Hominid butchers and biting crocodiles in the African Plio–Pleistocene

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Abstract

Zooarchaeologists have long relied on linear traces and pits found on the surfaces of ancient bones to infer ancient hominid behaviors such as slicing, chopping, and percussive actions during butchery of mammal carcasses. However, such claims about Plio–Pleistocene hominids rely mostly on very small assemblages of bony remains. Furthermore, recent experiments on trampling animals and biting crocodiles have shown each to be capable of producing mimics of such marks. This equifinality—the creation of similar products by different processes—makes deciphering early archaeological bone assemblages difficult. Bone modifications among Ethiopian Plio–Pleistocene hominid and faunal remains at Asa Issie, Maka, Hadar, and Bouri were reassessed in light of these findings. The results show that crocodiles were important modifiers of these bone assemblages. The relative roles of hominids, mammalian carnivores, and crocodiles in the formation of Oldowan zooarchaeological assemblages will only be accurately revealed by better bounding equifinality. Critical analysis within a consensus-based approach is identified as the pathway forward. More experimental studies and increased archaeological fieldwork aimed at generating adequate samples are now required.

Keywords: Zooarchaeology | Oldowan | Taphonomy | Cutmarks | Equifinality

Traces on bone surfaces play an important role in documenting humanity’s ever-broadening subsistence base. Prominent recent claims of stone tool use at ~3.4 million years (Ma) (1, 2), occupation of Eurasia by 2.6 Ma (3), and hominids in California at ~130 Ky (4) employ such evidence.

Experimental and naturalistic investigations in the 1980s led to a claimed dichotomy between U-shaped marks left on bones by “carnivore” teeth, and V-shaped traces (cutmarks) inflicted by stone tools (5, 6). Assertions that internal striation and shoulder marks were uniquely associated with cutmarks (7) were augmented by similar claims for percussion pits and associated striation (8, 9). Today these features are treated as “signature criteria” (10) and widely thought to accurately diagnose stone tool butchery.

Oldowan bone and lithic assemblages from Olduvai (~1.8 Ma) and other excavations have been intensively analyzed for decades and used in considerations of human evolution. Indeed, fundamentally different inferences about early hominid carcass procurement and butchery (e.g., hunting vs. scavenging) have been derived from such analyses of the very same assemblages (11, 12). Zooarchaeologists have largely followed the orthodoxy that stone tool modifications to bone surfaces are accurately diagnosable from mammalian carnivore damage, and routinely use carnivore to mean mammalian carnivore.

However, a few zooarchaeologists persistently doubted the proclaimed tool/carnivore dichotomy and cautioned against overreliance on microscopic techniques (13–15). Lyman consistently and prophetically cautioned that equifinality could cripple inferences about ancient behavior (16). Early experiments even revealed that animal trampling could mimic cutmarks (17). But with the tool/carnivore dichotomy meme embedded, paleoanthropological attention increasingly focused on subsistence.

It is now recognized that “linear marks” and other bone surface modifications can result from interacting agents that range from people to plants (18). On the basis of the mark(s) alone, it is often difficult to distinguish among the modifying objects (the tooth surface, stone tool edge, or sedimentary particle) and their effectors (the bone chews, trampling animal, or hominid butcher). Decades of actualistic research have now demonstrated that equifinality cannot be reduced to insignificance with a few more technological advances or experimental studies (19). Indeed, rather than reducing equifinality, these studies have persistently shown the pervasiveness of equifinality.

This roadblock to knowledge is also a significant barrier to assessing claims about “archaeology” among living apes and monkeys (20). As the hominid fossil record pushed into the Late Miocene, living chimpanzees continued to be idolized as behavioral proxies for early hominids (21, 22). The discovery that chimpanzees break open nuts with wooden and stone hammers raised expectations that a technology even more rudimentary than the Oldowan would be found in >3.0-Ma deposits (23), inspiring an ongoing quest for mid–Pliocene artifacts and/or their bony traces.

