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News and Views

Five more arguments to invalidate the passive scavenging version of the carnivore-hominid-carnivore model: a reply to Blumenschine et al. (2007a)

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Introduction

In our original paper (Domínguez-Rodrigo and Barba, 2006), we clearly stated that the version of the carnivore-hominid-carnivore model that we falsified was the model most commonly defended, and the only one experimentally replicated, by Blumenschine and his collaborators and students (Blumenschine, 1986, 1995; Selvaggio, 1994; Capaldo, 1995, 1997, 1998; Blumenschine and Pobiner, 2006): hominid scavenging of kills that had been partially or completely defleshed and then abandoned by felids, with a third stage of consumption by bone-destroying hyenas after hominid abandonment. Blumenschine et al.'s (2007a) claim that the carnivore-hominid-carnivore model also embodies scavenging fully fleshed carcasses from natural deaths and confrontational scavenging of partially or fully fleshed carcasses or "power scavenging" (Bunn, 2001) is not applicable to our debate. We never claimed to test the untested (perhaps untestable) "power scavenging" hypothesis. Blumenschine (1986) established a feasible scavenging niche for hominids based on the possibility of scavenging marrow-bearing bones from felid-defleshed kills in riparian environments. This was called the carnivore-hominid-carnivore multi-patterned mode of site formation, which was experimentally replicated by Selvaggio (1994) and was employed to explain the formation of the FLK *Zinjanthropus* bone assemblage (Blumenschine, 1995). This model is the *only* one we challenged in our research.

Despite the evidence we presented against this passive scavenging hypothesis, Blumenschine et al. (2007a) assert that it remains unfalsified. Here we discuss the scientific evidence that they provide as support for their assertion.

Carnivore tooth-marking

Contrary to Blumenschine et al.'s claims, we never confused Selvaggio's "carnivore-first" and Blumenschine's (1988) "carnivore only" models. We discarded Selvaggio's model because it does not reproduce the felid-hominid-hyenid model defended by Blumenschine (1986, 1995) and Capaldo (1995, 1998). Selvaggio used multiple carnivore taxa in her carnivore-hominid and carnivore-hominid-carnivore experiments. Her sample was obtained by lumping carnivore types, bone-crunchers and flesh-eaters alike. Hominids could theoretically scavenge from flesh-eating felids but not from bone-crunching canids and hyenids. This interpretation is the core of Blumenschine's (1986) seminal work on the ecology of scavenging. Yet Selvaggio ignored the basic premises of the carnivore-hominid-carnivore scenario: that is, that hominids were scavenging *complete* (marrow-bearing) long limb bones from *felid* kills, since scavenging from canids and hyenids in African savannas yields few opportunities to exploit marrow-bearing long limb bones.

Therefore, the use of Selvaggio's tooth mark frequencies by Blumenschine et al. (2007a) is misleading. The values she

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reports are much lower than those reported for assemblages created and modified only by hyenas (Blumenschine, 1988, 1995) and higher than those reported exclusively for felids (Domínguez-Rodrigo et al., in press) probably because she is mixing high tooth-marking carnivores with low tooth-marking ones[1]. If hominids were acquiring the *complete* bones from her sample (with tooth mark frequencies <50%), specifically those derived from just felids (presumably, significantly less tooth marked), they would be even further reducing the frequency of tooth marks by breaking open the bones and generating multiple fragments. This is supported by recent studies by Domínguez-Rodrigo et al. (in press) showing that tooth mark frequencies on midshafts from carcasses first consumed by felids (cheetah, leopard, and lion), and then broken by humans, are *<15%*, even lower than frequencies in hammerstone-carnivore scenarios in which hyenas were secondary scavengers.

Furthermore, neotaphonomic studies of cut marks (Domínguez-Rodrigo, 1997) suggest primary access to carcasses by hominids at FLK *Zinjanthropus*. The only contradiction to this was the high percentage of tooth marks reported by Blumenschine. The revised lower frequency presented by us, together with the similar tooth mark sizes across all carcass sizes,[2] which match the size of hyena tooth marks (Domínguez-Rodrigo and Barba, 2006), reject the felid-hominid-hyenid model as an explanation for the assemblage at FLK *Zinjanthropus*.

