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Faunal remains from Porc-Epic: Paleoecological and zooarchaeological investigations from a Middle Stone Age site in southeastern Ethiopia

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Abstract

The Middle Stone Age (MSA) sediments of Porc-Epic Cave near Dire Dawa, Ethiopia, have produced a large assemblage of archaeofaunal remains dating to the later periods of the Late Pleistocene. As one of the few MSA faunal assemblages from East Africa subject to detailed analysis, it provides rare insight into the foraging behavior of the early modern humans in this region. The MSA fauna include taxa that were not historically present in the area, with the occurrence of reduncines and alcelaphines indicating widespread grasslands and proximity to a perennial source of water. The faunal analysis examined several lines of evidence, including breakage patterns, surface modification, and skeletal-element representation. By incorporating comparisons with multiple actualistic data sets, the analysis of the assemblage demonstrates that, while the influence of carnivores and other biotic agents was evident, the faunal remains were accumulated primarily by hominid activity. The skeletal-element representation at Porc-Epic includes an abundance of high utility bones, in contrast to the predominance of "head-and-foot" elements documented at other MSA and Middle Paleolithic (MP) sites. The MSA occupants of Porc-Epic effectively exploited a wide range of prey with more emphasis on small- and medium-sized mammals.

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Introduction

Driven by efforts to understand the origins of modern humans, the last two decades have witnessed an increasing interest in both the behavioral and hominid fossil records of the Middle Stone Age (MSA). Archaeological evidence has been used to demonstrate the extent of complexity or "modernity" of human behavior vis-à-vis the fossil and genetic records (Stringer, 2002; Henshilwood and Marean, 2003). Since the onset of the debate about the origin of modern humans, the practice of hunting has been considered an important benchmark for modern human behavior, corresponding to

a more advanced technology and a well-organized social system. As a result, zooarchaeological analyses of late Middle and Late Pleistocene archaeological sites have become an important part of the efforts to understand the origin of modern behavior.

A detailed summary of zooarchaeological investigations into the subsistence strategies of early modern humans and Neandertals is provided elsewhere (Marean and Assefa, 1999). Current zooarchaeological models illustrate a wide range of interpretations of the faunal record. Based on observations of the "head-and-foot"-dominated skeletal-element profiles and related "reverse utility curves" from a number of archaeofaunal assemblages, Binford (1984, 1985, 1991) suggested the continuation of obligate scavenging of large mammals into the Middle Paleolithic (MP) and MSA. The analysis of faunal assemblages from four MP sites in Italy

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documented shifts through time from head-dominated to a more complete skeletal-element representation and from old- to prime-age-dominated prey-mortality profiles (Stiner, 1994). Klein (1989; Klein and Cruz-Uribe, 1983, 1996) noted contrasting patterns of prey-mortality profiles between the MSA and the LSA sites of southern Africa, argued to indicate less proficient hunting technology and social organization on the part of MSA humans. Contrary to the arguments of the "obligate scavenging" model, Chase's (1986, 1989) analysis of faunal assemblages from a number of European MP sites indicates the practice of effective hunting by Neandertals. Likewise, based on a microscopic study of bone-surface modifications, Milo (1998) concluded that the MSA occupants of Klasies River Mouth had primary access to nutritious body parts from all size classes of mammals, indicating the practice of active hunting.

These different arguments reflect not only the diversity of approaches that have been applied to the faunal analysis of Neandertal and early modern human sites, but the lack of consensus among researchers in the interpretation of the faunal record. Based on detailed taphonomic studies of faunal assemblages from the Zagros Mountains and South Africa, Marean and colleagues (Marean and Frey, 1997; Marean, 1998; Marean and Kim, 1998; Marean et al., 2004) demonstrated how the exclusion of long-bone shafts as "non-identifiable fragments" biases skeletal-element profiles, often resulting in "head-and-foot" -dominated reverse utility curve patterns (Marean and Frey, 1997; Pickering et al., 2003; Marean et al., 2004). This bias has resulted in the interpretation of scavenging behavior at many of the sites discussed above.

So far, the role of East African archaeofaunal assemblages in our understanding of faunal exploitation strategies of MSA humans has been marginal (Clark, 1982; Marean and Assefa, 2005). All of the models briefly discussed above are based on archaeofaunal samples from other regions of the Old World, mainly Eurasia and South Africa, where many MP/ MSA cave sites have been studied. The East African region has produced some of the key evidence for the anatomical evolution of both archaic and modern Homo sapiens (White et al., 2003; McDougall et al., 2005), as well as the earliest traces of the MSA (Deino and McBrearty, 2002). Compared to other regions of the continent, the MSA in East Africa has the longest and most continuous record. The Late Pleistocene deposits at Porc-Epic Cave, Ethiopia, have yielded a large sample of artifacts and faunal remains that shed light on the adaptive strategies of East African populations during the terminal stages of the MSA. This paper examines the faunal exploitation strategies of the MSA occupants of Porc-Epic Cave. Because there have been so few studies of MSA faunal assemblages from East Africa, the faunal assemblage from Porc-Epic provides rare insight into subsistence behavior during this important period in modern human evolution.

Location

Porc-Epic Cave is located 3 km south of Dire Dawa (Fig. 1), one of the largest cities in Ethiopia, situated at the

northeastern end of the Chercher Highlands within the Harar Plateau and adjacent to the Rift Valley. Along the western and southern margins of Dire Dawa, the great fault scarps of the plateau form a series of low hills composed of large, broken-faulted blocks of Upper Jurassic limestone (Brown, 1943). Porc-Epic Cave is located 2.5 km northeast of Babo Terara at an elevation of close to 1450 m, near the top of a hill called Garad Erer which rises steeply on the eastern edge of the massive wadi Laga Dächatu. A recent study of Mesozoic sediments of the Dire Dawa region identified the thick limestone bed within which Porc-Epic Cave is located as part of the Antalo Limestone Succession, which was formed during the Oxfordian of the Upper Jurassic (Bosellini et al., 2001).

Situated 9 m below the top of the ridge and about 140 m above the wadi on a steep slope, Porc-Epic Cave is strategically positioned for its prehistoric occupants to have monitored prey movement alongside the rugged gullies and ridges and in the nearby meandering riparian woodland. The cave is difficult to access from every direction. Access from the top requires climbing through a vertical 9-m fissure. From the wadi, a hike of 140 m along a steep loose-gravel talus covered with thorn bushes is necessary. There is no clear geomorphologic evidence for assuming a different topographic setting of the Porc-Epic area during the MSA occupation of the site. Accordingly, despite the advantages provided by the cave's commanding view, its inaccessibility may have posed challenges to its prehistoric occupants, particularly in increasing the cost of transport of prey animals.

Ecologically, the site is located at an ecotone between two physiographic units—the southeastern escarpments and the rift valley depression (Wolde-Mariam, 1972). Within a radius of 15 km of the site, the elevation of the surrounding area varies from about 1000 to 2200 m. With a current average annual temperature of 24.8 °C, Dire Dawa is in one of the hottest regions of the country. The area is quite dry, even if it receives rain in two seasons—July to September and March to May (Wolde-Mariam, 1972)—recording an average annual rainfall of 617 mm.

In his analysis of the biodiversity of the eastern Chercher Highlands and the adjacent areas of the Rift Valley, Ingersol (1968) identified five major topographic regions (Fig. 2) defined by altitudinal, climatic, land use, and physiogeographic factors. The contemporary biotic settings provide an important frame of reference for understanding human behavioral responses to varying environmental conditions (Potts, 1994). Porc-Epic is located within what Ingersol called the foothill region. In its floral composition, the foothill region supports acacia woodland and scrub-dominated vegetation that includes Acacia tortilis, Acalypha fruticose, Cissus quadrangularis, Grevia sp., Solanum sp., and Acacia senegal, in order of their relative abundance (Ingersol, 1968). Adjacent to Dire Dawa, the massive plain of the rift (Afdem) is primarily an area of open grassland and wooded steppe with scattered acacia trees and pockets of riparian woodland (Wolde-Mariam, 1972; White, 1983). The high altitudinal areas of the Chercher Highlands maintain an afroalpine ecosystem, dominated by Juniperus trees. While patches of montane evergreen forest

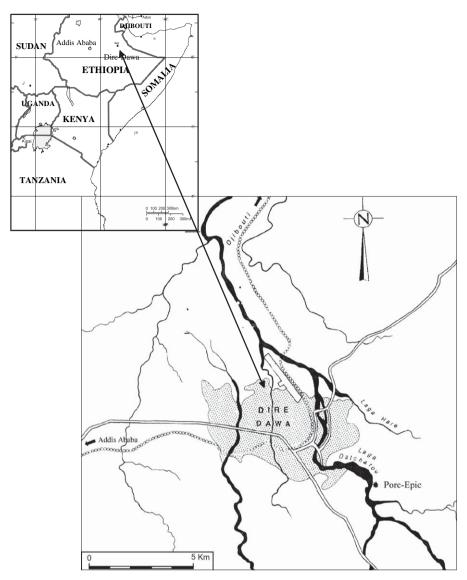


Fig. 1. Location of Porc-Epic (modified from Pleurdeau, 2001).

are abundant in higher elevation areas, montane grasslands and thickets are also widespread throughout intermediate areas of Chercher Highlands.

As illustrated in Fig. 2, in its modern-day settings, the foot-hill region supports the most diverse type of large mammalian fauna in the area. Of the different species of large mammals presently inhabiting the Chercher Highlands and adjacent areas, the tragelaphines, such as lesser kudu (*Tragelaphus imberbis*), greater kudu (*T. strepsiceros*), and bushbuck (*T. scriptus*), appear widely distributed throughout the savanna, woodland/scrub, and deciduous scrub zones of lower and intermediate altitudes. These same areas support the sub-desert adapted species Soemmerring's gazelle (*Gazella soemmerringi*) and beisa oryx (*Oryx beisa*) alongside gerenuk (*Litocranius walleri*) and warthog (*Phacochoerus aethiopicus*) (Ingersol, 1968; Kingdon, 1989). The high-altitude areas support a subspecies of bushbuck, Menelik's bushbuck (*T. scriptus meneliki*). Among small mammals, a variety of species of

dik-dik (*Madoqua*) and klipspringer (*Oreotragus*) preferentially inhabit the foothill region. Other small mammals, such as Abyssinian hare (*Lepus habessinicus*) and Abyssinian hyrax (*Procavia habessinica*), have been documented from all ecological regions.

Among the equids, occurrences of Grevy's zebra (*Equus grevyi*) and wild ass (*E. africanus*) have been reported from Afdem Plains in the Rift Valley. Of the two species of suids documented in the Porc-Epic area, the warthog (*Phacochoerus aethiopicus*) is equally abundant in lower and intermediate ecological zones, whereas the bush pig (*Potamochoerus porcus*) is confined to the high-elevation areas of the montane forest (Ingersol, 1968; Bolton, 1973; Yalden et al., 1984).

The Late Pleistocene record of the East African region documents major climatic changes that resulted in considerable shifts in floral and faunal composition and distribution (Hamilton, 1982). In general, paleoecological evidence from the last 20 kyr is very well-known in the Porc-Epic region

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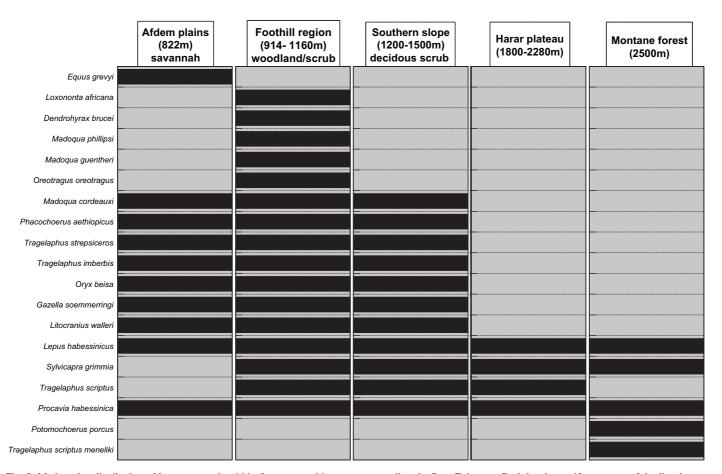


Fig. 2. Modern-day distribution of large mammals within five topographic zones surrounding the Porc-Epic area. Dark bands specify presence of the listed taxa.

(Nillson, 1940; Potter, 1976; Gasse and Street, 1978; Gasse et al., 1980; Messerli et al., 1980; Gasse and Fontes, 1989; Benvenuti et al., 2002), and it can be reasonably used to make projections of paleoenvironmental conditions during the least known warm and cold phases of the Late Pleistocene.

The period of occupation at Porc-Epic Cave, based on different lines of chronological evidence discussed below, corresponds to the Last Glaciation, which was characterized by a drier and more arid climate than is known for the region today. Low temperature (Gasse and Street, 1978; Messerli et al., 1980) and increased aridity might have caused the compression of altitudinal vegetation belts (Hamilton, 1982; Brooks and Robertshaw, 1990). This in turn may have encouraged humans to exploit diverse resources along the steep vertical gradients. The faunal evidence from Porc-Epic shows that, during its occupation by MSA humans, the site was close to highly diverse habitats, including thickets, montane forest, grassland, woodland, and sub-desert steppe.

History of excavation and stratigraphic sequences

The total area of Porc-Epic Cave shown in Fig. 3 covers an area of 182.5 m². Of this total, the 115 m² toward the center and front of the cave showed the greatest use by the prehistoric occupants. The first excavation at Porc-Epic Cave was conducted in 1929 by the French prehistorians Henri de Montfried and Père Teilhard de Chardin (Teilhard de Chardin, 1930; Breuil et al., 1951), who are considered pioneers (Brandt, 1986) of the systematic excavation of Later Stone Age (LSA) and MSA sites in the Horn of Africa. In 1933, Teilhard de Chardin and Paul Wernert continued an extended excavation at Porc-Epic, while Abbé Breuil et al. (1951) studied the much younger rock paintings on the roof of the cave. The area covered by the 1933 excavation is estimated to be 57.5 m². In 1974, after an interval of 40 years, a team led by Clark (Clark and Williamson, 1984) carried out a 1×6 m test excavation with the purpose of clarifying the sedimentary history of the cave and conducting a pilot study on the archaeological remains. In the following years, Williamson pursued an exhaustive excavation of the cave in an area of more than 50 m², producing a large sample of artifacts and faunal remains, the latter of which is the subject of the research reported here. Collections from earlier excavations are not available at the Ethiopian National Museum, and thus they could not be incorporated into this analysis. More recently (in 1998), a group of geologists and archaeologists led by H. de Lumley conducted a short field project, with the objective of reconstructing the stratigraphic sequences at Porc-Epic Cave and applying newly introduced chronometric dating methods. Details from this most recent phase of the project have yet to be published.

