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Taphonomy story of a modern African elephant *Loxodonta africana* carcass on a lakeshore in Zambia (Africa)

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ABSTRACT

A modern African elephant carcass was monitored taphonomically on a shallow lakeshore during dry and wet seasons of 2010–2011. The young adult female died on the lakeshore during the hot dry season of early October 2010. African lions were first to scavenge on the carcass, feeding on the intestines and inner organs that were accessed through the anus. Spotted hyenas also scavenged on the fresh carcass, with an emphasis on the feet and leg bones; one foot was scavenged with the toes eaten and metapodials half chewed. In addition, hyenas chewed on exposed leg bones resulting in bite mark damages in the softer bone spongiosa and bite scratches on one humerus joint. Following an initial scavenging phase by large and small carnivores where the fresh meat and softer material was eaten and the majority of the bone damage occurred, the desiccated remains were abandoned on the lakeshore as a more or less intact carcass with the thick hide covering the mostly articulated skeletal elements. The carcass was briefly revisited and secondarily scavenged by hyenas in mid-November 2010 when the first rains softened the remains. During the seasonal flood from December 2010 through May 2011, the carcass was submerged. By the beginning of the following dry season in June 2011, the remaining skeletal material lay scattered over an area of 20 × 25 m. The main concentration of bones, however, including most of the larger bones and two articulated sections of the vertebral column, remained within a 10 × 10 m area where the carcass had last been scavenged. Although the elephant died of natural causes, the skull was damaged on Day 2 post-mortem when wildlife authorities removed the single tusk. In late September 2011, nearly one year post-mortem, no additional bone damage attributable to scavenging by large predators could be found, although some of the smaller bones were missing. Following the scavenging period, environmental factors e.g., flooding, temperature and humidity changes resulted in additional carcass scattering and damage, including cracks and flaking in some bones.

1. Introduction

Taphonomic studies of modern remains lend invaluable context to the understanding of archaeological material. In particular, the influence of large carnivores on elephant bone taphonomy is of interest as it relates to fossil elephant skeletons and hyena bone accumulated fossil sites. However, although numerous fossil elephant skeletons have been described from fossil Late Pleistocene (Eemian-Interglacial) lakeshore environments (Diedrich, 2010, 2012a, 2012b), there exist few records monitoring the disposition of modern elephant carcasses. Of these, one chronicled the disposition of a *Loxodonta africana* carcass in a savannah environment in Kenya (Coe, 1978) and others examined modern elephant carcass disposition on lakeshores (Haynes, 1987, 1988, 2004). Additional studies have documented the relative influences of carnivores versus Middle Palaeolithic (Weber and Litt, 1991) or Late Palaeolothic humans (Haynes and Krasinski, 2010) on Late Pleistocene carcass decompositions on shallow lakes and lakeshores.

This paper describes the monitoring of a modern *L. africana* carcass that died and was deconstructed on the shore of an unnamed shallow and seasonal lake in a savannah environment in western Zambia adjacent to Kafue National Park, Africa, (Fig. 1). The Kafue National Park covers a total of 22,480 km^2 and is situated entirely on a plateau. It houses one of the highest diversity of fauna species in Zambia including 23 large herbivore species and 11