Significance

The idea that early Australopithecus shaped stone tools to butcher large mammals before the emergence of Homo around 2 million years ago has excited both primatologists and archaeologists. Such claims depend on interpreting modifications found on the surfaces of fossil bones. Recent experiments involving the feeding of mammal carcasses to modern crocodiles have revealed that equifinality—the creation of similar products by different processes—is more important than previously appreciated by zooarchaeologists. Application of these findings to Ethiopian fossils casts doubt on claims for the earliest large mammal butchery and indicates the need for reassessment of all Oldowan-associated bone assemblages to determine the degree to which equifinality compromises earlier interpretations of hominid subsistence activities and their role in human evolution.


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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1716317114/-/DCSupplemental.
Two recent *Nature* cover articles proclaimed just such evidence. Dubbed "The First Cut," one cover featured a photo of linear marks on the surface of a small bone shaft fragment eroded from Pliocene Ethiopian sediments at Dikika (1). Controversy immediately arose because the marks were interpreted by the discovery team as "unambiguous stone-tool cut marks for flesh removal and percussion marks for marrow access." (p. 857). Critics interpreted the traces as trampling damage (24, 25) rather than butchery marks. The second cover, "The Dawn of Technology," shows two allegedly shaped stones from Kenya dating to ∼3.4 Ma (2). Were stone tools made and used by hominids to butcher large mammals much earlier than previously thought?

**Crocodiles: Equifinality Expanded**

In his seminal 1981 book on the meaning of Paleolithic assemblages, Binford (13) recognized four types of "tooth marking." He noted some equifinality regarding carnivore tooth vs. stone tool marks on bones. He did not mention crocodiles as bone modifiers. Even the most comprehensive current atlas of bone modification agents (18) emphasizes the effects of crocodile digestion more than the marks that crocodile teeth leave on bones of their prey.

Paleontologists working on Plio–Pleistocene African bone assemblages have long recognized crocodile presence, and indeed, diversity (26). However, the taphonomic impact of crocodiles was only recently recognized by zooarchaeologists, first with Njau (27) and Njau and Blumenschine (28)'s publications of experimental results from captive crocodile feeding. Their actual work followed the earlier traditions described above, focusing on establishing signature criteria by which crocodile activity could be uniquely identified, rather than emphasizing how their bite traces can mimic marks classically and exclusively attributed to defleshing, disarticulation, and percussion with stone tools.

Njau's findings complement data from fields spanning alligator taphonomy (29), forensics (30), and Mesozoic paleontology (31), further raising this specter of equifinality. The revelation that traces left by crocodile teeth can match those previously thought to be diagnostic of stone tool butchery is a significant expansion of equifinality that threatens the binary orthodoxy employed by African zooarchaeologists to sort technological hominids.

Our observations on experimentally modified modern bones and fossils (below and SI Appendix, SI Text, Figs. S1–S12, and Table S1) confirm how pervasive this equifinality can be. We apply our findings to three time-successive occurrences of modified bones from the Plio–Pleistocene paleontological record of the Middle Awash study area of Ethiopia. Our team's sustained research efforts there are summarized in refs. 32–34. We present below, in chronological order, modified mammalian bones from sediments dated to ∼4.2 Ma, ∼3.4 Ma, and ∼2.5 Ma. Our findings have broad implications for claims of hominid butchery of large mammals in waterside Plio–Pleistocene African settings.

This issue has so far been underappreciated by zooarchaeologists working on small assemblages from Plio–Pleistocene sediments deposited in proximity to crocodile-infested swamps, rivers, and lakes. We call for a more comprehensive, critical, assemblage-level zooarchaeological reassessment of the relatively small samples of modified fossil bones from Plio–Pleistocene African waterside localities.

**Crocodile Modification of Middle Awash Fossils**

Middle Awash Asa Issie locality 2 dates to 4.2 Ma (33). The remains of ∼50 *Australopithecus anamensis* specimens are among ∼650 genetically identifiable vertebrate fossils collected.

Specimen ASI-VP-2/420 is a distal hominid humeral shaft whose fracture morphology and adherent matrix indicate perimortem breakage (Fig. 1 and SI Appendix, Fig. S3).