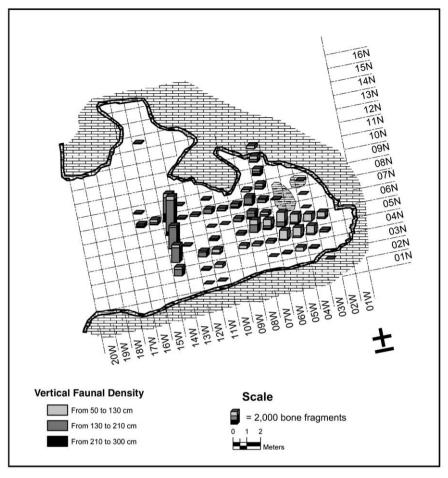
Important discoveries from the 1933 excavation at Porc-Epic included a hominid mandible (Vallois, 1951; Boule and Vallois, 1957; Tobias, 1962; Bräuer, 1984) found in association with a large sample of stone tools (Perles, 1974) and other vertebrate faunal remains. Findings from this phase of excavation are not, however, very well-described.

The 1974 excavation at Porc-Epic had two principal objectives: recovery of MSA artifactual remains and reconstruction of the stratigraphic sequence (Clark and Williamson, 1984; Clark, 1988) to address earlier suspicions (Breuil et al., 1951) of possible intrusion and admixture of the overlying LSA sequence with the MSA sediment.

Details of the depositional history at Porc-Epic Cave are discussed elsewhere (Clark and Williamson, 1984; Pleurdeau, 2003). To provide a concise picture of the sedimentary sequence at the cave, Fig. 4 illustrates the stratigraphic layers exposed at the eastern section of the 1974 grid. The MSA assemblage came from the calcareous breccia (4A in Fig. 4), which in some quarters of the cave measures up to 1.5-m thick. Prior to the deposition of the main dripstone (5 in Fig. 4), the upper horizon (4B in Fig. 4) of the breccia layer was cemented by lateral seepage. Subsequently, a major dripstone (5 in Fig. 4) sealed the MSA-bearing breccia layer (Clark and Williamson, 1984). In the center and toward the entrance of the cave, however, post-dripstone stream activity and subsequent erosion resulted in the removal of weakly consolidated deposits to a depth of about a meter. This was followed by the deposition of post-dripstone LSA and Neolithic sediments that unconformably overlie the MSA deposits. Thus, while natural mixing of LSA and Neolithic remains with older deposits is possible toward the entrance of the cave, where the sediment is weakly consolidated, the main MSA deposit is well protected from such actions by the dripstone (Clark and Williamson, 1984), Sampling selected squares that were part of the 1975/76 excavation, a recent microstratigraphic study (Pleurdeau, 2003) at Porc-Epic identified a series of stratigraphic horizons and layers, the lithographic features of which match the ones described by Clark and Williamson. These include the different horizons in the breccia layer that, with the exception of the upper horizon, are exceptionally rich with artifacts and faunal remains.

Obsidian hydration dating (Michels and Marean, 1984) provided three ages of $61,202 \pm 958$, $61,640 \pm 1083$, and $77,565 \pm 1575$ years BP for the MSA occupation. Accelerator mass spectrometry (AMS) analyses recently applied to three samples of gastropod shell fragments provided a different age range. Samples were taken from three different layers: 160-170 cm (5N-6W), 180-190 cm (4N-14W), and 270-280 cm (7N-16W) below datum. The AMS dates reported from Beta Analytic on the above three samples provided conventional radiocarbon ages of 33,700 \pm 300 (Beta - 193517), 35,600 \pm 350 (Beta - 193516), and >43,200 (Beta - 193518), respectively. The dates fit with the stratigraphic sequence in the cave, indicating a lack of feasible influence on the reported AMS dates that may be attributable to the old carbon reservoir effect or "old shell" problem (Rick et al., 2005). Given the disparity of the results from the different dating methods, however, the MSA occupation at Porc-Epic will be considered here to date generally to the Last Glaciation.

The analysis of thousands of artifacts from the 1974 excavation documented diverse types of retouched and utilized stone tools, with high proportions of points and scrapers. Possible evidence of hafting was found, with about 15% of the



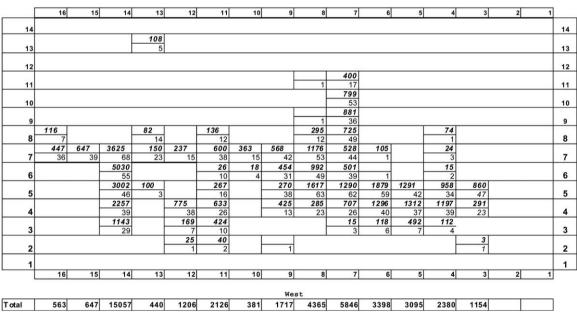


Fig. 3. Faunal distribution and density at Pore-Epic Cave. Columns show density of faunal remains classified in each of three arbitrary vertical horizons. The table at bottom shows counts of faunal remains included in the analysis (upper) and bone-bearing quadrants (lower) classified by grid squares from top to bottom.

points exhibiting damage at the proximal end. The types of stone tools and the predominantly Levallois technology appear to persist throughout the MSA sequences, indicating an absence of major changes in the techniques of stone tool production during the course of the MSA occupation (Clark and Williamson, 1984; Clark, 1988). A recent study of the artifacts from the 1975/76 excavation confirmed these initial findings (Pleurdeau, 2001, 2003).

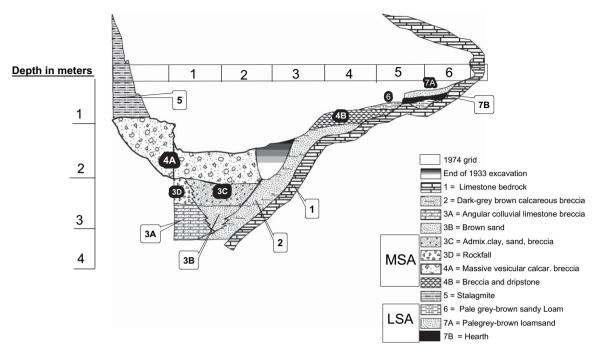


Fig. 4. Eastern profile of the 1974 excavation (modified after Clark and Williamson, 1984).

Characteristics of the fauna and methods of analysis

Taphonomic research is necessary in order for zooarchaeologists to recognize post-mortem processes (Gifford, 1981), which highlight the history a faunal assemblage from both behavioral and ecological perspectives. A legitimate understanding of the faunal exploitation strategies by prehistoric humans requires that taphonomy and zooarchaeology be pursued as "synergistic" (Lyman, 1994) analytical approaches. As noted by Behrensmeyer (1991), the sedimentary context and major features of a faunal assemblage, such as breakage patterns, taxonomic representation, and skeletal-element profile, provide essential lines of evidence from which to infer the taphonomic history of a vertebrate accumulation. Observations from actualistic studies have helped to identify human and other biological processes that are responsible for the accumulation of faunal remains (Behrensmeyer, 1991). The analysis from Porc-Epic follows this general framework in reconstructing major taphonomic history of the faunal assemblage.

There is no documentation that discusses the specific or general procedures of excavation that Williamson undertook at Porc-Epic. In compiling the available data derived from the excavation labels, it became clear that the excavation was dug in arbitrary 10-cm levels with each grid square divided into four quadrants ($50 \text{ cm} \times 50 \text{ cm}$). The total excavation area approaches 50 m^2 . From a total of 1590 bone-bearing quadrants (38.125 m^3), more than 57,000 fragments of large mammal bone were recovered from the MSA levels, making this—to the best of this author's knowledge—the largest of all published MSA faunal assemblages from Africa. From the collection, it appears that the excavators retained all concretions that contain bones, irrespective of size. Coming from a limestone cave deposit, the bulk of the bone and tooth fragments are coated with

calcium carbonate. At the initial curatorial stage of my project, every fragment with calcium carbonate coating was cleaned using a weak solution of glacial acetic acid (CH₃COOH). The small groups of bones that were heavily embedded in breccia could not be incorporated into this analysis due to the difficulty of cleaning their hardened matrix. Highly fragmented specimens, measuring less than 10 mm long, were also excluded from the analysis, with the exception of diagnostic fragments often belonging to very small mammals, such as hyraxes and hares. Subsequently, a total number of more than 42,000 bone fragments from different sections of the cave (Fig. 3) were subjected to a detailed taphonomic analysis.

The faunal remains were concentrated towards the center of the cave (Fig. 3). Deposits within the grid squares from 13W to 09W were focal areas of previous excavations. In Fig. 3, the paucity of bones from these grid squares results from samples from earlier phases of excavation being unavailable for inclusion in the analysis. The rear portion of the cave yielded a modest sample of faunal remains. Depth-wise, the largest portions of bones from the rear section of the cave come from the upper and middle sections of the excavation. The stratigraphic sequences as revealed at the witness section of the excavation are not clear enough to delineate separate observational or analytical units. The vertical distribution of the faunal remains appears continuous, lacking any noticeable clustering or breaks (Fig. 5; for details see, Assefa, 2002). As a result, this analysis treats the whole assemblage as a single aggregate unit. As noted earlier, the lithic analyses by Clark and Williamson (1984) and Pleurdeau (2003) also indicate the lack of a major shift in the composition of end-products and techniques of production throughout the occupation sequence.

At the first step of the documentation process, each faunal specimen was classified into two broad categories of identifiable

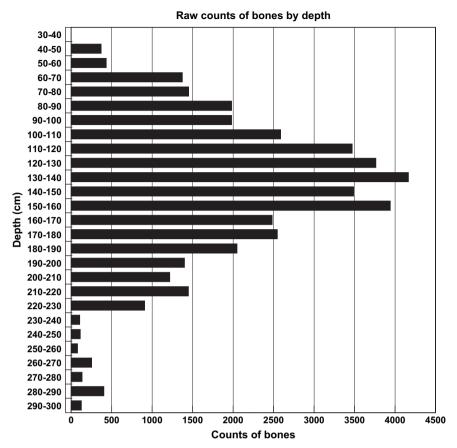


Fig. 5. Count of bones per 10-cm vertical layer.

(to element and/or size class) and non-identifiable remains. All specimens were examined for breakage patterns, weathering, and traces of burning. The recording of fragmentation and breakage properties followed the procedure established by Villa and Mahieu (1991) to distinguish between fresh- and dry-bone breakage. Data collected for the fragmentation and breakage study included measurements of length, width, and, for each long-bone fragment, the maximum circumference (Bunn, 1983), as well as the occurrence of fresh breaks. Weathering sequences were classified according to the stages proposed by Behrensmeyer (1978).

Evidence of burning was recorded using the color schemes outlined in the experimental study of Buikstra and Swegle (1989) to distinguish between fleshed-, green-, and dry-bone burning. All non-identifiable bones were also assigned to one of the following four categories: long-bone fragment, non-identifiable fragment, long-bone flake (with bulb of percussion), and cranial fragment. Long-bone fragments were further assigned to the three fragment codes (Blumenschine and Selvaggio, 1988): epiphyseal fragment, near-epiphysis fragment, and shaft.

Each fragment was assigned to a size class category (1A, 1, 2, 3, and 4). The last four size class categories follow Brain's (1981) scheme of classification, while the size class 1A represents very small mammals, including mainly hyraxes and hares, which weigh less than 4.5 kg. The rest of the size classes include groups of mammals ranging from Grevy's zebra to buffalo (size class 4: 400–850 kg live weight); topi to African

wild ass (size class 3: 150–400 kg live weight); reedbuck to warthog (size class 2: 20–150 kg live weight); and Salt's dikdik to Dorcas gazelle (size class 1: 5–20 kg live weight).

All of the fragments that could be identified to skeletalelement were subjected to more thorough documentation. In addition to taxon and size class, other variables, such as side and state of fusion were recorded for such fragments. In an attempt to incorporate as many bone fragments as possible into the skeletal-element profile, the documentation of this group of fragments employed a more comprehensive strategy of recording recognizable landmarks, using a relational database system developed by Marean et al. (2001) and hereafter referred to as the "fraction summation approach." This approach incorporates faunal documentation procedures that have been outlined by other researchers (Dobney and Rielly, 1988; Morlan, 1994). Under this system, each element has a series of defined anatomical zones, many first defined by Morlan (1994) as zones and features of skeletal elements. The data entry system defined the boundaries of features and zones in each skeletal-element (Marean et al., 2001) with the objective of sampling all portions of each element, which otherwise could have been ignored as non-identifiable fragments. Zonal definitions were also modified from Morlan's scheme to counterbalance density-related intra-zone differences and to sample portions of long bones that are experimentally proven to sustain the ravaging impact of carnivores (Marean and Spencer, 1991). In the course of faunal documentation, the estimated fraction of each preserved zone or feature on

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identifiable fragments was entered into the database. The sum of those fractions provides the basis for deriving the minimum number of elements (MNE).¹

All bone fragments were subjected to detailed examination for surface-modification marks. Judging from differences in the distribution and depth of parallel grooves found on many of the faunal remains, it is very likely that both large and small rodents were responsible for many of the observed rodent tooth marks. The depth and width of the gnaw marks were recorded according to three discrete categories: shallow, moderate, and deep (Brain, 1980). Such distinctions were used to distinguish the involvement of larger- from smaller-sized rodents in the process of faunal accumulations.

The taphonomic literature contains a wealth of information on diagnostic features of carnivore vs. human modified bones (Binford, 1981; Shipman, 1989; Blumenschine, 1995; Fisher, 1995), the procedure for documenting signatures by different bone-modifying agents (Blumenschine et al., 1996), and approaches to the analysis and presentation of the data (Brain, 1981; Lyman, 1987; Gifford-Gonzalez, 1991; Milo, 1998). I used the diagnostic criteria for tooth marks and cut marks as outlined by Blumenschine et al. (1996). The author participated in a series of blind tests similar to those described and advocated by Blumenschine et al. (1996). Diagenetic marks, which can sometimes resemble tooth marks, were excluded from the analysis. The documentation of surface modification was conducted using a binocular microscope at 8-40× magnification. Once identified with confidence, the presence of tooth marks or cut marks on each faunal fragment was recorded by tallying non-adjacent individual marks or closely spaced clusters, which, as argued by Lyman (1987), represent separate instances of bone modifications. Cut marks on identifiable long-bone fragments were recorded according to their position along the element: proximal end, shaft, and distal end. As noted by a number of authors (e.g., Lyman, 1987), the use of the number of identifiable specimens (NISP) in tabulating butchery marks is prone to bias due to the possibility of differential fragmentation. To minimize such bias, this analysis employed derived measures of abundance, such as MNE and minimum animal units (MAU), to evaluate butchery activities.

