



Evidence of early butchery of giant lemurs in Madagascar

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Abstract

We report here definitive evidence of butchery, most probably associated with hunting, of giant extinct lemurs by early human settlers in Madagascar. Specimens of *Palaeopropithecus ingens* and *Pachylemur insignis* from two sites in southwestern Madagascar, Taolambiby and Tsirave, show classic signs of butchering. We compared these to the bones (also from Taolambiby) of butchered *Propithecus verreauxi*, a lemur still living in the region. The characteristics of the tool-induced extinct-lemur bone alterations (sharp cuts and chop marks near joints, oblique cuts along the shafts, spiral fractures, and percussion striae) suggest skinning, disarticulation, and filleting. Conclusive evidence of megafaunal modification by humans in Madagascar was limited previously to a few hippo and elephant bird bones and one extinct aye-aye tooth. New evidence comes not from archaeological sites, but from specimens collected in the early 1900s, without stratigraphic records, at “subfossil” sites (i.e., sites renowned for their late Pleistocene or Holocene fossils, often lacking human artifacts). Whereas these are hardly the most ideal samples for analysis of this kind, careful scrutiny of the characteristics of the cut marks has allowed us to document butchery beyond any reasonable doubt. One bone with definitive cut marks has been dated to the very earliest part of the human period in Madagascar. Continued, careful research on the bones in subfossil collections is warranted.

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Introduction

The role of human hunting in the extinctions of the giant lemurs of Madagascar is the subject of intense debate (Burney, 1999). The coexistence of humans and megafauna on Madagascar is incontrovertible, and most, if not all, of the megafaunal extinctions occurred after humans colonized the Great Red Island (Burney et al., 2004). The global synchronicity of human arrival and megafaunal decline, and the naïveté of the fauna at first contact, have been invoked as evidence that hunting by humans was the primary cause of megafaunal extinction (Martin, 1967, 1984; Walker, 1967a). Large body size and diurnal habits would have made the megafauna easy hunting targets for humans. However, the dearth of direct evidence for butchery at archaeological sites in Madagascar and the absence of a game-dependent Stone Age culture (Dewar and Wright, 1993) argue against a human overkill (or “Blitzkrieg”) hypothesis (Dewar, 1984). Indeed, the pattern of extinction speaks against Martin’s (1967, 1984) prediction of a rapid extinction wave, since many species survived the advent of humans by at least a thousand years (Burney, 1999; Burney et al., 2004). And, whereas there is recent folk memory of the existence of megafauna (Godfrey, 1986; Burney and Ramilisonina, 1999) and even of rituals associated with their killing (Molet, 1951; Haring, 1979), the conspicuous absence of their skeletal remains from archaeological sites spanning the last 1000 years bears testimony to a culture that did not depend on megafaunal hunting for its subsistence. Instead, giant lemurs and other megafauna may have succumbed to natural or human-induced habitat modification or to diseases introduced by humans or their commensals (Humbert, 1927; Mahé and Sourdat, 1972; Dewar, 1984; MacPhee and Marx, 1997; see review by Burney, 1999). Indeed, a key factor contributing to megafaunal extinctions worldwide may be slow reproductive rates, not large body size per se (Johnson, 2002; see also Dewar, 1984).

To date, direct evidence of butchery of giant lemurs in Madagascar is sparse. Battistini and Vérin (1967) suggested that perforations on two *Archaeolemur* skulls may be direct evidence of

human hunting, but their published drawings are inconclusive. Walker (1967a) similarly attributed a frontal fracture on the skull of an *Archaeolemur majori* from Andrahomana in southeast Madagascar (BMNH M7374) to human agency, but radiocarbon dating has since shown this specimen to precede the human period (3975 ± 53 ^{14}C yr BP; P.S. Martin, pers. comm.).

Several specimens of megafauna at subfossil sites in southwest Madagascar (Lamboharana, Itampolo, Ambolisatra/Andolononby) show evidence of human modification. At Lamboharana, Guillaume Grandidier (1902, 1928) discovered pierced incisors of *Daubentonia robusta*, which appeared to have been worn as charms (see also MacPhee and Raholimavo, 1988). A human modified *Aepyornis* tibiotarsus from Itampolo has been dated to the early human period (1880 ± 70 ^{14}C yr BP; Burney, 1999). Neither of these provide evidence of butchery, but rather indicate postmortem utilization of the bones or teeth. Informative as these artifacts may be as elements of the material culture of the early human settlers of Madagascar, they do not offer any insight into hunting or butchering practices.

However, Grandidier (1905) and MacPhee and Burney (1991) described human-modified hippo bones from Lamboharana and Ambolisatra/Andolononby. These bones date to the early human period (including a femur dated at 2020 ± 300 ^{14}C yr BP, another at 1740 ± 50 ^{14}C yr BP, and a third at 1970 ± 90 ^{14}C yr BP) and show chop marks that were apparently made when the bones were “green,” and thus comprise evidence for megafaunal butchery (see Landon, 1996 for similar evidence of butchery in North America). Nevertheless, these sparse data are insufficient to fully support Martin’s hunting hypothesis (MacPhee and Burney, 1991).

Although direct evidence of human hunting is slim, indirect evidence of early large-scale megafaunal hunting is found in the pollen records of Madagascar. On the basis of pollen of introduced plants (such as *Cannabis*) in sediment cores, we know that humans arrived in Madagascar by ca. 2000 years ago (Burney et al., 2004). Human arrival is followed almost

immediately by a precipitous decline in megafaunal biomass, as indirectly measured in sediment cores by spores of the coprophilous fungus, *Sporormiella* (Burney et al., 2003), a fungus that cannot complete its life cycle in the absence of the dung of large animals. This decline predates by several centuries an apparent increase in the frequency or severity of fire (evidenced by a peak of charcoal microparticles in sediment cores), and it predates by 1000 years evidence of the introduction of cattle (Burney et al., 2003, 2004). Human hunting is a likely (although not the only possible) cause of the initial megafaunal decline, as hunting can explain the preferential disappearance of large-bodied animals virtually immediately after humans colonized the island and well before the rise in charcoal microparticles.

If there was an initial megafaunal collapse due to hunting, then direct evidence of megafaunal butchery should be sought in the regions that were first settled by humans and in the period immediately following human arrival. The best evidence of megafaunal butchery should be located not at the later archaeological sites, but at paleontological sites dating to between 2300 and 1600 years ago. Recently, we announced the discovery of cut marks indicative of butchery on some bones of *Palaeopropithecus ingens* at Taolambiby, and dating from the earliest part of the human period in Madagascar (Perez et al., 2003). A number of subfossil sites that have yielded at least some bones, shell, or other organic materials date from the early human period. Many of these are in the Southwest – the region apparently first settled by people (reviewed in Burney et al., 2004). They include Ambolisatra/Andolononby, Itampolo, and Lamboharana (the sites at which modified hippo and other megafaunal bones have been found; MacPhee and Burney, 1991), but also Ampoza, Bemafandry, Behavoha (or Bevoha), Tsiandroina, Taolambiby, and Tsirave (Fig. 1). The latter have been previously interpreted as largely or entirely paleontological rather than archaeological (but see Raison and Vérin, 1967). We review in detail the evidence that giant lemurs were butchered, describe the butchery practices, and explore their possible implications.