Tooth-marking and microbial bioerosion

As Blumenschine et al. (2007a: 421) correctly state, ‘‘the term [bioerosion] is used predominantly to describe modifications made by microbes and marine invertebrates,’’ but they do not mention that these modifications are mostly documented on geological materials and marine animals (see extensive references at http://www.wooster.edu/geology/bioerosion/BioerosionBiblio.pdf), and that many different processes have been lumped together under the term ‘bioerosion.’ Neumann (1966:92) defined bioerosion as ‘‘the destruction and removal of consolidated mineral or lithic substrate by the direct action of microorganisms.’’ Most bioerosion research has been conducted on calcium carbonate substrates, such as limestone. The modifications produced may involve the chemical modification of substrates, but frequently they do not. Biotic agents producing microscopic boring and tunneling in bones, morphologically similar to that documented in geological contexts, have also been referred to as bioerosion (see summary in Davis, 1997). The tunneling has been explained by the action of hyphae of saprophytic fungi (Marchiafava et al., 1974; Hackett, 1981; Piepenbrink, 1984, 1986; Child et al., 1993; Greenlee, 1996; Sharmin et al., 2003). However, tunneling is merely one of many processes that may affect bones at both the micro and macroscopic levels. For this reason, most researchers studying bone modification by microbial agents do not usually refer to these modifications as bioerosion. In the list of references provided by Blumenschine et al. (2007a), only Davis (1997) and Trueman and Martill (2002) do so. Some prefer other terms, such as microscopic focal destruction (Hackett, 1981; Child, 1995; Hedges et al., 1995). Similar processes at the macroscopic level, such as tunneling by earthworms or roots, are, for example, referred to as bioturbation (Denys, 2002).

None of the previous applies to the variety of macroscopic marks generated by metabolites of fungi and bacteria, which is why we did not previously include the extensive literature on bioerosion that Blumenschine et al. (2007a) cite. It is important to stress that the marks we report are not caused by single hyphae of individual fungi, which is the case in most of the references cited by Blumenschine et al. (2007a: 422), who argue that fungal marks can only generate ‘‘surface channels and pits [that] have widths typically around 10 microns, with examples up to 100 microns.’’ By contrast, we described macroscopic biochemical marks (measuring several mm in width and having lengths that vary from a few mm to even more than 1–2 cm) caused by the excretion of metabolites by fungal colonies. These marks show oval shapes (probably representing the original fungal colonies) and ‘‘score-like’’ shapes. This is likely due to the fact that mycelial fungi use plant roots (mycorrhizae) as support while accessing the bone, and the metabolites produced by them (through their hyphae) create bone surface modifications reflecting the shape of these roots (see ‘‘Protocols’’ below). Most of these marks do not involve macroscopic boring or tunneling. In this case, the term ‘‘biochemical’’ is far more specific than bioerosion and includes moderately to intensively erosive processes such as modification by digestive acids (Fernández-Jalvo et al., 2002), as well as other processes such as bone staining and degradation that do not involve any ‘‘erosion’’ at all.

Protocol of our experiments with fungi

Blumenschine et al. (2007a: 422) believe there are deficiencies in our experiments and ask about ‘‘the source and initial surface condition of the bones, the conditions to which the box of bones were exposed, and the manner in which the authors securely linked staining and bone erosion to fungal colonization as opposed to many other organisms known to bioerode bone.’’ Here we provide a description of the experiments, further outlined in a recent book (Domínguez-Rodrigo et al., 2007).

[1] One reason that contributes to Selvaggio’s high tooth-marking frequencies is that she lumps together carnivore-broken bone fragments and complete bones prior to human processing. Fragments are more tooth-marked than complete bones, and hominids would ignore them since they would be resource-free. Furthermore, most of her experiments are based on small carcasses, more easily fragmented (and tooth-marked) by felids than the larger carcasses represented at FLK *Zinjanthropus*.