A deep, partially matrix-filled, steep-sided, bifurcate, V-shaped, pivoted pseudocut with internal striations (see ref. 35 for terminology) marks the distolateral diaphysis. More superficial, U-shaped marks lie a few millimeters proximally. A 20-μm-long, V-shaped groove with terminal snap pits at both ends lies 3 mm distal to the bifurcate mark. A large, matrix-filled, jagged-edged pit is nearby. Taken in isolation, several of these modifications could be interpreted as evidence of stone tool percussion and slicing. However, given the context of this fossil and the characteristics and distribution of ancient surface modifications on even this small fragment, the preponderance of evidence leads us to conclude that these modifications are likely crocodile induced, rather than made by stone tools (which are unknown at any occurrence of this antiquity).

The Pliocene Maka MAK-VP-1 locality is spatially larger and paleontologically richer than Asa Issie (34). A total of 753 genetically identifiable surface and in situ vertebrate specimens is currently available from the Maka Sand Unit, a stratum also containing the embedded SHT tuff at ∼3.4 Ma. The assemblage from these fluvialite sands includes 27 *Australopithecus afarensis* specimens as well as crocodile remains and many other fossils exhibiting evidence of being bitten in the form of diamond-shaped (bisected) pits, hook scores, and pivoted drag-snags (ref. 35 and SI Appendix, Figs. S4 and S5; such modifications are also present on bones from penecontemporaneous paleontological localities in the nearby Hadar study area).

MAK-VP-1/3 is a left hominid humerus recovered in 1990 (ref. 34 and Fig. 1 and SI Appendix, Fig. S4). Surface preservation is imperfect, but ancient modifications include several deep linear
marks with V-shaped cross-sections and multiple internal striae. Scanning electron microscope (SEM) images were immediately acquired and assessed by zooarchaeologists expert in mark identification. These experts diagnosed the Maka marks as having been made by stone tools. However, mark distribution did not correspond to an anatomically expected pattern of tissue removal during butchery. Other fossils with obvious crocodile modifications were also collected from this stratum (SI Appendix, Figs. S6 and S7), and no stone artifacts have ever been found in this or adjacent strata. Given this discordance, we withheld judgment for two decades, concerned that equifinality might prevent identification of the modifying agent. Njau’s initial results (27) and our subsequent analyses have now combined with contextual data to allow attribution of the surface modifications on the Maka hominid humeral shaft to perimortem crocodile biting. Fig. 2 illustrates our inferences regarding analogous crocodile modification on penecontemporaneous vertebrate fossils from Dikika (1) and Hadar.

The third Middle Awash case reassessed for the possibility of crocodile modification involves faunal elements from the ~2.5 Ma Hadar A.L. locality 1 necessary to interpret and illustrate as exhibiting stone tool percussion and chopping damage (Fig. 3 and SI Appendix, Figs. S6 and S7). An in situ equid femur was described as exhibiting “... stone-tool cut marks indicative of dismemberment and filleting...” (ref. 36, p. 627). Seven years before the perspective of Njau’s experimental work with crocodiles became available (27), these modified fossil bones were interpreted within the then-dichotomous zooarchaeological paradigm of mammalian carnivore chewing vs. butchery with stone tools. Our inferences were widely endorsed (24, 39), but here we reassess these specimens in light of the experimental work now available on crocodile bone modification (context and specimens detailed in Fig. 3 and SI Appendix, Figs. S6–S11).

The unbroken but heavily modified Bouri fossilized equid femur BOU-VP-11/15 recovered from fine, water-lain sand shows marks similar to those made by crocodiles in actualistic and fossil contexts (27, 40). These marks include drag-snags (with and without striations), pseudocuts (with and without snags), and bisected perforations into thin cortex near the epiphyses. Slice marks with internal striae are deeply V shaped. Given its near-shore context, the overall patterning of marks, and the absence of in situ artifacts, we judge that crocodile biting created many—perhaps even all—of the marks on this equid femur.

The associated ungulate tibial midshaft specimen BOU-VP-11/14 is more difficult to interpret (Fig. 3 and SI Appendix, Fig. S8). We now appreciate that internally striated, irregular pits associated with deep negative flank scars on outer midshaft surfaces can result from crocodile biting and that these cannot always be distinguished from hammerstone percussion. Associated V-shaped linear pseudocutmarks made by crocodile teeth also frequently bear internal striae (27, 35). The BOU-VP-11/14 modified tibial shaft shows a plethora of damage types. More than 40 separate modifications of this 18-cm-long midshaft include curvilinear and straight pseudocuts as well as U-shaped grooves and V-shaped linear striations. Irregular pits with internal striations are present. Bisected pits expected of crocodile tooth perforation are absent, but thin cortex and underlying cancellous bone best suited to capture these are unavailable on this nonepiphysial midshaft.

