Standardizing terms for crocodile-induced bite marks on bone surfaces in light of the frequent bone modification equifinality found to result from crocodile feeding behavior, stone tool modification, and trampling.

Jackson Njau Department of Geological Sciences, Indiana University, Bloomington, Indiana; The Stone Age Institute, Bloomington, Indiana

Henry Gilbert Anthropology, Geography, and Environmental Studies, California State University, East Bay; Human Evolution Research Center, University of California, Berkeley

¶ These authors contributed equally to this work.

Introduction

Bone modifications have been used to infer Late Pleistocene hominid behavior since the 19th century (Lartet, 1860). Studies of bone modification in zooarchaeological assemblages have subsequently been characterized by waves of dramatic discovery, over-interpretation, broad dissemination, and controversy. In most cases, more modest interpretations and deeper understanding of diverse taphonomic processes have followed.

For example, Dart's claims for an "osteodontokeratic culture" (Dart, 1949, 1957) gave way to a detailed understanding of the patterning of bony element distribution due to carnivore activity (Brain, 1967). Discoveries of dense concentrations of crude stone artifacts in association with fossil mammal bones in Africa during the 1960's elicited claims of "home bases" at which Oldowan hominids were purported to have manufactured tools, processed carcasses, and communally consumed meat (Isaac, 1978; Leakey, 1959; Leakey, 1971). This view was challenged by Binford (Binford, 1981a), who contended that these Early Pleistocene archaeological occurrences were palimpsests of predator and hominid activities. The ensuing controversy brought forth rigorous actualistic studies aimed at understanding hominid carcass acquisition behaviors on the basis of carnivore tooth marks, marks made by hominid butchers (Blumenschine and Selvaggio, 1988; Brain, 1981; Bunn, 1981; Potts and Shipman, 1981) and trampling (Andrews and Cook, 1985; Behrensmeyer et al., 1986; Olsen and Shipman, 1988).

Unfortunately, the dichotomous characterization of mammalian carnivore chewing versus early hominid tool use that emerged in the 1980s has proven misleading. Trampling animals (Behrensmeyer et al., 1986; Domínguez-Rodrigo et al., 2009; Domínguez-Rodrigo et al., 2010; Olsen and Shipman, 1988), vultures (Fetner and Sołtysiak, 2013; Marín−Arroyo and Margalida, 2012; Reeves, 2009), carnivorous lizards (D'Amore and Blumenschine, 2009), and Crocodylians (Njau, 2012), have all been demonstrated to be capable of creating 'mimics' as forewarned by Shipman and Rose (Shipman and Rose, 1983a, 1983b). We now know that ***equifinality***, the potential for different modifiers to leave the same physical signatures on bone, widely affects interpretations of the zooarchaeological record (James and Thompson, 2015; Lyman 2004).

Despite long-standing cautions about equifinality among the modification agents in Paleolithic contexts and despite the ubiquity of crocodiles among African faunas, these animals have only recently gained notoriety as major taphonomic agents in the fossil record (Njau and Blumenschine, 2006). Currently there is no standardized terminology applied to the marks they leave. Crocodiles accumulate bones in depositional environments that promote fossilization (Njau and Blumenschine, 2006). They were also abundant in most depositional environments that captured fossil assemblages spatially associated with early hominids (Brochu and Storrs, 2012).

Actualistic studies

Actualistic work with living Crocodylians has firmly established their role not only as modifiers of bones but also as primary contributors to paleoanthropologically relevant assemblages (Baquedano et al., 2012; Davidson and Solomon, 1990; Drumheller-Horton, 2012; Njau, 2006, 2012; Njau and Blumenschine, 2006; Thompson et al., 2015; Westaway et al., 2011). Perhaps the most important finding of the initial actualistic work on modern crocodiles was that many of the marks produced are individually indistinguishable from mammalian carnivores and hominids with stone tools. Crocodile feeding behaviors do leave some specific bone modifications that are highly distinctive relative to a large repertoire of potential mimics (Table 1), allowing accurate diagnoses in moderate to large fossil assemblages when a contextual/ configurational approach is used. (Binford, 1981a; Domínguez-Rodrigo et al., 2010; White, 1992) is employed.