[2] If caused by felids, tooth mark size would be expected to vary according to felid type; that is, small carcasses would be attributed to leopards or cheetahs (or similarly sized saber-tooth felids), and large carcasses would be attributed to lions (or *Homotherium*). Felid type can be well-differentiated in the dimensions of tooth pits on dense cortical bone as shown by Selvaggio and Wilder (2001) and Domínguez-Rodrigo and Piqueras (2003). Also, primary access by felids would contradict the interpretation that carcasses were fleshed, as has been shown by the study of cut marks.

Twenty defleshed (with metal knives) and demarrowed (with a metal butcher's cleaver) equid and bovid bones were placed in a cardboard box in a dark storage room (beginning February 2003) to assess bone decay in the absence of the bone-modifying agents usually present in soils (e.g., pH, microbes, insects). When placed in the box, bones were mostly clean with some miniscule fresh scraps of tendon, periosteum, and flesh remaining; they had been broken (leaving clean-cut chopping marks), washed, partially dried, and were checked to ensure that they bore no biochemical or other marks, and that butchery-marks were properly identified. After three months, spongy structures identified as fungi were observed around the patches of periosteum, as well as on some bare bone patches. In subsequent months, these structures decayed and had disappeared completely by the eighth month, leaving behind dark stains, which were easily distinguishable from the surrounding surface. In 36 cases, surface color but not cortical structure had been affected; however, a few marks ($n = 4$), particularly the more elongated ones, began flaking the outermost cortical layer.

The marks shown in our previous paper (Domínguez-Rodrigo and Barba, 2006: Fig. 2) were analyzed for bacterial and fungal content, together with 8 more marks showing bone discoloration. The bone specimens had several dark oval-shaped marks. When observed under the microscope, these marks showed a dark central nucleus that became lighter towards the periphery. A total of 10 micro-samples were obtained from 10 different marks with a probe containing a sterile solution. Samples were obtained only from marks analyzed, and also from the mark-free surface as a control. The mark samples were placed in isolated Petri plaques where fungi and bacteria could develop. The plaques were incubated for a few days so that the microbial components of the samples could grow.

After 48 hours, all plaques (except those controls containing samples from the mark-free surfaces) showed rapid growth of mycelial fungi (Fig. 1). Bacteria were also documented, though at much lower frequencies, in all samples. The fungi documented belong to a diversity of taxa (Table 1). This proves that the dark staining of the bone surface corresponds to the action of diverse fungi. The dark pigmentation of some marks indicates prolonged exposure of the area to the acidic action of fungi. The degree of contamination is expressed as CFU (Colony Forming Units)/cm^2, where CFU corresponds to the average number of units forming colonies of fungi or bacteria. The values shown in Fig. 1 indicate the degree of contamination observed both in agar-based (nutrient-rich) plaques, as well as laminated plaques.

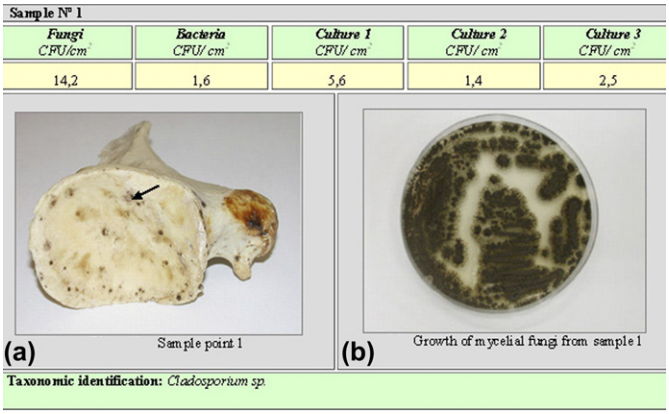

Fig. 1. Example of biochemically-analyzed macroscopic marks experimentally created on bone by fungi and bacteria. The probe of the mark (1a) sampled remaining fungi and they were reproduced in the laboratory (1b). See text for explanation.