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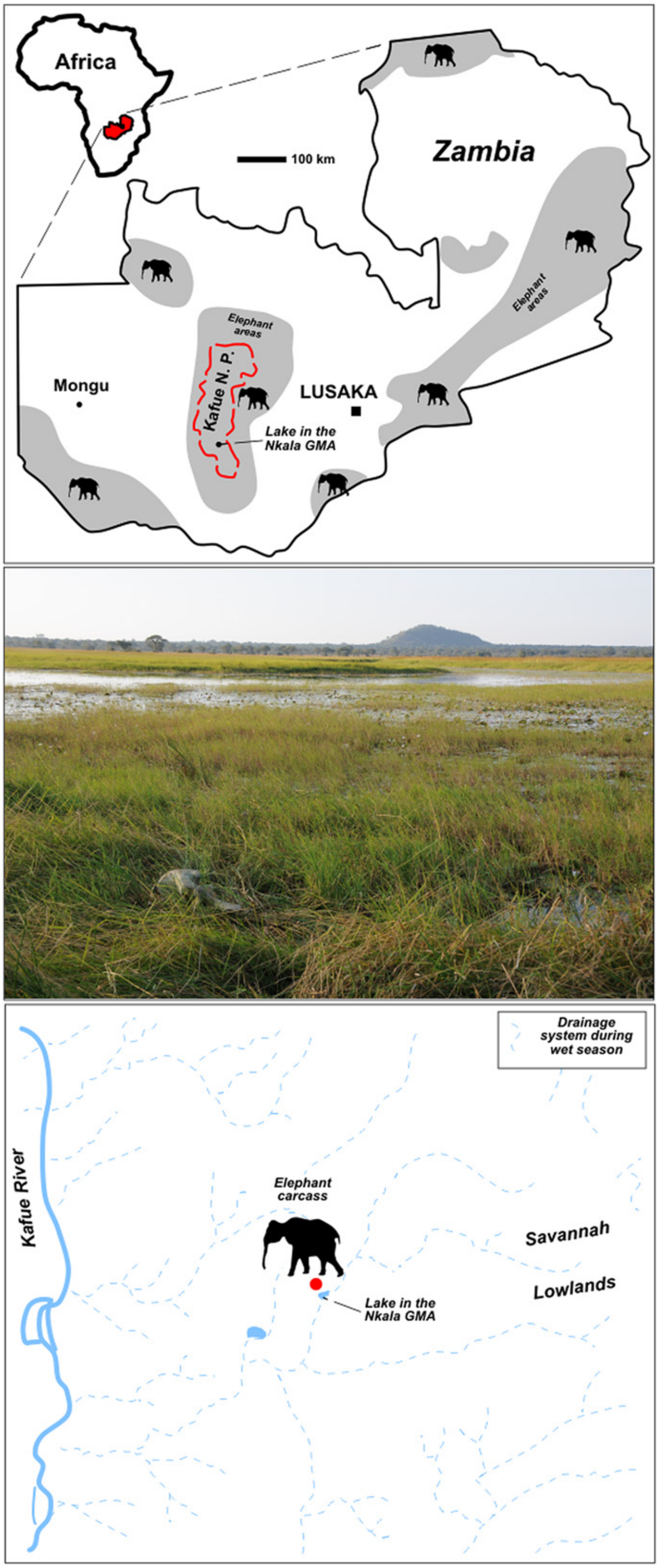

Fig. 1. Study area and modern elephant carcass locality, an unnamed small shallow lake in the Nkala Game Management Area, adjacent to Kafue National Park, Zambia (south-central Africa). During wet season the lakes expand and drainage system is active.

species of carnivores that include lion, leopard, cheetah, spotted hyena, side-striped jackal and wild dog. Kafue National Park is home to more then 2000 elephants, representing 10% of Zambia's total elephant population estimated at 20,000 animals.

Initial scavenging by contemporary large predators, e.g., African lion *Panthera leo leo* and spotted hyena *Crocuta crocuta crocuta*, and later environmental factors, influenced the ultimate fate of the modern elephant carcass. The purpose of this monitoring was to provide a taphonomic comparison to 24 fossil elephant skeletons and skeletal remains found in and on a lakeshore dating from the Late Pleistocene Eemian-Interglacial site Neumark-Nord Lake 1 in Central Germany. In the latter case, steppe lion *P. leo spelaea* and Ice Age spotted hyena *Crocuta crocuta spelaea* remains were found among the skeletons of their largest prey, the straight tusked elephant *Palaeoloxodon antiquus* (Diedrich, 2010, 2012a, 2012b).

2. Materials and methods

The modern elephant carcass was found opportunistically on the day of death (10 October 2010) in Nkala Game Management Area, 6 km east of Kafue National Park, Zambia, 15°55.058′S, 25°58.698′E, elevation 1001 m (Fig. 1). The following day, Zambia Wildlife Authority used a small axe to remove the single tusk, thereby damaging half of the cranium. Thereafter, all subsequent damage to the carcass was the result of scavenging by natural predators, and the elements.

Monitoring of the carcass was performed by one of the authors (PAW) daily for the first two weeks, and thereafter twice weekly for the next month until the end of November 2010. Each site visit was performed during daylight hours and the general condition of the carcass as well as the extent and location of scavenging on the carcass by lions and hyenas was quantified. At the end of each visit, the bare ground around the immediate area of the carcass was cleared of old tracks and scats by brushing the dirt with branches. Due to the secretive nature of large carnivores outside of National Parks, direct observations of carnivores visiting the elephant remains were conducted mostly at night with the aid of night-vision goggles. The remains were extensively photographed on four occasions: October 2010, November 2010, May 2011, and lastly in late September 2011 (Figs. 2–4).

Spatial disposition of the remains one year post-mortem were systematically photographed in a ca. 1 × 1 m grid layout. Each photograph was subsequently analysed to identify individual bones or bone fragments, and results rendered into a map (Fig. 5). Individual bones were then examined and photographed to qualify and quantify bite marks and damages as detailed in Figs. 5 and 6.