Results

Taxonomic representation

Due to the highly fragmented nature of the faunal assemblage, taxonomic identification could be based only on dental remains. At Porc-Epic, the representation of dental remains is remarkably low compared to postcranial bones and consists primarily of isolated and fragmented specimens. Based on the small sample of diagnostic dental remains, Table 1 lists the taxa of large mammals represented in the faunal assemblage, updated from Assefa (2002).

Altogether, the number of mandibular and maxillary bones with three or more teeth still embedded to the alveolar process amount to only 21 specimens. Of these, 13 are hyrax and hare, while the remainder are from small antilopines and neotragines.

The list in Table 1 includes a diverse range of large mammal species, the majority of which are still present within the immediate vicinity of Porc-Epic (Ingersol, 1968; Yalden et al., 1984). A few of them, such as *Alcelaphus buselaphus* and *Syncerus caffer*, no longer inhabit the area due to possible environmental degradation caused by both natural and cultural factors. On the other hand, the historical distribution of some of the species on the list (*Damaliscus* spp., cf. *Aepyceros*, *Redunca* spp., *Kobus* spp., *Kobus* cf. *ellipsiprymnus*, *Gazella granti*, *Giraffa camelopardalis*, and *Taurotragus oryx*) did not include the area around Porc-Epic, indicating that a different faunal and floral composition existed at the time of the MSA occupation of the site.

The different species of reedbuck (Redunca spp.), waterbuck (Kobus spp.), and topi (Damaliscus korrigum) could have lived in an area of abundant green forage, possibly along the edaphic grasslands and floodplains of the Dächatu River or, in the case of some species of Redunca, the rugged ridges and valleys of the escarpment. The other ungulate taxa include mixed feeders (Aepyceros melampus, Gazella granti, and Taurotragus oryx) and browsers (Giraffa camelopardalis), all sharing the same habitat of open woodland or bushland. Along with the physiogeographic zones of both the Awash Valley and the Chercher Highlands, the lower- and intermediate-elevation areas may have provided favorable habitat for the ungulate taxa listed above, including the alcelaphines and the equids. Other species of grazers, such as Syncerus caffer and Alcelaphus buselaphus, inhabit more diversified habitats, including mosaics of grassland, thickets, and woodlands, as well as the fringes of open woodlands and partially wooded small valleys. The rest of the ungulates are mainly browsers and frugivores, the majority of which would have occupied the scrub- and acacia-dominated thickets zone.

In general, the occurrence of specific ungulate taxa indicates that the modern semi-arid and thicket-dominated area of Porc-Epic previously supported more grazing animals than what has been documented during historic times. From a taphonomic perspective, the disproportionate paucity of craniodental remains of medium and large mammals may be explained in terms of the selective transport of body parts. However, one would not expect the skeletal-element representation of small animals to be biased by transport decisions, considering that it is easy to transport them whole and they maintain a "high ratio of edible meat to live weight" (Stahl, 1982). Accordingly, plausible explanations for the rarity of craniodental remains for very small animals have yet to be explored.

Faunal fragmentation and breakage patterns

Recent taphonomic studies (Capaldo, 1997; Marean et al., 2000) have categorized faunal transformations into two major phases—nutritive and non-nutritive. The nutritive phase deals with the relatively brief but complex stage of faunal

¹ The data entry and MNE calculation programs are available upon request from Curtis Marean (curtis.marean@asu.edu).

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Table 1
Taxonomic representation derived from dentitions¹

Order	Family	Tribe	Genus and species	Lowe	er limb	Uppe	er limb	Indeterminate	NISP
				Isolated	In-socket	Isolated	In-socket		
Artiodactyla	Bovidae	Bovini	Bovini indet.	8		2		1	11
-			Syncerus caffer	4		1	1	1	7
		Tragelaphini	cf. Tragelaphus	4					4
			Tragelaphus cf. imberbis	2					2
			Tragelaphus cf. strepsiceros	1	3				4
			Tragelaphus strepsiceros	2	2	1			5
			cf. Taurotragus	1	1	1		2	5
			Taurotragus oryx	3		1			4
		Alcelaphini	Alcelaphini indet.	11	5	4			20
			Damaliscus sp.			5			5
			Alcelaphus cf. buselaphus	1	1	1			3
		Aepycerotini	cf. Aepyceros		3				3
		Reduncini	Reduncini indet.	1					1
			Redunca sp.	1	5				6
			Kobus sp.	1			2		3
			Kobus cf. ellipsiprymnus	1		1			2
		Antilopini	Antilopini indet.	3	6	1	5		15
			Gazella sp.	2			1		3
			Gazella cf. granti	1					1
			Gazella granti	1		1			2
			Gazella cf. soemmerringi		4				4
			cf. Litocranius			3			3
		Neotragini	Neotragini indet.		8		1		10
		_	Madoqua sp.		2				2
	Suidae		Phacochoerus aethiopicus	5	1	1	3		10
	Giraffidae		Giraffa camelopardalis	1					1
Perrisodactyla	Equidae		Equus sp.	7	1	2			10
Primates	Cercopithecidae		Cercopithecus sp.	3	3	1	2		9
	•		Papio sp.	1	6	2			9
	Hominidae		Homo sapiens	1					1
Lagomorpha	Leporidae		Lepus capensis	1	26		4		31
	-		Lepus cf. capensis	1	4	2			7
Hyracoidea	Procavidae		Procavia capensis		17		11		28
-			Procavia cf. capensis	3	5		1		9
Rodentia	Hystricidae		Hystrix sp.	1					1
Carnivora	Canidae		Canis sp.	1	1				2
	Hyaenidae		Hyaena sp.					1	1

¹ The NISP includes individual counts of teeth attached to alveolar process.

transformation that lasts from the death of the animal to its complete consumption or the depletion of all its nutrients. Faunal transformations during the nutritive phase are typically related to the extraction of nutrients by biological agents such as carnivores and humans. The non-nutritive phase encompasses all subsequent post-burial stages in which the modification of bones by different actors is not related to extracting resources. In general, nutritive faunal transformations occur while bones are still fresh; non-nutritive transformations occur after they become dry.

When subjected to dynamic and static loading, fresh and dry bones react in predictably different manners (Johnson, 1985). Fresh long-bone diaphyses react in a "tensile-shear failure" or a spiral fracture. Depleted of its moisture content and with altered microstructure, dry bone reacts in a "horizontal tension failure" characterized by "perpendicular, parallel, or diagonal breaks" (Johnson, 1985; Villa and Mahieu, 1991). Villa and Mahieu (1991) established a number of criteria for distinguishing between green- and dry-bone breakage.

Green-bone breakage is characterized by oblique fracture angles and curved or V-shaped fracture outlines. On the other hand, right angle fractures and transverse fracture outlines are typical of dry-bone breakage. At Porc-Epic, more than 95% of the long-bone fragments exhibit curved fracture outlines and oblique fracture angles, indicating that they were broken almost exclusively while in the nutritive stage.

Generally, bone breakage and fragmentation patterns are considered to be poor indicators for singling out the role of a particular biotic agent in the accumulation of a faunal assemblage (Myers et al., 1980; Bunn, 1983; Bartram and Marean, 1999; Outram, 2001; but see Pickering et al., 2005). Unlike the action of any other agent of faunal fragmentation, however, hammerstone breakage of bones by humans results in a high degree of bone fragmentation and is frequently found on marrow-rich bones of the appendicular elements (Bunn, 1983). Particularly at constrained sites, such as caves and rock-shelters, bone-breaking actions of hyenas on marrow-rich long bones potentially produce clusters of shaft fragments (Gifford-Gonzalez,

1989; Marshall and Pilgram, 1991). Following Bunn's (1983) procedure of documenting the circumference of long-bone faunal fragments using three general categories—I, II, III (less than half, more than half, and complete, respectively)—Fig. 6 shows the extent of long-bone fragmentation at Porc-Epic.

The long bones of both medium and larger mammals at Porc-Epic are all highly fragmented. These groups of mammals show a higher degree of long-bone fragmentation, possibly due to increased application of hammer-stone breakage for extracting rich marrow resources. In contrast, the long bones of smaller mammals, specifically the forelimbs, are more complete. Given the minimal marrow content of small mammal long bones, their relatively complete representation may reflect the lack of interest of consumers in accessing these nutrients (Binford, 1981; Yellen, 1991b). Conversely, a high proportion of fairly complete small mammal long bones may also reflect the involvement of raptors such as owls and eagles in the accumulation of a faunal assemblage (Andrews, 1990). A clearer picture of the role of different biotic agents in the accumulation of faunal remains of all sizes emerges from the study of surface modification.

Surface modification

Systematic study of bone-surface modification provides insight into the sequence and intensity of faunal consumption by different agents. Research into human- and carnivore-induced modification marks, in particular, have played a central role in the reconstruction of faunal exploitation strategies by establishing the order in which humans and carnivores exploit and discard faunal resources (Binford, 1981; Bunn and Kroll, 1986; Blumenschine, 1988, 1995; Shipman, 1988; Blumenschine and Selvaggio, 1991; Oliver, 1994; Selvaggio, 1994b). After

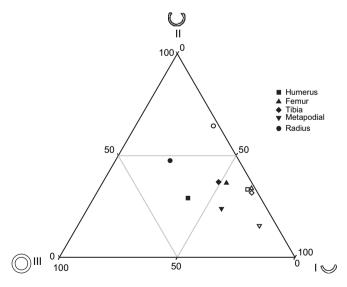


Fig. 6. Long-bone fragmentation and circumferential completeness. The ternary scatter plot shows the relative proportion of long-bone fragments in the three categories of circumferential completeness: Class I (100% complete), Class II (>50% complete), and Class III (<50% complete). Closed and open symbols represent long-bone fragments of smaller (size 1A and size 1) and larger (size 2 and size 3) mammals, respectively.

reviewing the influence of raptors and rodents on the accumulation and distribution of faunal remains at Porc-Epic, the following sections examine the role of carnivores and humans in a dual-patterned site formation process (Capaldo, 1995; Egeland et al., 2004).

Different species of raptors roost within caves and shelters and often produce the accumulation of small mammal bones (Andrews, 1990). Modifications such as corrosive damage, polish marks, and beak and talon depressions are diagnostic of bones from pellets and roosts of raptors (Hockett, 1991; Sanders et al., 2003). Only a very insignificant portion of the faunal sample from Porc-Epic exhibits any of these types of bone damage. Conversely, butchery marks and traces of burning observed on large numbers of hyrax and hare bones are indicative of human accumulation for at least some of the small mammal sample. However, as demonstrated in a number of actualistic studies (Brain, 1981; Hockett, 1991), traces of bone damage by raptors not only tend to be scarce, but also show considerable inter- and intraspecific variation. Therefore, establishing the contribution of raptors to faunal accumulations requires observations of bone damage combined with other lines of evidence, such as patterns of body part representation (Cruz-Uribe and Klein, 1998).

Hare and hyrax body-part frequencies at Porc-Epic were compared to the data sets from Cruz-Uribe and Klein's (1998) recent study of modern South African eagle roost collections and fossil samples comprising the same species of small mammals (Fig. 7). Although limited strictly to eagles, Cruz-Uribe and Klein's investigation of roost samples documented patterns of body-part representation that differed between hyrax and hare. The majority of postcranial bones of size class 1A mammals at Porc-Epic were too fragmented for secure identification to species, so the assemblage cannot be evaluated according to the species-specific characteristics observed by Cruz-Uribe and Klein (1998). Instead, the combined hare and hyrax sample at Porc-Epic was compared to the combined hare and hyrax sample from the modern eagle-roost collections and from the site of Die Kelders Cave 1, South Africa.

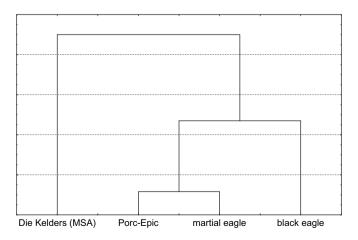


Fig. 7. Cluster analysis of skeletal-element representation of size 1A mammals from the roosts of two species of eagle and from Die Kelders compared with Porc-Epic.

On the basis of the cluster analysis, hyrax and hare skeletalelement representation at Porc-Epic shows greater similarity to the samples from the eagle roosts than to the Die Kelders faunal remains, which Cruz-Uribe and Klein (1998) determined to be a non-raptor accumulated assemblage. The major difference in the pattern of skeletal-element representation between roosts of the martial eagle (Polemaetus bellicosus) and the black eagle (Aquila verreauxi) is in variable representation of long bones and an uneven forelimb/hindlimb ratio. Such differences were typically observed between hare and hyrax samples, which cannot be directly applied to interpret samples from Porc-Epic, as the postcranial remains from the two species are undifferentiated. The close similarity in the abundance of skeletal elements between the samples from Porc-Epic and modern eagle roosts, however, indicates that a raptor may have contributed to the accumulation of hyrax and hare bones at Porc-Epic. On the other hand, traces of burning and cut marks (discussed in the following sections) signify that humans were also responsible for the presence of many of the hyrax and hare bones. From these observations, it appears that both raptors and humans contributed to the accumulation of hyrax and hare bones in the MSA layers of Porc-Epic.

Table 2 summarizes the relative proportion of bones exhibiting modification marks by rodents, carnivores, and humans. The bones of all size classes of animals at Porc-Epic exhibited signs of rodent gnawing, with the smallest size classes showing the least gnawing. Rodents regularly utilize bones for the nonnutritive purpose of sharpening their teeth. Among them, the porcupine (Hystrix sp.) is the only African species known to habitually accumulate bones in their lairs (Brain, 1980, 1981). Bones accumulated by porcupines show distinctive patterns, including high proportions of axial bones and horns, a predominance of complete bones, and invasive gnawing marks, particularly on larger bone fragments (Brain, 1980, 1981). The predominance of comminuted bone fragments and the high representation of limb bones from Porc-Epic differ from the characteristics of porcupine-accumulated assemblages. Moreover, in all size classes, the bulk of rodent-gnawed bones (>85%) exhibit small and sporadic modification marks that seem more consistent with the actions of mouse-sized rodents. Such small rodents are not known to accumulate bones, but they may move and modify bones collected by other agents. Persistent movement of bones by small-sized mammals may create

Table 2
Percentage of faunal remains with modification marks by rodents, carnivores, and humans, categorized by size class and anatomical units

		Rodent tooth mark	Carnivore tooth mark	Cut mark
Size	1A	7.2%	24.9%	8.7%
	1	12.9%	23.4%	7.4%
	2	19.8%	24.9%	10.1%
	3	21.0%	19.1%	11.3%
	4	20.2%	11.3%	13.0%
Anatomical	Axial	17.3%	20.7%	8.5%
unit	Forelimb	17.5%	28.7%	12.3%
	Hindlimb	15.6%	30.4%	15.6%

"second-order natural assemblages" (Hoffman and Hays, 1987), which could potentially result in a differential spatial concentration of gnawed bones. The distributions of rodent-gnawed bones from Porc-Epic show minimal clustering, implying insignificant effect of spatial displacement due to the actions of rodents (Assefa, 2002).