Table 1
Micro-organisms identified in several marks on the surface of the experimental bone and the metabolites excreted by them which produced these marks

Micro-organisms identified in the 10 samples		
Fungi	*Caldosporium* sp. *Penicillium* sp. *Aspergillus niger* *Mucor* sp. *Penicillium chrysogenum* *Alternaria* sp. *Actinomyces* sp. *(fungal bacteria)*	
Bacteria	*Micrococcus* sp. *Bacillus cereus* *Bacillus subtilis* *Micrococcus roseus*	
Micro-organism	Metabolic substance excreted	Intensity of development in the sample analyzed
Cladosporium	Acetic acid, lactic acid, proteases	High
Penicillium	Citric acid, oxalic acid, lactic acid lipases	High
Aspergillus	Citric acid, oxalic acid, lactic acid, fumaric acid, malic acid	Moderate
Alternaria	Acetic acid, amylases, proteases	Moderate
Actinomyces	Lactic acid, piruvic acid, acetic acid	High
Bacillus	Lactic acid, gluconic acid, amylases	High
Micrococcus	Lactic acid, acetic acid, lipases	Moderate

We conclude that the bone surfaces are affected by dark circular marks caused by mycelial fungi, with bacteria playing a decidedly smaller role. Both fungi and bacteria produce metabolites (listed in Table 1) during their growth, which are excreted on the bone. These metabolic products include: organic and inorganic acids, enzymes, pigments, and toxins. The marks are the result of these metabolites biochemically altering bone surfaces. These metabolites change the pH of the surfaces onto which they are excreted, usually towards more acidic values. The development of metabolites on the analyzed bones was so brief that micro-fissures and flaking developed only minimally. However, as witnessed by the examples in which flaking had already begun, we infer that had they been exposed to metabolic acids over a longer period of time than that documented in the present study, the cortical surface would have begun more intense exfoliation and marking (see Fig. 2).