3. Taphonomy

The modern *L. africana* elephant carcass was monitored in relation to species of scavenger present (as determined by direct observation, tracks, and scats), the anatomical location of scavenging activities and resultant bone damage, bite mark types, and ultimate disposition of the skeleton one year post-mortem following seasonal floods. Three distinct stages of decomposition of the carcass and skeleton were documented over different seasons during which time the carcass was subjected to dry, flooded, and dry conditions, respectively.

3.1. Large predator scavenging stage

The carcass was first scavenged by large predators two days after death, and first photographed 10 days post-mortem (Fig. 2)

Fig. 2. A. Modern African elephant *Loxodonta africana* carcass 20 October 2010, Day 10 post-mortem in an initial carcass destruction stage being mainly non-decomposed, at which lions and hyenas first ate B. the trunk, C. the feet, and D–F. started disconnecting the legs at their joints and G. inner organs/intestines eaten starting from the anus (the latter typical for lions). Most of the Late Pleistocene Neumark-Nord elephant carcasses were left in this initial stage of carcass destruction (photos: P.A. White).

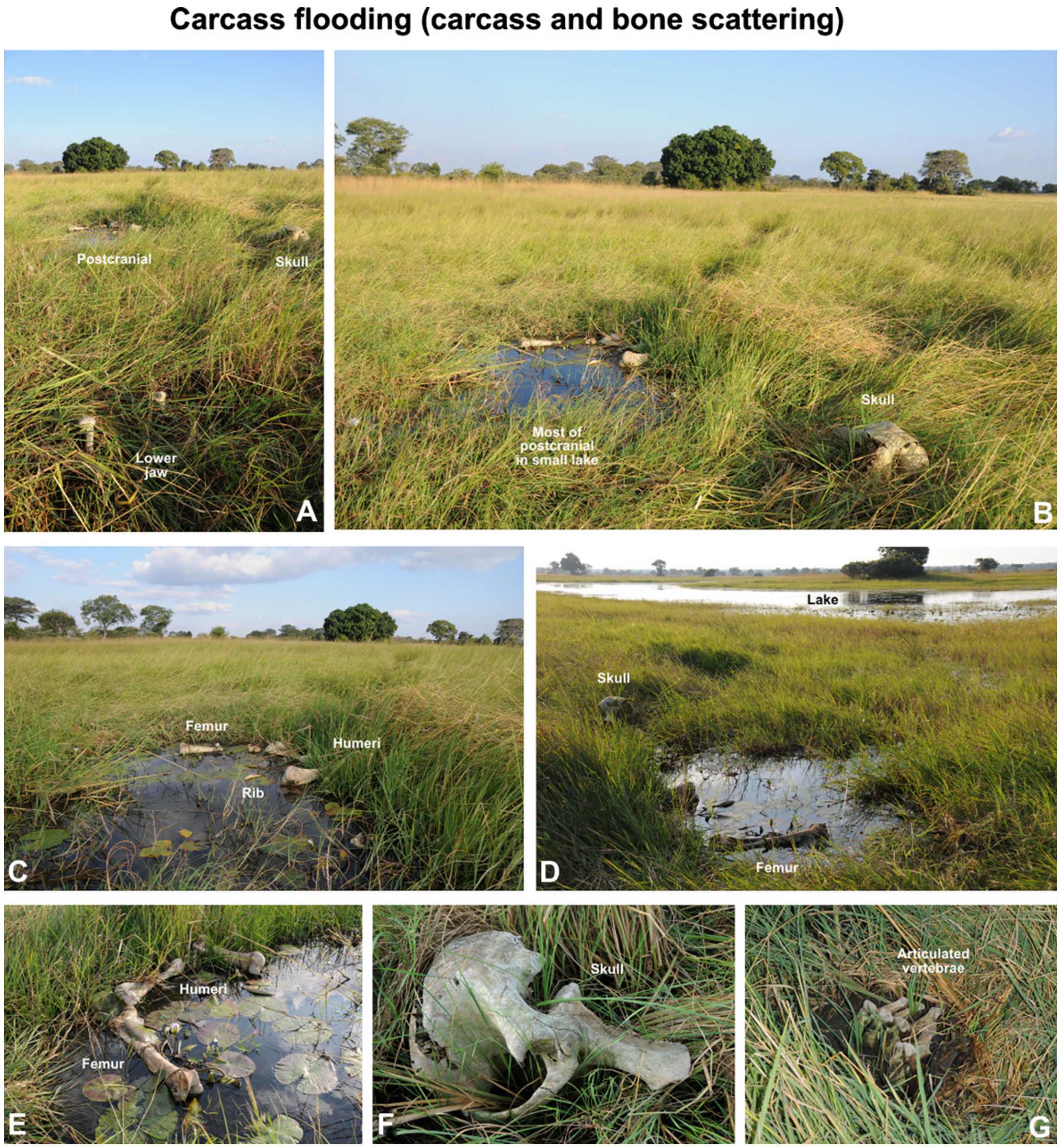

Fig. 3. A–F. Modern African elephant *Loxodonta africana* carcass 2 May 2011, Day 204 post-mortem under flooding carcass destruction stage being decomposed nearly completely, G. whereas some vertebral column remains remained articulated (photos: P.A. White).