Materials and methods

Localities and ages

We examined bones of extinct and extant lemurs collected from two subfossil sites (Taolambiby and Tsirave) in southwest Madagascar, at least some of which are likely to date to the early human period on the island (Fig. 1). These fossils were collected in the early and mid 1900s by Methuen (Taolambiby), Lamberton (Tsirave and Taolambiby), and Walker (Taolambiby). Fossiliferous sedimentary layers have been exposed at both sites by recent stream erosion (Walker, 1967b; Raison and Vérin, 1967), although at Taolambiby, the original deposits containing the primates appear to have been excavated or eroded away. Descriptions of the stratigraphy at Taolambiby are available (Walker, 1967b; Raison and Vérin, 1967; Tattersall, 1973), and in 2004 an expedition to Taolambiby by David Burney and crew exposed a long stratigraphic sequence that contains in its lower layers a potentially integrated sequence of data from pollen, seeds, bones, and shells. Of special interest for the reconstruction of events surrounding the subfossil extinctions are the decline of dung-fungus spores, representing megafauna, and the increase in charcoal particles, presumably at about the time of human arrival. Tsirave, located about 20 km south of Beroroha on the Isahena River, was briefly described by Lamberton (1930, 1931) in oral presentations to the Académie Malgache, but no detailed description of its stratigraphy is available. A single radiocarbon date on a subfossil lemur tooth collected by Lamberton at Tsirave gives an age of 2194 ± 70 BP (Burney et al., 2004).

Paul Ayshford Methuen was one of the first European explorers to visit Taolambiby, a site he called “Antolanbiby.” Two radiocarbon dates, on a lower molar of *Megaladapis madagascariensis* (2713 ± 44 ^{14}C yr BP) and a radius of *Palaeopropithecus ingens* (2325 ± 43 ^{14}C yr BP; see Perez et al., 2003; Burney et al., 2004), suggest that Methuen’s collection spanned the arrival of humans on Madagascar. Neither Methuen nor Lamberton recorded any stratigraphic information for the specimens they collected at Taolambiby, but the

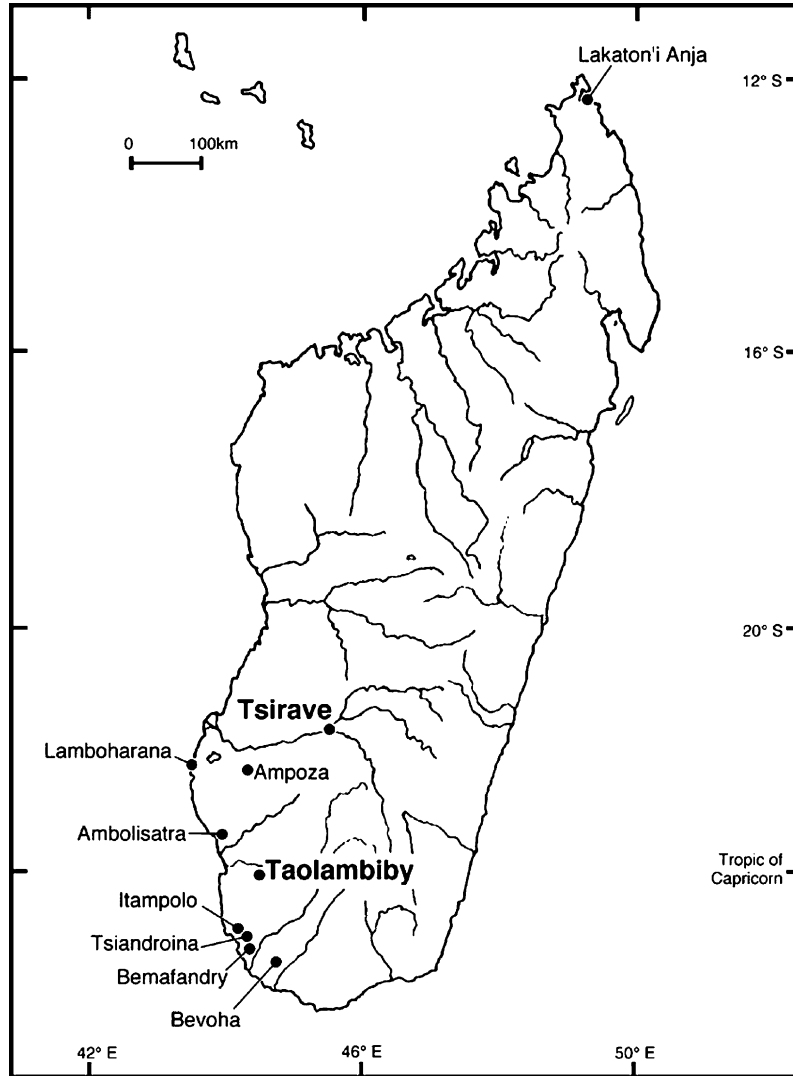


Fig. 1. Map of Madagascar showing subfossil sites mentioned in the text, and highlighting Taolambiby and Tsirave.

taxa in each collection (see below) suggest that both are likely to represent the same time frame.

Walker's collection from Taolambiby retains the most stratigraphic information and differs from earlier collections in its focus on extant lemurs and relative dearth of specimens of extinct lemurs. Much of the Walker collection may be drawn from a later period when the giant lemur species were locally extinct or very rare. The abundance of extant lemur (*Propithecus*) bones in Walker's collection may be explained, at least in

part, because Walker recognized cut marks on these remains and sought to collect them (pers. comm., 2005). Walker (1967b, p. 443, and pers. comm.) did not excavate at Taolambiby but rather found bones along the stream bank eroding out of a layer called the "black sands" — a fossiliferous and humic layer 50 cm thick and separated from the modern soil by 60 cm of "white and brown sands with alternating leached and humic layers." The *Propithecus* bones, a *Palaeopropithecus* ulna, and a jaw of an *Archaeolemur* were found

along ~20 m of outcrop on the west side of the stream depicted on Walker's Taolambiby site map (1967b, p. 440; see also Raison and Vérin, 1967). Occasional bones were found in a deeper layer of "fawn sands." Specimens of *Pachylemur* (including a humerus and a jaw) collected at Taolambiby during the following year by Paul Martin and others (housed at the United States National Museum, Washington, D.C.) derive from the fawn sands and from sediments up to a foot below the fawn sands (P. Martin, unpublished collection notes). Although the time depth of the Walker collection is unknown, a single, radiocarbon-dated, modified *Propithecus* humerus (TAO-66-1) is historic in age (Burney et al., 2004) and falls within the modern range of size variation for this taxon.

Collections and samples

As mentioned, our samples were drawn from three collections: (1) Paul A. Methuen's collection from Taolambiby, made in 1911 and housed at the Oxford University Museum of Natural History, UK (Godfrey et al., 2001); (2) Charles Lambertton's collections from both Tsirave and Taolambiby, housed at the Université d'Antananarivo, Madagascar (Lamberton, 1930, 1931, 1933); and (3) Alan Walker's collection from Taolambiby, now housed at the University of Massachusetts, Amherst (Walker, 1967b).

Methuen's collection includes five extinct lemur species (*Palaeopropithecus ingens*, *Mesopropithecus globiceps*, *Archaeolemur majori*, *Megaladapis madagascariensis*, and *Pachylemur insignis*) and several species of extant lemurs (*Propithecus verreauxi*, or Verreaux's sifaka, and *Lemur catta*, the ring-tailed lemur), along with other vertebrates (including the rare, extinct aardvark-like *Plesiorcycteropus madagascariensis*, extinct pygmy hippos and elephant birds, and the extinct carnivore *Cryptoprocta spelea*). *Palaeopropithecus* is the most common lemur in the Methuen collection, followed by *Pachylemur*. Because in 1911 associations of postcrania and crania of giant lemurs were poorly understood, many of Methuen's taxonomic identifications (reported in Jenkins, 1987) were erroneous. Methuen's

collection entered into obscurity until it was re-discovered almost a century later (Godfrey et al., 2001).