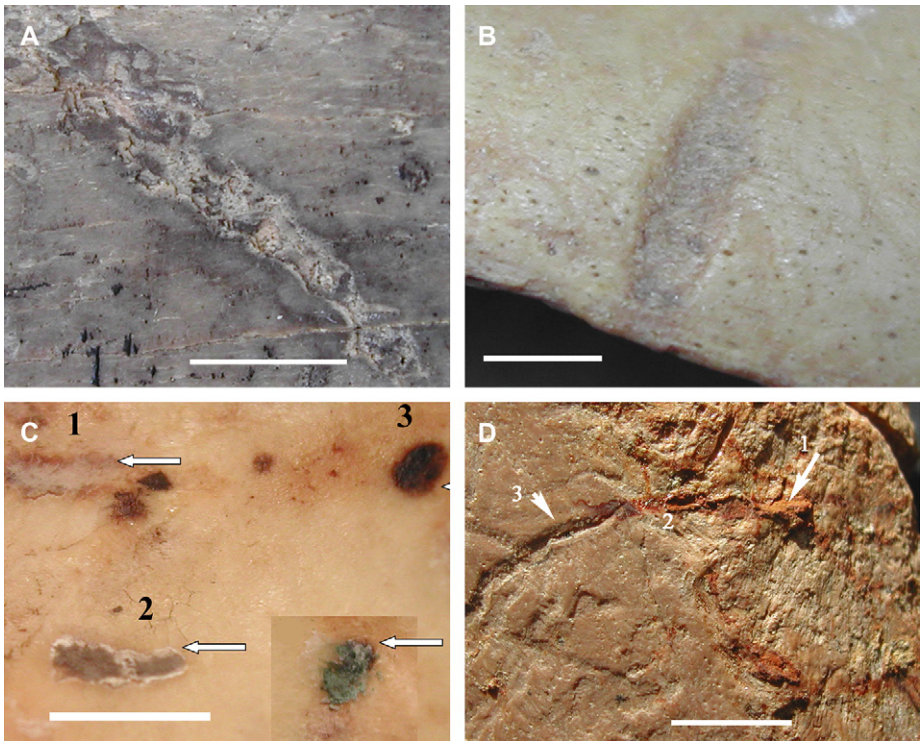

Fig. 2. A, Specimen from FLK *Zinjanthropus* identified by Blumenschine (1995) as having a typical tooth mark, as identified by him, and used by Domínguez-Rodrigo and Barba (2006) as an example of a biochemical mark. B, Tooth score created by hyenas and post-depositionally invaded by fungi from the Maasai Mara hyena den collection (National Museums of Kenya). Notice the numerous differences between marks A and B. The fungi-invaded tooth mark (B) preserves a U-shape and symmetrical trajectory, has walls on the sides showing the mark was created by crushing, and the inside of the groove is affected by discoloration where fungi were deposited; these traits all indicate that the mark was created by a carnivore. By contrast, the biochemical mark (A) preserves an asymmetrical shape and irregular trajectory, shows no crushing but rather partial exfoliation, with the original cortex visible inside parts of the groove, and has discoloration both inside and outside the mark outline; these traits suggest that it was biochemically created. C, Examples of experimentally-created biochemical surface modifications on modern bone (1–3). In one of the marks (3), fungi were documented to have appeared during the experiment, and later stained the underlying bone surface. These marks appear as pits and scores with different degrees of modification (reflected in different color tones). Arrows show the diagnostic color outline, which contrasts with the interior of the mark (Domínguez-Rodrigo and Barba, 2006). D, Biochemical score caused by a root in an archaeological specimen from the middle Pleistocene site of Cuesta de la Bajada (Spain): 1, carbonated remains of root; 2, staining of the bone surface by the root; 3, groove caused by prolonged exposure to the action of the root fungi, showing winding trajectory, asymmetry of groove, and discoloration of the inside of the groove and of the mark outline. Scale = 1 cm.

Our study demonstrates that fungi and bacteria can create macroscopic marks on bone surfaces, marks that show strong similarities to those we identified on the FLK *Zinjanthropus* fossils (Figs. 2 and 3).

What are biochemical marks?

Blumenschine et al. (2007a) claim that tooth marks invaded by fungi could be misidentified. They further claim that our low frequency of tooth marks at FLK *Zinjanthropus* could be the result of not identifying tooth marks that were stained by fungi as secondary colonizers. They interpret biochemical marks as "tunnels," "channels," and as microscopic pitting far smaller than tooth pitting, concluding that "the anatomical patterning and morphology of microbial bioerosion on bone surfaces are also not evocative of carnivore tooth-marking" Blumenschine et al. (2007a: 422). Contrary to this interpretation, biochemical marks can also be macroscopic, especially those caused by fungal and bacterial metabolites, as we have experimentally demonstrated. The process generates cortical exfoliation with or without staining and very frequently affects the outermost layers of bone. There is also a substantial literature recognizing both microscopic and macroscopic pitting, such as the so-called "dissolution pits" which can overlap and become even larger than tooth pits (Pathou-Mathis, 1989; López González et al., 1997; Henderson et al., 2002; Arnett, 2003; Trueman et al., 2004; Gaudzinski, 2005; Yravedra, 2006).

In our previous paper (Domínguez-Rodrigo and Barba, 2006), we outlined a clear set of criteria derived from archaeological and experimental samples[3] to differentiate tooth marks from biochemical marks. These criteria can also be used to differentiate tooth marks with staining caused by fungi or bacterial invasion from biochemical marks (Fig. 2). Useful criteria for distinguishing tooth marks include: the depth of crushed cortical layers, an overall symmetry of the mark's trajectory, a lack of exfoliation, staining of the inside of the mark (and not just the

[3] These criteria were established using samples of known carnivore damage from experiments by Domínguez-Rodrigo for tooth marks and the samples of biochemical marks presented here. Biochemical marks were also documented in prehistoric bones under root casts (see Fig. 2) from the middle Pleistocene site of Cuesta de la Bajada (Spain), currently under study.