Methods

Illustrations and photos of crocodile bite marks were produced from an experimentally derived collection of crocodile-bitten bones aggregated under controlled conditions (Njau, 2006, 2012; Njau and Blumenschine, 2006). Using ammonium chloride to coat the bones in a long-known paleontology and archaeology photography technique called the "Williams Process" (Ridgway, 1938), we rendered the surfaces of the croc-chewed bones an opaque, pure white that revealed all subtle detail of the modifications. We then used multidirectional, non-diffuse lighting with yellow and blue filters. Using image processing software we converted the color images to black and white, each of the color channels converted separately to enhance contrast. Using these images as a background, we then traced the marks to emphasize the diagnostic elements of the bone modifications. The illustrations and photographs they were based on are presented in Figures 1 and 2.

Discussion

Crocodylians have relatively small stomachs and regularly kill animals larger than they can devour (Cott, 1961; Doody, 2009). They also compete aggressively for subdued prey when hunting in groups, frequently violently dismembering a kill. Crocodiles amputate body parts and partially crush them, but do not use their teeth for producing a food bolus. Rather they swallow partially crushed animals and animal parts without prolonged chewing (Busbey, 1989). Crocodiles pulverize swallowed food during digestion, leaving feces without recognizable bones (Fisher, 1981).

Carcass parts not swallowed are often left behind by crocodiles when dropped in the chaos of group feeding (Njau and Blumenschine, 2006). These remains end up in river, lake, and waterhole environments commonly inundated by sediment-laden floodwaters. Fluctuating water tables in

Crocodylian modifications	Mammalian Carnivores	Stone tools	Reptiles	Trampling	Avian carnivores
Shoulder marks	NR	Y	NR	Y	NR
Multiple, fine, parallel striations within main groove	NR	Y	Y	Y	NR
V-shape cross section mark	NR	Y	Y	Y	Y
Periosteal crushing/ subcambial spawling, sometimes with associated striations and/or V-shape cross section mark	Y[1]	Y	NR	NR	NR
Bone flake removal usually associated with deep pit and/ or fracture on midshaft	NR	Y[2]	NR	NR	NR
Multiple fine parallel striations across broad area of bone	NR	Y	Y	Y[3]	NR
Drag-snags	NR	Y	NR	NR	NR
Pivoted V-shape cross section mark	NR	NR	NR	NR	NR
Pivoted V-shape cross section mark	NR	NR	Y	NR	Y
Hook marks (scores)	NR	NR	Y	NR	NR
Pits	Y	Y	Y	Y	NR
Bisected pits or marks	NR	NR	NR	NR	NR
Striation pivots	NR	NR	Y	NR	Y

Table 1. Crocodylian modifications compared to other agents of bone modification that leave similar marks. Y=present; **NR**=not reported. [1] Mammalian carnivores can cause removal of periosteum and damage to underlying bone surfaces, but adjacent striae, internal striae, associated V-shaped marks are not documented. [2] Hammerstone percussion can flake away bone from cortical surfaces. [3] As figured in Dominguez-Rodrigo et al. (2009) and Dominguez-Rodrigo et al. (2010), areas of parallel striae or microabrasions that are wider than about 1.5 cm are highly characteristic of trampling but not reported for other agents. (Behrensmeyer et al., 1986; Blumenschine, 1995; D'Amore and Blumenschine, 2009; Domínguez-Rodrigo et al., 2009; Domínguez-Rodrigo et al., 2010; Drumheller-Horton, 2012; Fetner and Sołtysiak, 2013; Njau, 2006, 2012; Potts and Shipman, 1981; Shipman and Rose, 1983a, 1983b; White, 1992)

regions with seasonally flooded, crocodile-infested river and lake environments cause calcium carbonate precipitation (Achyuthan et al., 2007) that can subsequently enhance fossilization. Bones dropped by Crocodylians are thus well-represented in fossil records from wetland settings, and these bones often bear characteristics of crocodile feeding traces, including distinctive bite marks produced by sharp carina along tooth edges (Njau, 2006; Njau and Blumenschine, 2006).