In the 1930s, Charles Lambertton, one of the most successful fossil hunters in Madagascar, built an extensive collection of subfossil specimens from a half dozen sites in southwest Madagascar. At Tsirave, Lambertton found specimens of many extinct primate species, including *Pachylemur insignis*, *Archaeolemur majori*, *Hadropithecus stenognathus*, *Mesopropithecus globiceps*, *Megaladapis* spp., *Daubentonia robusta*, and several extant primate species, including *Propithecus verreauxi* and *Lepilemur* spp. (Tattersall, 1973; Vuillaume-Randriamanantena, 1983; Godfrey et al., 1999). Of these, *Pachylemur insignis* is the best represented, with a minimum number of individuals of 57 – eight times the minimum number of the next most abundant primate species, *Archaeolemur majori* (Vuillaume-Randriamanantena, 1983). At Taolambiby, which he called Betioky Tulear, Lambertton found the same extinct species that Methuen had recovered, with the exception of *Mesopropithecus*. *Pachylemur* and *Palaeopropithecus* are the best represented extinct primates in Lambertton's Taolambiby collection (Vuillaume-Randriamanantena, 1983).

Alan Walker's collection includes mostly extant lemurs (especially *Propithecus verreauxi*), but also isolated bones of extinct taxa, including *Pachylemur*, *Archaeolemur*, and *Palaeopropithecus*. But here, it is the bones of extant lemurs that are of primary interest, precisely because, as Walker recognized, many show signs of butchery. The extant lemur taxa in this collection (*Propithecus verreauxi*, *Lemur catta*, and *Lepilemur leucopus*) are still found in nearby forests.

In all, 297 bones or bone fragments from all three collections were microscopically examined for surface modification by one of us (VRP) at the University of Massachusetts and Hampshire College, Amherst. These included bones with scratches or fractures of various sorts borrowed from the Methuen (n = 22) and Lambertton (n = 3) collections as well as the entire Walker collection (n = 272). For logistical reasons, no attempt was made to microscopically study the entire Methuen or Lambertton collections; rather,

only selected bones with signs of natural or human modification were chosen. However, the entire Methuen collection, which comprises approximately 90 primate specimens (including long bones, metapodials and phalanges, and skull and jaw fragments), was initially examined at Oxford by LRG, who corrected mistaken prior taxonomic attributions and then borrowed the long bones (but not the jaws, metapodials, or phalanges) of *Palaeopropithecus*, several *Megaladapis* jaw fragments, and several partial postcrania of *Pachylemur* for microscopic examination by VRP. The Lambertton collection was initially examined in Antananarivo by NV and LRG, with special attention paid to all non-fragmentary femora of *Pachylemur* (a total of 96 specimens from eight subfossil sites). Fifty-seven of these were from Tsirave, but only two were from Taolambiby. A subsample of six femora from Tsirave (and none from Taolambiby) exhibited signs of peri- or postmortem damage. Three of the six were borrowed for microscopic examination by VRP. Finally, the entire Walker collection was examined and checked for accuracy of taxonomic attributions by LRG, and all of the primates (with the exception of a few fragmentary bones of nocturnal lemurs) were then subjected to microscopic analysis by VRP. The primates included one partial long bone of a *Palaeopropithecus*, two of *Pachylemur*, 265 bones (or partial bones) of *Propithecus verreauxi*, and 4 *Lemur catta*. The elements of *Propithecus* included femora, tibiae, fibulae, patellae, calcanei, tali, entocuneiforms, a mesocuneiform, ectocuneiforms, cuboids, metatarsals, proximal phalanges, middle phalanges, humeri, ulnae, radii, metacarpals, clavicles, one scapula, innominates, vertebrae (cervical, thoracic, lumbar, and caudal), and cranial fragments (occipital, auditory bullae, maxillae, mandibles, and partial skulls).

Microscopic analysis

We used a 7–90 power zoom trinocular microscope with an external fiber optic light source to identify cut marks, tooth marks, and percussion marks using criteria established in bioarchaeology, zooarchaeology, forensics, and taphonomic sciences (White, 1992; Lyman, 1994; Blumenschine

et al., 1996; Pijoan and Mansilla, 1997; Reichs, 1998; Reitz and Wing, 1999; Lupo and O'Connell, 2002). The presence or absence of cut marks, chop marks, spiral fractures, flaking, pitting, scarring, and scraping was recorded for each element. In addition, evidence of natural taphonomic processes such as weathering, root damage, and carnivore and rodent gnawing was recorded. Once a bone was identified as having definitive cut marks, drawings were made with the location and orientation of the features accurately represented. In addition, we recorded cut mark location (anterior, posterior, medial, or lateral), position (proximal, distal, or somewhere near the middle of the shaft), length, width, depth, floor shape (V or U), and orientation (whether the cut was made parallel to, at an oblique angle to, or perpendicular to the long axis of the shaft).

When possible, a vinyl polysiloxane impression (mold) was made of the cut marks using 3M Imprint II, a hydrophilic material designed for precise dental impressions, which we used to make accurate negative impressions. Casts were made from these molds using an epoxy resin. With an Isomet low-speed saw, we thin-sectioned casts of these marks and from these sections the geometry of the molded cut marks (maximum depth, width, and other general morphological characteristics) was documented using a stereomicroscope fitted with a bio-imaging video screen and measurement software. This level of precision is ideal for identifying and analyzing perimortem processing (Walker and Long, 1977; Walker, 1978; Binford, 1981; Bunn, 1981; Bromage and Boyde, 1984; Bunn and Kroll, 1986; Lyman, 1987; Milo, 1998; Ubelaker, 1998; Perez, 2003). This process was unsuccessful for the specimens of *Palaeopropithecus* in the Methuen collection because these bones had been impregnated with wax, as was standard curatorial policy at some museums during the early 1900s. Multiple attempts (using ether or low-level heat generated from a Fostec light source with a dual flexible gooseneck spot lens) to remove the wax without damaging the bones were successful in improving cut mark visibility for microscopic work; however, molding continued to be impossible. Estimates of the depth and shape of these cut marks could be made, although with less precision than

would have been possible had we been able to cast these features. It is also possible that we have underestimated the number of cut marks on these bones, as the wax was thick in places and only removed in regions where cuts were apparent.

Identification of butchery-produced cut and chop marks

We identified features as “butchering marks” only when they met two strict “tests”: (1) There must be “patterning or redundancy.” In other words, the same type of marks must be found in the same region of bone and within the same species; and (2) There must be some sign of “purposefulness,” such as an anatomical necessity for the tool marks to occur in a given location (Guilday et al., 1962). Because splintering, spiral fractures, and percussion striae can be caused by nonhuman agents, these were not taken as definitive evidence of human processing. We recognize that, when animals are butchered, most of their bones may show no signs of butchery. The major appendicular elements are the most likely elements to have cut or chop marks, but even these elements can lack telltale signs of butchery, if the flesh is sufficiently thick that tools do not cut all the way through it.