at which stage the thick skin was more or less intact (Fig. 2A–B). The trunk was eaten, as were the intestines and inner organs; the latter being accessed from the anus rather than the ventral side (Fig. 2A, G). The skin area around the anus exhibited zig-zag margins (Fig. 2G), and a small amount of bite damage was visible through the anal opening on the pelvis. All of the feet had been fed upon, with the result that the entire right forefoot and the pedal bones (metapodials and phalangae) from both hind feet were absent. Of the left forefoot, two metacarpi were partially preserved being half-chewed with zig-zag margins at the exposed edge (Fig. 2C). The lower part of the right front leg was slightly dislocated with the ulna protruding through the hide. The ulna had been distally chewed with large bite impact marks in the upper shaft area (Fig. 2D). The right humerus showed large elongated bite scratches of approximately 6–8 mm in width on the distal joint surface (Fig. 2F) with a small amount of chew marks apparent on the outer lateral side (Fig. 2E). Round–oval impact bite marks, and wide elongated scratch marks coupled with oval to triangular bite depressions in bone compacta areas were noted on the pelvis (Fig. 2G), two metatarsals (Fig. 2C), one ulna (Fig. 2D), and one humerus joint (Fig. 2G) and were attributed to spotted hyenas and to a lesser extent lions.

Apart from soft tissue, the only bones initially absent from the site were from the elephant's feet, which appeared to have been fed upon by hyenas on-site as indicated by fresh tracks. Bones from both hind feet were absent (except one calcaneus/astragalus), and the entire right forefoot was missing. The left forefoot was half-eaten, and the remaining carpalia were present prior to the onset of the rains and seasonal floods.

Fig. 4. A–E. Modern African elephant *Loxodonta africana* carcass 30 September 2011, Day 355 post-mortem after flooding conditions in the final stage of being decomposed (photos: P.A. White).

Following detection of the elephant carcass by scavengers on Day Two post-mortem, lions fed on the carcass for the next five days. Spotted hyenas continued to scavenge on the elephant carcass for six additional days after the last lion visited, as indicated by daily monitoring of carnivore tracks. By Day 14 post-mortem, the elephant carcass was largely desiccated and all easily accessible soft tissue had been removed by small scavengers that included side-striped jackal *Canis adustus*, African civet *Civettictis civetta*, large-spotted genet *Genetta genetta*, and several species of vultures. The remains, which consisted of the mostly articulated skeleton draped in the dried hide, were largely abandoned by scavengers at that time.

3.2. Secondary scavenging stage

In mid-November 2010, the carcass was moistened by the season's first rains and was immediately revisited by spotted hyenas. Over the next four days, hyenas chewed on and removed additional material (mostly softened hide and sinew) from the desiccated carcass. Hyenas also chewed on and damaged distal portions of the dorsal and lateral vertebral processes of some