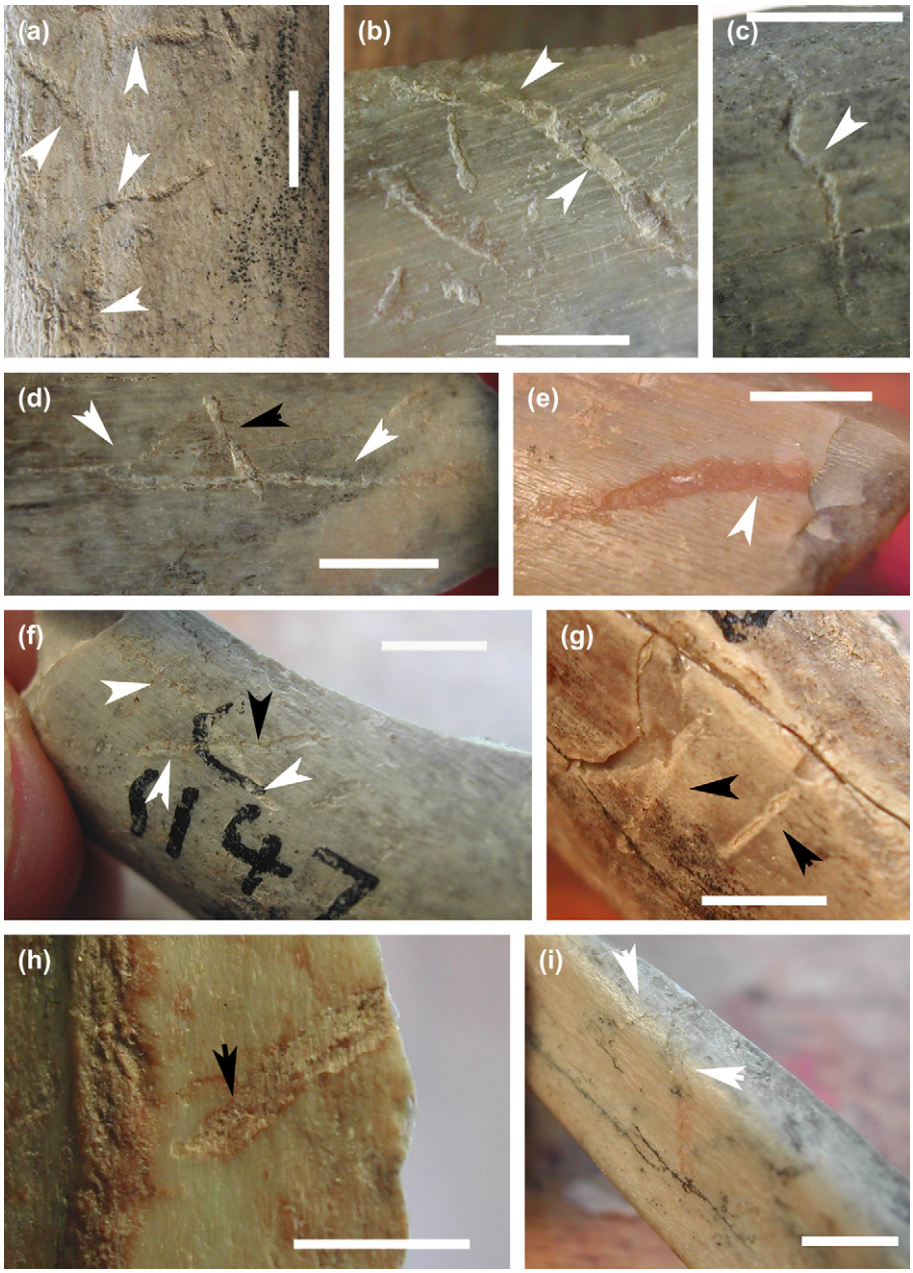

Fig. 3. Some specimens from FLK *Zinjanthropus* identified by Blumenschine (1995) as having tooth marks and argued by Domínguez-Rodrigo and Barba (2006) to be biochemical marks caused by the action of mycelial fungi either in colonies (pits) or attached to plant roots (scoring). Most of these marks could probably also be referred to as bioturbations (Denys, 2002). The specimen numbers are: C1180 (a), D70 (b), K16 (c), E60 (d), C769 (e), C1147 (f), B139 (g), F189 (h) and C894 (i). Notice the winding trajectory and variable width of scores (arrows in a, c, i), the discoloring of the existing upper layer (arrows in b, d, e, f, g), the interrupted trajectory of the groove, with the absence of crushing and existence of exfoliation of upper layer(s) (black arrows in d, f, g, h), and the same exfoliating process with winding trajectory of groove and incipient dendritic pattern covering more than one side of the bone (i). Scale = 1 cm.

outline of the groove, as would be the case with biochemical marks), and in particular, the clearly U-shaped cross-section of the tooth mark *versus* simple shallow exfoliation in a biochemical mark. We can confidently claim that in no instance did we mistake a stained tooth mark with a strictly biochemical mark (see Fig. 2 for an example of their differences).