When reviewing modification marks by larger biotic agents, carnivore tooth marks constitute the most common type of surface modification in the faunal assemblage at Porc-Epic (Table 2). As shown in more detail in Table 3, carnivore modification is present on virtually every type of skeletal-element in all size classes of mammals. In general, however, the proportions of carnivore-modified bone fragments varied within and between different size classes. Inflated percentage values in some of the elements may be an artifact of small sample size (refer to NISP figures in the next section). For instance, there is only a single thoracic vertebra identified to size class 4 mammals, which also happens to exhibit a tooth mark. Thus, the percentage value for this class of body part, as shown in the table, is inflated to 100%.

A number of experimental studies (Blumenschine and Selvaggio, 1988; Selvaggio, 1994b; Capaldo, 1997) and naturalistic and ethnoarchaeological observations (Blumenschine, 1988; Lam, 1992; Dominguez-Rodrigo, 1997) have produced data sets that assist in reconstructing the order and degree of human and carnivore involvement in the accumulation of faunal resources. Blumenschine's (1988) pioneering experimental study found distinct differences in the abundance of tooth marks on long bones depending on whether humans or carnivores had first access. Faunal fragments subjected to initial carnivore consumption exhibit high frequencies of tooth marks at all portions of long bones-epiphysis, near-epiphysis, and mid-shaft. In contrast, bones from which meat and marrow were first removed by humans followed by post-discard ravaging actions of hyenas exhibit few tooth marks on diaphyseal (mid-shaft) portions. The experimental study distinguishes the above two consumption sequences as carnivore-first and hominid-first models, respectively.

Figure 8 compares the frequency of tooth-marked bones from Porc-Epic to the results from Blumenschine's (1988) controlled experimental study. The abundance of tooth marks on the faunal remains from Porc-Epic is uncharacteristically low at epiphyseal and near-epiphyseal portions of long bones. On the other hand, tooth-marked mid-shaft fragments constitute 18.8%, 13.5%, and 18.1% of the small, large, and complete mammal samples, respectively (Fig. 8). These values are much closer to the experimental data set sampling hominid-first simulated sites (15%) than the carnivore-first controlled samples (up to 70%).

Further comparative investigation of similar experimental studies and naturalistic observations (Fig. 9) indicates that the percentage of tooth-marked mid-shaft fragments from Porc-Epic is closer to the limits of the 95% confidence intervals for most hominid-first samples. Overall, the frequency of tooth-marked bone fragments from Porc-Epic is more consistent with patterns of bone damage from assemblages accumulated by hominids. The slightly higher frequency of tooth-marked

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Table 3
Proportion of faunal fragments with carnivore tooth marks, according to body part and size class¹

Anatomical unit	Skeletal element			Size class		
		1A	1	2	3	4
Cranial	Cranial	_	29	31	_	_
	Maxilla	_	_	_	_	_
	Mandible	13	20	17	35	50
Axial	Atlas	_	_	20	100	_
	Axis	_	_	29	_	_
	Cervical	17	33	38	20	_
	Thoracic	_	33	20	20	100
	Lumbar	_	17	19	_	_
	Caudal	_	13	14	_	_
	Sacral	_	50	_	33	_
	Rib	50	22	23	21	22
	Vertebra indet.	29	16	16	17	7
Forelimb	Scapula	30	27	17	32	_
	Humerus	27	28	33	31	41
	Ulna	22	22	32	21	_
	Radius	29	36	31	11	_
	Metacarpal	17	40	27	22	14
	Cuneiform	_	_	20	_	_
	Lunate	_	_	_	_	_
	Scaphoid	_	_	_	_	_
	Unciform	_	_	_	_	_
Hindlimb	Pelvis	20	26	27	18	33
	Femur	33	34	32	31	19
	Patella	_	_	_	_	_
	Tibia	30	33	32	23	5
	Metatarsal	25	24	32	32	_
	Astragalus	_	13	_	_	_
	Calcaneus	_	36	50	_	_
	Naviculo-cubiod	_	_	_	_	_
	External cuneiform	_	_	_	_	_
	Internal cuneiform	_	_	_	_	_
Phalanx	1 st phalanx	_	25	29	9	_
	2 nd phalanx	_	13	15	_	_
	3 rd phalanx	_	9	13	21	_
Metapodial indet.	Metapodial	57	26	32	27	22
Long-bone fragment	Long-bone fragment	18	21	23	16	5
Cranial fragment	Cranial fragment	_	45	15	_	_
Non-ID fragment	Non-ID fragment	23	23	30	24	_

Numbers in the table refer to the percentage of tooth-marked bone fragments.

fragments suggests carnivore influence at Porc-Epic, but this nonetheless appears to be very marginal, for the most part limited to the attrition of bones discarded by humans.

Systematic study of the distribution, orientation, and frequency of cut marks has allowed researchers to establish the timing of access to carcasses by human consumers. This analysis of the Porc-Epic assemblage benefits from integrating such actualistic studies. Reviewing the data from Table 4, evidence of butchery activities is evident for all size-class mammal remains, including the hares and hyraxes. Small and large mammals both show a high concentration of butchery marks on their hindlimb and forelimb bones, which, as discussed in more detail in the following section, include the most nutritious body parts. Axial bones (excluding ribs) and lower limb elements in all size classes exhibit a low-to-moderate frequency of butchery marks.

Comparing the overall pattern of tooth mark and cut mark abundance on faunal samples from Porc-Epic with Selvaggio's

(1994a) experimental data sets, which model secondary access to carcasses by humans, reveals interesting contrasts. In the experimental study (Fig. 10), the proportions of both tooth marks and cut marks on epiphyseal and near-epiphyseal fragments are higher when compared with the mid-shaft fragments. The faunal remains from Porc-Epic show the opposite pattern, with greater concentrations of both tooth marks and cut marks on mid-shafts. Significant differences between the experimental study and the faunal sample from Porc-Epic are documented by the chi-square test for independence: χ^2 (3, n = 2592) = 10.77 (p < 0.05) and χ^2 (3, n = 2592 = 13.10 (p < 0.05) for cut-marked and toothmarked fragments, respectively. The result of the chisquare test clearly suggests that the abundance of tooth marks and cut marks on different portions of long bones from Porc-Epic are not consistent with patterns of bone damage expected if humans had only secondary access to carcasses.

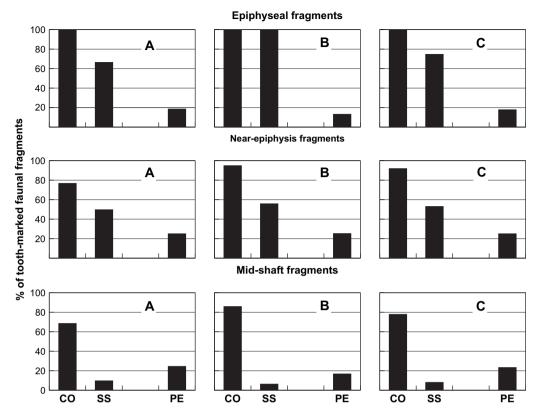


Fig. 8. Frequency of carnivore tooth marks by long-bone portions at Porc-Epic compared with the experimental control samples of Blumenschine (1988). Symbols: A, size 1 and 2; B, size 3 and 4; C, all size groups (1–4). CO = carnivore only; SS = hominid-first simulated sites; and PE = Porc-Epic.

To evaluate the alternative possibility—that humans had primary access to carcasses—it is necessary to conduct further comparative analysis against data sets from actualistic studies that model humans as primary agents of faunal modification

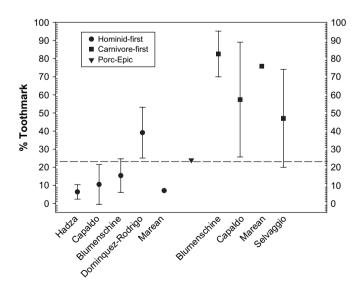


Fig. 9. Percentage of tooth-marked long-bone shaft fragments from Porc-Epic compared with data from controlled experimental studies (Selvaggio, 1994b; Blumenschine, 1995; Dominguez-Rodrigo, 1997; Marean et al., 2000) and ethnographic observations. The 95% confidence intervals of the means are shown. Data for the experimental data sets are from Lupo and O'Connell (2002: Table 10); Porc-Epic = 24%.

and accumulation. Figure 11 illustrates data from such comparative analyses: the frequency of long-bone shaft fragments bearing one or more cut marks in different simulated assemblages. As noted in the recent review by Lupo and O'Connell (2002; see also Dominguez-Rodrigo, 2003), simulated samples generated by different researchers essentially lack the resolution for distinguishing human versus carnivore primary access to carcasses. Such ambiguity limits the applicability of some of these studies as reliable guides to faunal consumption strategies of Plio-Pleistocene humans. Compared to results from these experimental studies (Capaldo, 1997; Dominguez-Rodrigo, 1997; Lupo and O'Connell, 2002), the cut mark data from Porc-Epic fall within an overlapping range predicted by both human-first and carnivore-first models. Nonetheless, when compared to experimental data sets that projected distinct differences in the relative proportion of cut marks between human-first and carnivore-first assemblages, the cut mark data from Porc-Epic show clear association with the former (Assefa, 2002). Dominguez-Rodrigo's (1997) experimental study documented such distinctions in the frequency of cut marks on the upper-limb elements, and the high proportion of cut-marked femora and humeri from Porc-Epic is consistent with observations of human-first control samples. Accordingly, despite limitations in the effectiveness of controlled samples, the cut mark data from Porc-Epic favor humans as the likely agent of faunal accumulation. This observation is consistent with what was noted earlier in reference to the frequency and placement of tooth marks.

Table 4 Frequency of cut marks by skeletal element¹

			Size 1A			Size 1							Size 2	2				Size 3	3		Size 4						
BONE	Portions	Butchering segments	Cut mark (counts)	MAU	MCF	rMCF	crMCF	Cut mark (counts)	MAU	MCF	rMCF	crMCF	Cut mark (counts)	MAU	MCF	rMCF	crMCF	Cut mark (counts)	MAU	MCF	rMCF	crMCF	Cut mark (counts)	MAU	MCF	rMCF	crMCF
Cranial											i								i .			·					
Cranial Fragment		a	-	0.5	!		:	-	2.5	<u> </u>	<u> </u>	i	-	2		0.00	i .	-	0.5		0.00	<u> </u>	-	-			
Mandible		Cranial	-	5				2	4			0.00	1	5.5	0.18	0.00	0.00	-	1		0.00	0.00	-	0.5		0.00	0.00
Axial skeleton Atlas			-	2.		0.00			3		0.00		3	2.	1.50	0.07			1		0.00					0.00	\longrightarrow
Axis		Occiptal to Axis	-	-	-		0.00		1		0.00	0.00	-	2	1.50	0.00	0.07		1		0.00	0.00		-	-	0.00	0.00
Cervical Thoracic		Cervical Thoracic	- 1	0.14	0.83	1.00	1.00 0.00		0.4		0.00	0.00	- 3	0.8	4.23	0.00	0.00	-	0.2		0.00	0.00	-	0.2		0.00	0.00
Lumbar		Lumbar	-	- 0.14	-	0.00	0.00	- -	0.07		0.00	0.00	10	1.33	7.52	0.18	0.18	-	0.14		0.00	0.00	-	0.07		0.00	0.00
Caudal		Sacrum	-	-	-		0.00	-	0.8		0.00	0.00	-	0.9		0.00	0.00	-	0.1		0.00	0.00	-	-	-	0.00	0.00
Sacral Rib		Rib	-				0.00	- 2	1.07	1.87	1.00	1.00	- 11	0.4	9.65	0.00	0.00	1	0.6	2,5641	1.00	1.00	-	-		0.00	0.00
MCF total					0.83				07	1.87					22.89					2.56					0.00		
Forelimb		Scanula		4.5	0.22	0.07	0.07	2	7.5	0.27	0.04	0.04	10	9.5	1.05	0.06	0.06	11	1.5	7.3333	0.37	0.37		0.5		0.00	0.00
Scapula Humerus	PE	Scapula Shoulder	-	3	0.22	0.07	0.00	-	5	0.27	0.00	0.04	-	1	1.03	0.00	0.00	-	-	1.3333	0.00	0.00	-	0.5		0.00	0.00
	PS		-	2		0.00			4		0.00		-:-	1		0.00		-	- :	_	0.00			- :		0.00	
	MS DS	Humerus	3	6	0.50	0.16	0.38	38 5	10.5	3.62 0.45	0.55	0.62	37 22	10.5	3.52 3.67	0.19	0.38	8	4	2 7	0.10	0.46	12	0.5	12	0.57	0.57
	DE		1	3	0.33	0.11		6	12	0.50	0.08		-	2.5		0.00		-	0.5		0.00		-	0.5		0.00	
	PE PE	Elbow	-	4 8.5		0.00	0.11		4.5 4.5		0.00	0.08	2	2.5	1.00	0.00	0.05	-	0.5		0.00	0.00	1	0.5		0.00	0.00
radius	PS		-	9		0.00	0.11	-	5.5		0.00	0.00	-	2		0.00	0.05	-	0.5		0.00	0.00	-	0.5		0.00	0.00
	MS DS	Radioulna	10	28.5 2	0.35	0.11	0.44	15 1	25 1.5	0.60	0.09	0.19	16 6	23.5 2.5	0.68 2.40	0.04	0.16	4	4.5	0.8889	0.05	0.05	-	-		0.00	0.00
	DE		-	0.5	1.00	0.00	0.44	-	1.3	0.07	0.10	0.19	-	0.5	2.40	0.13	0.10	-			0.00	0.03	-	-		0.00	0.00
Carpals	DE	Wrist	-	-		0.00	0.00	-	1		0.00	0.00	-	2.5	0.25	0.00	0.02	-	0.5		0.00	0.00	-	-		0.00	0.00
Metacarpal	PE PS		-	0.5		0.00	0.00	-	2		0.00	0.00	- 3	8.5 1.5	0.35	0.02	0.02	-	0.5		0.00	0.00	-	0.5		0.00	0.00
	MS	Metacarpal	-	2		0.00		3	6.5	0.46	0.07		38	7	5.43	0.29		7	5	1.4	0.07		4	0.5	8	0.38	
	DS DE	Metacarpal distal	-	0.5		0.00	0.00		5		0.00	0.07	2	5.5	0.43	0.02	0.31	1	1	11	0.05	0.12	- 1	0.5	1	0.00	0.38
MCF total		Metacarpar distai		0.0	3.07	0.00	0.00			6.57	0.00	0.00		5.5	18.90	0.02	0.02			19.62	0.00	0.00			21.00	0.05	0.05
Hindlimb		P.1.	_		0.64	0.06	0.01	20	2.6	0.01	0.15	0.15		2.2	1.00	0.05	0.05			2 0000	0.10	0.10				0.00	0.00
Innominate Femur	PE	Pelvis Hip	9	3	1.00	0.06	0.06		36 5	0.81	0.17	0.17	32	32	1.00	0.07	0.07	- 13	4.5 0.5	2.8889	0.18	0.18	-	-		0.00	0.00
	PS		13	3.5	3.71	0.35			10		0.00		41	19	2.16	0.14		1	3.5	0.2857	0.02		1	0.5	2	0.11	
	MS DS	Femur	26	40.5 3.5	0.64	0.06	0.41	75	58 5	1.29	0.28	0.28	173 5	59.5 9	2.91 0.56	0.19	0.37	41 16	14.5 4.5	2.8276 3.5556	0.18	0.42	1	2.5 0.5	0.4	0.02	0.24
	DE		-	3		0.00		-	3.5		0.00		-	2.5		0.00		-	-		0.00		-	-		0.00	
Patella Tibia	PE	Knee		0.5		0.00	0.00	1	1	0.33	0.00	0.07	-	2		0.00	0.00	-	0.5		0.00	0.00		-		0.00	0.00
	PS		6	11	0.55	0.05	0.00	- 8	17.5	0.46	0.10	0.07	10	19.5	0.51	0.03	0.00	10	7	1.4286	0.09	0.00	2	1	2	0.11	0.00
	MS DS	Tibia	-	2.5		0.00	0.05	- 4	2 6.5	0.62	0.00	0.23	6	2	3.00	0.20	0.23	-	- 15		0.00	0.09	-	0.5		0.00	0.11
	DE		-	2.5		0.00	0.05	1	5	0.62	0.13	0.23	7	5	1.40	0.00	0.23	1	1.5	0.6667	0.00	0.09	-	-		0.00	0.11
Astragalus		A 1.1 .		-		0.00			3	0.00	0.00		-	2	0.50	0.00			1	0	0.00			1	0	0.00	
Calcaneus Small tarsals		Ankle		-		0.00		-	4	0.00	0.00		1 -	2	0.50	0.03			0.5	0	0.00			0.5	0	0.00	
Metatarsal		L				0.00	0.00		8.5		0.00	0.04	3	12	0.25	0.02	0.14	-	3.5	-	0.00	0.04		-		0.00	0.00
	PS MS	Metatarsal	- 4	0.5 1	4.00	0.00		5	2.5 5	1.00	0.00		- 27	3.5 11	2.45	0.00 0.16		18	1	2.25	0.00		- 5	0.5	10	0.00	
	DS			0.5		0.00	0.38		6		0.00	0.21	-	7		0.00	0.16	2	1	2	0.13	0.27	-	-		0.00	0.54
MCF total	DE	Metatarsal end	-	0.5	10.54	0.00	0.00	-	5.5	4.76	0.00	0.00	2	6.5	0.31	0.02	0.02	-	1.5	15.00	0.00	0.00	1	0.5	2	0.11	0.11
Phalanx	Γ				10.54					4.70					15.05					15.90					18.40		$\overline{}$
1st Phalanx 2nd Phalanx 3rd Phalanx			-	0.125 0.125 -	:			3	4.3 1.8 1.3	0.70			6 3 -	2.9 2.2 2.1	2.04 1.39			3 1	1.1 0.8 1.1	2.82 1.23			1 - -	0.2 0.3 0.1	4.21		