Many of the marks on the Bouri tibia fall squarely within the widened zone of equifinality between crocodile biting and stone tool modification. Differential diagnosis is therefore problematic,
Bone surface modifications on ~2.5-Ma-old fossilized ungulate bones from Bouri, visualized by photographs, SEM, and confocal microscopy. (A–E) The BOU-VP-11/14 bovid tibia showing numerous marks. (F–H) The BOU-VP-11/12 alcelaphine mandible exhibits long curvilinear marks across its postero-medial surface. Before experimental work on crocodile bite marks (refs. 27, 28, and 35 and SI Appendix, Figs. S1 and S2), such deep, V-shaped, internally striated marks and forceful production of jagged pits with internal striae and large external cortical flaking were considered diagnostic of stone tool use by early hominids and differentiated from marks made by mammalian carnivores. However, even the limited currently available experimental data on crocodylians indicate that assessment of individual marks on small fragments drawn from inadequate samples of fossil bones (1) can be problematic. See text for a detailed consideration of the equifinality plaguing behavioral interpretation of such specimens and SI Appendix, Figs. S7–S13 for a broader consideration of spatial, stratigraphic, and taphonomic contexts.

Both at the level of the individual mark and across the entire element. Even if the dubious proposition that individual marks can each be unambiguously attributed to one agent or another, the relative timing of their formation would remain in doubt without mark overlap. Hence, we cannot attribute the marks on this BOU ungulate tibial shaft with certainty to either hominids, crocodiles, or to a potential contribution of both agents acting in sequence.

The BOU-A21 occurrence within BOU-VP-12 is located ~250 m to the NW (SI Appendix, Fig. S9). It presents similar interpretative challenges. An excavated medium-sized alcelaphine bovid mandible (BOU-VP-12/11; Fig. 3 and SI Appendix, Fig. S10) found in situ with hominid remains was noted to bear “... three successive, curvilinear striae on its postero-medial surface; these striae are unambiguous cut marks made by a sharp stone flake, presumably during tongue removal...” (ref. 36, p. 627). Reassessment of this specimen must now also consider both crocodile biting and trampling as possible additional modifiers.

There is polishing accompanied by superficial random striae adjacent to the long, linear marks on this Bouri fossil mandible. Such modifications are indicative of abrasion before burial, and some of the other excavated specimens also show such superficial damage. For the mandible, mark superimposition indicates at least some surface abrasion, most likely from trampling. The induced random striae contrast strongly with the set of much longer, subparallel, curvilinear marks that contain multiple (up to eight) straight and continuous internal striae (Fig. 2 and SI Appendix, Fig. S10). These marks are ancient (still matrix obscured in places), shallow, wide, and U shaped in profile, but physical and hydraulic abrasion can lower the relief and change the cross-sections of stone tool cutmarks (41). Despite the lowered overall relief from abrasion, obvious parallel shoulder marks accompany the two longest marks.

The overall length and pattern of the curvilinear marks on the BOU-VP-12/11 bovid mandible’s postero-medial surface has not yet been matched in either trampling or crocodile studies. The anatomical placement of the marks is consistent with tongue removal. Other specimens from the surface adjacent to this excavation in silt-grained sediments also bear marks (SI Appendix, Fig. S11). Those eroded from nearby outcrops (SI Appendix, Fig. S12) provide additional evidence of butchery in the form of more typical stone tool cutmarks. Although these Hatayae Member specimens exhibit marks apparently diagnostic of stone tool butchery, associated in situ artifacts (the sien qua non of hominid presence) are still lacking (SI Appendix, Fig. S13). Accurate assessment of the relative roles of trampling, crocodile biting, and butchery by hominids in the Hatayae Member will obviously require larger fossil samples.

