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 consilience-based approach is identified as the pathway forward. More experimental studies and increased archaeological fieldwork aimed at generating adequate samples are now required.

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 Miocene 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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The authors declare no conflict of interest.

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See Commentary on page 13066.

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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 actualistic 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 ancient mammalian carnivore traces from marks made by 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 zooarcheologists 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 generically 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-mm-long, V-shaped groove with terminal snag 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 generically 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 (bifurcated) 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 cuts with internal striae and the deep, V-shaped profiles of most linear marks. Formerly thought diagnostic of cutmarks made by stone tools, such linear features are now known from crocodilian feeding experiments. Note that an interpretation of any one of these marks in isolation would lead to the impasse of equifinality described in the text. The anatomical, association, geochronological, stratigraphic, and sedimentological contexts of these hominid fossils are interpreted as constituting a preponderance of evidence that the modifications are best attributed to crocodiles. F and G are casts. See text and SI Appendix, Figs. S4 and S5 for further details.

**Fig. 1.** Bone surface modification marks on Pliocene hominid humeri from the Middle Awash study area, Ethiopia, visualized by photographs, SEM, and confocal microscopy. (A and B) The ∼4.2-Ma-old ASI-VP-2/420 distal humerus bears a jagged matrix-filled pit, shallow U-shaped grooves, and a long, straight score with snap pits at both ends. Straight, deep, V-shaped, intersecting linear marks with internal striae are illustrated. (C–F) The anterior surface of Maka humerus MAK-VP-1/3 exhibits linear bone modifications and bisected pits near its distal epiphysis. Note the presence of multiple internal striae and the deep, V-shaped profiles of most linear marks. Formerly thought diagnostic of cutmarks made by stone tools, such linear features are now known from crocodilian feeding experiments. Note that an interpretation of any one of these marks in isolation would lead to the impasse of equifinality described in the text. The anatomical, association, geochronological, stratigraphic, and sedimentological contexts of these hominid fossils are interpreted as constituting a preponderance of evidence that the modifications are best attributed to crocodiles. F and G are casts. See text and SI Appendix, Figs. S4 and S5 for further details.
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. S5 and S6), 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.

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 striations are deeply V shaped. Given its near-shore context, the overall pattern of marks, and the absence of in situ artifacts, we judge that crocodile biting created many—or 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, 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).

A reassembled bovid tibial midshaft from the surface of Bouri locality 11 was first interpreted and illustrated 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 third Middle Awash case reassessed for the possibility of crocodile modification involves faunal elements from the ~2.5 Ma Hatayae Member of the Bouri Formation (36). This small fossil collection was made within 500 m of remains attributed to Australopithecus garhi (37). Oldowan cores and flakes were found on the surface of nearby eroding sediments, but excavations failed to recover in situ stone tools. Abundant and in situ stone tools of even greater antiquity are present at Gona, <100 km to the north, associated with cutmarked bones (38).

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,
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 interpretive challenges. An excavated medium-sized alcelaphine bovid mandible (BOU-VP-12/11; Fig. 3 and SI Appendix, Fig. S10) found in situ with hominin remains was noted to bear “… three successive, curvilinear striae on its posteromedial 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 sine 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 modifers. 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 processes such as pre- and postfossilization surface alterations (including 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 zooarchaeological samples (42). Even larger Oldowan assemblages from well-known and intensively analyzed younger occurrences 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 because 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 hominid activity or to mammalian carnivores.

Methodologically, the zooarchaeological attraction to reductionist quantitative emphasis on individual marks persists. For example, a recent review of bone modification studies remains focused on the individual mark, proposing “standardization” 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 (44). Another recent study concludes that three modern surface topography visualization methods yield equivalent results, but again fails to address equifinality by ignoring crocodiles (46). The quest for technological “solutions” to removing equifinality also obviously fails if actualistic and prehistoric sample sizes are inadequate. It is already 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 approaches built on reductionist character quantification of individual mark attributes too often fails when published claims of diagnostic criteria (47) are falsified by new actualistic studies. Even bottom-up, assemble-level assessments still rely on investigator decisions too often based on inadequate compensation for equifinality in small samples.