¹ Cut mark counts are the numbers of butchering marks by element. Following Milo (1998): MCF, mean cut-mark frequency = cut-mark counts/MAU; rMCF, relative mean cut-mark frequency = MCF (segment or portion)/sum of MCF (of animal unit); crMCF, combined relative mean cut-mark frequency = sum of rMCF of adjacent disarticulation or filleting segments. Other abbreviations are as follows: PE = proximal end, PS = proximal shaft, MS = middle shaft, DS = distal shaft, DE = distal end.

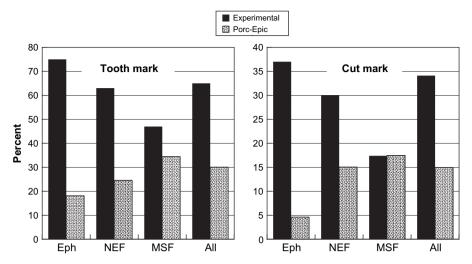


Fig. 10. Comparison of the frequency of tooth-marked and cut-marked long-bone fragments from Porc-Epic with Selvaggio's (1994a) experimental data set modeling secondary access to carcasses by humans. Eph = epiphysis; NEF = near-epiphysis fragment; MSF = mid-shaft fragment.

There is a general consensus among researchers (Binford, 1981; Bunn and Kroll, 1986; Lupo, 1994) that the placement and abundance of cut marks on skeletal elements is indicative of specific butchering activities. Cut marks on phalanges and lower-limb bones of larger mammals indicate the practice of skinning, while similar marks on ends of long bones and almost anywhere on most axial bones are associated with the disarticulation or dismemberment of carcasses. Similarly, cut marks on muscle-rich sections of certain elements such as the mid-shaft portions of long bones imply the practice of defleshing/filleting of meat (Binford, 1981; Marean and Assefa, 1999). To evaluate such activities, I followed Milo's (1998) approach of quantifying cut mark abundance using the combined relative mean cut mark frequency (crMCF) observed on each skeletal-element. This method is an effective approach

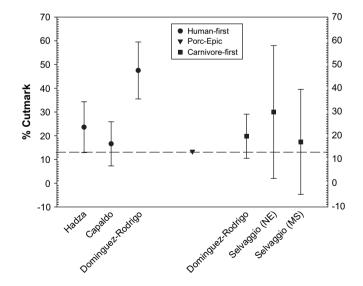


Fig. 11. The frequency of long-bone shaft fragments bearing one or more cut marks from Porc-Epic compared with similar data sets from controlled samples modeling initial access to carcasses by humans and carnivores. Data for experimental studies taken from Lupo and O'Connell (2002: Table 6); Porc-Epic = 13.4%. Abbreviations are the same as in Figure 9.

to comparing the relative abundance of cut marks across adjacent body parts of the same size class mammals.

At Porc-Epic, there is a similar pattern of cut mark distribution and abundance among mammals of all size classes (Table 4; Fig. 12). Mammals of size class 2, however, exhibit greater recurrence of cut marks on the axial elements. In contrast, among mammals of size classes 1 and 3, ribs are the only axial bones that show evidence of butchering activities. Traces of skinning activities on lower-limb elements (metapodials) and phalanges are present on faunal remains from mammals of all size classes. Despite a clear disparity in their sizes, the other two groups of mammals, size 1A and size 4, exhibit a similar pattern of relatively high concentration of cut marks on lower-limb elements, implying butchery activity related to skinning.

On the other hand, comparisons of cut mark concentrations within anatomical units (i.e., forelimb and hindlimb) consistently show (Fig. 12) the highest figures at muscle-rich segments that are identified by Milo (1998) as filleting zones. This pattern is evident on all size classes. Regular practice of defleshing or filleting could be possible only if the MSA occupants of the site had primary access to carcasses.

Skeletal-element abundance

Patterns of skeletal representations in archaeofaunal assemblages provide critical evidence about faunal exploitation strategies of prehistoric humans (Isaac, 1978; Binford, 1981, 1984; Potts, 1983, 1988; Bunn, 1986). Issues and controversies surrounding theoretical and methodological background to the application of skeletal-element profiles for understanding faunal exploitation strategies are discussed elsewhere (Lyman, 1985; Binford, 1988; Bunn et al., 1988; O'Connell and Hawkes, 1988; Grayson, 1989; Marean and Frey, 1997; Marean and Cleghorn, 2003; Munro and Bar-Oz, 2004). This analysis takes into account the underlying taphonomic and methodological issues raised by these groups of researchers in line with the analytical approaches for reconstructing the timing of access and carcass transport strategies using skeletal-element profiles.

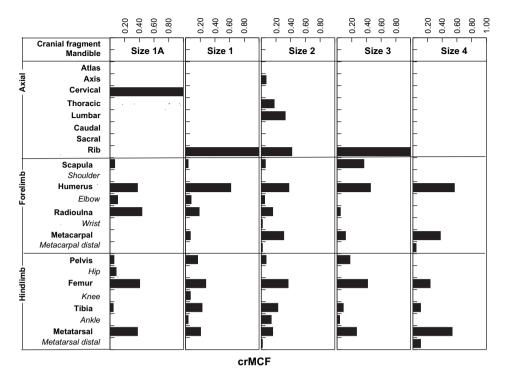


Fig. 12. Distribution of combined relative cut-mark frequency (crMCF) at the three major anatomical and economical units (axial bones, forelimb, and hindlimb) categorized by segments of disarticulation and filleting. Excluding axial bones, labels in bold represent filleting segments; labels in italics represent disarticulation, segments. The classification of different portions of each segment follows Milo's (1998: Table 6) scheme. Abbreviations are the same as in Table 4.

Examining the overall pattern of representation, Table 5 lists the skeletal-element frequencies for faunal remains by size class. Almost half of the faunal remains from Porc-Epic (about 45% of the 42,712 total specimens) are too fragmentary to identify to skeletal-element or to size class. The table lists the identifiable specimens, of which 63% could be identified only to general categories, such as long-bone fragment or non-identifiable fragment. Accordingly, even though the fraction-summation approach was employed, the number of specimens that could be identified to skeletal-element was limited to about 20% of the total faunal sample.

As shown in Table 5, on the basis of MNEs and MAUs, size 2, size 1, and size 1A mammals are the most abundant, in that order. There are relatively few size 3 mammals, and even fewer size 4 mammals. For all size classes, the meatiest body parts, such as upper-limb bones, scapulae, and pelves, are well represented. Using MNE, the femur is the most abundant element for all size classes. In size 1 and size 2 animals, the next most common element is the pelvis, which is also the second highest ranking nutritive element. In addition to the femur, other long-bone elements are well represented in the assemblage.

The inclusion of long-bone shaft fragments in the analysis of faunal remains generally results in higher counts of long bones (Marean, 1998; Marean and Assefa, 1999). The analytical advantage of employing "fraction-summation" lies primarily in its ability to incorporate shaft fragments into the quantification of long-bone abundance. The results presented in Fig. 13 show that the mid-shaft portion produces the highest MNE counts for nutritive long bones (femur, humerus, and radius), regardless of size. This is particularly evident for the

femur. Unlike the other long-bone elements, metapodials are relatively well-represented by epiphyses. This is consistent with the higher structural density of the ends of metapodials compared with those of other long-bone elements such as the femur and humerus (Lam et al., 1998). Throughout all size classes, the tibia is represented by an unusually high frequency of the proximal shaft, compared to the middle shaft portions of the element (Fig. 13).²

Among the other bones, pelves and, to a lesser degree, scapulae are well represented (Table 5). This may reflect their high utility and their association with other high-utility bones—the femur and humerus. The remaining axial bones—vertebrae and ribs—and cranial bones make up a very small portion of the faunal remains at Porc-Epic. Small bones such as tarsals and carpals are also under-represented in the assemblage.

The overall pattern of skeletal-element representation at Porc-Epic is different from the "head-and-foot"-dominated-pattern reported from many other MSA/MP sites (Klein, 1976; Binford, 1984, 1989, 1991; Stiner, 1994). A clear understanding of such a pattern of representation requires closer examination of behavioral and taphonomic factors that could have shaped the abundance of different body parts in one way or another. The following sections explore the principal factors that are known to have major influences in composition and abundance of skeletal elements at archaeological sites.

² It is possible that some unforeseen error in the documentation process, such as lack of consistent documentation of the internal foramen, resulted in the anomalous representation of the proximal and mid-shaft portions of tibia.