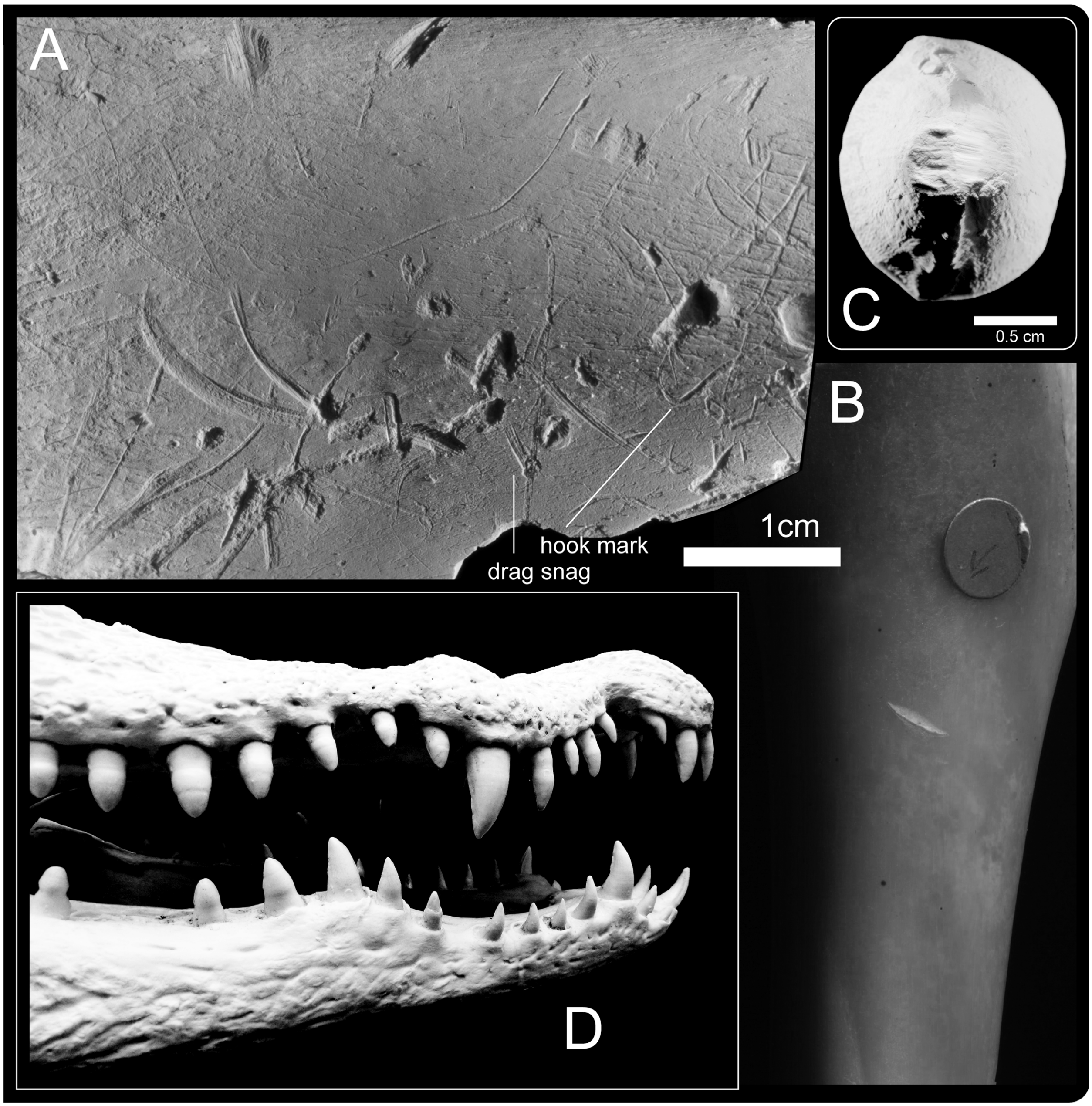

Figure 1 Crocodile bitten bones with (A), a dense cluster of diverse modifications and (B), a single, isolated pseudo cut. Posterior crocodile teeth often have dull, irregular, worn or fractured occlusal surfaces *in vivo* (C and D) and anterior teeth often retain strong, sharp blade-like crests (carina) mesially and distally. Crocodile mandible and maxilla are not scaled.

One of the most well known feeding-associated behaviors is the "death roll," whereupon a Crocodylian spins in the water in order to dismember prey grasped between its teeth. This involves rapid full-body pivots. Crocodiles also use side-to-side head swinging motions accompanied by strong biting and crushing when attacking prey and removing flesh and body parts for consumption (Busbey, 1989).Upon cessation of prey struggle, Crocodylians routinely clamp prey between their teeth and wait for extended periods of time without further manipulation, resuming biting and crushing again only if the prey renews its resistance.

Teeth of crocodiles, particularly anterior and freshly erupted teeth, have sharp mesial and distal crests (carina) that function to grasp, cut, and thereby disarticulate (Poole, 1961). Cheek teeth are used in crushing and anchoring prey (see Figure 1). These lack distinctive carina and tend to wear flat, exhibiting more deeply corrugated, buccolingually-linear occlusal striations as wear progresses (Drumheller-Horton, 2012; Njau, 2012). Swallowing is initiated using a series of upward head thrusts accompanied with repeated crushing bites that position the imminently-consumed animal portion in the pharynx and esophagus (Busbey, 1989).