Each Plio-Pleistocene assemblage is different from the next, so searching for a formulaic analytical “menu” for universal application seems pointless. Even a linear investigative process is often 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 considers each bone modification in the context of the bone fragment, 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.

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Supporting Information

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**SI Text**

**SI Materials and Methods.** Fossilized bones from all three Middle Awash Plio-Pleistocene occurrences described in the present study were initially examined in 1990 (and subsequently) by naked eye, then hand lens, and binocular microscope (Nikon SMZ645). Selected specimens were also evaluated via SEM and, more recently, digital microscope (Keyence VHX-600 3CCD). Images were generated by the latter instruments and standard digital photography under directional light.

We then assessed individual marks on selected specimens with a confocal profilometer. Molds were made with President MicroSystemTM (Coltene-Whaledent) regular body dental impression material after cleaning the fossil surfaces with cotton swabs soaked in distilled water (acetone was used for cleaning bone surfaces with consolidant or matrix). Positive casts were then poured using Epo-Tek 301 epoxy resin and hardener (Epoxy Technology). Multiple adjoining scans were taken at 20x magnification using a Sensofar Plu Neox Confocal Imaging Profiler housed in the Paleoanthropology Imaging Lab at the University of Tübingen. Scans were analyzed using the SensoMAP software, powered by Mountains Technology® from Digital Surf. Profiles of linear scores were taken at two loci along every linear groove, at 25%, 50%, 75% of the total length, plus the deepest point.

Fossil mark profiles were compared with marks from experimental crocodile feeding and stone-tool-assisted butchery. Profiler samples from Njau’s crocodile feeding experiments were analyzed as high-resolution casts (1, 2). Experimental butchery was conducted on a skinned sheep half-carcass (retaining hind limbs) with the intention of both disarticulating and defleshing. Simple flakes (some retaining cortical surface) were knapped by YS on rhyolite cobbles and were completely unmodified. Residual meat was removed from bones using standard maceration protocol—a 24 hr storage at 50° Celsius, followed by cleaning with a solution of 5% KOH, which does not affect the bone surface.

**SI Approaches to the identification and illustration of bone surface modifications.** The quest for methods to provide certainty of diagnosis at the level of the individual mark has been a long one in zooarchaeology. Early approaches at agent identification employed dental impression compounds to mold and then generate epoxy casts for visualization and measurement of linear groove cross-sections (3). Despite Binford and Stone’s warning of a “high-tech” craze (4, p. 472) four decades ago, adoption of SEM soon became the analytical and illustrative standard, allowing assessment of micromorphological attributes of individual marks (5-8). Later, hand lens magnification (10x-16x) under strong incident light, supplemented by low power binocular microscopy were suggested as adequate for systematic study of bone modification (9).

The more recent application of confocal microscopy and profilometry data (today’s faster and cheaper SEM substitute) in bone surface modification studies (e.g., 10) has further enhanced identification, visualization, and measurement of individual marks. However, such narrow, even microscopic focus on the dimensions and characters of each individual bone modification has still failed to overcome equifinality among the various modifying agents acting in prehistory (11).

A new 3D quantitative approach has recently been proposed as capable of capturing “previously unmeasurable diagnostic features of bone surface modifications (e.g., roughness, volume or microscopic differences in depth)” (10, p. 9), and thereby distinguishing among agents of bone modification. This new 3D quantitative method was claimed to accurately classify stone tool cut marks and mammalian carnivore tooth marks 97.5% of the time (10, p. 9). Even at the level of the individual mark, proponents of this method (10) did not include crocodylian modified bone to test the method’s efficacy at reliably distinguishing between crocodilian bite marks and cut marks inflicted by stone tools.

We employed this method to obtain high-resolution 3D quantitative data, and independently appraise the method’s diagnostic efficacy (12). Results from our pilot study using a similar instrument and software (including the Contour Analysis module) and following the same procedures detailed in (10) already indicate that the newly proposed 3D quantitative method is not entirely capable of sorting crocodile bite marks with V-shaped cross sections and relatively deep and narrow grooves from similar marks produced by stone tools (Table S1, Fig. S1). Despite the small size of our pilot samples, these already indicate the need for more rigorous testing of such methods using additional experiments. Whereas the approach does appear to standardize measurement, its narrow focus on the morphological attributes of the individual mark limits its ability to reduce equifinality.