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Table 5

Raw and derived skeletal element data from Porc-Epic

	Size 1A				Size 1				Size 2					Siz	e 3		Size 4				
BONE	NISP	MNE	MAU	%MAU	NISP	MNE	MAU	%MAU	NISP	MNE	MAU	%MAU	NISP	MNE	MAU	%MAU	NISP	MNE	MAU	%MAU	
Horn Core	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	
Cranium	1	1	0.50	1.2	7	5	2.50	4.3	16	4	2.00	3.4	3	1	0.50	3.4	0	-	-	-	
Upper Dentition	25	5	2.50	6.2	20	4	2.00	3.4	16	4	2.00	3.4	23	7	2.50	17.2	6	3	0.50	16.7	
Lower Dentition	70	11	5.50	13.6	53	7	3.50	6.0	76	14	7.00	11.8	55	16	4.00	27.6	14	4	1.50	50.0	
Mandible	47	1	5.00	12.3	76	8	4.00	6.9	141	11	5.50	9.2	23	2	1.00	6.9	2	1	0.50	16.7	
Atlas	2	2	2.00	4.9	5	3	3.00	5.2	5	2	2.00	3.4	2	1	1.00	6.9	0	-	-	-	
Axis	0	-	-	-	1	1	1.00	1.7	7	2	2.00	3.4	1	1	1.00	6.9	0	-	-	-	
Cervical (3-7)	6	6	1.20	3.0	3	2	0.40	0.7	21	4	0.80	1.3	5	1	0.20	1.4	1	1	0.20	6.7	
Thoracic	2	2	0.14	0.4	3	1	0.07	0.1	25	1	0.71	1.2	5	2	0.14	1.0	1	1	0.07	2.4	
Lumbar	0	-	-	-	6	2	0.33	0.6	27	8	1.33	2.2	4	2	0.33	2.3	2	2	0.33	11.1	
Sacral	0	-	-	-	2	2	0.40	0.7	3	2	0.40	0.7	3	3	0.60	4.1	0	-	-	-	
Caudal	0	_	_	-	8	8	0.80	1.4	14	9	0.90	1.5	1	1	0.10	0.7	0	_	_	_	
Scapula	20	9	4.50	11.1	44	15	7.50	12.9	167	19	9.50	16.0	25	3	1.50	10.3	1	1	0.50	16.7	
Rib	6	_	-	-	180	30	1.07	1.8	752	32	1.14	1.9	460	11	0.39	2.7	27	-	-	-	
Humerus	49	13	6.50	16.0	137	24	12.00	20.7	260	22	11.00	18.5	86	9	4.50	31.0	17	3	1.50	50.0	
Radius	108	57	28.50	70.4	237	5_	25.00	43.1	328	47	23.50	39.5	45	9	4.50	31.0	8	1	0.50	16.7	
Ulna	27	22	11.00	27.2	41	16	8.00	13.8	156	14	7.00	11.8	29	2	1.00	6.9	0	-	-	-	
Carpals	0		-		2	2	1.00	1.7	17	5	2.50	4.2	1	1	0.50	3.4	0	_	_	_	
Metacarpal	10	4	2.00	4.9	95	14	7.00	12.1	234	17	8.50	14.3	71	1	5.00	34.5	16	2	1.00	33.3	
Pelvis	51	28	14.00	34.6	184	72	36.00	62.1	253	64	32.00	53.8	34	9	4.50	31.0	3	2	1.00	33.3	
Femur	207	81	40.50	100.0	483	116	58.00	100.0	747	119	59.50	100.0	158	29	14.50	100.0	21	6	3.00	100.0	
Patella	0	-	-	-	2	2	1.00	1.7	4	4	2.00	3.4	1	1	0.50	3.4	0	_	-	-	
Tibia	119	22	11.00	27.2	291	36	18.00	31.0	543	40	20.00	33.6	155	14	7.00	48.3	21	2	1.00	33.3	
Fibula	0		_		0	_	-	_	0	-		-	0	_	_	_	0	_	_	-	
Astragalus	0	_	_	_	8	6	3.00	5.2	4	3	1.50	2.5	2	2	1.00	6.9	2	2	1.00	33.3	
Calcaneum	0	_	_	_	11	8	4.00	6.9	8	4	2.00	3.4	1	1	0.50	3.4	1	1	0.50	16.7	
Metatarsal	8	3	1.50	3.7	106	18	9.00	15.5	285	24	12.00	20.2	112	16	8.00	55.2	14	2	1.00	33.3	
Small Tarsals	0	_		-	0	-	1	-	4	2	1.00	1.7	2	2	1.00	6.9	3	2	1.00	33.3	
Phalanges	2	1	0.13	0.3	83	35	4.38	7.5	101	24	3.00	5.0	46	1	1.25	8.6	7	2	0.25	8.3	
	760	1	0.13	0.5	2088	33	1 1.50	,	4214	21	2.00	5.0	1353	-	1.23	0.0	167				
	'00								l				1333				107				
Cranial Fragment	1		i	ì	20		ì	i	20		i		0		i		0		ì	\Box	
Long Bone Fragment	315				4308				7624				1946				125				
Non-ID Fragment	13		İ	İ	142			İ	253		İ	i	34		İ	i l	5		İ	i l	
			ļ	ļ.			!	ļ			ļ				ļ	ļ			!	ļ	

Ethnographic studies (Binford, 1978; Yellen, 1991a) and naturalistic and experimental research (Blumenschine, 1991; Marean and Spencer, 1991; Blumenschine et al., 1994) have documented that nutritional attractiveness of bones is the principal factor that determines the relative abundance of skeletal elements transported to archaeological sites (O'Connell and Hawkes, 1988; Metcalfe and Barlow, 1992; Bartram, 1993). Perkins and Daly (1968) invoked the concept of the "schlepp effect," stating that "the larger the animal and farther away it is killed, the fewer of its bones will get schlepped (dragged) back to the camp, village, or other area" (Daly, 1969: 149). Pertinent to this assumption is that a high concentration of high-utility elements at an archaeological site is a sign of primary access to carcasses by humans [for a review of alternative explanations, see O'Connell and Hawkes (1988), Monahan (1998), and Marean and Cleghorn (2003)].

Binford (1978) was the first to derive utility indices for the different anatomical units of small-to-medium mammals (sheep and caribou) based on their meat, grease, and marrow content. He (Binford, 1978, 1981) outlined a series of models relating utility indices to skeletal-element abundance to aid in distinguishing between hunted and scavenged assemblages and among the different carcass-transport strategies employed by predators. For faunal assemblages accumulated through hunting or confrontational scavenging, utility models predict

a positive relationship between skeletal-element abundance and bone utility, while the reverse is expected for passively scavenged assemblages (Metcalfe and Jones, 1988; Blumenschine and Madrigal, 1993; Emerson, 1993; Outram and Rowley-Conwy, 1998).

Figure 14 plots the relationship between the standardized food utility index [(S)FUI; Metcalfe and Jones, 1988] and skeletal-element abundance (% MAU) for Porc-Epic. For the purposes of this analysis, I used Metcalfe and Jones's (1988) caribou-based (S)FUI, which I prefer due to its inclusion of complete long-bone elements instead of just portions.

Utility and skeletal-element abundance in all size classes show a clear positive relationship consistent with a hunted assemblage. The accompanying table lists the Pearson's and Spearman's correlation coefficients and their *p*-values for each plot in the figure. For all size classes, both tests show a positive relationship between the two variables. However, the difference in statistical significance (*p*-values) between the Pearson's and Spearman's correlation coefficients is unusual. Ostensibly, such variation could be a reflection of the different types of scores that the two measures of relationships rely upon in calculating correlations. As a parametric test, the Pearson's correlation is applied to score data, whereas the non-parametric Spearman's correlation uses ranked data. Determining which test to use depends on the appropriate type of scale (ratio vs.

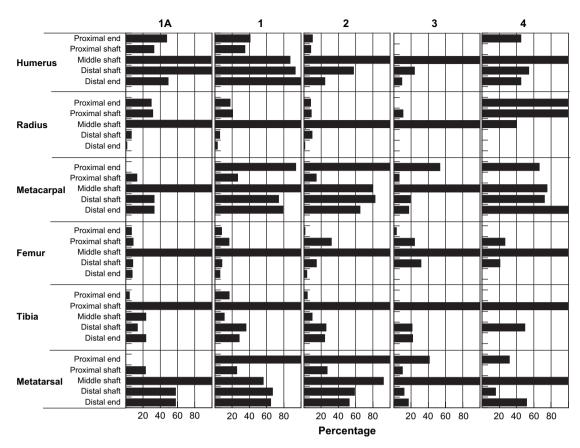


Fig. 13. Percent MNE by portions of long-bone elements from Porc-Epic.

ordinal) for variables under consideration. The fraction-summation approach that has been used to generate the skeletal-element abundance in this analysis is additive (Grayson, 1984) and also provides a natural zero point (Lyman, 1994). Therefore, it is plausible to consider the scale of the measurement as a ratio scale, which in turn partly justifies the application of Pearson's product-moment correlations. Consequently, despite the differences with the Spearman's rank correlations, the Pearson's correlation coefficients and *p*-values are considered more appropriate for testing the skeletal-element abundance from Porc-Epic. The result from the Pearson's correlation coefficient values clearly indicate that, irrespective of size classes, the faunal remains from Porc-Epic exhibit a statistically significant positive relationship with utility values.

Of all the skeletal elements, the abundance of the femur (indicated consistently in the upper right corner of the Fig. 14 graphs) has a disproportionate influence on the value and significance of the Pearson's correlation coefficients for all size classes. If the femur is excluded from the analysis, the relationships between utility and element abundance become much weaker, with values similar to the Spearman's rank correlation coefficients. This clearly indicates that the observed significant relationship is dictated by the presence of the femur and that the MSA occupants of Porc-Epic preferentially transported this element due to its high nutritional value.

Comparing the actual abundance of skeletal elements against the expected abundance based on regression, long-bone elements and other fleshy bones such as the pelvis occur at higher frequencies than predicted. In contrast, axial bones are under-represented throughout all size classes, while cranial bones occur at approximately their predicted abundance. Among size 3 and 4 mammals, both upper- and lower-limb elements, including the metapodials, are more abundant than is predicted by their utilities. This abundance of metapodials among larger mammals, similar to what Binford (1984) documented at Klasies River Mouth, would indicate preferential transport of large mammal lower-limb bones over those of smaller mammals. The greater absolute marrow content of the metapodials of larger mammals may have influenced their selection for transport.

In accordance with Marean and Cleghorn's (2003) recommendation, conducting utility analysis separately on what they sorted as high- and low-survival elements portrays positive relationships with food utility (for more details, see Assefa, 2002). However, a statistically significant positive relationship was observed only with high-survival or structurally denser elements, which for the most part comprises long bones. This result calls for closer investigation into the influence of density on patterns of faunal representation at Porc-Epic.

In a faunal assemblage, deletion of cancellous elements and epiphyseal fragments results from both carnivore-ravaging and sedimentary in situ destructions, which are both mediated by the relative density of bones (Lyman, 1985; Lam et al., 1998). A number of actualistic studies provide a framework for assessing the influence of carnivore ravaging on archaeological faunal assemblages. Figure 15 compares the proportion of

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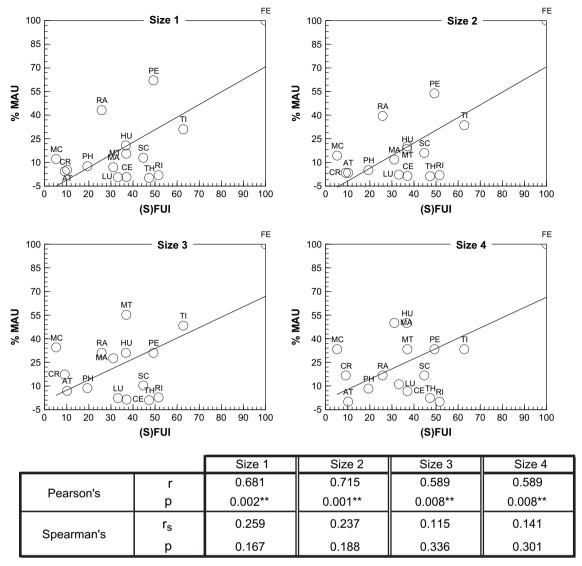


Fig. 14. Relationship between standardized utility index and skeletal-element abundance of different size classes. The table shows Pearson's and Spearman's correlation coefficient values and their associated *p*-values for each scatter plot. Abbreviations: CR = cranial; MA = mandible; AT = atlas; CE = cervical vertebrae; TH = thoracic vertebrae; LU = lumbar vertebrae; SC = scapula; RI = rib; HU = humerus; RA = radius; MC = metacarpal; PE = pelvis; FE = femur; TI = tibia; MT = metatarsal; PH = phalanges. ** indicate significant *P*-value.

epiphyseal and shaft fragments from Porc-Epic against experimental data sets derived by a number of researchers modeling hominid-only, hominid-to-carnivore, and carnivore-only consumption of bones. Faunal assemblages that have been exposed to initial consumption by carnivores (carnivore-only) or post-discard ravaging by carnivores (hominid-to-carnivore) both show extensive deletion of epiphyseal fragments. The faunal assemblage from Porc-Epic clearly exhibits analogous impacts due to the action of carnivores. However, Fig. 15 cannot provide a clear picture concerning the sequences of carcass consumption between humans and carnivores.

The simulated study by Marean and Spencer (1991) provides valuable data sets on the ravaging impact of carnivores on bones initially consumed and discarded by humans. Figure 16 plots the % MAU abundance of portions of three long-bone elements (tibia, femur, and metatarsal) from Porc-Epic against their respective percentage change after

carnivore attrition. In the scatter plot, a negative linear relationship indicates major post-discard attritional impact by carnivores, resulting in the deletion of cancellous/spongy portions of long bones. The observations from Porc-Epic show such a negative relationship for mammals of all size classes. Percentage change and % MAU show the most statistically significant relationship in size 2 and size 3 mammals $[r=-0.464 \ (p=0.041) \ \text{and} \ r=-0.588 \ (p=0.011),$ respectively]. 3

Inferentially, the loss of ends at Porc-Epic is a pattern of density-mediated destruction that is likely due to both carnivore-ravaging and in situ destruction, but perhaps weighted toward the former. The above comparative analysis particularly

³ The Spearman's corrections are $r_s = -0.440$ (p = 0.09) and $r_s = -0.492$ (p = 0.06) for size 2 and 3 mammals, respectively.

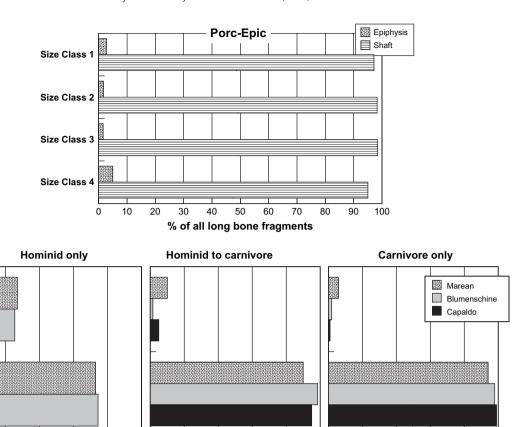


Fig. 15. Proportion of epiphyseal and shaft (including near-epiphysis) fragments from Porc-Epic compared with experimental studies modeling carnivore ravaging. Based on data compiled in Marean et al. (2000).

40

60 % of all long bone fragments

80

0

20

40

60

80

100

20

O

indicates that the influence of carnivores on the skeletal-element representation at Porc-Epic is more consistent with the patterns of post-discard damage or deletion, following initial consumption and modification by humans.

40

60

80

In general, the pattern of skeletal-element representation in mammals of all size classes, dominated by nutritionally highranking body parts, indicates primary access to carcasses by the MSA occupants of Porc-Epic. In accordance to the economic utility model, the composition of skeletal elements at Porc-Epic can be understood in terms of selective transport of the choicest elements by the MSA occupants of the site.