Patterned crocodile feeding behaviors include side-to-side head thrusting, death-rolling, passive and prolonged clenching in powerful jaws, upward head thrusting to position food in the rear of the gullet, and crushing in preparation for swallowing. This feeding sequence regularly leaves highly distinctive patterns of bone modification (Drumheller-Horton, 2012; Njau and Blumenschine, 2006; Westaway et al., 2011). Figure 2 illustrates a diversity of modifications to cow bones bitten by crocodiles under controlled actualistic conditions and presents a description of these modifications.

Bisected pits, rounded pits, and **jagged pits** are associated with crushing, grasping, and holding between teeth. Anterior crocodile teeth tend to leave **bisected pits**, and cheek (distal) teeth are more rounded, stout, and frequently worn. These teeth impose extreme compressive force, often producing **rounded pits**. **Jagged pits** often lack morphology that can be related to tooth position. Torsional forces applied against incompletely gripped bones that slip on clasped jaws during side-to-side head thrusting and clockwise-to-counterclockwise death roll pivots appear from actualistic experiments to leave **hook marks (scores)**, **pivoted drag-snags**, **striation pivots**, and **pivoted psuedo-cuts**. **Drag-snags**, **periosteal/subcambial spalling and bone flaking**, **pseudo-cuts,** and **striations** of various orientations and depths are all associated with the above-described behaviors and tooth anatomies, and are common in crocodile-modified bone assemblages.