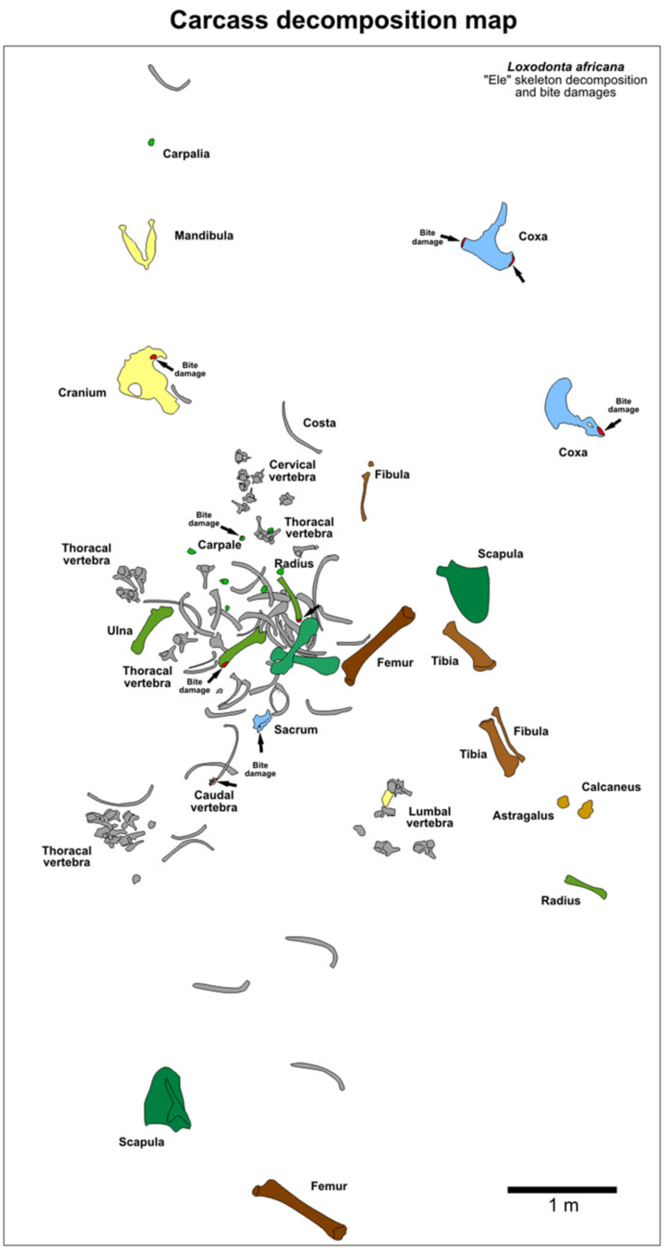

Fig. 5. Map sketch of the bones in the final stage of decomposition and bones with bite damages. Drawn from photos taken 30 September 2011, Day 355 post-mortem (bone elements – skull = yellow, fore limbs = green, hind limbs = brown, axial skeleton = grey, pelvis = blue; map: PaleoLogic). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cervical and lumbar vertebra that had been newly exposed as the elephant's hide dried and contracted.

3.3. Flooding stage

From December 2010 to April 2011, the carcass was subjected to the hot, wet season and lay submerged by the seasonally flooding lake during the majority of that time period. Wet season photographs were obtained in early May 2011 when the seasonal floodwaters had partially receded to expose the larger bones. At that stage, the hide along with all other soft material was entirely absent, and the bones were scattered in high grass (Fig. 3A–B). The small depression in which the elephant carcass was initially found was now a shallow lake in which only the largest bones were visible above the water's surface (Fig. 3C–E). Although the cranium, some long bones, and still-articulated vertebral column remains could be seen (Fig. 3E–G), tall grass and 1 m-deep water rendered detection and mapping of all of the osteological material impossible at that time.

3.4. Final disarticulation stage

By late May 2011, continued recession of the seasonal floodwaters gradually exposed more of the elephant skeleton on the shallow lakeshore. Grazing ungulates shortened the grass, thereby helping to expose the scattered bones. However, some of the smaller bones remained hidden under the grass until well into the next dry season. Thus, assessment of the final deconstruction was conducted in late September 2011, Day 355 post-mortem, when all of the remaining bones were apparent at which time they were photographed and mapped (Figs. 4 and 5). The disarticulated skeleton was scattered over an area of 20 × 25 m, although the majority (95%) of the bones were concentrated within a smaller 10 × 10 m area. One femur was found 10 m from the main concentration, while some thoracic vertebrae were found largely articulated in place (Fig. 4D).

4. Discussion

In regions of modern Africa, lions that specialize on hunting elephant have been reported (Joubert, 2006; Loveridge et al., 2006). Modern spotted hyenas are capable of killing small elephant calves (Kruuk, 1972). Moreover, both of these species of large carnivores are known to scavenge freely on elephant carcasses whenever available. While small portions of soft tissue are likely consumed by a variety of scavengers including small carnivores (*C. adustus*, *C. civetta*, *G. genetta*) and birds (vultures), the size of most elephant bones and toughness of the hide precludes species other than the largest carnivores from accessing and scavenging bony material. This is supported both by direct observations of large carnivores scavenging on elephant carcasses, as well as the size and extent of bite mark damage left on the remaining bones. The wide (4–6 mm) and elongated bite marks, large (ca. 110 mm) oval-round bite impact marks on the sacrum, and zig-zag margins on one fibula bone shaft and the pelvic bones found on the modern Zambian elephant carcass (Figs. 6 and 7) are similar to the large bite mark types on the Neumark-Nord Lake 1 fossil site attributable to Late Pleistocene hyenas and lions (Diedrich, 2012b). It is hypothesized that modern spotted hyenas *C. crocuta crocuta* and African lions *P. leo leo* are primarily responsible for modern elephant *L. africana* carcass destruction, with small carnivores and vultures playing a much lesser role.