We provide additional information on zooarchaeological, depositional, and configurational contexts of individual fossil specimens discussed in the main text in Supporting Information Figs. S1-S13, in which we provide additional illustrations of equifinality among different agents of bone modification, particularly crocodiles.
Fig. S1 Confocal profilometry scan and data from a single mark on the 2.5 Ma bovid tibia from Bouri depicted in the text Fig. 3E. (A) 3D model of mark; (B) “Studiable” (defined by Mountains(R) software for a stack of confocal scans rendered as an image, surface, or surface image ready to be further analyzed; and as “…a 2-D visual representation of x-y-z coordinates for each measured point” [10]) of mark with form of bone removed; (C) ‘Volume of a hole’ measurements of mark; (D) Distance measurements of mark; (E) Area of a hole from the profile extracted from the deepest point of the studiable shown in D; (F) Contour analysis showing opening angle and floor radius from the portion of the deepest profile that is highlighted on the “area of a hole” studiable shown in (E). Data presented in Table S1 were collected on individual marks using the same software, protocols, and functions, including the contour analysis.
Fig. S2. Modern crocodiles as bone modifiers. (A) A modern Crocodylus niloticus maxilla and mandible illustrate enormous size and shape variation among the teeth of even a single animal. Posterior teeth (B) more often have dull, irregular, worn, or fractured occlusal tips, whereas anterior and recently erupted teeth often retain sharper tips and blade-like crests (carina) mesially and distally (also see text Fig. 2 and Fig. S3 for fossil examples). As a result, even the teeth of a single crocodile are capable of making a wide variety of marks on bones. (C) A single modified bone surface that displays variety of marks known to have been produced by biting crocodiles in a controlled feeding experiment. These marks (reproduced with permission from Fig. 1, p. 4 of reference 2) include pseudo cuts with V-shapes as well as irregular pits that mimic stone tool hammerstone percussion pits. Taken in isolation (or on small fragments of limb and/or rib bone shafts), several of these marks would mimic stone tool contact. Encouraging attempts have been made to differentially diagnose the variety of marks already demonstrated to be made by crocodiles by a limited number of experiments (2). Additional experiments under more naturalistic conditions (and particularly with larger living crocodiles) will better circumscribe the range of bone surface modifications produced during crocodile feeding, and will likely expand the equifinality already evident.
Fig. S3. Bone surface modifications on the 4.2 Ma Au. anamensis left humerus (ASI-VP-2/420) from Asa Issie, Middle Awash, Ethiopia. (A) Anterior and posterior views of the distal left shaft. Note the ancient fracture and carbonate matrix still adhering to the radial fossa, and an irregular pit on the dorsal surface. (B) The dorsal surface of the fossil shows a double-ended drag-snag, several curvilinear, shallow, U-shaped grooves, and two intersecting linear grooves that are straight-sided and V-shaped in profile. Internal striae are present here as they often are in modern and fossil bones modified by crocodiles (text Fig. 2; Figs. S2-3). (C, D) Confocal microscopy images and profiles. For this hominid humerus, the variety of adjacent tooth pits, drag-snags, and hook marks provide context that makes an inference of crocodile agency most likely.
Fig. S4. Context and bone surface modification marks on the 3.4 Ma *Au. afarensis* humerus, (MAK-VP-1/12) from Maka, Middle Awash, Ethiopia. (A) The 1990 discovery of this specimen showed it to have eroded from the Maka Sand Unit, fracturing and scattering on the surface. The recovery operation resulted in 11 conjoint pieces (B) comprising most of the adult bone. Only two of these exhibit more diagnostic tooth pits. (C) The restored specimen in anterior view shows several linear marks described and illustrated in text Fig. 1. Here, the overall photograph, the obliquely illuminated high resolution plaster cast, the macro-photograph of the original fossil, and the SEM image show post-fossilization periosteal spalling. Note the microscopic longitudinal linear striae within the macroscopically illustrated linear mark. Had this humeral shaft been recovered without the two distal fragments, such marks might have been interpreted as evidence of Pliocene cannibalism rather than crocodile damage. It is obvious that the more completely preserved the fossil surface, the greater the chance that diagnostic modifications such as tooth punctures above trabecular bone will be captured. Because of equifinality, reliance upon a few marks on small shaft fragments absent a consilience approach to the overall context of the modification is not recommended for determining how bone assemblages are formed.