Any of these modifications can contain internal parallel and sub-parallel striations within the main mark. Such striations have long played a central role in the interpretation of hominid butchery activities (Blumenschine, 1995; Blumenschine and Selvaggio, 1988; Bunn, 1981; de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005; McPherron et al., 2010; Potts and Shipman, 1981). Once thought to be diagnostic of stone tool butchery (as opposed to mammalian carnivore chewing) (Blumenschine and Selvaggio, 1988; Potts and Shipman, 1981; Thompson et al., 2015), the finding that they are ubiquitous in crocodile modified assemblages (Njau, 2006; Njau and Blumenschine, 2006) alters

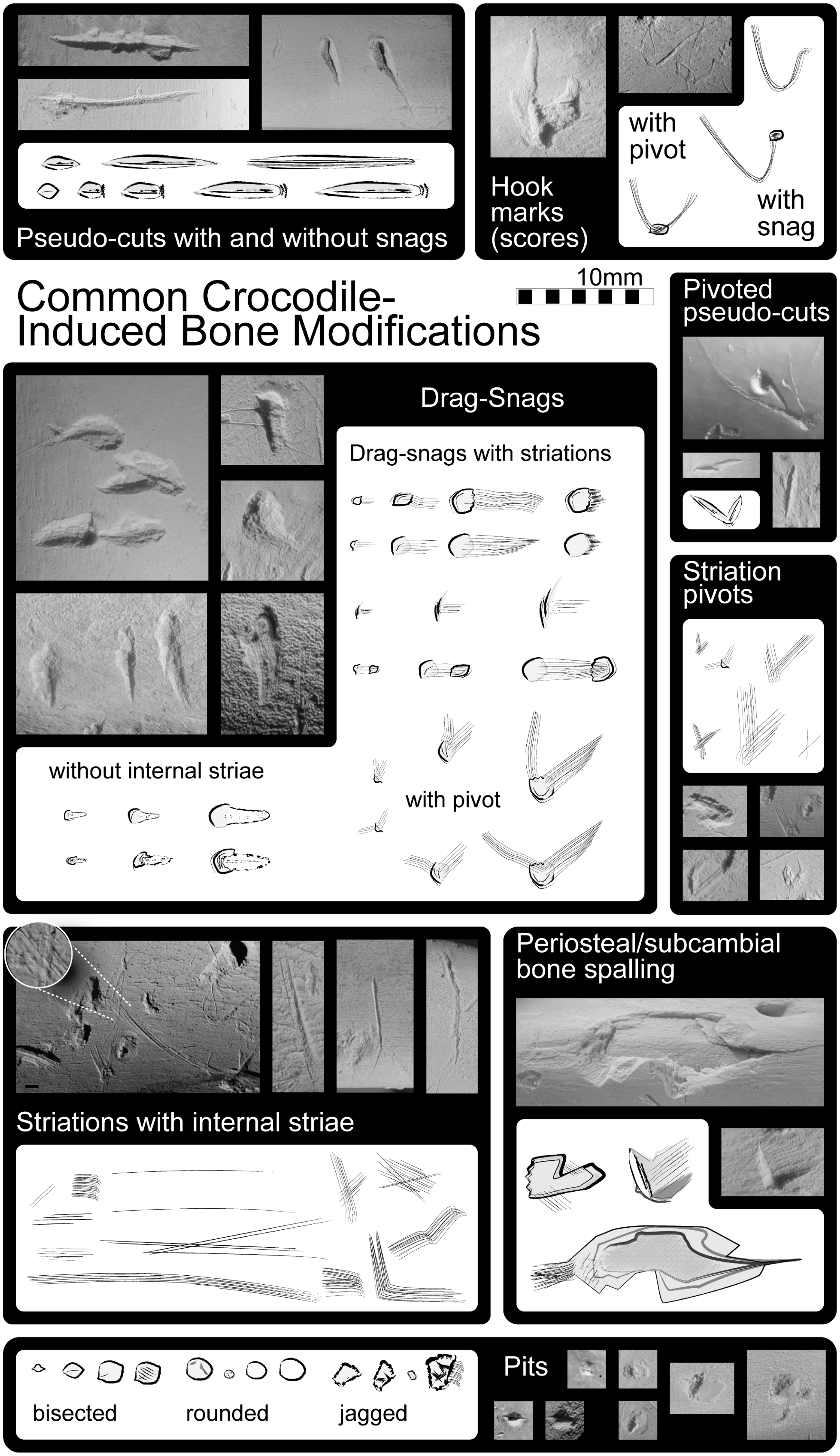

Figure 2 Illustrations and photographs of common crocodile-induced bone modifications. Photographs are of bite marks made by crocodiles on bovid bones in a controlled setting.

the way that many assemblages must be interpreted.