The placement, orientation, and form of cut marks were used to identify the types of tools that produced the marks, as well as to infer butchering practices (following Binford, 1981; Bunn, 1981; Bromage and Boyde, 1984; Lyman, 1987; Selvaggio, 1994, 1998; Perez, 2003) as there is a direct correlation between tool type and mark characteristics (Walker and Long, 1977; Shipman, 1981; Olsen, 1988; Blumenschine et al., 1996; Greenfield, 1999). Cuts produced by bifacially flaked or re-touched opportunistic lithic blades demonstrate extreme variability in their cross-sectional morphology due in part to these implements’ convoluted or serpentine cutting edges, which tends to produce wide and asymmetrical kerfs (Walker and Long, 1977; Potts and Shipman, 1981; Shipman and Rose, 1983; Olsen and Shipman, 1988; White and Toth, 1989; Blumenschine et al., 1996; Perez, 2002). In contrast, smooth-edged metal knives leave more

uniform marks that tend to have deeper profiles and narrow, V-shaped kerf walls, and with either no striations or with very uniform striations (Fig. 2; Walker and Long, 1977; Shipman, 1981; Maples, 1986; Olsen, 1988; Blumenschine et al., 1996; Reichs, 1998; Greenfield, 1999). Although metal knife blades taper to an edge, tending to be V-shaped in cross section, the same blade can produce both V- and U-shaped kerf floors depending on how the knife is wielded during the butchering process. This is because an action such as chopping involves the transfer of considerable force from the blade to the bone, which compresses the cortex, leaving a U-shaped floor. Depending on the angle of insertion of the knife, the direction of the force being applied, and the dullness of the edge of the blade, cuts with U-shaped floors but smooth walls also can be produced when metal blades are drawn across the surface of the bone. Unmodified lithic flakes or uniform stone blades, like metal knives, may also produce symmetrical, V- or U-shaped cuts with smooth walls. However, there is less consistency in cuts made by these lithic tools because their edges tend to deteriorate and collapse resulting in broader, irregular kerf walls, more similar to those produced by bifacially flaked tools. The shape and features of cuts produced by lithic tools depend heavily on the degree of friction, and dynamic or static

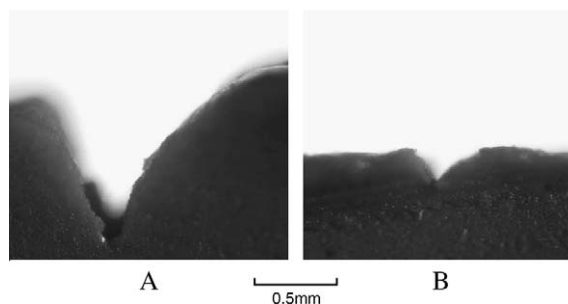


Fig. 2. Casts showing cross-sections of cut marks on: A) A left femur of a *Pachylemur insignis* from Tsirave (UA 3059, Lambertson collection). B) A long bone fragment of *Propithecus verreauxi* from Taolambiby (Walker collection). Both photographs were taken at 100 \times . Note the V-shaped profiles and smooth sides of the kerf walls of both cuts.

loading (Maples, 1986; Lyman, 1987; Reichs, 1998; Greenfield, 1999).

In contrast to cut marks, chop marks are clefts or notches generated by the force of impact of a blade on bone. These tend to have adhering or hinged flakes around the primary injury. They also produce fracture lines and considerable wastage (small segments of bone split from the area of impact) along with extensive fracturing. When striations are present, they are generally parallel to each other and to the direction of the implement strike (Mathieu and Meyer, 1997; Reichs, 1998; Greenfield, 1999). Another factor that can affect chop marks is the size of the animal (or bone) being butchered. Due to differences in bone thickness, the long bones of small and large-bodied animals fragment differently during percussion processing (Bartram and Marean, 1999).

Statistical analyses and interpretation

The cut and chop mark data for the long bones were entered into an SPSS (Version 12) database and the correlation structure of the variables (location, orientation, length, width, and floor shape) was examined. We compared cut mark characteristics and distributions for extinct and extant species. Independent-sample t-tests (for cut mark lengths) and non-parametric tests (for ordinal traits) were conducted to test the significance of differences in the metric attributes of marks with V- vs. U-shaped floors. We used accounts in the literature and personal observations of modern Malagasy hunting and butchery practices to help us interpret the results.

Results

Table 1 summarizes the occurrence of marks of various types on the lemur bones in our sample. In total, 10 of the 28 specimens of extinct lemurs that we examined microscopically, and 77 of the 269 specimens of extant lemurs, show definitive signs of butchery in the form of cut and/or chop marks. Bones in our sample exhibited very few nonhuman taphonomic changes. Neither the extinct nor extant specimens exhibited any carnivore damage or any evidence of scavenging by rodents. Sedimentary abrasions (or other postmortem damage) appeared to be present on some ($n = 9$) of the *Palaeopropithecus* bones from Taolambiby as well as the *Megaladapis* bones and two of the *Pachylemur* bones we examined. Bones of lemurs in the Walker collection were remarkably free of modifications other than those attributable to human butchery.

Figure 2 shows the cross sections of some of the marks on bones of extinct and extant lemurs that we have identified as cut marks. The shape of the kerfs on these bones suggests the use of a sharp-edged, metal implement that compressed the cortex to the sides as it was drawn across the surface of the bone (Walker and Long, 1977; Shipman, 1981; Maples, 1986; Olsen, 1988; Blumenschine et al., 1996; Reichs, 1998; Greenfield, 1999). Although few of the specimens in our sample have been directly dated, available radiocarbon dates are consistent with our assessment of types of marks. Of the three radiocarbon dates obtained on specimens in our sample, only two fall in the human period, and these are the two with cut marks (a *Palaeopropithecus* radius and *Propithecus*

Table 1
Number of elements with marks, by taxon, and mark type

Taxon	Number of elements examined	Sedimentary abrasion marks	Nonhuman predation or scavenging marks	Cut marks only	Cut marks and chop marks	Chop marks only	Total with definitive butchery
<i>Palaeopropithecus</i>	20	9	0	6	2	0	8
<i>Pachylemur</i>	6	2	0	0	2	0	2
<i>Megaladapis</i>	2	2	0	0	0	0	0
<i>Lemur</i>	4	0	0	0	0	0	0
<i>Propithecus</i>	265	0	0	8	3	66	77
Total	297	13	0	14	7	66	87

humerus). A *Megaladapis* jaw that predates the human period bears only sedimentary damage.

Patterns of butchery

Table 2 lists the definitive butchery-induced cut or chop marks on specimens of extinct lemurs at both Taolambiby and Tsirave, as well as those of *Propithecus* (sifakas) at Taolambiby. We provide here our assessment of the activities related to their production. Hand and foot bones with cut or chop marks, as well as small bone fragments, are omitted from this list.

Palaeopropithecus

Of the 20 long bones of *Palaeopropithecus* from Taolambiby examined here, eight (or 40%) have definitive cut or chop marks. One is an ulna from the Walker collection (TAO-66-43), with two chops and an associated cut lying in the plane of the chop marks. The bone was sliced through the shaft near the distal end, which is all that remains of it in the collection. We cannot assume a stratigraphic association of this ulna with the butchered *Palaeopropithecus* material that Methuen collected at the same site. The latter include a humerus of an infant with both a distal cut mark and a chop mark (Fig. 3A), and a humerus of an adult with a total of 18 cut marks (proximal, distal, and along the midshaft) (Fig. 4). Five additional long bones of adult *Palaeopropithecus* with cut marks were part of a series of fifteen elements with the same original catalogue number (OUM 14346, now OUM 14346a) that may have come from the same stratigraphic layer or context. These include an adult humerus, radius, ulna, and two tibiae. In all, a total of 45 cut marks and three chop marks were identified on eight bones of *Palaeopropithecus* from Taolambiby (Table 2).

The cut marks vary in length from 2.3 to 14.5 mm for the *Palaeopropithecus* sample, with a mean of 5.6 mm and a standard deviation of 2.3 mm. Most match what Binford (1981), Jelinex (1993), Lyman (1987), and others identify as disarticulation and skinning marks. Disarticulation marks are registered near the joints and tend to be oriented across the long axis of the bone, either obliquely or at 90 degrees (Fig. 5). All

Palaeopropithecus long bones with cut marks show evidence of disarticulation at the proximal and/or distal ends. Filleting marks produced by the removal of muscle are present on three bones: an ulna (OUM 14346a L, Fig. 5), a humerus (OUM 14342a A), and a tibia (OUM 14346a C). There are 10 bones in the OUM 14346a series that lack chop or cut marks. They do show other signs of possible human modification (as most bear spiral fractures and some have percussion striae). About 75% of all of the *Palaeopropithecus* long bones or bone fragments in the Methuen collection bear spiral fractures. Postmortem scratches (probable sedimentary abrasions) occur on some elements, but there is no evidence of carnivore chew marks or rodent damage.