Fig S5. Inferred crocodile damage to a fossil ungulate humerus (MAK-VP-1/754) at the Pliocene MAK-VP-1 locality, Maka, Middle Awash, Ethiopia. (A) Bone modifications show the intensity of biting. (B) More magnification on the photograph and confocal microscopic images illustrates the wide variety of linear midshaft marks. Several match the marks on the Maka *Au. afarensis* humeral fragment illustrated in text Fig. 1 and Fig. S5, the hominid humerus collected from the same stratum in 1990.
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Fig. S6. Context of the BOU-VP-11/14 ungulate tibia and excavated BOU-VP-11/15 equid femur. The Hatayae Member of the Pliocene Bouri Fm. of the Middle Awash (~2.5 Ma) has yielded numerous modified bones. Following the 1997 discovery of *Au. garhi*, extensive archaeological surveys were followed by excavations. None of these excavations recovered stone tools from *in situ*, but yearly visits did encounter freshly eroded artifacts (e.g. the core tool shown in Fig. S13. (A) Highly modified mammal bones (B, C) were found on the surface of the BOU-VP-11 locality, ~500 meters SE of the *Au. garhi* cranial holotype (Fig. S9). These occurrences are atop the dated MOVT (Maoleem Vitric Tuff) (8) volcanic ash with indurated upper contact seen in (A) as a resistant horizontal band immediately underlying softer sandy sediment that yielded the fossils. (D-G) Excavations into this massive sandy horizon produced little additional fish and turtle bone along with a surface-modified equid femur. Some of its modifications were initially interpreted as stone-tool-inflicted percussion and cut marks when published in 1999 (8). Subsequent experimental studies of modifications made by modern crocodiles raise serious concerns about signature-criteria assessment of such individual marks (see text and Fig. S7 for details). The 1998 excavation into a similarly placed stratum at the partial hominid skeleton from BOU-VP-11 lies in the distance at the white vehicle shown in (G).
Fig. S7. Bone surface modifications of the BOU-VP-11/15 equid femur. Recovered in situ within an excavation adjacent to the BOU-VP-11/14 bovid tibia surface recovery location (Fig. S6), this nearly intact equid femur (A) (distal end at top) exhibits a plethora of bone modifications now known to be made during crocodile feeding activities. The presence of multiple linear scores with internal striations (D, F) initially led to the inference that this femur had been processed using stone tools (8). However, subsequent actualistic studies of marks made by crocodile biting demonstrated the production of linear marks with internal striations. These feeding experiments (1, 2, 14) allow a contextual assessment of the overall patterning of marks on the specimen (e.g., compare them with those on the Hadar equid tibia in text Fig. 3). We therefore now infer that many of the marks on the Bouri femur were made by ancient crocodile teeth. These include diagnostic drag-snags (E), as well as round (B) and bisected (C) tooth punctures through the thin cortex surmounting spongy bone at the metaphyses.
Fig. S8. Bone surface modifications of the BOU-VP-11/14 ungulate tibia illustrate issues of equifinality. (A) Four views of the tibial shaft show a diversity of linear and irregular bone markings. Crocodile feeding experiments have so far failed to replicate the deep ecto-cortical conchoidal fracture (B) (cast on right) and associated deep pits with associated internal striae (C) (cast on right) seen on the Bouri tibia (see also text Fig. 3 and Fig. S1) and initially interpreted as evidence of forceful stone hammer percussion. However, the equid tibia from Hadar illustrated in text Fig. S2 and the excavated equid femur in Fig. S7 bear similar traces alongside other diagnostically crocodilian damage patterns. Given these cautionary examples and the specimen’s lack of metaphyseal ends likely to capture diagnostic traces attributable solely to crocodiles, we conclude that modifications on this Bouri ungulate tibia fall into the zone of equifinality in terms of the agent(s) that made them. See text for details.
Fig S9. Context of the BOU-A21 hominid and fauna. An overview (view NNW) of the Bouri Formation’s Hatayae Member sediments encompasses the holotype *Au. garhi* cranial location (arrow on right) and the BOU-A21 partial hominid skeleton discovery (left arrow) both stratigraphically immediately above the ~2.5 Ma Ar/Ar dated MOVT volcanic marker horizon (the light-colored band dipping to the west). The 1996-97 discovery of associated hominid skeletal parts on the surface (at feet of standing person at lower left) led to comprehensive surface collections of additional hominid and faunal remains, followed by excavations that recovered *in situ* fossils. The most notable excavated finds are *in situ* hominid fossils spatially and stratigraphically associated with modified faunal bones, including an alcelaphine bovid mandible (text Fig. 2; Fig. S10).