The description of crocodile-induced above provides a helpful tool, but it is necessary to note that bone assemblages modified by Crocodylians usually display combinations of these overlapping modification types. This makes a typological taxonomy or an identification key impractical. The crocodile behaviors are patterned (death rolling, clench-gripping, bone-crushing, side-to-side head-shaking, swarm-feeding, and frequent dropping of body parts) and this leaves typical combinations of features that can be diagnostic. In spite of equifinality, a combination of **bisected pits,** deep **rounded pits**, **pivoted drag-snags**, and **striation pivots** on an individual bone or in a larger assemblage is good evidence of Crocodylian activity; these types of bone modifications have not been demonstrated to occur with stone tools or mammalian carnivores. **Hook marks (scores)** and **pivoted psuedo-cuts** are also highly distinctive, although similar marks can be produced by Komodo dragons and avian scavengers (D'Amore and Blumenschine, 2009; Fetner and Sołtysiak, 2013).

Crocodile bite force is strong, over 3 times stronger than *Crocuta crocuta* (Erickson et al., 2012), the spotted hyaena. Crocodiles can alter bone surfaces just as effectively as other powerful agencies, even heavy stone tools. Excessive, deep **periosteal/ subcambial spalling** and/or large cortical bone-piercing pits (punctures), sometimes associated with removal of bone flakes and deep cracks, make such marks resemble stone tool-induced percussion traces (Erickson et al., 2012). The bite force attained by sharp anterior teeth is sufficient to create deep **pseudo cuts** with V-shaped traces on bone surface.

Some other crocodile marks mimic modifications induced by stone tools. **Jagged pits** induced by Crocodylian teeth can resemble percussion pits produced by hammerstones used to extract marrow, although differential diagnosis may be possible with functionally associated percussion striae produced by repeated hammerstone/anvil pairings (White, 1992). Crocodile-induced pits can also resemble tooth pits produced by mammalian carnivores (Sala and Arsuaga, 2013; Sala et al., 2014). **Drag-snags** can look very similar to stone tool-induced percussion pits and associated striae and can also mimic mammalian carnivore damage. Crocodile-induced drag snags frequently retain long, arching, curving, or pivoting marks with deep grooves/striae. The maintenance of significant bite force in unison with torsional force often gives crocodile marks a distinctly ‘plowed’ appearance, where adjacent bone has been dramatically compressed, crumpled, peeled, or flaked-off (Figure 2). Configurations of multiple trampling marks on a single bone can prove to be indistinguishable from those produced by the teeth, jaws, and behavior patterns of feeding crocodiles.

Although Crocodylian tooth marks are common on limb bone parts unprotected by overlying soft tissue during biting, they can occur virtually anywhere on any bone (including in hollows such as the olecranon fossa of the humerus). Crocodile-induced bone modifications depend upon the intensity of the behaviors described above. As a result, they can be broadly distributed across bone surfaces. Indeed, dense configurations of typologically diverse, randomly oriented marks can exist on a single crocodile-bitten bone (See Figures 1 & 2). Considered together, a pattern of such marks can be very diagnostic. However, most affected bones from crocodile-modified assemblages have only one or a few tooth marks. Without context, such isolated crocodile modifications are frequent ly indistinguishable from those made by other agents (Sala and Arsuaga, 2013; Sala et al., 2014).