In particular, the scavenging of the modern *L. africana* elephant's feet with half-chewed metapodials and missing phalangae is reminiscent of the bone damages documented at the Neumark-Nord Lake 1 fossil site (Diedrich, 2012b) that are believed to be the result of hyenas feeding on the thick fat layer as has been observed in modern Africa. The zig-zag margins on the thick skin around the anal opening, and bite mark damages on the pelvic bones (Figs. 6 and 7) are believed to be mainly the result of scavenging by lions. Photo documentations of African lions scavenging on elephants suggest that lions preferentially begin feeding from the anus (Fig. 8A–B). On a second fresh modern elephant carcass found opportunistically during this study, two male lions were photographed on Day 3 post-mortem preferentially opening and feeding from the anus, despite the abdomen having been cut open by humans (Fig. 8B). The lions initially prevented hyenas from accessing the kill (note the elephant's intact feet). Only following

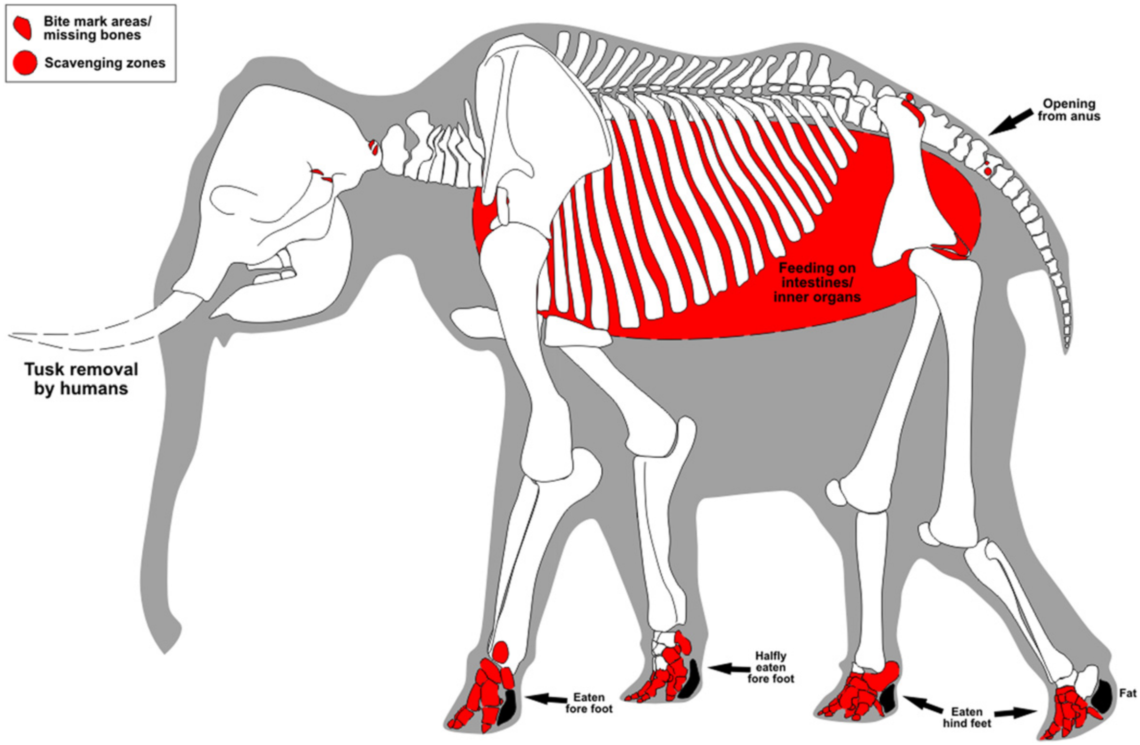

Fig. 6. Damaged bones of the Modern African elephant *Loxodonta africana* carcass. Drawn from photos taken 30 September 2011, Day 355 post-mortem (plate: PaleoLogic).

the lions' departure six days later did hyenas begin to feed on the elephant at which time they immediately targeted the feet.

The initial feeding on elephant intestines by African lions and spotted hyenas has been previously reported (Schaller, 1972; Coe, 1978; Joubert, 2006) but only rarely documented in the carcass and skeletal record i.e., in Kenya (Coe, 1978). The current study demonstrates in detail this feeding strategy on modern elephant carcasses (Figs. 2 and 8) in addition to qualifying scavenger versus fluvial flood damage in a unique way.

Inner organ and intestine feeding has been documented in the Neumark-Nord Lake 1 fossil site, where such feeding by lions/ hyenas is accompanied by bite mark scratches on the inner side of the vertebral columns of at least two elephant carcasses (Diedrich, 2012b). Although lions were known to have fed through the anal opening on the monitored carcass from Zambia, bite marks were not apparent on the inner side of the vertebral column. It is possible that the exact anatomical position of an individual elephant when it dies will influence the ability of large carnivores to access certain internal bones, and thus, influence which specific bones may be damaged before the hide is completely desiccated and the carcass abandoned. Additionally the season of death, as well as the number of scavengers present, may be expected to influence the condition of the carcass and thus, the duration and extent of scavenging and resultant bite damage.