Megaladapis

Neither of the *Megaladapis* bones from Taolambiby (Methuen collection) was interpreted as having butchery-related cut or chop marks. Both show postmortem scratches. A mandible has postmortem damage (a small scratch) on the external surface of the horizontal ramus, anterior to the insertion of the masseter muscle. There was no carnivore or scavenger damage on either of the specimens of *Megaladapis* that we examined.

Pachylemur

Of the six bones of *Pachylemur insignis* that we examined, two (or 33%), including a femur from Taolambiby (OUM 14341, Methuen collection) and another from Tsirave (UA 3059, Lambertson collection), have definitive cut marks (Tables 1-2). These features average 5.0 mm (SD = 1.9 mm) in length and vary from 3.0 to 9.3 mm.

The femur from Taolambiby is fragmentary; only its proximal portion remains, and it bears a chop mark, a cut mark, and a spiral fracture. The femur from Tsirave is complete, and has 5 cut marks (including two along the midshaft indicative of filleting) as well as a chop mark (Fig. 3B). The chop mark, located at the distal end of the femur, is very similar in appearance and location to the chop mark on the infant humerus of *Palaeopropithecus ingens* described above (cf. Fig. 3A and B). Most distinctive are the two horizontal cuts across the posterior face of the femoral

Table 2

Lemur subfossil bones (excluding hand and foot bones) with definitive butchery-induced cut or chop marks, and inferred activities related to their production

Taxon and specimen number	Bone	Site	Number and position of cut marks showing evidence of disarticulation/fragmentation.	Number and position of cut marks showing evidence of filleting.	Presence and distribution of chop marks showing evidence of disarticulation/fragmentation.
<i>Palaeopropithecus</i> OUM 14342A	Humerus	Taolambiby	4 Proximal, 9 Distal	5 Midshaft	
<i>Palaeopropithecus</i> OUM 14342B	Humerus	Taolambiby	1 Distal		Distal
<i>Palaeopropithecus</i> OUM 14346a A	Humerus	Taolambiby	4 Proximal		
<i>Palaeopropithecus</i> OUM 14346a C	Tibia	Taolambiby	2 Proximal, 3 Distal	3 Midshaft	
<i>Palaeopropithecus</i> OUM 14346a D	Radius	Taolambiby	1 Proximal		
<i>Palaeopropithecus</i> OUM 14346a G	Tibia	Taolambiby	2 Proximal, 4 Distal		
<i>Palaeopropithecus</i> OUM 14346a L	Ulna	Taolambiby	4 Proximal	2 Midshaft	
<i>Palaeopropithecus</i> TAO-66-43	Ulna	Taolambiby	1 Distal, in plane of chops		Distal
<i>Pachylemur</i> OUM 14341	Femur	Taolambiby	1 Proximal		
<i>Pachylemur</i> UA 3059	Femur	Tsirave	1 Proximal, 4 Distal	2 Midshaft	Distal
<i>Propithecus</i> TAO-66-1	Humerus	Taolambiby	1 Proximal, 2 Distal, 1 Midshaft		
<i>Propithecus</i> TAO-66-2	Humerus	Taolambiby	1 Proximal		Proximal
<i>Propithecus</i> TAO-66-3	Femur	Taolambiby	3 Proximal		
<i>Propithecus</i> TAO-66-4	Femur	Taolambiby	1 Distal		Distal
<i>Propithecus</i> TAO-66-5	Femur	Taolambiby	1 Midshaft		
<i>Propithecus</i> TAO-66-6	Tibia	Taolambiby	3 Midshaft		
<i>Propithecus</i> TAO-66-7	Femur	Taolambiby	1 Distal		
<i>Propithecus</i> TAO-66-8	Tibia	Taolambiby	3 Proximal		Proximal
<i>Propithecus</i> TAO-66-9	Clavicle	Taolambiby	2 Lateral, 1 Medial		
<i>Propithecus</i> TAO-66-10	Tibia	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-11	Tibia	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-12	Tibia	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-13	Tibia	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-14	Tibia	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-15	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-16	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-17	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-18	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-19	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-20	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-21	Femur	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-22	Femur	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-23	Femur	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-24	Femur	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-25	Femur	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-26	Femur	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-27	Femur	Taolambiby			Distal

(continued on next page)

Table 2 (continued)

Taxon and specimen number	Bone	Site	Number and position of cut marks showing evidence of disarticulation/fragmentation.	Number and position of cut marks showing evidence of filleting.	Presence and distribution of chop marks showing evidence of disarticulation/fragmentation.
<i>Propithecus</i> TAO-66-28	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-29	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-30	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-31	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-32	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-33	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-34	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-35	Fibula	Taolambiby			Midshaft
<i>Propithecus</i> TAO-66-36	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-37	Femur	Taolambiby			Distal
<i>Propithecus</i> TAO-66-38	Tibia	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-39	Tibia	Taolambiby			Midshaft
<i>Propithecus</i> TAO-66-40	Tibia	Taolambiby			Midshaft
<i>Propithecus</i> TAO-66-41	Femur	Taolambiby			Proximal
<i>Propithecus</i> TAO-66-42	Tibia	Taolambiby			Distal
<i>Propithecus</i> TAO-66-44	Clavicle	Taolambiby	1 Lateral		
<i>Propithecus</i> TAO-66-45	Patella	Taolambiby	1 Edge		

OUM = Oxford University Museum of Natural History, Methuen Collection. UA = Université d'Antananarivo, Madagascar, Lambertson Collection. TAO-66 = Taolambiby 1966 Walker Collection (now housed at the University of Massachusetts, Amherst, Department of Anthropology).

condyles (Fig. 3B). A single motion would have produced these cuts, as they are perfectly aligned. That action would have served the purpose of severing the lower from the upper leg at the knee joint.

Two additional specimens of *Pachylemur* from Taolambiby (a distal femur and a partial innominate) show no evidence of butchery. These belong to the Walker collection; they are broken, but there is no sign that this was deliberate. We also found no sign of butchery-induced cut marks on two additional femora of *Pachylemur* from Tsirave (belonging to the Lambertson collection). One (UA FPL 67) shows evidence of trowel or shovel damage. There are several cuts on this bone that were clearly made by humans, but: (1) they are very wide; (2) their walls and floors are almost square; (3) the cuts appear to serve no purpose; they occur at random orientations on the middle of the shaft – nowhere near muscle origins or insertions; (4) the cuts clearly bisect a sedimentation mark, thus indicating that the bone had been free of soft tissue and scratched by sediments prior to their being made by humans; and (5) the floors of the cuts appear to be lighter in color than the bone surface. The other

bone (UA 3102) shows sedimentary abrasions. There was no carnivore or scavenger damage on any of the specimens of *Pachylemur* that we examined.



Fig. 3. A) Right humerus of an infant *Palaeopropithecus ingens* (OUM 14342B, Methuen collection, originally catalogued as OUM 14343), showing chop marks. B) Left femur of an adult *Pachylemur insignis* from Tsirave (UA3059, Lambertson collection), showing chop and cut marks made during disarticulation. Note the alignment of the cut marks on the medial and lateral condyles.