Discussion and conclusions

Epiphysis

Shaft

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The archaeological faunal assemblage from Porc-Epic provides rare insight into the ecology and economy of Middle Stone Age populations in this region of East Africa. Dating to the Last Glacial, the MSA fauna from Porc-Epic is dominated by small- and medium-sized mammals representing a diversity of species. While no extinct species were unequivocally identified, the faunal assemblage includes a number of taxa that did not occur historically in this region. This includes some species of alcelaphines (Alcelaphini indet., Damaliscus spp., Alcelaphus cf. buselaphus) and reduncines (Redunca spp., Kobus ellipsiprymnus). From a paleoecological perspective, the former groups of taxa indicate that, at the time of its occupation, the Porc-Epic area supported grazing animals in a more open, grassland-dominated habitat. Likewise, the presence of waterdependent taxa, such as the reduncines and Syncerus caffer, indicate proximity to a perennial source of water close to the site, possibly from the springs of Lägäharré and Lägädol or the adjacent Dächatu River, which is now active only during the rainy seasons. Represented in the immediate surroundings of Porc-Epic is an altitudinal gradient of ecological regimes that appears to have provided a rich and diverse source of prey for the MSA occupants of the site. Located high on a steep slope, Porc-Epic would have provided its residents with a commanding view for monitoring the movement of prey within the surrounding rugged valleys, banks of the Dächatu River, and patches of plains. In particular, the Dächatu River potentially attracted a wide array of animals that could have been a major source of prey for the occupants of Porc-Epic. The series of broken valleys surrounding the cave might have been convenient grounds for ambush hunting.

The patterns of fragmentation indicate that most of the bones were broken while still fresh, i.e., in the nutritive stage, consistent with marrow extraction by humans. The abundant tooth marks and cut marks observed in the sample indicate that a variety of agents, including rodents, carnivores, and humans,

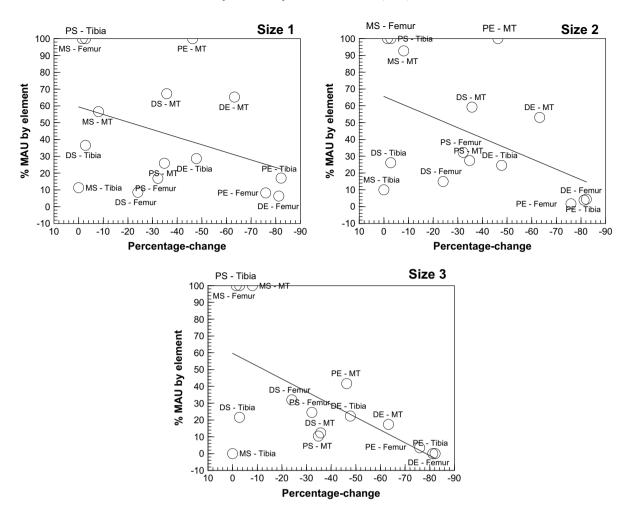


Fig. 16. Relationship between the relative abundance of portions of femur, tibia, and metatarsal and their expected percentage change due to carnivore ravaging. PE = proximal end; PS = proximal shaft; MS = middle shaft; DS = distal shaft; DE = distal end. Size class 4 is excluded due to small sample size.

contributed to the modification of the assemblage. Small rodents were responsible for the majority of gnaw marks. The frequency of carnivore tooth marks was more consistent with actualistic models in which carnivores had access to bones that had been previously exploited by humans, rather than those in which they had primary access to bones.

While a large proportion of the faunal sample—particularly the remains of the smaller mammals—exhibits cut marks, the significance of such marks is difficult to interpret. The placement and frequency of cut marks unequivocally indicate invariant practice of defleshing. In general, the patterns of surface modification support the interpretation that the human occupants of Porc-Epic had early access to prey carcasses and were the primary accumulators of the faunal assemblage.

The element frequency of the very small mammals—hares and hyraxes—is consistent with collection by raptors, but the presence of cut marks on many of their bones indicates that they were also a focus of human exploitation. Carnivores deleted many of the cancellous elements and portions of long bones, so a reliable estimate of skeletal-element abundance could be derived only from structurally dense elements or portions thereof, such as the mid-shafts of long bones. In contrast to many previous studies of MP/MSA faunal assemblages, this

analysis of the Porc-Epic fauna incorporated the quantification of long-bone shaft fragments. The skeletal-element profile from Porc-Epic shows an abundance of high-utility elements, a pattern distinct from the "head-and-foot" dominance documented at most other MP/MSA sites. For all size classes, middle shaft fragments of long bones produced the highest MAUs, and the femur was by far the most abundant element in the assemblage. In fact, the disproportionate abundance of the femur results in a statistically significant relationship between skeletal-element abundance and utility in parametric correlations, whereas the non-parametric correlations were not significant. Combined with the cut mark evidence, skeletal-element representation indicates that the MSA occupants of Porc-Epic effectively exploited the local fauna, discarding low-utility elements at the points of encounter and transporting the high-utility bones back to the site. Likewise, the low representation of lowerlimb elements, particularly the small, compact carpal and tarsal bones for all size classes, contrasts with what some authors predicted of patterns of faunal representations from ambush sites or encounter spots (e.g., Lupo and O'Connell, 2002).

Overall, the faunal assemblage at Porc-Epic consists of structurally dense and more resistant body parts, among which the upper-limb elements and other nutritive body parts constitute the most common elements among all size classes. Considering its location high on a steep slope, Porc-Epic Cave cannot have been strategically suitable as a kill site or an ambush spot. Regardless, if the cave had been used as a kill or ambush site or if its MSA occupants had been limited to secondary access to carcasses, the representation of low-utility but dense body parts such as the cranial bones and the lower-limb extremities should approach the proportion of the upper-limb elements. Alternatively, the most feasible explanation for the predominance of the latter group of elements is the selected transport of nutritionally high-ranking elements to a residential base, which Porc-Epic Cave must have represented to its MSA occupants.

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References

- Andrews, P., 1990. Owls, Caves and Fossils: Predation, Preservation, and Accumulation of Small Mammal Bones in Caves, with an Analysis of the Pleistocene Cave Faunas from Westbury-Sub-Mendip, Somerset, UK. The University of Chicago Press, Chicago.
- Assefa, Z., 2002. Investigations of faunal remains from Porc-Epic: A Middle Stone Age site in southeastern Ethiopia. Ph.D. Dissertation, State University of New York at Stony Brook.

- Bartram, L.E., 1993. Perspectives on skeletal part profiles and utility curves from eastern Kalahari ethnoarchaeology. In: Hudson, J. (Ed.), From Bones to Behavior. Southern Illinois University, Carbondale, pp. 115–137.
- Bartram, L.E.J., Marean, C.W., 1999. Explaining the "Klasies Pattern": Kua ethnoarchaeology, the Die Kelders Middle Stone Age archaeofauna, long bone fragmentation and carnivore ravaging. J. Archaeol. Sci. 26, 9–29.
- Behrensmeyer, A.K., 1978. Taphonomic and ecological information from bone weathering. Paleobiology 4, 150–162.
- Behrensmeyer, A.K., 1991. Terrestrial vertebrate accumulations. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy: Releasing the Data Locked in the Fossil Record. Plenum, New York, pp. 291–327.
- Benvenuti, M., Carnicelli, S., Belluomini, G., Dainelli, N., Di Grazia, S., Ferrari, G.A., Iasio, C., Sagri, M., Ventra, D., Atnafu, B., Kebede, S., 2002. The Ziway-Shala lake basin (main Ethiopian rift, Ethiopia): a revision of basin evolution with special reference to the late Quaternary. J. Afr. Earth Sci. 35, 247–269.
- Binford, L.R., 1978. Nunamuit Ethnoarchaeology. Academic Press, New York. Binford, L.R., 1981. Bones: Ancient Men and Modern Myth. Academic Press, New York.
- Binford, L.R., 1984. Faunal Remains from Klasies River Mouth. Academic Press, New York.
- Binford, L.R., 1985. Human ancestors: changing views of their behavior. J. Anthropol. Archaeol. 4, 292–327.
- Binford, L.R., 1988. Fact and fiction about the *Zinjanthropus* floor: data, arguments, and interpretations. Curr. Anthropol. 29, 123–149.
- Binford, L.R., 1989. Isolating the transition to cultural adaptations: an organizational approach. In: Trinkaus, E. (Ed.), Emergence of Modern Humans: Biocultural Adaptations in the Late Pleistocene. Cambridge University Press, Cambridge, pp. 18–41.
- Binford, L.R., 1991. The human revolution: behavioral and biological perspectives on the origins of modern humans. J. Field Archaeol. 18, 111–115.
- Blumenschine, R.J., 1988. An experimental model on the timing of hominid and carnivore influence on archaeological bone assemblages. J. Archaeol. Sci. 15, 483–502.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behavior. Nature 333, 763–765.
- Blumenschine, R.J., 1991. Hominid carnivory and foraging strategies and the socio-economic function of early archaeological sites. Philos. Trans. R. Soc. Lond. B Biol. Sci. 334, 211–219.
- Blumenschine, R.J., Selvaggio, M., 1991. On the marks of marrow bone processing by hammerstones and hyaenas: their anatomical patterning and archaeological implications. In: Clark, J.D. (Ed.), Cultural Beginnings: Approaches to Understanding Early Hominid Life-ways in the African Savannah. Union Internationale des Sciences Préhistoriques et protohistoriques Monographien Band 19, pp. 17–32.
- Blumenschine, R.J., Madrigal, T.C., 1993. Variability in long bone marrow yields of East African ungulates and its zooarchaeological implications. J. Archaeol. Sci. 20, 555–587.
- Blumenschine, R.J., Cavallo, J., Capaldo, S.D., 1994. Competition for carcasses and early hominid behavioral ecology: a case study and conceptual framework. J. Hum. Evol. 27, 197–213.
- Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determination of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. J. Hum. Evol. 29, 21–51.
- Blumenschine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of interanalyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. J. Archaeol. Sci. 23, 493-507.
- Bolton, M., 1973. Notes on the current status of and distribution of some large mammals in Ethiopia. Mammalia 37, 562–586.
- Bosellini, A., Russo, A., Assefa, G., 2001. The Mesozoic succession of Dire Dawa, Harar Province, Ethiopia. J. Afr. Earth Sci. 32, 403–417.
- Boule, M., Vallois, H.V., 1957. Fossil Men. The Dryden Press, New York.
- Brain, C.K., 1980. Some criteria for the recognition of bone-collecting agencies in African caves. In: Behrensmeyer, A.K., Hill, A.H. (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology. University of Chicago Press, Chicago, pp. 107–130.

- Z. Assefa | Journal of Human Evolution xx (2006) 1-26
- Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.
- Brandt, S.A., 1986. The Upper Pleistocene and early Holocene prehistory of the Horn of Africa. Afr. Archaeol. Rev. 4, 41–82.
- Bräuer, G., 1984. The Afro-European *sapiens* hypothesis and hominid evolution in East Asia during the late Middle Pleistocene and Upper Pleistocene. Cour. Forschungsinst. Senckenb. 69, 145–165.
- Breuil, H., Teilhard de Chardin, P., Wernert, P., 1951. Le Paléolithique du Harar. L' Anthropologie 55, 219–230.
- Brooks, A.S., Robertshaw, P., 1990. The glacial maximum in tropical Africa: 22,000 to 12,000 BP. In: Gamble, C., Soffer, O. (Eds.), Low Latitudes. The World at 18,000 BP, vol. 2. Unwin Hyman, London, pp. 121–169.
- Brown, B., 1943. Palaeontology of Harrar Province, Ethiopia. Bull. Am. Mus. Nat. Hist. 82, 7–13.
- Buikstra, J.E., Swegle, M., 1989. Bone modification due to burning: experimental evidence. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Institute for Quaternary Studies, University of Maine, Orono, pp. 247–258.
- Bunn, H.T., 1983. Comparative analysis of modern bone assemblages from a San hunter-gatherer camp in the Kalahari Desert, Botswana, and from a spotted hyena den near Nairobi, Kenya. In: Clutton-Brock, J., Grigson, C. (Eds.), Animals and Archaeology. British Archaeological Reports International Series, Oxford, pp. 143–148.
- Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. J. Hum. Evol. 15, 673–690.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai gorge, Tanzania. Curr. Anthropol. 27, 431–452.
- Bunn, H.T., Bartram, L.E., Kroll, E.M., 1988. Variability in bone assemblage formation from Hadza hunting, scavenging, and carcass processing. J. Anthropol. Archaeol. 7, 412–457.
- Capaldo, S.D., 1995. Inferring carnivore and hominid behavior from dualpatterned archaeological assemblages. Ph.D. Dissertation, Rutgers University.
- Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. J. Hum. Evol. 33, 555–597.
- Chase, P.G., 1986. The Hunters of Combe Grenal: Approaches to Middle Paleolithic Subsistence in Europe. British Archaeological Reports International Series 286, Oxford.
- Chase, P.G., 1989. How different was Middle Paleolithic subsistence. In: Mellars, P., Stringer, C. (Eds.), The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans. Princeton University Press, Princeton, pp. 321–337.
- Clark, J.D., 1982. The cultures of the Middle Paleolithic/Middle Stone Age. In: Clark, J.D. (Ed.), The Cambridge History of Africa: From the Earliest Times to c. 500 BC. Cambridge University Press, New York, pp. 248–340.
- Clark, J.D., Williamson, K.D., 1984. A Middle Stone Age occupation site at Porc-Epic Cave, Dire Dawa (east-central Ethiopia), Part I. Afr. Archaeol. Rev. 2, 37-64.
- Clark, J.D., 1988. The Middle Stone Age of East Africa and the beginnings of regional identity. J. World Prehist. 2, 235–305.
- Cruz-Uribe, K., Klein, R.G., 1998. Hyrax and hare bones from modern South African eagle roosts and the detection of eagle involvement in fossil bone assemblages. J. Archaeol. Sci. 25, 135–147.
- Daly, P., 1969. Approaches to faunal analysis in archaeology. Am. Antiq. 34, 146–153.
- Deino, A.L., McBrearty, S., 2002. ⁴⁰Ar/³⁹Ar dating of the Kapthurin Formation, Baringo, Kenya. J. Hum. Evol. 42, 185–210.
- Dobney, K., Rielly, K., 1988. A method for recording archaeological animal bones: the use of diagnostic zones. Circaea 5, 79–96.
- Dominguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge (Tanzania): an experimental approach using cut mark data. J. Hum. Evol. 33, 669–690.
- Dominguez-Rodrigo, M., 2003. On cut marks and statistical inferences: methodological comments on Lupo & O'Connell (2002). J. Archaeol. Sci. 30, 381–386.
- Egeland, C.P., Pickering, T.R., Dominguez-Rodrigo, M., Brain, C.K., 2004. Disentangling Early Stone Age palimpsests: determining the functional