Fig. S10. Surface modifications and context of the BOU-VP-12/11 bovid mandible illustrate issues of equivaility.
Successive curvilinear scores on the posteromedial parts of this alcelaphine mandible (A) were found partially covered by adhering carbonate matrix, and were interpreted as cutmarks made by stone tools (B). Anatomical placement and subparallel disposition of multiple linear striations documented within the long, parallel grooves seen in the SEM images of these marks support this conclusion. Because this fossil and some others from the excavation show fine random striations and polishing sometimes created by trampling of other animals, it is possible that agents besides hominin butchers were responsible for the observed modifications (although marks of such length, with such internal striae have not been documented in actualistic trampling cases; see main text for a more detailed discussion). Surfaces of spatially associated, anciently fractured medium size mammal bones from this horizon (B, C) are most often entirely obscured by adhering carbonate matrix, embedded within massive, silty, fine-grained sediments; only one of these fragments (C) was macroscopically rounded and edge-polished, showing that in addition to trampling and mammalian carnivore damage, fragments in the bone assemblage were only little subjected to hydraulic and physical abrasion before fossilization. Occurrences in South African cave breccia deposits with minimal integrity and resolution are behaviorally far less useful than such stratified, in situ assemblages (15). However, even relatively minimally-disturbed lakeside occurrences such as BOU A21 can also exhibit pre-fossilization modifications resulting from the actions of several biological and physical agents over weeks to years prior to burial. Differential diagnosis of among these modifications requires excellent bone preservation and careful preparation, large assemblages upon which to assess patterns of damage, and thorough actualistic experiments and adequate blind testing. Past events and relative agency (including hominin butchery) will only be accurately illuminated by such a balanced and comprehensive consilience approach. See text for details.
Fig S11. Small bone shaft fragment from the surface of the BOU A21 excavation. This fragment, seen here in SEM (A, B) and confocal (C) imagery, bears a short but deep, V-shaped (D) linear mark that would typically be considered to reflect ancient chopping motion of a sharp edge against fresh bone. Without additional anatomical context, it probably falls into the zone of equifinality between chopping marks left by stone tools and damage by crocodile teeth.
Fig. S12. The ventral surface of a large mammal rib shaft (cf. hippopotamid) found eroding from sediments above the MOVT within the BOU-VP-12 Hatayae Member locality at Bouri. The anatomical dispositions and individual characteristics of these successive marks are strong indicators of butchery with stone tools and contrast with marks left by alternative agents of bone modification.
Fig. S13. Surface artifact from BOU-VP-12. This specimen was found upon a resurvey of eroding outcrops ~70m WNW of the BOU-A21 locality and SSW the BOU-VP-12/130 Au. garhi holotype discovery location (see Fig. S9). It had freshly weathered from fine grained, near-shore sediments immediately above the MOVT sometime between our December 1998 excavations at BOU-VP-11 and its November 1999 discovery shown here. The unabraded stone tool is a core made on dark, welded volcanic material with phenocrysts. None of the Hatayae Member excavations have so far yielded stone tools in situ, probably due to the low artifact density on the seasonally inundated lake margin landscape, the rarity possibly related to the great distances of this location from raw material sources (8).
Table S1. Measurements of variables collected*

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*Measurements based on Plio-Pleistocene surface-modified fossils from the Middle Awash study area, experimental butchery using unmodified stone flakes, and crocodile bite marks from actualistic experiments; metrics collected on studiables generated by confocal profilometer and using protocols and software described in detail for a new 3D quantitative analysis proposed by Pante and colleagues (10).
SI Appendix

References