Blumenschine et al. (2007a: 424) suggest that we "did not identify tooth-marking if a specimen bore alleged 'biochemical marks,' a standard that will always underestimate tooth mark frequencies." In fact, their interpretation of our data (Domínguez-Rodrigo and Barba, 2006: Table 1) is wrong. In several instances we identified both tooth marks and biochemical marks on the same specimen. In our initial sample of 725 long limb bone specimens from the FLK *Zinjanthropus* collection, we discarded 26 (3%) only because of ambiguity in the identification of marks. We confidently identified 97% of the sample used by Blumenschine (1995)—containing several specimens that bore both tooth- and biochemical marks—which makes the sample more than ample for comparison with experimental frameworks.

Blumenschine et al. (2007a) also assert that our low tooth mark identification is somehow related to our lower percussion mark identification. We stress that these frequencies result from two very different causes. Despite the fact that Capaldo provided a ''virtually identical estimate of percussion mark frequencies on long bone midshafts to that obtained by Blumenschine in his independent analysis of FLK *Zinjanthropus*,'' (Blumenschine et al., 2007a: 424) this does not preclude the possibility that both may be over-identifying percussion marks. Following Turner (1983), Pickering and Egeland (2006) divided percussion marks into two classes: pits (associated with striae) and striae fields, and they reported that most percussion marks created by them were pits (>80%). This is especially true in midshafts where 85% were pits. Striae fields without pits are a common signature of trampling, as we have recently documented in a modern hyena den (work in progress). All the faunal assemblages from Olduvai Bed I and Bed II bear traces of trampling and abrasion to various degrees (Domínguez-Rodrigo et al., 2007). This made us cautious in the identification of percussion marks, and a few microscopic striae fields were not identified by us as percussion marks because they could also correspond to natural abrasion marks. Until this equifinality issue is resolved, we advocate a more conservative approach to the identification of percussion marks, instead of overestimating these marks as we contend that Capaldo did at FLKN 1–2, where we confirmed only 12 pits with associated microstriations, in contrast with the hundreds of specimens with isolated striae fields that he identified as percussion marks (Blumenschine et al., 2007b).

Misidentifications of tooth marks at FLK *Zinjanthropus*

Regardless of these other arguments, the most important issue is that in their reply to our paper, Blumenschine et al. (2007a) have not provided evidence to disprove our conclusion that they mistook biochemical marks for tooth marks. They say that ''crushing'' is clearly associated with tooth marks, but a large portion of the marks Blumenschine identified at FLK *Zinjanthropus* shows no crushing but only exfoliation (and in several cases, only discoloration). They provide no evidence that bones we identify as biochemically altered showed actual tooth marks. They did not even comment on one of the most controversial issues raised by us: that Blumenschine's ''typical'' tooth mark is nothing more than a biochemical mark (Domínguez-Rodrigo and Barba, 2006: Fig. 7), and several other marks in our Figures 3–5 remain unjustified by them. In our 2006 paper, the following images show specimens identified by Blumenschine (1995) as exhibiting tooth marks (catalog number in parentheses)[4]: Figures 3c and 3e (C1073), 3f (C1217); Figure 4b (B396), 4c (C729), 4d (C894); Figure 5a (D18), 5c (B147), 5e (M87). These are just a small sample of the marks we maintain were misidentified as tooth marks.

Blumenschine et al. (2007a) argue that we missed some references in our previous paper, that our experiment was of limited validity, and that we may not have been able to identify all the tooth marks in the FLK *Zinjanthropus* collection, but they do not provide compelling evidence that they identified tooth marks correctly. We believe that clear scientific evidence should be provided to support any interpretation, and we have, therefore, provided additional evidence to support our claims. In contrast to Blumenschine et al. (2007a), we provide some empirical evidence and show some more examples of marks that we argue Blumenschine (1995) misidentified (see Fig. 3). We ask readers to form their own opinion of the marks shown in these figures and the debate at hand.

[4] None of the specimens had marks other than those shown on these images that could potentially be interpreted as tooth marks.

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