These Middle Awash examples demonstrate that the limitations of equifinality and small sample size must be recognized when assessing claims regarding early hominid butchery and subsistence. Claims of stone tool use at Dikika (1) were based on marks on two small midshaft fragments from a surface collection (Fig. 2). They have been questioned by authors who also note that: “... Gona and Bouri stand as the earliest, best evidence of the tool-assisted reduction of large animal carcasses by hominins...” (ref. 24, p. 20933). We concur with that conclusion, but also agree with those whom they criticize (25). Among the latter, James and Thompson aptly note that a mere 14 specimens predating 2.0 Ma have even been claimed to have unequivocal stone tool cut and percussion marks (42), and as shown above, equifinality makes it impossible to eliminate crocodiles as the agent responsible for some of these marks.

Beyond Equifinality. Njau’s results (27) and ours indicate that stone tool cutmarks can be mimicked by crocodile biting as well as by trampling. Our work with fossils confirms that initial studies have not yet adequately explored the range of damage—the universe of equifinality—potentially created by crocodile biting. The equifinality already appears to extend beyond cutmarks to encompass even the irregular pits containing internal and external striae fields previously thought to be associated exclusively with hammerstone percussion. We predict an even greater expansion of equifinality when more crocodile experimentation with larger, hungrier animals and subsequent blind testing are conducted (43).

Meanwhile, it seems appropriate to abandon the quest to completely eliminate equifinality in many zooarchaeological contexts—particularly the ancient tropical and subtropical waterside locations in which crocodiles were potential bone modifiers. Simply dismissing equifinality by boldly asserting “high confidence” in mark diagnosis (1, 44) is a perilous pathway given the complex sedimentary and ecological envelopes containing the evidence of early hominids and their behaviors.

Logistically, the smaller the bone fragments themselves—and the smaller and more selective the fossil assemblage they comprise—the greater the risk that equifinality will lead to misinterpretation. The inferential potential of paleontological bone surfaces compared with their modern, relatively unaffected
actualistic counterparts is often further compromised by pro-
cesses such as pre- and postfossilization surface alterations (in-
cluding bioturbation); hydraulic and aeolian erosion; matrix
adhesion (often with attendant bone spalling); and damage
through matrix removal, molding, photography, and study.

How should these lessons be applied more broadly across
the earliest archaeological sites claimed to document large
mammal butchery with stone tools? Most occurrences are from
water-lain sediments and none of them have adequate
zoarchaeological samples (42). Even larger Oldowan assem-
blages from well-known and intensively analyzed younger oc-
currences such as Olduvai FLK 22 (“Zinj”) are plagued by
similar potential ambiguities. Each of these now requires more
holistic reconsideration at several analytical levels, in part be-
cause published “cutmark” data from this universe of sites were
compiled under the now dubious proposition that marks could
be attributed in dialectic fashion either to hominin activity or to
mammalian carnivores.

Methodologically, the zooarchaeological attraction to re-
ductionist quantitative emphasis on individual marks persists.
For example, a recent review of bone modification studies re-
 mains focused on the individual mark, proposing “standardiza-
tion” as the key to progress and lauding a typological approach
to mark identification based on “archetype” marks. The review
mentions crocodiles only by way of citation (45). Another recent
study concludes that three modern surface topography visuali-
ization methods yield equivalent results, but again fails to address
equifinality by ignoring crocodiles (46). The quest for techno-
logical “solutions” to removing equifinality also obviously fails if
actualistic and prehistoric sample sizes are inadequate. It is al-
ready evident that focus on the individual mark will always be a
pathway to the long-recognized but often ignored roadblock of
equifinality. There is probably not a technological fix to
this problem.

The quest to eliminate equifinality through bottom-up ap-
proaches built on reductionist character quantification of indi-
vidual mark attributes too often fails when published claims of
diagnostic criteria (47) are falsified by new actualistic studies.
Even top-down, assemblage-level assessments still rely on in-
vestigator decisions too often based on inadequate compensation
for equifinality in small samples.

Even if an assemblage is different from the next, so searching
for a formulaic analytical “menu” for universal application seems
pointless. Even a linear investigative process in the assessment—
stepping from marks, to specimens, to assemblage—is not the
best way of building the broad knowledge that we seek. Rather,
assessment and inference based on any fossil bone assemblage is
best accomplished through a series of feedback loops. Rather
than relying on inadequately established signature criteria, an
iterative hierarchical assessment of the individual mark, the
preserved bone, the assemblage, and the broader sedimento-
logical/associational/distributional contexts and patterns will be
the key to moving beyond equifinality.