Chew marks on the outer distal humerus joint of the modern Zambian elephant are similar to damages found in the fossil Pleistocene Neumark-Nord Lake 1 record (Diedrich, 2012b). The large bite marks on the Zambian elephant humerus and ulna/radius that penetrate deep into the spongiosa are common at the point of tendon insertion and relate to initial removal of the limbs from the carcass. Limb removal was documented in Kenya (Coe, 1978), but not observed at the Zambian carcass. The front legs are easier to remove from the carcass than the hind legs due to the latter's strong connection to the pelvis. Only hyenas seem to have developed a "slaughtering technique for body part removal" (Diedrich, 2012b) evidence of which can also be found in the disassembled remains of other large prey such as the woolly rhinoceros of the Late Pleistocene in Europe (Diedrich, 2012a). Hyenas remove and transport even large, heavy body parts from large prey carcasses in order to cache them and to feed their cubs in the dens as documented in the modern (e.g. Hayward, 2006) and Pleistocene record (e.g. Diedrich, 2012a). That the limbs were not removed from the Zambian elephant may have been influenced by the fact that the elephant died in the height of the hot, dry season leaving a relatively short time period until the hide was hardened by the elements to the point of being impenetrable even by the largest carnivores. This is supported by the observation that hyenas returned immediately to further scavenge on the carcass following the first rain. Bite marks on the pedal bones, chewed distal phalangae, and missing feet either in whole or part indicate that elephant feet were preferentially targeted both in modern (Figs. 2 and 8D) and fossil times (also fossil site Neumark-Nord lake 1: Diedrich, 2012b). The targeting of feet and missing foot bones may be attributed both to hyenas consuming the thick fat present in the pedal region, as well as the ability of large or small scavenger species to subsequently remove a relatively small food item once the thick skin of the foot has been opened and small pedal bones exposed.

In addition to scavenging by carnivores, final disarticulation and scattering of the bones appeared to have been further influenced by factors associated with the flooding stage. These include: 1) gradual movements of water during rainfall, runoff and as the shallow lake filled and receded, 2) scavenging of the remaining soft tissue by fish or aquatic invertebrates when the carcass lay submerged, 3) seasonal growth of thick grasses in the area in which the bones resided during the end of the wet season, and 4) inadvertent kicking or shifting of bones by ungulates grazing along the lakeshore as the lake receded.