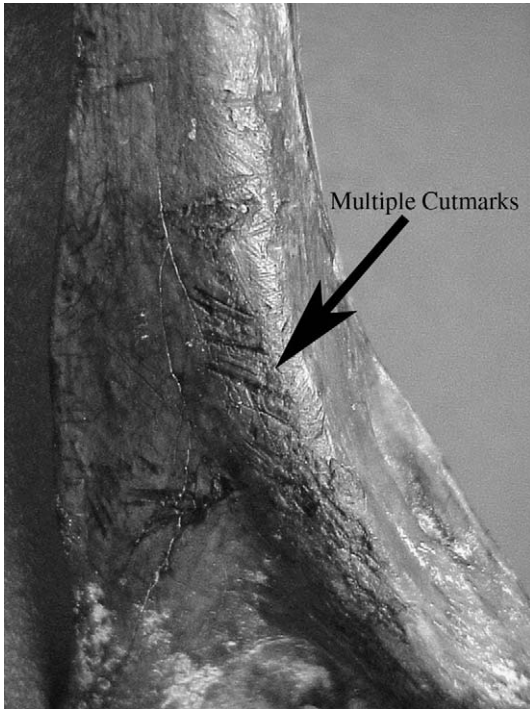


Fig. 4. Cut marks on the distal end of a *Palaeopropithecus ingens* left humerus (OUM 14342A) in the Methuen collection.

Propithecus

Of the 265 bones and bone fragments of *Propithecus verreauxi* in the Walker collection from Taolambiby that we examined, none showed sedimentary abrasions or evidence of carnivore or scavenger damage. There was abundant evidence of human butchery, however (Tables 1-2). Many bones are splintered and fragmented.

In all, 164 of 265 elements (or 62%) exhibit signs of probable butchery (cut marks, chop marks, or spiral fractures). A total of 22 cut marks are present on only eleven of these specimens. One has a cut mark, chop mark, and a spiral fracture (Fig. 6); three have both cut marks and spiral fractures (Fig. 7); two have both cut and chop marks; and five have cut marks only. The cut marks average 3.4 mm in length with a standard deviation of 2.4 mm. The elements with cut marks include two humeri, four femora, two tibiae, and one clavicle (see Table 2). Of elements *without* cut marks, a total of 66 have

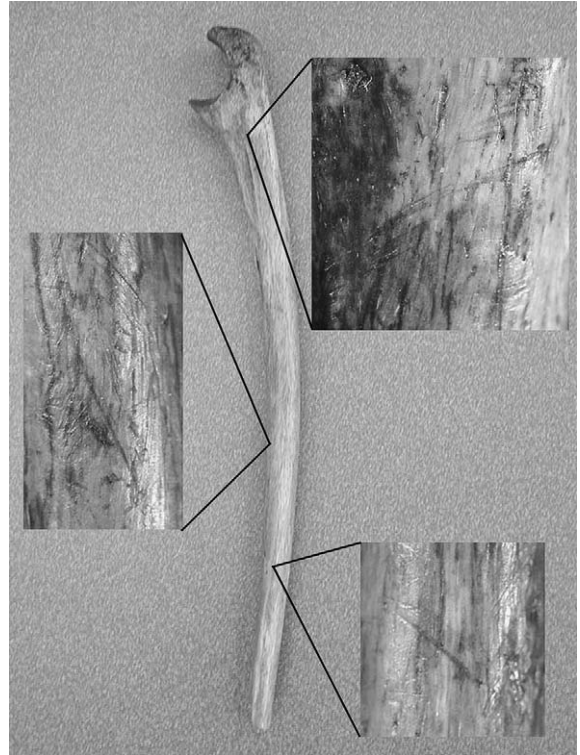


Fig. 5. Cut marks at three different locations on this right ulna of *Palaeopropithecus ingens* in the Methuen collection (OUM 14346a L) are highlighted.

chop marks. Five have chop marks and spiral fractures, and 61 have only chop marks.

Most of the cut marks on specimens of *Propithecus* in the Walker collection are located in the vicinity of joints. None (including those located in the middle third of the shaft) show definitive evidence of filleting. Instead, and regardless of location, these cut marks are generally short and oriented more or less perpendicular to the long axis of the shaft; those that are not (e.g., the cuts on the midshaft of TAO-66-6) appear to have produced the shattering of the bone. No *Propithecus* long bone shows a suite of oblique cuts running down the shaft, as occurs on some bones of *Palaeopropithecus*. We did find a single cut mark on a *Propithecus* distal femur running parallel to the long axis of a shaft – just proximal to the patellar groove. This appears to have been made in an effort to detach the patella.

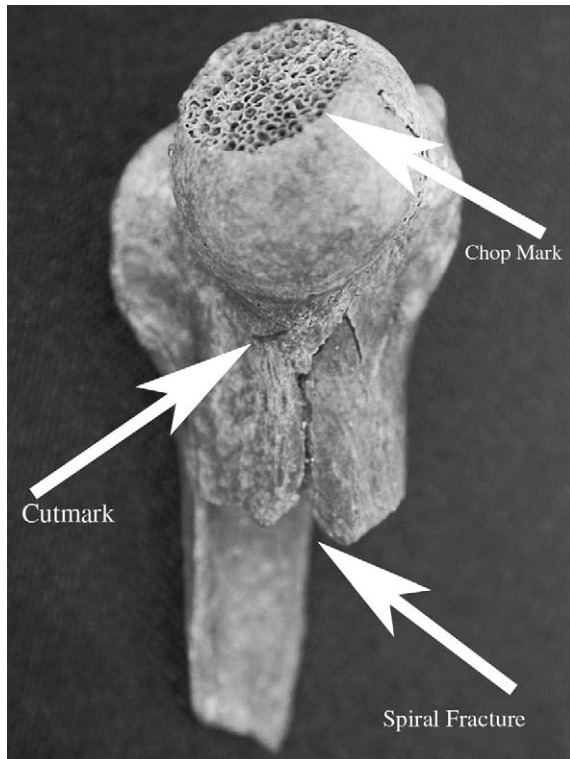


Fig. 6. Proximal portion of right humerus of *Propithecus verreauxi* from Taolambiby (TAO-66-2, Walker collection), showing a chop mark, cut mark, and spiral fracture. This humerus is beyond the upper limit of the size range of modern sifakas at Beza Mahafaly.



Fig. 7. Fragment of a femoral shaft of a *Propithecus verreauxi* from Taolambiby (TAO-66-5, Walker collection), showing a cut mark with an orientation oblique to the long axis of the shaft.

About half of the specimens of *Propithecus* with chop marks (36 total) are long bones. Of these, seventeen are femora, seventeen are tibiae, one is a fibula, and one is a humerus. The overwhelming majority (97.2%) are bones of the hindlimb. Other chop marks occur on foot bones (tali, calcanei, cuboids, entocuneiforms, metatarsals, and proximal phalanges), a clavicle, and small fragments of long bones, including additional fibular fragments. Chop marks on long bones show a striking consistency: (1) they are usually oriented perpendicular to the long axis of the shaft; and (2) they are located very near the joints or they pass through the joints (Fig. 8).