Binford (13) recognized this and advocated an approach often
termed “configurational” (although this term has deeper roots
and different meanings in evolutionary biology) (48). Dominguez-
Rodrigo et al. (24) described the configurational approach as
“holistic assessment” while ascribing claimed butchery marks on
two tiny Pliocene bone fragments to trampling damage. But
Binford’s approach was not just holistic in terms of assessment of
a bone within its provenance and assemblage contexts (see ref.
49 for expositions of these). Neither was it linear. It recognized
“... the potential feedback of applying a methodology and then
investigating the archaeological record in new ways...” (ref. 13,
p. 282). As Lyman prophetically appreciated, if we fail to build
“... multivariate interpretive models ... at large inclusive scales,
we may have a great deal of difficulty figuring out the behavioral
meaning of cut-marked bones of Plio–Pleistocene age...” (ref.
50, p. 1,731). As in historical sciences from forensics to astro-
physics, it is axiomatic that the more multistranded, adequately
verified, and independent the evidence, the more solid the built
inferences will be.

Equifinality will not be entirely eliminated at the level of the
individual mark on a bone. We therefore propose, at least for
occurrences in which crocodiles are potential agents of bone
modification, an approach that is configurational, broadly con-
textual (49), and comprehensive (51). Our goal should be what
E. O. Wilson has championed as “consilience” for each occur-
rence (52). In this regard, “context” thought of in the singular is
too simplistic and misleading to express the biophysical milieu in
which individual marks formed. A formal evaluation undertaken
via an iterative feedback process will usually be necessary in
circumstances where equifinality is a potential problem. For any
assemblage, such an iterative, cyclical, feedback approach cons-
iders each bone modification in the context of the bone frag-
ment, element, assemblage, geology, and ecology it occupies.
This approach will more accurately determine whether and how
hominids might have participated in the formation of any
prehistoric assemblage.

For tropical and subtropical waterside bone assemblages, the
consilience approach situates the question of butcher, cannibal,
or crocodile into a deeper and more comprehensive evidentiary
frame. In the legal forum, this is how forensic scientists help
prosecutors make their cases, whether the requirement is a
preponderance of evidence or establishment beyond doubt.
Asset assembly-level efforts to establish consilience as outlined above will not allow inferential robusticity without
adequate samples of fossil and contextual evidence. What can
currently be inferred soundly about hominin butcher before 2.0 Ma?
With the primary evidence still inadequate (42) nar-
rowly mark-focused approaches (53, 54), including recently
proposed “non-expert machine learning-based methods” (ref. 54,
p. 79) promise little illumination. Indeed, larger questions about
procurement, processing frequency across space and through
time, and myriad other important behavioral aspects remain in
the realm of speculation (55). Even for the iconic Pleistocene
FLK-22 (Zinj) occurrence excavated 57 y ago, Dominguez-
Rodrigo et al. ask: “Is there any other Plio–Pleistocene site
where the faunal assemblage could be identified as completely
(or mostly) accumulated and modified by hominins?” (ref. 56,
p. 260).

Nearly 40 y after serious taphonomic work began on Oldowan-
associated African Plio–Pleistocene bone assemblages, the big-
gest zooarchaeological challenge remains the notoriously small
samples of Plio–Pleistocene bone assemblages with insufficient
resolution—“consilience” and “resolution” (13). This barrier to knowledge produc-
ton is owed to several factors, ranging from the limited
availability of appropriate deposits to the inadequacy of field
exploration and from the increasing financial and career costs of
sustained field research (including excavation) to an academic
reward system increasingly linked to clickbait entertainment.
Worse, paleoanthropological funding is lavished on digital lab-
oratory technologies and quantitative methods even as vital
actualistic studies remain unconduted.

Only by redoubling archaeological fieldwork to generate ade-
quate samples, by conducting parallel experimental studies to
fully bound equifinality, and by critical analysis aimed at con-
silience can zooarchaeological studies generate more reliable
light on ancient events to allow a fuller assessment of the dy-
namics of interacting hominids, crocodiles, and other bone
modifiers whose combined actions produce the zooarchaeo-
logical record of hominin evolution.

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