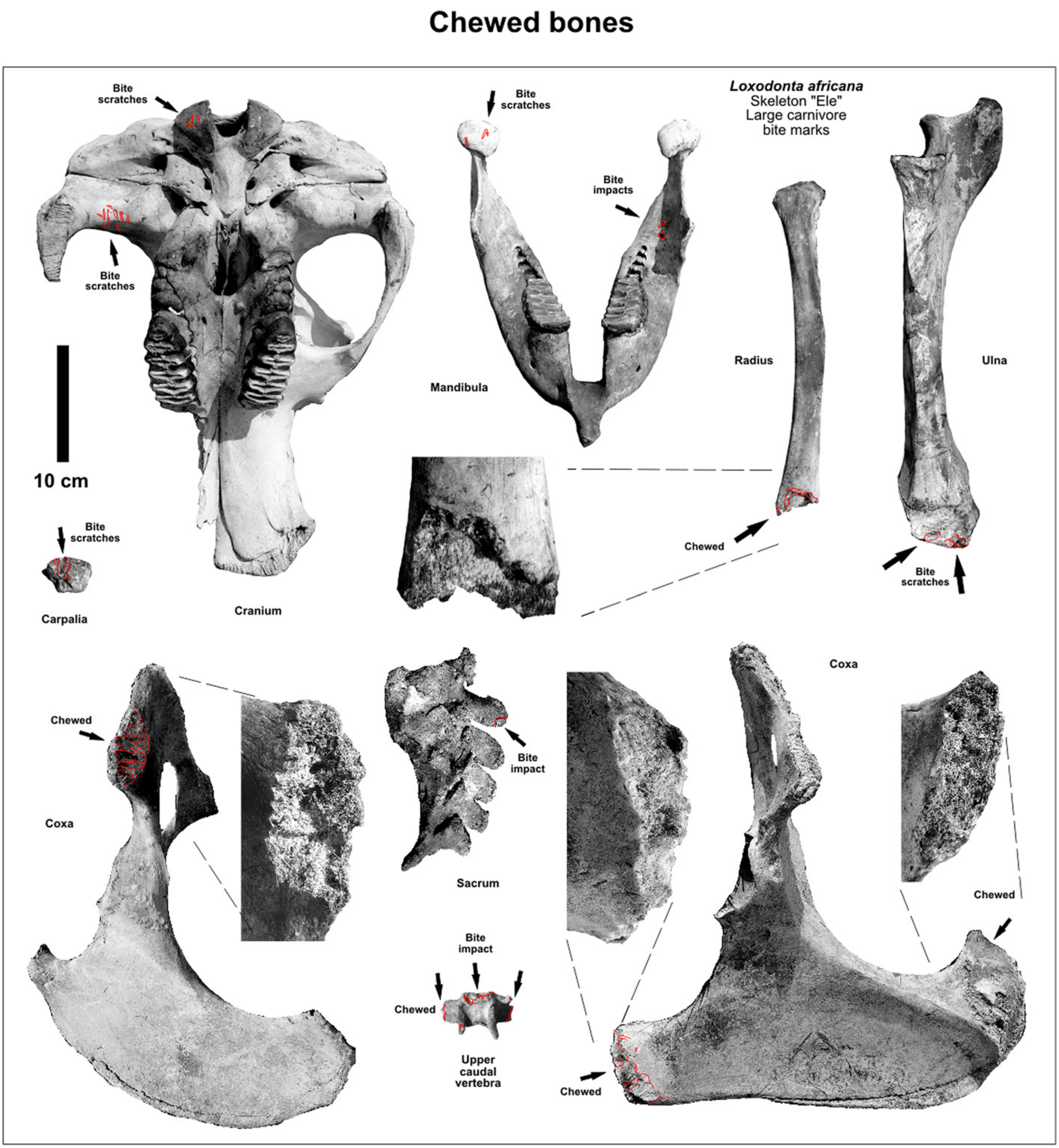

Fig. 7. Missing bones and bones with bite damages on the Modern African elephant *Loxodonta africana* carcass. Lions/hyenas accessed the intestines and internal organs starting from the anus; nearly all feet were eaten completely. The lone tusk was removed by humans (graphic: PaleoLogic).

Fig. 8. A. Modern African lion on elephant carcass feeding from the anus Ngorongoro Conservation Area, Tanzania (photo: B. Wilhelmi). B. Modern African lions (wearing a radio collar) feeding on a second Modern Zambian elephant carcass four days after it was killed by poachers. Lions fed on the meat and intestines through an anal opening that they created, despite the stomach having been already opened by humans. Lions guarded the carcass and prevented hyenas from feeding for the first several days. Note that the elephant's feet are still intact, Kafue, Zambia (photo: P.A. White). C. Modern spotted hyena clan feeding on an elephant carcass, Okavango Delta, Botswana (photo: © Christophe Courteau/naturepl.com), D. Modern spotted hyena eating an elephant foot, Masai Mara, Kenya (photo: S.A. Wahaj).

5. Conclusions

The carcass of a young adult female elephant on a savannah shallow lakeshore in Zambia was scavenged first by African lions and then spotted hyenas. Feeding behaviors of these two modern carnivore species scavenging on a modern African elephant resulted in patterns of bone damage and initial carcass disarticulation similar to those found in the analogous ancestral European species (Late Pleistocene *P. leo spelaea*, *C. crocuta spelaea* and their large prey *P. antiquus*). Following the scavenging period, seasonal flooding of the lakeshore then submerged the carcass for the duration of the wet season during which time decomposition of the remaining soft tissue was completed and additional scattering of the disarticulated skeleton occurred. One year after death, the majority of the clean and disarticulated skeleton still lay within a 10 × 10 m area corresponding to the location in which the elephant had died, although a few bones had been scattered over a broader 20 × 25 m area. The area of final carcass disposition described in this study is similar in size to those reported from Eemian elephant skeleton remains at the shallow Late Pleistocene Neumark-Nord Lake 1 in Europe.

Observations from the present study support past work which found that patterns of bone damage seen on elephant remains could be predicted and attributed to specific species of large carnivores (e.g., spotted hyenas feeding on elephant feet, African lions feeding on internal organs through the anal opening). However for very heavy carcasses with hard thick hides e.g., adult elephants, it is hypothesized that bone damage in some areas e.g., inner side of the vertebral column, may be dependent upon the exact position of the individual elephant at time of death as well as the season of death, since both factors will influence the subsequent ability of scavengers to access portions of the carcass.

In summary, in this study of the taphonomy of a modern day elephant carcass, one year post-mortem the documented bone damage as well as the final disposition of the skeleton was attributable to primary scavenging by large carnivores, secondary scavenging by smaller carnivores, and environmental factors e.g., final scattering of bones during seasonal floods.

Acknowledgements

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