- independence of hominid- and carnivore-derived portions of archaeofaunas. J. Hum. Evol. 47, 343.
- Emerson, A.M., 1993. The role of body part utility in small scale hunting under two strategies of hunting. In: Hudson, J. (Ed.), From Bones to Behavior. Southern Illinois University, Carbondale, pp. 138–155.
- Fisher, J.W., 1995. Bone surface modifications in zooarchaeology. J. Archaeol. Meth. Theor. 2, 7–68
- Gasse, F., Street, F.A., 1978. Quaternary lake level fluctuations and environments of the northern rift valley and Afar region. Palaeogeogr. Palaeoclimatol. Palaeoecol. 24, 279–295.
- Gasse, F., Rognon, P., Street, F.A., 1980. Quaternary history of the Afar and Ethiopian lakes. In: Williams, M.A.J., Faure, H. (Eds.), The Sahara and the Nile. A.A. Balkema, Rotterdam, pp. 361–400.
- Gasse, F., Fontes, J.-C., 1989. Palaeoenvironments and palaeohydrology of a tropical closed lake (Lake Asal, Djibouti) since 10,000 yr B.P. Palaeogeogr. Palaeoclimatol. Palaeoecol. 69, 67–102.
- Gifford, D., 1981. Taphonomy and paleoecology: a critical review of archaeology's sister discipline. Adv. Archaeol. Meth. Theor. 4, 365–437.
- Gifford-Gonzalez, D., 1989. Ethnographic analogues for interpreting modified bones: Some cases from East Africa. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Institute for Quaternary Studies, University of Maine, Orono, pp. 179–246.
- Gifford-Gonzalez, D., 1991. Bones are not enough: analogues, knowledge, and interpretive strategies in zooarchaeology. J. Anthropol. Archaeol. 10, 215–254.
- Grayson, D.K., 1984. Quantitative Zooarchaeology. Academic Press, New York
- Grayson, D.K., 1989. Bone transport, bone density, and reverse utility curves. J. Archaeol. Sci. 16, 643–652.
- Hamilton, A.C., 1982. Environmental History of East Africa: A Study of the Quaternary. Academic Press, London.
- Henshilwood, C.S., Marean, C.W., 2003. The origin of modern human behavior: critique of the models and their test implications. Curr. Anthropol. 44, 627–651.
- Hockett, B.S., 1991. Toward distinguishing human and raptor patterning on leporid bones. Am. Antiq. 56, 667–679.
- Hoffman, R., Hays, C., 1987. The eastern wood rat (*Neotoma floridana*) as a taphonomic factor in archaeological sites. J. Archaeol. Sci. 14, 325-337.
- Ingersol, R.H., 1968. The ecological stratification of mammals in the eastern Chercher Highlands of Harar province, Ethiopia. Ph.D. Dissertation, Oklahoma State University.
- Isaac, G.L., 1978. Food sharing and human evolution: archaeological evidence from the Plio-Pleistocene of East Africa. J. Anthropol. Res. 34, 311–325.
- Johnson, E., 1985. Current developments in bone technology. Adv. Archaeol. Meth. Theor. 8, 157–235.
- Kingdon, J., 1989. East African Mammals: An Atlas of Evolution in Africa, vol. 3, Part D: Bovids. University of Chicago Press, Hampshire.
- Klein, R.G., 1976. The mammalian fauna of the Klasies River Mouth sites, southern Cape Province, South Africa. S. Afr. Archaeol. Bull. 31, 75-98.
- Klein, R.G., Cruz-Uribe, K., 1983. The computation of ungulate age (mortality) profiles from dental crown heights. Paleobiology 9, 70–78.
- Klein, R.G., 1989. Biological and behavioral perspectives on modern human origins in southern Africa. In: Mellars, P., Stringer, C. (Eds.), The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans. Princeton University Press, Princeton, pp. 529–547.
- Klein, R.G., Cruz-Uribe, K., 1996. Exploitation of large bovids and seals at Middle and Later Stone Age sites in South Africa. J. Hum. Evol. 31, 315–334
- Lam, Y.M., 1992. Variability in the behavior of spotted hyaenas as taphonomic agents. J. Archaeol. Sci. 19, 389-406.
- Lam, Y.M., Chen, X., Marean, C.W., Frey, C.J., 1998. Bone density and long bone representation in archaeological faunas: comparing results from CT and photon densitometry. J. Archaeol. Sci. 25, 559–570.

- Z. Assefa | Journal of Human Evolution xx (2006) 1-26
- Lupo, K.D., 1994. Butchering marks and carcass acquisition strategies: distinguishing hunting from scavenging in archaeological contexts. J. Archaeol. Sci. 21, 827–837.
- Lupo, K.D., O'Connell, J.F., 2002. Cut and tooth mark distributions on large animal bones: ethnoarchaeological data from the Hadza and their implications for current ideas about early human carnivory. J. Archaeol. Sci. 29, 85-109.
- Lyman, R.L., 1985. Bone frequencies: differential transport, in situ destruction and the MGUI. J. Archaeol. Sci. 12, 221–236.
- Lyman, R.L., 1987. Archaeofaunal and butchery studies: a taphonomic perspective. Adv. Archaeol. Meth. Theor. 10, 249-337.
- Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.
- Marean, C.W., Spencer, L., 1991. Impact of carnivore ravaging on zooarchaeological measures of element abundance. Am. Antiq. 56, 645–656.
- Marean, C.W., Frey, C., 1997. Animal bones from caves to cities: reverse utility curves as methodological artifact. Am. Antiq. 62, 698–711.
- Marean, C.W., 1998. A critique of the evidence for scavenging by Neandertals and early modern humans: new data from Kobeh Cave (Zagros Mountains, Iran) and Die Kelders Cave 1 (South Africa). J. Hum. Evol. 35, 111–136
- Marean, C.W., Kim, S.Y., 1998. Mousterian large-mammal remains from Kobeh Cave: behavioral implications for Neanderthals and early modern humans. Curr. Anthropol. 39, 79–113.
- Marean, C.W., Assefa, Z., 1999. Zooarchaeological evidence for the faunal exploitation behavior of Neanderthals and early modern humans. Evol. Anthropol. 8, 22–37.
- Marean, C.W., Abe, Y., Frey, C.J., Randall, R.C., 2000. Zooarchaeological and taphonomic analysis of the Die Kelders Cave 1 layers 10 and 11 Middle Stone Age larger mammal fauna. J. Hum. Evol. 38, 197–233.
- Marean, C.W., Abe, Y., Nilssen, P., Stone, E.C., 2001. Estimating the minimum number of elements (MNE) in zooarchaeology: a review and a new image-analysis GIS approach. Am. Antiq. 66, 333–360.
- Marean, C.W., Cleghorn, N., 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. J. Taphonomy 1, 15-42.
- Marean, C.W., Domínguez-Rodrigo, M., Pickering, T.R., 2004. Skeletal element equifinality in zooarchaeology begins with method: The evolution and status of the "shaft critique.". J. Taphonomy 2, 69–98.
- Marean, C.W., Assefa, Z., 2005. The middle and upper Pleistocene African record for the biological and behavioral origins of modern humans. In: Stahl, A. (Ed.), African Archaeology: A Critical Introduction. Blackwell Publishing Ltd, pp. 93–129.
- Marshall, F., Pilgram, T., 1991. Meat versus within-bone nutrients: another look at the meaning of body part representation in archaeological sites. J. Archaeol. Sci. 18, 149–163.
- McDougall, I., Brown, F.H., Fleagle, J.G., 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. Nature 433, 733–736.
- Messerli, B., Winiger, M., Rognon, P., 1980. The Saharan and East African uplands during the Quaternary. In: Williams, M.A.J., Faure, H. (Eds.), The Sahara and the Nile: Quaternary Environments and Prehistoric Occupation in northern Africa. A.A. Balkema, Rotterdam, pp. 87–118.
- Metcalfe, D., Jones, K.T., 1988. A reconsideration of animal body-part utility indices. Am. Antiq. 53, 486–504.
- Metcalfe, D., Barlow, K.R., 1992. A model for exploring the optimal trade-off between field processing and transport. Am. Anthropol. 94, 340–356.
- Michels, J.W., Marean, C.A., 1984. A Middle Stone Age occupation site at Porc-Epic Cave, Dire Dawa (east-central Ethiopia), Part II. Afr. Archaeol. Rev. 2, 64–71.
- Milo, R.G., 1998. Evidence for hominid predation at Klasies River Mouth, South Africa, and its implication for the behavior of early modern humans. J. Archaeol. Sci. 25, 99-133.
- Monahan, C.M., 1998. The Hadza carcass transport debate revisited and its archaeological implications. J. Archaeol. Sci. 25, 405–424.
- Morlan, R.E., 1994. Bison bone fragmentation and survivorship: a comparative method. J. Archaeol. Sci. 21, 797–807.
- Munro, N.D., Bar-Oz, G., 2004. Debating issues of equifinality in ungulate skeletal part studies. J. Taphonomy 2, 1–14.

- Myers, T.P., Voorhies, M.R., Corner, R.G., 1980. Spiral fractures and bone pseudotools at paleontological sites. Am. Antiq. 45, 483–490.
- Nillson, E., 1940. Ancient changes of climate in British East Africa and Abyssinia: a study of ancient lakes and glaciers. Geogr. Ann. 22, 1–78.
- O'Connell, J.F., Hawkes, K., 1988. Hadza hunting, butchering, and bone transport and their archaeological implications. J. Anthropol. Res. 44, 113–161.
- Oliver, J.S., 1994. Estimates of hominid and carnivore involvement in the FLK *Zinjanthropus* fossil assemblage: some socio-ecological implications. J. Hum. Evol. 27, 267–294.
- Outram, A., Rowley-Conwy, P., 1998. Meat and marrow utility indices for horse (*Equus*). J. Archaeol. Sci. 25, 839—849.
- Outram, A.K., 2001. A new approach to identifying bone marrow and grease exploitation: Why the "indeterminate" fragments should not be ignored. J. Archaeol. Sci. 28, 401–410.
- Perkins, D., Daly, P., 1968. A hunter's village in Neolithic Turkey. Sci. Am. 219, 96–106.
- Perles, C., 1974. Réexamen typologique de l'industrie du Porc-Épic (Éthiopie): les pointes et piéces pointues. L' Anthropologie 78, 529–552.
- Pickering, T.R., Marean, C.W., Dominguez-Rodrigo, M., 2003. Importance of limb bone shaft fragments in zooarchaeology: a response to "On in situ attrition and vertebrate body part profiles" (2002), by M.C. Stiner. J. Archaeol. Sci. 30, 1469—1482.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2005. The contribution of limb bone fracture patterns to reconstructing early hominid behaviour at Swartkrans Cave (South Africa): archaeological application of a new analytical method. Int. J. Osteoarchaeol. 15, 247—260.
- Pleurdeau, D., 2001. Geston des matières premières et comportements techniques dans le Middle Stone Age Africain: Les assemblages lithiques de la grotte du Porc-épic (Dire Dawa, Éthiopia). Ph.D. Dissertation, Museum National D'Histoire Naturelle Laboratoire de Prehistoire.
- Pleurdeau, D., 2003. Le Middle Stone Age de la grotte du Porc-Epic (Dire Dawa, Ethiopie): gestion des matieres premieres et comportements techniques. L' Anthropologie 107, 15—48.
- Potter, E.C., 1976. Pleistocene glaciation in Ethiopia: new evidence. J. Glaciol. 17, 148–150.
- Potts, R., 1983. Foraging for faunal resources by early hominids at Olduvai Gorge, Tanzania. In: Clutton-Brook, J., Grigson, C. (Eds.), Animals and Archaeology. British Archaeological Reports International Series, Oxford, pp. 51–62.
- Potts, R., 1988. Early Hominid Activities at Olduvai. Aldine de Gruyter, New York.
- Potts, R., 1994. Variables versus models of early Pleistocene hominid land use. J. Hum. Evol. 27, 7–24.
- Rick, T.C., Vellanoweth, R.L., Erlandson, J.M., 2005. Radiocarbon dating and the "old shell" problem: direct dating of artifacts and cultural chronologies in coastal and other aquatic regions. J. Archaeol. Sci. 32, 1641.
- Sanders, W.J., Trapani, J., Mitani, J.C., 2003. Taphonomic aspects of crowned hawk-eagle predation on monkeys. J. Hum. Evol. 44, 87–105.
- Selvaggio, M.M., 1994a. Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. J. Hum. Evol. 27, 215–228.
- Selvaggio, M.M., 1994b. Evidence from carnivore tooth marks and stone tool butchery marks for scavenging by hominids at FLK Zinjanthropus Olduvai Gorge, Tanzania. Ph.D. Dissertation, Rutgers University.
- Shipman, P., 1988. Actualistic studies of animal resources and hominid activities. In: Olsen, S.L. (Ed.), Scanning Electron Microscopy in Archaeology. British Archaeological Reports International Series 452, pp. 261–285.
- Shipman, P., 1989. Altered bones from Olduvai Gorge, Tanzania: techniques, problems and implications of their recognitions. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Institute for Quaternary Studies, University of Maine, Orono, pp. 317–334.
- Stahl, P.W., 1982. On small mammal remains in archaeological context. Am. Antiq. 47, 822–829.
- Stiner, M.C., 1994. Honor Among Thieves: A Zooarchaeological Perspective on Neandertal Ecology. Princeton University Press, Princeton.

- Stringer, C., 2002. Modern human origins: progress and prospects. Philos. Trans. R. Soc. Lond. B Biol. Sci. 357, 563—579.
- Teilhard de Chardin, P., 1930. Observations géologiques en Somalie Française et Au Harrar. Société Géologique de France (Nouvelle série) 6, 5–12.
- Tobias, P.V., 1962. A re-examination of the Kanam Mandible. In: Mortelmans, G., Nenquin, J. (Eds.), Actes du IVe Congrès panafricain de Préhistoire et de l'étude du quaternaire. Musee Royale de L'Afrique Centrale, Tervuren, pp. 341–358.
- Vallois, H.V., 1951. La mandibule humaine fossile de la grotte du Porc-epic pres Dire Daoua (Abyssinie). L' Anthropologie 55, 231–238.
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. J. Hum. Evol. 21, 27–48.

- White, F., 1983. The Vegetation of Africa. UNESCO, Paris.
- White, T.D., Asfaw, B., DeGusta, D., Gilbert, H., Richards, G.D., Suwa, G., Howell, F.C., 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. Nature 423, 742–747.
- Wolde-Mariam, M., 1972. An Introductory Geography of Ethiopia. Berhanena Selam H.S.I. Printing Press, Addis Ababa.
- Yalden, D.W., Largen, M.J., Kock, D., 1984. Catalogue of the mammals of Ethiopia. 5. Artiodactyla. Monitore Zoologico Italiano: Italian Journal of Zoology 19 (Suppl.), 67–221.
- Yellen, J.E., 1991a. Small mammals: !Kung San utilization and production of faunal assemblages. J. Anthropol. Archaeol. 10, 1–26.
- Yellen, J.E., 1991b. Small mammals: post-discard patterning of !Kung San faunal remains. J. Anthropol. Archaeol. 10, 152–192.