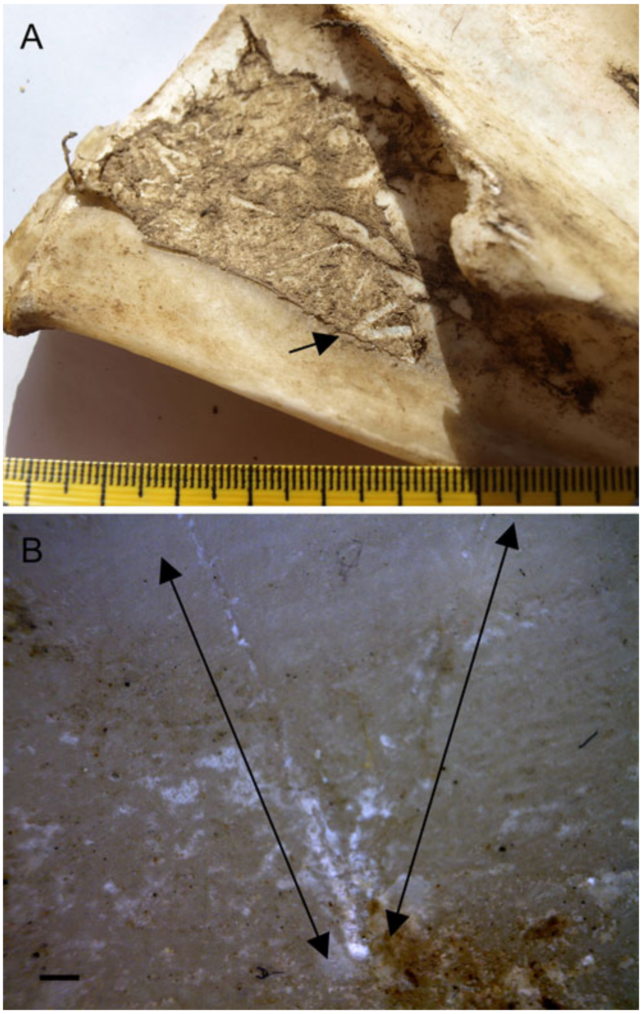

Fig. 7 **a** Tick (V)-shaped mark on the periostial surface of a suid scapula from a separate experiment caused by vulture defleshing of the carcass. **b** Tick (V)-shaped mark on the distal tibia of the deer carcass made by vultures. Scale, 1 mm

identical to those obtained in trampling experiments, a likely cause of those marks given the lithology of the stratigraphy associated with them (Domínguez-Rodrigo et al. 2010). Shallow grooves with microstriations showing linear and winding trajectories are also documented in bones modified by vultures, in addition to those that have been trampled. Vultures will thus need to be considered in future evaluations of some of these marks. The potential diversity of agents creating marks like some of those seen in the Dikika fossils advises even stronger caution in their interpretation than initially advocated by Domínguez-Rodrigo et al. (2010).

Conclusions

Vultures can inflict intensive damage to bone surfaces during the consumption of carcasses. Most of this damage is inconspicuous and needs the use of magnification to properly identify it. In several cases, marks are conspicuous and easily identified by naked eye. The anatomical distribution of marks created by griffon vultures affects the cranial, axial, and appendicular skeleton, avoiding only those parts that contain no flesh, such as metapodials and phalanges. Marks can occur in isolation or in groups and probably depend on the degree of competition in which vultures engage in order to consume the carcass. Some other experiments not reported here were conducted to test if the amount of available flesh determined the intensity of bone damage. The results indicate that bone surfaces are similarly modified in both cases (Domínguez-Solera 2010). Therefore, competition, expressed by the number of individuals that intervene in carcass consumption, may be a possible reason for the widespread occurrence of beak-inflicted marks on bone surfaces.

Marks created by vultures are diverse. Punctures have been documented on flat bones. Pits similar to those made by mammalian carnivores have also been documented. The most abundant type of mark, broad striations and scores with internal multiple parallel microstriations, probably caused by the microscopically irregular edge of the beak, frequently mimics some marks observed in trampling experiments.

This study has shown some of the bone modification patterns made by griffon vultures. Given that one carcass was used, the results shown here are only preliminary and certainly do not reproduce the range of variation characterizing vulture carcass consumption behavior and bone damage frequencies. Future work should aim at expanding the evidence of bone modification types shown in the present work and determining if other vulture taxa produce similar or different kinds of marks. The creation of such a referential framework could be used to estimate the degree of participation of vultures in prehistoric assemblages. Plug (1978) reported that not all bone collected from vulture nests was digested. Marín et al. (2009) have recently reported some digested bone from upper Paleolithic layers of El Mirón cave, thereby inferring that a representative part of the faunal assemblage was accumulated by vultures. The application of bone surface analyses to those assemblages could increase the evidence of vulture-modified bone and, therefore, provide a more complete estimate of their contribution. The present work shows that vultures need to be considered as potential taphonomic agents in future studies of prehistoric faunas.

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