Regarding the differential diagnosis of trampling versus Crocodylian damage, areas of parallel striae (or microabrasions) that are wider than about 1.5 cm along the perpendicular axis of the modification field (see Domínguez-Rodrigo et al. 2009, Figure F, and Domínguez-Rodrigo et al., 2010, Figure 9) (Domínguez-Rodrigo et al., 2009; Domínguez-Rodrigo et al., 2010) are not reported outside of trampling contexts. In crocodile-modified assemblages, such wide abrasion fields are exceptional, and thinner fields of parallel striae or microabrasions are common.

These observations, all derived from actualistic experiments, illustrate the roots of equifinality: because modifications result from the basic physics of contact and movement between bone surfaces and hard/irregular objects, these different agents can all leave similar marks. However, in assemblages of bones, and often even in single whole-bone specimens, only a contextual/configurational approach allows sound diagnoses between crocodile modifications and those made by mammalian carnivores, trampling, or stone tools. Beyond just individually diagnostic marks, crocodiles produce a distinctive pattern of modification, as described above.

Crocodylian modifications are increasingly recognized in prehistoric assemblages, from the Mesozoic through the Pleistocene (Boyd et al., 2013; Erickson et al., 2012; Erickson and Olson, 1996; Jacobsen, 1998; Longrich et al., 2010; Noto et al., 2012; Thompson et al., 2015). In some cases, modifications initially interpreted as cut marks produced by hominids have been questioned (Domínguez-Rodrigo et al., 2010; Domínguez-Rodrigo et al., 2012; Njau, 2012), The description of modifications presented here was inspired by the increasing recognition of Crocodylians as modification agents in the prehistoric record, a phenomenon especially important in zooarcaheology. The logical error of presuming that an archaeological assemblage is the uncomplicated representation of a single prehistoric moment has been called the 'Pompeii premise' (Ascher, 1961). The venerable Lewis Binford invoked this phrase often in addressing over-interpretation, and he described "integrity" as the degree to which single versus multiple agents are exclusively responsible for patterning on an archaeological assemblage (Binford, 1981a, 1981b). When modified bones come from depositional contexts where Crocodylians and trampling are demonstrated or highly likely, taphonomic deductions that hominids made the tools demand exceptional evidence for support. Thus, tool use claimed based on bone modifications found in archaeology-free sediments that date to earlier than the first *in situ* tools are controversial, specifically because crocodile biting and animal trampling are known to be capable of matching bone modifications made by stone tools (Andrews and Cook, 1985; Behrensmeyer et al., 1986; Domínguez-Rodrigo et al., 2009; Domínguez-Rodrigo et al., 2010; Domínguez-Rodrigo et al., 2005; Njau and Blumenschine, 2006; Olsen and Shipman, 1988).

Conclusion

As shown empirically from experimental studies (Baquedano et al., 2012; Drumheller-Horton, 2012; Njau, 2006; Njau and Blumenschine, 2006; Westaway et al., 2011), single, isolated bone modifications types produced by a stone tool, trampling, or a carnivorous mammal can be easily matched within an assemblage only ravaged by crocodiles. Equifinality of modification therefore becomes an imperative consideration when interpreting bone modifications from contexts with low integrity, and certainly if the assemblage derives from fossil crocodile-bearing deposits. This is particularly true for occurrences in time and space whence hominid agency is not testified by *in situ* lithics, or if there is an abundance of Crocodylian remains/traces in the stratigraphic/depositional neighborhood (i.e. Malassé et al.. 2016; McPherron et al., 2010, 2011). Fortunately, many crocodile-induced marks are distinctive and diagnostic (Drumheller-Horton and Brochu, 2014; Njau and Blumenschine, 2006). The description of marks outlined here, which includes new terminology for Crocodylian-specific modifications and a formalization of terms used in the literature, aims to provide a basis for the ongoing actualistic work that will be necessary to eliminate as much equifinality as possible for fossil bone assemblages from archaeological and non-archaeological sites (James and Thompson, 2015; Njau, 2012). Great care must be taken when diagnosing cut marks where crocodiles are present but no stone tools are found.

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*Corresponding author: Henry Gilbert, henry.gilbert@csueastbay.edu

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