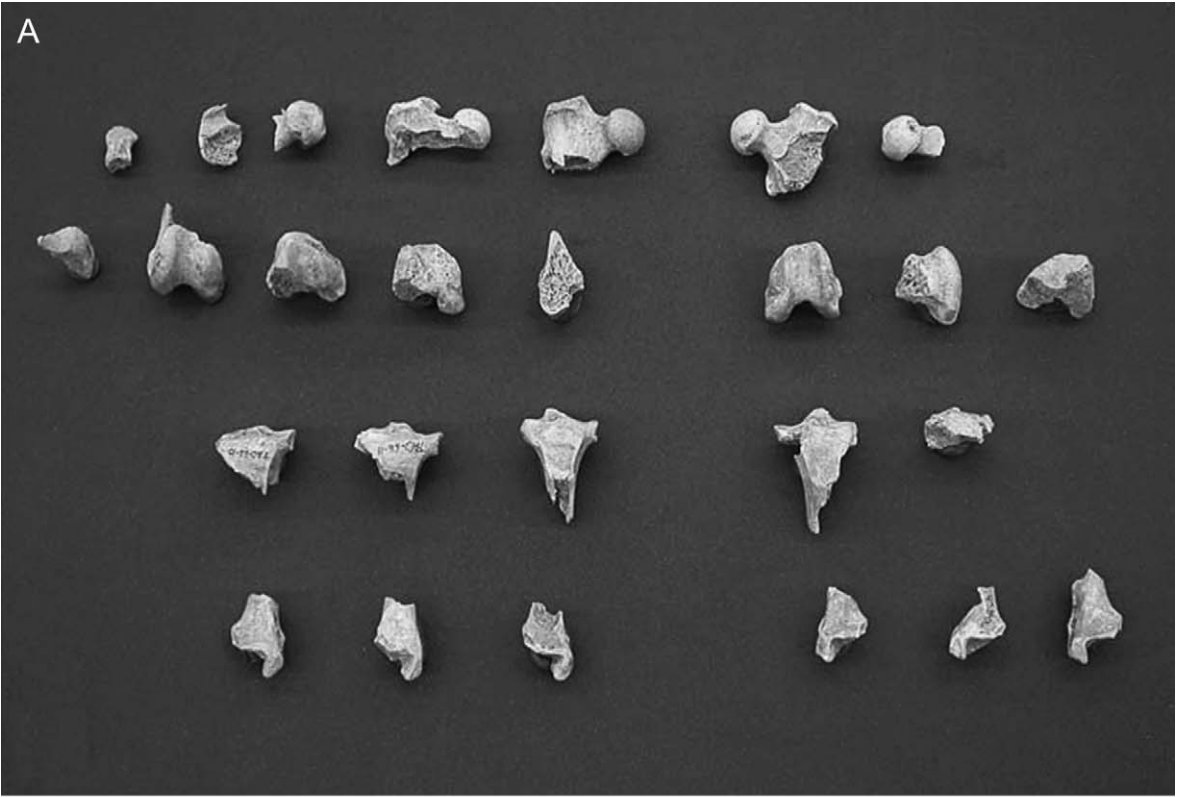
Lemur catta

There were very few bones of the ringtailed lemur or other extant primates in the Walker collection. Of the four fragmentary postcranial bones of *Lemur catta* that we examined, none showed any sign of butchery. Nor was there any sign of carnivore or scavenger damage.

Comparison of butchery patterns for extinct and extant mammals

The most striking differences between the butchery patterns on extinct and extant lemurs are the relatively higher frequencies of cut (as opposed to chop) marks and of oblique cuts located on the midshafts of long bones of extinct lemurs, and the higher frequencies of chop marks on the long bones of extant lemurs (Table 1). Forty percent (4/10) of the extinct species' bones in our sample with definitive evidence of butchery have chop marks, whereas 90% (69/77) of the sifaka bones with definitive evidence of butchery bear chop marks. Other distinctions are difficult to find. The great majority of cut marks on the long bones of all species (81% for the extinct sample, and 71% for the extant) are located at or near joints. Furthermore, all of the (admittedly few) chop marks on the long bones in our sample of extinct lemurs, and 92% on *Propithecus*, are located at or near joints. There is no preference for proximal vs. distal joints; the joints at both ends of the long bones were processed. There is no significant difference in the preponderance of U- vs. V-shaped cuts

A



B



across species. For pooled taxa, there are significant differences in the characteristics of cuts with U- and V-shaped floors. U-shaped cuts are deeper (Mann-Whitney U test, $p = 0.002$) and wider (Mann-Whitney U test, $p < 0.002$) than V-shaped cuts; cuts with U-shaped floors are also significantly longer than those with V-shaped floors (independent samples t-test, $df = 73$, $p = 0.02$). This suggests the use of a variety of cutting tools, or different methods of wielding the same cutting implement.

Methods of butchering large and small animals in rural Madagascar today may offer a model for past practices. At the site of slaughter, large animals (such as cattle) are skinned, the limbs are disarticulated using a large iron knife, and the organs removed. The head of the slaughtered animal is oriented toward the northeast (“zoro firarazana”) and a benediction is solicited from the ancestors. The butcher often uses two implements: a sharp knife to skin the animal and to remove the flesh from the bones, and an axe to chop through bones. The skin is removed from all parts except the fore- and hind-feet, which may be roasted with fur removed but skin intact. Parts of the cadaver may be distributed to villagers according to social rank, with the most-tender portions (for cows, the “vodi-hena”, or rump and thigh region) going to individuals holding the highest rank. Chopping near or through joints may aid in the process of disarticulation, and chunks may be roasted with the bone intact, or the muscle meat may be removed from the bones and distributed fresh for roasting or barbecuing. Alternatively, meat may be cut into thin strips and hung to dry for later consumption. Bones stripped of meat may be used in soups or stews.

Smaller animals (such as chickens, cats, and lemurs) are treated differently. The entire carcass is typically chopped into morsels that can be entered into a pot. Muscle is not removed from the bones prior to cooking. For birds, the head is consumed. For small mammals, the head is removed by cutting through the cervical vertebrae, and the hands and feet are also chopped off and discarded.

The *Propithecus verreauxi* at Taolambiby appear to have been prepared in a manner similar to small mammals today. They were hacked to pieces, apparently in preparation for cooking and consumption. An astoundingly high percentage (62%) of all elements of *Propithecus verreauxi* bones in the Walker collection have cut marks, chop marks, or spiral fractures (or some combination), and almost a third of the elements have chop marks. In contrast, only one *Palaeopropithecus* bone in the Methuen collection (the humerus of an infant) bears a chop mark, and that mark does not penetrate the entire shaft. Interestingly, the single specimen of *Palaeopropithecus* in the Walker collection does bear chops across the shaft, very like those on *Propithecus* bones in the Walker collection. There is no evidence of consumption of the heads of any primate and the abundant evidence of chop marks at the ankle of *Propithecus* suggests that the feet were also discarded. The characteristics and distribution of butchery marks on the long bones of *Propithecus* are consistent with expectations for bone fragmentation. “Bone fragmentation” refers to the reduction of a formerly complete element into a number of pieces (Capaldo, 1998, p. 312). There is no definitive evidence of filleting in *Propithecus*.

In contrast, the marks on long bones of *Palaeopropithecus* and *Pachylemur* are consistent with expectations for skinning, disarticulation, and filleting. The main difference between cut marks associated with disarticulation (on the proximal or distal end of the bone) vs. those associated with filleting is that the former tend to be more horizontal (i.e., cut across the shaft, perpendicular to the long axis of the shaft). All features that we attributed to filleting (more centrally located on the shaft) are oblique. We found no cut marks on extinct lemur long bones parallel to the long axis of the shaft, and only one on a far more extensive collection of butchered bones of the sifaka. Although there are chop marks on an infant *Palaeopropithecus* humerus in the Methuen collection and on an adult *Pachylemur* femur

Fig. 8. Selected fragmentary femora and tibiae of *Propithecus verreauxi* from the Walker collection, Taolambiby, with chop marks but no cut marks. A) Top row: Right and left proximal femora. Second row: Right and left distal femora. Third row: Right and left proximal tibiae. Bottom row: Right and left distal tibiae. B) Close-up of chop mark on left tibia (TAO-66-12), posterior view. The majority (62%) of the butchery marks on the long bones of *Propithecus* are chop marks. This contrasts with 10% of the butchery marks on the long bones of *Pachylemur* and 4% on the long bones of *Palaeopropithecus*.

in the Lamberton collection, the practice of slicing entirely through the limb bones either above, below, or through the joint articular surfaces was observed on only one of the *Palaeopropithecus* bones (the ulna in the Walker collection). The evidence of filleting suggests that muscle meat may have been removed from the carcasses of *Palaeopropithecus* and *Pachylemur* prior to cooking.

These differences in butchery practices may be related to the differences in the body sizes of the prey species themselves (ca. 45 and 10 kg respectively, for *Palaeopropithecus ingens* and *Pachylemur insignis*, and 3 kg for *Propithecus*; Jungers et al., 2002). Filleting may be practical for a large animal but may serve little purpose for a smaller one.

Discussion

Methuen's collection provides evidence of butchery of giant lemurs at a time when the mammalian species richness in Madagascar was much greater than it is today, and just after humans first arrived. Walker's collection at the same subfossil site provides evidence of butchery of extant lemurs in more recent deposits, when the larger-bodied lemurs were either locally extinct or exceedingly rare.

Propithecus is the largest-bodied of the lemurs that is still extant in the Southwest, and it is noteworthy that some of the butchered *Propithecus* bones in the Walker collection fall outside the range of size variation of specimens from the nearby forest of Beza Mahafaly, matching instead the larger size of specimens originally called *Propithecus verreauxoides* by Lamberton (1936). A recent body size diminution appears to have characterized southwestern *Propithecus*, as it did other lemur species (Godfrey et al., 1999).

Human butchery of wild lemurs neither implies nor precludes an economic dependence on domesticated animals. In some parts of rural Madagascar today where cattle are raised, wild birds and lemurs may be regular food items, while cattle and other larger-bodied domesticated mammals may be sacrificed only on special occasions (Goodman and Raselimanana, 2003). Hunting of wild lemurs occurs widely in Madagascar today, even in "protected" areas (Favre, 1996; Smith et al., 1997;

Hawkins, 1999; Randriamanalina et al., 2000; Mutschler et al., 2001; Garcia and Goodman, 2003; Goodman and Raselimanana, 2003). Arboreal quadrupedal lemurs (such as *Eulemur*, *Lemur*) are caught in arboreal traps or killed at short range by hunters bearing slings. Lemurs that locomote primarily by leaping (e.g., sifakas, or *Propithecus*) are less easily caught in arboreal traps than are smaller, quadrupedal lemurs. However, dogs may be employed to chase wild sifakas to exhaustion, rendering them easy targets for humans with slings (Goodman and Raselimanana, 2003).

We acknowledge that butchery does not necessarily imply hunting and consumption of lemur meat by humans. However, we believe that the circumstantial evidence in favor of both is compelling. First, there is no evidence of carnivore or scavenger damage on any of the bones with cut or chop marks. Secondly, the cuts and chops themselves indicate perimortem damage by sharp metal implements on fresh bone. Third, the cut and chop mark patterns (locations, orientations, mark floor shapes) observed on the subfossil bones suggest processing in preparation for cooking. Finally, there is indirect evidence of hunting pressure in the form of an early and precipitous decline in the abundance of *Sporormiella* (Burney et al., 2004). In addition, many of the now extinct and larger-bodied extant primate species appear to have undergone a recent diminution in body size, possibly associated with predation pressure (Godfrey et al., 1999).

Species bias in collections may itself be a by-product of selectivity in hunting. It is precisely those taxa that are most abundant in the Methuen and Walker collections that show clear signs of butchery (*Palaeopropithecus* in the case of the Methuen collection at Taolambiby, and *Propithecus* in the case of the Walker collection at Taolambiby). Habitat variation may explain differences in species abundance across sites, but it is also possible that such differences reflect an unnatural overrepresentation of preferred prey species at refuse sites near human camps or settlements.

We recognize that data on the stratigraphic context of Methuen's lemurs would have improved our ability to interpret the *Palaeopropithecus* cut marks. Taphonomists and zooarchaeologists

have long touted the importance of understanding the cultural and natural factors that influence the formation of faunal assemblages and the distribution of marks on skeletal material (Lyman, 1987; Yellen, 1991; Cruz-Uribe and Klein, 1994; Marean et al., 2000). Cultural factors include the number of people involved in processing prey, their methods of procurement, the number of prey processed in any given period of time, the tools used in processing (lithic or metal), processing taboos, and storage and processing techniques employed. Natural variables include processing site and habitation area, the time of year, ambient temperature, precipitation, and amount of natural light available (Yellen, 1977, 1991; Binford, 1981; Lyman, 1987; Bartram, 1993; Cruz-Uribe and Klein, 1994). O'Connor (1996) cogently argued that, to truly understand the distribution of cut marks on bones, one must take into consideration the “integrity” of any assemblage as a function of its deposition and diagenesis, along with the excavation methods utilized during the retrieval of the bones while *in situ*. Because we lack this information for the Methuen and Lambertson collections, we cannot use contextual information to establish human activities such as procurement, processing, or storage techniques, associated with the butchery of *Palaeopropithecus* and *Pachylemur*. Instead, careful attention must be paid to the details of the distribution and characteristics of marks on individual elements. On the basis of those details, hypotheses regarding processing techniques can be generated, hopefully for later testing at intact butchery sites. Meanwhile, by exercising special care in data collection and analysis, it may be possible to maximize the diagnostic potential of individual elements. The lack of specific site information and contextualization can be at least partially offset by attention to the details of mark morphology. We would maintain that, in the case of the Methuen and Lambertson collections, the evidence is so compelling that, even without stratigraphic contextualization, butchery of extinct lemurs can be affirmed. Butchery of *Palaeopropithecus* occurred at precisely the place and time (Southwest Madagascar, over 2000 years ago) where we might expect to find evidence of hunting and consumption

of giant lemurs, if indeed hunting contributed to their decimation.

Summary and conclusions

We report here the first definitive evidence of butchery of giant lemurs in Madagascar. Specimens of *Palaeopropithecus ingens* from Taolambiby (in southwestern Madagascar) and *Pachylemur insignis* from Tsirave (in south-central Madagascar) show classic signs of butchering. Bones of the still-extant *Propithecus verreauxi* from one of the same sites (Taolambiby) also show classic signs of butchering – particularly fragmentation. The characteristics of tool-induced bone alteration of extinct lemurs (sharp cuts near joints, spiral fractures, and percussion striae) suggest dismembering, skinning, and filleting. *Propithecus* exhibits a higher frequency of chop marks, and more features perpendicular (rather than oblique) to the long axis of the shaft than does *Palaeopropithecus*. Whereas differences in bone properties can result in differences in non-cultural taphonomic breakage that must be taken into consideration when analyzing paleontological assemblages for evidence of human butchery (Lyman, 1984, 1985, 1992; Grayson, 1989, 2001; Klein, 1989), the patterned differences observed here could not have arisen through variation in patterns of taphonomic breakage. Instead, the different modifications of extinct and extant lemur bones can be explained most easily as a byproduct of differences in processing techniques applied to large and small animals.

Madagascar experienced a dramatic loss of megafauna over the past two millennia. Gone are flightless elephant birds, pygmy hippopotamuses, giant tortoises, and approximately one-third of the lemur species (including all species weighing more than 10 kg). The role humans played in the extinction process is still hotly debated. Whereas we know that the great majority (if not all) of the Holocene megafauna were alive when humans first arrived in Madagascar (>2300 years before present), there is good evidence that at least some (including *Palaeopropithecus*) survived the advent of humans by 1500 years or more (see Burney, 1999; Burney et al., 2004). Some

researchers dismiss hunting as a major factor contributing to megafaunal extinctions on the grounds that the people who colonized Madagascar were fishermen, herders, and agriculturalists, not big game hunters. Our data on butchery suggest that hunting of lemurs may have been practiced by early inhabitants of Madagascar. They do not speak to the relative cultural importance of hunting, but they do demonstrate that a role for hunting in the extinction process cannot be summarily dismissed.

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